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A synthesis of marine predator migrations, distribution, species overlap, and use of Pacific Ocean Exclusive Economic Zones

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A synthesis of marine predator migrations, distribution, species overlap, and use of Pacific Ocean Exclusive Economic Zones.

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by

Autumn-Lynn Harrison

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Abstract

A synthesis of marine predator migrations, distribution, species overlap, and use of Exclusive Economic Zones in the Pacific Ocean.

by

Autumn-Lynn Harrison

Many marine predator populations are commercially important and are threatened by human activities. As a result, many of these populations are heavily depleted, declining, or are recovering from past depletion. Recovery and management of threatened and exploited marine predators are complicated by life histories that 1) span international waters, 2) are dynamic in space and time, and 3) are hidden from direct observation. My goal with this dissertation was to attain a synthetic understanding of the implications of marine predator migratory life histories on the spatio-temporal dynamics of distribution, species overlap, and residency in Exclusive Economic Zones of countries. I analyzed an electronic tracking dataset provided by the Tagging of Pacific Predators program that contained location data for pinnipeds, seabirds, sharks, tuna, turtles, and whales. This dataset included 257,133 daily locations recorded from 1,679 individuals representing 18 species of pelagic predators electronically tracked in the Pacific Ocean during an eight-year period.

Many marine predators are broadly recognized as exceptional migrants but there has been little integration of traditional migratory theory with the study of their movements. In chapter one, I examined whether theoretical nonlinear models of migration developed for ungulates and based upon a fundamental statistic of random walk theory (net squared displacement) provide a useful framework for quantifying and predicting marine predator migratory behavior. I found that migration models fit species as ecologically dissimilar as moose and Pacific bluefin tuna suggesting that a unified approach to quantifying migration across taxa and biomes may be possible.

The potential utility of marine protected areas (MPAs) for pelagic conservation is debated, especially for wide-ranging species with large, dynamic area requirements. In chapter two I used kernel density analysis to determine the spatial and temporal extents of the distributions and core habitats of marine predators and quantified patterns of species overlap that could help guide management strategies. I found that spatial management measures may not need to be prohibitively large to include major core habitats of wide-ranging species—at least in reference to the size distribution of large extant MPAs. However, to account for seasonal variability in distribution, spatial measures may need to be dynamic, numerous, and/or embedded within strategic multi-scale zoning strategies. Seals, sharks, tuna, and turtles had high probabilities of overlap with black-footed albatross and sooty shearwaters. Spatial conservation efforts targeted at seabirds could help focus ecosystem management in this vast pelagic realm.

Integrated international efforts are required to effectively manage threatened and exploited populations of wide-ranging species. In chapter three I used generalized additive mixed-effects models to investigate non-linear daily trends in the probability of occurrence in Exclusive Economic Zones (EEZs) and in the high seas, and to account for the effects of tagging location, tagging date, track duration, and autocorrelated time-series data. Ninety-four percent of Pacific Ocean EEZs were visited. Land-breeding populations were estimated to spend 14-33% of their annual cycles within the waters of their breeding EEZs, and 53 to 76% of the year in the high seas. In contrast, most fish and shark populations were estimated to spend less than a quarter of their annual cycle in international waters. My results describe the suite of countries with shared management responsibility throughout the year for each species, and detail when this responsibility commences and concludes.

Dedicated to the memories of my high-spirited grandmothers,

Frances Tyler Aaron and *Minnie Cooper Watts Harrison.*

Acknowledgements

I used data collected by an international team of researchers united as the Tagging of Pacific Predators (TOPP) program, a field project of the Census of Marine Life. From 2002-2009 TOPP researchers deployed electronic tags on over 4,000 marine predators including sharks, seals, seabirds, turtles, tunas, and whales. They devoted countless hours in the field, in the lab, and at their computers. They developed new technologies and analytical approaches, and published many important biological and ecological discoveries. My research would not have been possible without their contributions. I am indebted to every individual who contributed to the Tagging of Pacific Predators.

The Tagging of Pacific Predators project itself was the ambitious idea of Barbara Block of Stanford University, and Daniel P. Costa of the University of California, Santa Cruz. Barb's dedication to the project and the depth of her knowledge about tunas and pelagic ecosystems is inspiring. Her edits and support have been invaluable. I feel so much gratitude toward Dan, my Ph.D. supervisor. I thank him for believing that I could accomplish a project of this scope and for being excited about my ideas from our first meeting; for introducing me to all that is incredible about pinnipeds; for providing me with wonderful field experiences to strengthen my knowledge of marine predators; for facilitating my involvement in global high seas conservation efforts; for appreciating good design; and most importantly, for liking football.

I was fortunate to have a supportive Reading Committee. Scott Shaffer's work with sooty shearwaters inspired many of my questions. His unfailing support, encouragement, and camaraderie kept me going. Mark Carr exuded positivity and excitement. His sound edits greatly improved my work. In addition to my committee, other mentors who provided emotional and intellectual support were Jim Berkson and Ian Jonsen. Pete Raimondi and others in the Department of Ecology and Evolutionary Biology expended an incredible amount of time and energy to help me succeed.

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Chapter 1

Introduction

1.1 Broad context

The 193 parties to the United Nations Convention on Biological Diversity (CBD) have agreed to protect 10% of the world's marine ecoregions by 2020. Devastating statistics portend the collapse of global fisheries (Pauly, 1998; Myers and Worm, 2003), loss of marine biodiversity worldwide (Worm et al., 2006; Sala and Knowlton, 2006), and the decline of marine predators (Baum, 2003; Polidoro et al., 2008). Place-based management techniques have been advocated as a conservation tool in oceanic habitats (Mills and Carlton, 1998; Hyrenbach et al., 2000; Russ and Zeller, 2003; Oliver, 2004; Corrigan and Kershaw, 2008; Game et al., 2009) and for the conservation of wide-ranging marine predators (Hooker and Gerber, 2004; Hooker et al., 2011), but little has been done to implement this concept in practice. To be ecologically representative, and to address widespread threats to global marine biodiversity via overexploitation of pelagic fisheries (Myers and Worm, 2003) and climate change (Davies et al., 2009; Robinson et al., 2009), a global system of marine protected areas will include high seas ecosystems—those areas beyond any one nations jurisdiction. Less than 1% of the high seas is currently protected (Spalding et al., 2010).

Understanding where, when, and why organisms are where they are is a primary focus of ecology (Darwin, 1872; Elton, 1927), and of conservation (Myers et al., 2000). Traditional spatial conservation strategies, for example, the designation of protected areas, assume knowledge about where biodiversity is and require an understanding about how species are distributed, the environmental factors correlating with their presence, and how they are likely to be distributed in the future. Wide-ranging predators utilize vast and highly distributed habitats for foraging, migrating, and breeding, and many species are commercially important and threatened with extinction. A robust, integrated approach to identifying ecologically and biologically important areas for wide-ranging animals is lacking (Game et al., 2009).

In 2007, the CBD adopted scientific criteria for identifying ecologically or biologically significant marine areas in need of protection in open ocean waters and deep sea habitats (Annex 1 of CBD Decision IX/20): colloquially referred to as the Azores Criteria. The Global Ocean Biodiversity Initiative (www.GOBI.org), together with the CBD and many scientific and non-governmental partners, are currently evaluating potential areas of conservation importance in the high seas requiring a high level of protection through place-based management tools such as marine reserves. The relevance of ecosystem-based spatial techniques to management and conservation of wide-ranging marine animals, and the scale at which they will be implemented, depend upon knowledge about the spatial and temporal relationships between these animals and their dynamic environment, and on standardized techniques for their identification.

1.2 Dissertation outline

I was motivated to provide new synthetic ecological insights of the spatio-temporal dynamics of marine predator movements in the high seas, to relate marine predator migrations to general ecological theory developed from terrestrial migratory ecology, and to help fill information gaps identified by the CBD. I focused my research on the high seas of the North Pacific Ocean, the only region of the worlds oceans for which this analysis is possible due to the detailed and robust movement data available for 2500 individuals representing populations of 23 marine predator species electronically tracked during 2002-2009 by the Tagging of Pacific Predators program (TOPP, www.TOPP.org, Block et al., 2003, 2011).

Chapter One: Many marine predators are broadly recognized as exceptional migrants but there has been little integration of traditional migratory theory with the study of their movements. In chapter one, I examined whether theoretical models of migration developed for ungulates provide a useful framework for quantifying and predicting marine predator migratory behavior.

Chapter Two: The potential utility of marine protected areas (MPAs) for pelagic conservation is debated, especially for highly vagile species with large, dynamic area requirements and extensive migrations. My objectives were to explore the spatial and temporal extents of the distributions and core habitats of populations of eight species of wide-ranging predators in the North Pacific Ocean and to quantify patterns of overlap among species that could help guide efficient strategies for managing wide-ranging species within this vast pelagic realm.

Chapter Three: Integrated international efforts are required to effectively manage threatened and exploited populations of wide-ranging species. In chapter three my goal was to attain a robust understanding of the migratory phenologies of marine predators in relation to human political boundaries of the Pacific Ocean. Using a generalized additive mixed modeling approach, I identified the suite of countries with shared management responsibility throughout the year, and detail when this responsibility commences and concludes. This approach fully capitalizes on what biologging technologies do best: produce rich time-series data on individual animals who spend most of their lives hidden from direct scientific observation.

1.3 Background to the Tagging of Pacific Predators, a field program of the Census of Marine Life

Animals that spend large periods of their lives immersed or in flight long eluded scientific observation. Until recently, the underwater activities, pelagic habitats, and migration routes of wide-ranging marine species were a mystery. From the mid-1980's, technological advances enabled electronic tracking devices attached to marine animals to collect and store fine-scale animal movement and behavioral data (Kooyman, 2004, 2007). Smaller size, lower cost, longer battery life, and greater data storage capacity (Holland et al., 2001) allow a variety of data to be recorded by electronic tags including: three-dimensional location, swimming velocity, water temperature, heart rate, internal body temperature, and pressure (Block, 2005). Holland et al. (2001), Block (2005), Kooyman (2004, 2007), and (Nielsen et al., 2010) give detailed reviews of the evolution and nature of electronic tags for use in acquiring data about marine species in their natural environments. With these advances, ecological questions about the the underwater habits and vast movements of wide-ranging marine species became tractable. Tracking projects arose around the world in the early 2000's to harness biologging technologies for the pursuit of biological and ecological insight, and for attaining information relevant to conservation and management (see the 2008 theme section of Endangered Species Research [volume 4, numbers 1-2] for a recent anthology).

In 2000, the Tagging of Pacific Predators (TOPP; Block et al., 2003), a field program of the Census of Marine Life, undertook an unprecedented effort to simultaneously track thousands of Pacific Ocean pelagic predators, including tunas, pinnipeds, sharks, seabirds, whales, and turtles (Figure 2.1) using geolocation, ARGOS satellite telemetry, and GPS technologies (Block et al. 2011). The overarching goals were: 1) to reveal habitats, migration routes, and physiological capabilities of six guilds of marine predators, and 2) to understand the behavior of these animals in relation to physical and biological forces, and 3) to use knowledge gained to inform management and policy for the purpose of marine predator conservation. The effort involved hundreds of researchers from around the world in large-scale field efforts; the development and improvement of electronic tagging technology; and the development of sophisticated data acquisition, storage, analysis, and visualization systems (see Block, Costa, and Bograd 2010 for a summary of TOPP planning, initiation, and development).

From 2000-2009, TOPP researchers deployed electronic tags on 4,306 individuals representing 23 species of apex marine predators in the Pacific Ocean (Block et al., 2011). The TOPP effort resulted in a number of species-specific discoveries. These include: sooty shearwaters (*Puffinus griseus*, SOSH) travel the entire Pacific Ocean in an "endless summer" figure-eight migration (Shaffer et al., 2006); white sharks (*Carcharodon carcharias*, WS) migrate between the California coast and a high seas hotspot called the 'White Shark Cafè' (Weng et al., 2007; Jorgensen et al., 2010); salmon sharks (*Lamna ditropis*) have an expanded niche due to the thermal capacity of their muscles (Weng et al., 2005); California sea lions (*Zalophus californianus*) respond to El Nino years by venturing much farther from the coast than normal (Weise et al., 2006); black-footed albatross (*Phoebastria nigripes*) and Laysan albatross (*Phoebastria immutabilis*) segregate at-sea during the breeding season according to sea surface temperature (Kappes et al., 2010); and loggerhead sea turtles (*Caretta caretta*) are at a high risk of bycatch in artisinal fisheries off the coast of Mexico (Peckham et al., 2007). These species-specific research discoveries and more are summarized in Costa, Block, and Bograd (2010).

A broad multi-species synthesis of the full TOPP dataset was published in 2011 (Block et al., 2011). Due to changes in technology over the decade-long project and differences in sampling regime across species, a state-space modeling approach was taken to standardize species datasets for comparison. A Bayesian state-space model (Jonsen et al., 2005) was fitted to the tag data to derive regular, daily mean estimates of locations at sea while accounting for tag observation error (Block et al., 2011; Winship et al., 2011, *in press*). The state-space model also provided estimates of the uncertainty in the location estimates.

Block et al. (2011) identified multi-species hotspots in the California Current and North Pacific Transition Zone (Fig. 1.2) and linked pelagic habitats to these hotspots. Specifically, (Block et al., 2011) demonstrated that temperature and primary production were the primary physical forces that influence spatio-temporal distribution patterns of marine predators. The synthesis also presented the north-south seasonal migratory cycles of species within the California Current and described within-guild (tunas, sharks, and seabirds) segregation of species by temperature. A portion of my dissertation research contributed to the TOPP synthesis and I am a co-author of this manuscript (Block et al., 2011). My dissertation expands upon the broad conclusions of Block et al. (2011) with focused multi-species comparisons.

1.4 Study Species

Tunas: Pacific bluefin tuna, yellowfin tuna, albacore tuna

Fishes of the genus, *Thunnus*, (family *Scrombidae*) are endothermic, powerful swimmers. Their speed and power allows them to predate on quick prey including squid, herring, and mackeral. Centrally-located red aerobic muscle—and the accompanying system of counter-current heat exchangers—is the major source of metabolic heat (Graham 1975) and facilitated niche expansion of tunas into a broad range of thermal conditions (Block et al., 1993). There is a continuum of endothermy in this group (Block et al., 1993). Pacific bluefin tuna (*Thunnus orientalis*) and albacore tuna (*Thunnus alalunga*) are able to occupy colder waters in the Pacific Ocean (Polovina et al., 2001; Boustany et al., 2010) and yellowfin tuna are primarily confined to subtropical and tropical distributions (Schaefer et al., 2011). Schaefer et al. (2011) reported high site fidelity of yellowfin tuna in the southern California Current to very localized habitats and that despite the cosmopolitan distribution of the species throughout the Pacific, eastern stocks are distinct and localized. In contrast, Pacific bluefin tuna spawn in the Western Pacific between Okinawa and the Philippines and the Sea of Japan. Juveniles migrate to the eastern Pacific where they reside within the California Current for years (Kitagawa et al., 2007) before eventually returning to their natal waters to spawn (Boustany et al., 2010). They are commercially valuable and this has resulted in precipitous declines in bluefin tuna populations worldwide. Tags were deployed on tunas in the California Current.

Sharks: White shark, salmon shark, shortfin mako shark, thresher shark, blue shark

Sharks of the family *Lamnidae*, including white shark, salmon shark, and shortfin mako shark (*Isurus oxyrinchus*), are large, fast and powerful swimmers with pointed snouts, large, long mouths, and sharp teeth (Compagno, 2002). Their modified circulatory systems help them maintain high body temperatures, although the degree of endothermy varies among species. Shortfin mako sharks are not as highly adapted to endothermy as white and salmon sharks and are restricted to warm-temperate and tropical waters (Compagno, 2002). Salmon sharks in comparison have a broad thermal niche, and range from subarctic to subtropical waters during their annual cycle (Weng et al., 2005). Lamnids feed on a wide variety of bony and cartilaginous fishes, air-breathing marine vertebrates, and squid (Compagno, 2002), have low reproductive rates, and are taken in pelagic longlines and gill nets, sometimes for direct use of meat, oil, fins, hides, etc., and sometimes as incidental bycatch (FAO, 2010). As a group, they are of conservation concern (Dulvy et al., 2008).

Blue shark (*Prionace glauca*) is the most widely distributed of all sharks. It is primarily pelagic, but also utilizes temperate inshore kelp forests and tropical coastal waters (Vögler et al., 2012). The blue shark is the most commonly bycaught shark species in pelagic longline fisheries and because its meat is not considered high quality, is mostly taken for its fins (FAO, 2010). In the California Current, squid species are its primary prey (Preti et al., 2012).

In contrast to blue sharks and lamnid sharks, common thresher sharks (*Alopias vulpinus*) are predominantly coastal (Compagno, 2002). In the California Current, anchovies, sardines, and hake compose nearly 80% of their diet by weight (Preti et al., 2012). Thresher sharks are acrobatic, strong swimmers with a long caudal fin that complements the shark's body in length. Adults seasonally migrate within the California Current and Southern California is an important nursery area (Compagno, 2002). The species is targeted by sports fisheries in California, was formerly caught in a targeted gill net fishery off of California (before overfishing occurred in the late 1980s), and is bycaught in swordfish fisheries and prized for the quality of its meat (Compagno, 2002; FAO, 2010).

Tags were deployed on salmon sharks in Alaska and on white sharks near the Farallone Islands, California where they have been observed to predate on northern elephant seals (Pyle et al., 1996). Tags were deployed on mako, blue, and thresher sharks in the southern California Current.

Pinnipeds: Northern elephant seal and California sea lion

Pinnipeds are semi-aquatic marine mammals widely distributed in the world's oceans. Two of the three families (Phocidae and Otariidae) are highly pelagic. Phocids or earless seals, are the most pelagic pinnipeds. Their physiological adaptations enable them to dive deeply and for a long duration, and to undertake long foraging migrations. Otariids (sea lions and fur seals) are generally more coastally distributed, are better adapted to movement on land, conserve heat primarily via fur rather than blubber, and are maneuverable swimmers.

Northern elephant seals (*Mirounga angustirostris*) are sexually dimorphic deep-diving phocids with incomparable breath-holding and fasting abilities. Once depleted to the brink of extinction due to human harvest (Bonnel and Selander, 1974), northern elephant seals are now fully protected and populations have have rebounded and are increasing along the western North American coast. Mainland rookeries now exist where none were historically. Ano Nuevo State Reserve in California, U.S.A. is the largest. Northern elephant seals undertake biennial foraging migrations (Stewart and Delong, 1995; Le Boeuf et al., 2000). Females spend approximately 10 months at sea during the year; 85-90% of this time is spent submerged (Robinson et al., *In Press*). Elephant seal life history has been reviewed by Le Boeuf and Laws (1994). Females travel to the rookery to give birth and mate in early winter. Pups are weaned in late winter and females return to forage at sea for approximately 2 months. Females return to land for approximately 1 month to moult before departing again for their long foraging migration (approximately 8 months coincident with gestation). Males spend the winter on the rookery for breeding, after which they forage at sea for 4 months. After a 1 month summer moult, males return to sea for another four months.

California sea lion (*Zalophus californianus*) California sea lions are social, sexually dimorphic otariids that reside along the west coast of North America. Otariids with young are constrained in their foraging trip distance and alternate alternate between time spent ashore provisioning pups and multi-day foraging trips at sea (Costa, 1993). Because male sea lions do not provide parental care, they can travel farther from the seal rookery to forage than females and due to their larger body sizes, can dive to deeper depths and have longer duration dives than females (Kuhn, 2006; Weise et al., 2010). Sea lions commonly forage over the continental shelf, but Weise et al. (2006) reported that during an anomalous warm water year (resulting in delayed upwelling and decreased primary productivity in the California Current), male sea lions spent more time searching for prey, and some individuals made repeated foraging trips of up to 450 km off shore.

Procellariiform seabirds (petrels or tubenoses): Black-footed albatross, Laysan albatross, sooty shearwater

Procellariiformes are highly pelagic foragers with extraordinary flying abilities (Croxall et al., 2005; Shaffer et al., 2006). They are colonial and monogamous nesters and exhibit strong philopatry to their remote nesting islands. A single egg is typically laid per year (Lack, 1968, The 'Great' albatrosses may nest every other year) and they provide a high level of parental investment investment until the chick fledges. Both sexes incubate and rear chicks (Warham, 1990; Weimerskirch et al., 2000). Many procellariiformes are endangered due to introduced predators on breeding islands, marine pollution and debris ingestion, and direct incidental take as bycatch in pelagic fisheries. Black-footed and Laysan albatrosses are bycaught in large numbers in the Central and Western Pacific (Miller and Skalski, 2006; Lewison et al., 2009), consume a large amount of plastics from the Pacific Garbage Patch (Young et al., 2009) which they in turn feed to their chick often resulting in chick mortality. The order also includes one of the most populous species in the world, the sooty shearwater. Shearwaters are subsurface feeders and thus provide an interesting contrast to the surface-feeding albatrosses.

Rorqual whales: Blue whale, humpback whale

Rorquals are baleen whales with a cosmopolitan distribution. They are named for the folds of skin extending from the mouth to the navel, which allows their mouths to expand tremendously during lunge feeding (Orton and Brodie, 1987; Goldbogen et al., 2008). They feed mostly on schooling fish and crustaceans such as krill. In the eastern Pacific ocean, humback whales (*Megaptera novaeangliae*) migrate between tropical calving groups in Mexico and polar foraging grounds (Calambokidis et al., 2004). Calving grounds of blue whale (*Balaenoptera musculus*) are in Mexico and Central America and they forage off the California coast. In the summer, they aggregate in areas of high upwelling with consistently high densities of euphausiids (Croll et al., 2005), but Bailey et al. (2010) suggested that they may forage throughout their migration. Blue whales were once widely distributed throughout the Pacific and may be re-establishing traditional migration patterns from Mexico to British Columbia and Alaska that existed before severe population declines (Calambokidis et al., 2009). Both species were tagged off the coast of California.

Sea turtles: Leatherback turtle, loggerhead turtle

Sea turtles are large slowly-maturing and long-lived marine reptiles with streamlined bodies and large flippers adapted to their mostly pelagic life histories (Spotila, 2004). After decades to sexual maturity and at-sea mating, females return to land to lay eggs on beaches at night and return to sea after laying. Migration routes of Pacific populations of leatherback turtles (*Dermochelys coriacea*) are varied and can be trans-Pacific (Benson et al., 2011). All sea turtle species were an historical human food-source, and were culturally important to many human groups, and were heavily harvested for both meat and shell. Turtles have been heavily impacted by incidental catch. They are bycaught in high numbers in pelagic fisheries (Howell et al., 2008) and artisinal fisheries (Peckham et al., 2007). Severe population declines have been seen at Playa Grande, Costa Rica (Santidrián Tomillo et al., 2007), one of the TOPP leatherback tagging locations. Tags were deployed in Indonesian nesting locations, California foraging grounds, and Costa Rican nesting beaches.

1.5 Habitats of the North Pacific Ocean

Dominant habitats and oceanographic features of the North Pacific Ocean referenced throughout this dissertation include the major upwelling area bounded by the California Current Large Marine Ecosystem, the North Pacific Transition zone, and other large gyres and currents (Fig. 1.2). The North Pacific Transition Zone (NPTZ) is a 9000-km basin-wide oceanographic feature bounded by thermohaline fronts: to the to the south (28 to 34N), the Subtropical Frontal Zone and to the north (40 to 43N) by the Subarctic Frontal Zone (Roden, 1991). The transition zone migrates seasonally and interannually (Bograd et al., 2004) and is persistently exploited by a number of species including loggerhead turtles and albacore tuna,(Polovina et al., 2000, 2001); Pacific bluefin tuna (Boustany et al., 2010), albatrosses (Hyrenbach et al., 2002; Kappes et al., 2010), and elephant seals (Simmons et al., 2010) for its rich trophic linkages (Brodeur et al., 1999).

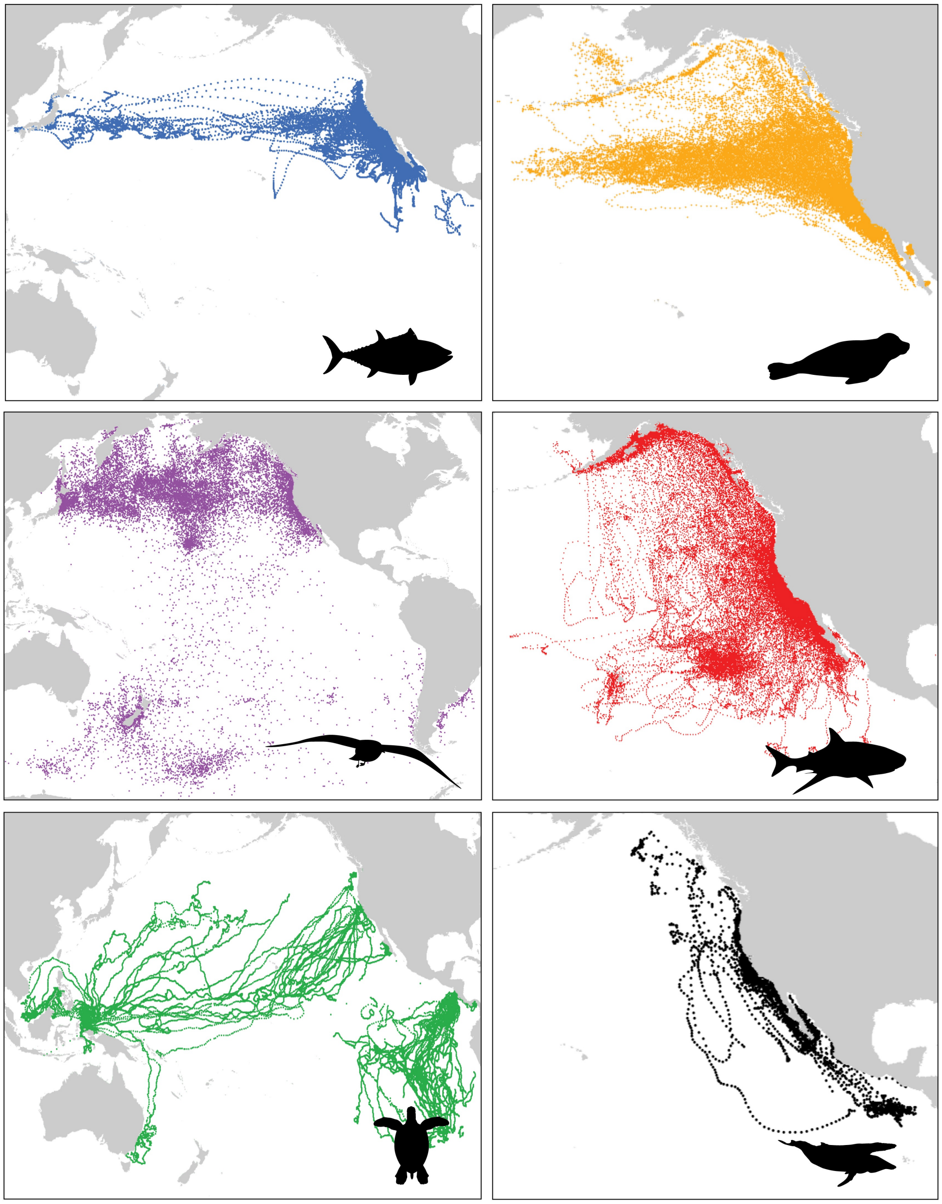

Figure 1.1: State-space modeled daily locations of a) tunas b) seabirds c) turtles d) pinnipeds e) sharks and f) whales electronically tracked in the Pacific Ocean during 2002-2009. Adapted from Block et al. (2011)

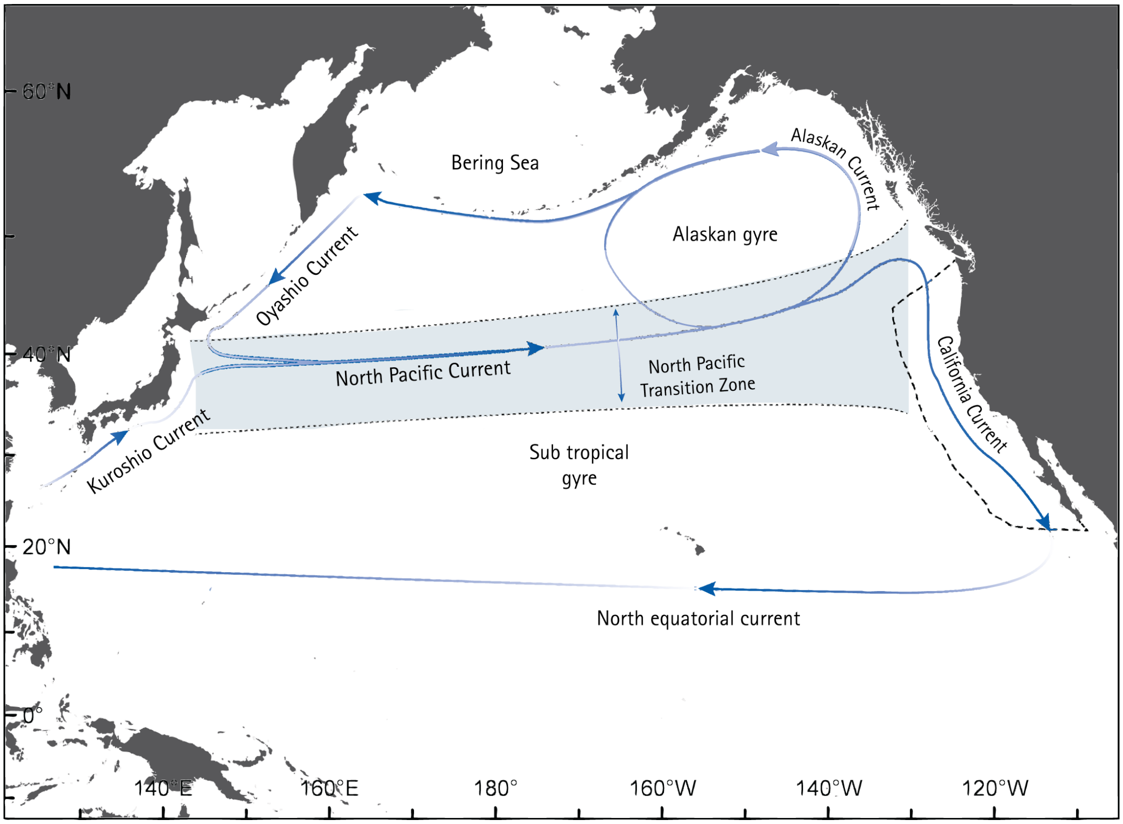

Figure 1.2: Dominant oceanographic features of the North Pacific Ocean. Two habitats frequently referenced in this dissertation included the North Pacific Transition Zone (shaded blue and delineated by dotted lines) and the California Current Large Marine Ecosystem, outlined in dashed lines. Adapted from Block et al. (2011)

Chapter 2

Are ungulate migration models applicable to marine predators?

Abstract

Integrated approaches are needed in migration biology. Systematically distinguishing migratory behavior from other types of movement requires theoretical approaches that are broadly applicable across taxa. Many marine predators are recognized as exceptional migrants but there has been little integration of traditional migratory theory with the study of their long-distance movements. A unifying migration modeling framework based upon random walk theory and the net squared displacement statistic was recently proposed. It has subsequently been used to estimate individual and population-level parameters of multiple ungulate species and to distinguish among various movement and ranging strategies by individuals. To examine their broad applicability, I fit these same theoretical models of animal migration to the movements of a group of marine predators that migrate long distances between coastal and pelagic habitats in the North Pacific Ocean. I found that observed functional forms of net squared displacement were similar to those of ungulates. Stop-over migration strategies during long-distance migration often resulted in non-convergence of models and loop or linear migration patterns were poorly fit. However, goodness of fit was high for sooty shearwaters, leatherback turtles, Pacific bluefin tuna, white sharks, and northern elephant seals during their 8-month

post-moult migration. That proposed migration models fit species as ecologically dissimilar as moose and Pacific bluefin tuna suggests that a unified approach to quantifying migration across taxa and biomes may be possible.

2.1 Introduction

Migratory life histories have evolved independently in many marine and terrestrial taxa (Alerstam and Hedenstrom, 2003). Marine animals are the record-setters. Upper trophic level marine predators are physiologically and biomechanically adapted for vagility. This enables them to exploit dynamic and patchily distributed foraging habitats at ocean basin scales and to have breeding habitats that are distantly separated from where they forage. Revolutionary advances in electronic tagging technology during the last decade have revealed extraordinary movements by a range of taxa: seabirds (Croxall et al., 2005; Shaffer et al., 2006; Kopp et al., 2011), marine mammals (Le Boeuf et al., 2000, Robinson et al., *in press*), sharks (Weng et al., 2005; Jorgensen et al., 2010), fish (Block et al., 2005; Boustany et al., 2010), and reptiles (Benson et al., 2011).

Migration is often described as a population phenomenon but the population-level outcomes of migration originate in individual behaviors. Consequently, there is an incredible amount of variation and evolutionary flexibility in migration (Alerstam and Hedenstrom, 2003). An extensive body of research on ungulates, insects, and songbirds has reduced this variation into conceptual, empirical, and theoretical definitions that should broadly apply across taxa (Dingle, 2006; Dingle and Drake, 2007). Migration is defined ecologically by population redistribution, usually a “to-and-fro” movement of partial or whole populations between locations that seasonally alternate in habitat suitability. For an individual, migration is typically distinguished from other movements by persistent, undistracted, and straight movement and by movements that are longer in duration and of far greater distance than those movements undertaken during normal activities (Dingle, 2006).

Random walks and diffusion models are the foundation of empirical definitions of individual movement (Kareiva and Shigesada, 1983). A framework for extending dispersal theory (Turchin, 1998) to migration was proposed by Bunnefeld et al. (2011). They proposed a suite of models derived from expected relationships between net squared displacement and time to distinguish among individual movement strategies (migration, home range, nomadism, one-way dispersal). They then used these models to estimate population level parameters. Given their conceptual and theoretical underpinnings, these models should be broadly applicable to any migrant.

My goal was to evaluate the applicability of current migration models for classifying marine predator movement behavior. Integration of theory and empirical studies in the field of migration biology is limited and models should be linked to data across taxa (Bauer et al., 2009; Gillespie et al., 2012). Many marine species are broadly recognized as exceptionally migratory but there has been little integration of traditional migratory theory with the study of their movements. Building upon single-species discoveries and the wealth of available tracking data available for marine predators (Block et al., 2011), I fit theoretical models of animal migrations developed for ungulates to the movements of a group of marine predators that migrate long distances between coastal and pelagic habitats in the North Pacific Ocean.

2.2 Methods

The daily time-series of animal locations used here were collected from 2003-2009 by the Tagging of Pacific Predators (TOPP), a field project of the Census of Marine Life. Block et al. (2011) and Winship et al. (2011) provide deployment details, tag types, the state-space model fitted to the raw electronic tagging data and the associated estimates of uncertainty. I analyzed data from species that use segregated coastal and pelagic habitats and that were successfully tracked between these two locations. This confined my analysis to the following populations of TOPP species: black-footed albatross (*Phoebastria nigripes*) and Laysan albatross (*P. immutabilis*) from Northwest Hawaiian Islands breeding colonies; female northern elephant seals (*Mirounga angustirostris*) from the Ano Nuevo breeding colony, California; leatherback turtles (*Dermochelys coriacea*) from the Playa Grande nesting beaches, Costa Rica; Pacific bluefin tuna (*Thunnus orientalis*) that were successfully tracked during their trans-Pacific migration from the California Current to Japan; salmon sharks (*Lamna ditropis*) tagged in coastal Alaska; sooty shearwaters (*Puffinus griseus*), tagged in New Zealand; and white sharks (*Carcharodon carcharias*) tagged in the Farallone Islands, California. For each species, tracks with long-duration gaps (longer than 2 weeks) were removed from analysis.

2.2.1 Movement models

For a given time (t), net displacement is the Euclidean distance between start and end locations. The square of this is a fundamental statistic used to summarize movement over long time scales (for example, of random processes, seed dispersal or animals). The mean net squared displacement is theoretically expected to increase linearly with time when movement processes are diffusive or nomadic (Fig. 2.1) and to asymptote when movement is spatially constrained, for example when migrating animals reach a foraging area and confine their movements within a home range .

Using this theoretical power law relationship between time and net squared displacement, migration strategies can be represented mathematically following Bunnefeld et al. (2011) and and Börger, *in press*.

a) Dispersal from location (a) to location (b) modeled as a logistic function:

$$NSD = \frac{\delta_b}{1 + exp(\theta_{ab} - t/\phi_{ab})} \tag{2.1}$$

b) Full migration from location (a) to location (b) and back to location (a) modeled as a double logistic (or positive-negative Richards) function:

$$NSD = \frac{\delta_b}{1 + exp(\theta_{ab} - t/\phi_{ab})} + \frac{-\delta_b}{1 + exp(\theta_{ba} - t/\phi_{ba})} \tag{2.2}$$

c) Mixed migration from location (a) to location (b) and back to a location (c) that differs from the initial location (a) modeled as a double logistic function with varying asymptote:

$$NSD = \frac{\delta_b}{1 + exp(\theta_{ab} - t/\phi_{ab})} + \frac{-\delta_c}{1 + exp(\theta_{bc} - t/\phi_{bc})} \tag{2.3}$$

In all equations, t is elapsed time, δ is the asymptotic height, θ is the timing at which migration has reached half of its asymptotic height, and ϕ is the time elapsed between reaching half and three-quarters of the migration. Extending Börger's approach (*in press*), I allowed for 8 parameters to be estimated to allow for flexibility in the slope of the curve and to include positive-positive sigmoidal functional forms.

I fit models to individual movements using nonlinear least squares regression available in the NLME package for R (R Development Core Team, 2012). For each individual, a best-fit model was selected (see further detail below). When distinct individual strategies were exhibited within a population, final population models were fit to these unique groups. For example, due to track attenuation, some individuals were tracked to a foraging area but the track ended before departure for the return migration. For these individuals, dispersal models were a more appropriate model of the observed data and parameters defining the "to" portion of the migration could be successfully extracted. When possible (i.e. when there was a high level of individual model convergence) nonlinear mixed effects models were used to estimate population-level migration parameters while accounting for individual effects.

Nonlinear models require a set of initial parameters. Models are sensitive to these values and a substantial amount of trial and error can be required to achieve convergence. Initial parameters were obtained through a combination of self-start functions for logistic, sequential logistic (double positive and double negative), and positive-negative Richard's functions available in the NLME and FlexParamCurve packages in R (R Development Core Team, 2012), and by visual inspection.

Although Bunnefeld et al. (2011) used Akaike's Information Criterion (Akaike, 1974) weights to select among competing models for each individual, multiple models often received similar support and AIC weights sometimes misclassified individuals to a migratory strategy that was obviously incorrect as indicated by visual examination of observed data (Bunnefeld et al., 2011; van Beest et al., 2011). A simulation study by Börger (*in press*) showed that the concordance correlation coefficient (CCC; Huang et al., 2009) provides a better assessment of goodness of fit than AIC weights and succeeded in classifying individuals to the correct simulated movement strategy 90% of the time. For each individual, I assessed the concordance of observed data to competing models using the CCC:

$$CCC = 1 - \frac{\sum_j (Obs. - Pred.)^2}{\sum_j (Obs. - \mu_{Obs.})^2 + \sum_j (Pred. - \mu_{Pred.})^2 + n_i(\mu_{Obs.} - \mu_{Pred.})^2} \tag{2.4}$$

Observed movement patterns are very complex and the form of the theoretical models required a high number of parameters to be fit. When convergence was not reached the CCC was set to zero.

2.3 Results

Observed patterns of one-way net displacement ranged from 2,000-8,000 km^2 (Fig. 2.2). The relationship between time and net squared displacement for all species appeared visually similar to theoretically expected relationships for migration or dispersal (Fig. 2.1).

Models successfully converged for 100% of leatherback turtles, 83% of sooty shearwaters, and 66% of Pacific bluefin tuna. For all other species, convergence success was between 40 and 50%). The highest concordance between observed and predicted patterns were obtained for Pacific bluefin tuna (dispersal models for truncated tracks and migration models for complete loops); leatherback turtles (dispersal model) and for sooty shearwaters (migration model) and for these species, population-level mixed effects models were fit with individual as a varying intercept effect (Fig. 2.3).

For northern elephant seal movement patterns, there was little support for either model (Fig. 2.4) during the post-breeding migration, but post-moult migrations were well-fit by the migration model (mean CCC = 0.72) . During the post-breeding migration, many migrations are continuous and loop-like, resulting in a near triangular NSD to time relationship, (Fig. 2.4e) that deviated visually from all proposed migration models. Triangular functional relationships were rarely fit (although see Fig. 2.4d) and were also commonly exhibited by salmon sharks. A full return migration that visually appeared ”migratory” (Fig. 2.4c) was misclassified as mixed migratory, and another (Fig. 2.4c) was fit by the migratory model (and visually appeared migratory), but the concordance was low (0.32) and the model underestimated the height of the asymptote by 200,000 km^2.

Sooty shearwater migration patterns were the most classically ”migratory” according to theory (Fig. 2.5), and to the goodness of fit of converged models (mean CCC = 0.96). When models failed to converge, individual movement patterns often contained a discrete stop-over in route to the final foraging destination (Fig. 2.5). Pacific bluefin tuna also had a high convergence rate, Abbreviated tracks were fit by the dispersal model and full migrations concorded with the migration model (Fig 2.6). A single tuna returned to the Pacific Northwest coast of the United States and stayed in residence there for over three months before returning south to it's tagging location in the California Current (Fig 2.6b). The goodness of fit between the observed locations and the mixed migratory model was high (CCC=0.83).

2.4 Discussion

I examined whether theoretical models of migration developed for ungulates provide a useful framework for quantifying marine predator migrations. Synthetic approaches to modeling marine predator movements have aimed to uncover unifying laws for optimal search strategies (Sims et al., 2008) given the highly heterogeneous distribution of prey in pelagic environments. For single-species, a focus has been the prediction of locations along an animal's movement trajectory where they are likely foraging (Jonsen et al., 2007; Breed et al., 2009; Wakefield et al., 2009) in order to formulate hypotheses about the environmental drivers of predator distribution. For these purposes, state-space models have superseded simple correlated random walk models because simple movement models are unable to detect a change in behavioral state (for example, from transiting to foraging on daily and weekly time scales). However, Bunnefeld et al. (2011) showed that the fundamental movement statistic explaining how well correlated random walk models fit observed movement behaviors—net squared displacement (Kareiva and Shigesada, 1983)—can be used to also predict large spatio-temporal state changes, for example, from migration to home range. Migration, a highly specialized type of movement, has received comparatively little attention in the marine predator movement literature.

The functional form of net squared displacement exhibited by many marine predators in this study match those of migratory ungulates (Bunnefeld et al., 2011). This was especially the case for species that undergo classic migrations (i.e. to-and-fro or "two worlds"). As a model of classic migration, the positive-negative logistic model had a high concordance with observed sooty shearwater movements. I extended Börger's (*in press*) approach to an 8-parameter Richards model which provided flexibility in the slope of arrival to and departure from the foraging range. This added flexibility better suits the behavior of some individuals shearwaters that may shift their movements around the Pacific Rim to two or three foraging locations, or shift their distribution within the California Current as the summer progresses (Fig. 2.5b).

Parameters estimated from the theoretical migration models are biologically interpretable. They are: the expected population net squared displacement from the nesting colony (Asymptote), the timing of migration when the predicted curve has reached 1/2 of its height (inflection points), and the duration of time spent on 1/2 of the migration (the scale). Shaffer et al. (2006) reported a highly synchronized equator crossing date of October 7 (+/- 5 days) by 19 of the sooty shearwaters used in this study. The positive-negative migration model fit to these plus an additional 5 individuals estimated the half-way point in the shearwater return migration to be October 5.

Stop-over locations during the long distance migrations of sooty shearwaters and Pacific bluefin tuna were evident in net squared displacement plots, but sometimes resulted in poor model fit, or a lack of convergence. This was the case for a shearwater that stopped over in the western Pacific before continuing to its final foraging range in Alaska (Fig. 2.5d; purple) and for a Pacific bluefin tuna. The tuna (Fig. 2.5d; purple) stopped over in the central Pacific for about two months before continuing its migration to Japan where it subsequently resided. Sequential logistic models (positive-positive or negative-negative) may be useful for modeling stop-over behavior. These are fit by Richard's equations and did sometimes converge with high concordance in dispersal models. A lack of convergence of individual models could have been due to the inappropriateness of the model, or more likely to improper initial start values that even after heavy adjustments through trial and error, did not yield convergence. The sensitivity of nonlinear models to start parameters is a limitation of this approach. To be broadly applied, a standard framework for quantify migration should be pragmatic for comparing hundreds or thousands of individuals with unique movement behaviors.

Many northern elephant seal migration patterns are linear or loop-like, resulting in triangular distributions of net squared displacement with time that were not well fit by a positive-negative logistic model. Northern elephant seals dive continuously during pelagic migrations and they forage at multiple locations during the track (Robinson et al., 2010). Using strict individual-based definitions, these foraging migrations are not considered migration. Ecologically, the population response that results from redistribution of individuals to a seasonally distant and ecologically distinct habitat is recognizable as migration. The migration model I used is based upon the conceptual idea that an animal migrates from a range with high resource availability for a particularly life history need (for example, breeding) to a separated range with high resource availability for a different life history need (foraging), and mostly suspends other biological needs until reaching its seasonal destination. This model represents bird, ungulate, and tuna long-distance migrations, but may not be applicable to animals for which the migration itself is the seasonal foraging range. Other species that favor coupled foraging/migratory strategies over stop-over or ranging strategies include predatory birds that hunt in flight. This fly-and-forage migration strategy (Strandberg and Alerstam, 2007) maximizes time spent migrating while simultaneously offsetting energy expenditure. Adjustments either to conceptual or quantitative definitions of migration is necessary to encapsulate long-distance, directed, linear/loop migrations and swim-and forage migrations.

Conclusions

Integrating and comparing theory across taxa and systems (marine vs. terrestrial) is one of the grand challenges of migration biology (Bowlin et al., 2010). Even daily foraging movements of some marine predators can be directed, fast, and extraordinary (Croxall et al., 2005)—typical indicators of migration—but should not be considered “migration” (Dingle, 2006). Systematically distinguishing migratory behavior from other types of movement requires theoretical approaches that are broadly applicable across taxa (Dingle, 2006; Bauer et al., 2009; Milner-Gulland et al., 2011). I showed that the migratory patterns of species as ecologically dissimilar as moose and Pacific bluefin tuna are well-fit by theoretical models based upon random walk theory, suggesting that a unified approach to quantifying and predicting migration across a range of taxa and biomes may be possible.

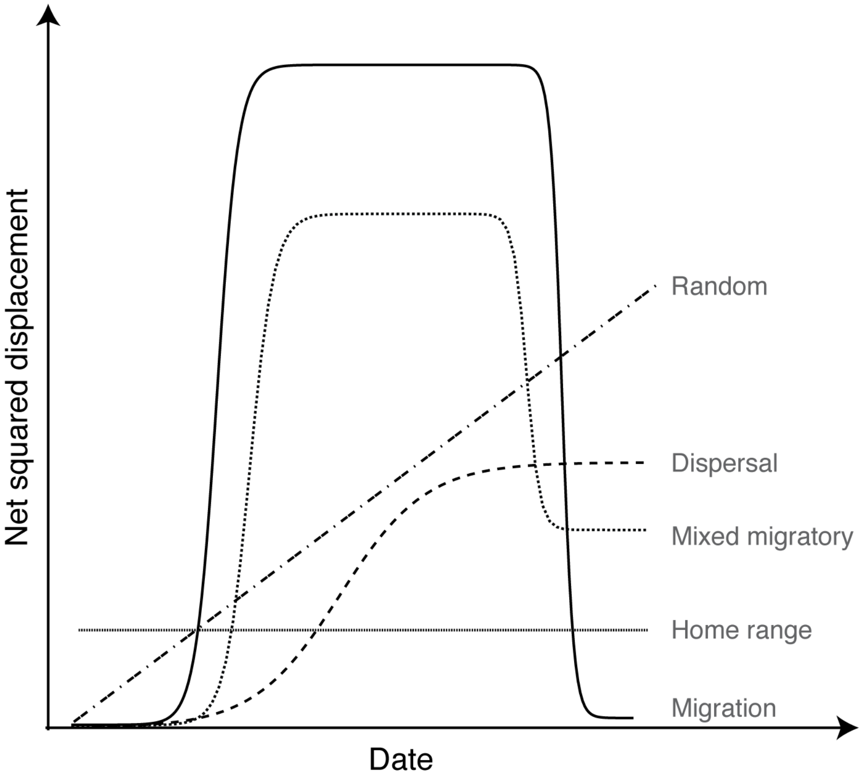

Figure 2.1: Theoretical models of animal movement behavior (Kölzsch and Blasius, 2008; Bunnefeld et al., 2011)

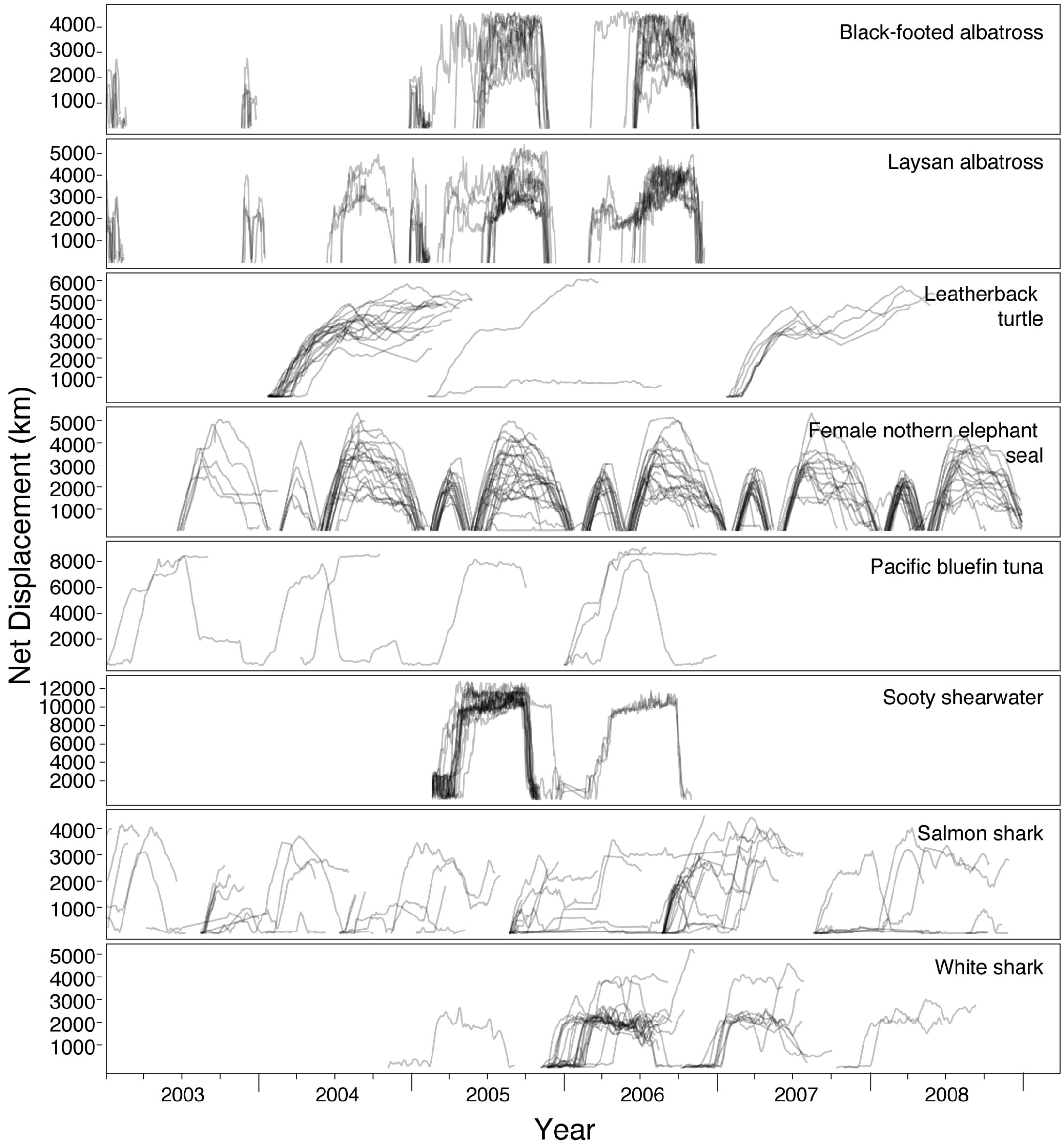

Figure 2.2: Net squared displacement (km^2) from tagging location by individuals of 8 marine predator populations electronically tracked from 2003-2008.

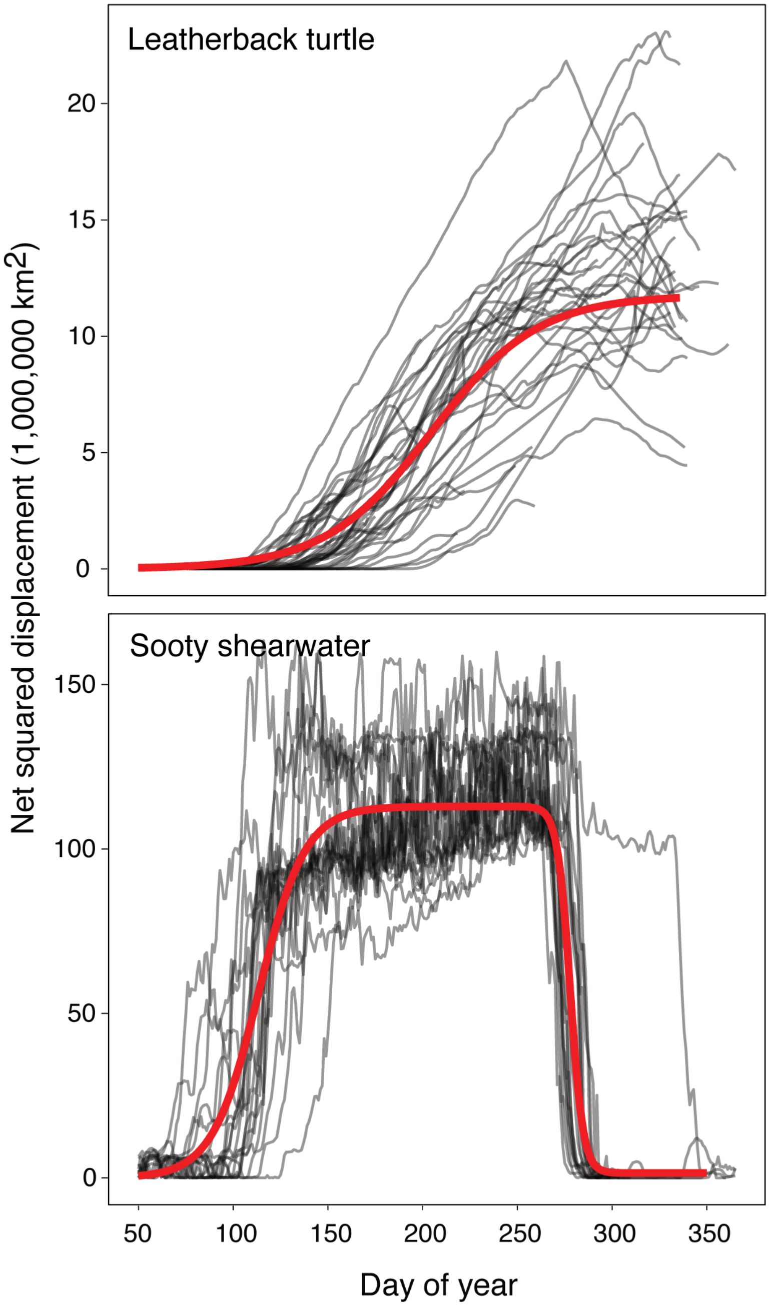

Figure 2.3: Dispersal (leatherback turtles - abbreviated tracks due to tag attenuation) and migration (sooty shearwater) models of net squared displacement and daily movements fit at the population level as a non-linear mixed effects model.

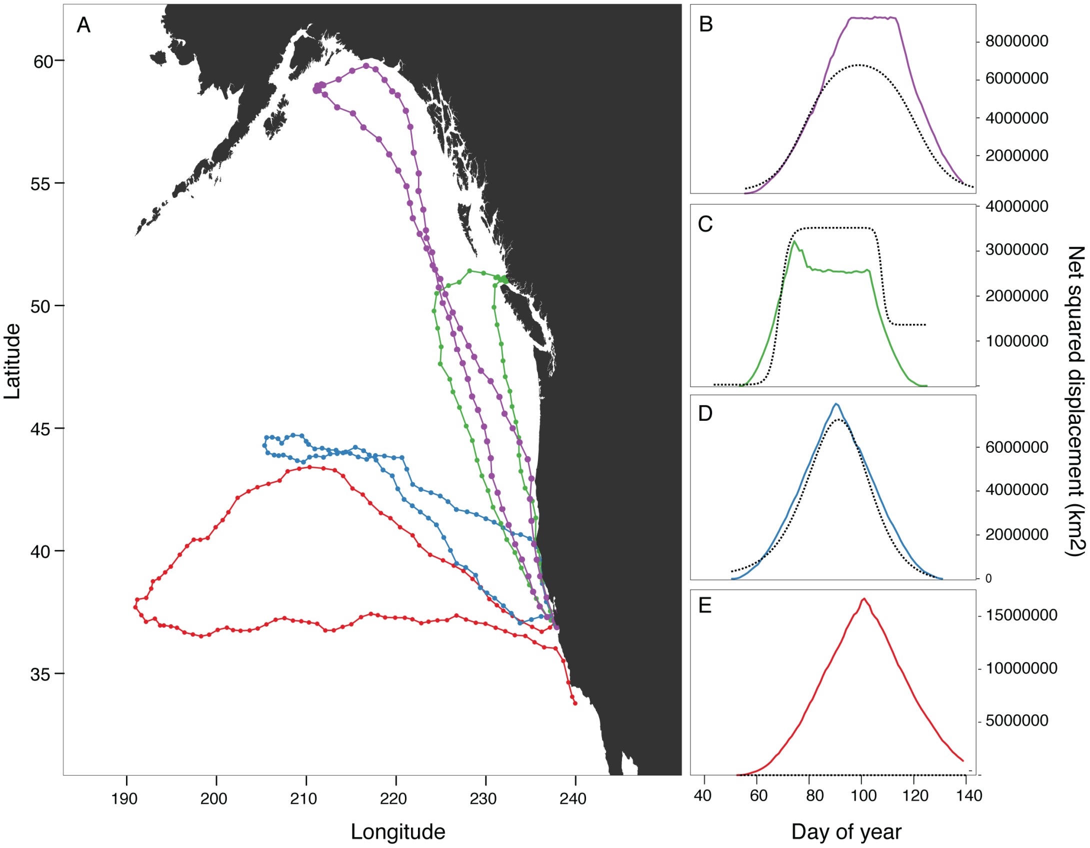

Figure 2.4: A) Select movements paths of female northern elephant seals electronically tracked during the post-breeding migration and B-E) non-linear least squares model fits. Dotted line indicates model prediction. Solid color line indicates observed net squared displacement (km^2) from nesting beach. A model fit of zero represents non-covergence.

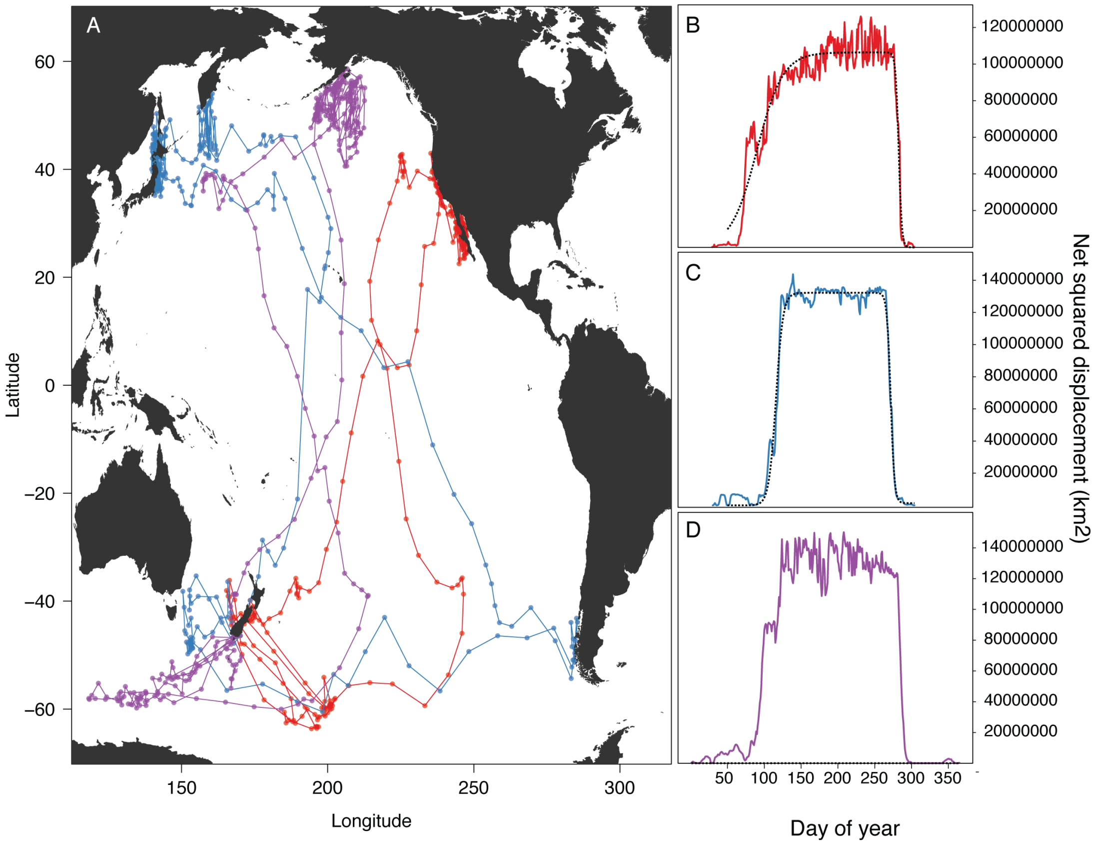

Figure 2.5: A) Select movement paths of sooty shearwaters electronically tracked during breeding forging trips and post-breeding trans-Pacific foraging migration and B-D) non-linear least squares model fits. Dotted line indicates model prediction. Solid color line indicates observed net squared displacement (km^2) from nesting colony. A model fit of zero represents non-covergence.

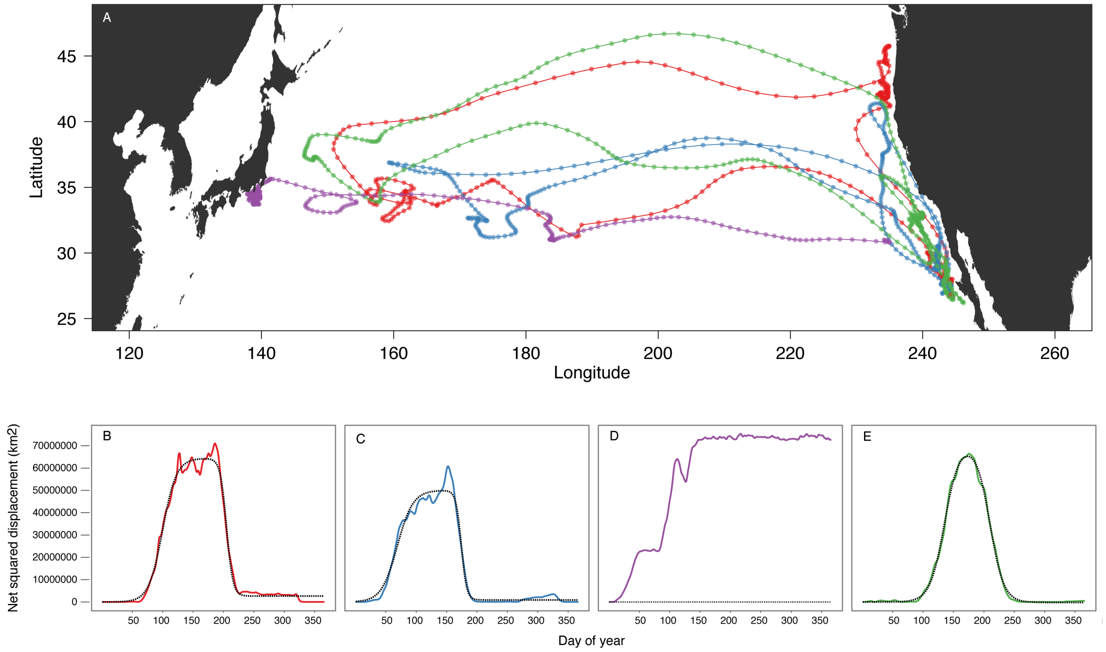

Figure 2.6: A) Select movement paths of Pacific bluefin tuna electronically tracked during their spawning migration and B-E) non-linear least squares model fits. Dotted line indicates model prediction. Solid color line indicates observed net squared displacement (km^2) from nesting colony. A model fit of zero represents non-covergence.

Chapter 3

Implications of size and spatio-temporal overlap of marine predator home ranges for pelagic MPA planning

Abstract

Upper trophic level marine predator populations have been heavily impacted by humans and they are assumed to be umbrella species for pelagic biodiversity. The potential utility of marine protected areas (MPAs) for pelagic conservation is debated, especially for highly vagile species with large, dynamic area requirements. My objective was to explore the spatial and temporal extents of the distributions and core habitats of populations of eight species of wide-ranging predators in the North Pacific Ocean and to quantify patterns of overlap among species that could help guide strategies for protecting multiple wide-ranging species within this vast pelagic realm. Using electronic tracking data provided by the Tagging of Pacific Predators, I estimated individual monthly home range sizes; monthly and annual area used by populations; monthly and annual estimates of area and location of core regions; effects of sample size on population area estimates; and monthly and annual probabilities of overlap among the eight species. Mean individual home range area was between 42,141 km^2 (SD = 41,895) for salmon sharks to 297,597 km^2 (SD=139,226) for sooty shearwaters. Seabirds were the most widely distributed taxa and their annual distribution encompassed 30-40% of the 64,550,459 km^2 North Pacific Ocean. However, density was highly concentrated in discrete regions that in total represented less than 7% of the North Pacific Ocean. The largest annual core regions were twice the size of the largest proposed MPA. Monthly core regions were numerous, varied in location and extent seasonally for all species, and were less than 250,000 km^2. Spatial management measures may not need to be prohibitively large to include major core habitats of wide-ranging species—at least in reference to the size distribution of large extant MPAs and the Convention on Biological Diversity goal of protecting a representative 10% of pelagic ecosystems. However, to account for seasonal variability in distribution, spatial measures may need to be dynamic, numerous, and/or embedded within strategic multi-scale zoning strategies. Seals, sharks, tuna, and turtles had high probabilities of overlap with black-footed albatross and sooty shearwaters. These two species may provide observable indication of the unobservable marine predator community beneath the surface. Spatial conservation efforts targeted at seabirds could help focus ecosystem management in this vast pelagic realm.

3.1 Introduction

Many large marine protected areas (MPAs) were gazetted in the past decade. Twenty-six MPAs are larger than 30,000 km^2 (Spalding et al., 2010)—the size of the Serengeti-Mara ecosystem. The Chagos Marine Protected Area in the Indian Ocean, established in 2010 by the United Kingdom, became the largest MPA at 544,000 km^2 (1.5 times larger than the Great Barrier Reef Marine Park, Australia). The first high seas network of MPAs—notable because it lies in a global commons—took effect in 2011 in the North Atlantic Ocean (total area: 285,000 km^2). And in November 2011, Australia announced plans for a 999,000 km^2 reserve in the Coral Sea. Proportionally, however, protected areas cover only 1.42% of global ocean area: 3.49% of Exclusive Economic Zone waters and less than 1% of high seas areas fall under protection (Spalding et al., 2010). The 193 signatories to the United Nations Convention on Biological Diversity (CBD) agreed in 2005 to protect 10% of the world's marine ecoregions by 2012. The rate of MPA establishment increased after 2005 (Wood et al., 2008; Spalding et al., 2010) but the 2012 target was not met. In October 2010, the CBD signatories agreed to extend the 2012 deadline to 2020.

The largest deficit in protection occurs in the pelagic realm (Game et al., 2009), especially in areas beyond national jurisdiction (Cullis-Suzuki and Pauly, 2010). Only a few of the ~6,000 MPAs extend off the continental shelf and despite the increasing trend in MPA size, the median MPA size is 1.6 km^2. Pelagic ecosystems have been heavily impacted (Halpern et al., 2008; Trebilco et al., 2011) but they are the least protected and least ecologically understood places on Earth. Global targets helped raise awareness of threats to pelagic environments and the movement to establish large, potentially dynamic, off-shore protected areas to address wide-spread threats to global marine biodiversity has gained traction with governments (Cressey, 2011), conservation organizations (Corrigan and Kershaw, 2008; Oliver, 2004), the United Nations, and the scientific community (Mills and Carlton, 1998; Hyrenbach et al., 2000; Russ and Zeller, 2003; Game et al., 2009).

The conservation of upper trophic level marine predators is a frequently cited justification for ever-larger marine protected areas (Hooker and Gerber, 2004; Hooker et al., 2011; Agardy et al., 2011). Marine predators have been heavily impacted by human harvest, overfishing, and incidental capture. Many species are of conservation concern due to population declines (Polidoro et al., 2008); range contraction has occurred for vulnerable commercial fish species (Worm and Tittensor, 2011) and marine mammals (Estes and Palmisano, 1974); and there is some evidence that when predators are extirpated from an area, cascading effects may cause further disruption to lower trophic levels (Estes and Palmisano, 1974; Myers et al., 2007). Predators can be charismatic flagships for ocean conservation, some are commercially or culturally valuable, and because of their wide distribution and hierarchical habitat selection at multiple scales (Fauchald and Tveraa, 2006), they are assumed to be umbrella species for pelagic biodiversity (Lascelles et al., 2012).

MPAs are now an accepted marine management tool and when they are enforced their successes are measurable (Claudet et al., 2008; Russ et al., 2004; Halpern et al., 2009; Lester et al., 2009; Babcock et al., 2010). However, most MPAs are small, coastal, and designed to conserve tropical reef and rocky near-shore habitats (Wood et al., 2008). The potential utility of MPAs for pelagic conservation is debated, especially for highly vagile species with large, dynamic area requirements. A reasoned contention is that protected areas will be impossible to implement and impractical to enforce at the spatial and temporal scales relevant to highly dynamic pelagic ecosystems and the predators they support (Kaplan et al., 2010; Agardy et al., 2011; Mora and Sale, 2011).

Determining the spatio-temporal scales at which pelagic spatial closures should be implemented to satisfy ecological requirements of wide-ranging marine predators depends upon knowledge of basic species ecology including the location and geographic extent of high use areas; the size of individual home ranges; variation in spatial distribution with season; and the extent of spatio-temporal overlap among species. "Calibrating protected area size and design to match home ranges of the species the protected area is intended to protect," is critical (Agardy et al., 2011). This study provides information necessary to perform such calibrations for 8 species of widely-distributed marine predators in the North Pacific Ocean.

Marine predators in the North Pacific exploit seasonally dynamic habitats within the transition zone chlorophyll front, the Alaskan and Subtropical Gyres, and the Alaska and California Currents (Block et al., 2011). The North Pacific Transition Zone (NPTZ; Roden, 1991; Bograd et al., 2004) in particular has been identified as a biodiverse region for marine predators in the high seas (Block et al., 2011), and is an area of importance for endangered (Polovina et al., 2004; Kappes et al., 2010) and commercially valuable species (Boustany et al., 2010). Taken together, the distribution of 17 species of marine predators electronically tracked by the Tagging of Pacific Predators (TOPP) project spanned nearly the entire North Pacific basin (Block et al., 2011) —a spatial extent that seems intuitively unmanageable by spatial closures, especially given its importance to international fishing fleets. However, the distributions of individual species varied in extent and location seasonally and there may be patterns of overlap among species that could help guide strategies for protecting multiple wide-ranging species within this continental-scale geographic area.

The objective of my study was to explore the spatial and temporal extents of MPAs that would be necessary to protect multiple species of predators in the North Pacific Ocean. I analyzed data for populations of eight species of widely distributed marine predators that were electronically tracked between 2002-2008 by the TOPP project (Block et al., 2011). I estimated 1) mean individual monthly home range sizes; 2) total monthly and annual area used by populations; 3) total monthly and annual estimates of area and location of high use regions; 4) effects of sample size on population area estimates; and 5) monthly and annual probabilities of overlap among the eight species.

3.2 Methods

3.2.1 Data summary

The populations of marine predator species included in this analysis are widely distributed throughout the North Pacific Ocean (Block et al., 2011): black-footed albatross (*Phoebastria nigripes*) and Laysan albatross (*Phoebastria immutabilis*), Pacific bluefin tuna (*Thunnus orientalis*), leatherback turtle (*Dermochelys coriacea*), female northern elephant seal (*Mirounga angustirostris*), salmon shark (*Lamna ditropis*), sooty shearwater (*Puffinus griseus*), and white shark (*Carcharodon carcharias*). The TOPP project, a recently completed electronic tracking project of the Census of Marine Life, provided modeled daily location datasets from individuals of these populations tracked during 2002-2008 (Block et al., 2011). Block et al. (2011) and Winship et al. (2011) describe in detail the model fitted to the raw TOPP data, and the associated estimates of uncertainty.

Animals were tracked as long as possible. Annual and multi-year tracks were obtained only for a small proportion of tagged individuals—most animals were tracked for 6 to 9 months. Tuna, shark, and leatherback turtle tracks ended due to battery failure, tag loss, or mortality/harvest, and for these species, there was generally an exponential attenuation of the number of active tags over time following deployment events. The TOPP Pacific bluefin tuna dataset includes 320 individuals, however, only 12 individuals were successfully tracked during their trans-Pacific migration—the remainder were juveniles distributed almost entirely within the California Current. Only the 12 trans-Pacific tuna migrants were included in my analysis and the tracks of these individuals were subset (if longer than a year) to the year in which the trans-Pacific migration occurred (beginning on 1 January).

Pinnipeds and seabirds breed on land and undergo moulting. To capture the full annual cycle of these species, tags were deployed multiple times in a given year (northern elephant seals: short post-breeding and long post-moult migrations; seabirds: short breeding and long post-breeding migrations). Typically, unique sets of individuals were tracked during each migration although some seals were tracked during both migrations in a given year, or during the same migration in multiple years. Tag failure was infrequent for these species and tags were recovered upon recapture of the animals. Sample sizes were similar during post-breeding and post-moult migrations of elephant seals. In contrast, sample sizes of albatrosses varied substantially between breeding and post-breeding stages. New Zealand sooty shearwaters on their post-breeding migrations arrive in the northern hemisphere during the second quarter of the year and return to their South Pacific Ocean breeding islands during the last quarter. I confined my analysis to their North Pacific Ocean locations.

In summary, tracking durations varied among individuals for tunas, sharks, and leatherback turtles for non-biological reasons and albatross sample sizes varied during breeding and post-breeding stages. Thus sampling effort varied throughout the year for many species (Table 3.1) and this required special consideration when estimating population distribution.

3.2.2 Distribution estimation

As a result of the non-standardized sampling regime for most species, and many potential biases introduced by it (Börger et al., 2006a; Walli et al., 2009; Block et al., 2011), I took the following steps to obtain robust distribution estimates: 1) I normalized the utilization distributions for each month and standardized the number of locations per individual contributing to the monthly utilization distribution estimates 2) I employed nonparametric kernel density estimation techniques (Silverman, 1986; Worton, 1989) to calculate monthly utilization distributions and 3) I summed the month-normalized utilization distributions to estimate the annual utilization distribution for each species.

Monthly dataset standardization

Because I was interested in estimating the population-level distribution resulting from individual movements, I treated the individual, rather than the daily location, as the sampling unit.

To avoid biases due to variability in the number of locations recorded for each individual, I standardized the individual contribution to monthly distribution estimates by including only those individuals that were tracked during the full month (individuals contributing 28 or more locations per month). Thus, for each month, I excluded individuals whose tracks were unnaturally abbreviated due to tag loss, tag failure, and/or harvest, whose tracks included large gaps, or whose tracks began only after the month had commenced. This effectively removed many (non-biological) sampling regime biases associated with estimating population-level effects from non-standardized individual movement time-series.

There were biologically relevant exceptions to this procedure. The number of monthly at-sea locations for seabirds undertaking multiple short trips to sea during brooding, or returning to or departing from their breeding colony, was typically less than 28, but I considered these locations representative of at-sea distribution during these months and retained them. Likewise, northern elephant seals may have been tracked at sea for fewer than 28 days in the months when they returned from or embarked upon a foraging migration. I considered pre/post-breeding and pre/post-moult partial-month tracks as representative of biological variability in individual arrival and departure dates to and from the rookery—and thus representative of the natural variability in individual contribution to at-sea population distribution during these months.

In total, 604 individuals contributed to this analysis (Table 3.1). I assumed that the individuals contributing to the utilization distribution in each month composed a random sample of the population.

Monthly utilization distributions

The best home range and population distribution estimators indicate where an animal may be found with some level of predictability during the duration of the study and provide an indication of importance of different areas to the animal (Powell, 2000). The most appropriate quantitative description of a home range is as a utilization distribution (UD)—a continuous probability distribution of an animals use of space (Van Winkle, 1975). Kernel density estimators have emerged as the most effective and objective technique for their estimation (Silverman, 1986; Worton, 1989; Seaman and Powell, 1996; Powell, 2000; Lichti and Swihart, 2011). Kernel estimators provide probability density functions that can be used in statistical analyses and make "near-optimal" use of limited data for generating ecologically meaningful conclusions about space-use (Matthiopoulos, 2003).

I employed nonparametric fixed kernel density estimation techniques (Silverman, 1986; Worton, 1989) to calculate monthly utilization distributions (pooled across years) for each population.

a) Kernel and grid selection:

Kernel density estimates (KDE) were calculated using the ks library (Duong, 2011) in R (R Development Core Team, 2012). I used a Gaussian kernel, and a grid resolution of 0.05 degree over which point samples of the probability density distribution were selected. Neither the kernel choice nor grid resolution greatly affects the estimated probability density distribution (Silverman, 1986). However, the choice of grid resolution does affect the subsequent calculation of overlap statistics that are themselves the result of integration of the density estimates over the same grid (Fieberg and Kochanny, 2005). I tested the adequacy of the initial grid selection (0.1 degree) following Fieberg and Kochanny (2005) to ensure integration of the estimated probability distributions to 1 for each KDE, and ultimately increased the resolution to 0.05 degree.

b) Bandwidth selection:

Kernel density estimates are very sensitive to bandwidth selection (Wand and Jones, 1995). I estimated utilization distributions separately using two bandwidth selection approaches.

First, I selected bandwidths for each KDE using a data-driven automatic selection approach (Silverman, 1986; Loader, 1999; Sheather and Jones, 1991). Such methods include the reference bandwidth, least-squares cross validation (LSCV), solve-the-equation, and plug-in-estimators. The reference bandwidth (Worton, 1995) is most frequently used, however I found that it substantially oversmoothed the utilization distribution, a common limitation (Seaman and Powell, 1996; Gitzen et al., 2006). The LSCV approach is typically recommended (Silverman, 1986; Seaman et al., 1999), and is particularly suggested for datasets with multiple clusters—for example, animals that frequent multiple geographically separated foraging areas. However, I found, as have other researchers (Amstrup et al., 2004; Hemson et al., 2005), that it failed to converge in most cases, likely because the large and highly clustered TOPP dataset contains many overlapping locations.

Plug-in methods (Sheather and Jones, 1991) are the most popular bandwidth selection tools in the statistical literature. Because plug-in methods estimate bandwidth based upon an initial normal model of the data, they perform well when the distribution of the dataset is indeed normal, i.e. there is a single center of activity. However, they tend to oversmooth when datasets contain multiple centers of activity.

Botev et al. (2010) introduced an improved Sheather-Jones plug-in method (ISJ) that avoids the normal reference rule, is computationally much faster than standard plug-in approaches (and most others that I explored), and outperforms the Sheather-Jones method for almost all standard test distributions. I used the bivariate ISJ algorithm (Botev et al., 2010) to select a bandwidth in both the latitudinal and longitudinal dimensions for each data subset (i.e. for each species/time-frame combination; Table A3). Bandwidths were calculated using the kde function (Botev et al., 2010) in Matlab (2010a).

For comparison and to evaluate bandwidth effects on monthly UD estimates and overlap indices, I also calculated each monthly KDE using a 1-degree bandwidth following the ad-hoc approach taken by BirdLife International (2004) in their Tracking Ocean Wanderers analysis.

Month-normalized estimates of annual population distribution

Because the sample of individuals was assumed to be representative of the population in each month, and sample size varied between months, months were normalized to obtain an estimate of annual space-use that was not directly biased by sample size and that ensured each month contributed equally to the annual estimate. Each monthly utilization distribution was standardized to integrate to 1. These were summed and divided by the total number of months with species records—12 in most cases, 7 for sooty shearwaters which were present in the North Pacific from April through October.

3.2.3 Area estimates

Population distribution and high use areas

I follow convention in defining the range of occurrence using the 100% probability contour of the utilization distribution, and the individual home range or population distribution using the 95% contour. The 95% contour is used to exclude rare sallies outside of the home range (Burt, 1943) that may greatly inflate perception of home range size. Areas of high use by animals are commonly delineated by the 50% and 25% contours of utilization distributions (Powell, 2000; Wilson et al., 2010). To distinguish "high use areas" from surface area, I refer to unique polygons within the 50% and 25% contours as core and focal regions, respectively, and their combined area as total core/focal area.

Geographic coordinates of 100%, 95%, 50% and 25% UD contours were transformed to planar Cartesian coordinates using an Albers equal-area conic projection (prime meridian, 180°; standard parallels, 10°N and 50°N; latitude of origin, 30°N) with units in kilometers. The area of all polygons within each contour were calculated in square kilometers using the calcArea function from the PBSmapping library (Schnute et al., 2010) in R (R Development Core Team, 2012). Area was calculated for population UDs, and for individual home ranges.

Relationship between sample size and area estimates

Kernel density estimation assumes that a true probability distribution exists, and that samples were drawn from and are representative of this distribution (Silverman, 1986). The validity of UD estimates is based upon their convergence with the true distribution as sample size increases. Theoretically, the relationship between the area of UD contours and sample size should asymptote as the estimated utilization distribution and the true probability distribution converge (Silverman, 1986; Kern et al., 2003; Laver and Kelly, 2008). To test whether there was an asymptotic relationship between area estimates and sample size and to obtain confidence intervals for mean area of the 100%, 95%, 50% and 25% contours (Kern et al., 2003), I took a resampling approach (Crowley, 1992). From each month's sample of individuals, I resampled 100 times with replacement a bootstrap sample of individuals following a regular sample size sequence from 1 to the maximum sample size. For each set of individuals in the bootstrap sample, the utilization distribution was estimated, contour polygons were projected and area calculated as in 2.3.1, and for each bootstrap sample, mean contour area and 95% confidence intervals were calculated.

3.2.4 Probability of overlap

I assessed the degree of similarity between utilization distributions using overlap statistics presented by Fieberg and Kochanny (2005) to quantify space-sharing between species. All statistics were calculated in R using a custom script adapted from the kerneloverlap function in the adehabitat package (Calenge, 2006) for R (R Development Core Team, 2012).

Space-sharing between species and groups of species: Area of overlap

A simple measure of space-sharing is the proportion of each species' distribution area shared with another species (Fieberg and Kochanny, 2005):

$$HR_{i,j} = A_{i,j,95}/A_{i,95}. \tag{3.1}$$

$HR_{i,j}$ is the area of overlap between the 95% contour areas of species i and j ($\mathrm{A}_{i,j,95}$) expressed as a proportion of the 95% contour area of species i ($A_{i,95}$) and ranges from 0 to 1 (100% overlap). The indices are directional—the proportion of species *i's* home range overlapped by species j typically does not equal the proportion of species *j's* home range overlapped by species i.

Although very straightforward, the HR measure of overlap has the disadvantage of ignoring each species' probability distribution (it assumes a uniform distribution). When densities are low within large areas of overlap, this measure overestimates the actual probability of finding the two species in the same place. To help extend this measure, I calculated area of overlap for three probability contours: 95%, 50% and 25%, however the assumption that species are distributed uniformly within each contour remains a difficulty.

Space-sharing between species and groups of species: Probability of overlap

To incorporate the utilization distribution into an index of overlap, I used a probabilistic measure; PHR:

$$PHR_{i,j} = \int\int_{A_i,95} UD_{j,95}(x,y)dxdy. \tag{3.2}$$

Equation 2 integrates over species *j's* utilization distribution (95% contour) within species *i's* distribution (95% contour). $PHR_{i,j}$ is the probability that species j will occur within species *i's* distribution. The index ranges from 0 to 1. This index is contrasted with area of overlap (2.4.1) in that it takes into account the full probability density function of the overlapping species (j). The two measures are equivalent when the overlapping species (j) exhibits nonrandom space-use (i.e. it is distributed uniformly throughout its distribution area). Species pairs with a large *area of overlap* may have a small *probability of overlap* if shared areas do not include high densities. Indices are directional (separate probabilities were calculated for each member of a species dyad).

3.3 Results

3.3.1 Utilization distributions

For comparison , I present in all tables and figures, utilization distributions (UD) and their area estimated both with the Improved Sheather Jones (ISJ) bandwidth and a 1-degree bandwidth. Areas referenced in the text are those estimated with the ISJ bandwidth only (Botev et al. (2010); Table A3).

Individual home ranges

Home range area

Mean individual home range area (95% contour of UD, Table 3.2) ranged from 42,141 km^2 for salmon sharks (SD=41,895) to 297,597 for sooty shearwaters (SD=139,226). Variability in mean estimates was high (Table 3.2). Mean individual home range size varied seasonally for all species (Fig. 3.1, Table A2). Mean individual monthly home ranges were the largest for seabirds...—up to 463,464 km^2 (SD=139,763, Table A2) in the boreal summer during post-breeding migrations. Other taxa had substantially smaller monthly individual home ranges. All non-seabird mean monthly home ranges were less than 200,000 km^2.

Core and focal area

Mean individual core area (Table 3.2) ranged from 12,123 km^2 for salmon sharks (SD=14,406) to 97,050 for black-footed albatross (SD=84,562), and mean focal areas ranged from 26,000-35,000 thousand km^2 for seabirds and 4,000-8,000 km^2 for all other species. Monthly mean individual core area of seabirds ranged between 80,000 and 200,000 km^2, and monthly mean individual focal area was less than 60,000 km^2. The largest seabird core and focal areas were recorded during the summer. Monthly mean individual core and focal areas of other taxa were often orders of magnitude smaller: less than 50,000 km^2 for core areas and less than 15,000 km^2 for focal areas.

Monthly population distribution

Distribution

Population distribution (95% of UD) varied throughout the year for all species (Figs. 3.2 and 3.3). Maximum monthly distributional area was less than 10 million km^2 (Fig. 3.4). Black-footed albatross monthly distribution was the largest—between 7 and 8 million km^2—from June through October (Fig. 3.4) when the centroids of their core and focal regions shifted north of 40° N (Fig. 3.5). Monthly distribution of each non-seabird species was less than 6 million km^2. In contrast to seabirds and seals, salmon sharks were most widely distributed during the first quarter of the year (Fig. 3.2, Fig. 3.4).

Core and focal area

Total monthly core area was less than 2 million km^2 (Fig. 3.4, Table A4) for black-footed albatross, less than 1.5 million km^2 for other seabirds and northern elephant seals, and less than 750,000 km^2 for all other species. The largest focal area was 681,812 km^2 for black-footed albatross in September (Fig. 3.4, Table A4). Monthly focal area of all other populations did not exceed 500,000 km^2.

Core and focal regions

Unique core and focal region size varied monthly (Fig. 3.6a), and within a month, there was large variability in polygon size for all species (Fig. 3.6b). Mean core region area was less than 300,000 km^2 for seabirds and northern elephant seals, less than 150,000 km^2 for white sharks, and less than 50,000 km^2 for other species. The size of unique focal regions was less than 200,000 km ^{2} for all species except sooty shearwaters.

Annual month-normalized population distribution

Distribution, core, and focal areas

On an annual basis, seabirds were the most widely distributed taxa (Figs. 3.7 and 3.8). Seabirds and Pacific bluefin tuna were the most widely distributed across the longitudinal extent of the Pacific (Fig. 3.2). Annual month-normalized areal extents (95% contour of UD) were 16.7 to 26.7 million km^2 (Table 3.3). Although sooty shearwaters had the largest areal extent, their total focal area was nearly 400,000 km^2 less than the total focal area of either albatross species. Salmon shark annual distribution, the next largest in size following seabirds (8.7 million km^2), was half the size of Laysan albatross distribution and despite their large range, salmon shark core and focal areas were the smallest (3.7 million km^2 and 34,000 km^2).

Core and focal regions

Core and focal regions (Figs. 3.7 and 3.8) were located in the California Current (all species except Laysan albatross); the NPTZ (seabirds, northern elephant seals, and bluefin tuna); the Kuroshio Current (sooty shearwater, Laysan albatross, and Pacific bluefin tuna), the Oyashio Current (sooty shearwater and Laysan albatross), the Gulf of Alaska (northern elephant seal, salmon shark, and all seabirds), and the eastern boundary of the North Pacific Gyre (white shark, leatherback turtle). Size of focal regions was variable for all species (Table 3.4). Focal region area ranged from 130 km^2 for northern elephant seals in the Aleutian Islands to 826,690 km^2 for Laysan albatrosses in the central NPTZ (Table 3.4). The largest core regions of seabirds and northern elephant seals ranged from 1.4 to 2.6 million km^2.

Bandwidth effects

Utilization distributions estimated with a 1-degree bandwidth were more highly smoothed in comparison to UDs estimated with the ISJ bandwidth (Figs. 3.2, 3.3, 3.7, and 3.8). Fewer unique focal regions were identified within each contour via a 1-degree bandwidth (Table 3.3), and the mean and median area of focal and core regions was in most cases substantially larger than those estimated with the ISJ bandwidth (Table 3.4). Maximum focal region area estimated by a 1-degree bandwidth was triple that of the ISJ estimation for salmon sharks. Core region area of black-footed albatross and salmon sharks estimated with a 1-degree bandwidth was double that estimated with the ISJ bandwidth. Sooty shearwater area estimated by a 1-degree bandwidth were similar or less than corresponding ISJ estimates. The mean ISJ bandwidth for sooty shearwaters—0.80 latitude and 1.01 longitude—was the closest to the 1-degree bandwidth (Table A3) and area estimated by the two bandwidths were similar for this species (Table 3.3, Table 3.4).

Relationship between sample size and area estimates

Sample size-area curves approached asymptotes for many species in many months (Fig A1-A8). Species for which large datasets were available (northern elephant seals, Fig. A4; salmon sharks, Fig. A6; and white sharks for half of the year, Fig. A8) had areas that approached an asymptote for 100%, 95%, and 50% contours at sample sizes of 20-60 individuals in most months and at 20 individuals for focal area. Northern elephant seal area estimates consistently approached an asymptote. For example, the mean bootstrapped estimate of the September utilization distribution area approached an asymptote between 20 and 40 individuals for the 25% and between 60 and 80 individuals for the 50% contour (Fig. 3.9). In contrast, only 24 individual sooty shearwaters were tracked in September, and with each added individual, the rate of area increase was high (Fig. 3.9). While the slope of the area to sample size relationship began to decrease as the maximum number of resamples was approached, an asymptote was not yet reached for the 50% contour in this example. Seabird area to sample size relationships generally tended toward an asymptote at maximum resample sizes, especially for the 25% contour. Among the seabirds, bootstrapped area estimates for Laysan albatross most frequently approached an asymptote. Monthly area estimates that did not appear to approach an asymptote given the sample size, or were highly imprecise due to individual variability, included those for white sharks during low sample size months (Fig. A8, June-September), Pacific bluefin tuna (Fig. A5), leatherback turtles (Fig. A3), and the outer contours of black-footed albatross (Fig. A1) and sooty shearwater (Fig. A7) utilization distributions.

3.3.2 Species Overlap

There were three general patterns of overlap between annual month-normalized distributions of species pairs:

a) A high area of overlap and a high probability of overlap (all seabird species with each other, leatherback turtle and white shark; salmon shark overlapped by northern elephant seal)

b) A high area of overlap but a much lower probability of overlap (northern elephant seal and salmon shark by black-footed albatross; northern elephant seal by salmon shark; and northern elephant seal and Pacific bluefin tuna by sooty shearwater).

c) A small area of overlap but a high probability of overlap (sooty shearwater by leatherback turtle; black-footed albatross and sooty shearwater by northern elephant seal, Pacific bluefin tuna, salmon shark, and white shark).

Probability of species overlap varied monthly (Fig. 3.10). Highest probabilities of overlap occurred with black-footed albatross, sooty shearwater, northern elephant seal, and salmon sharks. Mean probability of overlap of all species with black-footed albatross and sooty shearwater distributions was the highest when seabirds were widely distributed (Figs. 3.4 and 3.11). From June until October, four to six of the seven other species had a greater than 20% probability of co-occurring with black-footed albatross and sooty shearwaters (Fig. 3.11). During March and April, there was a high probability (greater than 60%) that black-footed albatross would overlap with northern elephant seal, and during the summer months (July-September), there was an 80% probability that northern elephant seals would overlap with the black-footed albatross distribution. White sharks had a high probability of overlap with northern elephant seals in the winter months. Black-footed albatross and sooty shearwater utilization distributions were the only to have high probabilities of being overlapped by Pacific bluefin tuna. There was a greater than 50% probability that Pacific bluefin tuna would overlap sooty shearwaters during much of the duration of sooty shearwater residency in the North Pacific (Fig. 3.10).

3.4 Discussion

This study provides a synthesis of the monthly spatial dynamics of eight migratory marine predator populations in the pelagic biomes of the North Pacific Ocean. These results are important for calibrating marine conservation efforts to the life histories of wide ranging species. The maximal extent of unique core regions was twice as large as the largest proposed marine protected area, and for all species, focal regions were of the scale of the largest MPAs (Spalding et al., 2010). Thus, spatial management measures may not need to be prohibitively large to include major core or focal regions of wide-ranging species—at least in reference to the size distribution of the largest extant MPAs and the Convention on Biological Diversity goal of protecting a representative 10% of pelagic ecosystems. However, to account for seasonal variability in distribution and risk exposure, and potential future distributional adjustments due to global climate change (Robinson et al., 2009), spatial measures intended to protect wide-ranging marine predators may need to be dynamic, numerous, and/or embedded within strategic, integrated, and adaptable macro-scale zoning strategies.

The ubiquity of wide-ranging marine predators has led other researchers to suggest their utility as indicator species (Sergio et al., 2008; Hooker et al., 2011; Lascelles et al., 2012). Seabirds were the most widely distributed taxa. Ultimately, their distribution is regulated by seasonal and annual variation in temperature and productivity, which influence where prey aggregate. Although normalized annual population ranges of seabirds encompassed 30-40% of the 64,550,459 km^2 North Pacific Ocean (Costello et al., 2010), density was highly concentrated in discrete regions within these ranges. The 50% contour of black-footed albatross distribution represented just 7% of the surface area of the North Pacific Ocean. Batten et al. (2006) observed that black-footed albatross and sooty shearwaters were ubiquitous in all of the key habitats of the North Pacific Ocean during summer surveys. In this study, seals, sharks, tuna, and turtles had high probabilities of overlap with black-footed albatross and sooty shearwaters. Thus, these two species may provide observable indication of the unobservable marine predator community beneath the surface. Spatial conservation efforts targeted at seabirds could help focus ecosystem management in this vast pelagic realm.

Black-footed albatross utilization distributions illustrate how inferences about species area requirements, location of high use regions, and potential exposure to risk change with the temporal scale of analysis. The annual core regions of black-footed albatross were the largest, and in total summed to 7% of the North Pacific Ocean's surface area. This annual utilization distribution normalizes monthly variability and indicated geographic regions that had consistently high density in multiple years or months (provided sampling regimes were standardized across months and years). The predominant annual core and focal regions of black-footed albatross were located in the central NPTZ and the northern California Current (Fig. 3.7). The largest focal region identified was in the California Current and was 1.3 million km^2. Monthly core regions were orders of magnitude smaller than their annual counterparts, were numerous (regardless of the bandwidth used in their delineation), and their centroids shifted location seasonally.

The westward extent of the black-footed albatross core area during the post-breeding period (July-October, Fig. 3.2) was not evident in the annual core distribution (Fig. 3.7) because of high densities in the California Current and central Pacific nine months of the year. Black-footed albatrosses are globally endangered (IUCN Red List of Threatened Species, v 2011.1) and considered at high risk of being bycaught by pelagic longline fisheries for tuna and swordfish in the western Pacific during the boreal summer (Waugh et al., 2012) and in the Central Pacific (Lewison et al., 2009; Huang and Yeh, 2011; Anderson et al., 2011). Protected area networks aim to ameliorate risks to wide-ranging threatened or endangered species by protecting seasonal high-use regions. Studies such as mine, that quantify population distribution at fine temporal scales reveal patterns that though ephemeral, may lead to important hypotheses about seasonal exposure of endangered species to risk.

A criticism of inferences made from marine tracking studies is that few individuals are tracked relative to the population's size, and often only for short periods of time. The robustness of kernel density estimates of space use is heavily influenced by sample size. The TOPP dataset was large enough to allow me to examine the effects of sample size on my results. Bootstrap estimates indicated that for the sample populations considered here, monthly estimates of home range size approached an asymptote with increasing sample size for many species in many months, especially for core and focal area estimates. My estimates of area for northern elephant seals, salmon sharks, white sharks (November, December, January-May), and seabirds (25% contours only), are likely to be accurate. Distribution area of species with large datasets (northern elephant seals, salmon sharks) approached an asymptote for 100% and 95% contours at sample sizes of 20-40 individuals in most months and at 20 individuals for core and focal area. The bootstrap analysis suggested that monthly areas for Pacific bluefin tuna and white sharks during some months (June-September) and outer utilization distribution contours for seabirds were likely imprecise or underestimated due to individual variability or small sample size. The sizes of seabird and Pacific bluefin tuna datasets were between 12 and 30 individuals. Based upon my bootstrap analysis, larger datasets are needed for seabirds and trans-Pacific migrant bluefin tuna to increase the precision and accuracy of monthly population area estimates. White shark population distribution is likely to be greatly underestimated from June through September.

Sample size and behavior should both factor into inferences made about area requirements estimated using different bandwidths. Improved-Sheather Jones bandwidths were smaller than 1 degree for most species in most months (Table A3), resulting in less kernel density smoothing and lower estimates of area than for the 1-degree bandwidth. When sample sizes are not sufficient for bootstrapped area estimates to approach an asymptote, use of a larger bandwidth to estimate area of population distribution will provide a less conservative estimate. Individual movement behaviour can also affect the inferences made about area requirements estimated with different bandwidths. For example, salmon sharks undertake directed north-south migrations and the longitudinal location of these migrations is variable among individuals (Weng et al., 2005). Mean monthly ISJ bandwidths were 0.10 latitude and 0.15 longitude (standard error = 0.01 and 0.02) and utilization distributions estimated with ISJ bandwidths (Figs. 3.2, 3.7) resulted in many disconnected polygons (representing individual home ranges). Utilization distributions estimated with a 1-degree bandwidth (Figs. 3.3, 3.8) were highly smoothed in comparison. In this case, a larger bandwidth would provide a less conservative estimate of total population distribution. Conversely, when albatrosses were aggregated during breeding (December, January, February), area estimates reached an asymptote at very small sample sizes. Thus, the ISJ bandwidth, which was much substantially smaller than 1-degree in these months, likely provided a more accurate estimate of area of total population distribution.

I followed recommended best practice in home range estimation (Laver and Kelly, 2008), and accounted for a non-standard sampling regime among individuals and species

(Börger et al., 2006a). The area-sample size bootstrap analysis that I conducted and the estimation of utilization distributions using two bandwidth selection approaches (a set of data-driven bandwidths and a constant ad-hoc bandwidth), go further than most marine telemetry studies in attempting to account for the variance induced by sampling regime and methodology. More work should be done to attribute variability in home range size to to separate components due to seasonal and inter-annual variability, choice of bandwidth, date of deployment, and individual variability in movement behaviors. This could be done using integrated modeling approaches suggested by (Börger et al., 2006a,b).

Conclusions

Success of spatial conservation efforts is critically dependent on appropriate spatio-temporal scaling of conservation efforts to animal life history, current and future risk, and potential for enforcement (Du Toit, 2010). Scale is central to the debate over whether spatial conservation measures could be useful tools for marine predator conservation. The primary concern is that pelagic MPAs scaled to the large, dynamic, and distributed area requirements of wide-ranging species will be impossibly large or too dynamic to be manageable. For the eight very wide-ranging species studied here, my results suggest that core habitats are within the areal extents of current MPA size but they are indeed highly dynamic. Habitat modeling approaches are extending our ability to make dynamic MPAs useful (Hobday et al.; Howell et al., 2008; Hobday et al., 2011) and sophisticated vessel monitoring systems provide an avenue for enforcement. I suggest that the debate over whether pelagic MPAs could be large or dynamic enough to satisfy area requirements for wide-ranging species should be refocused. The true problem is in the location of core habitats and their overlap with places and commercial processes that are also important to people. The Great Barrier Reef Marine Park is an example of an integrated zoning effort that applies dynamic or mitigative protective measures over a large static area while also balancing stakeholder sentiment. For marine predator conservation in areas of intensive fishing, like the North Pacific Transition Zone, strategic multi-scale strategies are needed.

Table 3.1: Number of individuals tracked in each month in the North Pacific Ocean. *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	BFAL	LAAL	LET	NELE	PBT	SS	SOSH	WS
JAN	25	29	11	83	11	62		58
FEB	21	21	10	103	11	62		52
MAR	2	6	10	110	11	64		49
APR	3	7	10	102	11	67	24	45
MAY	5	8	10	101	11	64	24	40
JUN	23	17	7	114	11	57	24	34
JUL	23	28	8	112	11	59	24	28
AUG	23	28	6	108	8	99	24	20
SEP	23	28	16	106	8	101	24	11
OCT	23	27	16	103	7	86	24	23
NOV	27	30	16	94	5	71	1	55
DEC	14	20	12	87	5	62		61
Total	70	73	16	231	12	113	24	65

Table 3.2: Area (km^2) within the 100%, 95%, 50% and 25% contours of monthly utilization distributions (ISJ bandwidths) estimated for individuals. *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	100%		**95%**		**50%**		**25%**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BFAL	306,672	270,801	285,462	255,018	97,050	84,562	33,273	29,120
LAAL	256,690	182,534	241,312	173,240	75,170	55,956	25,920	19,604
LET	106,172	55,747	85,066	42,939	23,914	14,020	8,138	5,320
NELE	75,976	60,297	62,701	47,581	19,231	16,656	6,874	6,781
PBT	100,742	67,934	91,382	62,825	25,719	20,903	8,391	7,930
SS	47,435	46,623	42,141	41,895	12,123	14,406	3,734	4,920
SOSH	320,284	144,597	297,597	139,226	95,666	56,104	34,439	23207
WS	65,684	53,546	56755	47,058	16,028	15,991	4,890	5,218

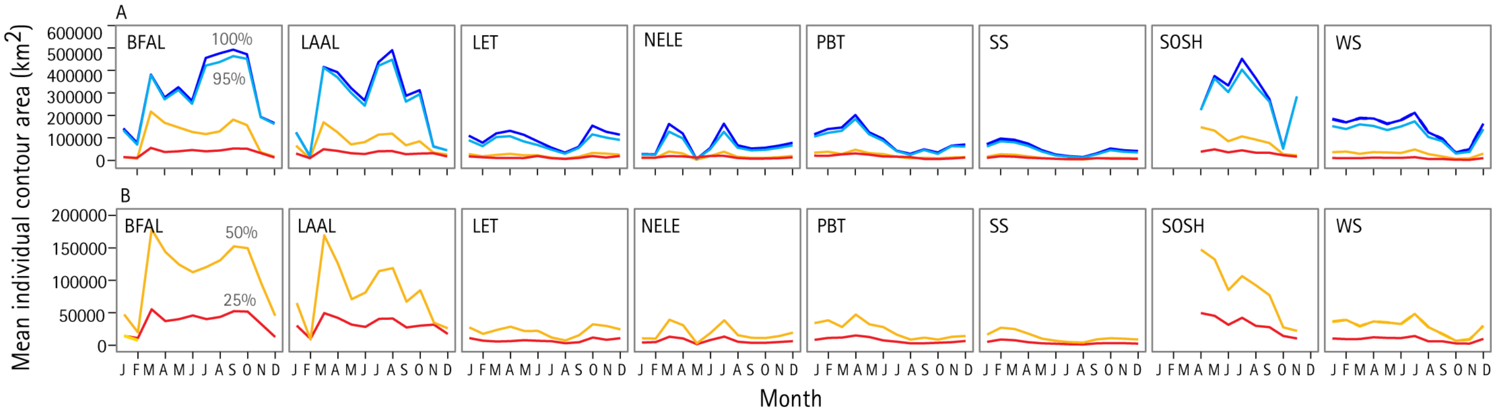

Figure 3.1: Area (km^2) within the A) 100%, 95%, 50% and 25% contours and B) 50% and 25% contours of monthly utilization distributions estimated for individuals (ISJ bandwidths). Values and standard deviations of means are presented in Table A1

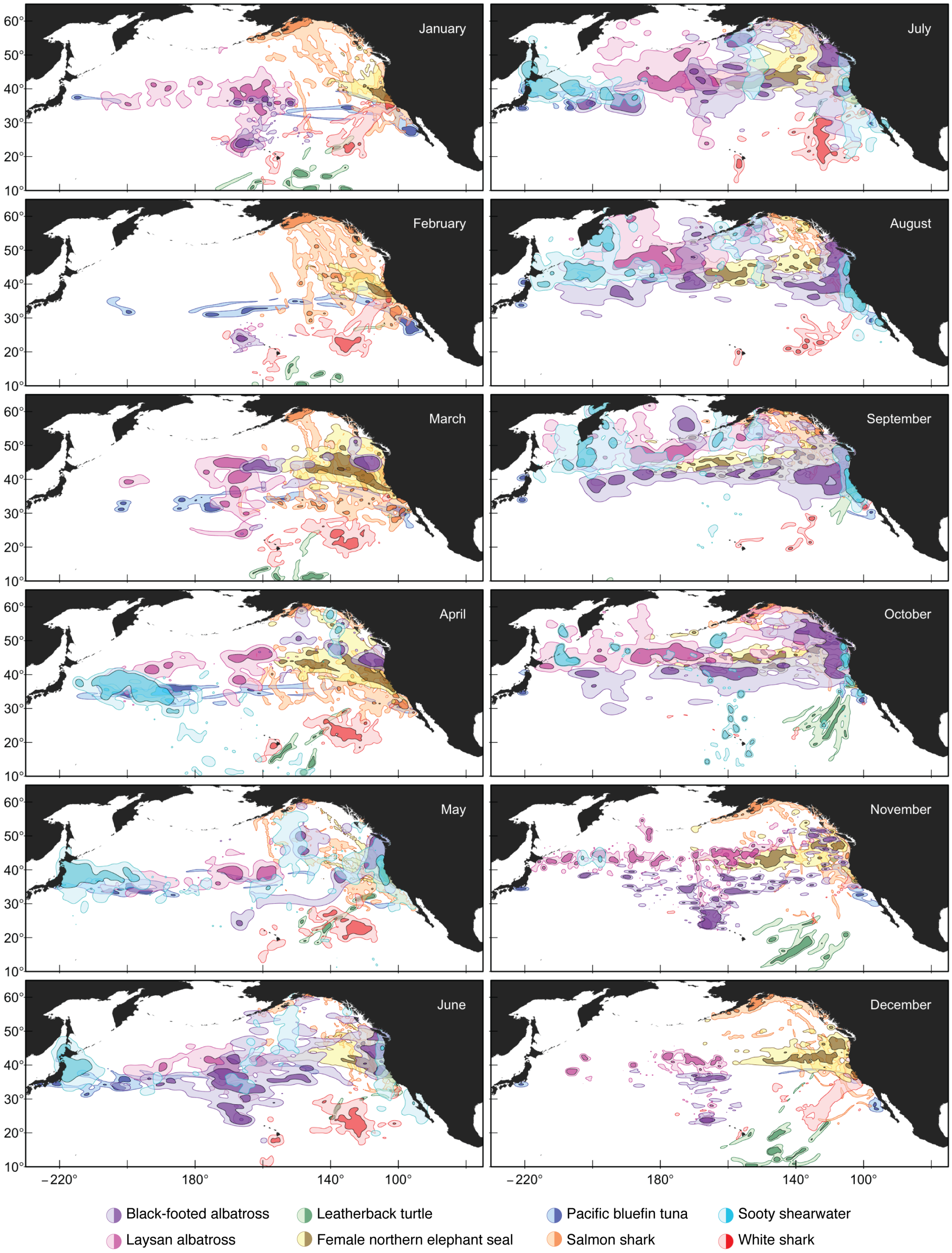

Figure 3.2: Estimated monthly utilization distributions (ISJ bandwidths) of 8 marine predator populations electronically tracked during 2002-2008. For each species, color gradients represent the 95% (light), and 50% (dark) UD contours.

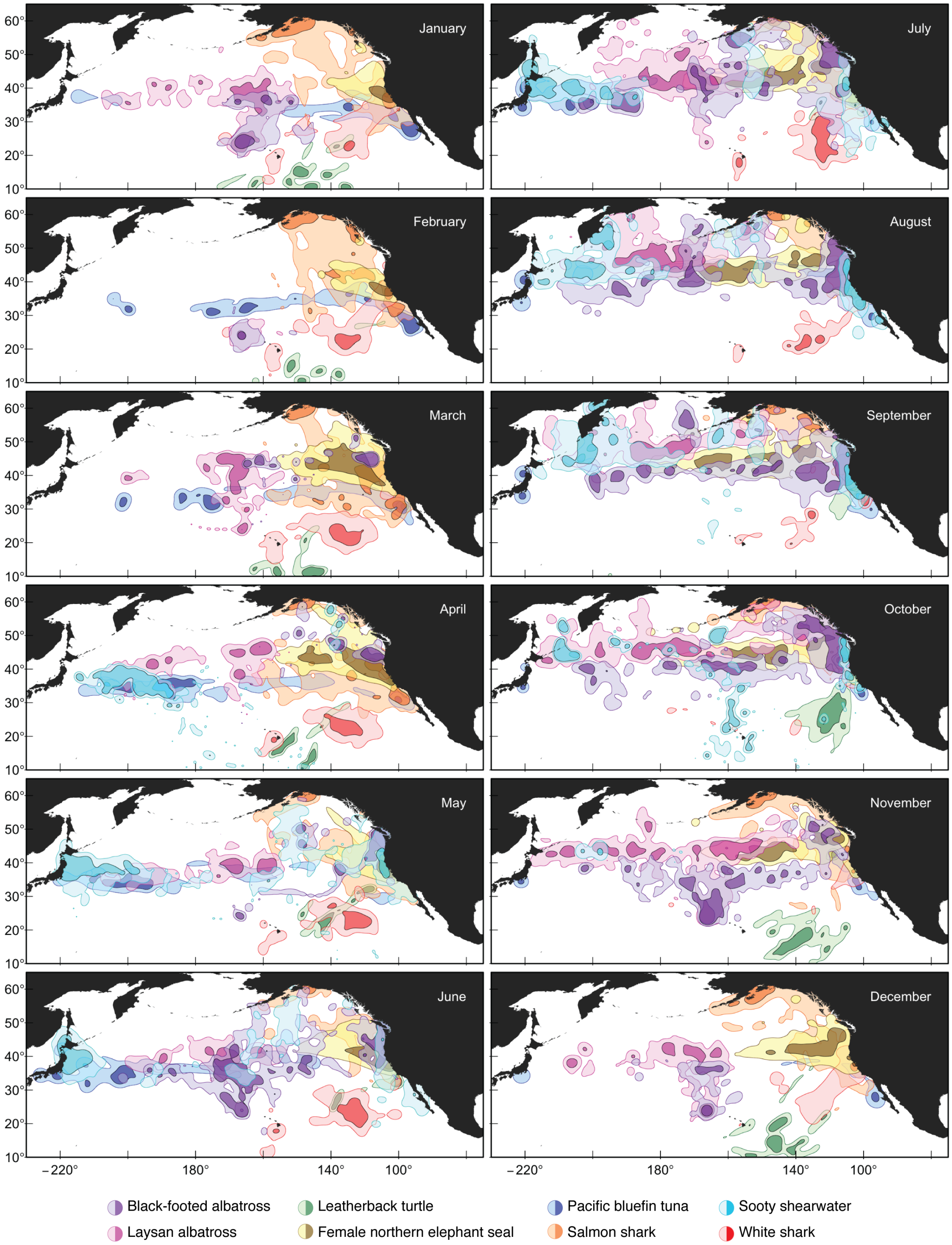

Figure 3.3: Estimated monthly utilization distributions (1-degree bandwidths) of 8 marine predator populations electronically tracked during 2002-2008. For each species, color gradients represent the 95% (light), and 50% (dark) UD contours.

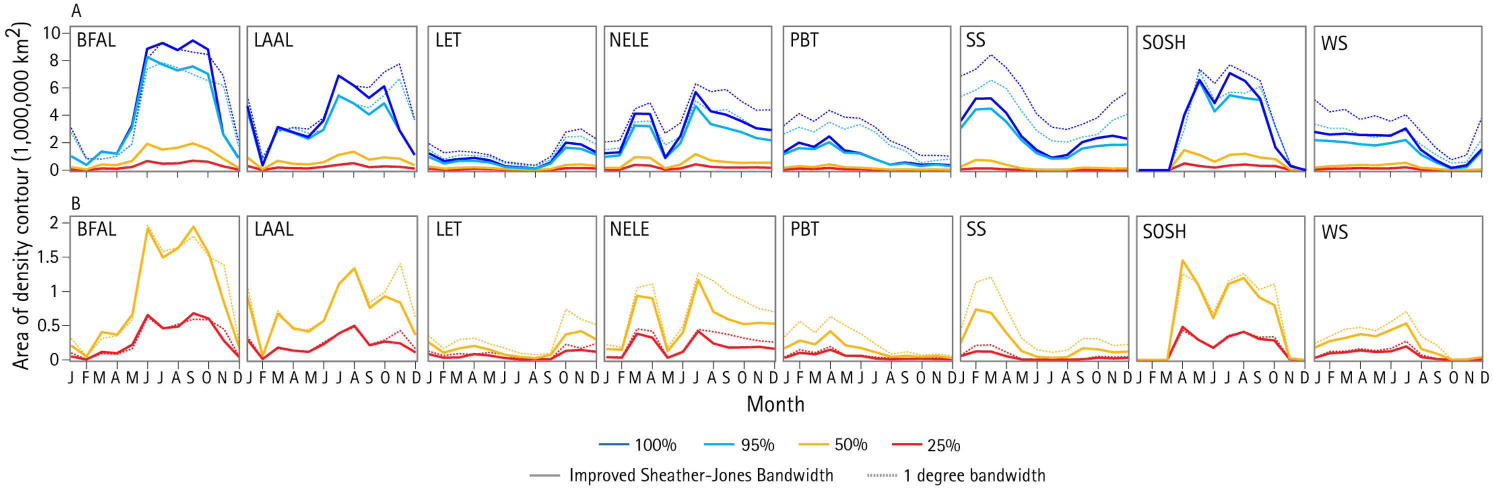

Figure 3.4: Total monthly area delineated by the 100%, 95%, 50% and 25% contours of population utilization distributions estimated with ISJ bandwidths and 1-degree bandwidths for 8 marine predator populations electronically tracked during 2002-2008.

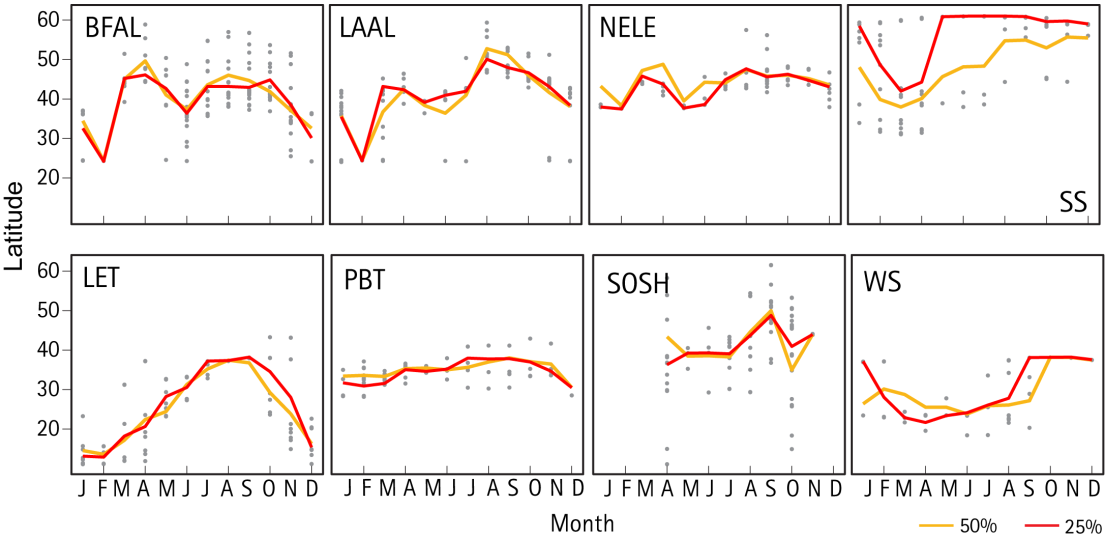

Figure 3.5: Latitude of polygon centroids within core (50% contour) and focal (25% contour) regions of monthly population utilization distribution estimates (ISJ bandwidths) of 8 marine predator populations electronically tracked during 2002-2008. Grey dots are latitudes of individual polygon centroids and lines represent means.

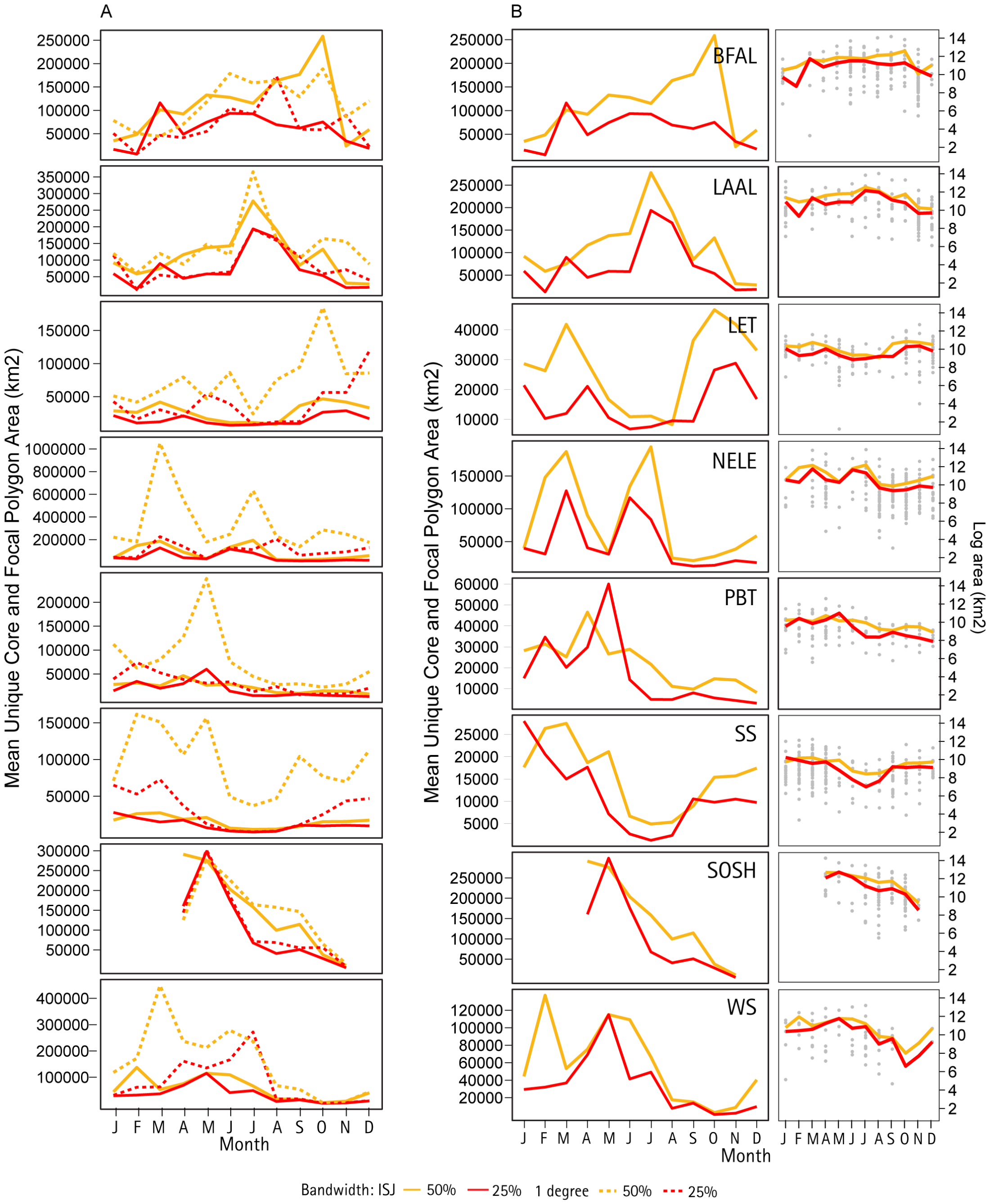

Figure 3.6: Mean area (scales vary by species) of unique polygons within core (50% contour) and focal (25% contour) regions of monthly population utilization distributions estimated with A) ISJ bandwidths and 1-degree bandwidths and B) ISJ bandwidths. For (B) the mean areas and areas of individual polygons (grey dots) are also presented on the log scale.

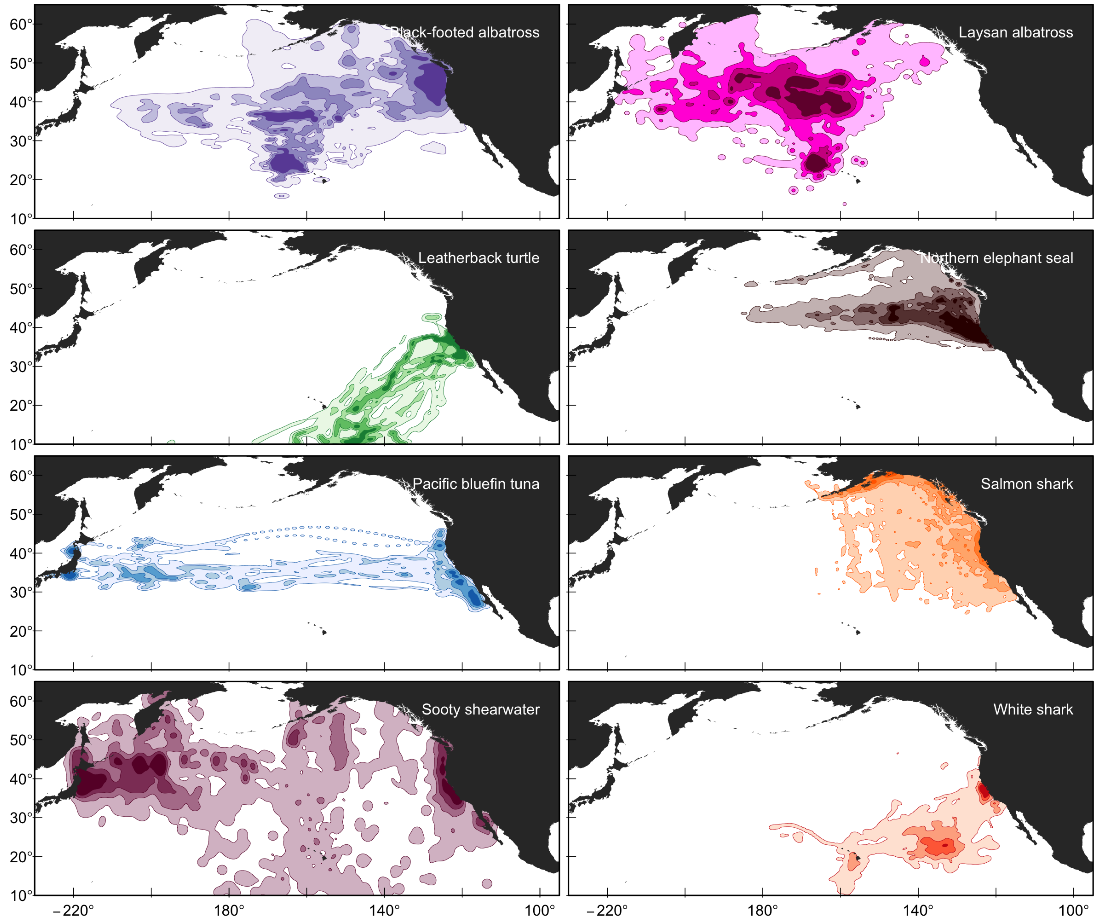

Figure 3.7: Estimated month-normalized annual utilization distributions (ISJ bandwidths) of 8 marine predator populations electronically tracked during 2002-2008. Color gradients represent from light to dark the 95%, 75%, 50% and 25% UD contours.

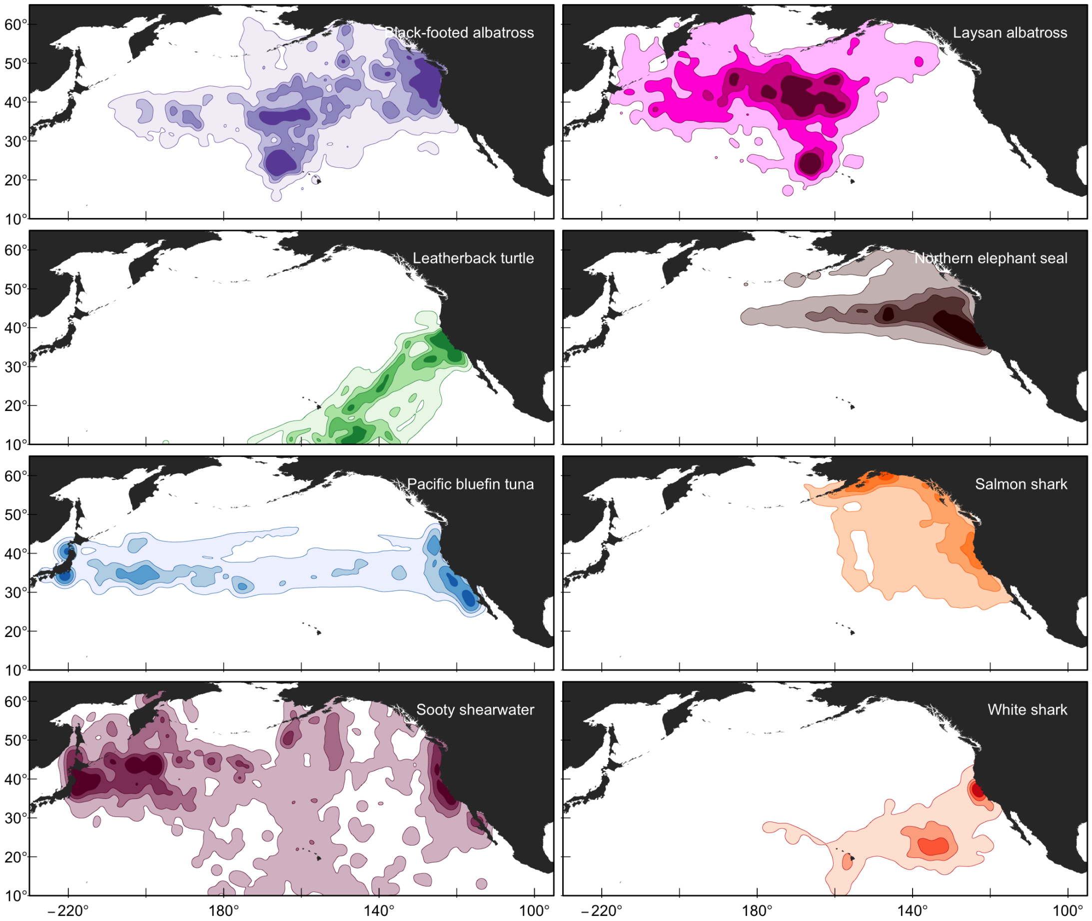

Figure 3.8: Estimated month-normalized annual utilization distributions (1-degree bandwidths) of 8 marine predator populations electronically tracked during 2002-2008. Color gradients represent from light to dark the 95%, 75%, 50% and 25% UD contours.

Table 3.3: Total area (km^2) and number of unique polygons within 100%, 95%, 50% and 25% contours of month-normalized annual utilization distributions estimated with ISJ and 1-degree bandwidths. *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	100%	**95%**	**50%**	**25%**
Improved Sheather-Jones bandwidth				
Total area under contour (km^2)				
BFAL	19,610,818	15,222,667	4,505,035	1,276,761
LAAL	16,721,920	13,377,183	3,123,068	1,265,381
LET	7,074,274	6,123,607	1,623,144	478,498
NELE	6,768,416	4,918,634	1,429,912	548,549
PBT	7,924,424	6,289,333	867,975	194,646
SS	8,652,646	5,906,446	365,120	33,771
SOSH	26,674,490	17,741,867	2,738,465	818,386
WS	6,755,187	4,224,759	420,406	69,606
Number of unique polygons within each contour				
BFAL	3	11	12	9
LAAL	16	16	12	10
LET	5	6	11	11
NELE	13	13	7	10
PBT	43	17	13	6
SS	14	16	11	4
SOSH	23	43	12	5
WS	5	19	3	2
1 degree bandwidth				
Total area under contour (km^2)				
BFAL	19,745,696	15,413,742	4,770,779	1,374,916
LAAL	17,501,226	13,840,020	3,202,441	1,378,264
LET	8,755,968	7,462,696	2,182,612	681,356
NELE	7,574,788	5,565,804	1,589,768	661,637
PBT	13,158,750	9,011,650	1,303,442	239,891
SS	10,135,499	6,837,073	606,938	68,376
SOSH	28,526,246	18,478,308	2,828,399	846,867
WS	8,031,142	5,103,706	492,323	93,778
Number of unique polygons within each contour				
BFAL	3	4	11	6
LAAL	8	6	4	5
LET	2	2	7	5
NELE	4	5	2	2
PBT	1	2	7	4
SS	1	4	4	2
SOSH	15	49	10	6
WS	2	3	2	1

Table 3.4: Summary statistics of area (km^2) of unique polygons within 50% and 25% contours of month-normalized annual utilization distributions. *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	Num.	**Range**		**Median**	**Mean**	**Std.Dev.**
		Min.	Max.			
Improved Sheather-Jones bandwidth						
50% contour						
BFAL	12	1,299	1,756,716	57,981	346,541	638,427
LAAL	12	739	2,571,320	16,233	260,256	734,128
LET	11	64	975,760	15,173	135,262	297,543
NELE	7	94	1,369,426	3,025	178,739	481,372
PBT	13	713	383,611	33,817	66,767	102,928
SS	11	230	189,761	3754	33,193	62,500
SOSH	12	3,511	1,913,543	23,885	228,205	552,178
WS	3	1,640	321,039	97,726	140,135	163,868
25% contour						
BFAL	9	1,998	553,440	19,692	141,862	206,525
LAAL	10	455	826,690	36,106	126,538	253,632
LET	11	798	226,602	11,867	43,500	69,877
NELE	10	130	446,585	2,238	49,868	133,016
PBT	6	5,903	80,991	23,688	32,441	25,915
SS	4	893	24,504	4,187	8,443	11,082
SOSH	5	25,672	340,063	147,035	163,677	139,036
WS	2	9,015	60,591	34,803	34,803	36,470
1 degree bandwidth						
50% contour						
BFAL	11	2,591	2,412,548	137,329	436,192	763,426
LAAL	4	12,518	2,733,527	228,198	800,610	1,300,787
LET	7	6,211	822,346	33,328	311,802	373,186
NELE	2	17,129	1,572,639	794,884	794,884	1,099,912
PBT	7	11,721	575,020	108,660	186,206	198,300
SS	4	10,761	326,811	134,683	151,734	161,456
SOSH	10	2,989	2,032,681	28,111	282,849	639,248
WS	2	175,582	316,741	246,162	246,162	99,815
25% contour						
BFAL	6	4,707	575,289	184,145	229,153	253,124
LAAL	5	54,924	890,470	98,043	275,653	353,709
LET	5	23,243	349,882	54,844	136,271	139,409
NELE	2	69,832	591,805	330,819	330,819	369,090
PBT	4	20,922	105,314	56,827	59,973	34,765
SS	2	3,983	64,393	34,188	34,188	42,716
SOSH	6	2,433	350,782	84,530	141,145	156,397
WS	1	93,778	93,778	93,778	93,778	0

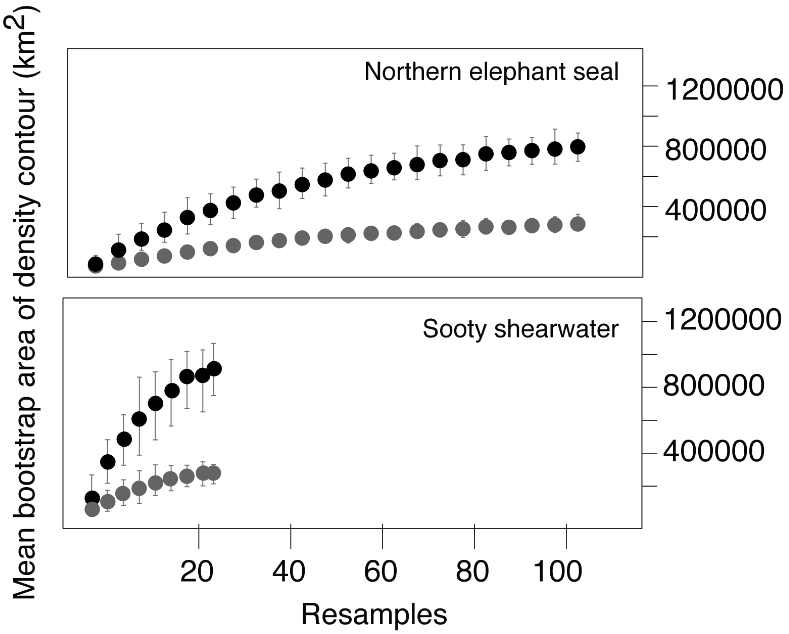

Figure 3.9: Bootstrapped estimates of area (km^2) as a function of sample size (number of individuals) for the 50% (black circles) and 25% (grey circles) contours of September population utilization distributions for female northern elephant seal and sooty shearwater. Circles are means and lines represent standard deviations.

Table 3.5: Proportion of area overlapped and directional probability of overlap between month-normalized annual utilization distributions of marine predator species pairs (row overlapped by column). *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	BFAL	**LAAL**	**LET**	**NELE**	**PBT**	**SS**	**SOSH**	**WS**
Proportion of area overlapped								
BFAL	1	0.53	0.04	0.33	0.22	0.33	0.47	0.03
LAAL	0.58	1	0	0.15	0.15	0.06	0.6	0
LET	0.11	0	1	0.07	0.16	0.21	0.32	0.46
NELE	0.96	0.39	0.07	1	0.13	0.63	0.45	0.05
PBT	0.58	0.35	0.14	0.12	1	0.28	0.64	0.11
SS	0.79	0.13	0.17	0.52	0.26	1	0.39	0.12
SOSH	0.41	0.48	0.09	0.13	0.21	0.14	1	0.06
WS	0.14	0.01	0.66	0.07	0.18	0.22	0.32	1
Probability of overlap								
BFAL	0.95	0.67	0.19	0.91	0.37	0.67	0.3	0.29
LAAL	0.54	0.94	0	0.21	0.2	0.12	0.47	0
LET	0.03	0	0.91	0.18	0.19	0.12	0.08	0.74
NELE	0.35	0.19	0.19	0.94	0.11	0.36	0.12	0.28
PBT	0.2	0.1	0.27	0.24	0.91	0.19	0.26	0.28
SS	0.33	0.02	0.34	0.72	0.31	0.93	0.13	0.35
SOSH	0.44	0.53	0.41	0.46	0.67	0.39	0.9	0.41
WS	0.02	0	0.49	0.16	0.16	0.11	0.08	0.93

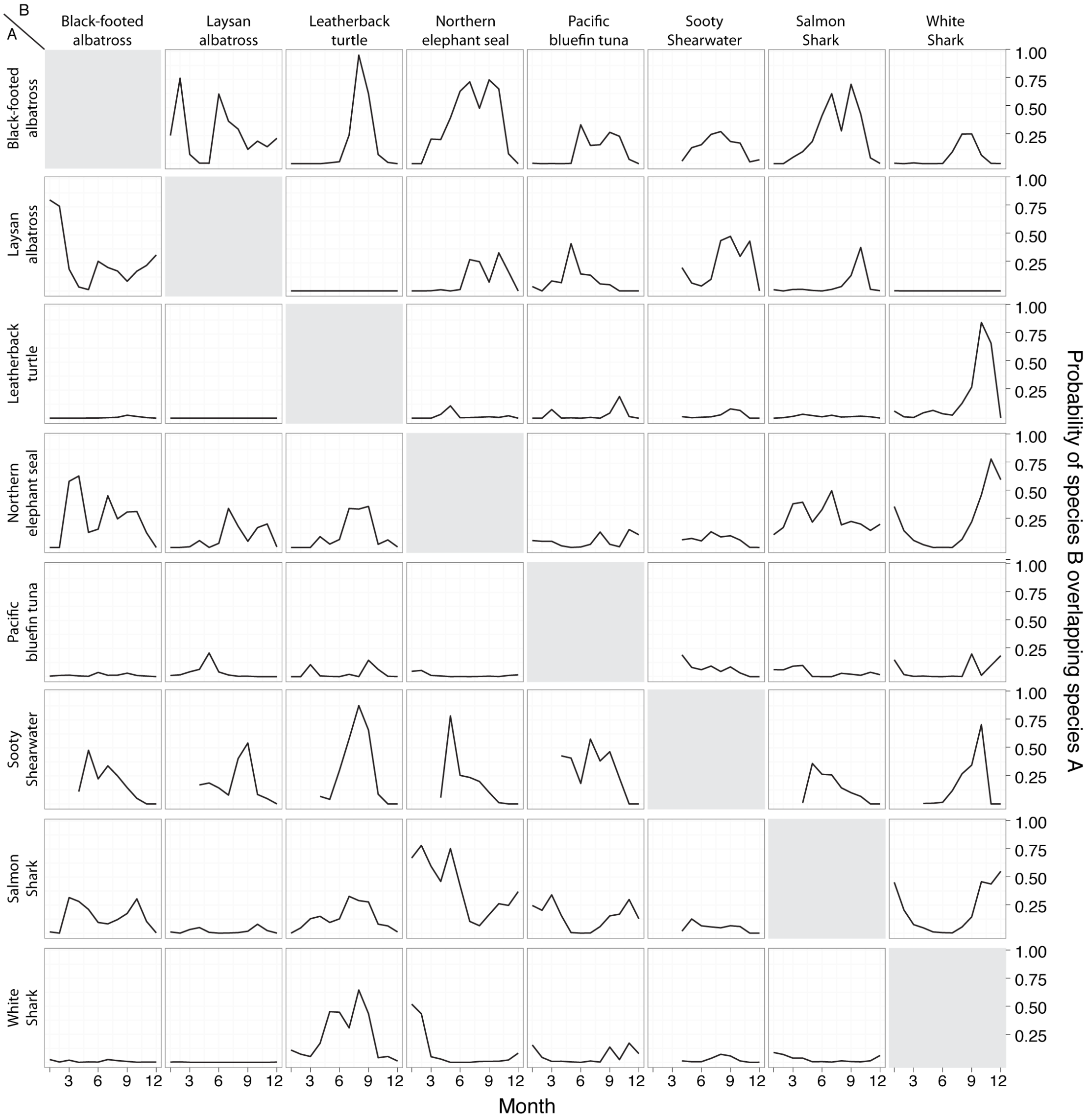

Figure 3.10: Directional monthly probability of overlap between pairs of 8 marine predator populations electronically tracked during 2002-2008.

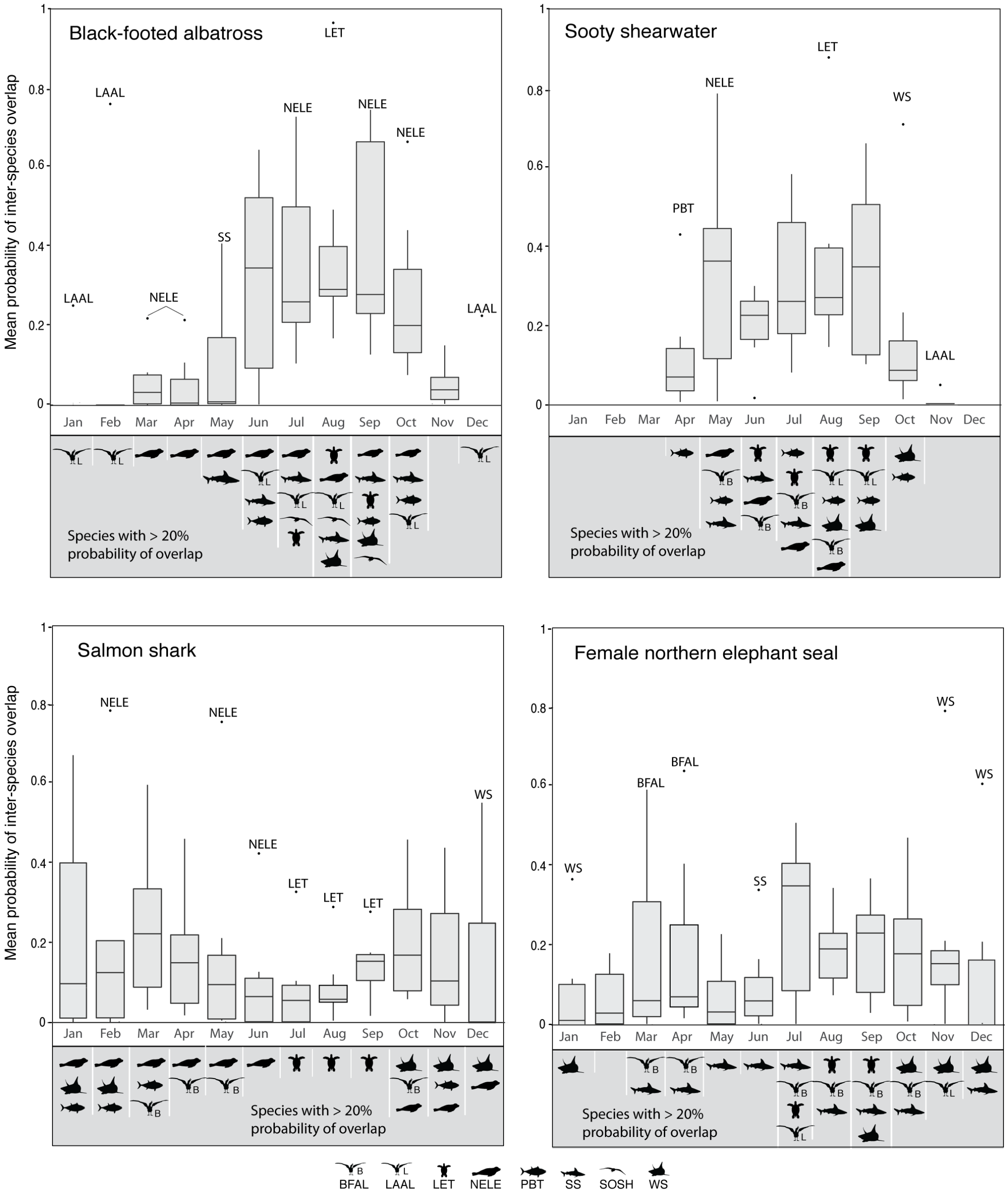

Figure 3.11: Monthly probability of inter-species overlap of four species of marine predators by seven other species electronically tracked during 2002-2008 in the North Pacific Ocean.

Appendix A

Table A1: Area (km^2) of individual monthly utilization distribution contours (ISJ bandwidths). *Codes:* **n**, sample size; **SD**, standard deviation.

	n	**100%**		**95%**		**50%**		**25%**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Black-footed albatross									
JAN	23	26,958	21,385	25,577	19,718	14,578	10,732	4,469	4,418
FEB	19	20,214	18,206	19,517	17,751	7,575	6,137	2,722	2,624
MAR	2	381,411	82,010	379,046	78,667	17,8581	51,118	55,353	36,519
APR	3	279,639	108,626	271,470	100,143	143,815	61,225	37,171	12,806
MAY	5	325,101	257,025	312,742	246,077	124,301	90,277	40,227	17,108
JUN	23	264,598	186,610	251,857	174,033	112,538	67,269	45,856	21,731
JUL	23	455,494	154,625	421,401	156,876	120,568	65,416	40,222	23,213
AUG	23	475,542	116,209	436,991	125,748	130,994	66,309	43,627	23,499
SEP	23	492,206	134,644	463,434	139,763	152,360	66,533	52,509	28,812
OCT	23	471,838	92,800	451,499	100,946	149,562	55,630	51,801	20,825
NOV	25	48,721	31,765	48,691	31,782	36,183	23,031	15,454	11,267
DEC	13	56,303	44,516	54,823	43,729	16,709	13,292	6,466	7,244
Laysan albatross									
JAN	26	123,994	68,747	122,548	68,800	64,923	37,577	22,973	16,857
FEB	16	19,630	15,080	18,575	13,404	8,773	6,654	3,702	3,861
MAR	6	415,454	196,682	412,709	199,506	169,274	117,349	49,398	32,699
APR	7	392,201	125,457	369,915	141,681	125,644	64,032	42,527	26,300
MAY	8	321,619	125,998	300,742	134,700	70,953	43,232	26,964	18,758
JUN	16	266,172	127,937	243,441	115,412	81,190	45,734	27,158	13,417
JUL	28	436,623	122,877	420,624	118,919	114,282	48,352	39,810	16,919
AUG	28	489,753	81,072	447,508	87,202	118,761	46,139	42,916	19,795
SEP	28	287,150	77,944	261,188	78,676	67,113	32,173	22,334	13,216
OCT	27	311,873	88,555	294,080	94,529	84,648	49,558	25,861	15,874
NOV	30	61,883	36,341	60,769	35,872	34,696	21,342	14,125	7,485
DEC	16	44,707	22,298	44,707	22,298	26,204	15,427	8,445	7,299
Leatherback turtle									
JAN	9	108,437	67,464	88,409	54,745	27,408	17,428	10,988	8,062
FEB	7	77,773	44,041	62,448	35,541	17,581	10,092	7,018	4,335
MAR	6	118,581	22,090	102,205	13,514	23,633	9,938	5,773	3,693
APR	6	130,030	37,657	106,250	25,942	28,573	5,223	6,377	3,209
MAY	6	112,634	57,465	83,177	42,503	21,947	13,690	7,743	3,803
JUN	3	84,048	6,037	67,500	7,223	22,119	2,608	6,835	3,257
JUL	3	56,194	34,235	47,211	28,695	11,884	7,403	6,192	2,679
AUG	3	33,813	29,551	29,182	25,213	7,356	6,280	3,104	2,688
SEP	16	59,218	31,658	54,202	28,622	15,463	8,900	4,634	3,184
OCT	16	152,602	39,633	114,116	31,855	32,201	11,314	11,835	4,011
NOV	15	125,777	62,369	100,098	51,649	29,682	19,050	8,436	5,696
DEC	10	113,141	53,118	89,771	40,386	24,477	14,555	10,798	6,368
Female northern elephant seal									
JAN	80	27,928	17,662	25,807	16,207	10,659	6,771	4,138	3,002
FEB	101	26,875	20,822	24,844	18,666	10,243	7,283	4,867	3,410
MAR	110	161,670	50,866	127,534	42,230	39,241	18,128	13,124	9,742
APR	102	119,630	51,823	97,946	41,527	30,817	18,596	10,406	8,512
MAY	88	5,789	8,615	5,536	8,051	3,001	3,723	1,663	2,003
JUN	112	54,819	24,385	49,415	21,994	19,084	8,461	8,140	3,956
JUL	112	162,994	49,617	127,026	38,272	38,423	17,523	13,280	8,364
AUG	108	67,057	34,065	56,228	28,873	15,480	12,164	5,345	5,219
SEP	106	52,878	31,267	44,365	27,169	11,463	9,990	3,678	3,768
OCT	103	56,137	31,123	46,750	26,230	11,124	9,697	3,769	3,627
NOV	94	65,368	31,651	55,550	27,956	14,132	9,928	4,976	4,259
DEC	87	77,998	35,045	66,379	30,461	19,413	11,881	6,293	4,741

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Table A2: *Continued from previous page*

	n	**100%**		**95%**		**50%**		**25%**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pacific bluefin tuna									
JAN	11	116,069	56,042	105,589	53,433	34,175	19,852	8,340	8,830
FEB	11	139,342	65,043	122,382	56,272	38,358	20,633	11,276	6,943
MAR	11	146,036	39,621	131,235	3,9833	28,093	20,364	11,852	9,708
APR	11	201,535	58,096	183,680	59,967	47,278	22,175	15,056	8,188
MAY	11	124,792	34,224	115,955	35,099	32,224	18,497	12,633	7,166
JUN	11	95,977	39,343	87,570	37,674	28,052	20,931	7,439	6,844
JUL	11	42,940	35,211	41,105	35,347	16,255	16,481	5,418	9,264
AUG	8	29,042	22,041	24,637	17,717	8,738	8,831	2,916	3,224
SEP	8	48,982	39,576	45,775	38,263	11,676	11,113	3,045	2,434
OCT	7	35,100	34,294	29,250	27,677	8,703	7,481	3,828	2,464
NOV	5	65,076	43,495	62,945	43,523	12,978	12,801	4,681	3,427
DEC	5	70,548	52,428	61,318	45,037	14,238	14,435	6,585	,7497
Salmon shark									
JAN	62	70,643	55,421	61,781	49,657	16,460	15,428	5,232	5,447
FEB	62	95,513	63,171	84,589	54,768	26,988	21,437	8,829	8,072
MAR	64	90,164	55,708	79,981	50,801	24,987	19,565	7,664	6,308
APR	67	72,975	58,063	64,234	52,682	17,857	17,350	4,656	4,721
MAY	64	43,888	34,783	39,261	32,280	10,144	10,659	2,970	3,380
JUN	57	24,582	18,506	22,216	17,885	6,794	7,828	2,304	3,194
JUL	59	17,175	15,486	15,991	14,999	4,784	6,025	1,498	1,900
AUG	97	13,153	16,514	12,373	15,925	4,140	6,258	1,194	1,867
SEP	100	29,464	22,928	27,010	21,422	9,080	8,675	2,915	3,665
OCT	84	51,095	34,379	45,147	32,537	10,785	11,162	3,351	4,551
NOV	71	43,472	32,337	37,910	30,405	9,990	10,796	3,170	3,854
DEC	61	39,993	31,550	34,924	29,163	8,857	9,783	2,467	3,246
Sooty shearwater									
APR	12	223,752	193,494	223,752	193,494	147,340	92,912	49,598	42,185
MAY	23	374,718	148,836	363,946	147,137	132,289	56,113	45,287	28,507
JUN	24	332,879	63,756	303,644	80,941	85,014	40,527	31,519	14,510
JUL	24	451,496	84,890	403,525	92,919	106,497	41,094	42,304	19,419
AUG	24	365,672	63,720	328,926	78,072	92,413	39,487	29,876	15,581
SEP	24	272,392	58,770	261,211	62,576	77,068	40,186	27,802	16,458
OCT	13	54,990	71,798	52,033	62,814	27,567	24,092	14,262	11,812
NOV	1	284,302		283,966		22,197		10,446	
White shark									
JAN	58	61,671	42,640	54,895	40,376	16,555	16,559	4,697	4,591
FEB	52	69,555	41,429	60,450	36,307	19,750	16,307	5,238	4,242
MAR	49	77,765	45,594	65,821	42,314	16,125	13,492	5,172	5,402
APR	44	97,361	48,737	82,528	43,792	22,326	14,692	7,424	5,179
MAY	40	95,802	50,911	80,112	44,087	21,372	16,758	6,142	5,080
JUN	34	105,134	52,141	89,497	45,697	22,838	13,306	7,104	4,421
JUL	28	129,219	66,416	111,293	57,700	31,102	22,173	9,404	7,932
AUG	20	53,540	39,235	47,759	35,404	12,366	14,522	2,773	2,972
SEP	11	44,429	47,732	40,083	45,193	10,647	13,261	2,794	4,146
OCT	22	8,562	11,133	7,515	10,645	2,576	5,731	1,168	2,868
NOV	55	11,332	10,408	10,097	9,782	3,210	5,378	1,112	1,490
DEC	60	39,742	29,697	36,348	29,631	11,587	12,309	4,280	5,577

Table A3: Improved Sheather-Jones (Costello et al., 2010; Botev et al., 2010) bandwidths used in kernel density estimation of monthly utilization distributions of 8 marine predator populations electronically tracked in the North Pacific Ocean 2002-2008. *Species codes:* **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **LET**, leatherback turtle; **NELE**, female northern elephant seal; **PBT**, Pacific bluefin tuna; **SS**, salmon shark; **SOSH**, sooty shearwater; **WS**, white shark.

	BFAL		**LAAL**		**LET**		**NELE**		**PBT**		**SS**		**SOSH**		**WS**	
	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long
JAN	0.22	0.30	0.62	1.01	0.24	0.55	0.11	0.11	0.10	0.58	0.15	0.20	0.52	0.63	0.17	0.21
FEB	0.10	0.80	0.29	0.36	0.21	0.49	0.12	0.21	0.17	0.88	0.17	0.24	0.71	1.68	0.19	0.24
MAR	1.09	2.03	0.67	1.78	0.20	0.49	0.31	0.57	0.12	0.76	0.14	0.22	0.87	1.90	0.20	0.24
APR	0.92	1.53	0.61	1.35	0.33	0.51	0.25	0.45	0.14	1.41	0.14	0.19	1.26	1.37	0.23	0.34
MAY	1.61	1.72	0.59	1.03	0.29	0.59	0.07	0.10	0.10	0.64	0.08	0.12	0.85	0.87	0.23	0.40
JUN	0.43	2.82	0.60	1.42	0.13	0.31	0.11	0.23	0.10	0.55	0.06	0.10	0.56	0.81	0.27	0.40
JUL	0.43	2.01	0.76	1.37	0.15	0.32	0.26	0.73	0.09	0.41	0.05	0.07	0.64	1.03	0.32	0.49
AUG	0.37	2.37	0.74	1.62	0.09	0.25	0.14	0.35	0.10	0.34	0.05	0.08	0.60	0.95	0.18	0.27
SEP	0.62	3.27	0.47	1.02	0.18	0.24	0.11	0.39	0.11	0.35	0.06	0.09	0.66	0.67	0.19	0.31
OCT	0.43	2.83	0.42	1.22	0.20	0.36	0.13	0.35	0.09	0.42	0.09	0.17	0.66	0.58	0.07	0.13
NOV	0.14	1.10	0.26	0.30	0.29	0.57	0.15	0.35	0.06	0.62	0.11	0.15	1.11	0.50	0.07	0.12
DEC	0.11	1.37	0.21	0.42	0.26	0.39	0.14	0.28	0.09	0.47	0.10	0.16	1.16	1.16	0.12	0.17
Mean	0.54	1.85	0.52	1.08	0.21	0.42	0.16	0.34	0.11	0.62	0.10	0.15	0.80	1.01	0.19	0.28
Std. Err.	0.13	0.26	0.05	0.14	0.02	0.04	0.02	0.05	0.01	0.09	0.01	0.02	0.07	0.13	0.02	0.03

Table A4: Area (km^2) of monthly utilization distribution contours (ISJ bandwidths) of marine predator species electronically tracked during 2002-2008 in the North Pacific Ocean.

	100%	**95%**	**50%**	**25%**	**100%**	**95%**	**50%**	**25%**
	Black-footed albatross				**Laysan albatross**			
JAN	1,016,184	1,009,942	208,987	49,573	4,673,894	4,366,478	919,486	295,541
FEB	376,286	376,284	48,590	6,484	338,599	337,467	58,588	12,640
MAR	1,347,161	1,333,777	405,392	116,186	3,147,163	3,063,407	673,843	179,258
APR	1,192,800	1,188,733	368,980	97,875	2,767,214	2,728,343	465,320	134,860
MAY	3,266,834	3,101,082	663,879	223,424	2,419,876	2,288,850	412,779	117,019
JUN	8,857,921	8,257,571	1,918,054	655,907	3,602,364	2,939,241	570,316	230,954
JUL	9,277,532	7,718,055	1,496,494	463,161	6,899,676	5,432,744	1,110,750	387,736
AUG	8,761,845	7,276,655	1,635,505	485,783	6,177,464	4,869,370	1,339,475	498,099
SEP	9,466,622	7,573,236	1,946,632	681,812	5,270,882	4,062,463	761,354	213,538
OCT	8,811,218	7,019,946	1,551,704	601,761	6,120,474	4,876,358	928,777	268,234
NOV	2,620,363	2,613,416	831,990	276,339	2,929,760	2,912,831	836,569	240,666
DEC	904,353	877,335	176,769	37,276	1,111,837	1,111,818	364,609	109,119
	Leatherback turtle				**Female northern elephant seal**			
JAN	1,215,702	957,823	257,738	85,669	1,216,502	953,160	159,821	40,004
FEB	665,259	476,928	105,238	30,923	1,301,878	1,072,397	147,799	31,223
MAR	807,157	676,364	167,207	35,997	4,121,824	3,255,115	935,854	382,529
APR	890,832	670,094	203,829	84,332	4,094,663	3,191,331	899,968	325,100
MAY	709,883	550,218	150,057	63,636	906,964	864,594	129,236	30,939
JUN	281,402	233,647	76,291	27,184	2,484,873	1,971,660	402,300	116,953
JUL	201,858	155,200	44,446	7,551	5,696,370	4,675,390	1,166,016	418,643
AUG	107,015	98,968	24,852	9,557	4,293,716	3,353,147	700,550	239,773
SEP	550,023	476,582	72,808	9,383	4,045,401	3,074,901	589,506	178,764
OCT	1,998,491	1,637,373	373,464	132,708	3,578,310	2,774,038	522,307	182,088
NOV	1,876,599	1,549,418	418,482	144,113	3,047,666	2,338,179	540,794	190,144
DEC	1,299,466	1,121,758	298,054	117,818	2,927,224	2,166,702	529,281	162,684
	Pacific bluefin tuna				**Salmon shark**			
JAN	1,304,780	1,146,789	168,925	29,945	3,575,636	3,055,839	246,802	55,967
FEB	1,998,998	1,603,594	281,999	103,940	5,223,893	4,434,110	737,519	123,277
MAR	1,695,838	1,525,603	226,727	80,626	5,231,220	4,488,632	686,729	119,923
APR	2,454,449	2,036,500	418,826	148,872	4,181,004	3,536,310	392,023	52,971
MAY	1,437,275	1,275,752	212,782	60,053	2,474,864	2,197,227	126,754	7,190
JUN	1,242,171	1,212,828	172,974	57,118	1,462,407	1,235,734	46,693	2,669
JUL	802,465	799,968	108,216	19,427	902,393	827,301	29,469	1,253
AUG	395,556	394,930	44,356	9,544	1,094,579	871,811	42,566	2,347
SEP	555,681	496,455	58,508	15,944	2,040,832	1,570,756	170,219	10,537
OCT	395,948	298,063	44,104	16,614	2,342,289	1,757,892	153,925	29,370
NOV	425,792	402,546	56,460	12,954	2,506,690	1,841,532	109,783	20,993
DEC	365,215	291,465	24,360	9,068	2,283,029	1,847,198	121,986	29,212
	Sooty shearwater				**White shark**			
JAN	1,304,780	1,146,789	168,925	29,945	3,575,636	3,055,839	246,802	55,967
FEB	1,998,998	1,603,594	281,999	103,940	5,223,893	4,434,110	737,519	123,277
MAR	1,695,838	1,525,603	226,727	80,626	5,231,220	4,488,632	686,729	119,923
APR	2,454,449	2,036,500	418,826	148,872	4,181,004	3,536,310	392,023	52,971
MAY	1,437,275	1,275,752	212,782	60,053	2,474,864	2,197,227	126,754	7,190
JUN	1,242,171	1,212,828	172,974	57,118	1,462,407	1,235,734	46,693	2,669
JUL	802,465	799,968	108,216	19,427	902,393	827,301	29,469	1,253
AUG	395,556	394,930	44,356	9,544	1,094,579	871,811	42,566	2,347
SEP	555,681	496,455	58,508	15,944	2,040,832	1,570,756	170,219	10,537
OCT	395,948	298,063	44,104	16,614	2,342,289	1,757,892	153,925	29,370
NOV	425,792	402,546	56,460	12,954	2,506,690	1,841,532	109,783	20,993
DEC	365,215	291,465	24,360	9,068	2,283,029	1,847,198	121,986	29,212

Table A5: Area (km^2) of monthly utilization distribution contours (1-degree bandwidth) of 8 marine predator populations electronically tracked during 2002-2008 in the North Pacific Ocean.

	100%	**95%**	**50%**	**25%**	**100%**	**95%**	**50%**	**25%**
				Black-footed albatross				**Laysan albatross**
JAN	3,083,047	2,731,894	313,296	101,300	5,410,904	4,726,703	1,080,687	342,864
FEB	844,026	774,872	50,608	6,803	888,696	784,127	61,246	11,126
MAR	797,275	794,386	311,300	93,167	2,828,752	2,791,095	717,935	165,270
APR	1,003,182	1,001,933	352,107	83,202	3,112,493	3,069,246	438,034	142,004
MAY	1,898,798	1,878,675	588,974	164,772	2,995,513	2,697,926	441,836	116,911
JUN	8,141,809	7,371,200	1,966,389	626,929	3,798,696	2,907,379	578,971	258,285
JUL	9,355,102	7,850,128	1,584,663	453,742	6,930,581	5,501,691	1,096,135	386,951
AUG	8,830,460	7,472,433	1,643,335	520,835	6,151,758	4,828,692	1,320,006	478,252
SEP	8,616,202	6,998,216	1,807,109	595,419	6,018,447	4,555,296	840,736	222,925
OCT	8,444,850	6,534,121	1,508,726	584,572	7,159,842	5,471,433	988,614	292,038
NOV	6,911,829	6,197,797	1,384,939	448,004	7,754,332	6,672,040	1,405,422	427,757
DEC	2,180,808	1,763,380	240,607	44,016	3,705,800	3,640,986	618,229	162,379
				Leatherback turtle				**Female northern elephant seal**
JAN	1,925,943	1,474,338	357,691	127,501	2,043,839	1,492,849	222,116	45,496
FEB	1,259,489	803,563	167,407	64,149	2150,078	1,600,380	180,085	42,405
MAR	1,385,519	1,094,917	296,222	90,630	4,474,900	3508089	1,052,676	452,880
APR	1,297,969	1,049,915	318,513	81,054	4,917,573	3,586,385	1,111,398	419,931
MAY	1,101,442	976,549	235,284	107,906	2,684,268	1,831,675	180,585	33,128
JUN	601,602	514,946	172,953	78,708	3,443,124	2,446,263	494,372	129,552
JUL	467,853	367,468	96,276	8,132	6,303,740	5,056,865	1,267,211	445,879
AUG	345,399	297,053	75,316	11,980	5,725,559	4,270,296	1,155,579	410,872
SEP	970,979	743,395	94,375	12,358	5,893,333	4,422,937	967,228	370,813
OCT	2,778,622	2,411,863	739,664	226,017	5,031,005	3,772,434	858,686	317,914
NOV	3,000,342	2,471,483	592,968	169,596	4,371,758	3,030,879	746,126	277,057
DEC	2,278,411	1,882,817	515,284	238,180	4,398,325	,2845,442	704,017	259,046
				Pacific bluefin tuna				**Salmon shark**
JAN	3,227,910	2,623,600	336,459	39,574	6,853,007	5,364,433	426,420	65,130
FEB	4,126,385	3,130,136	563,633	148,233	7,367,925	5,851,669	1,131,609	211,991
MAR	3,562,653	2,789,705	398,588	105,556	8,433,540	6,565,705	1,209,370	218,390
APR	4,353,107	3,506,133	633,437	193,774	7,483,680	5,975,353	746,410	111,179
MAY	3,868,757	2,986,894	498,786	61,778	6,062,803	4,331,452	313,444	12,546
JUN	3,786,991	3,328,908	380,806	67,422	4,103,391	2,880,555	148,110	2,869
JUL	3,163,388	2,791,122	224,866	38,894	3,139,200	2,134,153	111,360	1,724
AUG	2,146,423	1,787,356	83,416	23,676	2,961,745	2,039,262	141,118	2,614
SEP	1,690,493	1,417,085	118,779	19,863	3,342,618	2,411,653	312,463	11,099
OCT	1,072,078	533,630	67,499	16,970	3,819,373	2,586,390	308,356	50,713
NOV	1,076,244	697,266	86,740	25,948	4,974,451	3,637,968	208,952	43,688
DEC	1,013,907	813,578	55,044	20,511	5,712,248	4,094,520	225,673	46,920
				Sooty shearwater				**White shark**
JAN					5,148,717	3,358,376	236,370	31,297
FEB					4,252,850	3,055,500	343,939	123,539
MAR					4,431,984	3,047,817	449,210	126,252
APR	2,958,231	2,957,941	1,256,088	432,454	3,700,787	2,575,580	473,613	161,238
MAY	7,363,656	7,229,821	1,122,859	302,364	3,9713,70	2,388,444	425,458	135,212
JUN	6,322,887	5,092,869	680,909	186,466	3,562,581	2,607,842	557,239	166,510
JUL	7,684,995	5,697,938	1,149,991	356,516	4,045,970	2,873,784	708,775	272,168
AUG	7,123,568	5,619,946	1,259,689	412,164	2,819,713	1,860,288	341,120	70,808
SEP	6,527,853	6,095,943	1,026,326	331,203	1,608,915	1,117,701	215,849	17,822
OCT	3,167,724	3,159,199	1,109,814	336,393	748,348	508,603	3,090	964
NOV	371,216	370,710	31,646	16,498	1,088,057	575,578	8,816	3,223
DEC					3,813,659	2,242,854	44,519	10,995

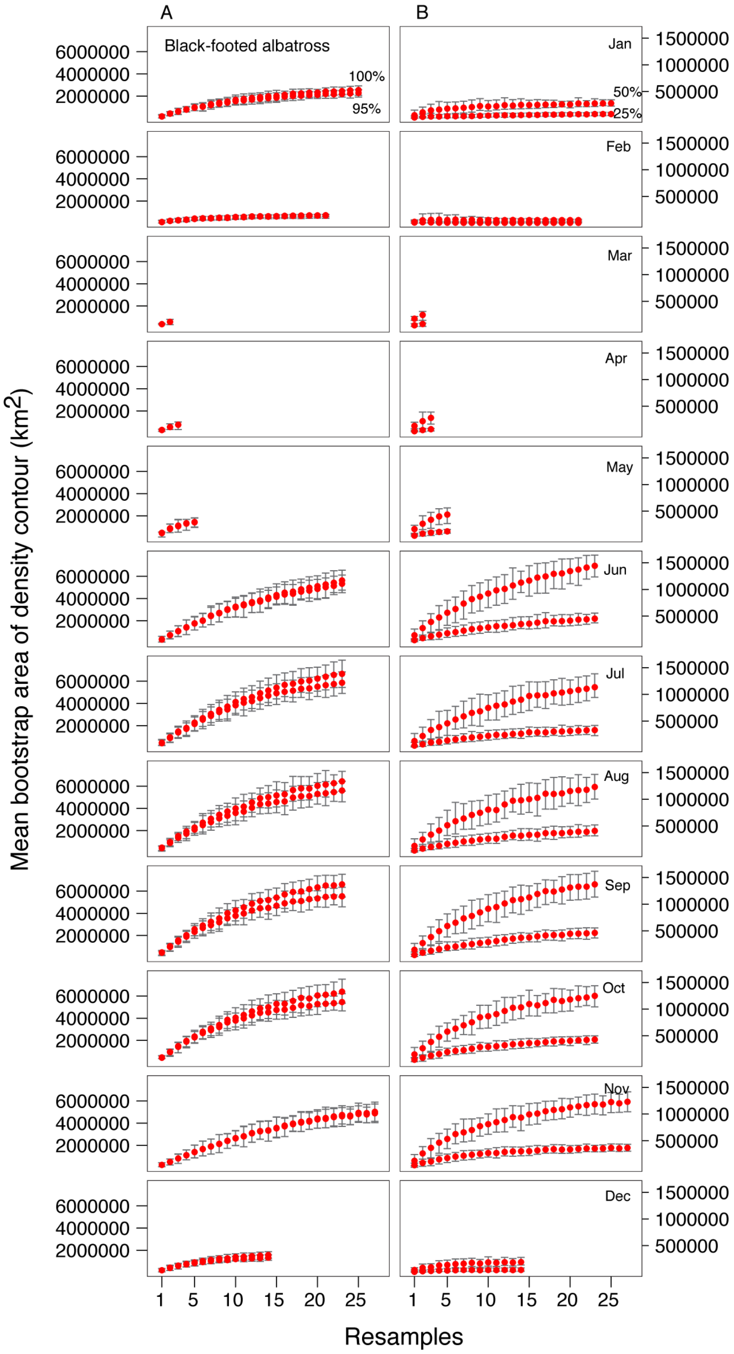


Figure A1: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of black-footed albatross population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

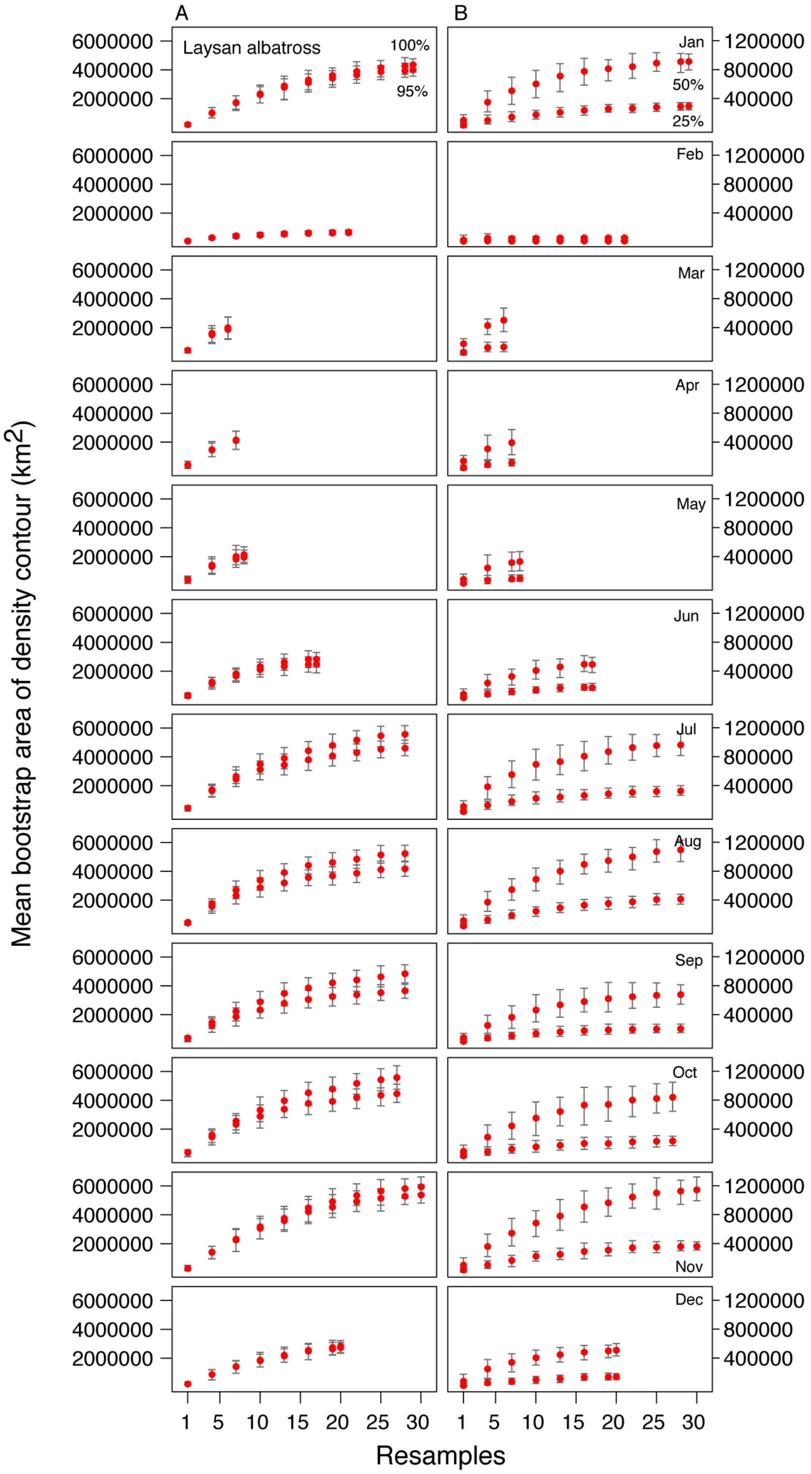


Figure A2: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of Laysan albatross population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

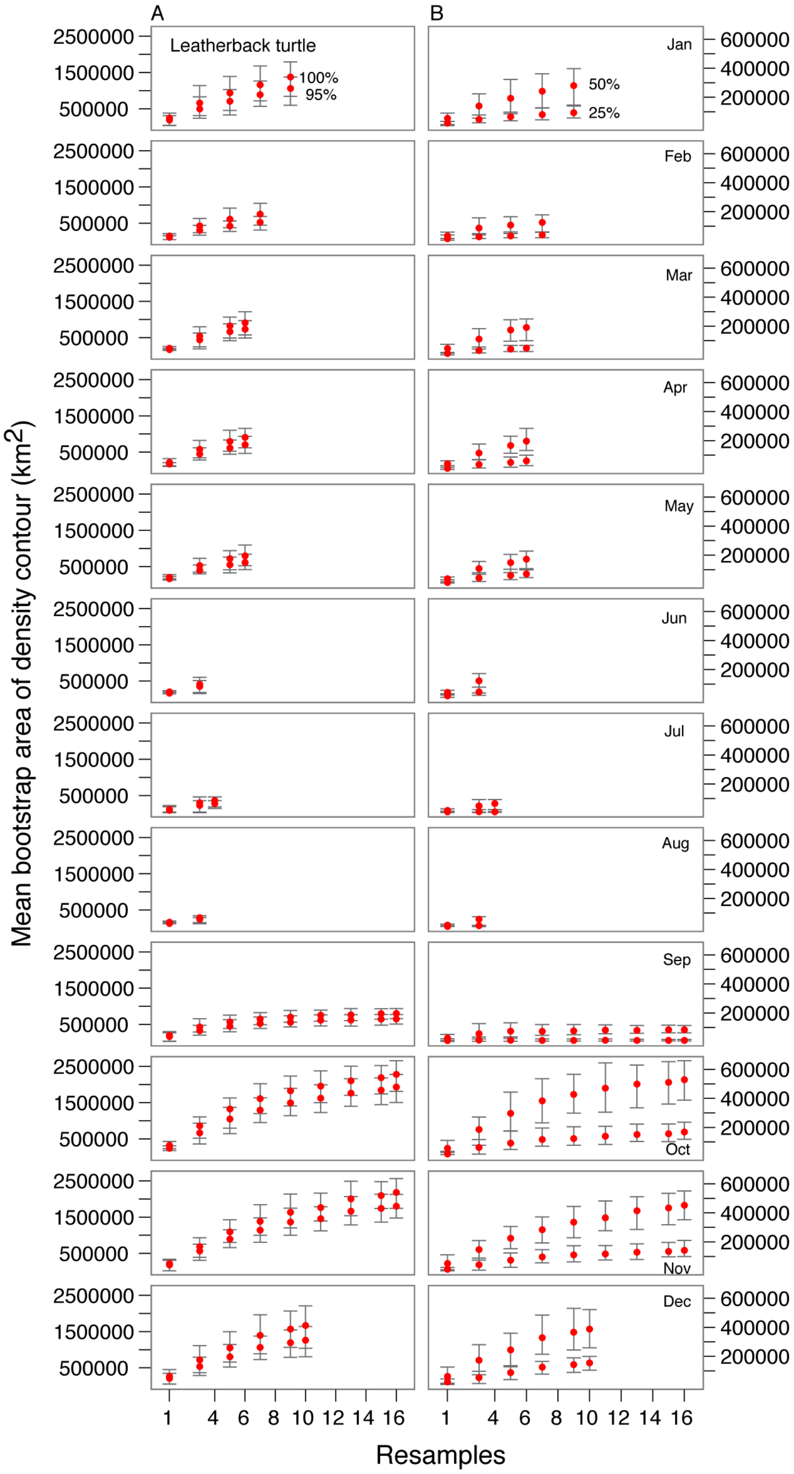


Figure A3: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of leatherback turtle population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

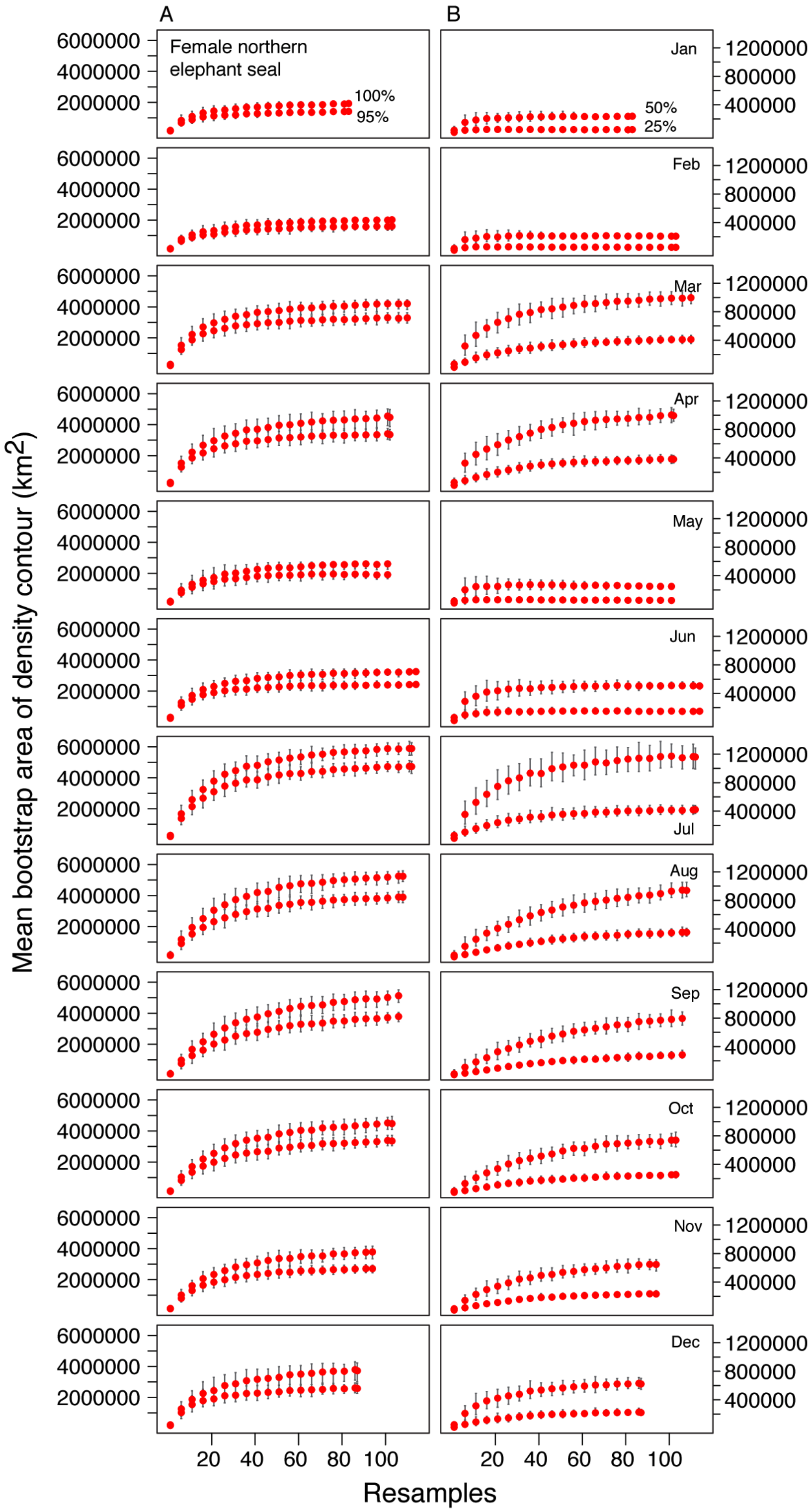


Figure A4: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of female northern elephant seal population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

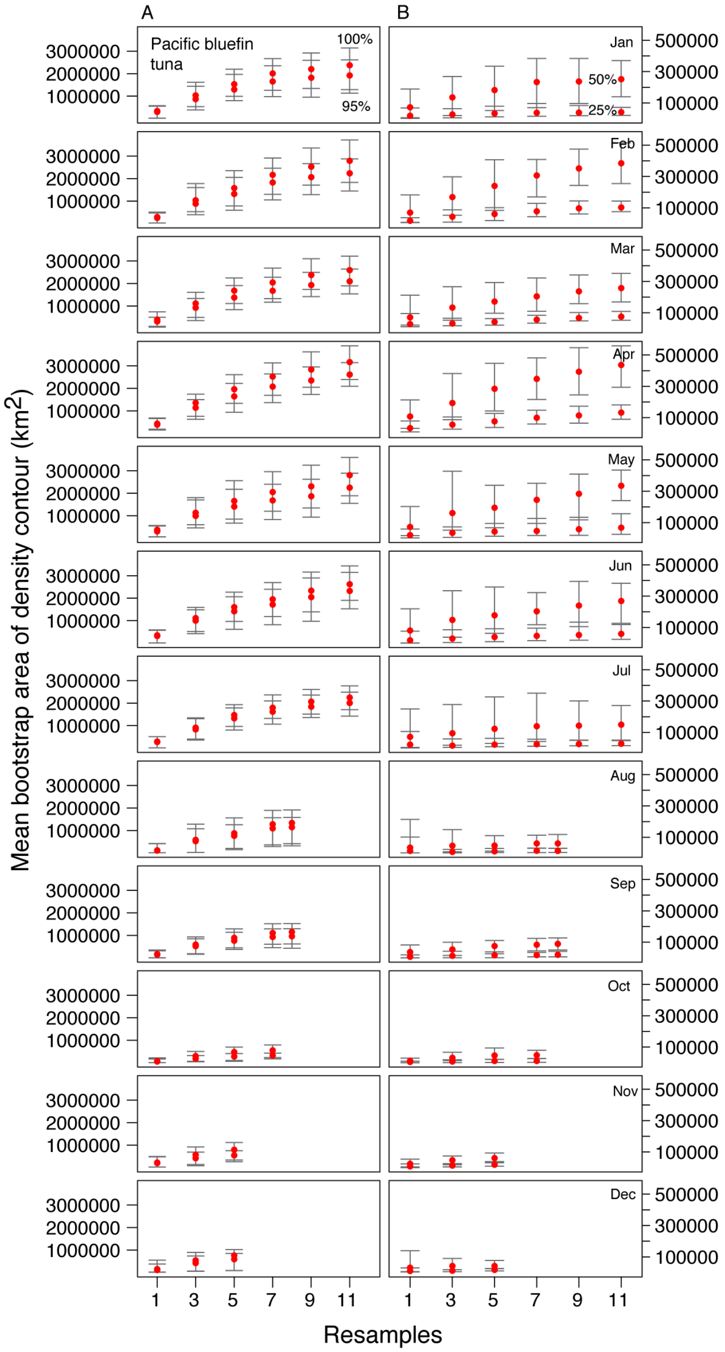


Figure A5: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of Pacific bluefin tuna (trans-Pacific migrants) population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

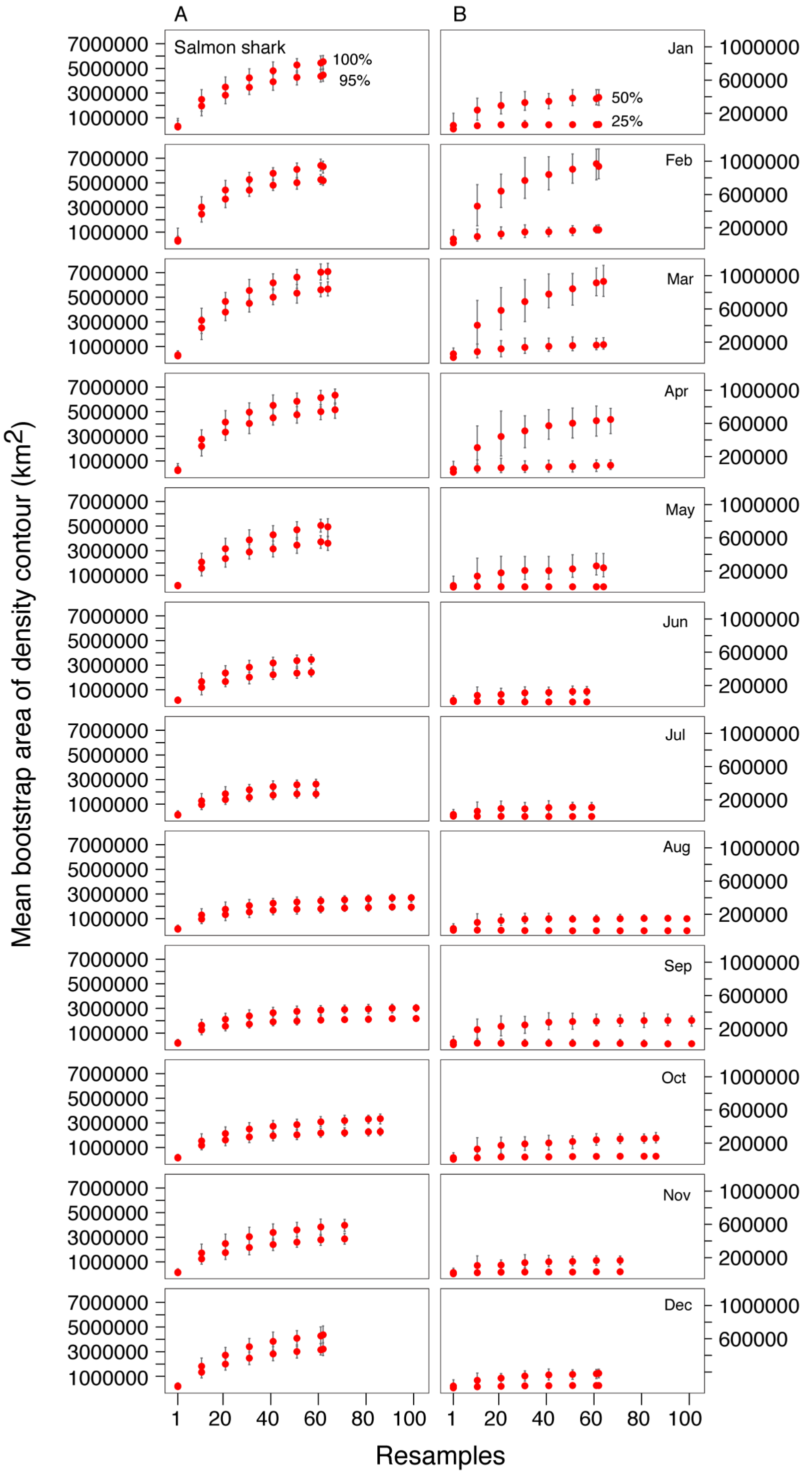


Figure A6: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of salmon shark population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

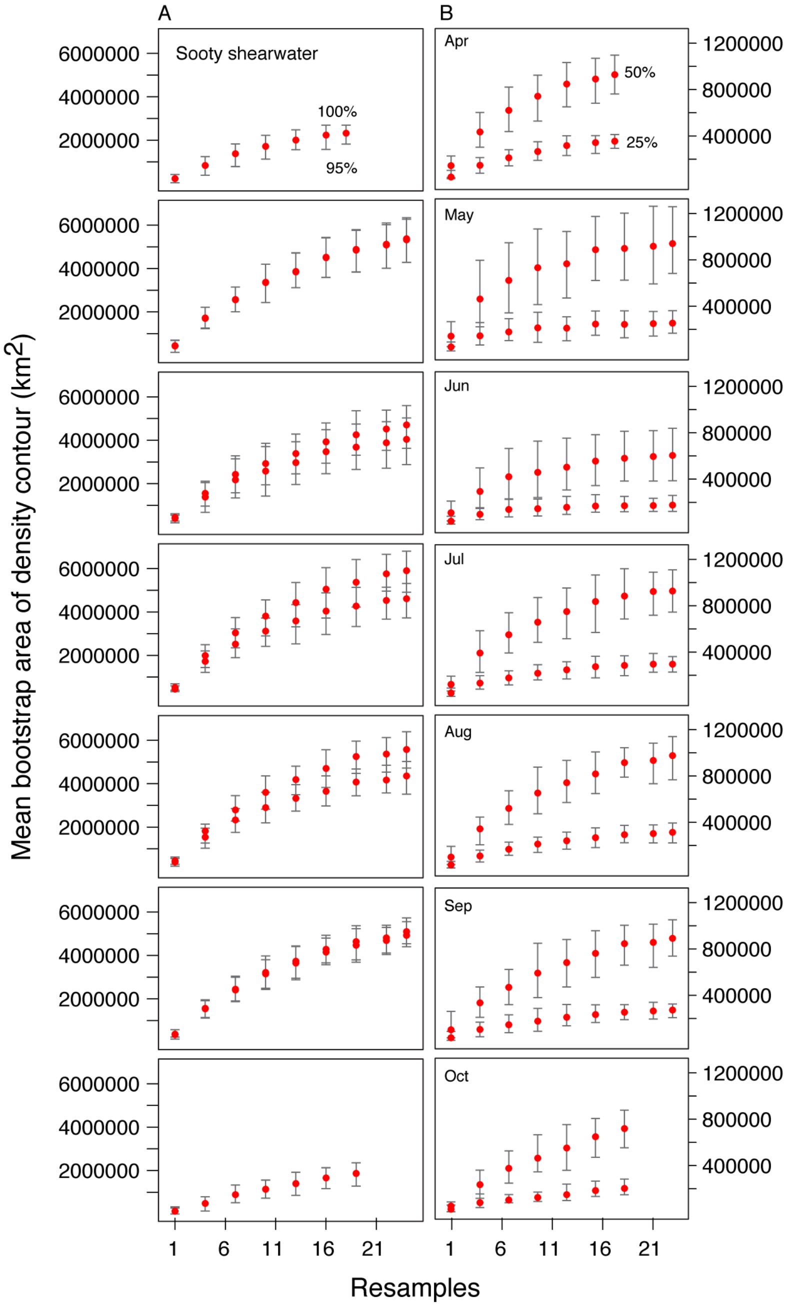


Figure A7: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of sooty shearwater population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

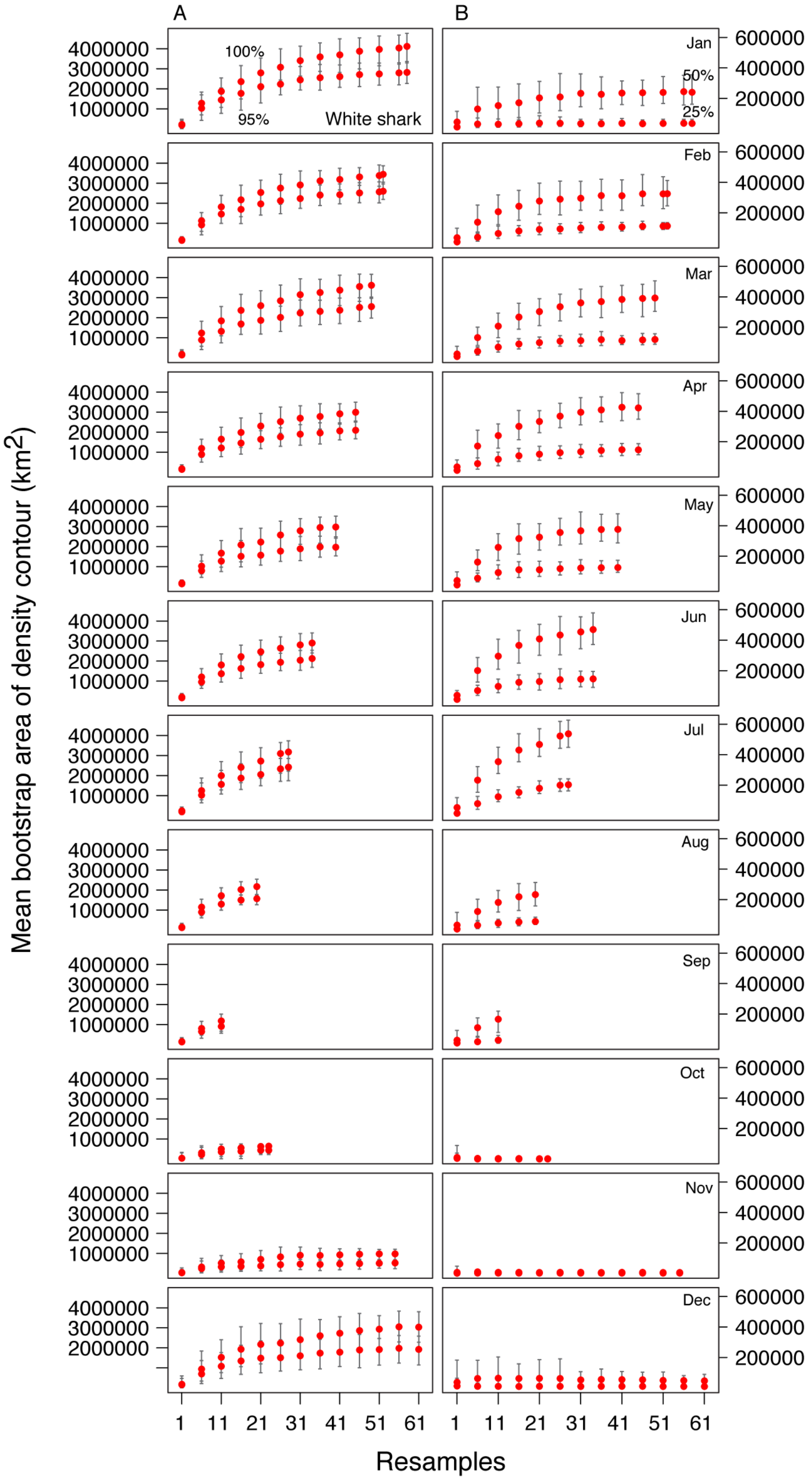


Figure A8: Bootstrapped estimates of area (km^2) of the 100%, 95%, 50%, and 25% contours of white shark population utilization distributions as a function of sample size (number of individuals). Circles indicate means and lines indicate standard deviations.

Chapter 4

Clarifying international responsibilities for managing wide-ranging marine predators

Abstract

Integrated international efforts are required to effectively manage threatened and exploited populations of wide-ranging species. Migratory marine predators spend most of their lives hidden from observation and we lack the information needed to support global efforts — a detailed understanding of when, and in which countries' Exclusive Economic Zones (EEZs) animals are found throughout their annual cycles. I analyzed tracking data collected from 2002-2009 from populations of 18 species of marine predators in the Pacific Ocean (1,679 individuals and 257,133 state-space modeled daily locations). I used generalized additive mixed-effects models to investigate non-linear daily trends in the probability of occurrence in each EEZ and in the high seas and to account for the effects of tagging location, tagging date, track duration, and autocorrelated time-series data. 94% of Pacific Ocean EEZs were visited. Land-breeding populations were estimated to spend 14-33% of their annual cycles within the waters of their breeding EEZs, and 53 to 76% of the year in the high seas. In contrast, most fish and shark populations were estimated to spend less than a quarter of their annual cycle in international waters. Results revealed defined periodic visits to specific countries and to the high seas;

the suite of countries with shared management responsibility; and when management responsibility commences and concludes throughout the year. Patterns were conserved over multiple years. I conclude that international management responsibilities over wide-ranging species become immediately transparent when temporal relationships between animals and their habitats are framed as continuous functions and synthesized for multiple populations.

4.1 Introduction

The physiological and biomechanical capabilities of marine predators enable them to track and utilize highly dynamic and/or dispersed resources. Seasonal migrations between breeding and foraging areas are part of many species' life history and these migrations can be vast journeys across ocean realms. Sooty shearwaters (*Puffinus griseus*) span the entire Pacific Ocean in an "endless summer" (Shaffer et al., 2006); white sharks (*Carcharodon carcharias*) migrate between the California coast and a high seas hotspot called the 'White Shark Café' (Weng et al., 2007; Jorgensen et al., 2010); and Pacific bluefin tuna (*Thunnus orientalis*) leatherback turtles (*Dermochelys coriacea*), and loggerhead turtles (*Caretta caretta*) breed on one side of the Pacific Ocean, but forage on the other (Bayliff, 1993; Boustany et al., 2010; Benson et al., 2011; Peckham et al., 2007).

Wide-ranging marine predators must traverse a crowded matrix of human activity and exploitation (Halpern et al., 2008; Trebilco et al., 2011). Many marine predator populations are commercially important and are threatened by human activities. As a result, many of these populations are heavily depleted (Lotze and Worm, 2009), declining (Myers and Worm, 2003; Butchart et al., 2004; Dulvy et al., 2008; FAO, 2010), or are recovering from past depletion (Read and Wade, 2000).

Recovery and management of threatened and exploited marine predators is complicated by highly migratory life histories that span international waters. Wide-ranging species fall under the purview of multiple municipalities, countries or international governing bodies (CMS, 1979). Sovereign jurisdiction over marine resources is delimited by Exclusive Economic Zones (EEZs), waters within 200 nautical miles of the shoreline of coastal nations (UNCLOS, 1982). Eighty-seven percent of world fisheries catch is from EEZs (Sumaila et al., 2007) but the effectiveness of fisheries management in most of the world's EEZs is considered sub-par (Mora et al., 2009). Ocean falling outside national jurisdiction, the 'high seas', remains a global commons with increasingly high human impact including illegal fishing (Agnew et al., 2009), ongoing bycatch of seabirds, marine mammals, and turtles in commercial fisheries (Kelleher, 2005), ineffective management (Cullis-Suzuki and Pauly, 2010), and little protection (Corrigan and Kershaw, 2008). There are no physical barriers separating the pelagic borders of adjacent states or between EEZs and the high seas.

Effective conservation and management of populations that straddle multiple EEZs and/or the high seas relies on transboundary cooperation (CMS, 1979). This includes cooperation among coastal nations and between coastal nations and high seas governing bodies such as regional fisheries management organizations (UNFSA, 1995). To make management tractable, cooperative strategies must consider when during the year species are more or less likely to fall under a nation or governing body's purview. However, for many marine predator populations, complete annual patterns of residency and migration have only recently been revealed (Block et al., 2011). Broad-scale multi-species analyses are needed to inform and encourage integrated ocean basin-scale management efforts.

Previous work has catalogued the presence of wide-ranging species within EEZs (for example Nicholls et al., 2000; Southall et al., 2006; Suryan et al., 2007; Copello and Quintana, 2009). Such studies have usually summarized counts of electronic tracking locations or the proportion of time spent within a few focal EEZs, often for a short duration or specific time of the year, and usually for a small number of individuals or a few species of interest, which have mostly been seabirds and turtles. Most studies did not capture patterns of use for the full annual cycle or for multiple life history stages (although see Phillips et al., 2005). Furthermore, little attention has been paid to movements and residency in the high seas.

Our goal was to attain a robust understanding of the migratory phenologies of marine predators in relation to human political boundaries of the Pacific Ocean taking advantage of the recently completed Tagging of Pacific Predators (TOPP) program (Block et al., 2011). The Pacific Ocean basin is the world's largest, and management effectiveness varies widely from excellent to poor within its EEZs (Mora et al., 2009). The Pacific Ocean also has the largest percentage of non-jurisdictional waters (60%) and the greatest number of countries (at least 42 depending on border disputes) having potential influence over the management of that ocean's wide-ranging species.

For wide-ranging animals spending most of their time submerged or on the wing, only electronic tracking techniques provide the data necessary to follow individuals through time. The Tagging of Pacific Predators dataset (Block et al., 2003) provided such information on the movement of 18 species of pelagic predators in the Pacific Ocean during a eight year period including tunas, pinnipeds, sharks, seabirds, whales, and turtles (Block et al., 2011). For each species in the TOPP dataset, and for multiple years, I asked: 1) Which EEZs were visited? 2) What is the proportion of time spent in each EEZ, and in the high seas? 3) When during the annual cycle was the species more or less likely resident in the high seas? 4) When during the annual cycle was the species more or less likely to fall under a given country's jurisdiction?

4.2 Methods

4.2.1 Data summary

From 2002 to 2009, TOPP researchers deployed 4,306 electronic tags which provided 1,791 individual animal tracks from populations of 23 species in the Pacific Ocean (Block et al., 2011). A Bayesian state-space model (Jonsen et al., 2005) was fitted to the tag data to derive regular, daily mean estimates of locations at sea while accounting for tag observation error (Block et al., 2011; Winship et al., 2011, *in press*). The state-space model also provided estimates of the uncertainty in the location estimates. I used a subset of this TOPP dataset; only species tracked over multiple years were included. The dataset analyzed here included 18 species, 1,679 individuals and 257,133 modeled daily locations (Table B1). Yearly sampling effort varied (Table B1). Tags were deployed within the boundaries of eight EEZs (Table 4.1; full deployment details: Block et al., 2011). There are multiple populations in the Pacific Ocean of many species considered here—I refer only to the specific populations and life history stages in the TOPP dataset (Block et al., 2011).

Variability in deployment date and track duration

Timing of tag deployments was multi-modal for some species (Fig. B2), and track duration varied among individuals (Fig. B3; Block et al., 2011). This variability in a tracking dataset can confound spatio-temporal analyses when deployment dates and track duration are unrelated to species life history.

Pinnipeds and seabirds: Distributions of deployment dates and track durations reflected these species' life histories. To capture the full annual cycle of land-breeding and moulting species, tags were deployed multiple times in a given year (northern elephant seals, *Mirounga angustirostris*: short post-breeding and long post-moult migrations; seabirds: short breeding and long post-breeding migrations). Typically, unique sets of individuals were tracked during each migration although some seals were tracked during both migrations in a given year, or during the same migration in multiple years. In general, tag failure was infrequent for these species and tags were recovered upon recapture of the animals.

Tunas, sharks, whales: For these species, deployment timing varied among years partially because of reasons unrelated to species' life history (sampling design considerations or cruise availability). Primary tagging months were: Pacific bluefin tuna, January, March, July-September, November-December; yellowfin tuna (*Thunnus albacares*), February, August, October-December; shortfin mako shark (*Isurus oxyrinchus*), June-August, November; blue shark (*Prionace glauca*), January-February, June-August, October-December; and salmon shark (*Lamna ditropis*), January, July-December. Because of a higher frequency of tag failure and the difficulty of targeted recapture, the distributions of track durations for these species were a function of tag attrition and harvest recapture. These datasets contained a high number of individuals tracked for less than a year, and a few individuals that were tracked for multiple years (Fig. B3).

4.2.2 Location classification

Global EEZ boundaries were obtained as shapefiles from the VLIZ Maritime Boundaries Geodatabase (v.5). Some EEZ boundaries between countries are disputed; full details of boundary delineation are available (VLIZ: http://www.vliz.be/vmdcdata/marbound/). Shapefiles were converted to polygon vectors using the MATLAB mapping toolbox (The MathWorks, R2010a). I developed a custom script based upon the inpoly function (Engwirda 2007) to classify each location as present or absent in each EEZ of the Pacific basin. I classified locations on an EEZ boundary as inside the EEZ. If a location was neither on land nor in an EEZ, I classified it as a high seas location. Disjunct EEZs for a given country were treated separately. For example, Hawaii and Alaska were each treated as unique to the mainland USA EEZ.

4.2.3 EEZ and high seas occurrence

For each species I calculated the total time spent in each EEZ and in the high seas, and the mean proportion of time spent by individuals of each species in each EEZ and in the high seas.

Statistical summaries of time spent in EEZs from electronic tracking data is influenced by the distribution of track durations and deployment dates. Early in a track, individuals have a high likelihood of being located within the tagging EEZ because they were tagged there. As time passes, individuals have the ability to disperse from the tagging location and the cumulative proportion of time spent within the tagging EEZ should level out to a more biologically representative proportion unaffected by the initial tagging event.

I explored the effects of track duration and deployment date in the TOPP dataset by calculating the cumulative proportion of time spent by each individual within primary EEZs and the high seas according to the relative day along each individual's track (i.e. days elapsed since deployment) and according to the month in which the animal was tagged. For example, most Pacific bluefin tuna were tagged in March, July-August, and November-December within the Mexican EEZ (Fig. B3; Block et al., 2011). Individuals tracked for less than 30 days spent 80-100% of their time within Mexico. Individuals tracked for greater than a year, spent 50% of their time in Mexico (Fig. B4a) with little change in this proportion as track length increased beyond a year. Tuna tagged in Mexico in November spent a higher proportion of their time in Mexico in the few months after being tagged than those tagged in July (Fig. B4b).

Thus, summaries of EEZ use from datasets with a high number of short or abbreviated tracks such as the tuna, shark, whale, and turtle datasets analyzed here may be skewed towards a high proportion of time spent within the tagging EEZ. Deployment date, especially coupled with a high number of attenuated tracks, can also affect interpretation of EEZ use. With respect to northern elephant seals, Laysan albatrosses (*Phoebastria immutabilis*), and black-footed albatrosses (*Phoebastria nigripes*), sample sizes were not always equal among the unique sets of individuals tracked during each of the migrations undertaken during their yearly cycles (Fig. B1) so averages of individual EEZ use were not necessarily representative of the annual cycle.

4.2.4 Modeled seasonal use of EEZs and the high seas

I used generalized additive mixed-effects models (GAMM; Wood, 2006) to investigate non-linear seasonal trends in the probability of being present in each EEZ while accounting for the effects of tagging location, tagging date, track duration, and autocorrelated time-series data. The response variable—the presence of an individual from the tagged sample in an EEZ—was modeled with a binomial error distribution and logit link. Although EEZ selection is a multinomial choice, functionally, most individuals use only one of two EEZs/high seas during a given period. Models were fitted using the 'mgcv' package (Wood, 2006) in R (R Development Core Team 2011) and formulated and selected as follows:

Fixed effects

Potential explanatory variables included continuous variables: day of year (DOY) and relative day along an individual's track (RELDAY); and factor variables: year (YEAR) and EEZ where tagged (tEEZ).

The suite of candidate models considered for each species depended upon its life history and the quality of its dataset (Table 4.2). Models were not developed for species who spent most of their time within a single EEZ (yellowfin tuna; common thresher shark, *Alopias vulpinus*; California sea lion, *Zalophus californianus*; loggerhead turtle), or for species whose datasets did not cover an entire annual cycle (humpback whale, *Megaptera novaeangliae*; northern fur seal, *Callorhinus ursinus*). RELDAY was considered for species tagged at varying times of the year across years and for species with highly variable tag attrition (fish, sharks, turtles, whales). YEAR was considered only for balanced datasets with full yearly coverage from multiple years (Table B1). Tagging EEZ was considered as a variable for species with deployments in multiple EEZs (Table 4.1).

For relevant datasets (Table 4.2), interactions between continuous variables and factor variables were modeled as varying-coefficient models (both the slope and intercept are allowed to vary, resulting in separate smooths fitted for each factor level, Hastie and Tibshirani, 1990).

For each species and candidate model, I fit separate binomial models for each focal EEZ.

Random effects

Individual was treated as a random, intercept effect.

Autocorrelation

A first-order autoregressive correlation structure was used to model the temporal dependence among within-individual errors.

Life history subsets

For some species, there was enough information to separately model genders and/or life history stages. Separate models were fitted for male and female northern elephant seals. Two model groups were also constructed for Pacific bluefin tuna. Group 1 included all PBT individuals. The second PBT model group included only those tuna that undertook trans-Pacific migrations to their natal waters for spawning (n=12).

Model Selection and Model Subsets

Comparison of binomial mixed-effects models is not straightforward (Bolker et al., 2009). Fitting of binomial GAMMs using the ‘gamm’ function of the mgcv library allows for autocorrelative error structures but produces a quasi-likelihood rather than a likelihood. Standard model selection methods such as the Akaike Information Criterion (Akaike, 1974, AIC) are thus unavailable for binomial GAMMs fitted via the ‘gamm’ function. The ‘gamm4’ function produces a full likelihood, but does not yet accommodate autocorrelative error structures, and exhibited convergence problems for many of the models I attempted to fit using this function. Simple random effects, but not autocorrelation, may be incorporated using the ‘gam’ function which does provide a likelihood (Wood, 2006).

In order to apply standard model selection techniques to binomial GAMMs that include an autocorrelative error structure, I first fitted each candidate model (Table 4.2) using the ‘gam’ function, with varying-intercept random effects incorporated as a simple smooth (Wood, 2006). I selected models based on AIC, null deviance explained, and the significance of explanatory variables. Selected models were then fitted using the ‘gamm’ function with an added autocorrelative error structure to determine appropriate confidence intervals (see Zuur 2009 for another example of this practical two-step approach to binomial generalized additive mixed model selection and fitting).

To explore the differences in model predictions from models that did and did not include year and tagging EEZ effects and interactions, I consider the former (models 1 and 2, Table 4.2) as a subset of simple models and the latter (models 3-16, Table 4.2) as a subset of complex models. For the relevant species, I select among models in each subset for further prediction.

Model predictions and model subsets

From fitted models I predicted the probability that a randomly selected individual from the tracked population would occur within select focal EEZs and the high seas on every day of the year. All predictions are unstandardized (i.e. daily predictions from the separate models fit for each EEZ were not standardized to sum to 1).

Predictions were made for each year and tagging EEZ when relevant (models 3-16, Table 4.2). For selected models that included relative day of track as a covariate, predictions were made over a specific range of relative days for each species. The range of relative days was chosen to minimize tagging effect, and to correspond with the deployment date of the average individual in that species' dataset (Fig. B2).

Predicted proportion of time spent in EEZs and the high seas

From selected model predictions, I estimated the proportion of the year spent in each focal EEZ and in the high seas for each tracked population. The daily predicted probabilities of occurrence for a random individual from the tracked population were summed over the course of a year and divided by 365.

4.3 Results

Individuals were tracked in 61 EEZs sovereign to at least 36 countries (Fig. 4.1; Table 4.1; Table B2); the rights to four EEZs visited by TOPP species are disputed. Leatherback sea turtles (two breeding populations) and sooty shearwaters (New Zealand breeding population) were tracked in the highest number of EEZs—38 and 37 respectively. Loggerhead turtles and California sea lions were tracked only within their tagging EEZ and the high seas. A proportion of individuals of all other species visited at least one EEZ in addition to their tagging EEZ (Table 4.1; Table B2). More than 90% of the individuals of the following species remained entirely within EEZs during their tracking duration: yellowfin tuna, thresher shark, California sea lion, and humpback whale. The high seas were visited by 47% (n=789) of all individuals, and by every species except humpback whale which were all tagged in the U.S. and on average tracked for only 47 days (Fig. B3). Because unique sets of individual northern elephant seals, Laysan albatrosses (*Phoebastria immutabilis*), and black-footed albatrosses (*Phoebastria nigripes*) were tracked during each of the respective migrations of their yearly cycles, for these populations, statistical summaries of individual EEZ use are not representative of individual use throughout the annual cycle.

Over 85% of all locations were in Mexico (33%), the high seas (28%), and the United States (23%); 72% of locations were within the boundaries of an EEZ (Table B3). These percentages are influenced by sample size differences among species (Table B1), and by track durations and deployment dates (Fig. B3, Fig. B2, Fig. B4). Greater than 85 per cent of locations of the following species were within a single EEZ: yellowfin tuna, California sea lion, and humpback whale.

4.3.1 Modeled daily probability of occurrence

Generalized additive mixed effects models accounted for sampling biases to predict daily EEZ and high seas use throughout the year (Fig. 4.2), and over multiple years (Fig. 4.5, Fig. 4.4).

Model Fit

Best-fitting models overall, and within the model subset that included year and tagging EEZ effects as covariates (models 3-16, Table 4.3) always included relative day of track and/or separate smooths for every year and tagging EEZ (for the relevant species, Table 4.2). From the simple model subset (models 1-2, Table 4.2), model 2 was always selected. Models explained 22% to 96% of null deviance. There was significant temporal autocorrelation in the residuals of all models.

Models with many covariates and interactions sometimes failed to converge when an autocorrelative error structure was added within a GAMM, especially for populations with either very large or very small datasets. The following models did not converge: models 12-16 for Pacific bluefin tuna, and models 10-16 for albacore tuna. For these species, final models were selected for prediction among those that converged. Models also did not converge for male northern elephant seals, or for female northern elephant seals tagged in Mexico due to a paucity of data throughout the annual cycle.

Confidence intervals were small for predictions from large tagging populations (PBT, SS, NELE), or populations with low individual variation (WS, LET tagged in Costa Rica), or at times of the year when individuals congregated for breeding (BFAL and LAAL, predictions of occurrence within the Hawaiian EEZ).

Seasonal patterns of visitation

Daily predictions of EEZ and high seas occurrence revealed defined periodic visits by marine predators to specific countries and to the high seas during the course of a year (Fig. 4.2). General patterns were conserved over multiple years (Fig. 4.5, Fig. 4.4).

Predictions represent the probability that an individual, randomly selected from the electronically tracked population, was present or absent in each EEZ and in the high seas on each day of the year, and can be interpreted as the expected proportion of the tracked population that was present or absent in each EEZ and the high seas. For example, there was a 20% probability that a randomly selected sooty shearwater from the tracked population occurred in Russian waters on September 1st, and a 40% probability that it was in the high seas (Fig. 4.2j).

The United States was home to Pacific bluefin and albacore tunas, mako and white sharks, and blue whales (*Balaenoptera musculus*, BLWH) during the latter half of the year, with a near 100% probability of individuals of these populations being located in the U.S. during this time. Individuals of the same populations were likely to reside in either the high seas or Mexico during the first half of the year. These populations were estimated to have spent a quarter to a third of their annual cycles within the U.S. EEZ.

Both northern and southern hemisphere seabirds converged in the waters of their breeding EEZ from October to November. Black-footed and Laysan albatrosses, female northern elephant seals, and leatherback turtles tagged in Costa Rica, also had a near 100% probability of occurring within these EEZs during the first quarter of the year before moving off shore or to other EEZs during April - September.

Land-breeding populations were estimated to spend 14-33% of their annual cycles within the waters of their breeding EEZs, and 53 to 76% of the year in the high seas (Table 4.4). In contrast, fish and shark populations were estimated to spend less than a quarter of their annual cycle in international waters. Exceptions were white sharks (Fig. 4.2b) and mature Pacific bluefin tuna returning to their natal waters for spawning.

Leatherback sea turtles and seabirds exhibited the most variability in predicted probabilities of EEZ use. During July - October, leatherbacks tagged in Indonesia had a 20% probability of visiting one of multiple EEZs (Fig. 4.2l). These patterns arose from individual variation in post-breeding destinations, rather than from individual movement among multiple EEZs (Benson et al., 2011). During this same time period, Laysan albatrosses and sooty shearwaters also had 20-30% probability of occurring within one of three EEZs: Japan, Russia, and Alaska. Separate groups of individual sooty shearwaters visited the California Current, Alaska, and the the western Pacific. In the western Pacific, those individuals that visited Japan from April to June were the same individuals that later ventured to Russia from July through September (Shaffer et al., 2006). Few individuals in this sample visited the U.S. or Alaskan EEZs (Fig. 4.2j).

Year effects

Models selected from the two model subsets—models with and without a year effect—predicted similar EEZ use patterns but yearly models did unveil a level of inter-annual variability. I qualitatively compared predictions from models 1 and 2, and models selected from the second subset (models 3-16) for the three species with the largest yearly datasets, Pacific bluefin tuna, female northern elephant seals, and salmon shark.

All pacific bluefin models (Fig. 4.3) predicted a similar pattern of use of waters in the Mexican and U.S. EEZs, however models 9 and 11 predicted a 10-20% probability that individuals stayed within the Mexican EEZ in September and October of 2004 and 2005, whereas models 1 and 2 predicted almost a complete exodus of the tracked population from Mexican waters in these months. Use of Canadian EEZs by female northern elephant seals was revealed by the selected model that included a year interaction (model 11), suggesting that in some years, use of Canadian waters (Fig. 4.4, 2005 and 2008) was more likely than predicted from the candidate model that did not include year effects (model 1, Table 4.2). General patterns were also similar for salmon shark (Fig. 4.5), but there was variability in arrival and departure windows. For example, the peak probability that a tagged salmon shark was in the U.S. EEZ occurred in either May (2004,2005), June (2006,2007), or July (2008).

4.4 Discussion

In the Pacific Ocean, 65 exclusive economic zones sovereign to 44 countries are entrusted with management responsibility of over 40% of Pacific Ocean waters. 94% of the Pacific's EEZs were visited by the 18 species analyzed here (Fig. 4.1). Jurisdictional complexity is considered the primary challenge to managing and conserving migratory species. To help elucidate jurisdictional responsibility over populations that are in need of more effective management in EEZs (Mora et al., 2009) and in the high seas (Cullis-Suzuki and Pauly, 2010), a number of studies have analyzed EEZ use by electronically tracked marine predators. Proportion of time spent in an EEZ or in the high seas, a metric useful for management and increasingly reported (Nicholls et al., 2000; Southall et al., 2006; Suryan et al., 2007; Copello and Quintana, 2009), is highly dependent upon track length, tagging EEZ, and date of tagging (Fig. B4). Previous research, when used as a basis for management decisions, should not be extrapolated beyond the time of year and typically short duration of the study and should be interpreted from the specific life history contexts of the species evaluated and the tagging methods employed. I synthesized individual movement patterns of populations of 18 species on a daily basis over multiple years to clarify international management responsibilities over these populations throughout the year.

4.4.1 Clarifying international management responsibilities for wide-ranging marine predator populations

Marine predators are driven to migrate ultimately by their life histories and proximally by the highly dynamic nature of oceanic habitats. Characteristics of migratory behavior can either facilitate or complicate the management process (Wilcove and Wikelski, 2008; Bowlin et al., 2010; Shuter et al., 2011). Many migratory species form large aggregations and exhibit seasonal fidelity to distinct locations. These tendencies make migratory species vulnerable to targeted over-exploitation but they also help focus management and recovery efforts on specific locations and time periods (Wilcove and Wikelski, 2008). However, the large multi-jurisdictional home ranges of migratory species also expose migrants to a wide range of threats and management regimes throughout their annual cycle (Reeves et al., 2004; CMS, 1979). To encourage integrated multi-species management strategies that specifically account for migratory phenology, I discuss ways in which understanding relationships between 18 populations of wide-ranging marine predators and the political jurisdictions of the Pacific Ocean throughout the year can help facilitate their management.

Which countries are responsible for management and when during the year does that responsibility commence and conclude?

During their annual cycle, some populations in this study remained almost entirely within the EEZs in which they were tagged. For example, California sea lions tagged in the United States expanded out to the high seas only in anomalous oceanographic years (Weise and Harvey, 2008), and at all other times, remained within the boundaries of the U.S. EEZ (Table 4.1). Yellowfin tuna spent most of their year within the Mexican EEZ (Table 4.1), and are generally known to migrate coastally within limited tropical areas in the eastern Pacific (Sund et al., 1981). Both populations are considered healthy;

management is relatively effective and regulated by the governments of the U.S. and Mexico.

In contrast, the governments of at least thirty-seven EEZs share the responsibility for managing the two Pacific populations of leatherback turtles; both populations are considered vulnerable to extinction (Sarti Martinez, 2011, 2000) and the Costa Rican population of leatherback turtles is considered one of the world's 11 most threatened sea turtle populations (Wallace et al., 2011). At least 38 countries share the responsibility for managing the New Zealand population of sooty shearwaters. However, residency within each EEZ is not equally probable during the year. Marine predators cue on predictable seasonal movements of oceanic habitats which in turn concentrates multiple individuals in specific ocean regions during defined time periods (Block et al., 2011). Only a portion of the basin's EEZs and international governing bodies has purview over specific species at any given time making optimal management strategies difficult to achieve.

Opportunities for management (and exploitation) of wide-ranging species within sovereign waters blink on and off. EEZ sovereignty may be highly punctuated in time—for example, the central Pacific island migration corridor of fast-moving sooty shearwaters (Fig. 4.2j). Or, a single EEZ may constitute an estimated half (or more) of yearly residency for a population (for example, salmon sharks in Alaska, Pacific bluefin tuna in Mexico, Table 4.4). For each population, I explicitly identified who is responsible for management and clarified when during the year that responsibility commences and concludes.

When is shared management responsibility asynchronous or synchronous, with whom, and for which populations?

Countries (or states and provinces) may have contemporaneous management responsibility over marine predator populations. For example, the individuals of the same endangered black-footed albatross population may visit either Alaska, Canada, the U.S. west coast, or the high seas from June through September. Or, during a given time period, an EEZ may have almost sole management responsibility. During January- March, and October - November, black-footed albatrosses are the exclusive management responsibility of the Northwest Hawaiian Islands, and specifically, the Papahānaumokuākea Marine National Monument. The Hawaiian (U.S.), Alaskan (U.S.), and Canadian governments, as well as the two Regional Fishery Management Organizations (RFMOs) that cover the north Pacific share responsibility for managing this population of albatross, but some EEZs have sole purview during their time window of the full population, and other countries simultaneously are responsible for management of subsets of the population. A similar pattern was exhibited by Indonesian leatherback turtles, who demonstrated individual variation in post-breeding movements to island EEZs of the south Pacific (Fig. 4.2i, Benson et al., 2011), but near exclusive residency in the Indonesian EEZ during their breeding period from June to August.

Mexico and the U.S. share management responsibility over juvenile Pacific bluefin tuna resident to the west coast of North America during their annual cycle. During narrow windows of time subsets of the population are likely to be resident in both countries, but in general, Mexico and the U.S. commend exclusive responsibility to each other twice during the annual cycle. All models predicted an August migration. By the end of August, there was a 50/50 chance of finding a tracked individual in either Mexico or the U.S. Thus, during the months of August and September, the U.S. and Mexico contemporaneously share responsibility. By the end of September, nearly all tagged tuna were within the United States, and management shifts to the U.S. for the months of October and November. These results align with previous research aimed at understanding seasonal movements of PBT with shifts in upwelling in the California Current (Domeier et al., 2005; Boustany et al., 2010; Block et al., 2011). When placed within the specific context of political boundaries, results delineate exactly when the trade-off in exclusive jurisdictional purview over this population occurs. Although both countries report to the Inter-American Tropical Tuna Commission, there is no extant regional agreement for Pacific bluefin management (ISC, 2008)

When are multiple populations or taxa concurrent within the same EEZ?

Among the six taxa of marine predators analysed here (tunas, sharks, pinnipeds, seabirds, turtles, whales), some were concurrently resident within the same EEZs (Fig. 4.2. For example, tunas, sharks, and whales occurred within the U.S. EEZ from July to November; female elephant seals, albatrosses, and leatherback turtles ranged throughout the high seas from April to November; and Laysan albatrosses and sooty shearwaters visited Russia from July through October. By synthesizing seasonal movement cycles across guilds, species, and populations, it is possible to take a big-picture approach to the management of wide-ranging species, and to create a portfolio of species within each EEZ during each month of the year.

How important are the high seas to marine predator populations?

The high seas are the world's last global commons (Russ and Zeller, 2003), RFMOs have mostly failed their mandates (Cullis-Suzuki and Pauly, 2010), which include managing for non-target species such as seabirds, turtles, and marine mammals in international waters, and the high seas are the least protected places on earth (Corrigan and Kershaw, 2008; Game et al., 2009). It is obvious that human activities in the high seas have been, and continue to be, a major threat to wide-ranging marine animals, but scientific information about high seas ecosystems is scant.

Global efforts to accumulate knowledge about this last frontier, such as the field projects of the Census of Marine Life, were a huge advance. Single-species focused research identified specific high use areas for marine predators within the Pacific Ocean high seas (Weng et al., 2005; Jorgensen et al., 2010; Kappes et al., 2010). In this study I synthesized, quantified, and compared the time spent in high seas ecosystems by marine predator populations throughout their annual cycles to inform current planning efforts for protected area networks in the high seas (Corrigan and Kershaw, 2008). All land-breeding populations (pinnipeds, seabirds, and marine turtles), white sharks, and adult Pacific bluefin tuna undertaking their transpacific migration, were estimated to spend more than half of their year in the high seas and Laysan albatrosses were estimated to spend three quarters of their year in the high seas.

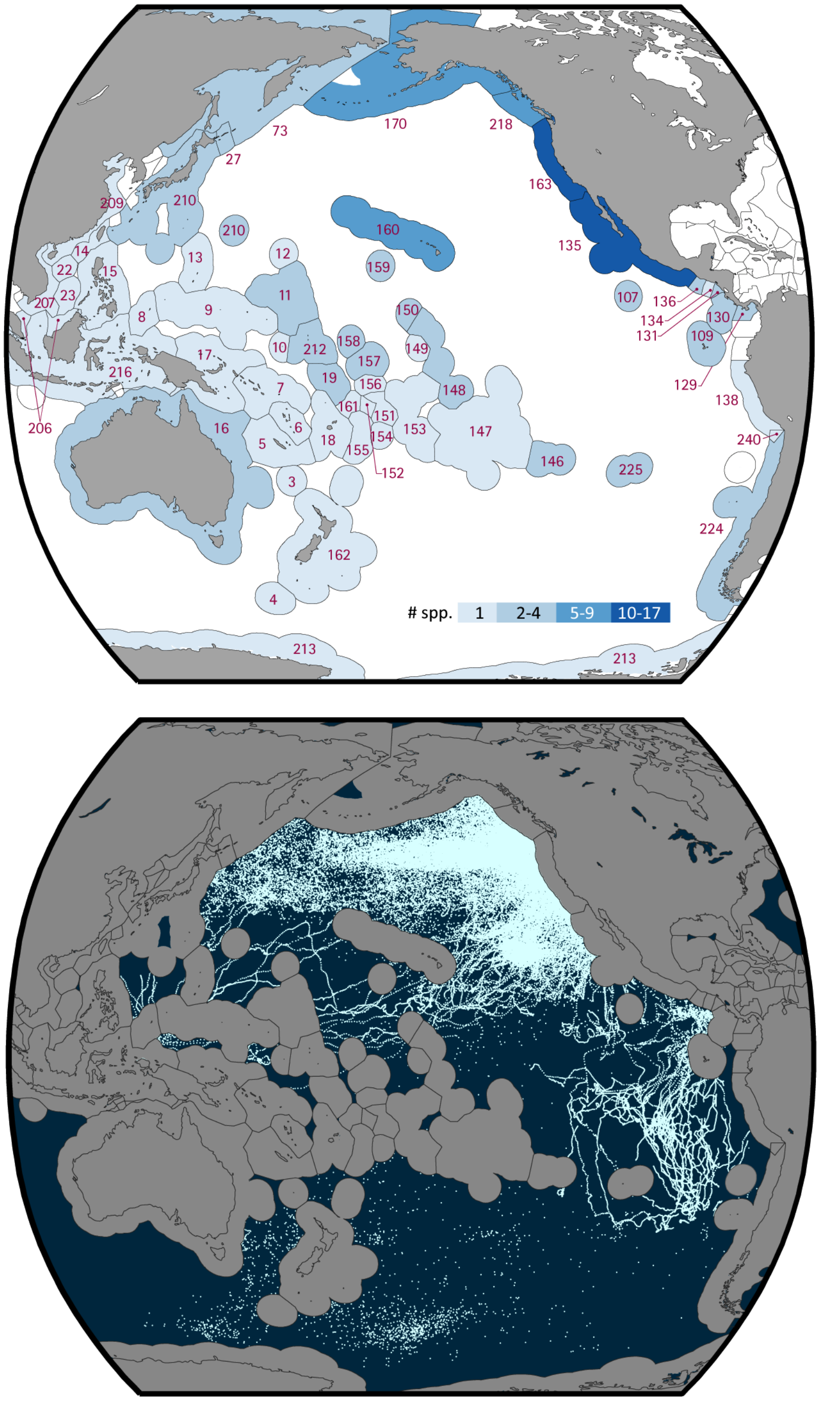
4.4.2 Methodological approach

The Tagging of Pacific Predators project was unprecedented in its scope and produced the world's largest multi-species, multi-year marine predator tracking dataset. The generalized additive mixed effects modeling approach (Wood, 2006) used to analyze temporal relationships with EEZs, and the specific covariates considered, accounted for many sampling imbalances and deployment effects unique to tracking datasets. However, caveats common to ecological research should be considered. Some datasets in this study were small (less than 25 individuals tracked), particularly in relation to full population size. For these species, model results are relevant only for the electronically tracked population. More tagging effort is needed in order to extrapolate to entire populations. For example, sooty shearwaters (one of the most abundant bird species in the world, with population estimates in the tens of millions) visit the California Current in numbers ranging from 2 to 4 million (Briggs and Chu, 1986) during the northern summer months. However, a greater proportion of the shearwaters tagged in New Zealand and tracked for their full migration as part of TOPP, spent their time foraging in Japan and Russia, rather than the eastern Pacific. Loggerhead turtles and albacore tuna are known to make use of the entire Pacific Ocean basin (Bowen et al., 1995; Polovina et al., 2001), however, most individuals of these populations were tracked for only a portion of their annual cycle, and/or sample sizes were small. Only a few species' datasets spanned more than four years, and there is still much to be learned about sex and age differences in migration patterns for all species.

The binomial models I used to represent daily probability of occurrence in EEZs and the high seas were useful, but for some of the species and populations I modeled, or for other applications, a multinomial approach would be better. A multinomial framework becomes more useful (and perhaps worth the complexity required) when multiple individuals use more than two EEZs over a given period. This is the case when high travel speeds allow individuals to exploit resources over very large scales, as albatrosses do, or when individuals are able to disperse to multiple EEZs because EEZs are geographically clustered, relatively small-scale, and adjoining (for example, the western Pacific population of leatherback turtles that may disperse to multiple island EEZs).

4.4.3 Conclusions and future directions

For 18 marine predator populations, I identified the suite of countries with shared management responsibility throughout the year, and detail when this responsibility commences and concludes. Using tracking data collected over the entire annual cycle, it is tractable to explicitly incorporate migratory phenology into integrated transboundary conservation and management strategies, and this should clarify international responsibilities. The methodological approach taken also accounted for many sampling imbalances and deployment effects unique to tracking datasets. Tracking data increasingly are collected in shared repositories (www.movebank.org; www.iobis.org; www.obisseamap.org). I present a pragmatic way to use these data for a range of marine management questions without limiting ecological spatial analyses to discrete chunks of time, for example season or month. The results are immediately interpretable. Many broad-scale analyses of tracking data—for example, use of habitat biomes, RFMOs, and marine protected areas, or overlap with threats —could be intuitively re-framed to view temporal relationships between animals and their habitats as the continuous functions that they are. This approach fully capitalizes on what biologging technologies do best: produce rich time-series data on individual animals who spend most of their lives hidden from direct scientific observation.



Exclusive Economic Zones

3	Norfolk Island (Australia)
4	Macquarie Island (Australia)
5	New Caledonia (France)
6	Vanuatu
7	Solomon Islands
8	Palau
9	Micronesia
10	Nauru
11	Marshall Islands
12	Wake Island (USA)
13	Northern Mariana Islands and Guam (USA)
14	Taiwan
15	Philippines
16	Australia
17	Papua New Guinea
18	Fiji
19	Tuvalu
22	Paracel Islands (Disputed)
23	Spratly Islands (Disputed)
27	Southern Kuriles (Russia-Japan Conflict Zone)
73	Russia
107	Clipperton Island (France)
109	Galapagos Islands (Ecuador)
129	Panama
130	Costa Rica
131	Nicaragua
134	El Salvador
135	Mexico
136	Guatemala
138	Peru
146	Pitcairn (UK)
147	French Polynesia (France)
148	Line Group (Kiribati)
149	Jarvis Island (USA)
150	Palmyra Atoll (USA)
151	American Samoa (USA)
152	Samoa
153	Cook Islands (New Zealand)
154	Niue (New Zealand)
155	Tonga
156	Tokelau (New Zealand)
157	Phoenix Group (Kiribati)
158	Howland Island and Baker Island (USA)
159	Johnston Atoll (USA)
160	Hawaii (USA)
161	Wallis and Futuna (France)
162	New Zealand
163	United States
170	Alaska (USA)
206	Malaysia
207	Viet Nam
209	China
210	Japan
212	Kiribati
213	Antarctica
216	Indonesia
218	Canada
224	Chile
225	Easter Island (Chile)
240	Area en controversia (Chile/Peru - Disputed)

Figure 4.1: a) Visited EEZs and b) high seas locations of 18 species of marine predators electronically tracked 2002-2009.

Table 4.1: Percentage of tagged individuals that visited EEZs and the high seas. EEZs visited by at least 20% of individuals from at least one species are listed. See Appendix A for full results and for percentage of locations within each EEZ. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WHS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater. Grey shading represents EEZs in which tags were deployed.

EEZ (*Sovereign*)	**PBT**	**YFT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**CSL**	**NFS**	**BLWH**	**HUWH**	**LET**	**LOT**	**BFAL**	**LAAL**	**SOSH**	**% All Ind.**	**Spp.**
HighSeas	24	7	55	39	56	67	7	85	85	2	78	27	0	89	13	70	65	100	47	17
Mexico	99	100	91	88	76	11	43	3	12	17	0	46	20	2	100	1	41	17	49	17
USA	71	10	82	100	83	44	100	100	97	84	33	100	100	19	0	23	24	25	60	17
Hawaii (*USA*)	<1	0	5	1	0	0	0	18	<1	0	0	0	0	13	0	100	59	79	12	10
Canada	<1	0	0	0	8	58	0	0	27	0	33	6	0	0	0	23	4	25	11	9
Alaska (*USA*)	0	0	0	0	0	100	0	0	15	0	100	0	0	0	0	17	21	38	13	6
Japan	2	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	3	58	2	4
Russia	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	1	14	63	2	4
Southern Kuriles	<1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	38	1	3
Phoenix Group (*Kiribati*)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	<1	25	<1	3
Costa Rica	0	0	0	0	0	0	0	0	0	0	0	2	0	48	0	0	0	0	3	2
Line Island Group (*Kiribati*)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	42	1	2
Australia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	21	<1	2
NewZealand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	1	1
Norfolk Island (*Aus.*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	1	1
Macquarie Island (*Aus.*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	<1	1
Palau	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0	1	1
Galapagos Islands (*Ecuador*)	0	0	0	0	0	0	0	0	0	0	0	0	0	43	0	0	0	0	2	1
French Polynesia (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	1	1
Cook Islands (*N.Z.*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	1	1
Tonga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	<1	1
Indonesia	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0	2	1
Tokelau (*N.Z.*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	<1	1
Number of individuals	299	224	22	67	59	113	14	65	281	135	9	52	15	93	16	70	134	24	1692	18
Number of EEZs visited	6	4	3	3	4	4	2	3	4	2	3	5	3	38	1	7	11	37	61	

Table 4.2: Species-specific candidate models of individual probability of occurrence in an EEZ or in the high seas. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WS**, white shark; **NELE**, northern elephant seal; **BLWH**, blue whale; **LET**, leatherback turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater. *Potential covariates:* **DOY**, day of year; **RELDAY**, relative day of track (days elapsed since the individual was tagged); **YEAR**, year in which location was recorded, **tEEZ**, EEZ in which the tag was deployed. Spline smoothers are represented by **s()**. All models included individual as a random effect.

Candidate Model		**PBT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**BLWH**	**LET**	**BFAL**	**LAAL**	**SOSH**
1	s(DOY)	×	×	×	×	×	×	×	×	×	×	×	×	×
2	s(DOY) + s(RELDAY)	×	×	×	×	×	×	×		×	×			
YEAR and tEEZ effect														
3	s(DOY) + YEAR	×	×	×		×			×		×			
4	s(DOY) + tEEZ	×	×						×		×		×	
5	s(DOY) + tEEZ + YEAR	×	×						×		×			
6	s(DOY) + s(RELDAY) + YEAR	×	×	×		×					×			
7	s(DOY) + s(RELDAY) + tEEZ	×	×								×			
8	s(DOY) + s(RELDAY) +YEAR + tEEZ	×	×								×			
DOY/YEAR interaction														
9	s(DOY) x YEAR + YEAR	×	×	×		×			×		×			
10	s(DOY) x YEAR + YEAR + tEEZ	×	×						×		×			
11	s(DOY) x YEAR + s(RELDAY) + YEAR	×	×	×		×					×			
12	s(DOY) x YEAR + s(RELDAY) + YEAR + tEEZ	×	×								×			
RELDAY/tEEZ interaction														
13	s(DOY) x tEEZ + tEEZ	×	×						×		×		×	
14	s(DOY) + s(RELDAY) x tEEZ + tEEZ	×	×								×			
15	s(DOY) + s(RELDAY) x tEEZ + tEEZ +YEAR	×	×								×			
DOY/YEAR interaction & RELDAY/tEEZ interaction														
16	s(DOY) x YEAR + s(RELDAY) x tEEZ + YEAR + tEEZ	×	×								×			

Table 4.3: Models of individual occurrence within EEZs and the high seas. These selected models are the models with the lowest AIC score within each model subset. Models with the lowest overall AIC score among all candidate models (both subsets) are indicated with an asterisk. *Species codes:* **PBT**, Pacific bluefin tuna; **ALT,** albacore tuna; **WS**, white shark; **SS**, salmon shark; **MS**, mako shark; **BS**, blue shark; **BLWH**, blue whale; **NELE**, female northern elephant seal; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater; **LET**, leatherback turtle. *Column codes:* **n** (number of locations); **Model** (candidate model: see Table 3); **Null. Dev.** (proportion of null deviance explained); **EDF** (estimated degrees of freedom).

Species	n	EEZ	Model	AIC	Null. Dev.	EDF
PBT	65,459	Mexico	2	46846	0.47	286.07
			11*	42065	0.53	343.87
		USA	2	41328	0.51	278.9
			11*	37226	0.56	348.9
		High seas	2	12069	0.61	187.4
			11*	10265	0.70	241.3
ALT	4,664	Mexico	2	2486	0.63	35.4
			6*	2476	0.53	34.0
		USA	2	1493	0.72	36.4
			9*	1391	0.74	39.4
		High seas	2	2486	0.63	35.4
			6*	2653	0.63	39.4
WS	11,971	USA	1	4256	0.73	68.60
			2*	2866	0.82	75.76
		High seas	1	6637	0.60	69.27
			2*	6041	0.64	77.78
		Hawaii	1	2346	0.57	46.63
			2*	1597	0.72	45.84
SS	29,802	Alaska	2	23703	0.43	125.0
			11*	13834	0.59	177.0
		High seas	2	21316	0.37	119.7
			11*	18664	0.56	166.6
		USA	2	3162	0.75	98.7
			11*	2180	0.84	147.3
		Canada	2	10735	0.31	115.9
			11*	6159	0.59	162.3
MS	14,990	Mexico	2	10613	0.46	81.4
			11*	9612	0.50	117.5
		USA	2	10885	0.48	82.0
			11*	9350	0.46	124.8
		High seas	2	6321	0.54	65.1
			11*	5300	0.51	86.0
BS	5,756	Mexico	1	3661	0.51	62.8
			2*	3403	0.55	69.7
		USA	1	4187	0.47	63.9
			2*	3405	0.57	72.9
		High seas	1	4127	0.42	59.8
			2*	2894	0.60	59.0

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Species	n	EEZ	Model	AIC	Null. Dev.	EDF
BW	4,689	Mexico	1	2936	0.49	47.4
			2*	2438	0.59	62.1
		USA	1	1265	0.82	46.0
			2*	1071	0.85	58.3
		High seas	1	838	0.82	30.3
			2*	259	0.96	35.9
NELE	16,218	USA	1	16218	0.51	259.00
			10*	13835	0.59	304.72
		High seas	1	20543	0.51	257.86
			10*	18664	0.56	309.00
		Alaska	1	3162	0.75	135.18
			10*	2180	0.84	139.92
		Canada	1	7266	0.51	182.42
			10*	6159	0.59	205.25
BFAL	4,237	Hawaii	1*	1158	0.58	52.31
		USA	1*	1820	0.38	28.70
		High seas	1*	4435	0.22	58.55
		Alaska	1*	1473	0.43	27.55
		Canada	1*	1724	0.30	29.15
LAAL	5,894	Hawaii	1*	1208	0.52	53.4
		Alaska	1*	2730	0.32	36.3
		Russia	1*	1881	0.45	34.0
		High seas	1*	5110	0.22	52.4
SOSH	6,597	New Zealand	1*	2880	0.42	29.8
		High seas	1*	8192	0.11	29.8
		Japan	1*	1521	0.67	26.2
		Russia	1*	1863	0.51	29.3
		Alaska	1*	786	0.61	24.2
LET	11,373	Costa Rica	2	1361	0.59	48.45
			9*	1233	0.89	57.53
		High seas	2	2525	0.62	50.56
			9*	2324	0.84	66.54
		Galapagos	2*	2822	0.38	47.09
			9	2861	0.45	55.40
LET	9,398	Indonesia	2*	2904	0.69	38.5
			9	3757	0.89	56.7
		High seas	2	5279	0.62	37.7
			9*	5218	0.84	57.3
		Palau	2	2526	0.38	37.3
			9*	2495	0.45	49.0
		Micronesia	2	1979	0.38	34.0
			9*	1974	0.45	44.2
		Philippines	2*	2019	0.38	31.5
			9	2235	0.45	43.0
		USA	2*	22.7	0.38	18.0
			9	39	0.45	15.5

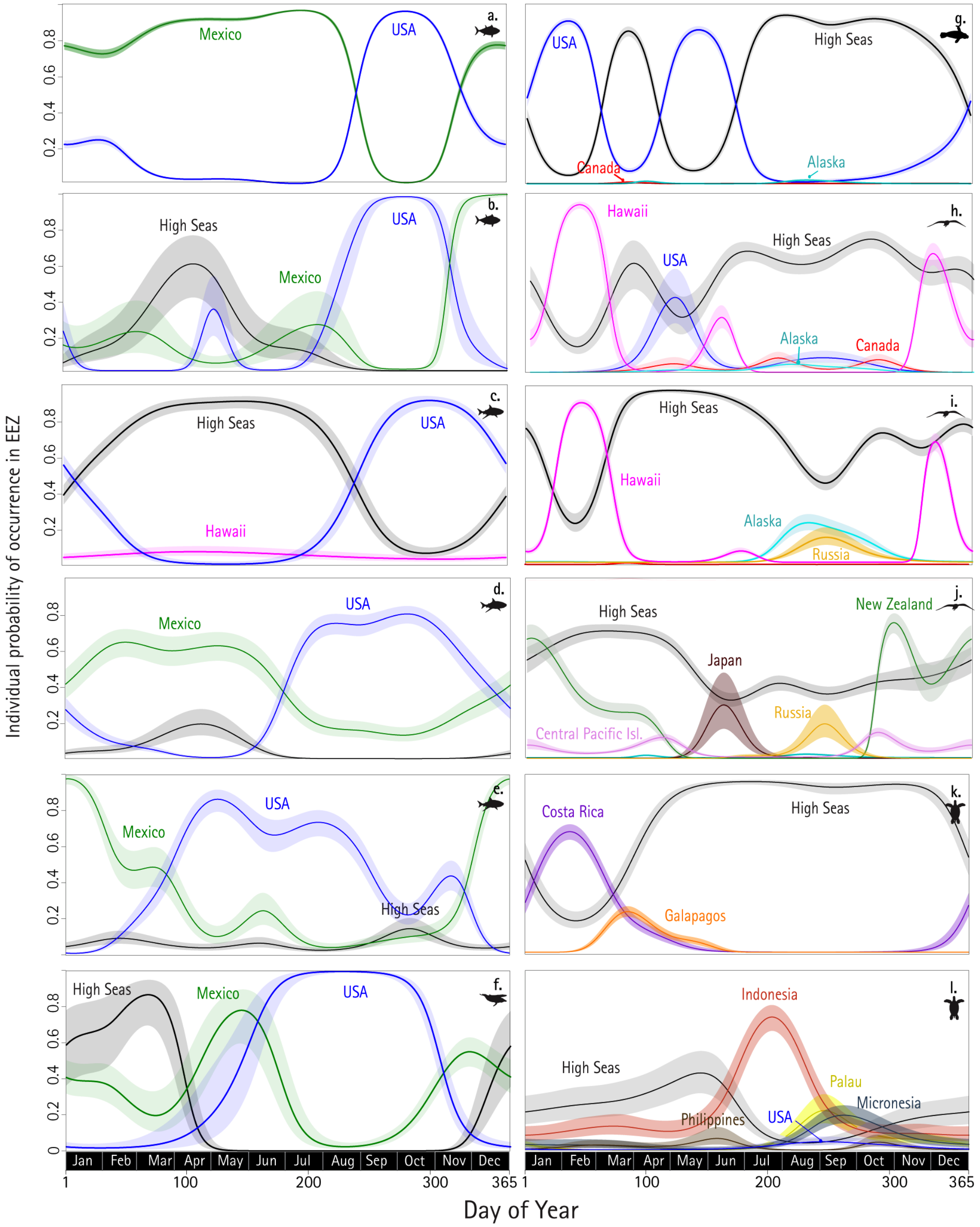

Figure 4.2: Model-predicted probability of a randomly selected individual from the tracked population occurring in Pacific Ocean EEZs and high seas on each day of year. a) Pacific bluefin tuna; model (m) 2 b) albacore tuna; m2; c) white shark; m2; d) mako shark; m2; e) blue shark; m2; f) blue whale; m2, g) female northern elephant seal; m1; h) black-footed albatross, m1; i) Laysan albatross, m1; j) sooty shearwater, m1 k) leatherback turtle tagged in Costa Rica, m1; l) leatherback turtle tagged in Indonesia, m1. Model details: Table 4.2.

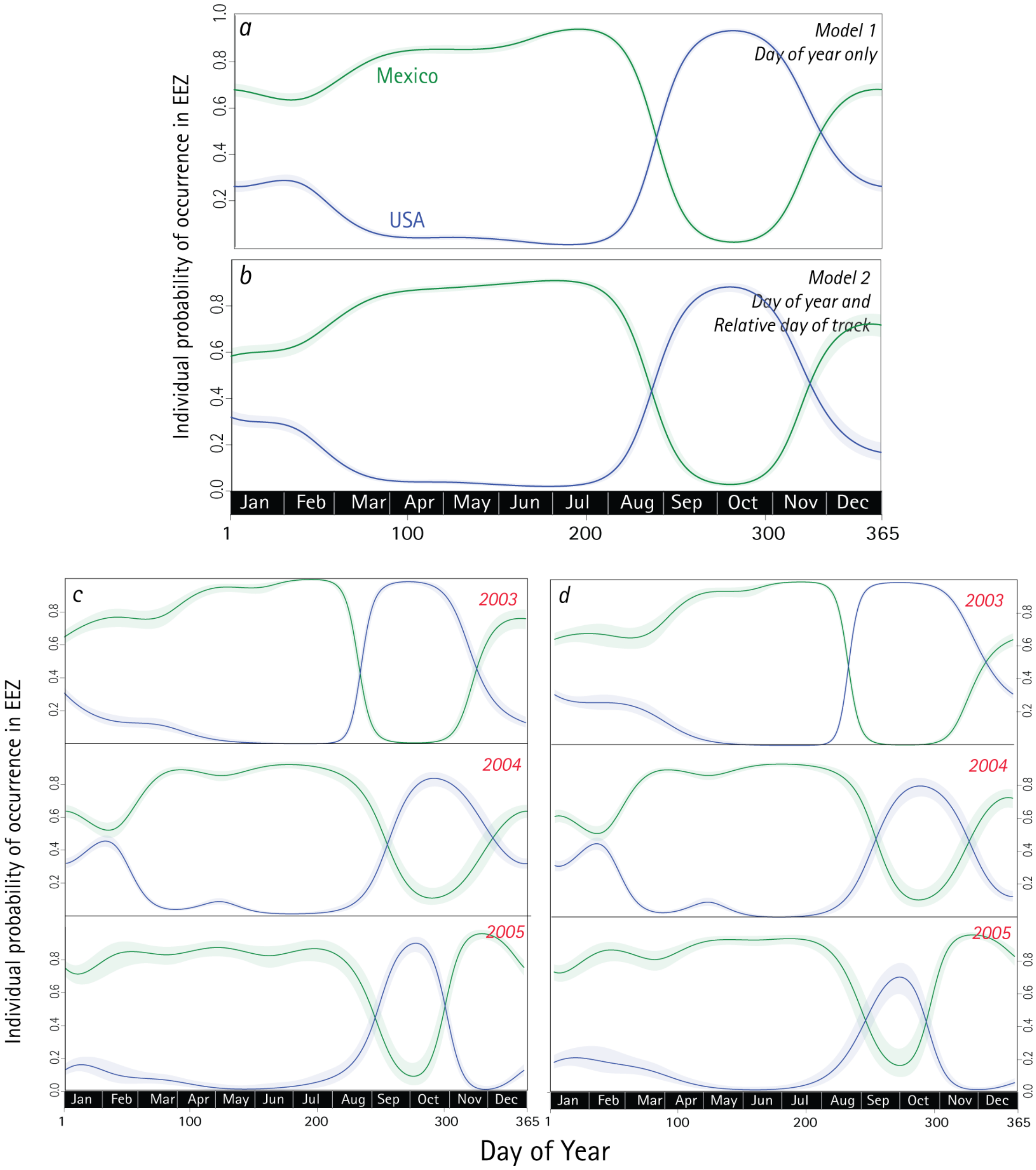

Figure 4.3: Model-predicted individual Pacific bluefin tuna probability of occurrence in Pacific Ocean EEZs and high seas on each day of year for a-b) all years combined (candidate models 1 and 2); c) 2003-2005 (candidate model 9); and d) 2003-2005 (candidate model 11).

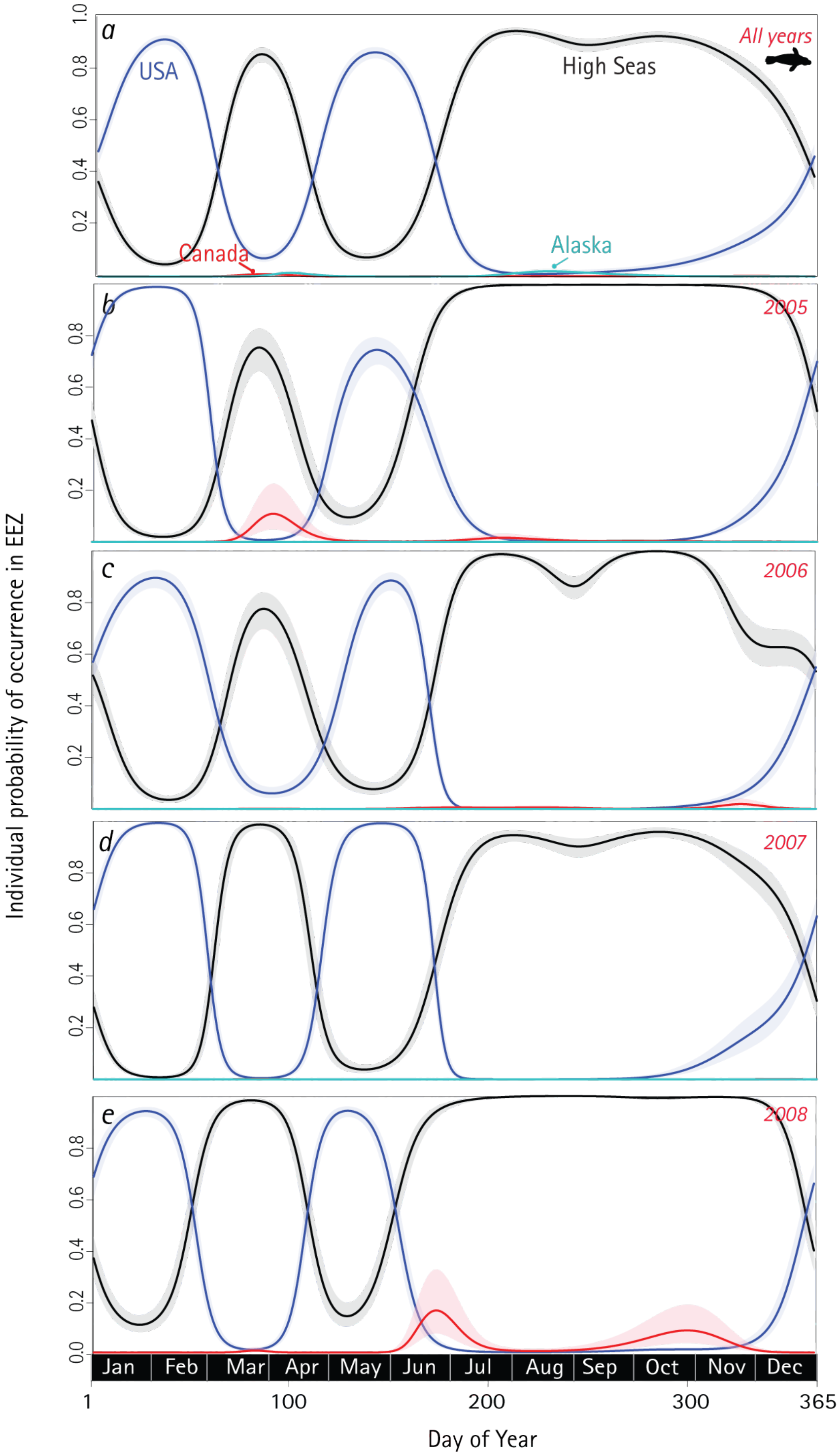

Figure 4.4: Model-Predicted individual female northern elephant seal probability of occurrence in Pacific Ocean EEZs and high seas on each day of year for a) all years combined (candidate model 1) and b-f) 2005-2008 (candidate model 11).

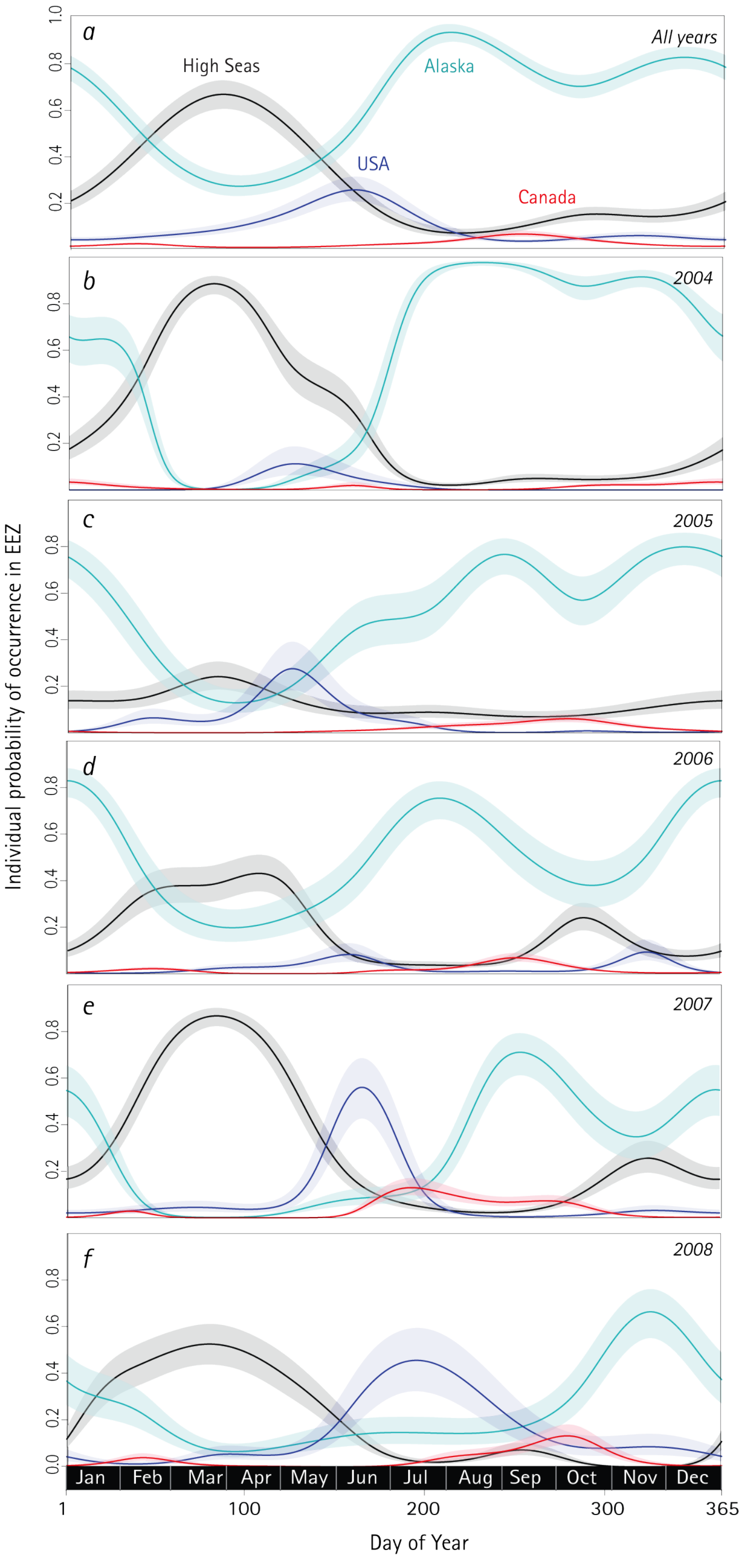

Figure 4.5: Model-predicted individual salmon shark probability of occurrence in Pacific Ocean EEZs and high seas on each day of year for a) all years combined (candidate model 2) and b-f) 2004-2008 (candidate model 10).

Table 4.4: Modeled proportion of a year marine predator populations of 12 species spent within focal EEZs. *Species codes:* **PBT**, Pacific bluefin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **WS**, white shark; **NELE**, female northern elephant seal; **BLWH**, blue whale; **LET(Ind)**, leatherback turtle tagged in Indonesia; **LET(CR)**, leatherback turtle tagged in Costa Rica; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater

	PBT	ALT	WS	SS	MS	BS	NELE	BLWH	LET(Ind)	LET(CR)	BFAL	LAAL	SOSH
High Seas		23.4	57.7	24.3	14.1	25.8	63.5	23.7	20.3	76.3	52.6	71.1	48.9
USA	30.1	25.5	36.2	10.8	27.4	41.9	33.0	46.0	1.6		7.0		0.1
Mexico	64.9	36.8			47.7	31.9		33.7					
Alaska				46.6			<1					4.8	0.1
Canada				5.0			1.3				2.6		
Hawaii			5.9								21.6	17.7	
Russia											1.3	2.4	2.2
Central Pac.Isl.													3.0
Japan													2.9
New Zealand													23.7
Indonesia									20.8				
Micronesia									5.4				
Philippines									2.1				
Palau									4.8				
Malaysia									0.9				
Costa Rica										14.4			
Galapagos										3.7			

Appendix

Table B1: Number of tags deployed, number of individuals with active tags, and number of daily location estimates by year and species for the analysed subset of the TOPP dataset (Block et al. 2011). *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater

	PBT	YFT	ALT	MS	BS	SS	TS	WS	NELE	CSL	NFS	BLWH	HUWH	LET	LOT	BFAL	LAAL	SOSH	TOTAL
Tags deployed																			
2002	45	13	0	0	4	10	0	1	4	0	0	0	0	0	0	4	5	0	86
2003	80	22	7	4	3	14	0	2	6	32	0	0	0	0	0	16	34	0	220
2004	6	40	8	15	19	20	4	7	36	14	0	18	7	31	0	4	9	0	238
2005	78	62	5	6	1	26	2	21	61	43	0	14	8	23	4	33	74	24	485
2006	16	53	0	13	12	24	4	21	56	21	9	7	0	8	12	13	11	0	280
2007	8	17	0	12	11	16	1	7	40	17	0	11	0	31	0	0	0	0	171
2008	59	17	2	5	1	3	3	0	51	8	0	2	0	0	0	0	1	0	152
2009	0	0	0	12	8	0	0	0	27	0	0	0	0	0	0	0	0	0	47
Total	292	224	22	67	59	113	14	59	281	135	9	52	15	93	16	70	134	24	1,679
Active tags																			
2002	46	13	0	0	4	10	0	5	4	0	0	0	0	0	0	4	5	0	91
2003	120	28	7	4	3	24	0	3	7	32	0	0	0	0	0	18	39	0	285
2004	96	56	15	17	20	32	4	9	41	18	0	18	7	31	0	4	13	0	381
2005	89	92	10	19	13	43	2	28	82	47	0	18	8	39	4	37	79	24	634
2006	47	88	3	16	12	52	5	42	85	52	9	10	1	22	16	13	11	5	489
2007	25	33	0	17	13	39	5	23	55	29	5	14	0	39	3	0	0	0	300
2008	65	29	2	17	4	21	4	4	66	17	0	8	0	23	0	0	1	0	261
2009	4	11	0	20	9	11	0	0	39	8	0	0	0	0	0	0	1	0	103
Daily locations																			
2002	4,916	548	0	0	479	1,121	0	543	321	0	0	0	0	0	0	35	75	0	8,038
2003	22,369	2,833	338	613	452	2,455	0	168	1,034	1,096	0	0	0	0	0	247	458	0	32,063
2004	18,735	4,696	2,357	2,285	843	3,439	429	464	5,312	542	0	1,289	286	6,431	0	22	565	0	47,695
2005	8,685	8,977	1,653	2,900	1,142	5,836	287	1,696	9,110	1,910	0	1,130	392	4,588	484	1,927	2,732	5,104	58,553
2006	4,787	5,271	243	1,667	538	7,412	434	6,037	7,155	2,073	619	766	9	3,336	1,478	2,006	2,033	1,493	47,357
2007	2,411	3,288	0	2,741	1,222	4,748	565	2,489	4,836	1,023	272	1,085	0	6,584	230	0	0	0	31,494
2008	2,782	2,341	73	3,172	356	3,392	237	574	6,150	658	0	419	0	3,726	0	0	20	0	23,900
2009	774	1,035	0	1,612	724	1,399	0	0	2,275	203	0	0	0	0	0	0	11	0	8,033
Total	65,459	28,989	4,664	14,990	5,756	29,802	1,952	11,971	36,193	7,505	891	4,689	687	24,665	2,192	4,237	5,894	6,597	257,133

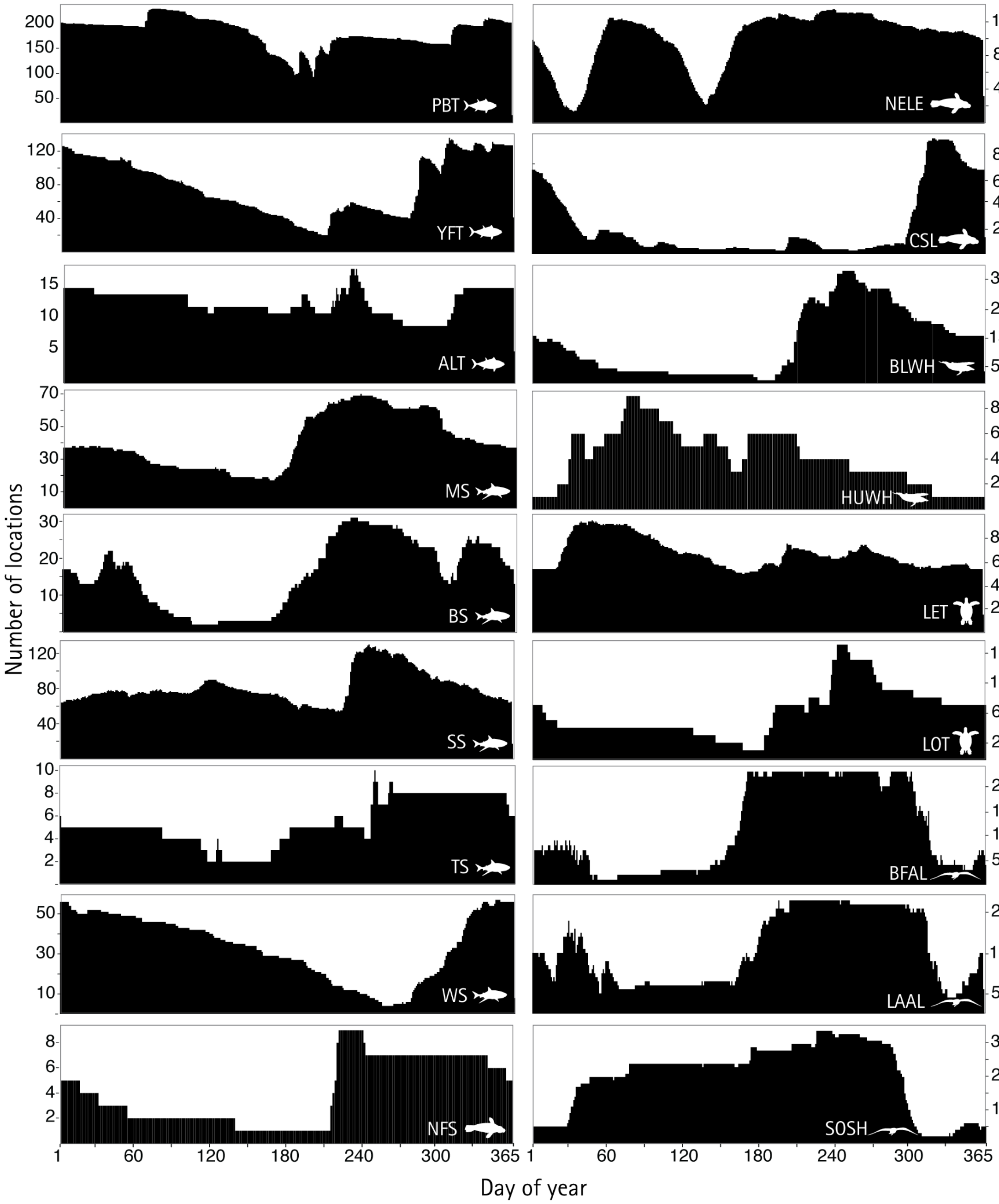

Figure B1: Frequency histograms of electronic tagging locations available for every day of the year during the tagging period 2002-2009. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater

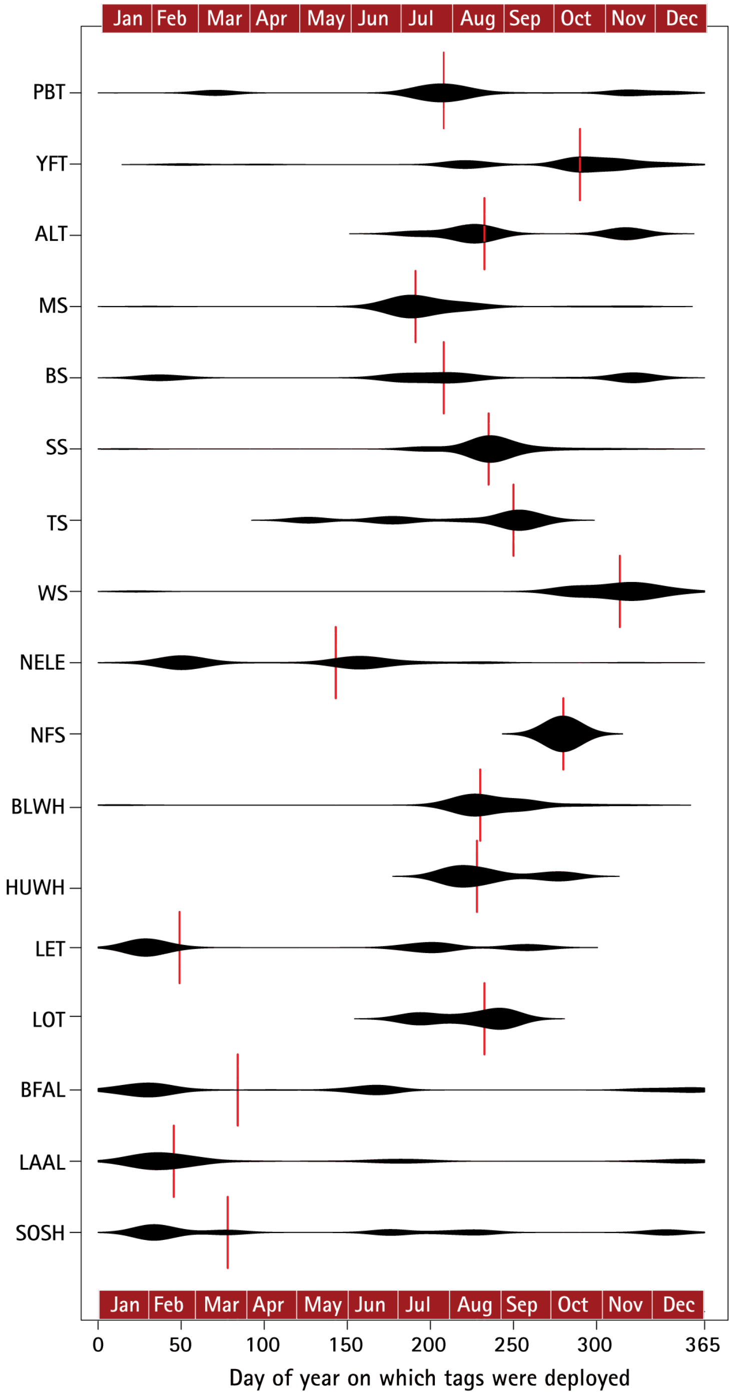

Figure B2: Distribution of tag deployment dates by species. Vertical red lines indicate mean deployment date. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **THS**, thresher shark; **WS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater.

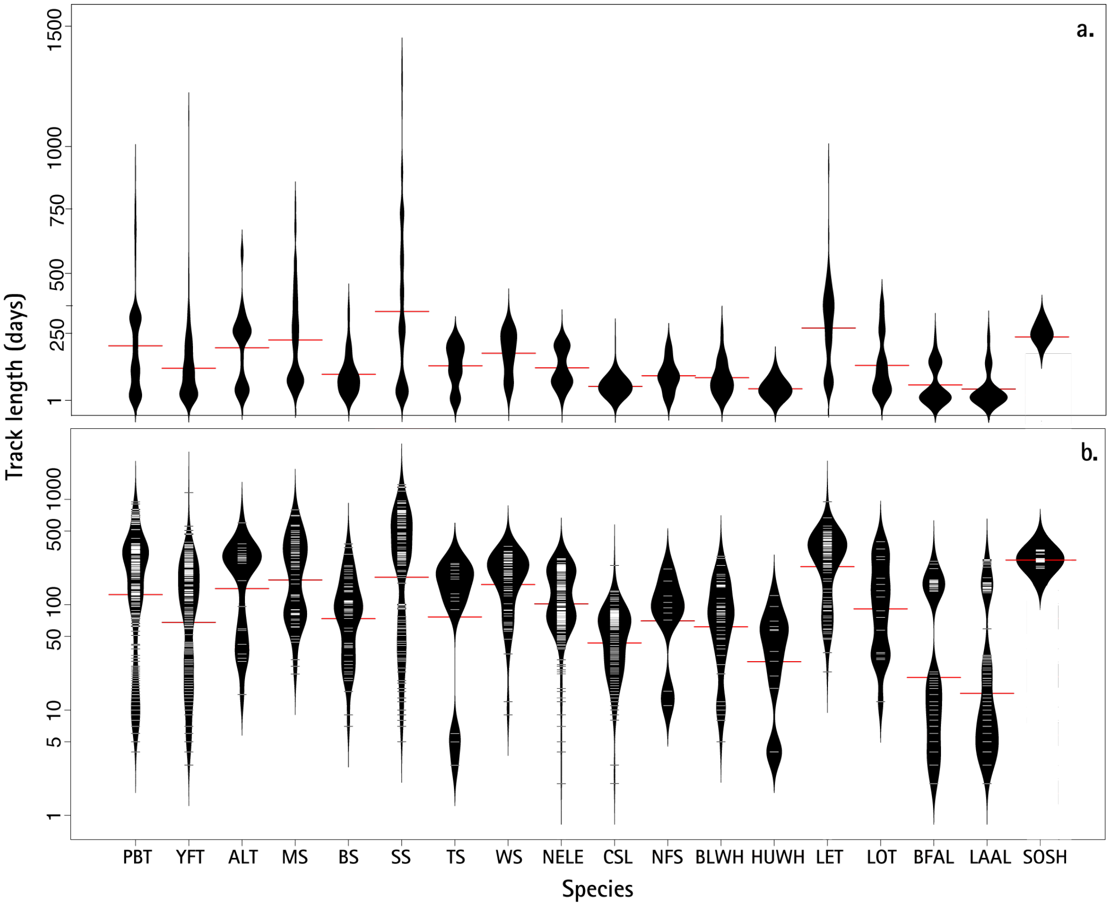

Figure B3: Distribution of individual tracking durations by species a) on a linear scale and b) on a log scale. Red lines indicate median track length; white lines represent individual track durations. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **THS**, thresher shark; **WS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater.

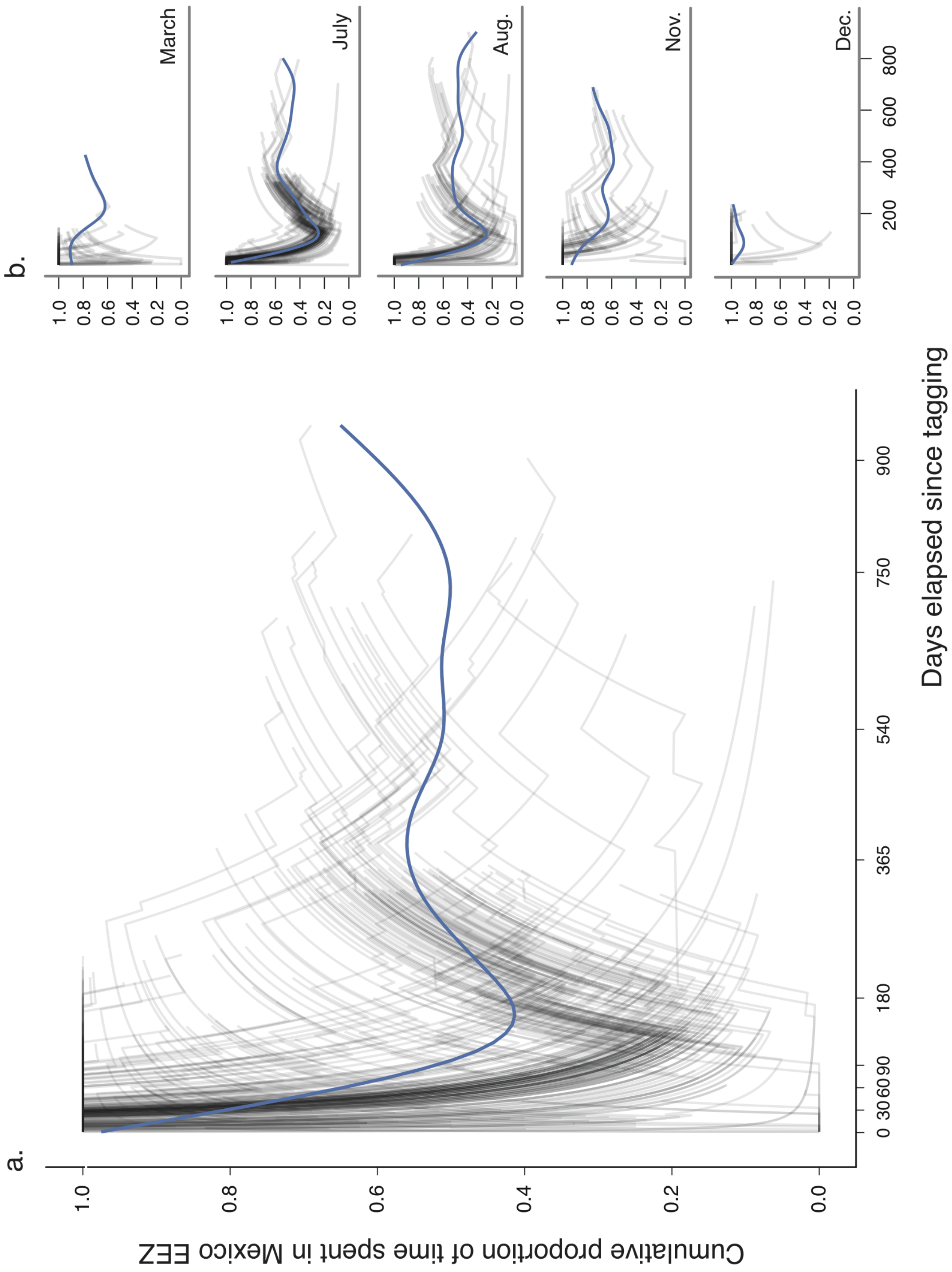

Figure B4: a) Cumulative proportion of time spent in Mexican EEZ by individual Pacific bluefin tunas while tracked and b) grouped by tag deployment month. Blue lines are smooths of the data (loess) representing the population mean.

Table B2: Percentage of tagged individuals tracked within EEZs and the high seas. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WHS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater. Grey shading represents deployment EEZs.

EEZ (*Sovereign*)	**PBT**	**YFT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**CSL**	**NFS**	**BLWH**	**HUWH**	**LET**	**LOT**	**BFAL**	**LAAL**	**SOSH**	**% Tot.**	**Spp.**
United States	71	10	82	97	83	44	100	98	97	84	33	92	100	19	0	23	24	25	60	17
High Seas	24	7	55	39	56	67	7	85	85	2	78	27	0	89	12.5	70	65	100	47	17
Hawaii (USA)	<1	0	5	1	0	0	0	18	<1	0	0	0	0	13	0	100	59	79	12	9
Canada	<1	0	0	0	8	58	0	0	27	0	33	6	0	0	0	23	4	25	11	9
Alaska (USA)	0	0	0	0	0	100	0	0	15	0	100	0	0	0	0	17	21	38	13	6
Russia	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	1	14	63	2	4
Johnston Atoll (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	2	17	1	4
Japan	2	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	3	58	2	4
Southern Kuriles (Russia-Japan Conflict Zone)	<1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	38	1	3
Clipperton Island (France)	0	<1	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	4	<1	3
Guatemala	0	< 1	0	0	0	0	0	0	0	0	0	2	7	0	0	0	0	0	<1	3
Phoenix Group (Kiribati)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	<1	25	<1	3
Kiribati	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	<1	8	<1	3
Marshall Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	4	1	2
Australia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	21	<1	2
Tuvalu	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	<1	2
Costa Rica	0	0	0	0	0	0	0	0	0	0	0	2	0	48	0	0	0	0	3	2
Nicaragua	0	0	0	0	0	0	0	0	0	0	0	2	0	17	0	0	0	4	1	2
Pitcairn (UK)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	13	<1	2
Line Group (Kiribati)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	42	1	2
Palmyra Atoll (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	8	<1	2
Howland Island and Baker Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	13	<1	2
Chile	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	17	<1	2
Easter Island (Chile)	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	4	<1	2
Desventuradas (Chile)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	<1	2
Norfolk Island (Australia)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	1	1
Macquarie Island (Australia)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	<1	1
New Caledonia (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1	1
Vanuatu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	<1	1
Solomon Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	<1	1
Palau	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0	1	1
Micronesia	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	1	1

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Table B2 – Continued

EEZ (*Sovereign*)	**PBT**	**YFT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**CSL**	**NFS**	**BLWH**	**HUWH**	**LET**	**LOT**	**BFAL**	**LAAL**	**SOSH**	**% Tot.**	**Spp.**
Nauru	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	<1	1
Wake Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1	1
Northern Mariana Islands and Guam (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	<1	1
Taiwan	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	<1	1
Philippines	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	<1	1
Papua New Guinea	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	<1	1
Fiji	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	<1	1
Paracel Islands (Disputed)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1	1
Spratly Islands (Disputed)	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	<1	1
Galapagos Islands (Ecuador)	0	0	0	0	0	0	0	0	0	0	0	0	0	43	0	0	0	0	2	1
Panama	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	<1	1
El Salvador	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	<1	1
Peru	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1	1
French Polynesia (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	1	1
Jarvis Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	<1	1
American Samoa (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	<1	1
Samoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	<1	1
Cook Islands (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	1	1
Niue (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	<1	1
Tonga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	<1	1
Tokelau (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	<1	1
Wallis and Futuna (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	<1	1
New Zealand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	1	1
Malaysia	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	<1	1
Viet Nam	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	<1	1
China	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1	1
Antarctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	<1	1
Indonesia	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0	2	1
Area en controversia (Chile/Peru - Disputed)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	<1	1
Number of individuals	292	224	22	67	59	113	14	59	281	135	9	52	15	93	16	70	134	24	1,679	18
Number of EEZs visited	6	4	3	3	4	4	2	3	4	2	3	5	3	38	1	7	11	37	61	

Table B3: Percentage of tracking days within EEZs and the high seas. *Species codes:* **PBT**, Pacific bluefin tuna; **YFT**, yellowfin tuna; **ALT,** albacore tuna; **MS**, mako shark; **BS**, blue shark; **SS**, salmon shark; **TS**, thresher shark; **WHS**, white shark; **NELE**, northern elephant seal; **CSL**, California sea lion; **NFS**, northern fur seal; **BLWH**, blue whale; **HUWH**, humpback whale; **LET**, leatherback turtle; **LOT**, loggerhead turtle; **BFAL**, black-footed albatross; **LAAL**, Laysan albatross; **SOSH**, sooty shearwater. Grey shading represents deployment EEZs.

EEZ (*Sovereign*)	**PBT**	**YFT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**CSL**	**NFS**	**BLWH**	**HUWH**	**LET**	**LOT**	**BFAL**	**LAAL**	**SOSH**	**% Tot.**
Mexico	61	94	51	34	33	1	33	<1	5	8	0	28	13	<1	92	<1	4	2	33
High Seas	6	3	26	16	29	25	<1	63	63	<1	25	17	0	54	8	64	67	49	28
United States	32	2	23	49	37	16	67	32	20	92	20	54	87	3	0	10	2	8	24
Alaska (USA)	0	0	0	0	0	51	0	0	5	0	51	0	0	0	0	9	11	3	7
Canada	<1	0	0	0	1	7	0	0	6	0	4	<1	0	0	0	8	0	1	2
Costa Rica	0	0	0	0	0	0	0	0	0	0	0	<1	0	8	0	0	0	0	1
Indonesia	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	1
Japan	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	11	1
Hawaii (USA)	<1	0	<1	<1	0	0	0	6	<1	0	0	0	0	1	0	9	5	1	1
Philippines	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	1
American Samoa (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Antarctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Area en controversia (Chile/Peru)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Australia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	<1
Chile	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	1	<1
China	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Clipperton Island (France)	0	<1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Cook Islands (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1
Desventuradas (Chile)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Easter Island (Chile)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
El Salvador	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Fiji	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
French Polynesia (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	<1
Galapagos Islands (Ecuador)	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	<1
Guatemala	0	<1	0	0	0	0	0	0	0	0	0	<1	<1	0	0	0	0	0	<1
Howland and Baker Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Jarvis Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Johnston Atoll (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	<1	<1	<1	<1
Kiribati	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	<1	<1	<1
Line Group (Kiribati)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Macquarie Island (Australia)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Malaysia	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	<1

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Table B3 – Continued

EEZ (*Sovereign*)	**PBT**	**YFT**	**ALT**	**MS**	**BS**	**SS**	**TS**	**WS**	**NELE**	**CSL**	**NFS**	**BLWH**	**HUWH**	**LET**	**LOT**	**BFAL**	**LAAL**	**SOSH**	**% Tot.**
Marshall Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	<1	<1
Micronesia	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	<1
Nauru	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
New Caledonia (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
New Zealand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	<1
Nicaragua	0	0	0	0	0	0	0	0	0	0	0	<1	0	<1	0	0	0	<1	<1
Niue (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Norfolk Island (Australia)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Northern Mariana Is. and Guam (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Palau	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	<1
Palmyra Atoll (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Panama	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	<1
Papua New Guinea	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Paracel Islands (Disputed)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Peru	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Phoenix Group (Kiribati)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	<1	<1	<1
Pitcairn (UK)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Russia	0	0	<1	0	0	0	0	0	0	0	0	0	0	0	0	<1	8	8	<1
Samoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Solomon Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Southern Kuriles (Russia-Japan)	<1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	<1
Spratly Islands (Disputed)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Taiwan	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Tokelau (New Zealand)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Tonga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1
Tuvalu	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1	<1
Vanuatu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Viet Nam	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Wake Island (USA)	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	0	<1
Wallis and Futuna (France)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Total number of tracking days	65,459	28,989	4,664	14,990	5,756	29,802	1,952	11,971	36,193	7,505	891	4,689	687	24,665	2,192	4,237	5,894	6,597	257,133

Chapter 5

General Discussion

5.1 Broader implications

The work I presented here is an important first step toward understanding the spatio-temporal dynamics of the community of predators in the North Pacific and will directly contribute to developing basin-wide high seas management strategies. Marine animals with wide-ranging life histories are difficult to manage. They cross international boundaries, they have large, dynamic, and distributed area requirements, and their migrations take them to places that are also valuable to fisheries. Because marine predator behavior has been difficult to study *in situ*, management efforts are often based on scant information. I directed my research at answering a question posed directly by the Convention on Biological Diversity. Where are the ecologically and biologically significant areas in the high seas? I have presented results at CBD, Global Ocean Biodiversity Initiative, and BirdLife International workshops. I ensured that the work I did would be directly useful by asking leaders of these programs what information was needed and by participating directly in their efforts. The strengths of my dissertation are in its direct applicability; synthetic, standardized, multi-species spatio-temporal approaches; and visually intuitive presentation. My work fully capitalizes on what biologging technologies do best: produce rich time-series data on individual animals who spend most of their lives hidden from direct scientific observation. I presented pragmatic and rigorous ways to use tracking data for a range of theoretical and management-focused questions and I am optimistic that my work will help improve the tractability of marine predator management.

5.2 The challenges of working with large multi-species tracking datasets

The Tagging of Pacific Predators was unprecedented in its scope. Despite its many achievements, working with tracking data, combining them for different species and time frames, and robustly estimating space-use can be statistically problematic for a number of reasons (Aarts et al., 2008). In addition to experimental design limitations, coordinating research efforts across many universities in multiple countries also resulted in incomplete transfer of information or institutional knowledge between partners. I therefore faced a number of analytical challenges in trying to draw robust and meaningful conclusions about the spatio-temporal dynamics of the TOPP predators. I outline below steps I took to ameliorate biases and describe challenges that are insurmountable when synthesizing data from animals with diverse life histories. I also provide recommendations for other large-scale tracking programs and some of the lessons I learned.

1) Tracking data represent some life history stages or sexes very well, and neglect others.

This is a common limitation of ecological research in general, especially for wide-ranging species and predators that spend most of their lives in habitats that are inaccessible to humans. Every effort should be made to include multiple life history stages and sexes in research programs, but this isn't always possible for various reasons. For fully marine species, sampling is limited to what researchers are able to catch at sea. This ability in turn is partially limited by knowledge about marine predator life history, which for some species was scant prior to TOPP. TOPP specifically targeted species for which there were either established research programs, or a large body of knowledge to support efforts and the potential each species had for carrying tags.

My conclusions are limited mostly to adults, only to female salmon sharks because sexes are segregated (females in the eastern Pacific, males in the western Pacific), and only to female northern elephant seals because male tracks were few, and to juvenile Pacific bluefin tuna (with the exception of the small number of trans-Pacific migrants). Although we are still very far from a complete understanding of the spatial dynamics of entire populations and life histories of some species, the TOPP project was a huge advance and provided the foundation for future targeted studies focused on specific sexes and life history stages about which we still know very little.

2) Track durations for many species were skewed toward short tracks. This posed a very large challenge for my work, and for Block et al. (2011). Variability in track length among individuals can confound spatio-temporal analyses when tracking duration are unrelated to species life history. Individuals were tracked as long as possible. For a small number of salmon sharks, tracks were three years long. For most Pacific bluefin tuna, tracks were less than 9 months. Harvest rates of tagged Pacific bluefin tuna were high (in some years, 70%). In chapters 2 and 3 I describe in detail the approaches I took to lessen the effects of variable sampling effort across individuals on my conclusions and Block et al. (2011) present a first-step simulation study to assess the effects of applying different weighting schemes to tracking data to recover the ”true” spatial distribution.

I believe this is an area requiring much more future research and very careful consideration by researchers. The effects on conclusions aren’t always obvious, and without an understanding of species life history or of how data were collected, can easily mislead. Tracking data increasingly are collected in shared repositories (www.movebank.org;

www.iobis.org; www.obisseamap.org) and will be accessible by many researchers who either have little experience with tracking data in general, or little experience with the species tracked. Biologists collect tracking data, but collaborations should be made with statisticians in analysing them. These are not easy datasets and improper attention to track duration distributions is common in marine tracking studies. As well, broad conclusions are sometimes drawn from tracking studies that last for only short durations. I attempted to carefully integrate time with space in my dissertation and hope that future work will be spent on simulating the effects of variable tracking durations on ecological conclusions.

3) Data accuracy

The data I analysed were modeled daily location data. Raw geolocation and ARGOS data were processed with state-space models (Jonsen et al. 2003, Jonsen et al. 2005), allowing direct incorporation of position error and providing robust location estimates comparable across taxa and tagging technologies. Model output includes a single average position estimate per day per usable track and 2000 Markov chain Monte Carlo (MCMC) estimates for each location. For each individual, I analyzed the mean track of all MCMC estimates; the full MCMC dataset was unavailable. Therefore, I could not incorporate estimated location error for each track into my analysis. Additionally, how to incorporate error into 2-dimensional analysis is not straightforward. Ideally, I would have classified every MCMC location as in or outside of an EEZ, and performed my analysis on the entire dataset. Ideally, I would have bootstrapped kernel density estimates for each individual from the entire 2,000 MCMC tracks estimated for each individual. It is assumed that these estimates would be similar to the kernel density distributions calculated for the mean tracks. Unfortunately, it is likely that only mean tracks will be deposited in tracking databases. The error-structure available from the state-space modeling approach taken in Block et al. (2011) will be unavailable to other researchers.

4) Sample size of individuals

A criticism of inferences made from marine tracking studies is that few individuals are tracked relative to the population's size, and often only for short periods of time. Obtaining meaningful sample sizes is a general challenge of ecological studies, and especially so for research on large animals. TOPP included a number of species that are commercially harvested. The greatest number of tags were deployed on Pacific bluefin tuna—655. Meaningful datasets were obtained from half of these, and most of those tracks were less than 9 months long. Tracks often ended because of harvest, not tag failure. The scale of the TOPP effort was already impressive both in terms of cost and labor. Larger sample sizes are desirable, but would have been difficult to obtain. A larger statistical challenge was dealing with imbalanced sample sizes across time periods of interest (years, seasons, etc) for many species. Due to unpredictability in tag attenuation, loss, and animal harvest, it was also difficult to obtain balanced datasets across time periods of interest (years, seasons, etc.) for most species.

For this dataset, I took efforts to quantify the effects of sample size on my conclusions. Based upon my bootstrap analysis, larger datasets are needed for seabirds and trans-Pacific migrant bluefin tuna to increase the precision and accuracy of monthly population area estimates. White shark population distribution is likely to be greatly underestimated from June through September. Confidence intervals were large around EEZ probability estimates for species with small sample sizes. For species with large enough sample sizes, I evaluated inter-annual variability in EEZ use predictions. I would have liked to evaluate inter-annual variability in species overlap statistics. Unfortunately, only two years of data were available for black-footed albatross and sooty shearwaters (and shearwater datasets were highly unbalanced across years). More tracking data is needed to extend the species overlap analysis. For many species, sample sizes were too small or unbalanced to have the power to discern differences among years.

5) Deployment schedules

Timing of tag deployments was multi-modal and/or inconsistent across years for some species. For species that are tagged in coincidence with fisheries or by baiting, there is an initial bias of calculated space-use toward the tagging location. In exploring my data, I saw large effects of multi-modal deployment schedules (high density around tagging areas during multiple times of the year). This was especially a problem for my EEZ analysis, in which I was calculating daily probability of space use. The generalized additive mixed effects modeling approach (Wood, 2006) used to analyze temporal relationships with EEZs, and the specific covariates considered, accounted for many sampling imbalances and deployment effects unique to tracking datasets. More work should be done to attribute variability in home range size to to separate components due to seasonal and inter-annual variability, choice of bandwidth, date of deployment, and individual variability in movement behaviors. This could also be done using a modeling approach.

6) The state-space modeled dataset

The state-space model fitted to the raw tag data did not include a land-mask. This was a large problem for me when calculating probability of EEZ use. Although the modeled dataset had been previously quality-controlled, land locations (and many other highly erroneous locations, for example, white sharks in India, or albatrosses north of the north pole) remained in the final modeled dataset. I reviewed every individual track (over 1700) to remove obviously erroneous positions (automated algorithms sometimes prevented me from finding other errors—I found a visual review of each track to be the most thorough way to spot errors). I considered positions on land (for fully aquatic species) to be within the EEZ of the country in which the location fell. However, a better approach would have been to explicitly prevent any modeled location (ever), from falling on land within the state-space model. It would not be pragmatic to quality control in this way for all MCMC tracks, and I fear that many of them would also include many erroneous locations.

7) Sharing knowledge

Coordinating research efforts across many universities, researchers, countries, and post-doctoral researchers and graduate students is difficult. Memorandums of understanding written at the outset can help clear confusions that may arise due to sharing of data. The dissemination of MOUs among entire research teams would unite researchers within a common framework. Effective procedures for documenting and sharing institutional knowledge should be established prior to embarking upon a long-term multi-lateral research project. For multi-species, multi-lab projects such as TOPP, syntheses across species rely very much on past individual experiences and knowledge. Many post-doctoral researchers and graduate students completed their work part of the way through the TOPP project and in some cases knowledge about dataset nuances is lost.

Bibliography

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., and Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31(1):140–160.

Agardy, T., Sciara, G. N. d., and Christie, P. (2011). Mind the gap Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Marine Policy*, 35(2):226–232.

Agnew, D. J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J. R., and Pitcher, T. J. (2009). Estimating the Worldwide Extent of Illegal Fishing. *PLoS ONE*, 4(2):e4570.

Akaike, H. (1974). A new look at the statistical model identification. *Automatic Control*, 19(6):716–723.

Alerstam, T. and Hedenstrom, A. (2003). Longdistance migration: evolution and determinants. *Oikos*.

Amstrup, S., McDonald, T., and Durner, G. (2004). Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin*, 32(3):661–679.

Anderson, O., Small, C., Croxall, J., Dunn, E., Sullivan, B., Yates, O., and Black, A. (2011). Global seabird bycatch in longline fisheries. *Endangered Species Research*, 14(2):91–106.

Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., McClanahan, T. R., and Russ, G. R. (2010). Marine Reserves Special Feature: Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences*, 107(43):18256–18261.

Bailey, H., Mate, B., Palacios, D., Irvine, L., Bograd, S., and Costa, D. (2010). Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, 10:93–106.

Batten, S. D., Hyrenbach, K. D., Sydeman, W. J., Morgan, K. H., Henry, M. F., Yen, P. P. Y., and Welch, D. W. (2006). Characterising meso-marine ecosystems of the North Pacific. *Deep-Sea Research Part II-Topical Studies In Oceanography*, 53(3-4):270–290.

Bauer, S., Barta, Z., Ens, B. J., Hays, G. C., McNamara, J. M., and Klaassen, M. (2009). Animal migration: linking models and data beyond taxonomic limits. *Biology Letters*, 5(4):433–435.

Baum, J. K. (2003). Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science*, 299(5605):389–392.

Bayliff, W. (1993). Growth and age composition of northern bluefin tuna, *Thunnus thynnus*, caught in the eastern Pacific Ocean, as estimated from length-frequency data. *Inter-American Tropical Tuna Commission Bulletin*, 20:503–540.

Benson, S. R., Eguchi, T., Foley, D. G., Forney, K. A., Bailey, H., Hitipeuw, C., Samber, B. P., Tapilatu, R. F., Rei, V., Ramohia, P., Pita, J., and Dutton, P. H. (2011). Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere*, 2(7):art84.

BirdLife International (2004). Tracking Ocean Wanders (PDF, 5 MB). pages 1–116.

Block, B., Costa, D., Boehlert, G., and Kochevar, R. (2003). Revealing pelagic habitat use: the Tagging of Pacific Pelagics program. *Oceanologica Acta*, 25(5):255–266.

Block, B., Finnerty, J., Stewart, A., and Kidd, J. (1993). Evolution of Endothermy in Fish - Mapping Physiological Traits on a Molecular Phylogeny. *Science*, 260(5105):210–214.

Block, B., Teo, S., Walli, A., Boustany, A., Stokesbury, M., Farwell, C., Weng, K., Dewar, H., and Williams, T. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature*, 434(7037):1121–1127.

Block, B. A. (2005). Physiological Ecology in the 21st Century: Advancements in Biologging Science. *Integrative And Comparative Biology*, 45(2):305–320.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A.-L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., Henry, R. W., and Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475(7354):86–90.

Bograd, S., Foley, D., Schwing, F., Wilson, C., Laurs, R., Polovina, J., Howell, E., and Brainard, R. (2004). On the seasonal and interannual migrations of the transition zone chlorophyll front. *Geophysical Research Letters*, 31(17):L17204.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., and White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3):127–135.

Bonnel, M. L. and Selander, R. K. (1974). Elephant seals: genetic variation and near extinction. *Science*, 184(4139):908–909.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. (2006a). Effects of sampling regime on the mean and variance of home range size estimates. *Journal Of Animal Ecology*, 75:1393–1405.

Börger, L., Franconi, N., Ferretti, F., and Meschi, F. (2006b). An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist*, 168:471–47185.

Botev, Z. I., Grotowski, J. F., and Kroese, D. P. (2010). Kernel density estimation via diffusion. *The Annals of Statistics*, 38(5):2916–2957.

Boustany, A. M., Matteson, R., Castleton, M., Farwell, C., and Block, B. A. (2010). Movements of Pacific bluefin tuna (*Thunnus orientalis*) in the Eastern North Pacific revealed with archival tags. *Progress In Oceanography*, 86:94–104.

Bowen, B. W., Abreu-Grobois, F. A., Balazs, G. H., Kamezaki, N., Limpus, C. J., and Ferl, R. J. (1995). Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proceedings Of The National Academy Of Sciences*, 92(9):3731–3734.

Bowlin, M. S., Bisson, I. A., Shamoun-Baranes, J., Reichard, J. D., Sapir, N., Marra, P. P., Kunz, T. H., Wilcove, D. S., Hedenstrom, A., Guglielmo, C. G., Akesson, S., Ramenofsky, M., and Wikelski, M. (2010). Grand challenges in migration biology. *Integrative And Comparative Biology*, 50(3):261–279.

Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D., and Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (Halichoerus grypus) revealed by state-space analysis. *Ecology*, 90(11):3209–3221.

Briggs, K. and Chu, E. (1986). Sooty shearwaters off California - distribution, abundance and habitat Use. *Condor*, 88(3):355–364.

Brodeur, R., McKinnell, S., Nagasawa, K., Pearcy, W., Radchenko, V., and Takagi, S. (1999). Epipelagic nekton of the North Pacific Subarctic and Transition Zones. In *Progress in Oceanography*, pages 365–397. NMFS, Alaska Fisheries Sci Ctr, Seattle, WA 98115 USA.

Bunnefeld, N., Boerger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., and Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal Of Animal Ecology*, 80(2):466–476.

Burt, W. H. (1943). Territoriality and Home Range Concepts as Applied to Mammals. *Journal Of Mammalogy*, 24(3):346–352.

Butchart, S. H. M., Stattersfield, A. J., Bennun, L. A., Shutes, S. M., Akçakaya, H. R., Baillie, J. E. M., Stuart, S. N., Hilton-Taylor, C., and Mace, G. M. (2004). Measuring global trends in the status of biodiversity: Red List indices for birds. *PLoS Biology*, 2(12):e383.

Calambokidis, J., Barlow, J., FORD, J. K. B., Chandler, T. E., and Douglas, A. B. (2009). Insights into the population structure of blue whales in the Eastern North Pacific from recent sightings and photographic identification. *Marine Mammal Science*, 25(4):816–832.

Calambokidis, J., Steiger, G., Ellifrit, D., Troutman, B., and Bowlby, C. (2004). Distribution and abundance of humpback whales (Megaptera novaeangliae) and other marine mammals off the northern Washington coast. *Fishery Bulletin*, 102(4):563–580.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197(3-4):516–519.

Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-M., Dimech, M., Falcón, J. M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P. J., Stobart, B., Vandeperre, F., Valle, C., and Planes, S. (2008). Marine reserves: size and age do matter. *Ecology Letters*, 11(5):481–489.

CMS (1979). Convention on the Conservation of Migratory Species of Wild Animals. pages 1–99.

Compagno, L. (2002). Sharks of the World: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). Food and Agriculture Organization of the United Nations, Rome.

Copello, S. and Quintana, F. (2009). Spatio-temporal overlap between the at-sea distribution of Southern Giant Petrels and fisheries at the Patagonian Shelf. *Polar Biology*, 32(8):1211–1220.

Corrigan, C. and Kershaw, F. (2008). Working Toward High Seas Marine Protected Areas. Technical report, Cambridge, U.K.

Costa, D. (1993). The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposia of the Zoological Society of London*, 66:293–314.

Costello, M., Cheung, A., and de Hauwere, N. (2010). Surface Area and the Seabed Area, Volume, Depth, Slope, and Topographic Variation for the World's Seas, Oceans, and Countries. *Environmental Science & Technology*, 44(23):8821–8828.

Cressey, D. (2011). Uncertain sanctuary. *Nature*, 480:166–167.

Croll, D. A., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R., and Tershy, B. R. (2005). From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, 289:117–130.

Crowley, P. (1992). Resampling Methods for Computation-Intensive Data-Analysis in Ecology and Evolution. *Annual Review Of Ecology And Systematics*, 23:405–447.

Croxall, J. P., Silk, J. R. D., Phillips, R. A., Afanasyev, V., and Briggs, D. R. (2005). Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science*, 307(5707):249–250.

Cullis-Suzuki, S. and Pauly, D. (2010). Failing the high seas: A global evaluation of regional fisheries management organizations. *Marine Policy*, 34(5):1036–1042.

Darwin, C. R. (1872). *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London, 6th edition.

Davies, T. J., Purvis, A., and Gittleman, J. L. (2009). Quaternary Climate Change and the Geographic Ranges of Mammals. *The American Naturalist*, 174(3):297–307.

Dingle, H. (2006). Animal migration: is there a common migratory syndrome? *Journal of Ornithology*, 147(2):212–220.

Dingle, H. and Drake, V. A. (2007). What is migration? *BioScience*, 57(2):113–121.

Domeier, M., Kiefer, D., Nasby-Lucas, N., Wagschal, A., and O'Brien, F. (2005). Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. *Fishery Bulletin*, 103(2):292–306.

Du Toit, J. T. (2010). Considerations of scale in biodiversity conservation. *Animal Conservation*, 13(3):229–236.

Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martinez, J., Musick, J. A., Soldo, A., Stevens, J. D., and Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation-Marine And Freshwater Ecosystems*, 18(5):459–482.

Duong, T. (2011). ks: Kernel smoothing. *R package version 1.8.2.*

Elton, C. S. (1927). *Animal Ecology.* Macmillan Co., New York.

Estes, J. A. and Palmisano, J. F. (1974). Sea otters: their role in structuring nearshore communities. *Science*, 185(4156):1058–1060.

FAO (2010). *State of World Fisheries and Aquaculture, 2010.* Food & Agriculture Org, Rome.

Fauchald, P. and Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern. *Oecologia*, 149(3):383–395.

Fieberg, J. and Kochanny, C. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal Of Wildlife Management*, 69(4):1346–1359.

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., Bustamante, R., Possingham, H. P., and Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends In Ecology & Evolution*, 24(7):360–369.

Gillespie, R. G., Baldwin, B. G., Waters, J. M., Fraser, C. I., Nikula, R., and Roderick, G. K. (2012). Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution*, 27(1):47–56.

Gitzen, R. A., Millspaugh, J. J., and Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal Of Wildlife Management*, 70(5):1334–1344.

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., Oleson, E. M., Schorr, G., and Shadwick, R. E. (2008). Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *Journal Of Experimental Biology*, 211(23):3712–3719.

Halpern, B. S., Lester, S. E., and Kellner, J. B. (2009). Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation*, 36(4):268–276.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., and Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319(5865):948–952.

Hastie, T. J. and Tibshirani, R. J. (1990). *Generalized Additive Models*. Monographs on Statistics & Applied Probability. Chapman and Hall/CRC, London, 1 edition.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., and MacDonald, D. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with leastsquares crossvalidation. *The Journal of Animal Ecology*, 74(3):455–463.

Hobday, A. J., Hartog, J. R., Spillman, C. M., Alves, O., and Hilborn, R. (2011). Seasonal forecasting of tuna habitat for dynamic spatial management. *Canadian Journal Of Fisheries And Aquatic Sciences*, 68(5):898–911.

Hobday, A. J., Hartog, J. R., TIMMISS, T., and FIELDING, J. Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery. *Fisheries Oceanography*, 19(3):243–253.

Holland, K. N., Kajiura, S., Itano, D., and Sibert, J. (2001). Tagging techniques can elucidate the biology and exploitation of aggregated pelagic species. *American Fisheries Society Symposium*, pages 211–218.

Hooker, S., Cañadas, A., Hyrenbach, K., Corrigan, C., Polovina, J., and Reeves, R. (2011). Making protected area networks effective for marine top predators. *Endangered Species Research*, 13(3):203–218.

Hooker, S. K. and Gerber, L. R. (2004). Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna. *BioScience*, 54(1):27–39.

Howell, E. A., Kobayashi, D. R., Parker, D. M., Balazs, G. H., and Polovina, J. J. (2008). TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endangered Species Research*, 5(2-3):267–278.

Huang, H.-W. and Yeh, Y.-M. (2011). Impact of Taiwanese distant water longline fisheries on the Pacific seabirds: finding hotspots on the high seas. *Animal Conservation*, 14(5):562–574.

Huang, S., Meng, S. X., and Yang, Y. (2009). Assessing the goodness of fit of forest models estimated by nonlinear mixed-model methods. *Canadian Journal of Forest Research*, 39(12):2418–2436.

Hyrenbach, K., Fernandez, P., and Anderson, D. (2002). Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series*, 233:283–301.

Hyrenbach, K., Forney, K., and Dayton, P. (2000). Marine protected areas and ocean basin management. *Aquatic Conservation-Marine And Freshwater Ecosystems*, 10(6):437–458.

ISC (2008). Report of the Pacific bluefin tuna working group workshop. Technical report.

Jonsen, I. D., Flemming, J. M., and Myers, R. A. (2005). Robust state-space modeling of animal movement data. *Ecology*, 86(11):2874–2880.

Jonsen, I. D., Myers, R. A., and James, M. C. (2007). Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, 337:255–264.

Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., van Sommeran, S. R., Fritz-Cope, C., Brown, A. C., Klimley, A. P., and Block, B. A. (2010). Philopatry and migration of Pacific white sharks. *Proceedings Of The Royal Society B-Biological Sciences*, 277(1682):679–688.

Kaplan, D., Chassot, E., Gruss, A., and Fonteneau, A. (2010). Pelagic MPAs: The devil is in the details. *Trends In Ecology & Evolution*, 25(2):62–63.

Kappes, M. A., Shaffer, S. A., Tremblay, Y., Foley, D. G., Palacios, D. M., Robinson, P. W., Bograd, S. J., and Costa, D. P. (2010). Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress In Oceanography*, 86(1-2):246–260.

Kareiva, P. and Shigesada, N. (1983). Analyzing insect movement as a correlated random-walk. *Oecologia*, 56(2-3):234–238.

Kelleher, K. (2005). Discards in the world's marine fisheries: an update. Technical report, Rome.

Kern, J., McDonald, T., Amstrup, S., Durner, G., and Erickson, W. (2003). Using the bootstrap and fast Fourier transform to estimate confidence intervals of 2D kernel densities. *Environmental and Ecological Statistics*, 10(4):405–418.

Kitagawa, T., Boustany, A. M., Farwell, C. J., Williams, T. D., Castleton, M. R., and Block, B. A. (2007). Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. *Fisheries Oceanography*, 16(5):409–421.

Kölzsch, A. and Blasius, B. (2008). Theoretical approaches to bird migration. *The European Physical Journal-Special Topics*, 157(1):191–208.

Kooyman, G. (2007). Animal-borne instrumentation systems and the animals that bear them: Then (1939) and now (2007). *Marine Technology Society Journal*, 41(4):6–8.

Kooyman, G. L. (2004). Genesis and evolution of bio-logging devices: 1963–2002. *Memoirs of National Institute of Polar Research*, 58:15–22.

Kopp, M., Peter, H., Mustafa, O., Lisovski, S., Ritz, M., Phillips, R., and Hahn, S. (2011). South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Marine Ecology Progress Series*, 435:263–267.

Kuhn, C. (2006). *Measuring At Sea Feeding to Understand the Foraging Behavior of Pinnipeds*. PhD thesis, University of California, Santa Cruz.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. Methuen, London.

Lascelles, B., Langham, G., and Ronconi, R. (2012). From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe, *In press*. *Biological Conservation*.

Laver, P. N. and Kelly, M. J. (2008). A Critical Review of Home Range Studies. *Journal Of Wildlife Management*, 72(1):290–298.

Le Boeuf, B., Crocker, D., Costa, D., Blackwell, S., Webb, P., and Houser, D. (2000). Foraging ecology of northern elephant seals. *Ecological Monographs*, 70(3):353–382.

Le Boeuf, B. J. and Laws, R. M., editors (1994). *Elephant seals: population ecology, behavior, and physiology*. University of California Press.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airame, S., and Warner, R. R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, 384:33–46.

Lewison, R. L., Soykan, C. U., and Franklin, J. (2009). Mapping the bycatch seascape: multispecies and multi-scale spatial patterns of fisheries bycatch. *Ecological Applications*, 19(4):920–930.

Lichti, N. I. and Swihart, R. K. (2011). Estimating utilization distributions with kernel versus local convex hull methods. *Journal of Wildlife Management*, 75(2):413–422.

Loader, C. (1999). Bandwidth selection: Classical or plug-in? *Annals of Statistics*, 27(2):415–438.

Lotze, H. K. and Worm, B. (2009). Historical baselines for large marine animals. *Trends In Ecology & Evolution*, 24(5):254–262.

Matthiopoulos, J. (2003). Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos*, 102(2):367–377.

Miller, T. J. and Skalski, J. R. (2006). Estimation of seabird bycatch for North Pacific longline vessels using design- and model-based methods. *Canadian Journal Of Fisheries And Aquatic Sciences*, 63(8):1878–1889.

Mills, C. and Carlton, J. (1998). Rationale for a system of international reserves for the open ocean. *Conservation Biology*, 12(1):244–247.

Milner-Gulland, E. J., John M Fryxell, P., and Sinclair, A. R. E. (2011). *Animal Migration: A synthesis*. Oxford Univ Press.

Mora, C., Myers, R. A., Coll, M., Libralato, S., Pitcher, T. J., Sumaila, R. U., Zeller, D., Watson, R., Gaston, K. J., and Worm, B. (2009). Management Effectiveness of the World's Marine Fisheries. *PLoS Biology*, 7(6):e1000131.

Mora, C. and Sale, P. (2011). Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series*, 434:251–266.

Myers, N., Mittermeier, R., Mittermeier, C., Da Fonseca, G., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772):853–858.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. (2007). Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. *Science*, 315(5820):1846–1850.

Myers, R. A. and Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423(6937):280–283.

Nicholls, D., Murray, M., Butcher, E., and Moors, P. (2000). Time spent in exclusive economic zones of southern oceans by non-breeding wandering albatrosses (*Diomedea* spp.): Implications for national responsibilities for conservation. *Emu*, 100:318–323.

Nielsen, J. L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M., and Sibert, J., editors (2010). *Tagging and Tracking of Marine Animals with Electronic Devices (Reviews: Methods and Technologies in Fish Biology and Fisheries)*. Springer, softcover reprint of hardcover 1st ed. 2009 edition.

Oliver, J. (2004). IUCN/WCPA/WWF High Seas Marine Protected Areas Project Steering Committee. Technical report.

Orton, L. and Brodie, P. (1987). Engulfing Mechanics of Fin Whales. *Canadian Journal Of Zoology-Revue Canadienne De Zoologie*, 65(12):2898–2907.

Pauly, D. (1998). Fishing Down Marine Food Webs. *Science*, 279(5352):860–863.

Peckham, S. H., Maldonado Diaz, D., Walli, A., Ruiz, G., Crowder, L. B., and Nichols, W. J. (2007). Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS ONE*, 2(10):e1041.

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., and Bennett, V. J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*, 86(9):2386–2396.

Polidoro, B. A., Livingstone, S. R., Carpenter, K. E., Hutchinson, B., Mast, R. B., Pilcher, N., de Mitcheson, Y. S., and Valenti, S. (2008). Status of the World's Marine Species. In Vie, J.-C., Hilton-Taylor, C., and Stuart, S. N., editors, *The 2008 Review of the IUCN Red List of Threatened Species*, pages 1–12. IUCN, Gland, Switzerland.

Polovina, J., Balazs, G., Howell, E., Parker, D., Seki, M., and Dutton, P. (2004). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography*, 13(1):36–51.

Polovina, J., Howell, E., Kobayashi, D., and Seki, M. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress In Oceanography*, 49:469–483.

Polovina, J. J., Kobayashi, D. R., Parker, D. M., Seki, M. P., and Balazs, G. H. (2000). Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997-1998. *Fisheries Oceanography*, 9(1):71–82.

Powell, R. (2000). Animal home ranges and territories and home range estimators. In Boitani, L. and Fuller, T., editors, *Research techniques in animal ecology: controversies and consequences*, pages 65–110. Columbia Univ. Press, New York.

Preti, A., Soykan, C. U., Dewar, H., Wells, R. J. D., Spear, N., and Kohin, S. (2012). Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current. *Environmental Biology Of Fishes*.

Pyle, P., Anderson, S. D., and Ainley, D. G. (1996). Trends in white shark predation at the South Farallon Islands, 1968–1993. In Klimley, A. P., editor, *Great white sharks: the biology of Carcharodon carcharias*, pages 375–379. Academic Press, Inc.

R Development Core Team (2012). R: A language and environment for statistical computing.

Read, A. and Wade, P. (2000). Status of marine mammals in the United States. *Conservation Biology*, 14(4):929–940.

Reeves, R. R., Smith, T., Josephson, E., Clapham, P., and Woolmer, G. (2004). Historical observations of humpback and blue whales in the North Atlantic Ocean: clues to migratory routes and possibly additional feeding grounds. *Marine Mammal Science*, 20(4):774–786.

Robinson, P. W., Simmons, S. E., Crocker, D. E., and Costa, D. P. (2010). Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal. *Journal Of Animal Ecology*, 79(6):1146–1156.

Robinson, R., Crick, H., Learmonth, J., Maclean, I., Thomas, C., Bairlein, F., Forchhammer, M., Francis, C., Gill, J., Godley, B., Harwood, J., Hays, G., Huntley, B., Hutson, A., Pierce, G., Rehfisch, M., Sims, D., Santos, B., Sparks, T., Stroud, D., and Visser, M. (2009). Travelling through a warming world: climate change and migratory species. *Endangered Species Research*, 7:87–99.

Roden, G. I. (1991). Subarctic-subtropical transition zone of the North Pacific: Large-scale aspects and mesoscale structure. *US National Marine Fisheries Service, NOAA Technical Report*, 105:1–38.

Russ, G., Alcala, A., Maypa, A., Calumpong, H., and White, A. (2004). Marine reserve benefits local fisheries. *BioScience*, 14(2):597–606.

Russ, G. R. and Zeller, D. C. (2003). From *mare liberum* to *mare reservarum*. *Marine Policy*, 27(1):75–78.

Sala, E. and Knowlton, N. (2006). Global Marine Biodiversity Trends. *Annual Review of Environment and Resources*, 31(1):93–122.

Santidrián Tomillo, P., Vélez, E., Reina, R. D., Piedra, R., Paladinos, F. V., and Spotila, J. R. (2007). Reassessment of the leatherback turtle (*Dermochelys coriacea*) nesting population at Parque Nacional Marino Las Baulas, Costa Rica: Effects of conservation efforts. *Chelonian Conservation and Biology*, 6(1):54–62.

Sarti Martinez, A. (2011). *Dermochelys coriacea. IUCN Red List of Threatened Species, v 2011.1.*

Schaefer, K. M., Fuller, D. W., and Block, B. A. (2011). Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. *Fisheries Research*, 112(1-2):22–37.

Schnute, J. T., Boers, N., Haigh, R., and Couture-Beil, A. (2010). PBSmapping: Mapping Fisheries Data and Spatial Analysis Tools. *R package version 2.61.9.*

Seaman, D., Millspaugh, J., Kernohan, B., Brundige, G., Raedeke, K., and Gitzen, R. (1999). Effects of sample size on kernel home range estimates. *Journal Of Wildlife Management*, 63(2):739–747.

Seaman, D. and Powell, R. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77(7):2075–2085.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., and Hiraldo, F. (2008). Top Predators as Conservation Tools: Ecological Rationale, Assumptions, and Efficacy. *Annual Review Of Ecology Evolution And Systematics*, 39:1–19.

Shaffer, S. A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D. R., Sagar, P. M., Moller, H., Taylor, G. A., Foley, D. G., Block, B. A., and Costa, D. P. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings Of The National Academy Of Sciences*, 103(34):12799–12802.

Sheather, S. and Jones, M. (1991). A Reliable Data-Based Bandwidth Selection Method for Kernel Density-Estimation. *Journal of the Royal Statistical Society Series B-Methodological*, 53(3):683–690.

Shuter, J. L., Broderick, A. C., Agnew, D. J., Jonzen, N., Godley, B. J., Milner-Gulland, E. J., and Thirgood, S. (2011). Conservation and management of migratory species. In *Animal Migration: A synthesis*. Oxford Univ Press.

Silverman, B. W. (1986). *Density estimation for statistics and data analysis*. Monographs on Statistics and Applied Probability. Chapman & Hall, New York.

Simmons, S. E., Crocker, D. E., Hassrick, J. L., Kuhn, C. E., Robinson, P. W., Tremblay, Y., and Costa, D. P. (2010). Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*. *Endangered Species Research*, 10:233–243.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. Z., Brierley, A. S., Hindell, M. A., Morritt, D., Musyl, M. K., Righton, D., Shepard, E. L. C., Wearmouth, V. J., Wilson, R. P., Witt, M. J., and Metcalfe, J. D. (2008). Scaling laws of marine predator search behaviour. *Nature*, 451(7182):1098–1102.

Southall, E. J., Sims, D. W., Witt, M. J., and Metcalfe, J. D. (2006). Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the north-east Atlantic. *Biological Conservation*, 132(1):33–39.

Spalding, M., Wood, L., Fitzgerald, C., and Gjerde, K. (2010). The 10% target: where do we stand. In Toropova, C., Meliane, I., Laffoley, D., Matthews, E., and Spalding, M., editors, *Global Ocean Protection: Status and Future Possibilities*. Brest, France: Agence des aires marines protegees, Gland, Switzerland, Washington, DC and New York, USA: IUCN WCPA, Cambridge, UK : UNEP-WCMC, Arlington, USA: TNC, Tokyo, Japan: UNU, New York, USA: WCS. 96pp.

Spotila, J. R. (2004). *Sea turtles: A complete guide to their biology, behavior, and conservation*. Johns Hopkins University Press.

Stewart, B. and Delong, R. (1995). Double migrations of the northern elephant seal, *Mirounga angustirostris*. *Journal Of Mammalogy*, 76(1):196–205.

Strandberg, R. and Alerstam, T. (2007). The strategy of fly-and-forage migration, illustrated for the osprey (textitPandion haliaetus). *Behavioral Ecology and Sociobiology*, 61(12):1865–1875.

Sumaila, U. R., Zeller, D., Watson, R., Alder, J., and Pauly, D. (2007). Potential costs and benefits of marine reserves in the high seas. *Marine Ecology Progress Series*, 345:305–310.

Sund, P. N., Blackburn, M., and Williams, F. (1981). *Tunas and their environment in the Pacific Ocean: a review*, volume 19 of *Oceanography and Marine Biology - An Annual Review*. Aberdeen University Press, Aberdeen.

Suryan, R. M., Dietrich, K. S., Melvin, E. F., Balogh, G. R., Sato, F., and Ozaki, K. (2007). Migratory routes of short-tailed albatrosses: Use of exclusive economic zones of North Pacific Rim countries and spatial overlap with commercial fisheries in Alaska. *Biological Conservation*, 137(3):450–460.

Trebilco, R., Halpern, B. S., Flemming, J. M., Field, C., Blanchard, W., and Worm, B. (2011). Mapping species richness and human impact drivers to inform global pelagic conservation prioritisation. *Biological Conservation*, 144(5):1758–1766.

Turchin, P. (1998). *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer, Associates, Inc.

UNCLOS (1982). United Nations Convention on the Law of the Sea. pages 1–202.

UNFSA (1995). United Nations Fish Stock Agreement. pages 1–40.

van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., and Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal Of Animal Ecology*, 80(4):771–785.

Van Winkle, W. (1975). Comparison of Several Probabilistic Home-Range Models. *Journal Of Wildlife Management*, 39(1):118–123.

Vögler, R., Beier, E., Ortega-Garcia, S., Santana-Hernández, H., and Valdez-Flores, J. J. (2012). Ecological patterns, distribution and population structure of Prionace glauca (Chondrichthyes: Carcharhinidae) in the tropical-subtropical transition zone of the north-eastern Pacific. *Marine Environmental Research*, 73(C):37–52.

Wakefield, E. D., Phillips, R. A., and Matthiopoulos, J. (2009). Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, 391:165–182.

Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Mortimer, J. A., Seminoff, J. A., Amorocho, D., Bjorndal, K. A., Bourjea, J., Bowen, B. W., Briseño Dueñas, R., Casale, P., Choudhury, B. C., Costa, A., Dutton, P. H., Fallabrino, A., Finkbeiner, E. M., Girard, A., Girondot, M., Hamann, M., Hurley, B. J., López-Mendilaharsu, M., Marcovaldi, M. A., Musick,

J. A., Nel, R., Pilcher, N. J., Troëng, S., Witherington, B., and Mast, R. B. (2011). Global conservation priorities for marine turtles. *PLoS ONE*, 6(9):e24510.

Walli, A., Teo, S. L. H., Boustany, A., Farwell, C. J., Williams, T., Dewar, H., Prince, E., and Block, B. A. (2009). Seasonal Movements, Aggregations and Diving Behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) Revealed with Archival Tags. *PLoS ONE*, 4(7):e6151.

Wand, M. and Jones, M. (1995). *Kernel smoothing.* Monographs on Statistics and Applied Probability. Chapman & Hall.

Warham, J. (1990). *The petrels: their ecology and breeding systems.* Academic Press.

Waugh, S. M., Filippi, D. P., Kirby, D. S., Abraham, E., and Walker, N. (2012). Ecological Risk Assessment for seabird interactions in Western and Central Pacific longline fisheries. *Marine Policy*, 36(4):933–946.

Weimerskirch, H., Barbraud, C., and Lys, P. (2000). Sex differences in parental investment and chick growth in Wandering Albatrosses: Fitness consequences. *Ecology*, 81(2):309–318.

Weise, M. J., Costa, D. P., and Kudela, R. M. (2006). Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. *Geophysical Research Letters*, 33(22).

Weise, M. J. and Harvey, J. T. (2008). Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management. *Marine Ecology Progress Series*, 373:157–172.

Weise, M. J., Harvey, J. T., and Costa, D. P. (2010). The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, 91(4):1004–1015.

Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A., and Block, B. A. (2007). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology*, 152(4):877–894.

Weng, K. C., Castilho, P. C., Morrissette, J. M., Landeira-Fernandez, A. M., Holts, D. B., Schallert, R. J., Goldman, K. J., and Block, B. A. (2005). Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science*, 310(5745):104–106.

Wilcove, D. S. and Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing? *PLoS Biology*, 6(7):1361–1364.

Wilson, R., Hooten, M., Strobel, B., and Shivik, J. (2010). Accounting for Individuals, Uncertainty, and Multiscale Clustering in Core Area Estimation. *Journal Of Wildlife Management*, 74(6):1343–1352.

Winship, A. J., Jorgensen, S. J., Shaffer, S. A., Jonsen, I. D., Robinson, P. W., Costa, D. P., and Block, B. A. (2011). State-space framework for estimating measurement error from double-tagging telemetry experiments. *Methods in Ecology and Evolution*, page In press.

Wood, L. J., Fish, L., Laughren, J., and Pauly, D. (2008). Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx*, 42(03).

Wood, S. (2006). *Generalized Additive Models: An Introduction with R (Chapman & Hall/CRC Texts in Statistical Science)*. Chapman and Hall/CRC, 1 edition.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., and Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800):787–790.

Worm, B. and Tittensor, D. P. (2011). Range contraction in large pelagic predators. *Proceedings of the National Academy of Sciences*, 108(29):11942–11947.

Worton, B. (1995). Using monte-carlo simulation to evaluate kernel-based home-range estimators. *Journal Of Wildlife Management*, 59(4):794–800.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70(1):164–168.

Young, L. C., Vanderlip, C., Duffy, D. C., Afanasyev, V., and Shaffer, S. A. (2009). Bringing Home the Trash: Do Colony-Based Differences in Foraging Distribution Lead to Increased Plastic Ingestion in Laysan Albatrosses? *PLoS ONE*, 4(10):e7623.