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ON THE FORMATION OF A CONSERVATION HOTSPOT FOR JUVENILE NORTH PACIFIC LOGGERHEAD SEA TURTLES (CARETTA CARETTA)

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ABSTRACT

ON THE FORMATION OF A CONSERVATION HOTSPOT FOR NORTH PACIFIC LOGGERHEAD SEA TURTLES (*CARETTA CARETTA*)

DANA K. WINGFIELD

This research examined the incorporation of highly productive regions within the marine system. I combined historical conservation literature, remotely sensed oceanography, ship based surveys, satellite tagged animals, and statistical models to explore an integrated approach to the identification of key oceanic regions that require incorporation into current marine conservation strategies.

In my first chapter, I undertook a literature review of the term "hotspot", one of the most common ways by which scientists ascribe conservation prioritization in the marine and terrestrial systems. My results showed that marine literature has identified important areas of biodiversity and productivity (i.e. high primary production that results in trophic linkages and species aggregations) are in need of protection from human threats. However, current non-governmental organizations focus primarily on biodiversity, thus missing important areas of productivity for marine conservation.

In my second chapter, I demonstrated how remotely sensed oceanography, ship-based surveys, and satellite tagged animals can help to identify the formation

of such a "productivity hotspot". Specifically, I examined the connection between physical forcing (surface winds and vertical Ekman upwelling), sea-surface temperature, primary production (chlorophyll-*a* concentrations), retentive features of fronts and dynamic height, and prey abundance (red crabs) in the spatial and temporal concentration of the critically endangered North Pacific juvenile loggerhead sea turtle (*Caretta caretta*) within its foraging habitat off the Pacific coast of Baja California.

Finally, in my third chapter, I identified habitat selection of loggerheads to better understand the species preference within suitable habitat. I sampled several environmental variables (depth, sea-surface temperature, and chlorophyll-*a*) within 'preferred' versus 'avoided' turtle habitat. Results from a generalized additive model showed the statistical importance of all three variables in the prediction of loggerhead presence within suitable habitat off of Baja California. I then incorporated prey distribution to fully explore the connection between a highly migratory species and its environment. These results show how knowledge of threatened and endangered species habitat use within a productivity hotspot can help to more efficiently identify and prioritize critical areas for conservation.

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INTRODUCTION

There is a widespread consensus that we are facing a global conservation crisis (Pimm et al 1995: Myers et al. 2000, Millenium Ecosystem Assessment 2005; Jackson 2008). Threats to species, species interactions, and the services provided by those interactions have been significantly elevated by human actions, and accelerating the wide scale loss of ecosystem functions and ecosystem services (Ceballos et al. 2005; Hooper et al. 2006). For this reason, conservation scientists have sought to restore and protect invaluable resources through conservation prioritization schemes.

One of the earliest ways by which to prioritize conservation was by Norman Myers. In 1988, Myers coined the term "biodiversity hotspots" to identify geographical regions of "exceptional concentrations of endemic species undergoing exceptional loss of habitat" (Myers 1988). The goal of Myers and colleagues was to pinpoint geographical areas – hotspots of biodiversity – that would protect the largest number of endangered species within a relatively small area yielding the highest return per dollar invested (Myers 1988, Myers et al 2000). Over the past twenty years, the term has evolved to symbolize how scientists identify and prioritize conservation efforts in the marine and terrestrial systems.

However, the fundamental differences in the processes that shape each ecosystem result in different threats and thus, conservation targets. The terrestrial system is dominated by habitat destruction and the risk of extinction; the marine system is most affected by over-exploitation of marine productivity, resulting in population declines. Important marine megafauna such as marine mammals, fishes, and sea turtles aggregate within areas of high primary production ocean (e.g. upwelling centers, fronts, and eddies), that serve to spatially and temporally concentrate forage species. Recent studies have documented the loss of ecologically important species within these hotspots of marine productivity (Schipper et al. 2008, Worm et al. 2003). Compared to coral reef systems, these areas are lower in biodiversity, but have greater fishing pressure. In fact, these highly productive areas hold immense economic importance, as they account for more than half the world's fisheries production (Valavanis et al. 2004).

The use of "biodiversity hotspots" as a strategy to counter species loss in the terrestrial system has worked well, as the goal closely matches its target to protect species from extinction. However, if the main focus in the marine system is the protection of over-exploited species, we must ask: how well do biodiversity hotspots match the target of halting population declines within the most heavily exploited regions of the ocean? Specifically, are we missing important areas in the ocean based on the current focus conservation prioritization, and if so, how do we define these areas in such a highly dynamic system?

For my dissertation, I examine these questions at three integral levels. In the first chapter, I present the results of a detailed meta-analysis on the use of the term "hotspot" in conservation literature since the inception of the term (Myers 1988). I then compare these findings to the conservation objectives of some of the most influential non-governmental organizations (NGOs) to show how important areas of productivity are currently being left out of marine conservation schemes. For example, Marine Protected Areas (MPAs) can be very effective in protecting coastal marine biodiversity; however the huge ranges of many pelagic species make the model used for coastal MPAs an unrealistic management tool. This is unfortunate, because pelagic species that make up 70 million tons/year of marine fisheries yields (Pauly et al. 2002), have been even more poorly managed and have experienced more severe declines than many coastal fisheries.

Areas of high productivity are expansive and ephemeral, and the comprehensive conservation of all productivity hotspots in the ocean is unrealistic. In response to the difficulty of forming expansive pelagic protected areas, some scientists, fishery managers, and conservation organizations have advocated Ecosystem Based Management (EBM) techniques, which offer a more holistic approach through the protection of trophic interactions (Pikitch et al. 2004; Crowder et al. 2008). These approaches must rely on an understanding of the physical and biological processes that concentrate pelagic species during key life history stages (i.e.breeding, juvenile feeding, etc.).

In chapter two, I seek to identify the trophic linkages in the distribution of one such pelagic species during its most population-sensitive life history stage

(Crouse et al. 1987) -- the North Pacific juvenile loggerhead sea turtle (*Caretta caretta*). Using remotely sensed satellite oceanography and ship based surveys, I identify the bottom-up processes that create complete relationship between physical forcing, primary production, prey species, and loggerhead movement, off the Pacific coast of Baja California, Mexico.

Finally, in chapter three I demonstrate an approach that combines two of the most common techniques in marine species habitat use (remotely sensed oceanography and satellite tagging capabilities), to statistically predict loggerhead presence based on key environmental parameters. In this way, it is possible to identify the most important areas within productive waters for a more efficient conservation management within marine productivity hotspots.

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CHAPTER 1: ARE WE MISSING IMPORTANT AREAS IN MARINECONSERVATION? REDEFINING CONSERVATION HOTSPOTS IN THE OCEAN

ABSTRACT

For over 20 years, scientists have used ‘hotspots’ to call attention to areas of high biological diversity threatened by human activity. The concept of biodiversity hotspots has helped guide development of conservation priorities in the terrestrial environment where the focus is often on extinction risk. But in marine systems, differences in processes, extinction, and threats require alternative approaches to setting priorities. Zones of high primary production in the ocean concentrate ecologically and economically important species; yet these areas often are not congruent with hotspots of marine biodiversity. Nonetheless, ‘productivity hotspots’ provide important ecosystem functions and services, and are the most heavily exploited regions of the ocean. We conducted a comprehensive review of the conservation hotspot literature and compared that to areas identified in conservation objectives of non-governmental organizations. Marine scientists recognize the importance of biodiversity and productivity for conservation, but few NGOs implement strategies based on productivity hotspots. We argue that identifying and protecting areas of high primary productivity, coupled with biodiversity, is necessary to efficiently allocate limited marine conservation resources.

INTRODUCTION

Threats to global biodiversity have been significantly elevated by human actions, and extinctions are accelerating (Pimm et al 1995: Millenium Ecosystem Assessment 2005; Underwood et al. 2008). Extinctions, range contractions, and population declines have all led to wide scale loss of ecosystem functions and ecosystem services (Ceballos et al. 2005; Hooper et al. 2006). Thus, for aesthetic, moral and, economic reasons extensive efforts are underway to protect biodiversity (Myers et al. 2000; Millenium Ecosystem Assessment 2005; Brooks et al. 2006; and others).

Because conservation dollars are scarce, biologists have sought to identify conservation efforts that maximize return on investment. One of the earliest and most influential efforts was the 'hotspots' approach (Myers 1988), identifying geographic regions of "exceptional concentrations of endemic species undergoing exceptional loss of habitat" (Myers 1988). Specifically, in order to be designated as a 'hotspot', criteria required that an area must contain > 0.5% of the world's total vascular plant species as endemics, and have lost at least 70% of its original habitat (Myers 1988; Myers et al 2000). The primary goal of the biodiversity hotspots approach was to identify the most at risk areas in the terrestrial system, where the greatest number of endemic species could be protected per conservation dollar invested (Myers 1988; Myers et al 2000; Myers 2003).

Since its inception twenty years ago, the original hotspot definition has evolved as researchers have expanded upon and revised the metrics. In practice, hotspots now describe a geographical area (terrestrial or marine) ranking highly in one or more of the following biological criteria: species richness, species endemism (range-rarity), number of rare or threatened species, complementarity, taxonomic distinctiveness, and degree of habitat loss (Reid 1998; Brummitt 2002; Possingham & Wilson 2005). Criticism of the hotspots approach has pointed to the lack of congruence between hotspots based on different biological criteria, and the difficulties in setting conservation priorities when different types of diversity hotspots do not overlap (Harcourt et al. 2000; Kareiva & Marvier 2003; Orme et al. 2005; Possingham & Wilson 2005). In its most general sense, conservation biologists use 'hotspots' as a value-laden term to call attention to important areas of biodiversity under imminent threat (Myers 1988; Prendegast 1993; Mittermeier et al. 1998; Reid 1998; Myers et al. 2000, 2003; Roberts et al. 2002; Karieva & Marvier 2003). The term has become so prevalent within academia, that nearly 1,000 articles have been published in conservation literature since Myers first coined the term in 1988 (Figure 1). Thus, after 20 years of use, 'hotspots' have become a fixture within conservation biology to guide global conservation efforts.

The focus on biodiversity in conservation planning has been appropriate for terrestrial systems, where reducing extinction risk has been the primary conservation strategy (Baillie et al. 2004; Bode et al. 2008). But anthropogenic extinction is less prevalent in marine systems (e.g. Dulvey et al. 2003) where humans are more likely to drive changes in food web structure and function

(Steele 1985, 1991; Cohen 1994; Carr et al. 2003). For this reason, it is logical that prioritization strategies developed for terrestrial systems may not be appropriate for marine systems. Nonetheless, 'hotspot' prioritization criteria are increasingly being applied to marine ecosystems. Because currently the use of biodiversity hotspots is one of the most influential prioritization frameworks, we examine whether this approach adequately encompasses potentially important regions for marine conservation. Specifically we: 1) review the inherent differences in biophysical processes between the two systems that should be considered in conservation prioritization, 2) review differences in how human activities alter biodiversity and ecosystem processes, functions and services in marine vs. terrestrial systems, 3) explore how academics have used the term in terrestrial and marine conservation publications to prioritize important areas for conservation, and 4) refer to the objectives of some of the most influential conservation organizations to examine whether productivity 'hotspots' should also be included as a marine conservation priority.

TERRESTRIAL AND MARINE PROCESSES

Biodiversity and Primary Production

There are fundamental differences in the spatial scale, variability, and degree of threat found in terrestrial and marine systems that effect the prioritization of areas for conservation (Steele 1985, 1991; Beddington et al. 1994; Cohen 1994; Levin 1994; Allison et al. 1998; Carr et al. 200; Shuring et al. 2006). Dynamic coupling between physical and biological processes in marine systems spread interactions over spatial and temporal scales much larger than those found in terrestrial systems (Hyrenbach et al. 2000). On land, high biodiversity is more geographically confined because the dominant primary producers on land are multicellular organisms that have developed specialized vascular systems and long life cycles (Tang 2008). These terrestrial plants turnover slowly causing species to aggregate within stable areas of high primary production. This spatial discreteness with limited dispersal in terrestrial systems leads to regions of both high productivity and diversity, (Carr et al. 2003; Hooker & Gerber 2004), including diversity in upper trophic levels (Hutchinson 1959; Rosenzweig 1995; Zhao et al. 2006). As a result, Richmond et al. (2007) and Gaston (2000) found that the global distribution of terrestrial biodiversity generally increases with net primary production. This coupling is advantageous; in protecting hotspots of species biodiversity, regions of high primary production are also included, protecting the ecosystem functions and services provided by each.

In contrast, the majority of marine primary production comes from non-vascular, unicellular organisms with short life spans and rapid turnover. Biological responses are more closely coupled to physical processes (Steele & Henderson 1994). While there are geographically predictable locations of high productivity and high diversity in the ocean (e.g. seamounts, reefs, upwelling regions, and intertidal zones), the lateral transport of energy, resources, and organisms leads to a patchier environment, complex migratory behaviors, and less clearly biogeographically defined habitats (Levin 1994; Carr et al. 2003; Lourie &

Vincent 2004). As a result, marine biodiversity occurs on much larger spatial, functional, and genetic scales (Palumbi et al. 2009). While oceanic areas of high productivity may have high biodiversity, the two are not necessarily congruent. Some of the most productive marine regions (e.g. the North Atlantic, Polar Seas) are relatively depauperate in species diversity (Leslie 2005; Schipper et al. 2008). Many highly productive/low diversity oceanographic features (upwelling sites, frontal gradients, eddies) form critical ecosystem linkages between trophic levels. Defined as "productivity hotspots" (Valavanis et al. 2004), these areas serve to spatially and temporally concentrate forage species (e.g. krill, pollock, and menhaden), and high abundances of economically important target species (e.g. tuna and billfishes), as well as threatened marine species (e.g. sea turtles, seabirds, sharks, and marine mammals), which creates the potential for bycatch in these highly valuable fisheries. Although productive areas such as upwelling regions account for only 0.1 percent of the ocean surface (Ryther 1969), they support up to 50 percent of the world's fisheries production (Valavanis et al. 2004). While they may lack the level of endemism, richness, or stability of marine biodiversity hotspots (see Roberts et al. 2002), these "productivity hotspots" are geographically distinct from important areas of high conservation value and intense exploitation by humans.

Human-induced Threats

Threats resulting from the interaction between human activities and ecosystem functions have greatly accelerated population declines in both systems

(Brooks et al. 2006; Worm et al. 2006). Habitat loss through deforestation and agricultural development has dominated the terrestrial system, producing rates of extinction 1000 times greater than pre-human levels (Pimm et al. 1995; IUCN 2007). In contrast, while several studies have shown the mass depletion through overharvest of pelagic sharks, billfish, and tunas (e.g. Myers & Worm 2003; Worm et al. 2005), and coastal species have been depleted by as much as 90% of historical values (e.g. Lotze et al. 2006; Jackson 2008), there have only been 10-16 global marine extinctions specifically attributed to anthropogenic impacts (Dulvy et al. 2003; Del Monte-Luna et al. 2007). To adequately address marine conservation concerns, regions of high productivity must also be included in conservation priorities.

Ecosystem Functions and Services

In both marine and terrestrial systems, the loss of these diverse and productive biota threatens a wide variety of irreplaceable ecosystem goods and services with an estimated worth of $33 trillion per year (IUCN 2007). Because anthropogenic threats to these resources will only intensify with growing population demand, it is critical to invest in their maintenance (Pimm et al. 1995; Myers et al. 2000; Carr et al. 2003; Lotze et al. 2006; Worm et al. 2006; Halpern et al. 2008; Jackson 2008; Palumbi et al. 2009). But human activities threaten marine vs. terrestrial ecosystems differently and thus there are differences in the efficacy of biodiversity vs. productivity hotspots to ameliorate these impacts. In marine systems direct exploitation by humans is the primary threat, while habitat destruction is the primary driver of extinction. Large scale fishing not only depletes target species, but can damage critical benthic habitats and reduce populations of non-target species taken as bycatch. Because of the overlap in biodiversity and primary production in the terrestrial system, the designation of biodiversity hotspots for important areas on land generally offers an umbrella of protection to the wide range of ecosystem functions and services. But because important areas of productivity are often decoupled from regions of high biodiversity, effective marine conservation must also include areas of high primary productivity as well as areas of high biological diversity (Table 1) (data from de Groot et al. 2002 and MEA 2005).

METHODS AND ANALYSES

We reviewed all academic peer-reviewed publications from 1988-2007 that use the term for the purposes of conservation (*[Biosis Previews and Web of Science; keywords: "hotspot" and/or "hot spot" and "conservation"]).* For consistency, book chapters, proceedings, and non-English journal articles were removed from our database. We acknowledge that this is not an all-inclusive review of all hotspot references, however we felt it was a comprehensive collection of publications through two highly used and widely accessible search engines.

We then compared the percentage of marine defined hotspots of biodiversity versus productivity with a published synthesis of global marine conservation planning cases by Leslie (2005), to determine how biodiversity and productivity have been incorporated into marine conservation organizations.

Lastly, we generated a map of the spatially summed mean global net primary productivity (NPP) from 1998-2007 using the SeaWiFS ocean color sensor (8-day, 9km resolution) and AVHRR Pathfinder sea surface temperature data (same resolution) as inputs to the Vertically Generalized Productivity Model (VGPM; Behrenfeld & Falkowski, 1997). We defined the upper 10% and 25% areas of NPP globally (referred to as "productivity hotspots"). These productivity hotspots are where economically and ecologically important species concentrate to form ecosystem linkages and provide valuable goods and services to human well-being. We then overlaid these results with the 2005 Conservation International boundaries for marine hot spots. We used standard GIS methods to determine the overlap between "productivity hotspots" and "biodiversity hotspots".

RESULTS

TERRESTRIAL VS. MARINE HOTSPOTS LITERATURE REVIEW

Over the past twenty years, the hotspots concept has been the subject of hundreds of academic publications, and has influenced conservation policy and on-the-ground conservation actions. In the process, "hotspots" has become a symbolic term to call attention to important areas under threat, and, although originally defined to prioritize biodiversity loss on land, it is increasingly used to identify important marine conservation areas (Roberts et al. 2002; Myers 2003).

However, because a focus on marine biodiversity alone may not protect the most important areas of the ocean, we compared how scientists ascribe biological importance (i.e. biodiversity vs. productivity) to the term 'hotspot' in each system. We evaluated all academic peer-reviewed publications from 1988-2007 that define hotspots for conservation and compare how the term is used to prioritize important areas within each system. *([Biosis Previews and Web of Science; keywords: 'hotspot'and/or 'hot spot' and 'conservation']).*

The use of the term 'hotspot' has increased steadily, at least through 2006, with over 85% of the 943 studies applied to the terrestrial systems (Fig. 1). Over 87% of these terrestrial articles used 'hotspot' to identify biodiversity under threat, with 63.1% using the original Myers definition (Myers 1988; Myers et al. 2003). In contrast, the fewer articles published on marine hotspots in the past 20 years defined important marine 'hotspots' in terms of both biodiversity and productivity (defined as species abundance and primary production). Fifty-four percent of articles defined hotspots of marine biodiversity, while 38.1% used the term to define areas of high productivity (Figure 2). The presence of productivity hotspots within marine literature shows that academics appear to be modifying the original definition of hotspots to match the different conservation needs within marine systems.

DISCUSSION

ARE WE INCORPORATING PRODUCTIVITY INTO MARINE CONSERVATION STRATEGIES?

Because academic analyses have often guided international and government conservation strategies, we determined whether the primary objectives of conservation organizations aligned with those identified by the scientific literature. Traditionally, terrestrial organizations have closely matched academic targets, as biodiversity loss has been the foremost priority in terrestrial conservation strategies (e.g. Conservation International's Biodiversity Hotspots, WWF-US's Global 2000, IUCN/WWF-International's Centers of Plant Diversity, TNC's Conservation Initiatives, and Birdlife's Endemic Bird Areas) (Myers et al. 2000; Mittermeier et al. 1998; Olsen and Dinerstein 1998; Davis et al. 1994; TNC 2008; Birdlife International 2008, respectively). Although terrestrial in origin, many of these well-known organizations have now expanded to incorporate marine programs into their conservation portfolios and prioritization schemes. A synthesis of marine conservation planning approaches by Leslie (2005) found that few organizations are prioritizing important marine areas by objectives other than biodiversity (Figure 3). While some organizations are incorporating additional criteria in their priority-setting process (e.g. environmental and ecological factors, stock recovery, and endangered species) a primary focus on biodiversity conservation may exclude important marine regions of high productivity. Thus, important regions of high productivity are likely missing from prominent non-governmental marine conservation schemes (James et al. 1999; Murdoch et al.

2007).

We examined one of the most well-funded and influential priority-setting conservation NGOs worldwide, Conservation International (CI). Using the Biodiversity Hotspot approach (Myers 1988; Mittermeier et al. 1999; Myers et al. 2000) as its foremost strategy in conservation planning, CI has generated over $750 million of funding for terrestrial and marine conservation (Myers 2003). We chose the CI Hotspots approach as an example because it is the leader in conservation prioritization schemes globally, and has been used extensively by prominent conservation foundations and international conservation efforts (e.g. Global Environment Facility, World Bank), and many threatened ecosystem functions and services are protected under terrestrial biodiversity hotspot regions (Table 2). Specifically, we questioned: how well do marine biodiversity hotspot priorities protect the areas of the ocean that are most threatened by human action?

We mapped Conservation International's marine hotspots of biodiversity with the areas of greatest Net Primary Production (NPP) to identify exactly how well important areas of biodiversity and productivity overlap in each system, and thus, how effective a terrestrial-developed conservation strategy works in the marine system. CI's marine biodiversity hotspots cover 26.4% of the world's oceans, and include 20.5% of the upper 25% of annual oceanic NPP (Figure 4). But our results show that there is a mismatch between marine biodiversity and productivity, as there are large areas of primary productivity that do not overlap with CI's biodiversity hotspots. Notably, the productivity hotspots of the North

Atlantic sea, as well as the South American, and southern African coasts are absent from the biodiversity hotspot regions, yet these regions are some of the most highly exploited areas of the world's oceans (Halpern et al. 2008). By failing to include these areas, potentially important regions of high productivity and likely intense human exploitation may be excluded from conservation priority portfolios.

RE-THINKING MARINE CONSERVATION PORTFOLIOS

Results from this review show that the majority of marine conservation by NGOs and conservation foundations remains focused on the "coral triangle", where biodiversity is high but fishing pressure is low, compared to other locations where productivity is high (e.g. upwelling regions, fronts, eddies) and important marine megafauna (e.g. marine mammals, seabirds, sea turtles) aggregate. While biodiversity must be included as a factor in conservation planning, some of the main drivers of marine species decline (over-exploitation and pollution) are most intense in areas of high primary productivity, and are often overlooked in conservation prioritization schemes. Coastal and upwelling zones represent only a small percentage of the global ocean (Ryther 1969) and do not have the levels of species richness documents in terrestrial systems, but these productivity hotspots account for at least half of the world's fisheries production, as many highly migratory and economically important species use these areas (Valavanis et al. 2004). In comparison to the terrestrial system, inherent differences within a fluid environment and the highly transient nature of these species make their movements less identifiable within the marine realm. For this reason, inclusion of highly productive regions of the ocean, coupled with biodiversity, may serve as an umbrella in the protection of marine species and ecosystem services.

Emerging strategies in ecosystem-based management may be one type of opportunity to include important areas of biodiversity and productivity within the marine environment (Pikitch et al 2004; Crowder et al. 2008; EBM 2008). Large Marine Ecosystems (LMEs) are characterized by distinct bathymetry, hydrography, productivity, and collectively account for 95% of the world's annual fisheries yields. They contain the highest levels of global marine primary production, are where coastal destruction is most severe, and are also where eutrophication is increasing (Sherman & Duda 1999; Sherman et al. 2005). Thus, they provide an important target for marine conservation prioritization - where anthropogenic threats are driving species declines, and where the impending effects of climate change will most heavily affect ecosystem functions and services on which humans depend. Areas of biodiversity and productivity require a separate set of strategies for effective protection. While we do not provide a silver bullet approach to marine conservation, we have shown here the importance of maintaining highly productive areas of the ocean, and our current emphasis on biodiversity protection may fail to protect important regions with high levels of anthropogenic impact. In order to effectively prioritize and efficiently allocate limited resources within the marine system, conservationists must also focus on important areas of primary productivity within their conservation portfolios.

CONCLUSIONS

Since the inception of the term twenty years ago, hotspots have been used to call attention to the most important areas under threat that require immediate conservation action. Biodiversity hotspots have worked well in the terrestrial environment, where conservation goals are driven by biodiversity loss and extinction risk. But marine systems are driven by different processes, so threats and conservation goals that require different prioritization strategies. In terrestrial systems regions of high biodiversity and regions of high productivity often overlap. But intrinsic differences in marine processes lead to mismatches between high biodiversity, high productivity, and human impact. Inclusion of productivity hotspots in conservation priority portfolios would provide the opportunity to include important regions of high value for ecological function and services. Furthermore, such areas are often the focus of intense human exploitation. As we move forward in realizing the costs, benefits, and successes in conservation planning, we urge marine scientists and organizations to integrate regions of high productivity as an ecosystem-based approach for conservation prioritization.

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TABLE 1. Ecosystem functions, services, their threats in each system and the types of hotspots that could conserve them.

(Data from de Groot et al. 2002)

				Hotspot Type	
Ecosystem Function	**Ecosystem Service**	**Terrestrial Threat**	**Marine Threat**	**Terrestrial**	**Marine**
Climate Regulation	Maintenance of suitable climate	Habitat Loss, Pollution	Pollution	Biodiversity	Productivity
Disturbance Prevention	Buffering from natural hazards	Habitat Loss, Invasives	Exploitation, Pollution	Biodiversity	Biodiversity
Biological/Population Control	Disease resistance through genetic evolution	Habitat Loss, Pollution, Invasives	Exploitation	Biodiversity	Biodiversity, Productivity
Carbon Fixation	Consumption of plant and animal biomass; fuel	Exploitation, Habitat Loss	Exploitation	Biodiversity	Biodiversity, Productivity
Refuge/Reproduction	Maintenance of suitable habitat for wild plants and animals	Habitat Loss	Habitat Loss	Biodiversity	Biodiversity, Productivity
Pollination/Dispersal	Maintenance of diversity	Exploitation, Habitat Loss	Pollution	Biodiversity	Productivity
Nutrient Cycling	Maintenance of arable soils and crops	Habitat Loss	Pollution	Biodiversity	Productivity
Water Regulation/Supply	Maintenance of hydraulic cycle	Habitat Loss, Pollution	Pollution	Biodiversity	Biodiversity, Productivity
Medicinal Resources	Pharmaceutical and biochemical substances	Exploitation, Habitat Loss, Invasives	Pollution, Exploitation	Biodiversity	Biodiversity

FIGURE 1.1 Number of conservation hotspot publications from 1988 – 2007 (n = 966).

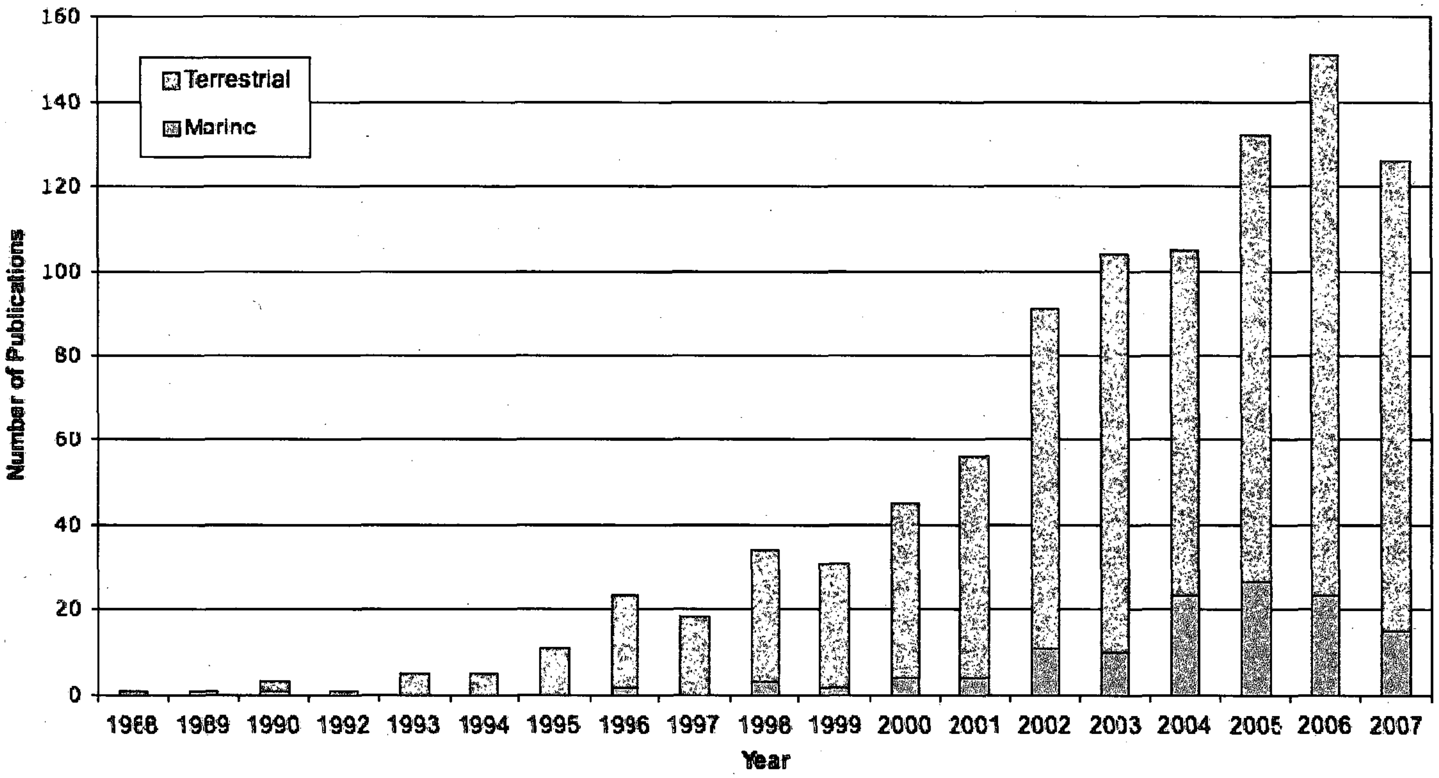

Terrestrial
Marine
Number of Publications
160
140
120
100
80
60
40
20
0
1988
1989
1990
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
Year

FIGURE 1.2 Number of conservation hotspot publications focused primarily on biodiversity vs. productivity

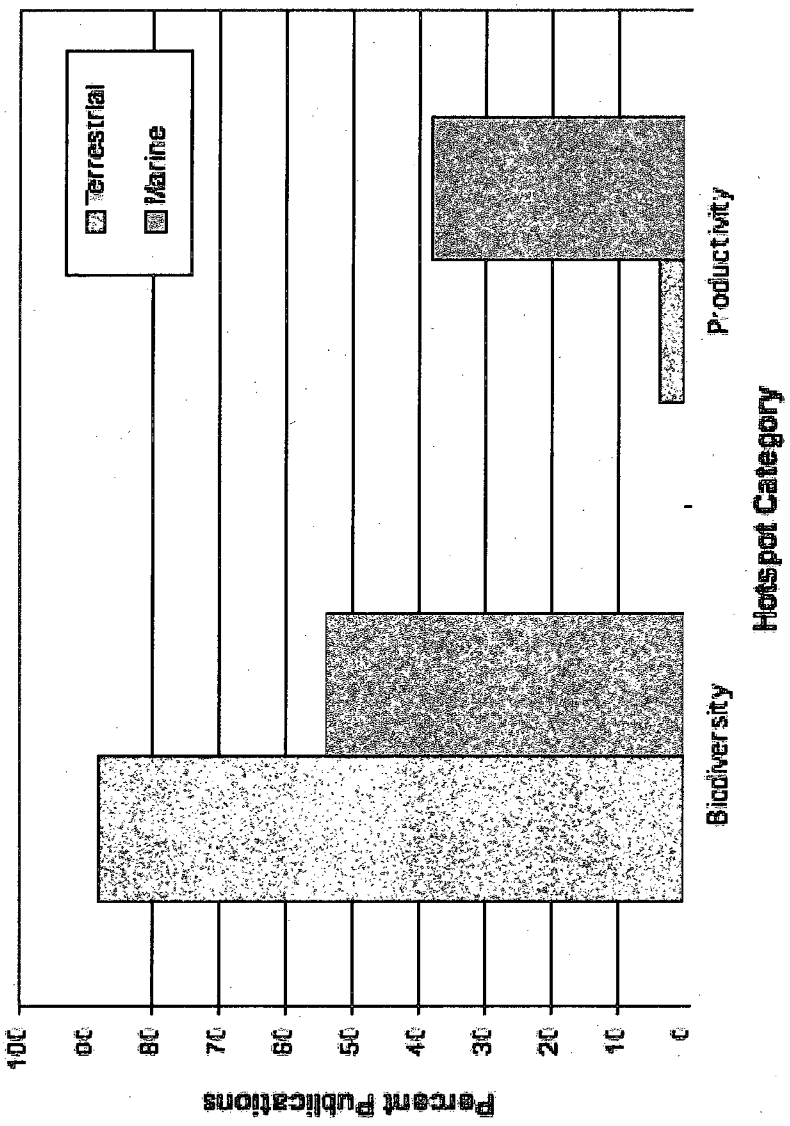

Percent Publications
100
90
80
70
60
50
40
30
20
10
0
Terrestrial
Marine
Biodiversity
Productivity
Hotspot Category

FIGURE 1.3 Primary conservation objectives of 27 marine conservation-planning cases at the local, regional, national, and global levels. *Data from Leslie (2005).*

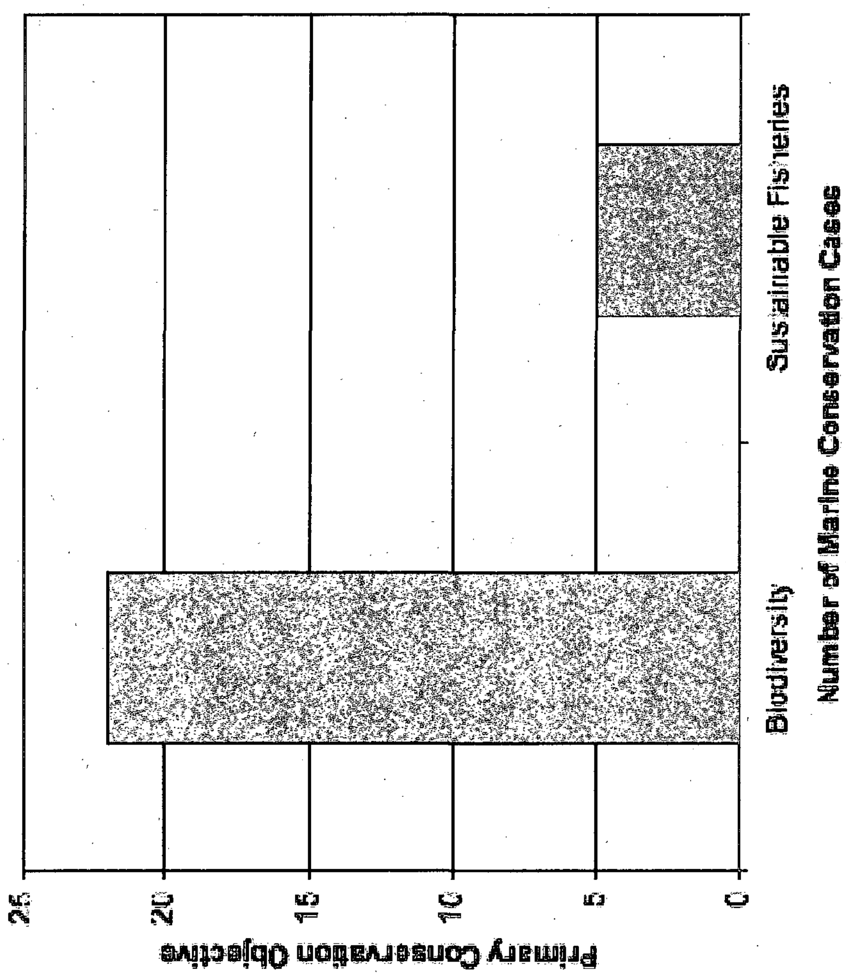
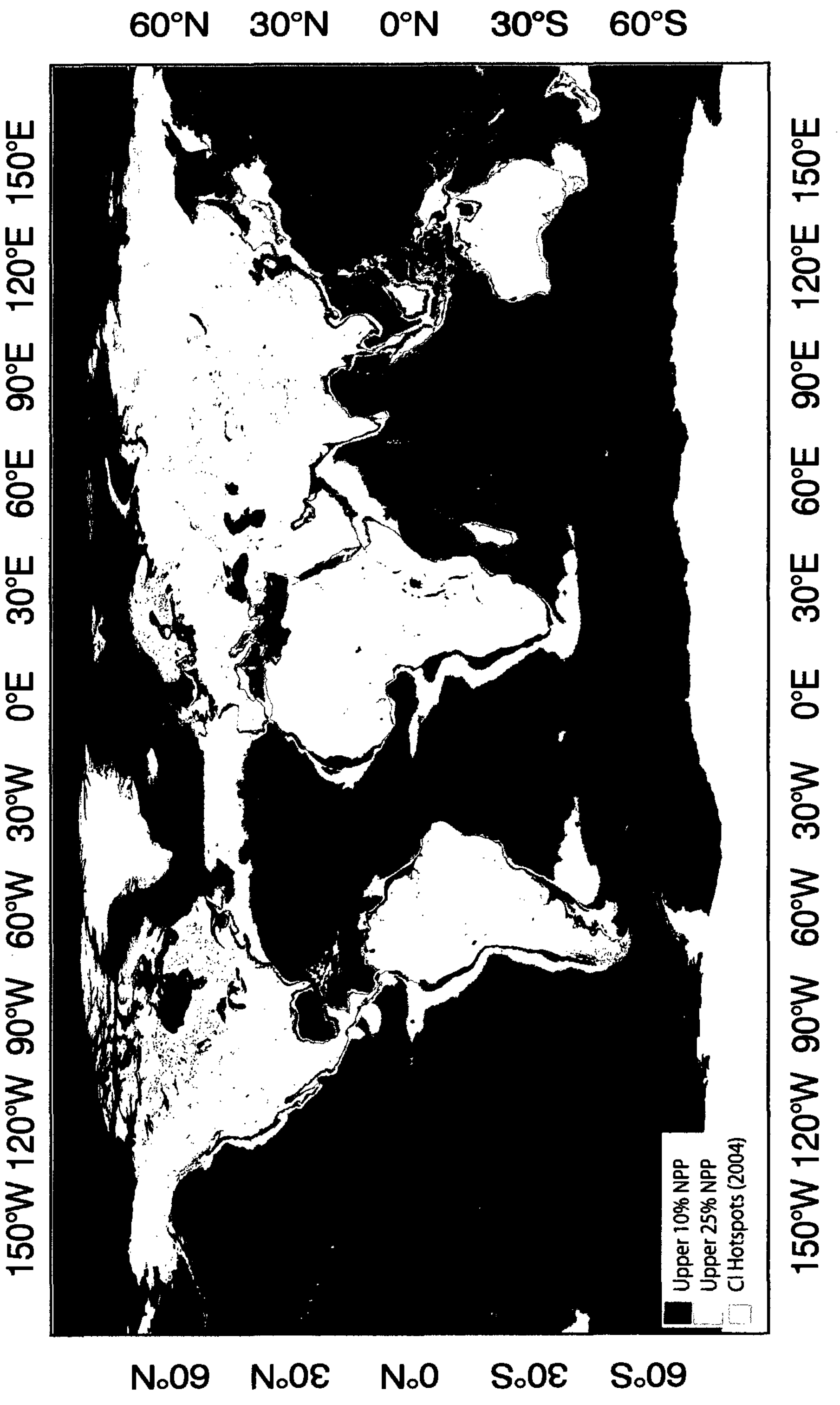

25
20
15
10
5
0
Primary Conservation Objective
Biodiversity
Sustainable Fisheries
Number of Marine Conservation Cases

FIGURE 1.4 Marine overlap between Conservation International's Biodiversity Hotspots and areas of greatest Net Primary Production ("Productivity Hotspots")


60°N
30°N
0°N
30°S
60°S
150°W
120°W
90°W
60°W
30°W
0°E
30°E
60°E
90°E
120°E
150°E
Upper 10% NPP
Upper 25% NPP
CI Hotspots (2004)

CHAPTER 2: FROM TAU TO TURTLES THE MAKING OF A TOP PREDATOR HOTSPOT

ABSTRACT

Biologically-rich regions of the ocean provide favorable conditions for the concentration of many large marine predators. These top predator hotspots are formed by the complex physical forcing mechanisms that are often several trophic levels removed from pelagic predators. Understanding how hotspots persist requires knowledge of the spatio-temporal linkages between physical forcing, biological responses, and predator utilization. Here we integrate remotely sensed oceanography, ship-based prey measurements, and satellite telemetry to show the formation of an upwelling shadow that promotes regional circulation patterns, enhanced primary productivity year-round, and the aggregation of prey that form a hotspot for endangered loggerhead sea turtles (*Caretta caretta*) off Baja California, Mexico. These results enhance our understanding of how migratory species utilize productive regions of the ocean and will contribute to the development of spatially explicit management strategies for marine conservation.

INTRODUCTION

Highly migratory species are known to associate with dynamic and productive areas of the ocean (coastal upwelling centers, fronts, eddies) (e.g., Worm *et al.* 2003; Polovina *et al.* 2006; Gremillet *et al.* 2008). Many species spend a portion of their life history utilizing these productivity 'hotspots' as they move between foraging and breeding grounds (Sydeman *et al.* 2006). Specifically, within eastern boundary currents, enhanced primary production at localized upwelling centers sustains dense concentrations of forage species that, in turn, provide optimal foraging opportunities for top predators (Croll *et al.* 2005). While several studies have established relationships between predator distribution and physical or biological variables like bathymetry, sea-surface temperature or chlorophyll (e.g., Tynan 1998; Ainley *et al.* 2005; Etnoyer *et al.* 2006; Polovina *et al.* 2006), pelagic predators are several trophic levels removed from the abiotic factors or the primary producers, such that these relationships may be indirect or unpredictable. Few studies have simultaneously measured the linkages between physical forcing, primary and secondary producers, and the pelagic predators that exploit them (Croll *et al.* 2005; Baumgartner & Mate 2005; Gremillet *et al.* 2008). Thus while dynamic physical oceanic processes may indirectly attract predators, understanding the formation of these productivity hotspots requires knowledge of the spatio-temporal linkages that serve to concentrate their prey within a patchy environment.

The Pacific coast of the Baja California Peninsula, Mexico, has been identified as a hotspot for ecologically and economically important species inhabiting the California Current System (CCS), including several species of tunas, elasmobranchs, sea turtles, seabirds, whales and other marine mammals (Etnoyer *et al.* 2006; Kitagawa *et al.* 2007; Peckham *et al.* 2007; Schaefer *et al.* 2007; Wolf *et al.* 2009). The pelagic red crab (*Pleuroncodes planipes*) is considered the principal intermediary in the energy flow from primary producers to a wide array of invertebrate and vertebrate predators, and probably serves as the link that attracts a diverse assemblage of top predators to the Baja California Peninsula (Longhurst *et al.* 1967; Longhurst 2004). Among these, juvenile loggerhead sea turtles (*Caretta caretta*) are unique in that they occur there year-round, remaining tightly aggregated off the coast for up to two decades before returning to their natal beaches off Japan to breed (Nichols 2000). Basic life history strategy would predict that juvenile loggerheads, which are not geographically constrained to centralized breeding grounds, should maximize fitness by seeking productive areas that optimize growth during their juvenile life history stage (Stearns 1992). Thus, the extended and localized presence of juvenile loggerheads off Baja California is indicative of a region of persistently favorable foraging conditions.

Red crabs are the primary prey of juvenile loggerheads (Ramirez-Cruz *et al.* 1991; Peckham & Nichols 2002), and they occur throughout the entire Baja California Peninsula (Aurioles-Gamboa *et al.* 1992). It has been hypothesized that strong ocean fronts act to concentrate red crabs, secondarily leading to increased abundance of foraging predators in this area (Longhurst 2004; Etnoyer *et al.* 2006). This study examines the trophic linkages between physical forcing and the distribution of juvenile loggerhead sea turtles as a model system to understanding the development and persistence of top predator foraging hotspots (Fig.1). Specifically, we combine a suite of remotely sensed and ship-based oceanographic measurements with long-term prey data sets and loggerhead satellite tracking to provide one of the first comprehensive assessments of the bottom-up creation of a top predator hotspot. In addition to understanding the ecological processes leading to a persistent predator hotspot, the results from this work will also provide the spatial and temporal information needed for the development of spatially explicit conservation strategies.

MATERIALS AND METHODS

Satellite transmitters were deployed on 41 juvenile loggerhead turtles captured off the coast of Baja California Sur, Mexico from 1997 to 2007. Position estimates and location accuracy were provided by the Argos satellite Location classes identified as 1, 2, or 3 were included in analysis. Remaining data positions were filtered based on a location class of A, B, and O and a maximum travel rate of 5 km h^{-1}. Location classes of Z were automatically discarded. Consecutive ARGOS locations were interpolated every 12 hours to reduce spatial autocorrelation (Tremblay *et al.* 2006). Weighted kernel density analysis of all filtered positions was used to derive highly utilized areas over the study period

(Worton 1989). Utilization distributions were calculated for the 25%, 50%, 75%, 100% contour intervals.

Hydrograhic surveys were conducted by the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program. Surveys occurred seasonally (January-February, April, July, and September-October). Sub-surface dynamic height (200/500 dbar) was derived from station data from 2000-2007. Red crab samples were collected from oblique net tows (Lavaniegos *et al.* 2003) and seasonally recorded from 2000-2008. Abundance was log-transformed and averaged at each station and gridded for spatial interpolation.

Gridded digital bathymetry at 30 arc-seconds was extracted from the SRTM30_PLUS global database (Becker *et al.* 2009). Remotely sensed oceanographic data were obtained for the study period from January 2000 - December 2007, except for frontal probability, a probability index that is calculated by the number of times a pixel is classified as a temperature front divided by the number of cloud free days for the given time period (Breaker *et al.* 2005). Frontal Probability was obtained from January 2001 - December 2007. Long-term climatologies were computed from remotely sensed satellite products. Satellite data used include: surface wind speed from QuikSCAT (25-km spatial resolution) and the derived vertical Ekman velocity from wind-stress curl (Risen and Chelton, 2008), Pathfinder sea surface temperature (SST, 4.4-km spatial resolution), SeaWiFS chlorophyll-*a* concentrations (1 km resolution) and GOES frontal probability index (10-day and 5-km temporal and spatial resolution, respectively). The geometric mean was used for surface chlorophyll-*a*, and values were log-normalized.

RESULTS

The predominant wind direction throughout the study area was from the northwest (Fig. 2a). Winds were most intense around the Point Eugenia headland, with a long-term mean of 7 m s^{-1}. Elevated vertical Ekman transport, driven by positive wind-stress curl, was localized at three main locations along the coast (northern Baja California, Ulloa Bay, and at the southern tip of the Baja California Peninsula). A small area of high vertical Ekman velocities was also seen in the lee of Guadalupe Island (Fig. 2b). Mean SST showed a strong north-south gradient, with increasing values equatorward (Fig. 2c). Long-term chlorophyll-*a* concentrations greater than 1 mg m^{-3} were found inshore along most of the coast (Fig. 2d). On average, the highest probability of SST fronts extended as a band along the coast, being narrowest off northern Baja California and widest south of Point Eugenia, especially offshore of Ulloa Bay (Fig. 2e). Sub-surface dynamic height contours showed a large cyclonic feature off the Point Eugenia at 28°N (Fig. 2f). The greatest mean abundance of adult pelagic red crabs was found within the continental shelf waters of Ulloa Bay and extending offshore from this location (Fig. 2g). Kernel density analysis of 41 juvenile loggerhead turtles tracked from 1997-2007 identified Ulloa Bay as the most highly utilized area off the entire Peninsula (Fig. 2h).

DISCUSSION

The prevailing oceanic conditions along the Baja California Peninsula are primarily determined by the interaction of persistent physical forcing with coastal topographic irregularities. Our results show that the complex geomorphology of Point Eugenia plays a particularly important role in coastal oceanographic patterns and ecosystem dynamics of the region, as suggested in previous studies (Hewitt 1981; Lynn & Simpson 1987; Lavaniegos 1994; Durazo & Baumgartner 2002; Batteen *et al.* 2003; Espinosa-Carreon *et al.* 2004). Dominant winds from the northwest sustain upwelling-favorable conditions year-round (Bakun & Nelson 1977), and are intensified at the Point Eugenia headland (Fig. 2a). The prominence of the headland shelters the southern portion of the Peninsula from direct wind exposure, most notably within the Ulloa Bay embayment just south of the point. This discontinuity in the wind field also generates persistent positive curl-driven upwelling within Ulloa Bay (Fig. 2b), similar to what has been documented in the lee of other major headlands, providing a significant source of nutrients to coastal ecosystems (Koracin *et al.* 2005; Rykaczewski & Checkley 2008). The year-round persistence of this positive wind-stress curl, tau (τ), leads to enhanced vertical Ekman transport, increased nutrient availability, and regionally elevated chlorophyll-*a* biomass year-round.

Previous studies have documented SST along the Baja California Peninsula, as cooler SSTs are associated with the strengthening of the equatorward flow of the CCS and the most intense northwesterly winds found during the spring and early summer upwelling maximum (Bakun & Nelson 1977; Lynn & Simpson 1987; Espinosa *et al.* 2004; Legaard & Thomas 2006). Wind-driven circulation in the lee of Point Eugenia is also a mechanism for advecting recently upwelled waters into a relatively calm, stratified area. This is evident in the warmer mean SST values within Ulloa Bay (Fig. 2c), which may in turn provide more suitable habitat for foraging marine species with thermoregulatory constraints such as sea turtles.

Variability in chlorophyll-*a* concentrations is associated with coastal upwelling intensity in the CCS (Espinosa-Carreon *et al.* 2004; Rykaczewski & Checkley 2008), and our results show a direct correspondence between localized areas of curl-driven upwelling and high chlorophyll-*a* concentrations (Figs. 2b, 2d). Despite the seasonal cycles, the long-term means of SST and chlorophyll-*a* identify Ulloa Bay as a distinct area of relatively warm surface temperatures and sustained productivity (Figs. 2c, 2d).

The prominence of Point Eugenia's headland separates the northern and southern portions of the Baja California coastline (Espinosa *et al.*, 2004). The coastal geometry and the strong vertical shear from the poleward flow of the California Undercurrent (CUC) are the primary mechanisms in the development of instabilities and meanders off the coast (Lynn & Simpson 1987; Batteen *et al.* 2003). Increased probability of SST fronts south of Point Eugenia (Fig.2e) may be reflective of the widened shelf and the convergence of the cool equatorward flow of the CCS with the warmer undercurrent. Persistent cyclonic eddy activity off Point Eugenia (Fig. 2f) is influenced by the CUC (Soto-Mardones *et al.* 2004), and the combination of frontal convergence with eddy retention provides favorable conditions for foraging species.

Red crabs primarily forage on phytoplankton and detrital matter (Aurioles *et al.* 1992). Localized within coastal upwelling sites of increased productivity, they exhibit a unique life history for a meroplanktonic species, as the adults have an extended pelagic stage lasting several years (Longhurst *et al.* 1967; Longhurst 2004; Robinson *et al.* 2004). They undertake a distinct inshore-offshore seasonal migration over the continental shelf, from winter-spring to summer-fall periods, reflecting the offshore Ekman transport and changes in food availability and water temperature in the second half of the year (Aurioles-Gamboa *et al.* 1992). However, recent research has shown that red crabs are also capable of maintaining high densities inshore within coastal upwelling sites irrespective of the season (Robinson *et al.* 2004; Gómez-Gutierrez *et al.* 2000). Although our data do not allow us to comprehensively describe the complex life history cycle nor the full range of red crab distribution off the entire Baja California Peninsula, it is clear from our study that adult pelagic red crabs are present year-round within Ulloa Bay (Fig.2g). Here, increased frontal probability and persistent cyclonic eddy activity create a region of localized convergence and retention for this micronektonic species.

Located within the lee of Point Eugenia's headland, Ulloa Bay represents a unique assemblage of physical and biological features that make this area an ecologically important hotspot for loggerhead sea turtles (Fig. 2h). As ectotherms, sea turtles have specific physiological constraints that must be balanced with foraging needs. For them, higher water temperatures are reported to be metabolically favorable as long as they do not approach upper thermal limits (Bjorndal 1980). Thermoregulatory costs conflict with enhanced prey detection, prey capture, ingestion, digestion, and absorption of food (Congdon 1989; Dunham *et al.* 1989). We suggest that foraging juvenile loggerheads are tightly aggregated within Ulloa Bay because it represents an "upwelling shadow" (Graham *et al.* 1992), providing relatively warmer waters within the embayment. The irregular shape of the coastline shelters Ulloa Bay from direct exposure to winds, while the wide continental shelf provide neritic habitat adequate for the juvenile life history stage (Musick & Limpus 1997). Persistent wind-curl-driven upwelling promotes enhanced primary production adjacent to Ulloa Bay, while the frontal structures formed by the poleward flow of the CUC and the local cyclonic circulation of surface waters helps to congregate food through surface convergences, and thus crabs as secondary producers throughout the entire year. The combination of these conditions would maintain high red crab abundances year-round, thus satisfying both foraging and thermal requirements for juvenile loggerheads.

CONCLUSIONS

The identification and understanding of the mechanisms driving marine predator hotspots is of increasing importance, as many of these species are threatened by commercial fisheries and unintentional capture, and also face climate-driven shifts in suitable habitat (Myers *et al.* 2003, Peckham *et al.* 2007; Jackson 2008). Marine Protected Areas (MPAs) that focus on vulnerable life history stages (i.e., breeding, juvenile foraging, etc.) have the promise to yield conservation benefits (Hooker & Gerber 2004); however there is little theoretical framework for the selection, design, and efficacy of MPAs for pelagic predators (Hooker & Gerber 2004), beyond "drawing lines around the features" Norse *et al.* (2005). To develop life-history based MPA models that can be realistically used by managers, advances in satellite oceanography that provide considerable spatial and temporal detail about when and where physical forcing leads to increased primary productivity, must be combined with advances in satellite telemetry that provide detailed information on the long-term movement patterns of pelagic predators at various life history stages over large spatial scales (Block *et al.* 2001; Etnoyer *et al.* 2006). This study shows the emerging capabilities of coupling these satellite-based data sets to characterize the unique combinations of bottom-up processes in the formation of a top predator hotspot. Knowledge of how these processes vary in space and time will allow for development of more effective marine conservation strategies.

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FIGURE 2.1 a) Juvenile loggerhead turtle tracks from 1997 – 2007 (n = 41), (b) mean red crab presence and corresponding mean abundance (log num/m^3) at each IMECOCAL cruise station (2000-2008).

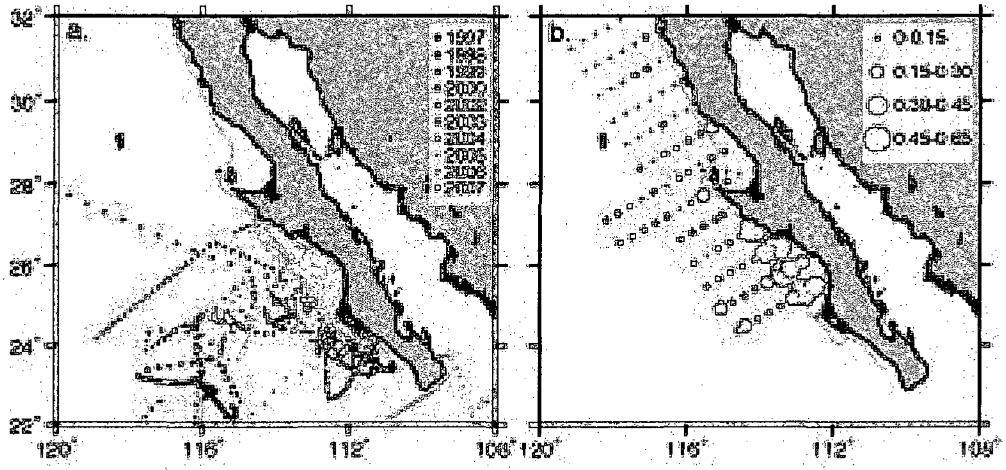
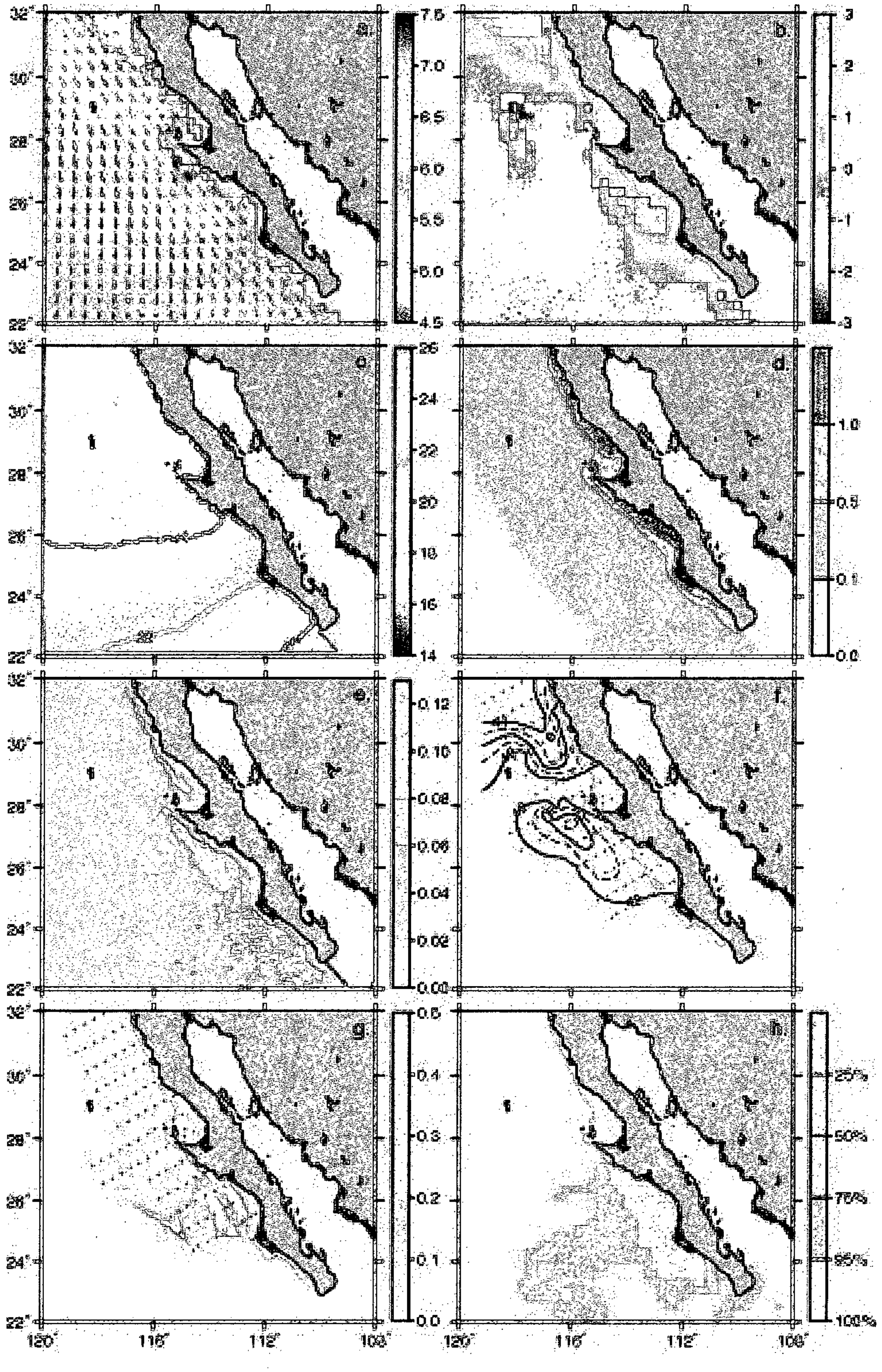
a.
1997
1998
1999
2000
2002
2003
2004
2005
2006
2007
b.
0-0.15
0.15-0.30
0.30-0.45
0.45-0.65
32°
30°
28°
26°
24°
22°
120°
116°
112°
108°

FIGURE 2.2 All-time means for a) surface winds (m/s); b) vertical Ekman transport (decimeters day^{-1}); c) sea-surface temperature (°C); d) chlorophyll-*a* (mg/m^3); e) Frontal Probability Index; f) dynamic height: 200/500dbar, (dyn-cm); g) gridded red crab distribution (log num/m^3); h) loggerhead sea turtle kernel density distribution


a.
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32°
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108°
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7.0
6.5
6.0
5.5
5.0
4.5
3
2
1
0
-1
-2
-3
26
24
22
20
18
16
14
1.0
0.5
0.1
0.0
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.5
0.4
0.3
0.2
0.1
0.0
25%
50%
75%
95%
100%

CHAPTER 3: PREDICTIVE HABITAT USE OF JUVENILE LOGGERHEADSEA TURTLES (*Caretta caretta*) OFF BAJA CALIFORNIA, MEXICO

ABSTRACT

Understanding of how species respond to and utilize their environment has been inherently difficult in the marine system. However, knowledge of the environmental conditions where they went, versus where they chose not to go is critical in the effective conservation and management of a species. Predictive habitat models have emerged as a means to identify the species-environment relationship where information on a population-level may be limited. In this study, we construct a spatially explicit habitat model to identify habitat selection of the critically endangered loggerhead sea turtle (*Caretta caretta*) off the Pacific coast of Baja California, Mexico. Specifically, we compare the home-range conditions of depth, sea-surface temperature, and chlorophyll-a concentrations of 30 satellite-tagged loggerheads over 10 years, against those conditions found outside of the habitat, as defined by the generation of simulated random-walkers. A generalized additive model (GAM) shows the significance of all three environmental variables to turtle response, and is used to spatially map the probability of loggerhead presence against the mean environmental conditions over the study period. We then overlaid a map of pelagic red crabs (*Pleuroncodes planipes*), the main prey source for Baja loggerheads, to fully describe optimal habitat. Our model identifies two explicit regions off the Baja California

Peninsula, Vizcaino Bay and Ulloa Bay as highly suitable for loggerhead habitat, however only Ulloa Bay combines these favorable environmental conditions and high prey abundance. The use of a statistical framework to identify available versus preferred habitat use may provide a more informative approach towards conservation strategies of pelagic species.

INTRODUCTION

A fundamental challenge in the physiological ecology of animals is optimizing conditions for physiological function within the context of of ecological constraints (Emlen 1966, MacAurthur & Pianka 1966). Often optimal locations for physiological processes such as metabolism and growth are not optimal within ecological constraints such as prey availability or predation; resulting in trade offs between physiological and ecological constraints. Trade offs may be particularly important for ectotherms, where thermo-regulatory requirements can significantly constrain movement and distribution. Several terrestrial studies have shown that reptiles deal with this problem by selecting habitats that may be a compromise between physiological and ecological optima (e.g. Huey 1991, Law & Dickman 1998, Regosen et al. 2003). The study of these tradeoffs has been more difficult in the marine environment due to the technical difficulties of monitoring animal movement, physiological condition, and the spatio-temporal scales of physical and biological processes in marine systems(Levin 1994, Steele & Henderson 1994).

The combination of recent advancements in electronic tagging of marine vertebrates with synoptic spatio-temporal measurements of marine habitats via satellite oceanography has provided new opportunities to examine physiological/ecological tradeoffs in marine vertebrates. Specifically, the combination of these data allow the characterization of environmental conditions in utilized vs. unutilized habitats, facilitating the development of simple predictive models of habitat preference resulting from physiological/ecological tradeoffs. Predictive habitat models have become a resourceful tool in understanding the species-environment relationship where ecological information may be limited (Guisan & Zimmerman 2000). Traditionally, predictive habitat models have been used in the terrestrial system to assess the effects of vegetation change or climatic variability on the distribution of organisms (Lischke et al. 1998, Kienast et al.1995, 1996, 1998, Guisan & Theurillat 2000, Guisan an&d Zimmerman 2000, Mladenoff et al. 1995, Mace et al. 1999, Shao & Halpin 1995, Corsi et al. 1999). Spatially explicit predictive models have recently been used in marine systems to define the environmental conditions that establish spatial habitat use. For example, Ferguson et al (2006) used a quantitative method to predict whale populations from oceanographic variables in the eastern tropical Pacific Ocean.

Characterizing habitat use of threatened species within highly utilized areas is critical to effective conservation actions over spatial and temporal scales. Highly productive regions of the ocean – "productivity hotspots" (Wingfield et al., submitted) serve to spatially and temporally concentrate foraging marine species (i.e. sea turtles, seabirds, and marine mammals). Likewise fisheries activities and incidental, bycatch can be high in these productivity hotspots, leading to precipitous declines of non-target species (Spotila et al. 2000, Baum et al. 2003, Lewison and Crowder 2003, Read et al. 2006). As a result, marine scientists, fisheries managers, and policy makers have begun to advocate conservation practices that focus on regions where pelagic predators concentrate at vulnerable life history stages (Norse et al. 2005, Pikitich et al. 2004, Hobday & Hartmann 2006). Thus, the combination of remotely sensed oceanography, satellite tags, and statistical models may not only characterize the habitats of where animals go, but also the ability to delineate potential habitats for conservation focus.

The waters off Southern Baja California are characterized as a transitional zone between the subarctic-influenced waters of the California Current System (CCS) and subtropical/equatorial water masses. Significant coastal upwelling occurs year-round, and these conditions collectively lead to persistent mesoscale physical oceanographic features (Hewitt 1981, Batteen et al. 2003). These physical oceanographic characteristics lead to consistently high primary productivity; these waters are the most productive of the entire CCS (Longhurst 2004, Legaard & Thomas et al. 2006). Several studies have shown that a diversity of pelagic vertebrates (e.g. elasmobranchs, tuna, sea turtles, seabirds, and whales, tuna, and sea turtles) consistently aggregate in this region (Etnoyer et al. 2006, Kitagawa et al. 2007, Peckham et al. 2007, Schaefer et al. 2007, Croll et al. in prep).

The biological productivity that sustains foraging pelagic species in this region has also resulted in significant overlap with indusrial- and small-scale fisheries, causing precipitous declines in non-target species (Peckham et al. 2007, Schaeffer et al. 2007). For example, juvenile loggerhead sea turtles aggregate at unusually high densities off the Baja California Sur coastline, exposing them to high bycatch risk in long-line and gillnet fisheries (Peckham et al 2006; Seminoff 2006). Peckham et al. (2007) estimated a minimum of 1,000 juvenile loggerhead turtles are incidentally taken in Southern Baja California artisanal fisheries bycatch each year. This is one of the highest known sources of mortality for the entire North Pacific loggerhead population, and has likely contributed to a 50-90% decline of loggerheads at their nesting beaches in Japan and their IUCN listing as the most endangered large marine vertebrates (Kamezaki et al. 2003). The persistence of juvenile loggerheads within a productivity hotspot off Baja California presents a unique opportunity to examine habitat selection of a pelagic predator. Figure 1 demonstrates this long-term residence of thirty satellite tagged loggerheads off Baja California from 1997-2007.

In general, it is believed that loggerheads undergo an ontogenetic shift from foraging in oceanic to neritic waters some time during their juvenile life history stage (Bolten et al. 2003). Some time after hatching from nesting beaches in Japan, North Pacific Loggerheads undertake a trans-oceanic migration to the Eastern Pacific and subsequently remain in neritic waters off Baja California year-round for up to two decades before returning again to their Western Pacific natal beaches (Peckham et al. 2007). Peckham et al. (2008) proposed that the neritic region off Southern Baja California provides energetically favorable thermal conditions and productive foraging opportunities. Because juvenile loggerheads are free of constraints to return to a central location (such as breeding or haulout areas), their extended and localized presence in these waters suggests conditions that likely serve to maximize survival and growth (Stearns 1992).

Aarts et al (2008) defined habitat as a collection of conditions within an environmental space that may be preferred or avoided. We used this definition to examine habitat selection in juvenile loggerhead sea turtles off Southern Baja California. We used spatially-explicit habitat models to examine the importance of a suite of environmental variables to the distribution of juvenile loggerheads. Specifically, we examined: 1) which environmental variables significantly correlate to loggerhead habitat; 2) what properties of these variables define the habitat that juvenile loggerheads prefer to occupy; and 3) how do these conditions differ with adjacent regions that they could realistically reach, but choose not to inhabit? We test the hypothesis that resident (non-migratory) juvenile loggerheads are randomly distributed off of Baja California against the alternative hypothesis that loggerheads preferentially select habitat that includes shallow (neritic) depths, thermally optimal conditions, and high abundance of food.

To test this hypothesis we compared the movement of satellite-tagged juvenile loggerheads to a theoretical population of individuals moving in a correlated random walk (CRW). The CRW approach generates animal movement data based upon a statistically generated distribution of step-lengths and turning angles (Kareiva and Shigesada 1983). This analytical approach has been applied across a range of species to relate differences in CRW individuals with individuals moving in response to environmental and landscape features (Kareiva and Shigesada 1983, Bergman et al. 2000, Morales et al. 2004, Aarts et al. 2008).

We defined preferred habitat through the utilization distribution of 10 years of observed turtle locations, and compared the underlying environment with the spatial extent of a simulated population of correlated random walkers to represent all possible locations a Baja California loggerhead could 'choose' to go without regards to their environment. We then determined the relationship between loggerhead presence and environmental conditions through a generalized additive model (GAM). Finally, we used this information to develop predictive maps of suitable loggerhead habitat to understand how this species exploits the waters off Baja California Mexico. Knowledge of how these juveniles utilize their habitat is also important for effective conservation management of the entire North Pacific loggerhead population.

MATERIALS AND METHODS

Loggerhead Tracks

Thirty juvenile loggerhead sea turtles were tracked from September 1997 to February 2007, with satellite platform transmitting terminals (PTT) (Wildlife Computers, Redmond, Washington, USA). Turtle carapaces were outfitted with satellite tags using a polyester resin and fiberglass cloth (Peckham 2008; Balazs et al. 1996). Movements were monitored through the Argos satellite system. Turtle positions were determined with the Argos classification system. Location classes identified as 1, 2, or 3 were included in analysis. All other raw data positions were filtered based on a location class of A, B, and O and a maximum travel rate of 5km h-1. Location classes of Z were automatically removed. Consecutive ARGOS location hits were interpolated every 12 hours to reduce spatial autocorrelation (Tremblay et al 2005, Peckham et al. 2007).

Utilization distributions (UD) represent the probability of animal occurrence within a defined home range. Utilization distributions were determined using a Gaussian kernel density analysis of all interpolated positions (Peckham 2008). An index of turtle residence probability per unit area by gridding the number of turtle positions multiplied by the number of individuals found within a 5km2 cell. Contours representing the percent area of habitat utilized were then generated from 1-99%. For display purposes, the UD contours at 25%, 50%, 75% and 95% were displayed (Figure 1).

Simulated Tracks

Correlated random walks (CRW) were generated to account for 'pseudo-absences' – places available in space and time that a turtle could choose to go, but did not. Therefore, random walkers show no preference to habitat (Aarts et al. 2008). Random walk trajectories were simulated using the 'adehabitat' package in R software program (The R Project for Statistical Computing, 2009). A minimum of 500 CRW simulations were generated per observed track and were allowed to move unconstrained except for on land, in which a new location along the track length was sampled with replacement. Each simulation started at the observed track latitude/longitude location, and was built iteratively so that the simulated movement was wrapped from a normal distribution. Each simulation along a track maintained the same distance, turning angle, and duration in time between successive relocations (Calenge et al. 2009). One drawback to methods such as this is the inability to account for hidden processes variables (e.g. regime shifts in movement and behavior), as noted in Royer et al. (2005), however for the purposes of our study, CRWs provide a statistical way to delineate turtle movement without regards to biological preference of habitat.

Prey Distribution and Abundance

Hydrograhic surveys were conducted by Investigaciones Mexicanas de la Corriente de California (IMECOCAL). Detailed IMECOCAL survey design and sampling methodology is provided in Lavaniegos (2006). Briefly, surveys occurred seasonally (January-February, April, July, September-October) and zooplankton samples were collected with bongo net. Adult pelagic red crab abundance was measured and recorded seasonally from 2000-2008 (Lavaniegos et al. 2006). Abundance was log-transformed and averaged at each station and gridded for spatial interpolation using MATLAB 2007a (Mathworks 2007). Boogaart (2003) noted that a central problem of spatial interpolation (e.g. kriging) is the uncertainty of having enough data to infer the true structure of a population.

However, this method is still known to be one of the best ways to linearly predict individual measurements using known observations (van den Boogaart 2003).

Environmental Data

Satellite data for sea-surface temperature and chlorophyll-a was extracted along the track of each observed and simulated turtle, using a 0.01° x 0.01° spatial grid under each track location. Products were sampled from the OceanWatch Thematic Real-time Environmental Distributed Data System (THREDDS) (PFEL 2009, Seminoff et al. 2008). Sea-surface temperature (SST) was obtained from NOAA's Advanced Very-High Resolution Radiometer (AVHRR) Pathfinder v5, using a 5-day, 4km spatial resolution; Chlorophyll-a concentrations (chl-a) from the Sea-Wide Field of Viewing System (SeaWiFS), using an 8-day, 1km spatial resolution. For SeaWiFS-derived surface chl-a, values were log-normalized for subsequent analyses. Two-minute (~4km), gridded digital bathymetry was extracted from the ETOPO2v2 (2006) database, provided by National Oceanic and Atmospheric Administration's National Geophysical Data Center.

The long-term temporal averages for SST and chl-a were computed over the tagging study period (September 1997 – February 2007) in order to generate a single environmental layer for each dynamic response variable to be used for habitat prediction. Because loggerheads have rarely been recorded in the Gulf of California and this region represents a much different oceanic regime, strongly influenced by tidal mixing and complex geomorphology, we excluded the region east of 110°W that encompassed the Gulf of California from our analysis. We also chose to exclude the area north of 31°N latitude, as our PTT data indicated that the region north of this latitude is not utilized by loggerhead sea turtles. Likewise, the extent of the simulated tracks did not reach north of this latitude.

Data Analysis

In order to identify the separation in environment between the observed turtles and simulated tracks, we first defined 'preferred' (high-use) habitat as the area within the 75% kernel density contour interval. All datasets were explored for normality, and chlorophyll-a was log-transformed prior to subsequent analyses. Density histograms of the environmental conditions sampled under observed tracks were compared to the conditions synchronously sampled in time under the simulated tracks (Figure 3).

Generalized Addiditve Models (GAMs) were used to relate turtle presence to environmental variables. A GAM is a nonparametric extension of a generalized linear model, in which the predictor variables may be transformed to identify non-linear relationships between an animal and its environment (Hastie & Tibshirani 1990) GAMs are often used when the response variable is binary, such as in the case of presence/absence data, and where the linear function of the predictor variables can be replaced with a smoothing function, allowing for a more flexible non-parametric fit between the response and predictor variables (Redfern et al. 2006, Redfern et al. 2008).

In preparation for fitting the GAM, all observed points were assigned a spatial reference value of 1 (presence), and simulated points were given a value of 0 (absence). Aarts et al. (2008) recommend a random sampling of at least twice as many absence points from the CRW to presence points. Thus, from an initial array of 500 "pseudo-absence" CRW points, we randomly sampled a subset of 5 CRW tracks per turtle.

Because models cannot be tested as "true" or "false, but rather assessed by the accuracy of their predictive power, cross-validation techniques must be applied to evaluate their overall predictive performance (Guisan and Zimmerman 2000, Elith et al. 2006). Cross-validation of our subsampled dataset was done by randomly selecting 2/3 of our data points for model calibration, and reserved the remaining 1/3 of the dataset for model evaluation (Guisan and Zimmerman 2000).

The GAM was fitted using the 'mgcv' package in the R statistics program and the MGET Toolbox within ArcGIS (Wood 2009, Roberts et al. *in review*), with a quasi-binomial distribution and the logit link function. The final model was included with spline smoothers to SST, log-transformed chlorophyll, and depth.

A Receiver Operator Curve (ROC), a diagnostic to test the performance of the model, was run on the remaining portion of the cross-validation dataset (1/3) set aside for evaluation (Aarts et al. 2008). The area under the curve represents the accuracy of the diagnostic test, and the closer the value is to 1.0, the more accurate the test is deemed to be (Tape, 2001).

The all-time temporal means of each environmental variable were layered on top of each other, and predictive habitat maps were generated by systematically incorporating the output of the statistical model into each cell of the layers to calculate a probability of turtle presence. The largest spatial resolution cell size (0.83° x 0.83°) of the environmental was used for consistency in generating habitat maps. We excluded distribution from our model, because of the spatial mismatch in data extent. Ship transects from IMECOCAL do not encompass the entire Pacific coast of the Baja California Peninsula; therefore we could not make an adequate statistical inference as to turtle presence based on red crab survey extent. We generated two types of predictive maps: binary (0 or 1 habitat suitability), and percent probability, were values ranged from 0 up to 1.

RESULTS

Figure 2 shows the spatial distribution of all observed loggerhead locations versus simulated points. The simulated locations show the wide spatial extent potentially available to a foraging loggerhead off of Baja California. Density histograms for depth, SST, and chl-a show a separation in the distribution of the environment sampled under the observed versus simulated tracks. Table1 lists a summary of the relationship between each environmental variable and the response variable, turtle presence. Results from our generalized additive model showed that depth and chlorophyll-a concentrations most significantly explained presence ($p \leq 0.001$), followed by sea-surface temperature ($p \leq 0.01$). Output model functions show the smoothed relationship between each predictor variable and the response (Figure 4). Dashed lines represent upper and lower limits of twice the standard error. Figure 4a suggests that SST follows a slight bow shape, with probability of presence greatest between 20-25°C, and decreasing with temperatures cooler and warmer than this range. Similarly, the probability of presence is greater in shallower depths, and an probability decreases with increase in chlorophyll Figures 4b and 4c. This indicates that turtles are inhabiting waters with lower chl-a concentrations.

The area under the ROC curve was found to be 0.95, suggesting a very good performance by the model.

The binary predictive habitat map identified the majority of the continental shelf waters as suitable habitat for juvenile loggerhead sea turtles (Figure 5). The probability of occurrence map showed Vizcaino Bay and Ulloa Bay as the two areas along the Pacific coast of Baja California that a turtle is most likely to be found, with predictions 0.6 and greater (Figure 6).

Gridded red crab distribution shows the highest abundances were found between 25°N and 28°N latitude, near Point Eugenia.

DISCUSSION

Predictive Habitat

Our understanding of marine animal movement has been greatly enhanced with advances in satellite telemetry. To date, most studies have used presence only observations to identify a relationship between an animal and the prevailing environmental conditions (Aarts et al. 208). However, the increase in quantitative analyses in spatial ecology now presents a statistical framework for ecologists to explore the space-use and preference of species on a population level, using predictive models to derive a relationship between environmental covariates and population distributions (Guisan & Zimmerman 2000, Aarts et al. 2008).

Long-term tag deployment of 30 juvenile loggerheads over a 10 year study period have shown a strong site fidelity to the coastal waters of Ulloa Bay, and our results indicate there is a clear separation in the environmental conditions of depth, SST, and chl-a between this home-range habitat, and the surrounding available habitat. Generally, we found that loggerheads preferred shallow depths, areas of lower chlorophyll concentrations and temperatures closest to 25°C.

The predictive model suggests that all three predictor variables (depth, SST, and chl-a) explain significant variability in turtle presence in the waters off of Baja California. These results correspond with recent studies in the North Atlantic and the Central North Pacific that show the influence of such variables as temperature, depth, and the magnetic field on the habitat selection of loggerhead sea turtles (Hawkes et al. 2007, Kobayashi et al. 2008).

Using our extrapolated relationship of these variables with turtle presence, we generated two types of spatially-explicit predictive maps that identify suitable versus unsuitable habitat (Figure 5) and the probability of loggerhead occurrence (Figure 6). The binary map identifies the majority of coastal waters off Baja California as suitable habitat. This is expected for depth and chlorophyll, as it is known that foraging juvenile loggerheads prefer neritic waters (Bolten 2003) where chlorophyll concentrations are generally high off Baja California (Espinosa et al. 2004). However, it is unrealistic to assume that we can protect the entire Pacific coast of Baja California from overlap with fisheries activity. For this reason, we used the probability of occurrence map to go a step further in identifying areas where it is most likely to find a turtle within the defined suitable habitat for conservation target (Figure 6). Two areas off the Pacific coast of the peninsula that show a higher probability of loggerhead presence are Vizcaino Bay and Ulloa Bay. Despite the fact that both of these regions satisfy the conditions of shallow depths and high chl-a concentrations for a foraging turtle, the strong site fidelity of loggerheads to Ulloa Bay required further inspection of preference between these two locations.

Potential Habitat: Vizcaino Bay and Ulloa Bay

We suggest two possible reasons why juvenile loggerheads would prefer the waters of Ulloa Bay over Vizcaino Bay. Firstly, average sea-surface temperatures within Vizcaino Bay are much cooler than those found within Ulloa Bay (less than 18°C compared to greater than 20°C, respectively) (Legaard and Thomas 2006). While this difference in temperature seems negligible, it has been determined that higher water temperatures are energetically more favorable for sea turtles in terms of growth, digestion, and maintenance of core body temperature, up to a 30°C thermal maxima (Bjordnal 1980, Coles and Musick 2000, Peckham et al. 2008). Additionally, Wingfield et al. (in prep - *ch2*) have identified Ulloa Bay as an "upwelling shadow" (see Graham et al. 1992), where the warmer, more thermally optimal SSTs and biomass are retained downcoast of a localized upwelling center.

This leads to the second suggested reason why Ulloa Bay provides more suitable habitat than Vizcaino Bay. Although Ulloa Bay more appropriately satisfies the thermal constraints of loggerheads while maintaining high chl-a concentrations, like most apex predators, juvenile loggerhead sea turtles do not forage directly on chlorophyll biomass. In fact, studies have shown that while inhabiting the waters off Baja California, loggerheads forage primarily on the pelagic red crab (*Pleuroncodes planipes*) (Villanueva 1991, Peckham and Nichols 2002). Phytoplankton comprise a major component of red crab diet (Aurioles et al. 1992), and the distribution of this micronecktonic species has been correlated to areas of increased coastal productivity (Longhurst et al. 1967, Aurioles et al. 1992, Robinson et al. 2004). Red crab concentrations have been documented in both Vizcaino Bay and Ulloa Bay (Gomez-Gutierrez et al. 2000, Aurioles et al. 1992), however results from our analysis of long-term ship based surveys of red crab biomass off the coast of Baja California highlight the abundance of this species off Ulloa Bay (Figure 7). Wingfield et al. (submitted) discusses in depth the development and retention of red crab abundance within this upwelling shadow, and it is this large concentration of prey within the warm, neritic waters of Ulloa Bay that creates the ideal habitat for a foraging juvenile loggerhead off the Baja California peninsula. While visual comparison in this study shows the potential overlap between high red crab abundance and the probability of turtle presence, a more detailed quantitative analysis must be undertaken to identify the correlation between these two variables.

This study explores a novel approach to the use of environmental predictors to identify the probability of species occurrence, on a population level. Because prey datasets are often unavailable to draw direct trophic linkages between the physical processes that serve to concentrate marine predators, these connections generally rely on biological proxies (i.e. sea-surface temperature and phytoplankton standing stock) to indirectly relate species to their environment.

For the purposes of this study, we used a very basic additive model that did not account for temporal variability or interaction terms. We used all-time averages for SST, chl-a, and red crab distributions as a first-step analysis, due to the long-term persistence of loggerheads within Ulloa Bay year-round. Future steps for this work will include the exploration of a more fully developed model with environmental covariates, such as the interactive influence of SST and Chl-*a*, further exploration in auto-correlation effects, and greater consistency between sampling of the environment along animal tracks (i.e. spatial and temporal resolution of satellite products), and the corresponding environmental layer for output predictive habitat maps.

CONCLUSIONS

Identification of species habitat use within areas identified as 'productivity' hotspots is a critical first step in the ability to conserve them. This is especially important for threatened and endangered species, where the implementation of marine protected areas and seasonal closures during vulnerable life history stages can greatly reduce extinction risk of an entire population. Spatially explicit habitat models such as the one used in this study offer a more robust statistical framework to make these indirect associations where population data is limited.

As a first-order approach to better understanding of a species habitat use, we have identified the basic habitat preference of the critically endangered loggerhead sea turtle throughout its long-term residence off of Baja California, Mexico. Significant threats to this population have been identified within the

Central North Pacific, and interaction avoidance has been a high priority of NOAA Fisheries (NMFS 2004, Gilman et al. 2006). However, effective conservation of this population requires an international focus on management, and the development of strategies that include protection from detrimental overlap within the waters off Mexico. Spatially-explicit predictive models may allow fisheries to use environmental correlates to identify areas of high avoidance throughout the year, and with further development, on a seasonal level as well as potential application to projected shifts in oceanic conditions of sea-surface temperature and productivity, with impending climate change. Further, it is hoped that these models can be expanded to identify critical habitat where species may choose to concentrate during vulnerable life history stages, and where the establishment of protected areas will be most effective.

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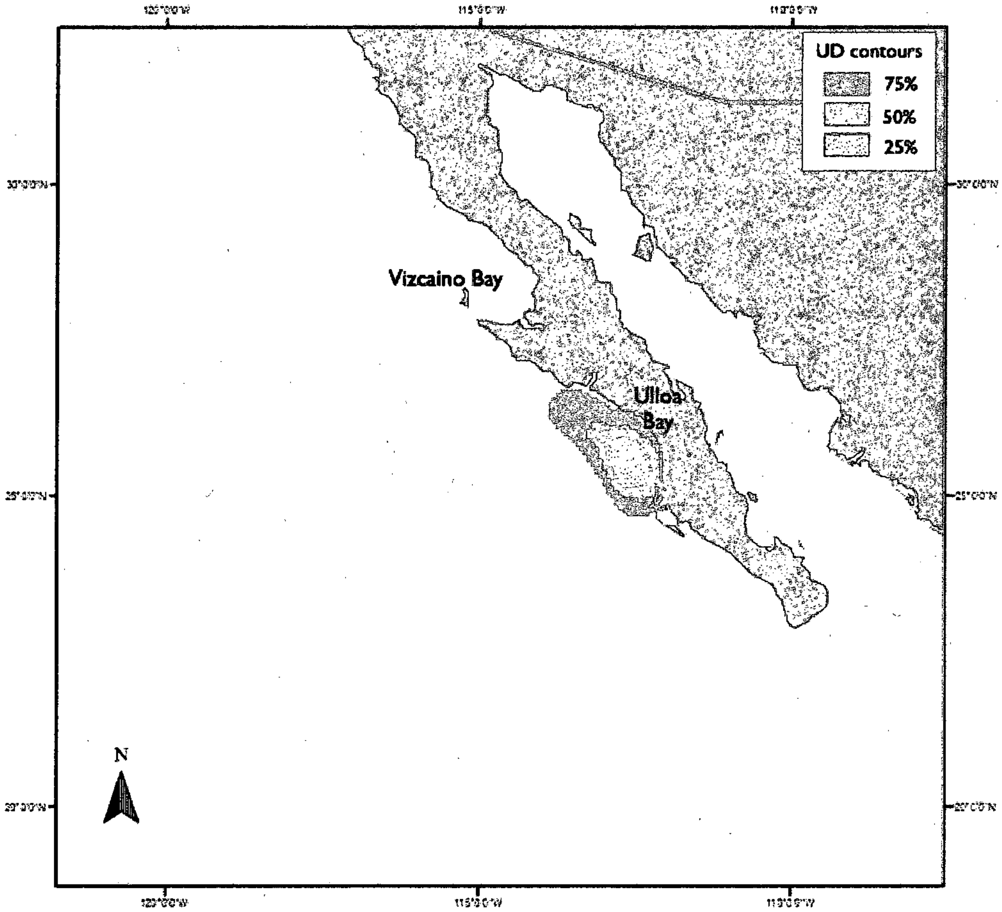
TABLE 3.1 Output summary for the final Generalized Additive Model (GAM).

Environmental Variable	**Effective degrees of freedom**	**F**	**Probability**
Sea-surface temperature	1.919	6.49	$p \leq 0.01$
Chlorophyll-a	1.953	185.69	$p \leq 0.001$
Depth	1.995	776.52	$p \leq 0.001$

FIGURE 3.1 Utilization distribution (UD) of thirty resident (non-migratory) juvenile loggerhead sea turtles at the 25%, 50%, and 75% contour intervals off Baja California, Mexico (1997-2007).



120°0'0"W
115°0'0"W
110°0'0"W
UD contours
75%
50%
25%
30°0'0"N
Vizcaino Bay
Ulloa Bay
25°0'0"N
N
20°0'0"N

FIGURE 3.2 Cumulative spatial distribution of all observed loggerhead locations (red) versus correlated random walk simulations (blue).

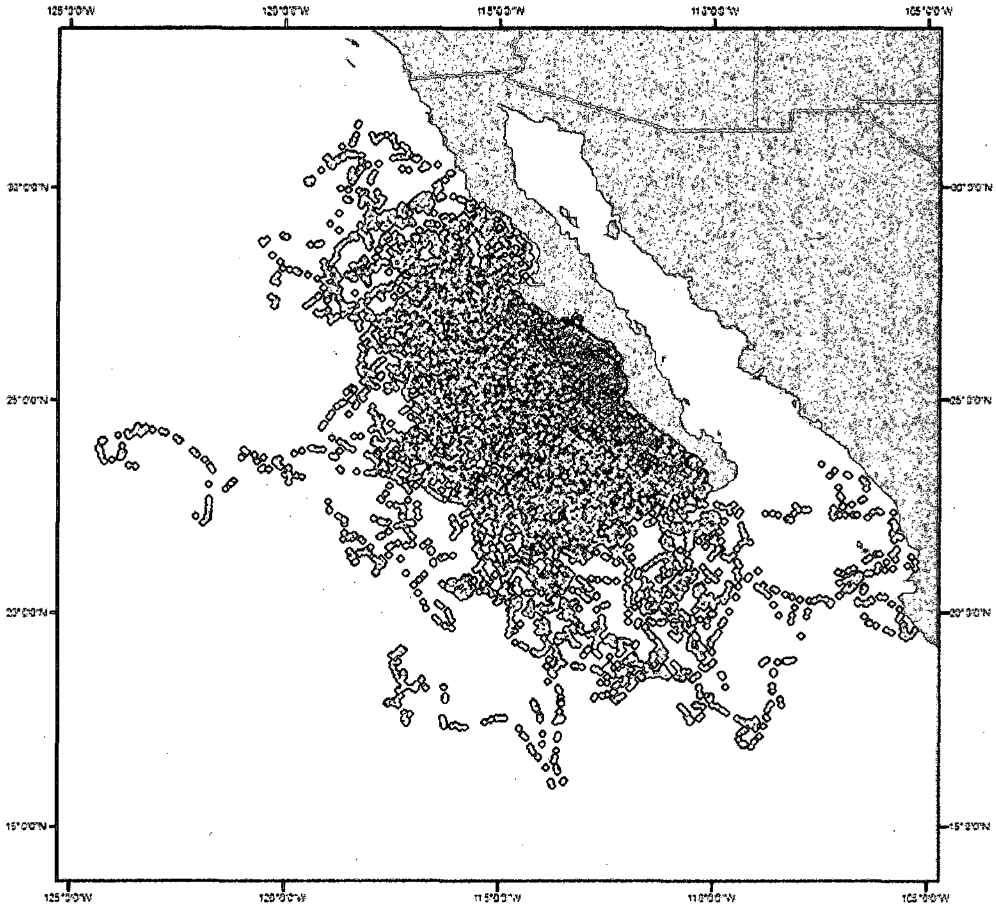
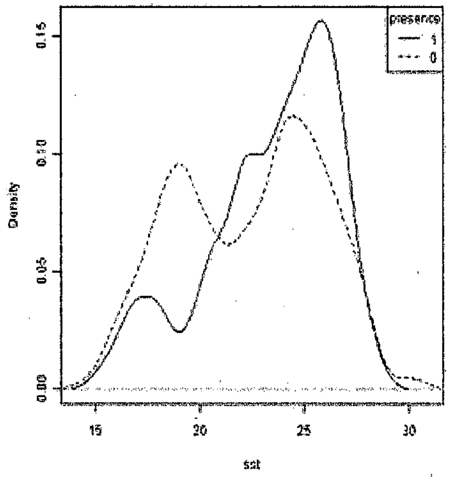
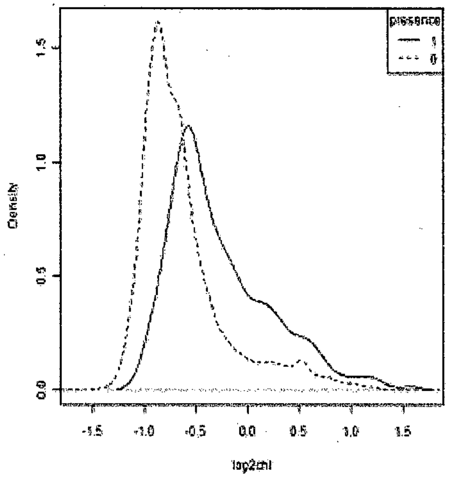

125°0'0"W
120°0'0"W
115°0'0"W
110°0'0"W
105°0'0"W
30°0'0"N
25°0'0"N
20°0'0"N
15°0'0"N

FIGURE 3.3 Density histograms of the environment sampled underneath of observed tracks ('presence') versus simulated tracks ('absence') for a) sea-surface temperature (°C); b) log-transformed chlorophyll-a concentrations (mg m^{-3}); and c) depth (meters).


presence
1
0
Density
0.00
0.05
0.10
0.15
15
20
25
30
sst


presence
1
0
Density
0.0
0.5
1.0
1.5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
log2chl

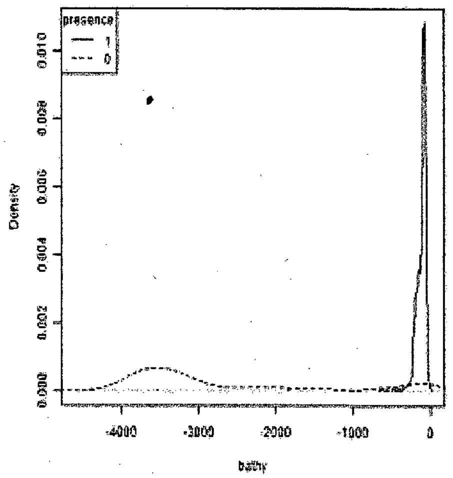
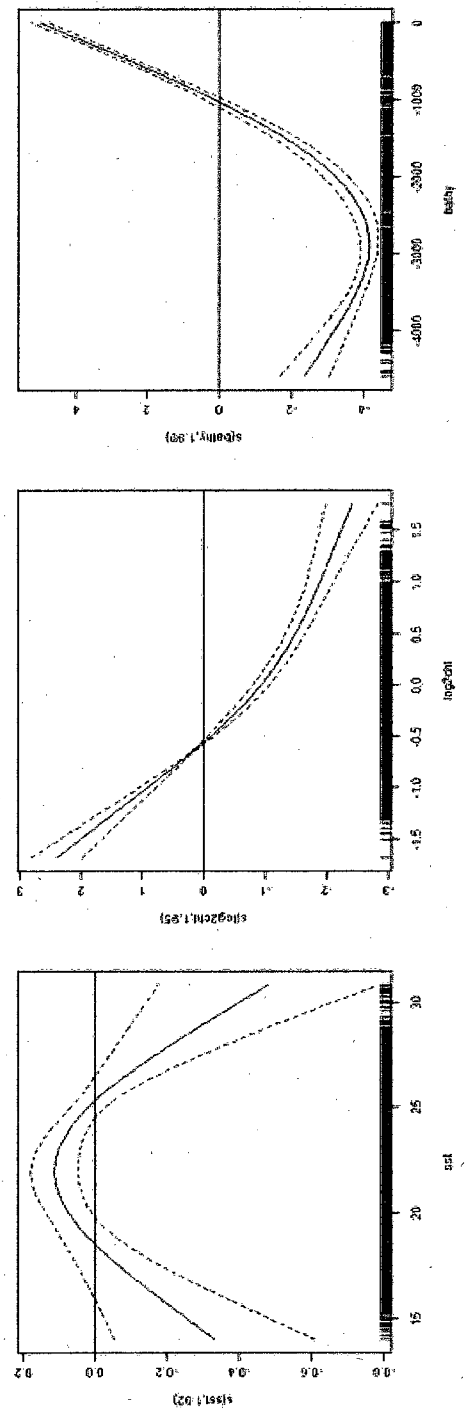

presence
1
0
Density
0.000
0.002
0.004
0.006
0.008
0.010
-4000
-3000
-2000
-1000
0
bathy

FIGURE 3.4 Generalized Additive Model functions of sea turtle presence in relation to a) sea-surface temperature; b) chlorophyll-a concentrations; and c) depth



s(bathy,1.99)
4
2
0
-2
-4
0
-1000
-2000
-3000
-4000
bathy
s(log2chl,1.95)
3
2
1
0
-1
-2
-3
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
log2chl
s(sst,1.02)
0.2
0.0
-0.2
-0.4
-0.6
-0.8
15
20
25
30
sst

FIGURE 3.5 Binary predictive habitat map showing suitable and unsuitable habitat as defined by the response of loggerhead presence to the environmental predictor variables of SST, Chl-*a*, and depth.

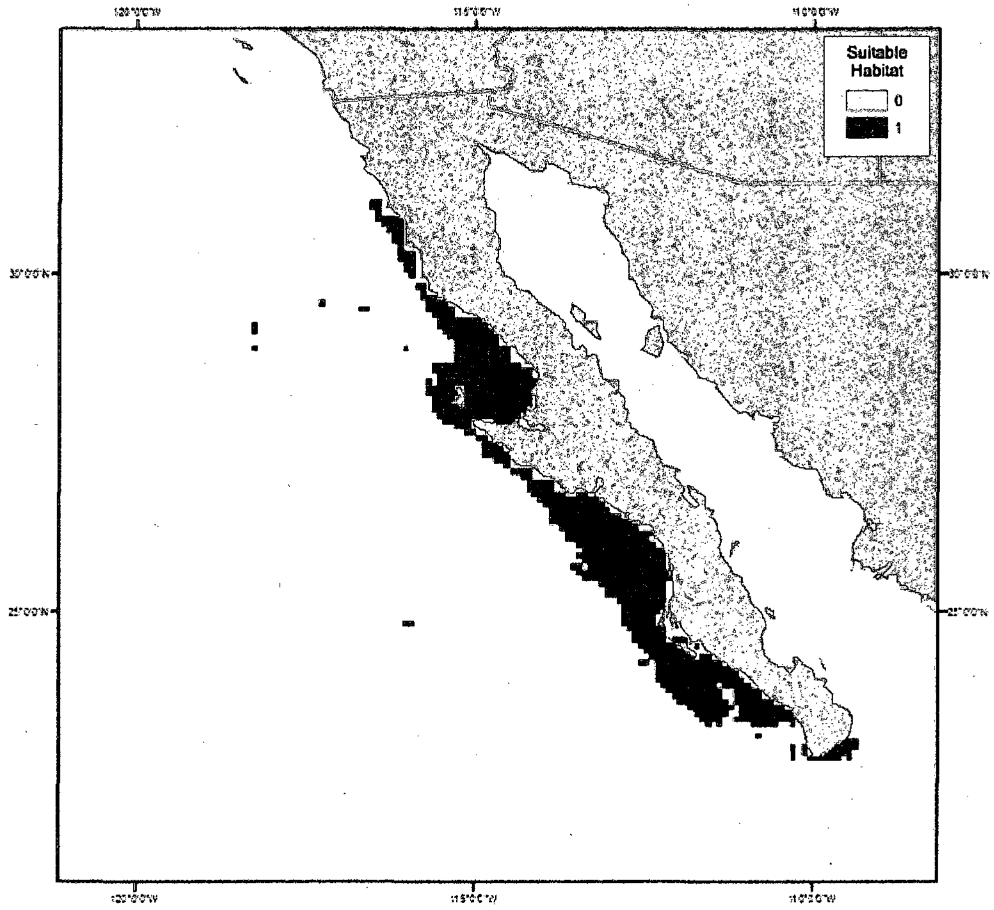

120°0'0"W
115°0'0"W
110°0'0"W
30°0'0"N
25°0'0"N
Suitable Habitat
0
1

FIGURE 3.6 Predictive habitat map showing the probability of loggerhead occurrence (0 -1), in relation to the environmental predictor variables of SST, Chl-a, and depth.

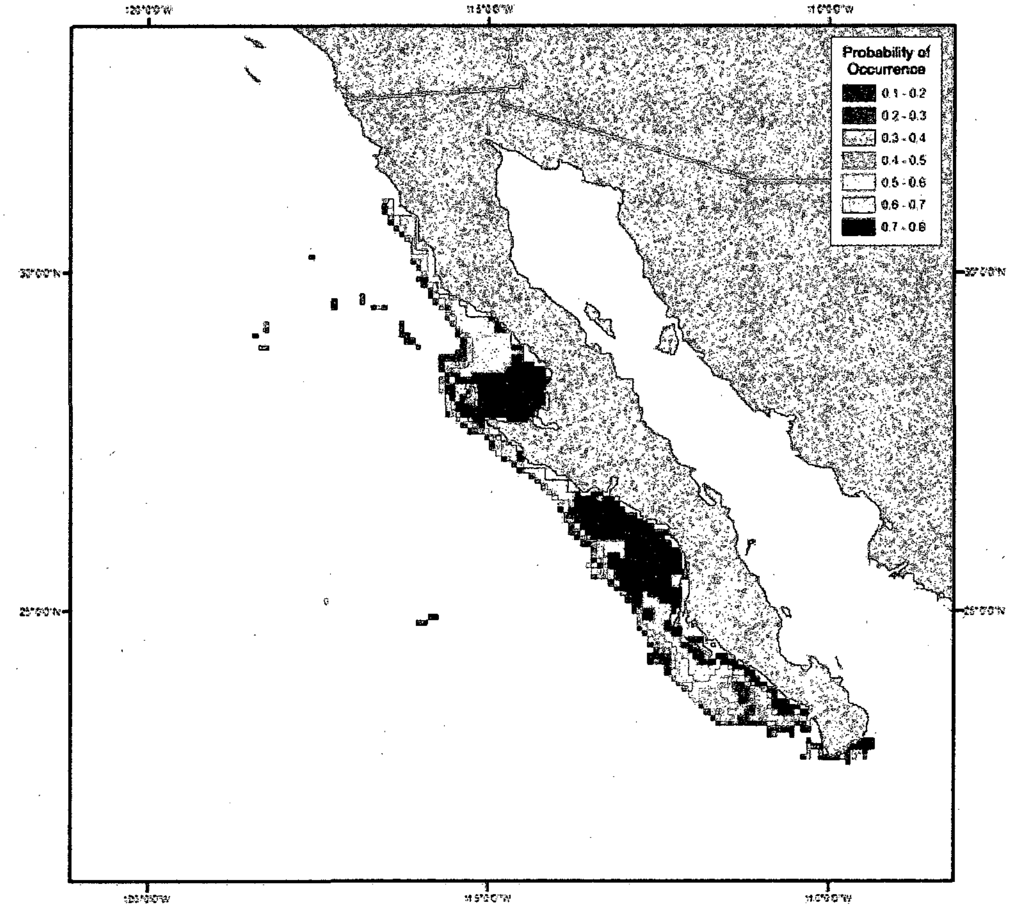
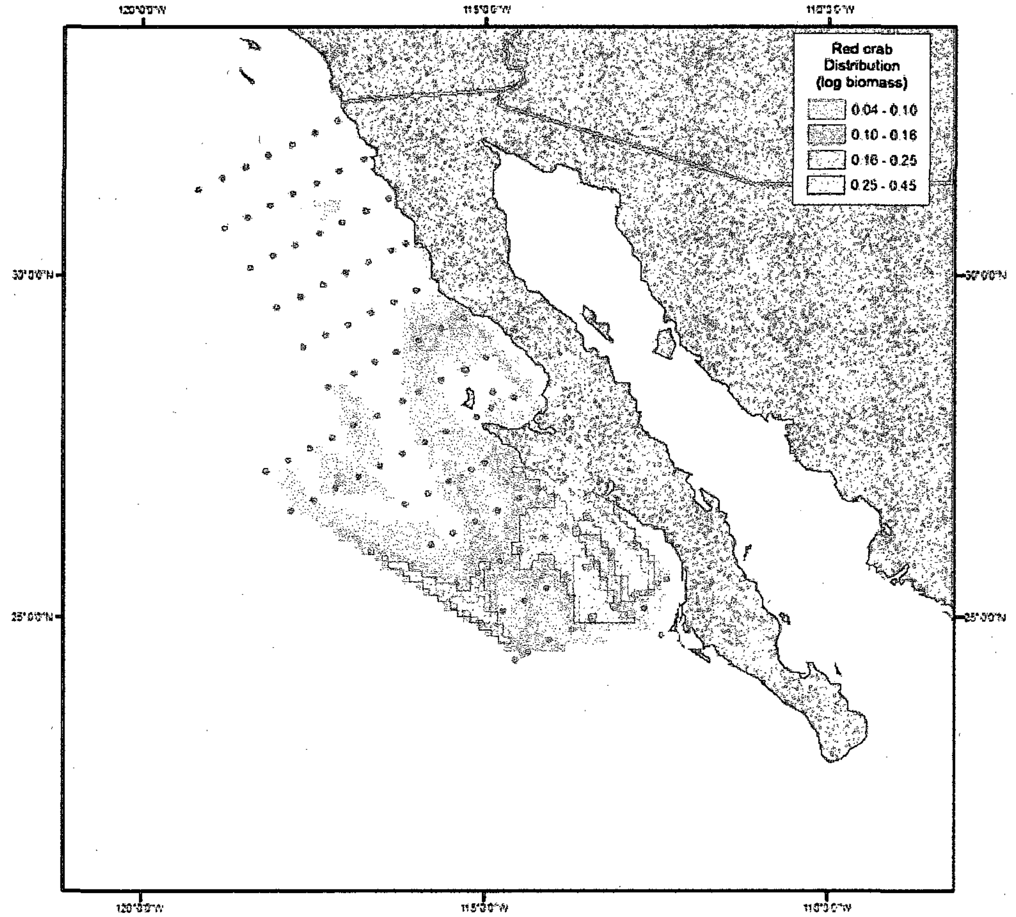
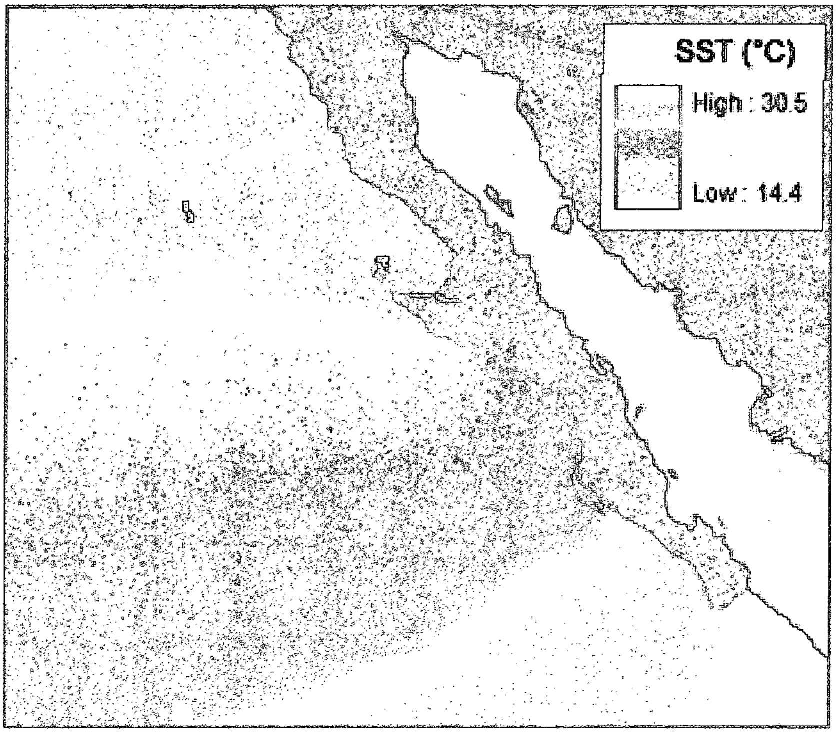

120°0'0"W
115°0'0"W
110°0'0"W
30°0'0"N
25°0'0"N
Probability of Occurrence
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8

FIGURE 3.7 All-time average of red crab abundance from IMECOCAL hydrographic surveys from 2000-2008 (log biomass).

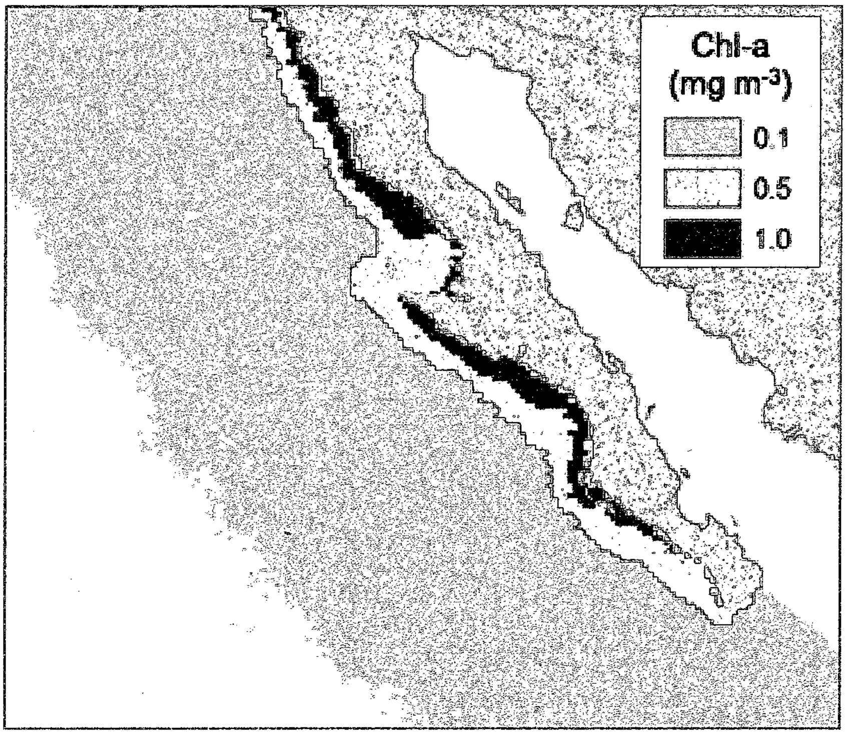

120°0'0"W
115°0'0"W
110°0'0"W
30°0'0"N
25°0'0"N
Red crab Distribution (log biomass)
0.04 - 0.10
0.10 - 0.16
0.16 - 0.25
0.25 - 0.45

APPENDIX 3.1 Temporal averages of environmental variables for the entire study period (09/1997 – 02/2007) for a) AVHRR Pathfinder sea-surface temperature (°C): monthly, 5km spatial resolution; b) SeaWiFS chlorophyll-a surface concentrations (log mg m-3): 8-day, 0.1 degree spatial resolution; c) ETOPO2v2 2 minute gridded bathymetry (~4km) in meters below sea level.

Appendix 3.1a)



Appendix 3.1b)



Appendix 3.1c)