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Ecosystem-based management for the oceanic commons: Applying the concepts of
ecosystem services, indicators, and trade-offs to make informed decisions

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Oceanography

by

Summer Lynn Martin

Committee in charge:

Professor Lisa Ballance, Chair
Professor Paul Dayton, Co-Chair
Professor Theodore Groves
Professor Stuart Sandin
Professor Lynne Talley

2014

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Co-Chair

Chair

University of California, San Diego

2014

DEDICATION

To my mom, who encouraged me to go away to college, find my passion in life, and pursue my dreams,

To my dad, who has always believed that I can accomplish anything,

To my family and friends, for their support while I was on this incredible journey,

To Lisa, for taking me under her wing, believing in me, encouraging me to explore, and investing so much of her time and energy in my development,

To Paul, for his dedication to teaching students about the importance of natural history,

To my mentors and colleagues, who inspire me every day,

To those with whom I worked on various field projects, for the incredible experiences, memories and inspiration to work in conservation.

EPIGRAPH

“The juggernaut of technology-based capitalism will not be stopped. Its momentum is reinforced by the billions of poor people in developing countries anxious to participate in order to share the material wealth of the industrialized nations. But its direction can be changed by mandate of a generally shared long-term environmental ethic. The choice is clear: the juggernaut will very soon either chew up what remains of the living world, or it will be redirected to save it.”

Edward O. Wilson
The Future of Life

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ABSTRACT OF THE DISSERTATION

Ecosystem-based management for the oceanic commons: Applying the concepts of ecosystem services, indicators, and trade-offs to make informed decisions

by

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Doctor of Philosophy in Oceanography

University of California, San Diego, 2014

Professor Lisa Ballance, Chair
Professor Paul Dayton, Co-Chair

The ocean provides numerous ecosystem services, or natural benefits, which are critical to the well-being of humanity. Over the last century, however, humans have had tremendous impacts on the ocean. Overexploitation of resources, habitat destruction, pollution and anthropogenic climate change jeopardize the ocean's ability to support a growing population.

The ocean will provide essential ecosystem services if human activities are managed sustainably. Traditional management, with its focus on single sectors or species, has often failed to conserve natural resources. Ecosystem-based management (EBM) has

been proposed as an alternative, holistic approach which considers the entire social-ecological system, including humans. It calls for maintaining healthy, productive and resilient ecosystems.

Implementation of marine EBM has largely focused on coastal areas. There has been much less emphasis on oceanic ecosystems. These systems represent a large proportion of the earth's surface and face complex challenges – they include oceanic commons, multiple jurisdictions, trans-boundary resources, and global services. For these reasons, a more holistic approach is needed.

This dissertation applies theoretical concepts of EBM to oceanic ecosystems in the eastern Pacific Ocean. Through analysis of long-term datasets containing biological, fisheries, oceanographic, and economic information, this research offers new perspectives to support oceanic EBM. The first two chapters focus on the eastern tropical Pacific (ETP), and the last chapter on the California Current Ecosystem. The chapters follow a progression from broad-scale, big-picture challenges to fine-scale, specific problems.

The first chapter provides an ecosystem-level perspective, focusing on broad-scale benefits provided by oceanic systems. It highlights and quantifies the variety of services in the ETP and sets the stage for further analysis of trade-offs. The second chapter focuses on the use of indicators to predict ecosystem characteristics that are associated with desired services. It demonstrates that tuna fishery metrics can be used as biological indicators for cetacean densities in the ETP. The third chapter focuses on fine-scale problems that arise when EBM goals conflict and decisions must be made. It provides a quantitative tool for assessing bycatch of protected species in fisheries.

Together, the results from the three chapters show promise for the implementation of EBM in oceanic ecosystems.

INTRODUCTION

Anthropogenic impacts on ocean ecosystems remain intense and global, despite a growing awareness that marine ecosystems are degraded (Worm et al. 2006, Halpern et al. 2008). Social, economic, and political pressures interact to impact marine ecosystems in complex ways. Traditional management of living marine resources has focused on single species or stocks of interest and has relied on single disciplines of expertise. This has resulted in a piece-meal understanding of marine ecosystems and, by failing to address the complex interaction of factors that impact living resources, it has often failed to conserve them. Ecosystem-based management (EBM) offers an alternative, holistic approach that considers humans as integral components of social-ecological systems, and not only in negative ways. EBM does not focus on a single species, sector, activity, or concern, but rather considers all of the benefits provided by an ecosystem and all of the impacts that humans have on that system. The primary goal of EBM is to maintain an ecosystem in a healthy, productive, and resilient condition so that it will continue to provide humans with the goods and services they want and need (McLeod et al. 2005).

A successful EBM approach requires implementation of several key concepts (McLeod and Leslie 2009). Humans should be viewed as inextricably linked to the natural world, thus forming social-ecological systems that are the focus of EBM. Resilience – the extent to which a system can absorb perturbations and still maintain its structure, function, and identity – should be investigated and understood. Management strategies should be: 1) based on input from monitoring, research, and

modeling, 2) adaptive over time, 3) focused on maintaining resilience of social-ecological systems in desirable states and eroding resilience of undesirable states, and 4) aimed at managing anthropogenic influences, rather than ecosystems themselves. The cumulative effects of different anthropogenic activities on the system should be assessed and the trade-offs associated with those different activities evaluated. To evaluate such trade-offs, economic valuation of ecosystem services (i.e., benefits humans obtain from ecosystems) can be used as a tool. And finally, prior to implementing an EBM approach, the legal and political landscape should be considered.

EBM has been embraced by government institutions, academics, and conservation entities around the world, but practical implementation has been difficult to achieve, particularly for oceanic systems (Ballance and Whitty 2010). Oceanic ecosystems, those seaward of the continental shelf, face a complex set of challenges. They include waters under the jurisdiction of multiple nations, as well as the oceanic commons; the living marine resources they include are often trans-boundary; enforcement of international agreements is extremely difficult; and the ecosystem goods and services they provide are truly global. Yet it is precisely because of these complicating factors, and because these oceanic ecosystems represent such a large proportion of the world's surface that is heavily utilized, that a more holistic approach needs to be developed.

The goal of this dissertation is to apply theoretical concepts of EBM to oceanic ecosystems in the eastern Pacific Ocean. Through the integration and analysis of several long-term datasets containing biological, fisheries, oceanographic, and economic information, this research presents new perspectives that are intended to support practical implementation of EBM for oceanic ecosystems. The first two-thirds of the research

focus on the eastern tropical Pacific (ETP) ecosystem as a case study, and the final third on a case study from the California Current Ecosystem (CCE). The chapters follow a progression from broad-scale, big-picture challenges to fine-scale, specific problems associated with EBM for oceanic ecosystems.

Chapter 1

An Ecosystem Perspective: Oceanic Ecosystem Services

The first chapter provides an ecosystem-level (in fact, a social-ecological system level) perspective, which focuses on understanding the broad-scale benefits that oceanic systems provide to humans. This perspective provides the foundation for an EBM framework. Understanding the full range of ecosystem services, and assigning monetary values where appropriate, offers an economic approach to evaluating trade-offs and informing decisions about natural resource use. This approach has been applied to coastal systems rather extensively (de Groot et al. 2012), but its application to oceanic systems is lacking. This chapter presents a case study application of the ecosystem services concept to the oceanic ETP. It integrates long-term datasets from the ETP that span nearly 100 years of commercial fishing (data from the Inter-American Tropical Tuna Commission), 35 years of market information on U.S. fish imports (data from National Marine Fisheries Service, NMFS), and 20 years of ship-based biological observations (data from NMFS). These rich data sources, along with other sources from the literature, markets, and recreational organizations, are used to quantify the major ecosystem services provided by the ETP – commercial fisheries, biodiversity, carbon storage, and recreational fishing – and provide a sense of the magnitude of economic value associated with each. The results indicate that ETP commercial fisheries may be worth an estimated \$2.7 billion annually;

sport fishing is likely worth at least \$1.2 billion annually; the potential value of natural carbon storage in the deep ocean and in large vertebrates is on the order of \$10 billion; and values associated with biodiversity in the region, while not quantified here, are likely on the order of \$1 billion based solely on ecotourism opportunities and conservation investments in the region. Our results illuminate the biological and commercial importance of the ETP in a global context, provide insights into the quantities and relative economic values of the major services, and contribute an initial assessment of ecosystem services that is important for future research and for implementation of EBM in the region.

Chapter 2

An Upper Trophic Level Perspective: Biological Indicators as Predictors

The second chapter focuses on the use of indicators that can be measured and monitored through time to predict other characteristics of an ecosystem that are associated with desired ecosystem services. Characteristics of ideal indicators include ease of measurement and accessibility of information. Some ecosystem services (e.g., fisheries productivity) may be relatively easy to measure and monitor, particularly for cases in which observer programs have already been implemented. In contrast, monitoring biodiversity or the status of top predator populations that are not the target of fisheries can be challenging and expensive, particularly for oceanic ecosystems. Identification and use of indicators based on linkages within the ecosystem is critical. The research in this chapter is also focused on the ETP and is aimed at understanding linkages among upper trophic level animals, specifically a heavily-fished tuna species and communities of oceanic cetaceans (whales and dolphins). By linking long-term datasets

that capture 20 years of biological observation (data from NMFS) and commercial fishing activity (data from IATTC), this research uses fishery metrics associated with yellowfin tuna (*Thunnus albacares*) as biological indicators for cetacean densities in the ETP. Key results include maps of predicted cetacean densities that are qualitatively similar to (and validated by) maps produced by models that include environmental variables. The approach used here can now be extended to develop similar indicators for seabirds and larval fishes. By providing measurable indicators of upper trophic level communities, this approach provides great promise for EBM in the oceanic ETP.

Chapter 3

A Protected Species Perspective: Making Informed Management Choices

The third chapter focuses on relatively fine-scale problems that arise when high-level EBM goals come into conflict and informed decisions must be made. For example, marine fisheries provide an important source of protein for billions of people globally, but they can also negatively impact populations of long-lived, slow-growing megafauna (e.g., marine mammals, sea turtles, seabirds, and sharks) through incidental bycatch. If EBM goals for a system include maintaining productive fisheries and healthy populations of megafauna, then conflicts in which a fishery threatens an endangered species require difficult decisions. These decisions should be informed by the best available science regarding the impact of one ecosystem service (the fishery, in this case) on the other (the endangered species, in this case). This chapter is focused on the CCE and uses a 20-year fisheries observer dataset (data from NMFS) to model and predict rare-event bycatch of endangered leatherback sea turtles (*Dermochelys coriacea*) and humpback whales (*Megaptera novaeangliae*) in the drift gillnet fishery off California. Bayesian model-

based methods are used to produce bycatch estimates with associated probabilities to characterize uncertainty. Results indicate that 50 to 153 leatherback turtles and 0 to 21 humpback whales were killed by the fishery from 1990 to 2009. Comparison of bycatch predictions to a regulatory threshold for humpback whales (0.113 deaths per year) suggests that the fishery warrants a “medium bycatch risk” classification; a threshold does not exist for leatherback turtles, but the probability of exceeding 2 deaths per year (a *de facto* expectation) is extremely low. The approach presented in this chapter can be used by managers to objectively and probabilistically classify fisheries with respect to bycatch impacts on species, and declare with a stipulated level of certainty that the fishery did or did not exceed estimated upper bounds. Making informed management choices related to trade-offs between fisheries and protected species is an important component of the EBM goal to employ adaptive management strategies.

LITERATURE CITED

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CHAPTER 1

**An ecosystem services perspective for the oceanic eastern tropical Pacific:
commercial fisheries, biodiversity, carbon storage and cultural services**

ABSTRACT

Degradation of marine ecosystems and loss of biodiversity through overexploitation of natural resources, habitat destruction, pollution, and anthropogenically-induced climate change have been well documented. The drivers these problems are economic in nature; until recently, ecosystem services have been assumed to hold value only if traditionally traded in markets. This has historically made decision-making for the marine environment simple. Society has extracted commodities that hold market value (e.g., fish) at the expense of ecosystem services that lack market value (e.g., biodiversity). Understanding the full range of ecosystem services, and assigning monetary values where appropriate, offers an economic approach to evaluating trade-offs and informing decisions about natural resource use. This approach has been applied to coastal systems, but its application to open ocean systems is lacking. Our research provides a case study application of the ecosystem services concept to an open ocean ecosystem, with a focus on the oceanic eastern tropical Pacific (ETP), an area of 21 million km² that includes waters of 12 nations and the oceanic commons. We analyzed the ETP in terms of production, distribution, and consumption of its major ecosystem services. We examined commercial fisheries as a key provisioning service, biodiversity (a measure of ecosystem resilience) as a key supporting service, carbon storage as a key regulating service, and examples of recreational uses (including recreational fishing) as cultural services. Using 35 years (1975-2010) of historical fisheries and economic data, we estimated a recent average market value of \$2.7 billion for the 10 most abundant commercially-fished species. We linked total catch and landings to specific countries, identifying Ecuador, Mexico, and Panama as key fishing nations, with the first 2 also

receiving 3/4 of total landings. Using a 20-year (1986-2006) dataset, we quantified species richness patterns and geographic extent for cetaceans, seabirds, marine turtles, and larval fishes, showing that the ETP contains over 1/3 of the world's species for the first 3 taxa, and that hotspots of diversity for cetaceans and seabirds exist hundreds of kilometers offshore. We estimated the value of carbon export to the deep ocean at \$12.9 billion per year, the lost value of carbon storage in two depleted dolphin populations at \$1.6 million, and the annual carbon storage value for total fishery removals (544,000 mt) at \$1.6 million. Finally, we highlighted the case of sport fishing from recent studies which suggest it is worth at least \$1.2 billion. Our results illuminate the biological and commercial importance of the ETP in a global context, offer insights into the relative magnitudes of economic value associated with its major ecosystem services, and contribute to the challenging but critical movement toward ecosystem-based management for the open ocean.

INTRODUCTION

Ecosystem services are the material and non-material benefits (i.e., goods and services) that people derive from the ecological processes of the planet's biosphere (Ehrlich and Ehrlich 1981, Costanza et al. 1997, Daily et al. 1997, Fisher et al. 2009). The oceans provide a wealth of ecosystem services that play a critical role in the survival and well-being of humanity (Ehrlich and Ehrlich 1981, Costanza et al. 1997, Daily et al. 1997, Costanza 1999). These services range in nature and scale, from provisioning (e.g., production of food, fuel or water) and regulating (e.g., regulation of climate, floods or disease) to supporting (e.g., nutrient cycling, oxygen production or habitat creation) and cultural (e.g., recreational, spiritual or aesthetic uses) (Millenium Ecosystem Assessment

2003). Key examples highlight the magnitude of their importance. First, the oceans provision a major food source – nearly 4.3 billion people obtain 15% of their animal protein from fish (UNFAO 2014). Two-thirds of total (freshwater and marine) annual fish production comes from the ocean, with 80 million tonnes captured in wild fisheries and 25 million tonnes produced through aquaculture (UNFAO 2014). Second, the oceans regulate climate by serving as a major carbon sink, absorbing nearly 50% of all anthropogenic carbon emissions (Sabine et al. 2004). This has dampened the immediate warming effects of greenhouse gases on the terrestrial biosphere. Third, marine organisms, most notably phytoplankton, account for nearly 50% of global primary production (Field et al. 1998). These primary producers support marine ecosystems by converting carbon dioxide into oxygen and particulate organic carbon (POC) for animals to consume. This process also starts the biological carbon pump, which transports a portion of POC from the surface layer to the deep ocean, where it is sequestered on timescales of hundreds to thousands of years (Henson et al. 2012). Fourth, the oceans provide a multitude of cultural services, including recreational opportunities (e.g., boating, diving, fishing and surfing) and spiritual, artistic, historical, and educational information (de Groot et al. 2002). These services have been historically important in human societies and in recent decades made marine tourism the fastest growing tourism sector in the world (Hall 2001). Globally, the economic value of all marine ecosystem services combined is estimated at \$50 trillion in 2011 \$US (Costanza et al. 2014).

In the last century, humans have had a tremendous impact on the ocean. Degradation of marine ecosystems and loss of biodiversity through the overexploitation of resources, habitat destruction, pollution and anthropogenically-driven climate change

has been well documented (Jackson et al. 2001, Dulvy et al. 2003, Pandolfi et al. 2003, Worm et al. 2005, Lotze et al. 2006, Worm et al. 2006, Halpern et al. 2008). The drivers of these problems are economic in nature; modern industrial society has largely made decisions about resource use without considering the negative impacts of its actions on the environment. Until recently, ecosystem services have been assumed to hold value only if traditionally traded in markets. This has historically made decision-making for the marine environment simple. Society has chosen to extract commodities that hold market value (e.g., fish) potentially at the expense of ecosystem services that lack market value (e.g., biodiversity). Adding to this problem is the fact that nature's benefits are often public goods to which individuals do not hold property rights. In many cases, including the case of commercial fishing, this has caused a race to exploit the resource without regard to its future or the impacts on the supporting ecosystem, resulting in the "tragedy of the commons" (Hardin 1968) and the current jeopardized state of many ecosystems. These impacts have diminished the ability of natural marine ecosystems to meet the demands of a growing human population (Worm et al. 2006).

The oceans will provide essential ecosystem services if human activities are managed sustainably into the future. Traditional marine management has focused on single sectors, species, or activities, and has relied on single disciplines of expertise. This approach has resulted in a piece-meal understanding of marine ecosystems and has often failed to manage or protect natural resources because it does not consider the complex interaction of social, economic, and political factors impacting those resources. Ecosystem-based management (EBM) offers an alternative, holistic approach that considers the entire system, rather than single sectors or species, and explicitly factors

humans into the equation (McLeod et al. 2005). It emphasizes managing anthropogenic activities to maintain healthy, productive and resilient ecosystems that provide the services that humans want and need.

An important step in implementing EBM is to employ an ecosystem services approach to understand the social-ecological system of interest. This involves identification and quantification of the natural benefits, human uses and impacts, relevant stakeholders, and monetary or cultural values associated with the various benefits. Application of this ecosystem services concept to marine environments has largely focused on coastal systems, including coral reefs, mangrove forests, salt marshes, seagrass beds, sand dunes, and beaches. This is apparent in the number of monetary value estimates that are available for coastal systems. Out of 275 estimates, 95% were relevant to coastal systems and only 5% pertained to the open ocean (de Groot et al. 2012). There has been much less emphasis on the open ocean because it is further offshore, more remote, and more difficult to study and manage. However, as management for open ocean ecosystems moves toward more holistic approaches, efforts to assess the ecosystem services they provide will need to progress.

The goals of this paper are to apply the concept of ecosystem services to an open ocean (e.g., seaward of the continental shelf, which we will refer to as “oceanic”) system, identify potential trade-offs in alternative uses of the system, and estimate monetary values where appropriate to facilitate this process. We use the eastern tropical Pacific (ETP) as a case study and target commercial fisheries as a key provisioning service, biodiversity as a key supporting service, Carbon dynamics as a key regulating service, and direct and indirect use by recreational fishers, ecotourists, and conservationists as

examples of key cultural services. Our results illuminate the importance of the ETP in a global context and contribute to the challenging but critical movement toward ecosystem-based management for the open ocean.

METHODS

Study Area

The oceanic eastern tropical Pacific (ETP) as used here is defined as the area seaward of the continental shelf, from the Americas west to approximately 150° longitude, and from the U.S.-Mexico border south to central Peru (Fig. 1). This area is roughly 21 million km², includes waters of 12 nations and the oceanic commons, and roughly corresponds to the area managed by two regional fishery management bodies: the Inter-American Tropical Tuna Commission (IATTC) and the Agreement on the International Dolphin Conservation Program. It has been used for more than 50 years as productive fishing grounds for yellowfin, bigeye, and skipjack tuna (*Thunnus albacares*, *T. obesus*, and *Katsuwonus pelamis*, respectively), and there has been a long history of interaction between the commercial tuna purse-seine fishery and pantropical spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*, respectively) (Wade et al. 2007). The ETP, as defined here, encompasses the entire range of the dolphin stocks impacted by the fishery. Because of the magnitude of the commercial fishery and the historical impacts on dolphin populations, the ETP has been well-studied and is relatively data rich compared to most other oceanic systems (Ballance et al. 2006 and references therein, Wade et al. 2007, Gerrodette et al. 2012).

Provisioning Services: Commercial Fisheries

The IATTC maintains an online source of publicly available data on commercial fisheries catches in the IATTC Convention area. Time series data range from 1918 through 2011, with data beginning in different years for different species groups. Metric tons (mt) of catch are aggregated by year, species group, vessel flag (country), and gear type. Combining all gear types and vessel flags, we calculated the mean, standard deviation, minimum, and maximum annual catch for each species group and for all species combined. Combining all species groups and gear types, we analyzed the distribution of total annual catch among vessel flags. Combining all species groups and vessel flags, we determined the percentage of cumulative total catch obtained by different gear types. We will refer to the fished species using their common names; Latin names are provided in Table 1.

The National Marine Fisheries Service (NMFS) Office of Science and Technology maintains an online database of foreign trade fisheries statistics. For fish imported to the U.S., data on total weight imported (in kilograms) and price paid (in U.S. dollars) are aggregated by year, taxon (species group), and export country. We focused on data corresponding to the top 10 species groups in terms of maximum annual catch (from the IATTC dataset as described above). Data were available from 1975 to 2010 on imports from IATTC member countries in Latin America (Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Mexico, Nicaragua, Panama, Peru, and Venezuela). We excluded IATTC member countries that are not located in Latin America (France, Japan, South Korea, Spain, and Vanuatu) because the NMFS data include all fish imported from a country, regardless of where the fish were caught. For Latin American

countries, we examined fishery profiles from the Food and Agriculture Organization of the United Nations to confirm that the large majority of fish are caught in the Pacific rather than the Atlantic; thus, we assumed that all U.S. imports from those countries were caught in the ETP.

For each of the 10 species groups, we calculated the annual price per metric ton using the U.S. imports data. We applied these annual prices to total annual catches to estimate the total market value for each year. Total market values were adjusted for inflation using the U.S. Inflation Calculator available online, which is based on U.S. government consumer price index data. All values are presented in 2010 U.S. dollars, thereby allowing for comparisons across years. Combining the 10 species groups, we produced a plot of cumulative annual catch and estimated market value (Fig. 4). We used linear regressions to analyze general temporal trends in catch and market value.

Focusing on yellowfin tuna as the top species in terms of cumulative catch over the years, we mapped total effort and catch by the purse-seine fishery over a 20 year period (1986-2006). Effort was measured as the number of purse-seine sets of 3 different types (on dolphin schools, floating objects, or schools of tuna unassociated with objects or dolphins); catch was measured in metric tons (mt) of fish caught. The data used in this analysis were provided by IATTC through a special agreement. The spatial resolution was 2° latitude by 2° longitude for most of the data; however, when effort in a grid cell was comprised of fewer than 3 vessels or was solely within one country's exclusive economic zone, the data were provided at a resolution of 5° to maintain confidentiality. For 5° by 5° cells, we divided the catch and effort by 6.25 (the number of 2° by 2° cells

in one 5° by 5° cell) to standardize values to the 2° by 2° cells. We binned the catch and effort data into 5 quantitative categories each to map them.

Data on the distribution of purse-seine fishery landings among different ETP ports in 2010-2011 were provided by IATTC for this study. Species groups represented by these landings data include albacore tuna, eastern Pacific bonito, bigeye tuna, black skipjack tuna, eastern Pacific and striped bonito, dolphinfishes, bullet and frigate tunas, Pacific Bluefin tuna, skipjack tuna, tunas not elsewhere included, and yellowfin tuna. We plotted the 2010-2011 mean annual percent of landings for each port. For each country, the data also included the percentage of landings brought to shore by vessels carrying the flag of that country. From this, we determined the proportion of landings in each country that is supplied by foreign vessels.

Supporting Services: Biodiversity

Data on cetaceans (whales, dolphins, and porpoises), seabirds, marine turtles, and ichthyoplankton (includes larval fishes, squids, and octopuses) were collected during vessel-based surveys of the ETP conducted by the Southwest Fisheries Science Center (SWFSC) of the National Oceanic and Atmospheric Administration's National Marine Fisheries Service between 1986 and 2006. Surveys took place between July and December, with most effort occurring between August and November. Cetacean data were collected using standard visual line-transect survey methods (Gerrodette and Forcada 2005). For this analysis, we used data from 1986-1990, 1998-2000, 2003, and 2006. Seabird data were collected using standard visual strip-transect survey methods (Ballance 2007). Our analysis includes seabird data from 1988-1990, 1998-2000, 2003, and 2006. Marine turtle data were collected during the cetacean line-transect surveys, and

data from 1998-2000, 2003, and 2006 were included here. Ichthyoplankton samples were collected daily using manta net tows (Vilchis et al. 2009). We included data from 1987-1990, 1998-2000, 2003, and 2006.

We used a spatial grid of 2° (roughly the distance the ship traverses in one day while conducting a survey) to investigate biodiversity patterns for cetaceans, seabirds, and larval fishes. Our metric of biodiversity was species richness, calculated for each 2° by 2° degree grid cell as the number of species observed over all data years. Sightings or specimens identified to order, family, or genus only counted toward the species tally if a species within that higher taxon had not already been observed in that cell. We used the same spatial grid for turtles, but we calculated sightings density instead of species richness because nearly all sightings were of olive ridley turtles (*Lepidochelys olivacea*). Survey effort (the number of hours the ship spent on survey effort for cetaceans, seabirds, and turtles, and total volume of water filtered by net tows) was also calculated per grid cell.

Regulating Services: Carbon export and storage

We estimated the amount of carbon (C) exported annually from the surface to the deep ocean in the ETP, and the potential market value of this carbon. The ETP as we have defined it has an area of approximately $2.1 \times 10^{13} \text{ m}^2$. Emerson et al. (1997) estimated that $24 \text{ grams of C m}^{-2} \text{ yr}^{-1}$ are exported from the surface to the deep ocean in an oligotrophic (nutrient poor) area in the Pacific Ocean. Portions of the ETP, notably, the Equatorial Cold Tongue and the Costa Rica Dome, are characterized by high nutrient concentrations relative to oligotrophic waters (Fiedler and Talley 2006), but we used this value as a conservative estimate for our calculations. The product of these quantities

estimates the amount of C exported annually in the ETP. After converting this quantity to metric tons (mt), we divided by 0.2729 mt, the amount of C in 1 mt of CO₂ (1 trading unit = 1 mt of CO₂ = 0.2729 mt of C + 0.7271 mt of O₂) to estimate the equivalent number of CO₂ trading units. To estimate the potential market value, we multiplied the CO₂ units by a range of prices from the European Union Allowances Emissions Trading System, currently the largest carbon market in the world (USIWG 2013, World Bank 2014). We used the recent average of \$7 per mt (with \$5 and \$9 as lower and upper limits) to estimate current potential value. For a potential future scenario, we used a much higher price of \$35 per mt, a recent estimate of the price required to achieve climate stabilization goals and pay for climate-change related damages. This price was also observed in an early phase of the market before the major economic downturn in 2008.

The tuna purse-seine fishery has potentially impacted the amount of carbon stored in populations of large vertebrates, specifically populations of fish that are targeted either directly or indirectly (Gerrodette et al. 2012) and populations of dolphins that were incidentally depleted as bycatch in the past (Wade et al. 2007). For the fish populations, we estimated the amount of C that is removed annually by applying a total body carbon content of 11.5% (Czamanski et al. 2011) to the annual purse-seine fishery biomass removals of 543,533 mt (Gerrodette et al. 2012). After converting from mt of C to equivalent CO₂ trading units, we applied the same range of market prices as above. For the depleted dolphin populations, we determined the decrease in standing stock biomass (mt) by taking the difference between the estimated pre-exploitation and current population sizes (Wade et al. 2007, Gerrodette et al. 2008) and applying a mean body mass of 65.4 kg and 52.5 kg for northeastern offshore spotted and eastern spinner

dolphins, respectively (Trites and Pauly 1998, Perrin et al. 2005). We applied a total body carbon content of 25% (based on an estimate for humans by Wang and Pierson (2010)) to that biomass, converted it to equivalent CO₂ trading units, and applied a market price of CO₂ to estimate the potential market value of the lost carbon.

Cultural Services: Recreational Fishing

The Billfish Foundation (TBF) exists to promote the conservation of billfish (marlins, sailfish, and swordfish) and associated species (e.g., tunas), healthy oceans, and a sustainable recreational fishing industry that targets these species. TBF lobbies for conservation-based management of both commercial fisheries and recreational fisheries as part of its strategy. Recently, TBF released a series of sport fishing socio-economic studies for 3 locations in Latin America: Los Cabos (Baja California Sur, Mexico), Costa Rica, and Panama (Southwick et al. 2008, Jimenez et al. 2010, Southwick et al. 2013). The purpose of these studies was to demonstrate the economic value of sport fishing to local economies. This effort, which included surveys of tourists at airports, anglers, hotels, restaurants, and local businesses, appears to be the first major attempt to quantify the economic impact of sport fishing in Latin America. The reports also aim to understand the factors appealing to international anglers traveling to those locations (mostly from the U.S.). We believe these reports, with their focus on highly migratory pelagic species, contain uniquely relevant information for understanding different uses of ETP ecosystem services. We summarize the important findings across the 3 reports as an example of key cultural services provided by this region.

RESULTS

Provisioning Services: Commercial Fisheries

Commercial fisheries operating in the ETP from 1918 to 2011 caught an estimated total of 28,281,645 mt (Tbl. 1). Of this estimated cumulative catch, 65% was captured using purse-seines, 18% by longlines, 9% with pole-and-line methods, and the remaining 8% with trolls, harpoons, gillnets, and hook-and-line methods. Annual catch ranged from 1,089 to 906,250 mt (mean = 300,869 mt, CV = 82%) across all years, with an increasing trend over time and high values in recent years that are often double the mean (e.g., 585,226 mt in 2011). Yellowfin tuna was by far the top species in terms of cumulative catch over time, mean annual catch, and maximum annual catch (Tbl. 1). It also had the largest range of annual catch amounts, with a minimum of 136 mt in 1919 and a maximum of 439,317 mt in 2002. Skipjack tuna had the next highest cumulative catch and mean annual catch, both of which were roughly 60% of those amounts for yellowfin tuna. In 2011, the skipjack catch exceeded that of all other species. Bigeye tuna was the third most important species, with cumulative and mean annual catches 33% and 52% of the yellowfin tuna amounts. Catch data for skipjack and yellowfin tuna began in 1918-1919, while data for bigeye tuna only date back to 1954. Together, these 3 species comprise 86% of the cumulative catch.

Twenty-seven different countries fished (legally, based on IATTC data) in the ETP from 1918-2011, each with a unique temporal trend in its annual catch (Fig. 2). Countries with the highest percentage of cumulative catch across all years included the U.S. (23%), Mexico (14%), Japan (13%), Ecuador (13%), Venezuela (6%), and Panama (4%). U.S. catch ramped up from the 1950s (Fig. 2a), peaked in the late 1970s when the

U.S. captured 60% of the total catch (Fig. 2b), and tapered to nearly zero in 2011.

Mexico's catch gradually increased from the 1960s to the 1980s and remained relatively steady thereafter (Fig. 2a); it was 22% of total catch in 2011 (Fig. 2b). Japan's catch was fairly consistent from the late 1950s through the early 1990s (Fig. 2a), but it decreased in the 2000s and only represented 2% of the total in 2011 (Fig. 2b). Ecuador's catch slowly increased from the 1960s onward (Fig. 2a); in 2011, it captured the largest portion of total catch (37%) (Fig. 2b). Venezuela began fishing in the early 1980s, increased its catch into the 1990s (Fig. 2a), and acquired an 8% share of total catch in 2011 (Fig. 2b).

Panama's relatively small fleet appeared in the 1970s, grew in the 2000s (Fig. 2a), and claimed 10% of total catch in 2011 (Fig. 2b). Colombia is represented in the "Other" categories in Fig. 2 because it only caught 1% of the cumulative catch; however, in 2011, its portion of total catch was 8%. Spain, Vanuatu, Korea, Peru, Taiwan, and Chile each caught 1-2% of the cumulative total. Spain, Korea, Nicaragua, and Taiwan each caught 1-2% of the 2011 total.

Increasing trends ($p < 0.01$) were observed in annual catch and market value from 1975 to 2010 for yellowfin, albacore, dolphinfish, swordfish, and the "all species" group that combined 10 species groups (Fig. 3, 4). Increases in catch and value were notably disproportionate for yellowfin tuna (only a 30% increase in mean annual catch but a 239% increase in mean annual value after 1990, when the dolphin-safe label was introduced in the U.S. (see Wade et al. (2007) for a brief review of the dolphin-safe label) and for "all species" (46% increase in catch and 226% increase in value after 1990).

There was a significant increase ($p < 0.001$) in the price per ton for yellowfin tuna over time, which was \$2,222 (mean annual price per ton) for 1975-1990 and \$5,492 for 1991-

2010. For “all species,” mean annual price per ton was \$3,111 across all years (range: \$1,431 - \$6,339, CV = 53%), but increased from \$1,932 for 1975-1990 to \$4,055 for 1991-2010. Mean annual market value increased from \$830 million for 1975-1990 to \$2.7 billion for 1991-2010, and was \$1.9 billion for the entire period (range: \$487 million - \$4.7 billion, CV = 76%). Trends for “all species” largely reflect trends for yellowfin tuna, as it comprises 46% of the cumulative catch in this period (Fig. 4).

Trends in annual catch and market value for the remaining species groups varied. Bonitos were the only group with significant decreases ($p < 0.01$) in both annual catch and market value (Fig. 3). There was no significant trend in catch for bluefin tuna, but value significantly increased ($p < 0.001$) (Fig. 3) due to an increase ($p < 0.10$) in the price per metric ton (mean of \$5,424 for 1989-1990 and \$10,853 for 1991-2010). For skipjack, bigeye, and elasmobranchs, annual catch increased significantly ($p < 0.001$), but there was no significant trend in value (Fig. 3), due to significant decreases ($p < 0.01$) in the price per ton for skipjack tuna (mean of \$1,836 for 1975-1990 and \$1,355 for 1991-2010) and elasmobranchs (mean of \$33,026 for 1975-1990 and \$3,820 for 1991-2010). The price per ton for bigeye tuna did significantly increase ($p < 0.01$), but a decreasing trend in catch over the years for which we had price data (2001-2010) probably canceled this effect, leading to the absence of significant change in the total value. There were no significant trends for the “tunas – other” group.

Typical supply and demand dynamics, in which the price per ton decreases with an increased supply of fish, were not apparent in all species groups. Skipjack tuna and elasmobranchs did follow these dynamics; however, the dynamics were reversed for yellowfin, bigeye, albacore, and dolphinfish. For these groups, the price per ton increased

as catch increased over time. For swordfish and bonitos, the price per ton did not change significantly through time, indicating an elastic demand that was not influenced by supply.

Spatial patterns in purse-seine fishery effort and yellowfin tuna catch were slightly different (Fig. 5). The highest concentrations of catch occurred between the southern tip of Baja California and Mazatlan, near the Costa Rica dome, and along the 10°N thermocline ridge. Concentrations of effort are also highest in those regions but have a broader geographic extent surrounding them and a clearer gradient of high values in the east and low values in the west.

ETP fishery landings in 2010-2011 were distributed across ports in the following countries (Fig. 5): Ecuador (51%), Mexico (25%), Colombia (9%), El Salvador (5%), Guatemala (3%), Costa Rica (3%), Venezuela (3%), and Peru (2%). Differences between 2010 and 2011 percentages were 0-2% for all port locations except Manta, Ecuador, where the percentage of total landings increased from 36% to 44%. The 2010-2011 mean percentages of landings that were brought to shore by vessels with the port's national flag were: Venezuela (100%), U.S. (100%), Mexico (96%), Colombia (75%), El Salvador (68%), Ecuador (62%), Guatemala (6%), Costa Rica (0%), and Peru (0%). The reverse order of this ranked list indicates how commonly foreign vessels land fish in these ports (i.e., landings in Peru were all from foreign vessels, whereas landings in Venezuela were all from domestic vessels). These percentages for each country varied 0-6% between years, with the exception of a 14% decrease for Ecuador. For the U.S., there were only data for 2011.

Supporting Services: Biodiversity

Cetacean species richness ranged from 1 to 16 species per grid cell (mean = 6.6, CV = 49%), excluding cells with no cetacean sightings (Fig. 6). Regions of high richness (12-16 species per cell) occurred off the southern of the tip of Baja California (near 109°W, 23°N), around the Costa Rica Dome (near 90°W, 9°N), and in the Panama Bight (near 81°W, 8°N). Intermediate richness (4-11 species per cell) was observed in the majority of remaining cells throughout the ETP. Survey effort ranged from 0.2 to 109.2 hours (0 – 9 survey days) per grid cell (mean = 31.7, C= 69%), with (by design) the highest levels of effort in the core of the ETP and the lowest levels near the western perimeter (Fig. 6). Nevertheless, qualitatively, patterns of richness do not simply reflect patterns of effort.

Seabird species richness ranged from 1 to 38 species per grid cell (mean = 15.8, CV = 48%), excluding cells with no seabird sightings (Fig. 7). Richness was generally highest within the Exclusive Economic Zones (EEZs) of the bordering countries (i.e., within 200 nm, or within 2 cells, from the shoreline), and along the 10°N thermocline ridge. Survey effort ranged from 0.04 to 103.5 hours (0 – 8.6 survey days) per grid cell (mean = 27.5, CV = 71%), with patterns nearly identical to those for cetacean effort.

Ichthyoplankton species richness ranged from 1 to 50 species per grid cell (mean = 8.5, CV = 94%), excluding cells with no larval specimens collected (Fig. 8). Sampling effort ranged from 52 to 13,283 m³ per grid cell (mean = 1,449, CV = 124%), and followed a similar east-west gradient with higher effort near the coasts.

Marine turtle sightings density ranged from 1 to 158 sightings per grid cell (mean = 14.6, CV = 189%), excluding cells with no turtle sightings. The highest density of

sightings occurred in EEZ waters off southern Mexico (Guerrero and Oaxaca), Guatemala, and Costa Rica (Fig. 9). Survey effort ranged from 0.2 to 72.2 hours (0 – 6.0 survey days) per grid cell (mean = 16.6, CV = 81%), with similar patterns to those for cetacean and seabird effort but with fewer areas of high and intermediate effort due to fewer years of data.

Regulating Services: Carbon Storage

Our conservative estimate for the amount of C exported from the surface to the deep ocean in the ETP was 5.0×10^{14} g or 5.0×10^8 mt of C per year (Tbl. 3). This was equivalent to 1.8×10^9 trading units of CO₂, which had a total value of \$12.9 billion per year (range: \$9.2 - \$16.6 billion per year) using an average carbon price (Tbl. 3). If the carbon price reaches \$35 per mt, as experts suggest it should in order to capture the social cost of carbon, then the ETP's export service would be worth \$64.7 billion per year.

The population of northeastern offshore spotted dolphins is estimated to have decreased by 76% from 3.6 million individuals in pre-exploitation years to 857,884 individuals in 2006. With an average body mass of 65.4 kg, the 2.74 million dolphins lost from the population represent a total biomass of 179,334 mt, of which roughly 44,834 mt was carbon. This carbon amount was equivalent to 164,286 mt of CO₂ trading units, with a total value of \$1,398,161 (range: \$998,687 - \$1,797,636). Spreading this value across the 2.74 million dolphins yields a potential carbon storage value per dolphin of \$0.42 (range: \$0.30 - \$0.54). At a carbon price of \$35 per mt, the value of the lost portion of the population would be \$5,750,003, or \$2.10 per dolphin.

The population of eastern spinner dolphins is estimated to have decreased by 41% from 1.8 million individuals prior to exploitation and 1,062,879 individuals in 2006. The

reduction of the population by 737,121 dolphins, with an average body mass of 52.5 kg, represented a loss of 38,699 mt total and 9,675 mt of carbon from the system. This was equivalent to 35,451 mt of CO₂ trading units worth a total of \$248,160 (range: \$177,257 - \$319,063) or \$0.34 per dolphin (range: \$0.24 - \$0.43). The value would be \$1,240,802, or \$1.68 per dolphin, if the carbon price were \$35 per mt.

Total fishery removals of 543,533 mt per year contained 62,506 mt of carbon. This was equivalent to 229,045 mt of CO₂ trading units with a potential value of \$1,603,313 per year (range: \$1,145,223 - \$2,061,402). Spreading this value across the 543,533 mt of fish caught yields a value of \$2.95 per mt of fish (range: \$2.11 - \$3.79). At \$35 per mt for CO₂, the potential carbon value for the fishery removals would be \$8,016,564, or \$14.75 per mt.

Cultural Services: Recreational Fishing

Sport fishing was estimated to bring \$634 million in expenditures to Los Cabos in 2007, \$467 million to Costa Rica in 2008, and \$97 million to Panama in 2011. This total of \$1.2 billion in expenditures in these 3 locations covered the cost of charter boats, lodging, food, transportation, tackle, fuel, and other fishing needs. The costs were incurred by an estimated 354,013 visitors who fished in Los Cabos, 283,790 who fished in Costa Rica, and 86,250 who fished in Panama. In Los Cabos, anglers paid an estimated \$1,785 per person during a trip. Of visitors who flew to these destinations, anglers represented 25% in Los Cabos (mostly American), 22% in Costa Rica (Americans and Canadians were surveyed), and 9% in Panama. In Los Cabos, visitors who fished were estimated to provide 24.1% of the total dollars injected into the local economy by tourism. Given the choice of 4 locations in the Atlantic (Bahamas and South Florida) and

Pacific (Cabo San Lucas in Mexico and Golfo de Papagayo in Costa Rica), 46% of anglers stated a preference for fishing in the Pacific locations if given the choice (35% preferred the Atlantic locations and 19% had no preference) (Southwick et al. 2008).

Anglers who had fished in Los Cabos revealed their perception that commercial fishing is detrimental to the quality of their experience. A large majority (88%) said they would be less likely to return to Los Cabos if commercial fishing for billfish increased, and more likely to return if commercial restrictions or bans were implemented.

DISCUSSION

Provisioning Service – Commercial Fisheries

For nearly 100 years, humans have commercially harvested fish from the ETP. This remote region of the ocean has provided at least 28 million mt of large pelagic fish as a food source to the world. To put this large amount of biomass into more familiar units, it is equal to 5.7 million African elephants (*Loxodonta africana*) – these are the largest extant terrestrial animals, weighing 5 mt on average. These elephants could stand in a single-file line at the equator and wrap around the earth nearly 10 times. Annually, the current production in the ETP is equal to 117,045 African elephants, which could form a single-file line about half as long as the Baja California peninsula. As a provisioning service, commercial fisheries production in the ETP has made a significant contribution to feeding the world, and it currently accounts for 1% of global marine capture fisheries production (80 million mt per year).

Numerous countries have benefited from commercial fishing in the ETP, particularly those with fishing fleets and processing ports that earn profits and create jobs. At least 27 countries have legally fished in the area over time. Historically, the key

players were the U.S. (which accounted for nearly a quarter of the historical biomass removals), Mexico, Japan, and Ecuador. In the last two decades, the U.S. and Japan have dropped from this list, and Panama, Venezuela, and Colombia have replaced them. Fishing fleets from Europe, Asia, the south and southwest Pacific, the Caribbean, and Africa have had a small presence. In terms of where the fish is landed after it is caught, Ecuador is by far the largest stakeholder with over half the annual landings coming into its ports. Mexico is also important in this regard, as its ports receive a quarter of annual landings. Panama is the only major fishing nation that does not also have ports with sufficient infrastructure to process landings. Now that all key fishing nations and ports are Latin American, perhaps the cooperation required for place-based management of the region is more feasible.

Our estimated market values for commercial fisheries are only intended to provide some perspective on the magnitude of value associated with this sector. The values are not precise – they are only based on market prices from imports to the U.S., thus they do not capture the full picture. Because the processing plants are private business entities, obtaining data on where they distribute the fish is difficult, but we know the fish are exported to many countries other than the U.S. Similarly, obtaining data on the price paid for fish is difficult. Therefore, we made use of the information available through NMFS on historical U.S. import prices of fish from the ETP (1975-2010) and extrapolated an estimated value for the whole fishery. From our synthesis of these data with the IATTC catch data, we estimated that the U.S. imports roughly 15% of the total ETP catch, across all species, which means that we used the price paid in the U.S. to extrapolate a value for the remaining 85% of the catch. As an additional caveat, the price

of yellowfin tuna increased dramatically in the U.S. after the implementation of dolphin-safe tuna labeling in 1990. Given these two issues, plus the fact that yellowfin tuna comprises nearly half the catch, we may have overestimated total market value across the 10 species groups (mean of \$2.7 billion per year after 1990). However, our goal was to understand the magnitude of market value for ETP commercial fisheries, not to provide the most accurate or precise estimate.

Temporal dynamics in annual catch and market value for the 10 individual species groups for 1975-2010 were complex. The species groups all impact one another and are also part of a global market. Not all species groups followed typical supply and demand dynamics; the ones with inelastic demand (e.g., swordfish) likely indicate that they are part of a much larger global market in which demand for the fish had not yet been saturated. Those with reversed dynamics, where the price per ton increased with increasing supply (e.g., yellowfin tuna), might reflect a change in the product or increase in the cost of fishing. For example, the U.S. label for dolphin-safe tuna essentially created a new product that potentially cost fishers more to catch due to increased time to locate schools of tuna unassociated with dolphins. Trends for all 10 species groups combined essentially reflect trends of the species with largest portions of catch from 1975 to 2010 – those were yellowfin (46%), skipjack (27%) and bigeye (17%).

Supporting Service – Biodiversity

The ETP contains high species richness of oceanic megafauna. Over 1/3 of the world's cetacean and seabird species and over 2/3 of marine turtle species occur in the region (Tbl. 2). Based on IUCN red list criteria, 17% of these cetacean species, 26% of the seabird species, and 100% of the marine turtle species are threatened to some degree

(critically endangered, endangered, or vulnerable) (Tbl. 2). Whereas seabirds and turtles spend a portion of their life cycle on land and are relatively easy to monitor, cetaceans reside completely in water, making it more difficult to assess their populations. Thus, nearly half (43%) of the ETP cetacean species lack sufficient data for assessing their conservation status. On a positive note, 59% of seabird species and 40% of cetacean species are designated as species of least concern (Tbl. 2).

The diversity of these taxa is spread throughout the entire region, from the EEZ waters of bordering nations westward to 150° W (nearly as far west as Hawaii). While the highest concentrations of turtle sightings and ichthyoplankton richness occurred near the coasts, some richness hotspots for cetaceans and seabirds were located hundreds of kilometers offshore (e.g., off Baja California, near the Costa Rica Dome, and near the 10°N thermocline ridge) (Figs. 5, 6). Regions of high diversity of cetaceans and seabirds overlapped with high and intermediate effort and catch by the yellowfin tuna purse-seine fishery. This is likely because productive fishing grounds are also productive feeding grounds for these apex predators. In many cases, this overlap leads to bycatch of these oceanic megafauna in commercial fisheries. This human threat is one of the reasons that ¼ of the cetacean, seabird, and turtle species in the ETP are classified with a “threatened” status on the IUCN’s Red List. Spatial patterns in diversity almost certainly change over seasons and years, but we did not investigate temporal dynamics here. Rather, our intention was to provide a baseline understanding of the magnitude, extent, and conservation status of the existing diversity.

Biodiversity is important in an EBM context because of its link ecosystem resilience. Resilience is defined as “the extent to which ecosystems can absorb recurrent

natural and human perturbations and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states” (Hughes *et al.* 2005). The role of biodiversity in ecosystem resilience has been a long-standing theme in ecology – one that has captured the interest of those concerned with recent environmental degradation and associated biodiversity loss (Holling 1973, Levin and Lubchenco 2008). The concept that biodiversity is linked to ecosystem resilience was first explored theoretically and later tested experimentally. Walker (1995) argued that ecosystem resilience is enhanced when each functional group of organisms consists of several ecologically redundant species, each of which responds differently to changes in the environment. This ecological redundancy provides a measure of safety in the face of disturbance, such that if one species is depleted, another will assume the same functional role. This is referred to as the “insurance hypothesis” because a higher number of species insures against the collapse of the system in the face of environmental fluctuation (Yachi 1999, Loreau *et al.* 2001). Indeed, marine ecosystems with fewer species are often functionally compromised, and those with more species are more likely to have functional redundancy (Steneck *et al.* 2002, 2004, Bellwood *et al.* 2004, Hughes *et al.* 2005). For example, studies have found species-rich kelp forests off the west coast of North America to be more resilient than the naturally species-poor kelp forests off the east coast (Steneck *et al.* 2002, 2004). However, it is important to recognize that a higher number of species theoretically would not confer resilience on the ecosystem if the species have similar responses to external pressures, such as overfishing and pollution (Chapin *et al.* 1997, Folke *et al.* 2004, Hughes *et al.* 2005). Thus, the diversity of functional groups, diversity of species in functional groups, and diversity within species and populations all appear to

be critical for generation and resilience of ecosystem services (Chapin *et al.* 1997, Luck *et al.* 2003, Folke *et al.* 2004).

Resilience of ecosystems is crucial for maintaining the continued flow of desirable services. While stakeholders of biodiversity in the ETP may not be as apparent as those associated with commercial fishing, there are indeed many of them. Those who benefit from a resilient ecosystem also benefit from biodiversity. For example, all of the countries with fishing fleets or major ports with processing facilities in the ETP benefit from a resilient ecosystem that continuously produces fish. Similarly, countries that import and consume the fish benefit from biodiversity. Additionally, benefits from non-use values (existence, option, and bequest) and passive use values (e.g., viewing and photographing) associated with ETP species are distributed to people around the world. There are also several conservation organizations (e.g., Conservation International, World Wildlife Fund, United Nations Environment Programme, MarViva, Migramar, and the Galapagos Conservancy) focused on the protection of biodiversity and vulnerable megafauna species in the ETP. These organizations have invested considerable sums of money (on the order of \$ millions) to support protected areas containing high diversity of species.

Regulating Service – Carbon Storage

Our estimates of carbon export from the surface to the deep ocean and the potential market value of that carbon are rough conservative estimates for a static system. The dynamics of this system are complex; however, we know that more productive ocean ecosystems are generally home to larger animals, starting with phytoplankton at the base of the food web, and relatively high abundance of top predators. These systems are

believed to be more efficient at exporting carbon out of the photic zone and into the deep ocean (Eppley and Peterson 1979). Thus, we can hypothesize that if fishing reduces the number of large animals present, we might expect less efficient transport of carbon to the deep and more recycling of nutrients in the surface layer, which would allow carbon to more easily transfer back to the atmosphere. What we do know is that if we had to pay for the ETP's natural service of transporting carbon from the surface layer to the deep ocean, where it is essentially locked up for relevant timescales, then we might have to pay \$16.2 billion. So if a human activity, such as fishing, disrupts that service or makes it less efficient, then society may want to pay to reduce the disruptive activity.

The dynamics associated with carbon storage in dolphins, tunas, or other large vertebrates are similarly complex. How the system changes in response to the removal of top predators is unknown. In our static example of dolphin and fish biomass extraction, removing these animals from the ocean means that the carbon is no longer stored there. Payments for Ecosystem Services (PES) schemes exist in which carbon polluters pay for the maintenance of ecosystems that naturally store carbon but might be degraded without compensation (e.g., payments to prevent rainforest destruction). Hypothetically, there could be a PES scheme in which polluters would receive a carbon credit by paying fishers in the ETP not to fish. In order for this type of scheme to function, we would need to know the marginal (per-unit) impacts of fishing on carbon storage. For example, if fishers left 100 mt of fish in the water (roughly 20% of current annual catch), this would be approximately 11.5 mt of carbon, which is equivalent to 42 mt of CO₂. We would want to know whether that 42 mt of CO₂ left in the water is worth the 42 mt of carbon released to the atmosphere if those fish were caught and consumed on land. At the current

average price of carbon, we calculated a potential marginal value of leaving the fish in the water as a carbon store to be \$2.95 per mt. The current mean annual market value of \$4,055 per mt (1991-2010, all species) is 3 orders of magnitude higher than this. To make it more valuable to leave all of the fish in the water when the mean market value of catching the fish is \$2.71 billion (1991-2010), the price of CO₂ would need to exceed \$11,820 per mt. This is a huge increase over the 2012 price of \$9 per mt used in our analyses.

Cultural Services – Recreational Fishing

Our treatment of recreational fishing focused on existing economic analyses of three major locations to highlight the magnitude of the industry and the potential for growth in the region. Combined, the economic value of sport fishing in these three locations (Los Cabos, Costa Rica, and Panama) was estimated at \$1.2 billion. This is nearly half the recent mean annual market value of the commercial fisheries (\$2.7 billion), and it does not include all known fishing locations. In Mexico, for example, there are other hotspots of sport fishing for billfish and tunas, including La Paz, Mazatlan, Puerto Vallarta, Manzanillo, and Acapulco. Opportunities also exist and may be growing in Ecuador (in Manta and the Galapagos). Sport fishing for billfish and tuna represents a major ecosystem service that should be quantified and valued in further detail.

We focused on sport fishing as the major cultural service provided by the ETP, but there are others that also deserve more detailed investigation in future studies. Ecotourism involving viewing and photographing of charismatic megafauna, such as whales, turtles, and seabirds is growing in the region. On a global scale, whale watching

is already estimated worth over \$2 billion and is expected to grow as an industry (Cisneros-Montemayor et al. 2010). Endangered and threatened species have been shown to hold significant value through different economic surveys (Richardson and Loomis 2009 and references therein), but these are not specific to the ETP. As one example of a hotspot for ecotourism involving ETP species, tourism in the Galapagos Islands brings more than 145,000 people and generates \$418 million annually, according to the Galapagos Conservancy. Given that the ETP contains 1/3 of the world's cetacean, seabird, and marine turtle species, we can speculate that the value of ecotourism opportunities alone might on the order of \$1 billion in the near future.

Trade-offs Among Ecosystem Services

Our analysis of the major ecosystem services provided by the oceanic ETP provides a new perspective for this large marine ecosystem and a baseline understanding for future research. We view this study as a first step toward answering important questions about trade-offs among the different services. An important next step is to improve our grasp on the linkages between each of the services and understand how marginal changes in one service might impact another (Fig. 10). For example, if commercial fisheries production decreased by one unit (e.g., 1 mt), how would this impact recreational fishing? Biodiversity? Carbon storage? Would these other services increase or decrease? Would the changes be linear or non-linear? For any change that occurs in another service, how much value is that change worth (in monetary or other terms)?

Commercial fishing has had a long history in the ETP – it is a big industry and its stakeholders have been important in making decisions about ETP resources. What we

hope we have demonstrated here is that commercial fisheries production is not the only major ecosystem service in the ETP. On the contrary, biodiversity, carbon storage, and recreational fishing are major services that also have significant values associated with them. These should be more fully understood and considered in management schemes for this region. The analysis presented here is intended to support a movement toward true ecosystem-based management, in which all ecosystem services, activities, and users are considered. Oceanic ecosystems have historically only been recognized for their contribution to commercial fishing, but they provide much more for the world.

ACKNOWLEDGEMENTS

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Chapter 1, in part, is currently being prepared for submission for publication of the material. Martin, Summer L.; Ballance, Lisa T.; Groves, Theodore. The dissertation author was the primary investigator and author of this material.

TABLES

Table 1. Summary of commercial fisheries catches in the ETP. “nei” = not elsewhere included. Data: IATTC public data.

Species group	Latin name	Data start	Cumul. catch (mt)	Mean annual catch (mt)	Std dev annual catch (mt)	Min ann. catch (mt)	Max ann. catch (mt)	Min ann. catch year	Max ann. catch year	2011 catch (mt)
Yellowfin tuna	<i>Thunnus albacares</i>	1919	12,656,133	136,087	109,585	136	439,317	1919	2002	202,762
Skipjack tuna	<i>Katsuwonus pelamis</i>	1918	7,657,572	81,464	75,650	499	298,323	1921	2008	279,007
Bigeye tuna	<i>Thunnus obesus</i>	1954	4,126,879	71,153	36,550	1,610	143,141	1954	2000	81,743
Albacore	<i>Thunnus alalunga</i>	1952	1,356,235	22,604	8,727	123	45,390	2011	2003	123
Bonitos	e.g., <i>Sarda</i> spp.	1949	429,700	6,931	5,094	1	18,652	2002	1967	7,958
Dolphinfishes	<i>Coryphaena</i> spp.	1971	283,613	6,917	12,035	8	57,465	1972	2009	1,718
Swordfish	<i>Xiphias gladius</i>	1945	448,808	6,699	5,673	504	21,340	2011	2010	504
Pac. bluefin tuna	<i>Thunnus orientalis</i>	1952	327,703	5,462	3,752	480	15,899	1991	1966	3,187
Blue marlin	<i>Makaira nigricans</i>	1954	245,669	4,236	2,061	212	12,043	2011	1963	212
Sharks, skates, rays	<i>Elasmobranchii</i>	1969	175,309	4,174	4,557	8	15,211	1969	2003	3,098
Striped marlin	<i>Kajikia audax</i>	1954	241,671	4,167	3,248	16	14,213	1955	1968	36
Tunas nei	Scombridae	1970	155,623	3,705	4,135	225	18,195	1991	1998	1,825
Black skipjack	<i>Euthynnus lineatus</i>	1964	54,873	1,247	1,165	5	4,359	1964	2009	2,197
Indo-Pac. sailfish	<i>Istiophorus platypterus</i>	1975	32,648	882	589	6	2,291	1990	1993	20
Unidentified marine fishes	Osteichthyes, Chondrichthyes	1961	38,353	834	984	6	4,956	1970	2003	684
Marlins, sailfishes, spearfishes, nei	Istiophoridae	1967	18,120	421	594	0	1,948	1976 1980	2001	21
Black marlin	<i>Istiompax indica</i>	1954	18,187	314	215	13	905	1954	1973	52
Carangids nei	Carangidae	1959	10,172	199	251	10	1,240	1970	1983	79
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	1986	4,377	182	145	0	519	1989	2010	NA
All Species			28,281,645	300,869	245,136	1,089	906,250	1921	2003	585,226

Table 2. Number of species in three taxa (cetaceans, seabirds, and marine turtles) that occur in the eastern tropical Pacific (ETP), with a comparison to the global number of species per taxon and the IUCN conservation status for ETP species.

	Cetaceans	Seabirds	Turtles
Global spp.	86	346	7
ETP spp.	30 (35%)	123 (35%)	5 (71%)
Critically Endangered	0 (0%)	4 (3%)	2 (40%)
Endangered	3 (10%)	10 (8%)	2 (40%)
Vulnerable	2 (7%)	19 (15%)	1 (20%)
Near Threatened	0 (0%)	14 (11%)	0 (0%)
Data Deficient	13 (43%)	3 (2%)	0 (0%)
Least Concern	12 (40%)	73 (59%)	0 (0%)

Table 3. Estimates of the quantity and potential market value of carbon that is exported from the surface to the deep ocean in the ETP (Emerson et al. 1997, USIWG2013, World Bank 2014).

Estimate	Description
$2.1 \times 10^{13} \text{ m}^2$	Area of ETP
24 grams of C $\text{m}^{-2} \text{ yr}^{-1}$	Oligotrophic C export estimate
5.0×10^{14} grams C yr^{-1}	<i>Conservative</i> C export estimate for ETP
5.0×10^8 metric tons C yr^{-1}	ETP estimate in metric tons per year
1.8×10^9 trade units CO ₂ yr^{-1}	CO ₂ trade units (CO ₂ = 27.29% C)
\$16.6 Billion yr^{-1}	Annual value (using \$9 price/mt)

FIGURES

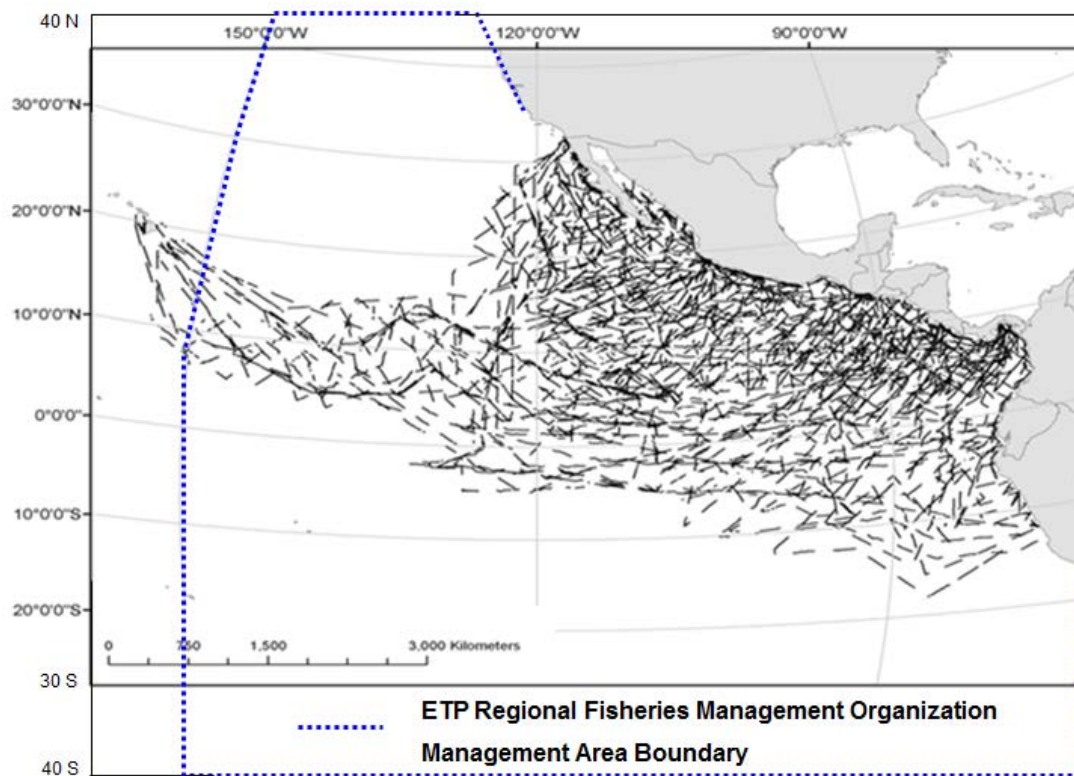


Figure 1. The oceanic eastern tropical Pacific (ETP) is defined as the area seaward of the continental shelf, from the Americas west to approximately 150° longitude, and from the U.S.-Mexico border south to central Peru. This area is roughly 21 million km², includes waters of 12 nations and the oceanic commons, and roughly corresponds to the area managed by two regional fishery management bodies: the Inter-American Tropical Tuna Commission (IATTC) and the Agreement on the International Dolphin Conservation Program (AIDCP). The area managed by the IATTC is outlined in blue; this is also the relevant area for AIDCP. National Marine Fisheries Service survey effort for assessing dolphin populations historically impacted by the tuna purse-seine fishery is shown by the ship tracklines in black.

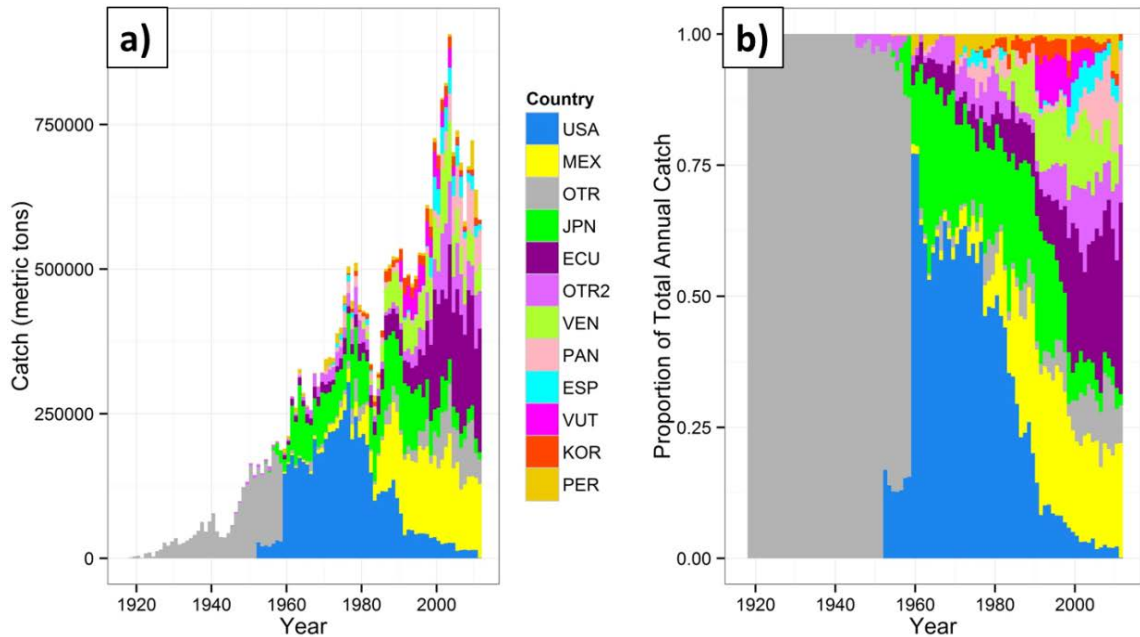


Figure 2. Distribution of annual commercial fisheries catch (mt) by vessel flags, for all species groups and gear types combined (1918-2011). The top 10 vessel flags by cumulative total catch are shown (USA=United States, MEX=Mexico, JPN=Japan, ECU=Ecuador, VEN=Venezuela, PAN=Panama, ESP=Spain, VUT=Vanuatu, KOR=Korea, PER=Peru). OTR pools data from various countries to protect the identity of individual vessels or companies (different groupings each year). OTR2 groups 17 countries not included in the top 10 list (Colombia, Taiwan, Chile, Canada, Costa Rica, Nicaragua, French Polynesia, China, Netherlands, Belize, Bermuda, El Salvador, Honduras, Guatemala, Cayman Islands, Senegal, Portugal). Data source: IATTC public data.

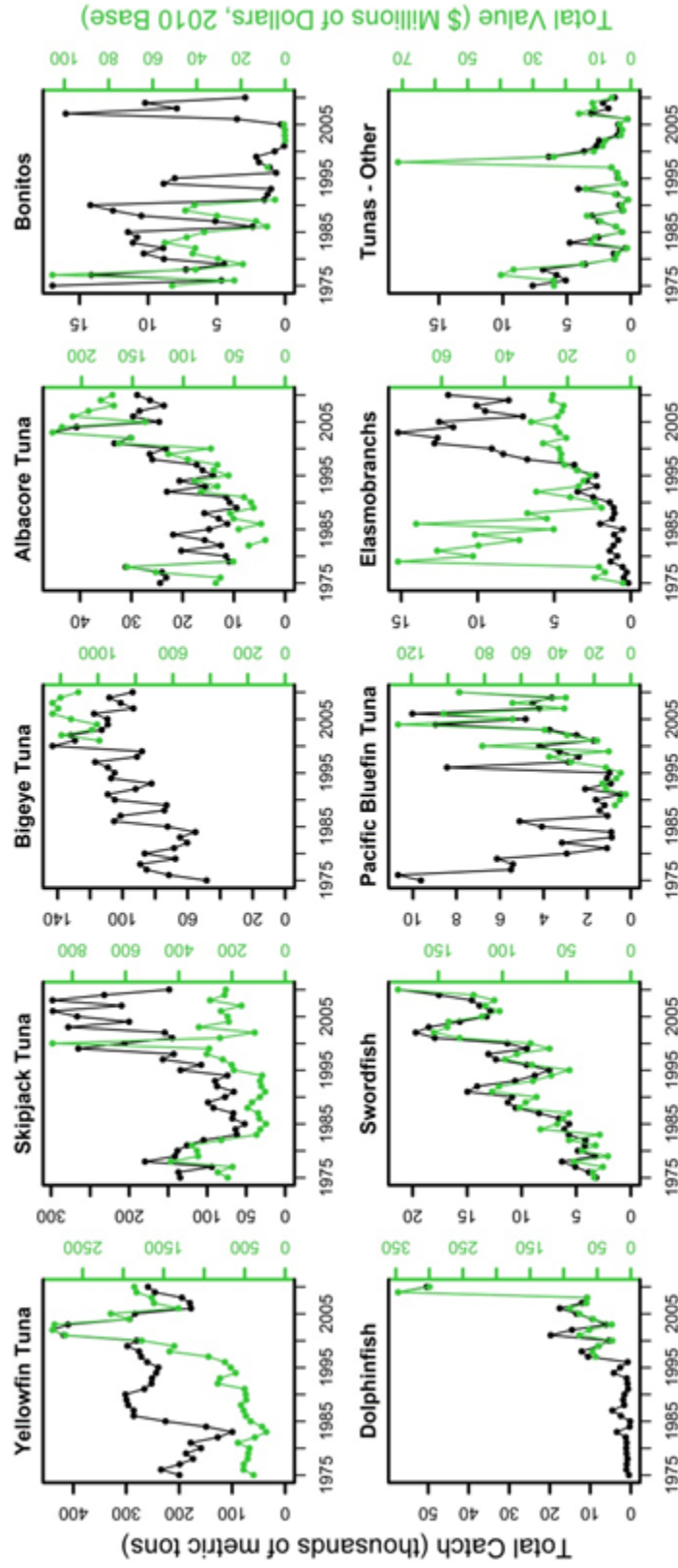


Figure 3. Total catch (black lines) and total estimated market value (green lines) for the top 10 commercially fished species groups (in terms of maximum annual catch) in the ETP across all gear types and countries. Note that there are differences in the scales on the left and right vertical axes, as well as differences across species groups. Breaks in the lines appear where no data were available. Data source: IATTC and NMFS public data.

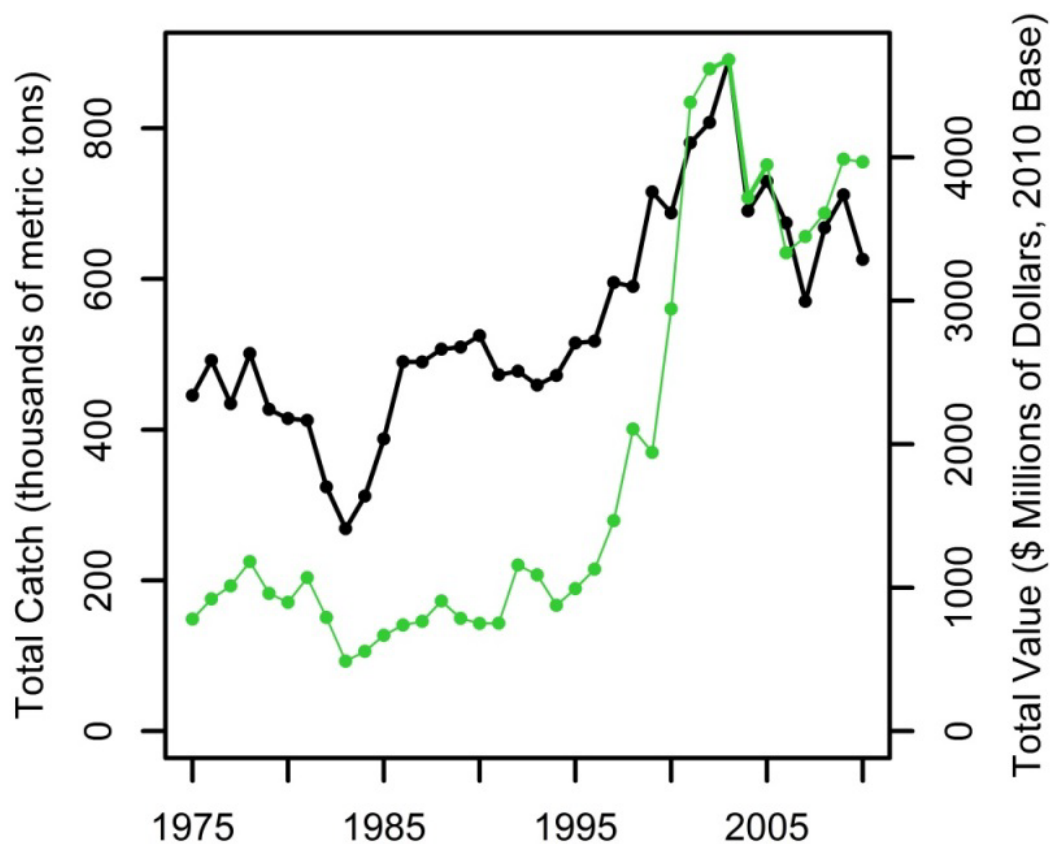


Figure 4. Cumulative totals for annual catch (black lines) and estimated market value (green lines) for the 10 commercially fished species groups from Figure 3 combined. Cumulative totals across all years were 19.6 million metric tons (mt) for catch and \$67.4 billion for market value. Mean annual catch was 544,247 metric tons (range: 268,796 - 891,019 mt; sd: 144,698 mt). Mean annual market value was \$1.9 billion (range: \$487 million - \$4.7 billion; sd: \$1.4 billion).

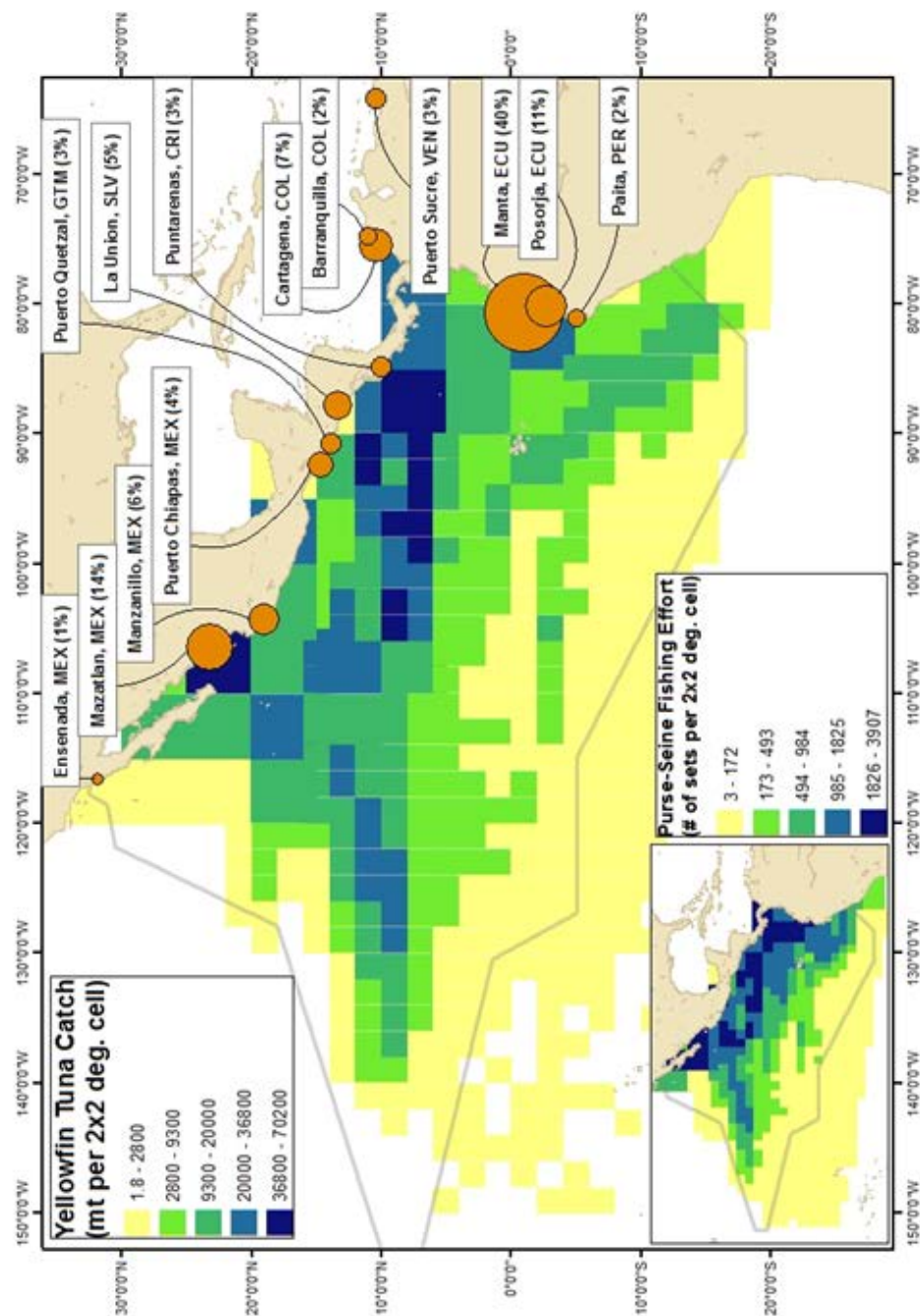


Figure 5. Yellowfin tuna catch (metric tons; large map) and effort (number of sets; inset map) from the commercial purse-seine fishery (1986-2006, all months). Percentages of annual landings at different ports are shown with proportional orange circles (2010-2011 data from IATTC). Country codes: MEX=Mexico, GTM=Guatemala, SLV=El Salvador, CRI=Costa Rica, COL=Colombia, VEN=Venezuela, ECU=Ecuador, PER=Peru. Data source: IATTC special release agreement.

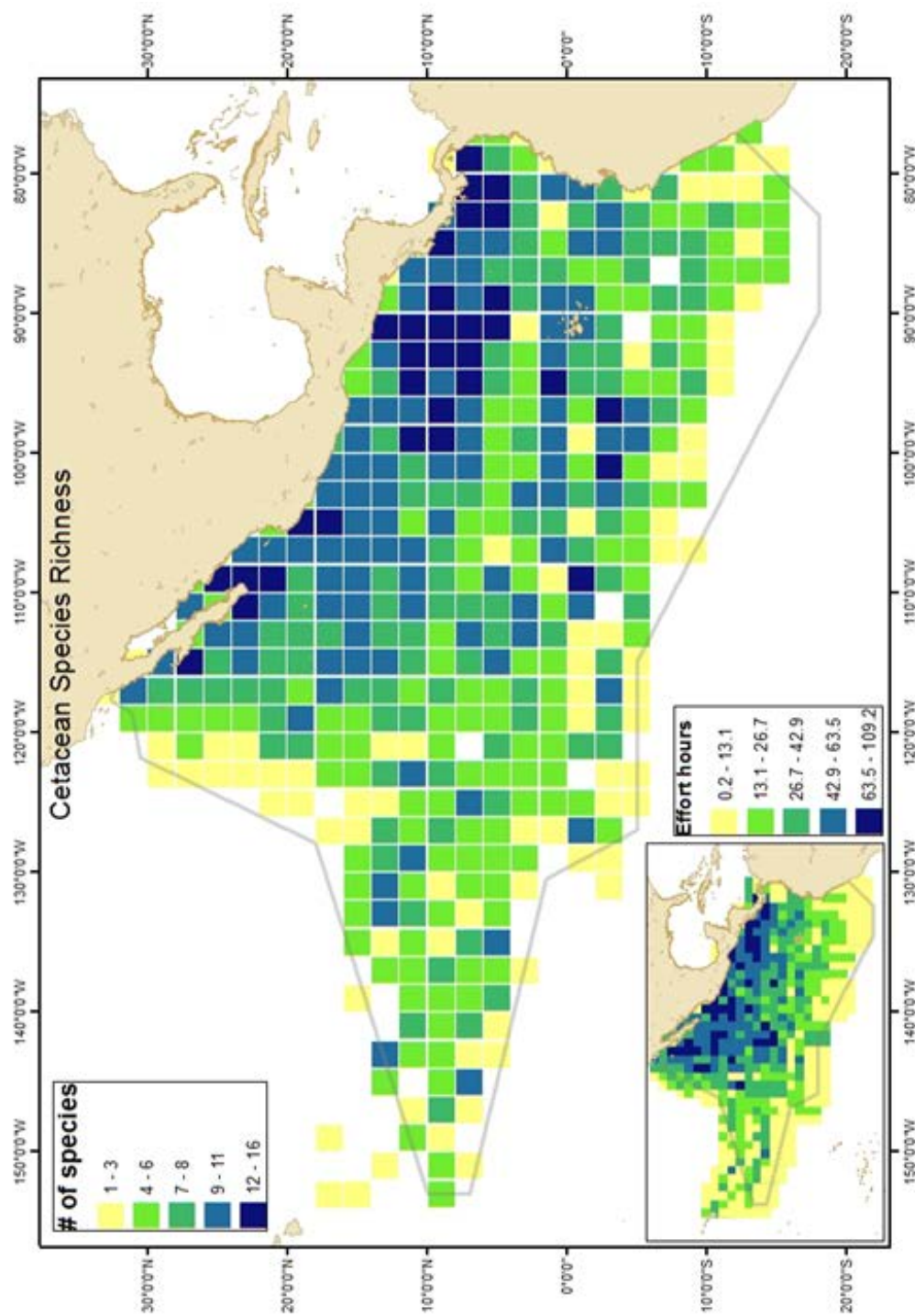


Figure 6. Species richness for cetaceans. Data from National Marine Fisheries Service surveys in 1986-1990, 1998-2000, 2003 and 2006 (primary months of effort were August through November).

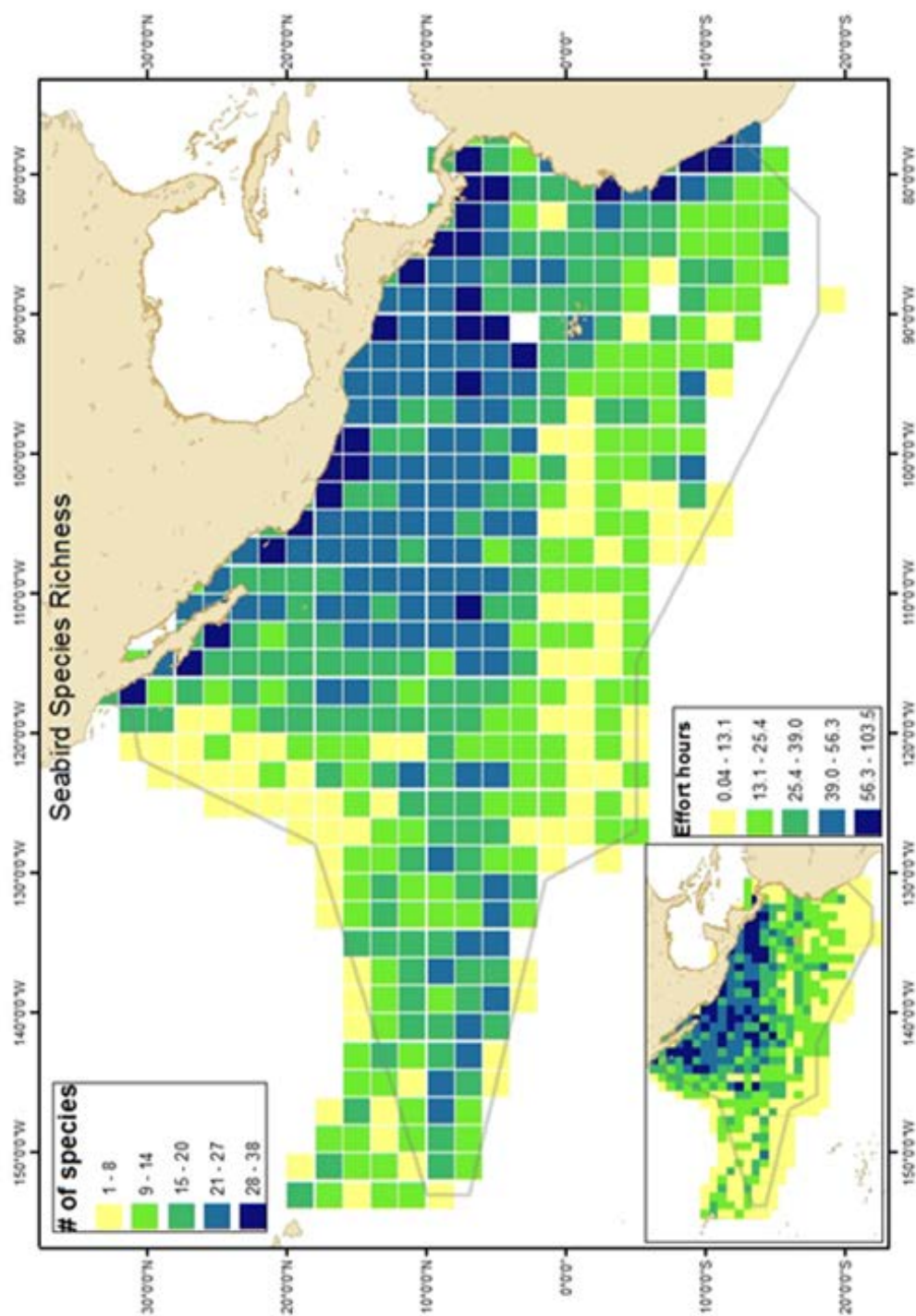


Figure 7. Species richness for seabirds. Data from National Marine Fisheries Service surveys in 1988-1990, 1998-2000, 2003 and 2006 (primary months of effort were August through November).

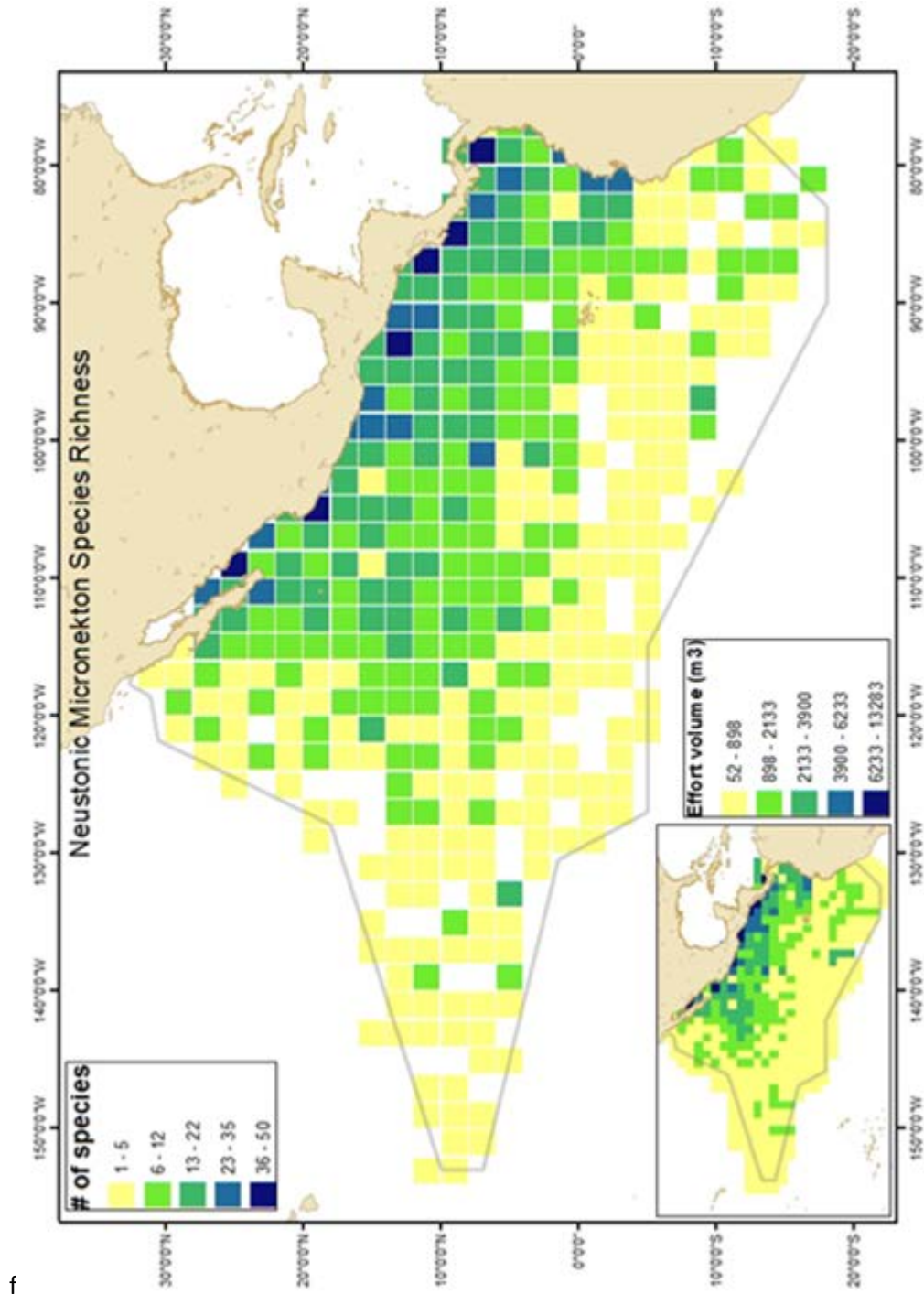


Figure 8. Species richness for ichthyoplankton (i.e., neustonic micronekton, including larval fishes, squids, and octopuses). Data from National Marine Fisheries Service surveys in 1987-1990, 1998-2000, 2003, and 2006 (primary months of effort were August through November).

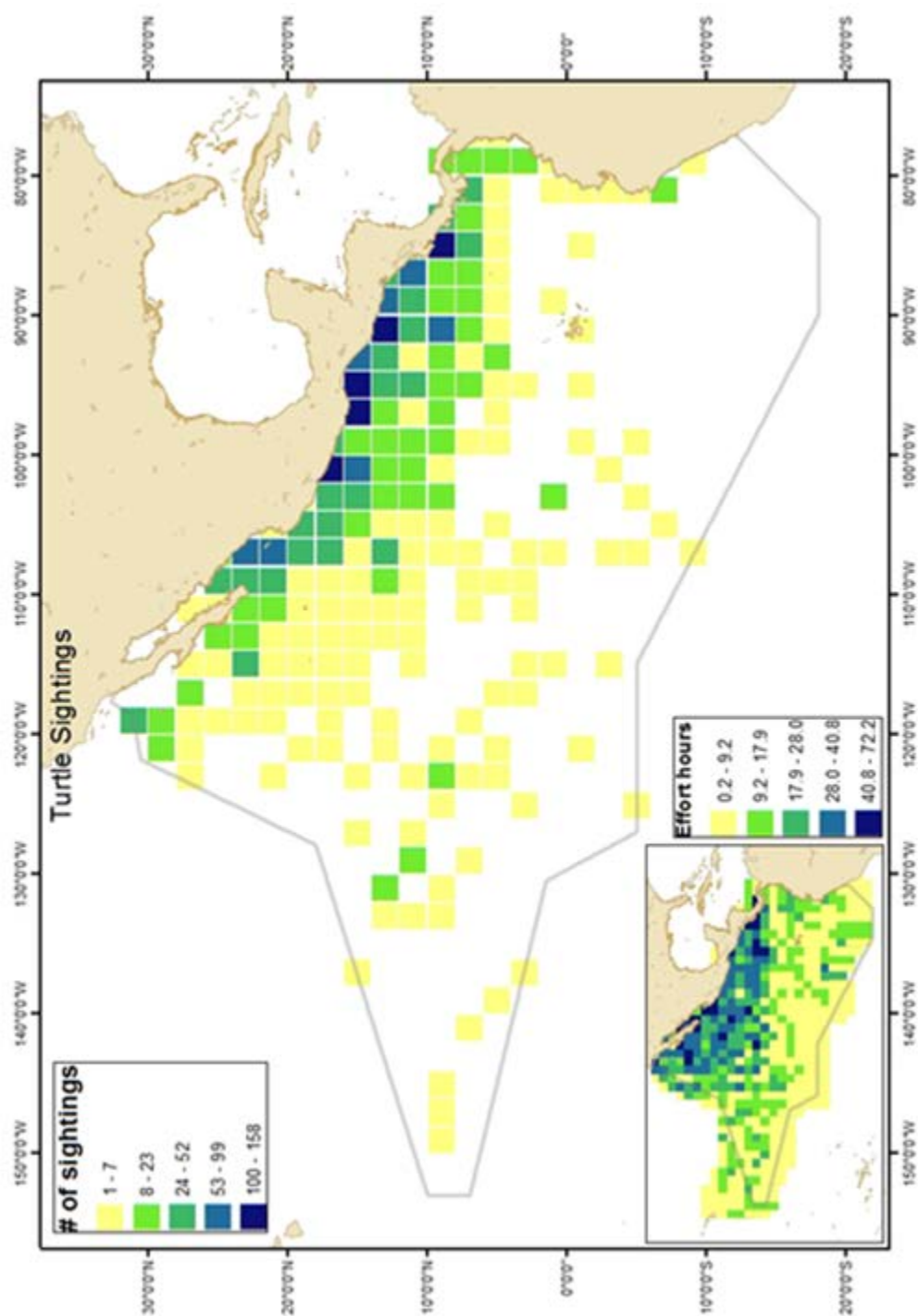


Figure 9. Sightings density for marine turtles. Data from National Marine Fisheries Service surveys in 1998-2000, 2003 and 2006 (primary months of effort were August through November).

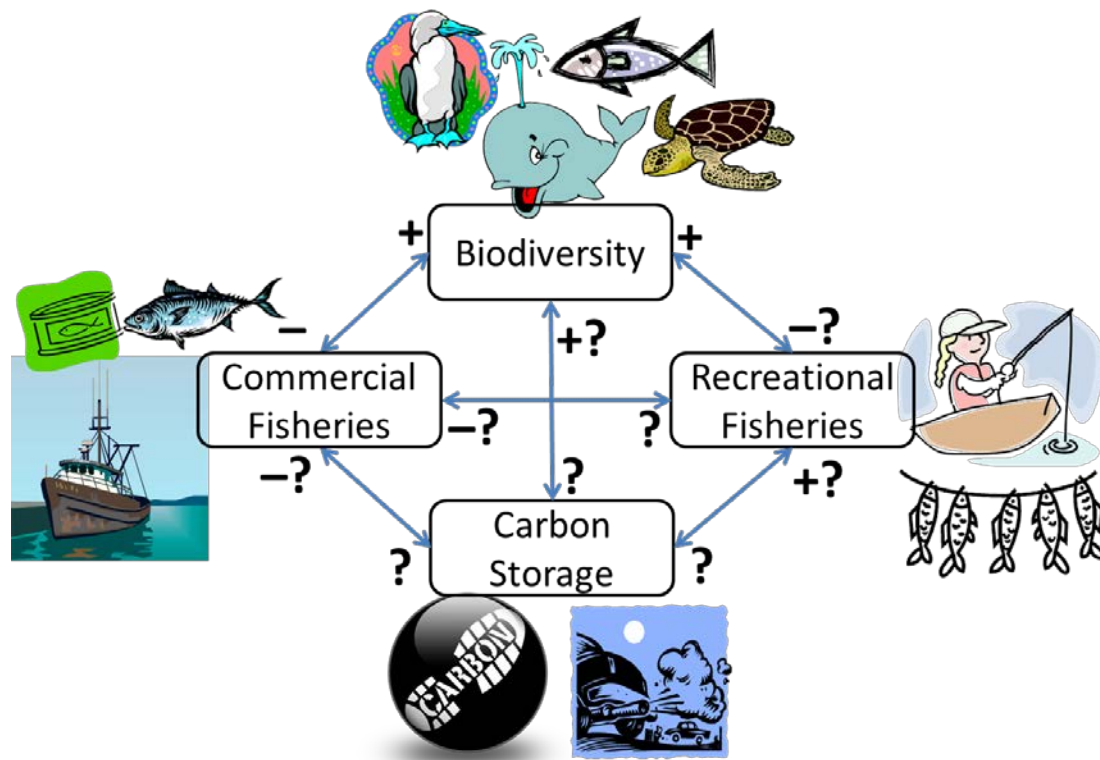


Figure 10. Conceptual diagram of linkages among major oceanic ecosystem services: commercial fisheries, biodiversity, carbon storage, and recreational fishing. Potential impacts of one service on another are indicated as positive (+), negative (−), or unknown (?).

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CHAPTER 2

**Yellowfin tuna (*Thunnus albacares*) as biological indicators of cetacean community
structure and densities in the oceanic eastern tropical Pacific**

ABSTRACT

A critical component of ecosystem-based management (EBM) for oceanic systems is the development and use of a comprehensive suite of indicators. Indicators can be ecological, economic or social in nature. Ideally, they use continuously measured, readily available data to provide insights into harder-to-measure ecosystem attributes. In this study, we used one set of biological metrics (fishery effort and catch metrics for yellowfin tuna, *Thunnus albacares*) to make predictions about other biological components (cetacean community structure and density) of the oceanic eastern tropical Pacific (ETP). This is different from the more common approach of using environmental variables (e.g., physical oceanographic variables) to make predictions about biological components of an ecosystem. We validated our approach with comparisons to previous studies that related physical variables to cetaceans in the ETP. Relationships between cetacean taxa and three types of purse-seine fishing methods (“dolphin”, “log,” and “school” fishing, based on what the net is set upon) were revealed through canonical correspondence analysis. Dolphin fishing metrics were mostly associated with offshore spotted and eastern spinner dolphins (*Stenella attenuata* and *S. longirostris orientalis*), rough-toothed dolphins (*Steno bredanensis*), and dwarf sperm whales (*Kogia sima*). Log fishing metrics were associated with sperm whales (*Physeter macrocephalus*), Bryde’s whales (*Balaenoptera edeni*), and short-finned pilot whales (*Globicephala macrorhynchus*). School fishing metrics were associated with blue whales (*Balaenoptera musculus*), bottlenose dolphins (*Tursiops truncatus*), Risso’s dolphins (*Grampus griseus*), and offshore common dolphins (*Delphinus delphis*). Predicted maps of cetacean densities are qualitatively similar to those developed using environmental variables, including sea

surface temperature and salinity, chlorophyll, mixed-layer depth, bathymetry, and distance to shore. Many of them capture historically observed ranges and sighting rates remarkably well. Our results provide incredible support for moving forward with this approach and applying it to other taxa (e.g., seabirds and larval fishes) for which long-term data exist in the ETP. This suite of indicators would facilitate predictions of communities and densities for these taxa in future years, demonstrating promise for EBM in this region.

INTRODUCTION

Management of living marine resources has traditionally focused on single species or stocks of interest and has relied on single disciplines of expertise. This approach has often failed to manage or protect marine resources because it does not consider the complex interaction of social, economic, and political pressures impacting those resources. Ecosystem-based management (EBM) has been proposed as an alternative, holistic approach to this traditional management style. EBM integrates principles from multiple disciplines in an approach that considers the entire ecosystem, including humans, and the cumulative impacts of different sectors and anthropogenic activities (McLeod et al. 2005). The primary goal of EBM is to maintain healthy, productive, and resilient social-ecological systems that continue to support humans by providing the services they want and need.

EBM has been embraced by government institutions, academics, and conservation entities around the world, but practical implementation has been difficult to achieve, particularly for oceanic ecosystems (McLeod and Leslie 2009, Ballance and Whitty 2010). Oceanic ecosystems, those seaward of the continental shelf, face a complex set of

challenges. They include waters under the jurisdiction of multiple nations, as well as the oceanic commons; the living marine resources they include are often transboundary; enforcement of international agreements is extremely difficult; and the ecosystem goods and services they provide are truly global. Yet it is precisely because of these complicating factors, and because these oceanic ecosystems represent such a large proportion of the world's surface that is heavily utilized, that a more holistic approach needs to be developed.

Resilience – the extent to which a system can absorb perturbations and still maintain its structure, function, and identity – is a guiding principle of EBM. Resilience-based EBM strategies should rely on input from scientific monitoring, research, and modeling, and should include regular evaluation to ensure that they are adaptive over time (McLeod and Leslie 2009). Evaluation allows managers to document, anticipate, and respond when the system is approaching a threshold that, if crossed, will tip it into an undesirable state. Determining what to evaluate is challenging. Theoretically, resilience can be measured mathematically by fitting a dynamic model to a time series, calculating equilibria and size of basins of attraction; however, this would require extraordinary data and is typically not feasible (Carpenter et al. 2001). Instead, it is more effective and feasible to develop indicators, or proxies, of ecosystem resilience which can be implemented in an EBM approach. The benefit of indicators is that they reflect changes in harder-to-measure ecosystem attributes (Niemeijer and de Groot 2008, Samhouri et al. 2009), one of these attributes being resilience. Thus, indicators only require one type of data to learn something about the ecosystem as a whole.

Indicators can be ecological, economic or social in nature, and they are critical to the implementation of EBM. A comprehensive suite of ecological indicators should: 1) include traditional indicators of physical and chemical processes, community structure, and biomass and relative abundance of ecologically and commercially important species, 2) incorporate information about the ecological processes that sustain biodiversity patterns (e.g., recruitment, dispersal, and cross-scale interactions), and 3) incorporate information on the relative abundances and composition of functional groups that have strong effects on ecosystem functioning (Leslie and Kinzig 2009). Indicators that are clearly defined and are relevant to key processes or drivers in the system are a powerful tool for EBM (Carpenter et al. 2001, Carpenter et al. 2005).

In the context of EBM, indicators have two important purposes. First, they provide something measurable that will reflect changes in the general state of the ecosystem. This requires that the indicators be concrete and measurable in practice (i.e., relatively easy to obtain, cost-effective, or widely available) (Samhuri et al. 2009). For an indicator to be effective, it has to be continuously measured, even when more thorough assessments of the ecosystem are prohibitively expensive. Second, indicators have the potential to predict changes in the economic value of the system. For example, if the yields of a fishery are related to another ecosystem component, then an indicator of the other component could provide insight into the yields of the fishery. The development of indicators, especially those that are process-related (i.e., reveal mechanisms of change), is the first step that scientists can take toward the implementation of EBM for oceanic systems (Levin et al. 2009, Samhuri et al. 2009).

The eastern tropical Pacific (ETP) is a model oceanic ecosystem on which to apply the concepts of EBM. It has a rich modern history of anthropogenic influence, particularly through industrial-scale commercial fishing. Interest in the productivity of the fishery and its impacts on the supporting ecosystem have led to the development of long-term data collection programs. Consequently, the ETP is well-studied relative to other large oceanic systems, and there are multiple long-term datasets available for the exploration of potential indicators. There are stakeholders invested in the future productivity of fisheries in the region (e.g., the Inter-American Tropical Tuna Commission (IATTC), which manages fisheries in the region) and stakeholders invested in the protection of the region's biodiversity and endangered species (e.g., the National Marine Fisheries Service, NMFS). The development of indicators to facilitate an EBM approach could help inform future management strategies for the ETP.

Yellowfin tuna (*Thunnus albacares*) have been hypothesized to be a keystone species in the ETP. Therefore, we explore the potential use of effort and catch metrics from the purse-seine fishery for this species as indicators of the broader biological ecosystem in the ETP. The fishery catches yellowfin tuna using one of three methods – by setting a massive purse-seine net around: 1) dolphins that have large-bodied yellowfin tuna swimming below them (“dolphin sets”), 2) floating objects, such as logs or man-made fish aggregating devices (“log sets”), or 3) schools of tunas unassociated with dolphins or floating objects (“school sets”). It is possible, and perhaps likely, that these methods of fishing occur in different oceanographic conditions or habitats, and attract different suites of species. The objectives of the present study are to investigate relationships between the three types of purse-seine fishing and the broader biological

ecosystem. We focus on cetaceans, some of which are known to have strong ecological linkages to yellowfin tuna (Ballance et al. 2006 and references therein), as representatives of top predators in the system.

METHODS

Study area

The ETP is defined here as the oceanic area seaward of the continental shelf, from the Americas west to approximately 150°W longitude, and from the U.S.-Mexico border south to central Peru (Fig. 1). This roughly corresponds to the region bounded by 150°W, 40°S, and 40°N, and the coasts of the Americas, in which living marine resources are managed by the IATTC, the Regional Fisheries Management Organization for the ETP (Fig. 1).

The ETP is characterized by several major oceanographic features that make it spatially heterogeneous (Fig. 1). It is located at the southern end of the California Current and the northern end of the Peru Current. These two eastern boundary currents feed into the westward flowing North Equatorial Current (10-15°N) and South Equatorial Current (near the equator), respectively. The North Equatorial Countercurrent (5-10°N) flows eastward between these two currents toward the Eastern Pacific Warm Pool, which has its western edge near 110°W and widens toward southern Mexico and Costa Rica in the east. There is a thermocline ridge near 10°N due to divergence along the boundary of the North Equatorial Countercurrent and the North Equatorial Current. To the southeast of the Eastern Pacific Warm Pool is the Costa Rica Dome, an upwelling feature centered near 89°W and 9°N (Fiedler and Talley 2006). Extending west along the equator from South America is the Equatorial Cold Tongue, characterized by Equatorial Surface Water

that is colder and saltier than the warm, low salinity Tropical Surface Water associated with the Eastern Warm Pool. The ETP is uniquely characterized by a sharp, shallow thermocline and a strongly depleted, shallow, and extensive oxygen minimum layer (Fiedler and Talley 2006).

Conditions in the ETP vary seasonally, inter-annually, and with El-Niño South Oscillation (ENSO) phases. There are three ENSO phases: El Niño, La Niña, and Neutral. During El Niño conditions, surface water temperatures increase and the typically shallow thermocline deepens as warm water from the west piles up in the east. During La Niña conditions, temperatures are cooler. The Eastern Pacific Warm Pool experiences relatively low seasonal and ENSO variability, while the Equatorial Cold Tongue experiences relatively high variability (Fiedler and Talley 2006).

Data sources

Data on purse-seine fishery effort and yellowfin tuna catch were collected by fisheries observers onboard fishing vessels. These data were provided by IATTC at a spatial scale of 2° latitude by 2° longitude and a monthly temporal scale for 1986 through 2006 through special agreement. Only data corresponding to NMFS survey years and months (see below) were used in this study. For each 2° x 2° grid cell and month, there are several effort and catch metrics. Effort metrics include: 1) the number of purse-seine vessel days spent in the area during the month, which includes all time spent transiting, searching, and conducting fishing operations, 2) the number of sets on yellowfin tuna associated with dolphins (“dolphin sets”), 3) the number of sets on yellowfin tuna associated with floating objects, including logs and man-made fish aggregating devices (“log sets”), and 4) the number of sets on yellowfin tuna schools that are unassociated

with dolphins or floating objects (“school sets”). Catch metrics include metric tons of yellowfin tuna caught on: 1) dolphin sets, 2) log sets, and 3) school sets. Catch-per-unit-effort (“CPUE”) was calculated as metric tons of catch per day of fishing effort. Using days rather than sets as the unit of effort here avoids dividing by zero sets. Instances of zero sets of one or two types of sets occur frequently in the data, as certain time/location combinations often favor only one type of set. The average number of sets per day is less than one, and the maximum is three.

Data on cetaceans were collected during shipboard research surveys conducted by NMFS from August through November between 1986 and 2006. The primary purpose of these surveys was to monitor the status and trends of dolphin populations historically impacted by the tuna purse-seine fishery. Surveys were planned and executed to systematically cover the entire range of the impacted dolphin populations. Visual observations of cetacean species and group sizes were made by rotating observers following standard line-transect methods (Gerrodette and Forcada 2005). Cetacean data were available for 10 years: 1986-1990, 1998-2000, 2003, and 2006. We limit this study to 19 cetacean taxa, all with at least 100 sightings over the 10 years. Latin and common names for these taxa are provided in Table 1; we will use common names throughout the paper.

This study overlays a spatial grid of 2° latitude by 2° longitude over the entire ETP. This grid cell size was selected for two reasons. First, this was the lowest level of spatial resolution that IATTC could release without compromising confidentiality of vessels and nations. Second, previous research suggests an absence of scale-dependence

in the response of some dolphin species to spatial variability of oceanographic habitat in the ETP at this and smaller scales (Redfern et al. 2008).

Depending on the analysis, data were aggregated temporally at one of three levels: 1) all data aggregated into one group, eliminating the temporal component and providing an average, or “climatological,” view, 2) by ENSO phase, aggregating data into three groups based on assignment of years into La Niña, El Niño, and Neutral categories, and 3) by individual year, grouping all data for each individual year together. ENSO phase assignment was based on the Oceanic Niño Index seasonal values for August to November (NOAA 2014) and confirmed with oceanographer P. Fiedler. Niña years include 1988, 1998, 1999, and 2000; Niño years include 1986, 1987, and 2006; Neutral years include 1989, 1990, and 2003.

Analytical approaches

A goal of EBM is to identify and utilize a comprehensive suite of ecological indicators; identifying indicators of community structure for ecologically and commercially important species is one element of that goal. To investigate general relationships between yellowfin tuna fishery metrics and the cetacean community in the ETP, we used canonical correspondence analysis (CCA). CCA is a multivariate statistical method that uses direct gradient analysis to relate a set of species data to a suite of predictor variables (ter Braak 1986). Our response metric is the number of sightings per hour for each of the 19 cetacean taxa for each sample site. The definition of “site” varies depending on the level of temporal aggregation used in the analysis. For the climatological analysis, sites are simply 2° x 2° grid cells. For ENSO analyses, sites are grid cells in a particular ENSO phase (e.g., grid cells in Niño years). For analyses of

individual years, sites are grid cells in each particular year (e.g., grid cells in 1990). These analyses were conducted using the community ecology package ‘vegan’ in the R statistical software environment.

Interpretation of CCA results focused on three main aspects: 1) the percentage of variance in the cetacean data (total and per taxon) that was explained by the yellowfin tuna metrics, 2) definition of the canonical axis space by the yellowfin tuna metrics, and 3) associations between cetacean taxa and yellowfin tuna metrics, and relative strength of those associations based on cetacean scores along the axes. Cetacean taxa with an axis score of 0.25 or greater for at least one of the first two canonical axes (those present on the triplots) were examined further to characterize their relationships with the yellowfin tuna metrics. Taxa with axis scores less than 0.25 for both axes (those taxa relatively close to the origin in the triplots) were not considered to have meaningful relationships with the axis space defined by the yellowfin tuna metrics in the analysis.

Another element of the EBM indicators goal is to develop indicators of relative abundance and biomass of species, particularly those that have strong effects on ecosystem functioning. To quantify specific relationships between the fishery metrics and cetaceans, which are top predators, we used generalized additive models (GAMs). GAMs are commonly used to relate environmental variables of a habitat to characteristics of a population, such as abundance or distribution (Forney et al. 2012). They are extended, nonparametric versions of generalized linear models (likelihood-based regression models) that replace the linear function which relates covariates to the response with an additive smooth function (Hastie and Tibshirani 1986). In our models, the response variable is the number of cetacean sightings per hour for a selected taxon. There are 6

predictor variables: DolpCPUE (for dolphin fishing, metric tons of catch per day of fishing effort), SchlCPUE (for school fishing), LogCPUE (for log fishing), DolpSets (number of sets on dolphins), SchlSets (number of sets on schools), and LogSets (number of sets on logs). ‘Year’ and ‘ENSO’ were used as categorical variables when aggregating the data at those levels. The number of sightings was modeled using a quasi-Poisson likelihood (mean proportional to variance), a log link function, and the number of cetacean survey hours as an offset. The use of effort as an offset in the model standardizes for variations in the level of effort across grid cells, effectively modeling sightings per hour (rather than number of sightings). These analyses were conducted using the modeling package ‘mgcv’ in the R statistical software environment.

Using the ‘year’ temporal aggregation, we built a model using all years of data except 2003. We left 2003 out of the model-building process so that we could validate the model by making predictions onto 2003 as an ENSO-Neutral year. The model results were used to make predictions for each cetacean taxon for 2003, both for grid cells that contained survey effort for the year and also grid cells that only had fishery data but no survey data. The result is a predicted map for each cetacean taxon, using only the yellowfin tuna metrics to make the predictions.

RESULTS

Canonical Correspondence Analysis (CCA)

Climatological Analysis (All Data Aggregated Temporally)

When the data were aggregated into one temporal group (the climatological view), the yellowfin tuna metrics explained 13.2% of the overall variance in the cetacean data (Fig. 2). Axis 1 (x-axis) was defined by school sets (SchlCPUE, SchlCatch, and

SchlSets) in the negative direction and dolphin sets (DolpCPUE, DolpCatch, and DolpSets) in the positive direction. Axis 2 (y-axis) was defined by dolphin sets in the negative direction (mainly DolpSets and DolpCatch) and log sets in the positive direction (mainly LogCPUE and LogSets). The three types of fishing occupied relatively separate areas in the axis space (Fig. 2). Appendix 1 shows that the cetaceans generally exhibited a unimodal response to Axis 1 and Axis 2, thus validating a primary assumption of the CCA method.

Cetacean taxa were grouped into three tiers based on their scores for Axis 1 and 2 (Fig. 2). The lowest tier contained taxa with scores below 0.25 for both axes. Coastal spotted dolphins, striped dolphins, Cuvier's beaked whales, killer whales, and mesoplodont beaked whales fell into this category. For these taxa, the variance explained by Axes 1 and 2 combined was low, ranging from 0.3 to 6.5% (mean = 1.8%). Appendix 2 provides a breakdown of the percent of variance explained by each of the first four canonical axes for each taxon. Axes 1 and 2 explain the largest portion of the variance for most taxa; therefore, we only focused on these two axes when interpreting results.

The middle tier contained taxa with a maximum axis score between 0.25 and 0.5 (Fig. 2). It included offshore spotted dolphins, offshore common dolphins, short-finned pilot whales, rough-toothed dolphins, sperm whales, Bryde's whales, and dwarf sperm whales. The variance explained by the tuna metrics ranged from 3.6 to 10.3% (mean = 6.7%).

The top tier contained cetacean groups with a maximum score above 0.5 for Axis 1 or 2 (Fig. 2). This included eastern spinner dolphins, whitebelly spinner dolphins, offshore spotted mixed with eastern spinner dolphins, offshore spotted mixed with

whitebelly spinner dolphins, Risso's dolphins, bottlenose dolphins, and blue whales. For these taxa, the tuna metrics explained from 4.0 to 29.1% of the variance (mean = 14.1%). As such, the analysis lends the most support to associations found between these taxa and the tuna metrics.

This analysis highlighted several relationships among cetaceans and tuna metrics (Fig. 2). 1) There were 5 taxa closely aligned with dolphin fishing metrics. In the top tier (taxa exhibiting the strongest relationships with tuna metrics), mixed schools of offshore spotted and eastern spinner dolphins, as well as pure schools of eastern spinner dolphins, were tightly linked to DolpCatch and DolpSets. In the middle tier, pure schools of offshore spotted dolphins, rough-toothed dolphins, and dwarf sperm whales were closely associated with DolpCPUE, DolpCatch, and DolpSets, respectively. 2) Four taxa were associated with school fishing metrics, including blue whales, bottlenose dolphins, and Risso's dolphins in the top tier, and offshore common dolphins in the middle tier. 3) Three taxa in the middle tier were most closely linked to log fishing metrics. Sperm whales were closely associated with LogSets, and Bryde's whales were closely linked to LogCPUE, as are short-finned pilot whales but to a lesser degree. 4) Pure schools of whitebelly spinner dolphins and mixed schools of offshore spotted with whitebelly spinner dolphins were both in the top tier with a strong position opposite school fishing metrics on Axis 1 and dolphin fishing metrics on Axis 2.

El Niño Southern Oscillation (ENSO) Analysis

The overall percent of variance in the cetacean data explained by the tuna metrics for the ENSO phases was similar to the climatological analysis and also across phases – 14.8% for the Neutral phase, 11% for El Niño phase, and 10.6% for La Niña phase (Fig.

3). Definition of the axis space varied across phases. Under Neutral conditions, Axis 1 was defined by school and log fishing on the negative end, and dolphin fishing on the positive end. Axis 2 was characterized by school and dolphin fishing in the negative direction, and log fishing in the positive direction. The Neutral axis space was the most similar to the climatological view. During El Niño conditions, Axis 1 was defined by school and log fishing on the negative side and dolphin fishing on the positive side. Axis 2 was not clearly defined in the negative direction, and was influence by all three types of fishing in the positive direction, although DolpSets has the most influence. Thus, there appeared to be weaker axis definition for El Niño conditions. Under La Niña conditions, Axis 1 was defined by log fishing in the negative direction, with no clear definition in the positive direction. Axis 2 was defined by dolphin fishing in the negative direction and school fishing in the positive direction. Here, the separation between dolphin and school fishing is clear, but log fishing and school fishing were not as clearly segregated as they were in the climatological view.

The amount of variance explained for each taxon was reflected by the axis scores they received, where higher scores indicated a higher proportion of variance explained. Compared with the three-tiered structure based on maximum axis scores in the climatological analysis (Fig. 2), Neutral conditions created the most similar structure and La Niña conditions the most different (Fig. 3). Under Neutral conditions, sperm whales, coastal spotted dolphins, and offshore spotted dolphins moved into the top tier (highest proportion of variance explained), while mixed offshore spotted with whitebelly spinner dolphins moved down into the middle tier (Fig. 3). Mesoplodont and Cuvier's beaked whales moved up from the bottom tier to the middle tier. Under El Niño conditions,

sperm whales, coastal spotted dolphins, and offshore spotted dolphins again moved up into the top tier, along with dwarf sperm whales, while bottlenose dolphins and blue whales moved down into the middle tier. Killer whales moved from the bottom tier into the middle tier. Under La Niña conditions eastern spinner dolphins, mixed offshore spotted with eastern spinner dolphins, and Risso's dolphins moved down into the middle tier, and offshore common dolphins, short-finned pilot whales, and sperm whales moved up into the top tier. Coastal spotted dolphins, striped dolphins, Cuvier's beaked whales, killer whales, and mesoplodont beaked whales all moved from the bottom tier to the middle tier. Bryde's whale moved down from the middle tier to become the only taxon in the bottom tier.

Relationships between the cetaceans and tuna metrics varied to different degrees across ENSO phases depending on the taxon. Under Neutral conditions, mixed schools of offshore spotted with eastern spinner dolphins, pure schools of eastern spinner dolphins, and pure schools of offshore spotted dolphins had strong (top tier) associations with dolphin fishing metrics (Fig. 3). Whitebelly spinner dolphins had a strong negative relationship with dolphin fishing and school fishing metrics. Coastal spotted dolphins showed a strong association with log fishing metrics. Risso's dolphins and sperm whales were strongly positioned between log and school fishing metrics. Blue whales and bottlenose dolphins had strong relationships with school fishing metrics.

Under El Niño conditions, strong relationships were maintained between dolphin fishing metrics and mixed schools of offshore spotted with eastern spinner dolphins, pure schools of eastern spinner dolphins, and pure schools of offshore spotted dolphins (Fig. 3). Dwarf sperm whales also showed a strong relationship with dolphin sets here. Pure

schools of whitebelly spinner dolphins and mixed schools of offshore spotted with whitebelly spinner dolphins again had strong negative relationship with dolphin fishing metrics. Coastal spotted dolphins appeared to have a strong relationship with school fishing metrics, though school fishing and log fishing metrics occupied similar axis space. Sperm whales and Risso's dolphins were strongly aligned with school sets.

Under La Niña conditions, the relationships weakened between dolphin fishing metrics and mixed schools of offshore spotted with eastern spinner dolphins, pure schools of eastern spinner dolphins, and pure schools of offshore spotted dolphins (Fig. 3). This was evidenced by these taxa dropping down into the middle tier of axis scores, indicating the relationships existed but were weaker. Pure schools of whitebelly spinner dolphins and mixed schools of offshore spotted with whitebelly spinner dolphins maintained their distance from dolphin sets and catch, but appeared to be strongly associated with DolpCPUE and LogCPUE. They typically occupied the space between those metrics, but that space was condensed here. Short-finned pilot whales were strongly linked to LogCPUE, and sperm whales were strongly positioned between log fishing and school fishing metrics. Offshore common dolphins were tightly and strongly associated with SchlSets and SchlCatch, while blue whales and bottlenose dolphins were top tier taxa oriented closest to SchlCPUE and distinctly opposite of log fishing metrics.

Analysis of One Selected Year for Each ENSO Condition

Of the three Neutral years (1989, 1990, and 2003), the analysis explained the highest percent of variance in the cetacean data (21.7%) for 2003. Thus, we used 2003 to as an example to demonstrate potential inter-annual variation that was lost when we grouped three years together into one analysis. For 2003, Axis 1 was clearly defined by

dolphin sets in the negative direction and school sets in the positive direction (Fig. 4).

Axis 2 was less well-defined, with log sets and dolphin CPUE in the negative direction and school CPUE in the positive direction. The separation between dolphin and log fishing was less clear in this year than when we aggregated the three Neutral years. There were still strong relationships between dolphin fishing metrics and mixed schools of offshore spotted with eastern spinner dolphins, pure schools of eastern spinner dolphins, and pure schools of offshore spotted dolphins (Fig. 4). Rough-toothed dolphins were also located with this group. These taxa were all separated from school fishing metrics along Axis 1 and from log fishing metrics along Axis 2. Mixed offshore spotted with whitebelly spinner dolphins were still strongly positioned between dolphin fishing metrics and log fishing metrics, though that space was condensed here. Short-finned pilot whales and Risso's dolphins were strongly associated with dolphin fishing and also nearby log fishing metrics. Cuvier's beaked whales were tightly linked to log fishing metrics. Bryde's whales were strongly positioned in between school fishing and log fishing metrics. Blue whales and sperm whales were strongly associated with school fishing metrics. Dwarf sperm whales and mesoplodont beaked whales were most strongly associated with school fishing metrics here.

For El Niño years, the analysis explained the highest percent of variance for 2006 (28.2%). In 2006, Axis 1 was defined by school sets on the negative side and dolphin metrics plus a small influence from log fishing metrics positive side (Fig. 4). Axis 2 was not well-defined in the negative direction and was defined by dolphin and school metrics in the positive direction. The separation between dolphin fishing and log fishing was not very clear here. Eastern spinner dolphins were still in the top tier, exhibiting a strong

relationship with dolphin fishing metrics only along Axis 1 (Fig. 4). Offshore spotted mixed with whitebelly spinner dolphins were associated with eastern spinner dolphins, which was unusual. Rough-toothed dolphins were also located in this group. Coastal spotted dolphins appeared to also have a strong relationship with dolphin fishing metrics, but on the positive side of Axis 2, opposite from eastern spinner dolphins. Offshore common dolphins exhibited this same association with dolphin fishing metrics, but with less strength. Sperm whales, Risso's dolphins, and Bryde's whales exhibited strong associations with school sets.

The highest percent of variance explained for La Niña years was 28.3% for 1988. In this year, Axis 1 was defined by dolphin fishing metrics on the negative side and school and log fishing metrics on the positive side (Fig. 4). Axis 2 was defined by dolphin and log metrics in the negative direction and school metrics in the positive direction. There was relatively clear separation of the three types of fishing in the axis space. Nearly all taxa were in the top tier, exhibiting strong relationships with the tuna metrics (Fig. 4). Only striped dolphins, Risso's dolphins, mixed offshore spotted with eastern spinner dolphins, and mixed offshore spotted with whitebelly spinner dolphins were in the middle tier, the latter two just missing the 0.5 cutoff for the top tier. Rough-toothed dolphins, bottlenose dolphins, offshore spotted dolphins, and pure schools of whitebelly spinner dolphins were all tightly associated with dolphin sets and catch. Eastern spinner dolphins were now associated with school fishing metrics and log fishing CPUE. Short-finned pilot whales and sperm whales were strongly associated with log sets and catch. Killer whales were also associated with log fishing metrics here. Cuvier's beaked whales were positioned between log and school fishing metrics. Offshore

common dolphins were tightly linked to school catch, while dwarf sperm whales were tightly linked to school fishing CPUE. Mesoplodont beaked whales, Bryde's whales, and blue whales were mostly associated with school fishing, but with influence from the dolphin fishing metrics.

Generalized Additive Models (GAMs)

Climatological Analysis (All Data Aggregated Temporally)

The panel plots in Appendix 3 depict the smoothed functions estimated by the models. These functions characterize the relationships between each tuna predictor variable and the response variable for the specified cetacean taxon. The response variable was always the number of sightings per hour of survey effort. The shapes of these smoothed functions were not overly complex, which facilitated a straightforward visual interpretation of the results. A flat line indicated that the predictor variable was probably not useful in explaining variation in the data for that taxon. A line that generally increased indicated a positive relationship between the predictor and the number of sightings of the taxon. Likewise, a line that generally decreased indicated a negative relationship between the two. Lines with inflection points indicated potentially more complex responses to increasing values of the predictor variables, but because the degrees of freedom were limited, these remained relatively straightforward to interpret.

The results from the model for mixed schools of offshore spotted with eastern spinner dolphins serve as a good example of how these plots were interpreted (Appendix 3). First, the smoothed response to the DolpSets predictor had a positive slope that was steeper at first and more gradual later, indicating that the number of sightings per hour of this taxon increased with the number of dolphin sets. The ETP purse-seine fishery does

indeed set its nets around this type of mixed school, so the positive relationship between DolpSets and number of sightings per hour makes intuitive sense. Second, the smoothed response for the DolpCPUE predictor was a downward sloping line, which indicates a negative relationship between DolpCPUE and the number of sightings per hour. This negative relationship could indicate that large, highly clumped schools of tuna are found in association with dolphin schools that are spread out over a large area. Next, the smoothed responses to the SchlSets and LogSets predictors had decreasing slopes, indicating negative relationships between those predictors and the number of sightings per hour. Because the data were aggregated temporally here, this indicates a spatial segregation between dolphin fishing and log and school fishing, a result corroborated by the CCA results. Lastly, the smoothed response lines for SchlCPUE and LogCPUE predictors were essentially flat and were not significant (Tbl. 2), indicating that they were not useful in explaining the variance in the data for this taxon.

The deviance explained by the models ranged from 0% to 56% (mean: 29%) (Tbl. 2). The models performed the worst for killer whales and Cuvier's beaked whales, explaining less than 10% of the deviance. Models for Bryde's whales, mesoplodont beaked whales, short-finned pilot whales, and sperm whales performed somewhat better (10-19%). For striped dolphins, Risso's dolphins, and mixed schools of offshore spotted with whitebelly spinner dolphins, the models performed reasonably well (20-29%). They explained 30-39% of the variance for dwarf sperm whales, offshore spotted dolphins, blue whales, and offshore common dolphins. For rough-toothed dolphins, whitebelly spinner dolphins, coastal spotted dolphins, eastern spinner dolphins, and bottlenose dolphins, the models performed quite well with an explained variance of 40-49%. The

best model (56%) was for mixed schools of offshore spotted dolphins and eastern spinner dolphins.

The importance of the 6 yellowfin tuna metrics varied across taxa (Tbl. 2). Taxa for which at least one dolphin fishing metric had the highest significance level ($p < 0.001$) included eastern spinner dolphins, whitebelly spinner dolphins, offshore spotted dolphins, mixed offshore spotted with eastern spinner dolphins, mixed offshore spotted with whitebelly spinner dolphins, bottlenose dolphins, rough-toothed dolphins, dwarf sperm whales, mesoplodont beaked whales, and short-finned pilot whales. Using the same criterion, school fishing appeared to be potentially important in explaining variation in striped dolphins, offshore common dolphins, rough-toothed dolphins, sperm whales, and blue whales. Similarly, log fishing metrics explained variation in eastern spinner dolphins, offshore spotted dolphins, offshore spotted with eastern spinner dolphins (MIXE), offshore spotted with whitebelly spinner dolphins (MIXW), striped dolphins, short-finned pilot whales, and bottlenose dolphins.

El Niño Southern Oscillation (ENSO) Analysis

The overall pattern in the importance of the 6 yellowfin tuna metrics was generally similar to the pattern in the climatological analysis, but some differences occurred within taxa (Tbl. 3). For example, in the climatological view, SchlCPUE was not important for whitebelly spinners or mixed schools of offshore spotted with eastern spinner dolphins; however, it had the highest level of significance during La Niña periods for both of these groups in the ENSO analysis.

The taxa for which the importance of dolphin metrics was robust across ENSO phases included: eastern spinner dolphins, whitebelly spinner dolphins, offshore spotted

dolphins, mixed schools offshore spotted and eastern spinner dolphins, mixed schools of offshore spotted and whitebelly spinner dolphins, rough-toothed dolphins, and dwarf sperm whales (Tbl. 3). Out of 6 possible combinations of ENSO phases and dolphin metrics (e.g., DolpCPUE for La Niña or DolpSets for Neutral conditions), these groups all had 5 or 6 that were significant. There were fewer taxa for which log fishing predictors were robust across ENSO phases, and these only had a maximum of 2 or 3 significant combinations of ENSO phases and log fishing metrics. These included eastern spinner dolphins, whitebelly spinner dolphins, offshore spotted dolphins, mixed offshore spotted and eastern spinner dolphins, and blue whales, most of which were primarily explained by LogSets rather than LogCPUE. Similarly, school fishing metrics were not as robust across ENSO phases, and the taxa influenced by these only had a maximum of 3 or 4 combinations of ENSO phases and school fishing metrics that were significant. These taxa included offshore spotted dolphins, coastal spotted dolphins, mixed schools of offshore spotted and eastern spinner dolphins, Risso's dolphins, offshore common dolphins, rough-toothed dolphins, sperm whales, Bryde's whales, blue whales, and mesoplodont beaked whales.

Analysis of Individual Years

When running the models on each year separately, most of the relationships between the cetaceans and the tuna predictors lost their consistency and robustness (Tbl. 4). Even most of the strong relationships tended to break down. Out of 20 possible combinations of year and dolphin metrics for each taxon, only 4 taxa had 10 or more significant combinations. Those were eastern spinner dolphins, whitebelly spinner dolphins, mixed schools of offshore spotted and eastern spinner dolphins, and

mesoplodont beaked whales. Only bottlenose dolphins exceeded this threshold for log fishing metrics, and no taxa exceeded it for school fishing metrics.

Model Predictions for 2003

The deviance explained by the models built using all years except 2003 ranged from 4.1% for killer whales to 55.6% for whitebelly spinner dolphins (mean = 20.1%) (Tbl. 5). The adjusted R-squared values ranged from 0 for killer whales to 0.42 for whitebelly spinner dolphins (mean = 0.13). GCV scores ranged from 0.04 for whitebelly spinner dolphins to 2.01 for striped dolphins (mean = 0.75). Compared to the climatological models, each of the tuna predictors was significant for fewer of the taxa. Year, as a predictor variable, appeared to be potentially significant for about half the taxa, although it was only significant at the highest level ($p < 0.001$) for four groups: offshore common dolphins, bottlenose dolphins, Bryde's whales, and blue whales.

The prediction maps for 2003 (Figs. 5-23) were divided into three qualitative categories ("good", "fair", and "poor") based on how well the model prediction corresponded to the 2003 survey observations. The "good" category was characterized by maps with a relatively high coincidence of high model predictions (red to orange cells) with high observed sightings per hour for 2003 (black to dark gray dots), and/or low model predictions (yellow cells) with low observed sightings per hour (light gray dots). This category included 10 taxa: offshore spotted dolphins, eastern spinner dolphins, offshore spotted mixed with eastern spinner dolphins, whitebelly spinner dolphins, offshore spotted with whitebelly spinner dolphins, sperm whales, rough-toothed dolphins, striped dolphins, blue whales, and Bryde's whales.

The “fair” category consisted of maps with intermediate coincidence of model predictions with observed sightings for 2003. This means that the model may have captured some obvious areas of high or low sightings, while missing others. This category included offshore common dolphins, short-finned pilot whales, Risso’s dolphins, dwarf sperm whales, killer whales, bottlenose dolphins, Cuvier’s beaked whales, and mesoplodont beaked whales.

The “poor” category included only the coastal spotted dolphin. The prediction for coastal spotted dolphins was unrealistic; this subspecies is restricted to coastal waters, but the model predicted areas of high sightings per hour offshore. Adding geographic or bathymetric constraints (e.g., latitude and longitude, or depth) to the model could alleviate this problem.

DISCUSSION

Interpretation of Patterns

Over-interpretation of results should be avoided for taxa that are challenging to survey in high sea states, particularly beaked whales and dwarf sperm whales. Additionally, caution should be taken when interpreting results from analyses in which data overlap is poor. For most of the models built with a single year of data, the tuna metrics failed to explain the cetacean data, which is attributable, at least in part, to the low degree of overlap between the two datasets at the annual level. For example, for many of the taxa, there are relatively few (less than 10) overlapping cells (i.e., cells that contain both fishery effort and cetacean survey effort) that contain observed sightings for these taxa in 2003. For all taxa, it is useful to compare the predicted maps to historical observations for additional context.

Yellowfin tuna purse-seine fishery metrics appear to have robust relationships with several cetacean taxa in the ETP. For example, the association between dolphin fishing metrics and mixed schools of offshore spotted and eastern spinner dolphins appears to remain stable across years and ENSO phases. Other less robust relationships exhibit inter-annual variability, potentially associated with ENSO phases. For example, model results showed that year was a significant predictor for some taxa (blue whales, offshore common dolphins, bottlenose dolphins, and Bryde's whales), suggesting that inter-annual variability, potentially associated with ENSO phases, may be important to these species. These species all feed on schooling fish or krill and may be influenced by variations in the strength of upwelling. Their behavior (or the behavior of the fishery) may change in under certain conditions, causing their relationships with the 3 types of fishing to change.

Comparison with Previous Research

Investigations into general relationships through canonical correspondence analysis revealed positive associations between dolphin fishing metrics and 5 taxa (mixed schools of offshore spotted with eastern spinner dolphins, pure schools of eastern spinner dolphins, pure schools of offshore spotted dolphins, rough-toothed dolphins, and dwarf sperm whales). There were also negative associations between dolphin fishing metrics and 2 taxa (mixed schools of offshore spotted with whitebelly spinner dolphins and pure schools of whitebelly spinner dolphins) along one axis, and a negative relationship with offshore common dolphins along the other. These relationships reflect those found by Reilly and Fiedler (1994) in a similar analysis performed with oceanographic variables instead of fishery variables as predictors.

Forney et al. (2012) constructed habitat-based spatial models for most of these ETP cetaceans using environmental variables, and used them to predict densities (Figs. 24-28). Their suite of candidate predictor variables included bathymetry, distance to shore, sea surface temperature, salinity, chlorophyll, and mixed-layer depth. The deviance explained by these models ranged from 5.6% to 38.8% (mean= 15.0%), which is similar to our model results (mean = 20.0%, range = 4.1 - 55.6%). The predicted maps by Forney et al. (2012) are qualitatively very similar to the predicted maps in the present study. There is remarkable resemblance in the areas predicted to have high and low densities for each taxon. There are a few notable differences. The southern range of whitebelly spinner dolphins might be better represented by the map from this study (Fig. 8 vs. Fig. 24). The maps for Risso's (Fig. 13) and bottlenose dolphins (Fig. 22) extend further offshore than maps in Forney et al. (2012) (Fig. 26), perhaps capturing more areas of relatively high density. The map for blue whales in this study (Fig. 10) does not fully capture the importance of the Costa Rica Dome, which is known to be important habitat for blue whales. This feature is more apparent in the Forney et al. (2012) maps (Fig. 27). For offshore common dolphins, the map in this study (Fig. 11) captures the high sightings area along the 10°N thermocline ridge near 120°W, which is not pronounced in habitat maps (Fig. 25).

Given that no geographic constraints (e.g., latitude, longitude, or grid cell number) or oceanographic variables were included as predictor variables in our models, they perform surprisingly well for most taxa. Comparing our prediction maps to the habitat-based maps produced by Forney et al. (2012) validates this. Additionally, comparing our prediction maps to maps of all historical sightings (Figs. 5-23, right panel)

shows that many of the models predict high sighting rates in areas that have historically had the highest observed sighting rates and low rates in areas where sightings have historically been low.

While Forney et al. (2012) used environmental variables to produce maps of predicted cetacean densities, we found that we could use tuna fishery metrics to produce similar maps, from which we can infer some general habitat associations. Examining our prediction maps for 2003 (Figs. 5-23, left panel) alongside a map of major oceanographic features (Fig. 1), the taxa can be aggregated into 5 groups: 1) Eastern Pacific Warm Pool associated (“warm pool taxa”); 2) anti-Eastern Pacific Warm Pool associated (“anti-warm pool taxa”); 3) coastal associated (“coastal taxa”); 4) upwelling feature associated – in particular with areas surrounding Baja California, the Costa Rica Dome, the Equatorial Cold Tongue, and the 10°N thermocline ridge (“upwelling taxa”); 5) those with wide distributions and no apparent strong connections to the first four groups (“widespread taxa”).

The “warm pool taxa” include offshore spotted dolphins, eastern spinner dolphins, dwarf sperm whales, mixed schools of offshore spotted with eastern spinner dolphins, and rough-toothed dolphins. “Anti-warm pool taxa” include pure schools of whitebelly spinner dolphins and mixed schools of offshore spotted with whitebelly spinner dolphins. “Coastal taxa” only includes the coastal spotted dolphin. “Upwelling taxa” includes Bryde’s whales, offshore common dolphins, short-finned pilot whales, Risso’s dolphins, bottlenose dolphins, blue whales, sperm whales (to some extent), striped dolphins (to some extent), and killer whales (to some extent). The “widespread taxa” group includes sperm whales (to some extent), striped dolphins (to some extent), killer whales, Cuvier’s

beaked whales, and mesoplodont beaked whales. These general habitat associations reflect those found in Forney et al. (2012).

Relevance of this Approach to EBM

In this study, we have used one set of biological metrics (tuna fishery metrics) to make predictions about other biological components of an oceanic ecosystem (cetacean community structure and relative abundance). This is different from the more common approach of using environmental variables (e.g., physical oceanographic variables) to make predictions about biological components of an ecosystem. Because we performed this analysis on an ecosystem for which there are multiple long-term datasets, we were able to validate our approach by comparing our results to previous studies that have related physical variables to the same taxa. Our approach did not use any physical variables to predict characteristics of cetacean populations (e.g., communities and sighting densities), but our results were qualitatively the same as previous studies that did use them. This exciting result provides incredible support for moving forward with our approach.

This research has demonstrated that yellowfin tuna fishery metrics can be used as indicators of the broader biological ecosystem in the ETP. Based on our findings, we can be confident about the approach developed here and its extension to other taxa. Specifically, our next steps will include similar investigations relating yellowfin tuna fishery metrics to seabirds and larval fishes in the ETP, for which we have comparable long-term datasets. Ultimately, our goal is to use these metrics to make predictions in future years when we have no survey data on cetaceans, seabirds, and larval fishes. By

developing measurable indicators of upper trophic level communities, this approach provides great promise for EBM in the oceanic ETP.

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Chapter 2, in part, is currently being prepared for submission for publication of the material. Martin, Summer L.; Ballance, Lisa T. The dissertation author was the primary investigator and author of this material.

TABLES

Table 1. Taxonomic information for cetaceans used in this study.

Common Name	Codes	Scientific Name
Eastern spinner dolphin	ESpin, 10	<i>Stenella longirostris orientalis</i>
Whitebelly spinner dolphin	WBSpin, 11	<i>Stenella longirostris longirostris</i>
Offshore spotted dolphin	OSpot, 2	<i>Stenella attenuata</i>
Coastal spotted dolphin	CSpot, 6	<i>Stenella attenuata graffmani</i>
Offshore spotted + eastern spinner dolphins	MIXE	<i>S. attenuata</i> + <i>S. longirostris orientalis</i>
Offshore spotted + whitebelly spinner dolphins	MIXW	<i>S. attenuata</i> + <i>S. longirostris</i>
Striped dolphin	STCO	<i>Stenella coeruleoalba</i>
Risso's dolphin	GRGR	<i>Grampus griseus</i>
Offshore common dolphin	DEDE	<i>Delphinus delphis</i>
Short-finned pilot whale	GLMA	<i>Globicephala macrorhynchus</i>
Bottlenose dolphin	TUTR	<i>Tursiops truncatus</i>
Rough-toothed dolphin	STBR	<i>Steno bredanensis</i>
Sperm whale	PHMA	<i>Physeter macrocephalus</i>
Bryde's whale	BAED	<i>Balaenoptera edeni</i>
Cuvier's beaked whale	ZICA	<i>Ziphius cavirostris</i>
Blue whale	BAMU	<i>Balaenoptera musculus</i>
Dwarf sperm whale	KOSI	<i>Kogia sima</i>
Killer whale	OROR	<i>Orcinus orca</i>
Mesoplodont beaked whales	Mesop	<i>Mesoplodon</i> spp.

Table 2. Summary results from GAM models with all data aggregated temporally into one group (climatological analysis). Models explain the indicated percent of deviance in the cetacean data. P-values for smoothed functions of yellowfin tuna metrics indicate whether each metric is important in explaining each taxon. Darker shades of green indicate higher levels of significance ($p < 0.001$ is darkest). “D”, “S”, and “L” signify dolphin, school, and log fishing, respectively. “CPUE” = metric tons of catch per day of fishing effort. “Sets” = number of times the purse-seine net was set in pursuit of tuna. Taxonomic information as in Table 1.

Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
Eastern spinner dolphin	47%	0.005	0.007	1.000	0.000	0.998	0.000
Whitebelly spinner dolphin	40%	0.000	0.118	0.100	0.007	0.986	0.276
Offshore spotted dolphin	32%	0.000	0.993	0.971	0.000	0.001	0.000
Coastal spotted dolphin	47%	0.118	0.011	0.005	0.041	0.030	0.999
Offsh. spot. + east. spinner	56%	0.000	0.183	1.000	0.000	0.005	0.000
Offsh. spot. + wb. spinner	29%	0.001	0.132	0.996	0.001	0.124	0.000
Striped dolphin	24%	0.011	0.000	0.205	0.104	0.989	0.001
Risso's dolphin	26%	0.002	0.121	0.489	0.103	0.018	0.077
Offshore common dolphin	34%	1.000	0.000	0.595	0.368	0.361	0.072
Short-finned pilot whale	18%	0.004	0.995	0.244	0.082	0.320	0.000
Bottlenose dolphin	46%	0.000	0.168	0.001	0.000	0.063	0.000
Rough-toothed dolphin	40%	0.000	0.000	0.050	0.001	0.003	0.063
Sperm whale	19%	0.993	0.204	0.077	0.998	0.001	0.037
Bryde's whale	10%	0.502	0.994	0.011	1.000	0.002	0.003
Cuvier's beaked whale	6%	0.178	0.998	1.000	0.992	0.592	0.083
Blue whale	33%	0.998	0.000	0.987	0.047	0.600	0.003
Dwarf sperm whale	30%	0.000	0.997	0.058	0.000	1.000	0.013
Killer whale	0%	1.000	0.999	0.999	0.999	0.997	0.997
Mesopl. beaked whales	14%	0.000	1.000	0.171	0.006	0.126	0.337

Table 3. Summary results from GAM models with data grouped by El Niño Southern Oscillation (ENSO) phase. Models explain the indicated percent of deviance in the cetacean data. P-values for smoothed functions of yellowfin tuna metrics indicate whether each metric is important in explaining each taxon. Darker shades of green indicate higher levels of significance ($p < 0.001$ is darkest). “D”, “S”, and “L” signify dolphin, school, and log fishing, respectively. “CPUE” = metric tons of catch per day of fishing effort. “Sets” = number of times the purse-seine net was set in pursuit of tuna. Taxonomic information as in Table 1.

ENSO Phase + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
Niña: East. spinner dolphin	39%	0.001	0.001	0.185	0.000	0.000	0.018
Niño: East. spinner dolphin	36%	1.000	0.995	1.000	0.015	0.404	0.015
Neutral: East. spinner dolphin	32%	0.029	0.998	0.078	0.005	0.248	0.005
Niña: Wb. spinner dolphin	60%	0.000	0.001	0.000	0.000	0.000	0.000
Niño: Wb. spinner dolphin	61%	0.000	0.573	0.013	0.000	0.218	0.003
Neutral: Wb. spin. dolphin	60%	0.000	0.777	0.001	0.000	0.158	0.000
Niña: Offsh. spotted dolphin	19%	0.025	0.999	1.000	0.000	0.019	0.000
Niño: Offsh. spotted dolphin	28%	0.097	0.065	0.428	0.054	0.992	0.000
Neutral: Offsh. spot. dolphin	24%	0.000	0.006	1.000	0.000	0.990	0.023
Niña: Coastal spotted dolphin	31%	0.161	0.005	0.135	0.999	0.026	0.072
Niño: Coastal spotted dolphin	98%	0.943	0.954	0.974	0.978	0.962	0.917
Neutral: Coastal spot. dolphin	56%	0.500	0.013	0.208	0.998	0.584	0.537
Niña: Offsh. spot. + east. spin.	44%	0.004	0.001	0.013	0.000	0.000	0.011
Niño: Offsh. spot. + east. spin.	44%	0.004	0.993	1.000	0.004	0.056	0.007
Neutral: Off. spot. + east. spin.	55%	0.000	0.010	0.992	0.000	0.141	0.000
Niña: Offsh. spot. + wb. spin.	30%	0.114	0.014	0.999	0.001	0.998	0.591
Niño: Offsh. spot. + wb. spin.	37%	0.006	0.768	0.992	0.021	0.212	0.056
Neutral: Off. spot. + wb. spin.	33%	0.002	0.446	0.998	0.002	0.014	0.034
Niña: Striped dolphin	10%	0.996	0.280	0.988	0.000	1.000	0.526
Niño: Striped dolphin	25%	0.996	0.225	0.007	0.000	0.065	0.991
Neutral: Striped dolphin	25%	0.032	0.997	0.000	0.489	0.996	0.029
Niña: Risso's dolphin	24%	0.047	0.076	0.037	0.998	0.157	0.998
Niño: Risso's dolphin	23%	0.999	0.108	0.010	0.300	0.001	0.999
Neutral: Risso's dolphin	19%	0.975	0.000	0.827	0.177	0.999	0.065
Niña: Offsh. common dolphin	36%	0.998	0.000	0.000	0.005	0.408	0.001
Niño: Offsh. common dolphin	31%	0.375	0.000	0.896	0.056	0.998	0.989
Neutral: Off. common dolphin	36%	0.299	0.000	0.002	0.994	0.999	0.183

Table 3. Summary results from GAM models with data grouped by El Niño Southern Oscillation (ENSO) phase. Continued.

ENSO Phase + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
Niña: Short-finned pilot whale	11%	0.067	0.999	0.213	0.999	0.991	0.026
Niño: Short-finned pilot whale	10%	0.998	0.037	1.000	0.315	0.999	0.087
Neutral: Short-fin. pilot whale	29%	0.000	0.295	0.307	0.019	0.998	0.023
Niña: Bottlenose dolphin	26%	0.059	0.347	0.390	0.999	0.150	0.374
Niño: Bottlenose dolphin	22%	0.128	0.999	0.004	0.000	0.589	0.998
Neutral: Bottlenose dolphin	32%	0.003	0.001	0.999	0.074	0.997	0.109
Niña: Rough-toothed dolphin	37%	0.000	0.000	0.999	0.000	0.000	0.002
Niño: Rough-toothed dolphin	19%	0.042	0.998	0.812	0.998	1.000	0.232
Neutral: Rough-tooth. dolphin	21%	0.002	1.000	0.999	0.001	0.004	0.999
Niña: Sperm whale	20%	1.000	0.536	0.989	0.179	0.002	0.182
Niño: Sperm whale	30%	0.996	0.999	0.998	0.177	0.000	0.000
Neutral : Sperm whale	32%	0.122	0.067	0.252	0.003	0.048	0.003
Niña: Bryde's whale	12%	0.991	0.288	0.233	0.999	0.066	0.283
Niño: Bryde's whale	22%	0.003	0.998	0.029	0.999	0.096	0.999
Neutral: Bryde's whale	7%	0.999	0.253	0.999	0.998	0.008	0.050
Niña: Cuvier's beaked whale	18%	0.561	0.099	0.994	0.999	0.115	0.469
Niño: Cuvier's beaked whale	7%	0.996	0.071	0.989	0.744	0.109	0.119
Neutral : Cuvier's beak. whale	15%	0.471	1.000	0.098	0.972	0.586	0.045
Niña: Blue whale	43%	0.020	0.005	0.062	0.375	1.000	0.011
Niño: Blue whale	46%	0.001	0.997	0.009	0.002	0.000	0.028
Neutral: Blue whale	52%	0.678	0.045	0.071	0.290	0.191	0.179
Niña: Dwarf sperm whale	27%	0.023	0.719	1.000	0.996	0.029	0.001
Niño: Dwarf sperm whale	34%	0.026	0.998	0.209	0.013	0.999	0.329
Neutral: Dwarf sperm whale	37%	0.006	0.997	0.644	0.079	0.997	0.743
Niña: Killer whale	9%	0.306	0.529	0.309	0.998	0.632	0.999
Niño: Killer whale	18%	0.094	0.000	0.999	0.603	0.999	0.522
Neutral: Killer whale	9%	0.993	0.989	0.331	0.024	0.899	0.115
Niña: Mesopl. beaked whales	9%	0.371	1.000	0.992	0.999	0.003	0.804
Niño: Mesopl. beaked whales	18%	0.313	0.019	0.121	0.111	0.042	0.006
Neutral: Mesopl. beak. whales	24%	0.004	1.000	0.239	0.047	0.995	0.001

Table 4. Summary results from GAM models with data separated by individual years. Models explain the indicated percent of deviance in the cetacean data. P-values for smoothed functions of yellowfin tuna metrics indicate whether each metric is important in explaining each taxon. Darker shades of green indicate higher levels of significance ($p < 0.001$ is darkest). “D”, “S”, and “L” signify dolphin, school, and log fishing, respectively. “CPUE” = metric tons of catch per day of fishing effort. “Sets” = number of times the purse-seine net was set in pursuit of tuna. Taxonomic information as in Table 1.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
1986 East. spin. dolphin	59%	0.998	0.144	0.009	0.011	0.003	0.321
1987 East. spin. dolphin	97%	0.652	0.641	0.902	0.973	0.768	1.000
1988 East. spin. dolphin	100%	0.000	1.000	1.000	0.000	1.000	0.000
1989 East. spin. dolphin	45%	0.094	0.999	0.244	0.999	0.080	1.000
1990 East. spin. dolphin	57%	0.344	0.999	0.259	0.058	1.000	0.999
1998 East. spin. dolphin	47%	0.016	0.368	0.098	0.047	0.996	0.020
1999 East. spin. dolphin	45%	0.291	0.575	0.999	0.577	0.101	0.383
2000 East. spin. dolphin	68%	0.005	0.074	0.992	0.000	0.998	0.998
2003 East. spin. dolphin	82%	0.901	0.974	1.000	0.919	1.000	0.845
2006 East. spin. dolphin	84%	0.996	0.209	0.163	0.045	0.281	1.000
1986 Wb. spin. dolphin	100%	0.000	1.000	1.000	0.000	1.000	1.000
1987 Wb. spin. dolphin	100%	1.000	1.000	1.000	1.000	1.000	1.000
1988 Wb. spin. dolphin	62%	0.075	1.000	0.999	0.546	1.000	0.996
1989 Wb. spin. dolphin	100%	0.000	1.000	0.852	0.000	1.000	1.000
1990 Wb. spin. dolphin	100%	0.000	0.000	1.000	0.000	1.000	0.000
1998 Wb. spin. dolphin	82%	0.769	1.000	0.869	0.867	1.000	1.000
1999 Wb. spin. dolphin	93%	0.578	0.228	0.259	0.775	0.999	0.999
2000 Wb. spin. dolphin	100%	0.000	0.999	1.000	0.000	1.000	1.000
2003 Wb. spin. dolphin	100%	1.000	1.000	1.000	1.000	1.000	1.000
2006 Wb. spin. dolphin	100%	0.000	0.000	1.000	0.000	1.000	0.000
1986 Off. spot. dolphin	33%	0.007	0.999	0.999	0.307	0.751	1.000
1987 Off. spot. dolphin	36%	0.193	0.999	0.002	0.040	1.000	0.993
1988 Off. spot. dolphin	62%	0.004	0.998	0.999	0.000	0.998	0.002
1989 Off. spot. dolphin	53%	0.000	0.217	0.377	0.999	0.006	0.249
1990 Off. spot. dolphin	36%	0.275	0.320	0.163	0.999	0.044	0.987
1998 Off. spot. dolphin	20%	0.007	0.037	1.000	0.002	1.000	0.998
1999 Off. spot. dolphin	0%	0.999	1.000	0.999	1.000	1.000	0.998
2000 Off. spot. dolphin	28%	0.267	0.998	0.156	0.287	0.088	0.999
2003 Off. spot. dolphin	55%	1.000	0.999	1.000	0.996	0.001	0.009
2006 Off. spot. dolphin	16%	0.205	0.999	1.000	1.000	0.575	1.000

Table 4. Summary results from GAM models with data separated by individual years.
Continued.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
1986 Coast. spot. dolph.	96%	0.996	1.000	1.000	1.000	0.999	1.000
1987 Coast. spot. dolph.	100%	1.000	0.000	1.000	0.000	0.000	1.000
1988 Coast. spot. dolph.	100%	1.000	1.000	1.000	1.000	1.000	1.000
1989 Coast. spot. dolph.	100%	1.000	1.000	1.000	1.000	1.000	1.000
1990 Coast. spot. dolph.	85%	0.199	1.000	1.000	1.000	0.972	1.000
1998 Coast. spot. dolph.	43%	0.011	0.053	0.632	0.046	0.999	0.997
1999 Coast. spot. dolph.	49%	0.999	0.279	0.234	0.295	1.000	0.999
2000 Coast. spot. dolph.	90%	1.000	0.999	0.017	0.005	0.315	0.335
2003 Coast. spot. dolph.	61%	0.053	0.863	0.594	0.013	0.790	0.131
2006 Coast. spot. dolph.	97%	0.266	1.000	0.999	0.324	1.000	0.440
1986 Off. spot. + e. spin.	59%	0.099	0.009	0.001	0.001	0.995	1.000
1987 Off. spot. + e. spin.	36%	0.141	0.999	1.000	1.000	0.033	1.000
1988 Off. spot. + e. spin.	100%	0.000	0.000	0.000	0.000	0.000	0.000
1989 Off. spot. + e. spin.	58%	0.000	0.008	0.104	0.001	0.997	0.172
1990 Off. spot. + e. spin.	55%	0.018	0.082	0.999	0.032	0.027	0.152
1998 Off. spot. + e. spin.	45%	0.998	0.998	0.241	0.066	0.002	0.497
1999 Off. spot. + e. spin.	46%	0.015	0.087	0.166	0.004	0.024	0.183
2000 Off. spot. + e. spin.	47%	0.005	0.999	0.020	0.004	0.003	0.996
2003 Off. spot. + e. spin.	66%	0.000	0.995	0.025	0.000	0.025	0.224
2006 Off. spot. + e. spin.	57%	0.044	0.665	0.077	0.025	0.388	0.997
1986 Off. spot + wb. spin.	90%	0.610	0.804	0.319	0.517	1.000	0.630
1987 Off. spot + wb. spin.	100%	0.000	0.000	1.000	0.000	0.000	0.000
1988 Off. spot + wb. spin.	74%	0.869	1.000	0.930	0.869	0.931	0.999
1989 Off. spot + wb. spin.	100%	0.000	1.000	0.000	0.000	0.999	0.000
1990 Off. spot + wb. spin.	92%	1.000	0.989	1.000	0.999	1.000	0.927
1998 Off. spot + wb. spin.	100%	0.000	1.000	1.000	1.000	0.000	0.000
1999 Off. spot + wb. spin.	43%	0.343	1.000	0.243	0.999	0.695	0.496
2000 Off. spot + wb. spin.	96%	0.937	0.935	1.000	0.854	0.906	0.967
2003 Off. spot + wb. spin.	100%	0.000	0.000	0.000	0.000	1.000	1.000
2006 Off. spot + wb. spin.	100%	0.000	0.000	0.000	0.000	0.000	0.000
1986 Striped dolphin	51%	0.020	0.998	0.001	0.060	0.823	0.021
1987 Striped dolphin	18%	1.000	0.999	0.012	0.117	0.556	0.586
1988 Striped dolphin	24%	0.999	0.999	0.999	0.999	1.000	0.014
1989 Striped dolphin	24%	0.119	0.615	0.101	0.364	0.999	1.000
1990 Striped dolphin	8%	1.000	0.998	0.046	0.999	1.000	0.999
1998 Striped dolphin	7%	0.999	0.999	0.997	0.999	1.000	0.115

Table 4. Summary results from GAM models with data separated by individual years.
Continued.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
1999 Striped dolphin	25%	0.999	0.002	0.999	0.022	0.998	1.000
2000 Striped dolphin	18%	1.000	0.344	1.000	0.002	0.988	0.063
2003 Striped dolphin	29%	1.000	0.075	0.996	0.207	1.000	0.022
2006 Striped dolphin	24%	0.064	0.431	0.009	0.999	0.999	1.000
1986 Risso's dolphin	3%	1.000	1.000	0.996	0.999	0.496	1.000
1987 Risso's dolphin	56%	0.860	0.088	0.229	0.018	0.998	0.143
1988 Risso's dolphin	31%	0.029	0.999	0.999	0.999	0.061	0.999
1989 Risso's dolphin	84%	0.002	0.019	0.058	0.002	1.000	0.843
1990 Risso's dolphin	80%	0.404	0.996	0.980	0.999	0.998	0.998
1998 Risso's dolphin	25%	1.000	0.250	0.270	0.417	0.559	0.999
1999 Risso's dolphin	60%	0.060	0.034	1.000	0.012	0.999	0.221
2000 Risso's dolphin	19%	0.999	1.000	1.000	0.999	0.025	0.127
2003 Risso's dolphin	48%	1.000	0.022	0.998	0.067	0.999	0.168
2006 Risso's dolphin	64%	1.000	0.161	0.316	0.052	0.000	0.295
1986 Off. comm. dolph.	95%	1.000	1.000	0.999	1.000	1.000	1.000
1987 Off. comm. dolph.	53%	1.000	0.060	0.028	0.256	0.001	0.207
1988 Off. comm. dolph.	93%	1.000	1.000	1.000	1.000	1.000	1.000
1989 Off. comm. dolph.	39%	0.999	0.648	0.047	0.023	0.352	1.000
1990 Off. comm. dolph.	83%	0.999	0.427	0.469	0.513	0.478	0.436
1998 Off. comm. dolph.	24%	0.131	0.999	0.105	0.999	0.999	1.000
1999 Off. comm. dolph.	45%	0.005	0.000	0.045	1.000	1.000	0.234
2000 Off. comm. dolph.	49%	1.000	0.003	0.292	0.137	0.091	0.996
2003 Off. comm. dolph.	23%	0.993	1.000	0.998	0.042	0.997	0.298
2006 Off. comm. dolph.	74%	0.047	0.395	0.079	0.078	0.741	0.124
1986 Short-fin. pilot wh.	79%	0.515	0.877	0.883	1.000	0.929	0.997
1987 Short-fin. pilot wh.	62%	0.085	0.316	0.162	1.000	1.000	0.540
1988 Short-fin. pilot wh.	93%	1.000	1.000	0.999	0.788	0.750	0.546
1989 Short-fin. pilot wh.	95%	0.948	0.964	0.851	0.911	0.944	1.000
1990 Short-fin. pilot wh.	90%	0.925	0.808	0.904	0.916	0.925	0.962
1998 Short-fin. pilot wh.	44%	0.183	0.999	0.999	0.226	0.410	0.603
1999 Short-fin. pilot wh.	58%	0.995	1.000	0.073	0.408	0.055	0.014
2000 Short-fin. pilot wh.	96%	0.813	0.797	0.902	0.888	0.722	0.960
2003 Short-fin. pilot wh.	92%	1.000	0.999	0.997	0.801	0.956	0.989
2006 Short-fin. pilot wh.	94%	1.000	1.000	1.000	1.000	1.000	0.998
1986 Bottlenose dolph.	36%	0.999	0.999	0.093	0.237	0.055	0.037
1987 Bottlenose dolph.	48%	0.085	0.999	0.169	0.116	0.008	0.041

Table 4. Summary results from GAM models with data separated by individual years. Continued.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
1988 Bottlenose dolph.	78%	0.909	1.000	0.741	0.988	1.000	0.918
1989 Bottlenose dolph.	50%	0.990	1.000	0.002	0.025	1.000	0.005
1990 Bottlenose dolph.	88%	0.802	0.817	0.866	0.810	0.976	0.814
1998 Bottlenose dolph.	64%	0.001	1.000	0.000	0.129	0.000	0.000
1999 Bottlenose dolph.	50%	0.316	0.592	0.007	0.993	0.999	0.003
2000 Bottlenose dolph.	31%	0.996	0.162	0.041	0.999	0.525	0.103
2003 Bottlenose dolph.	51%	0.010	0.492	0.997	0.121	0.004	0.412
2006 Bottlenose dolph.	68%	0.006	0.009	0.101	0.448	0.004	0.020
1986 Roug.-tooth. dolp.	51%	0.005	0.028	0.998	0.461	0.081	0.151
1987 Roug.-tooth. dolp.	60%	0.997	0.037	0.167	0.999	0.115	0.096
1988 Roug.-tooth. dolp.	100%	0.000	0.000	0.000	1.000	1.000	0.000
1989 Roug.-tooth. dolp.	13%	0.993	0.997	0.999	0.298	0.268	0.999
1990 Roug.-tooth. dolp.	39%	0.163	0.447	0.208	0.130	0.184	0.998
1998 Roug.-tooth. dolp.	37%	0.000	0.999	0.003	0.995	0.999	0.245
1999 Roug.-tooth. dolp.	45%	0.130	0.648	0.228	0.999	0.183	0.222
2000 Roug.-tooth. dolp.	85%	0.496	0.965	0.954	0.826	0.832	1.000
2003 Roug.-tooth. dolp.	33%	0.999	0.999	1.000	0.242	0.204	0.081
2006 Roug.-tooth. dolp.	92%	0.000	0.764	0.002	0.249	0.947	0.003
1986 Sperm whale	41%	0.321	1.000	0.018	0.006	0.022	0.997
1987 Sperm whale	45%	0.066	1.000	0.184	0.996	0.021	1.000
1988 Sperm whale	73%	0.039	0.027	0.998	1.000	0.004	0.024
1989 Sperm whale	81%	0.139	0.169	0.154	0.124	1.000	0.183
1990 Sperm whale	38%	0.016	0.379	0.317	0.999	0.999	0.031
1998 Sperm whale	99%	0.909	0.722	0.264	0.647	0.891	0.789
1999 Sperm whale	93%	0.804	0.995	0.963	0.896	0.877	0.994
2000 Sperm whale	100%	0.000	1.000	0.000	0.000	0.999	1.000
2003 Sperm whale	85%	1.000	0.365	0.969	0.654	0.809	0.915
2006 Sperm whale	100%	1.000	1.000	0.999	1.000	0.000	1.000
1986 Bryde's whale	75%	0.751	0.775	0.926	0.999	0.775	1.000
1987 Bryde's whale	58%	1.000	1.000	0.000	0.001	0.999	0.000
1988 Bryde's whale	95%	0.386	0.894	1.000	0.994	0.954	0.975
1989 Bryde's whale	60%	1.000	0.193	0.805	0.999	1.000	0.481
1990 Bryde's whale	15%	0.999	0.999	0.103	0.999	0.407	0.122
1998 Bryde's whale	0%	1.000	0.999	1.000	0.999	1.000	0.999
1999 Bryde's whale	59%	0.097	0.000	0.098	0.046	0.000	0.002
2000 Bryde's whale	43%	0.999	1.000	0.070	0.205	0.008	0.127

Table 4. Summary results from GAM models with data separated by individual years. Continued.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
2003 Bryde's whale	64%	1.000	0.149	1.000	0.533	0.088	0.573
2006 Bryde's whale	32%	0.999	0.463	0.110	0.999	0.027	0.998
1986 Cuvier's beak. wh.	30%	0.999	0.999	1.000	0.999	0.064	0.039
1987 Cuvier's beak. wh.	97%	0.888	0.989	0.940	0.907	1.000	1.000
1988 Cuvier's beak. wh.	100%	0.000	1.000	1.000	1.000	0.000	1.000
1989 Cuvier's beak. wh.	47%	0.293	0.758	0.999	0.999	0.999	0.384
1990 Cuvier's beak. wh.	0%	1.000	1.000	0.999	0.999	1.000	0.999
1998 Cuvier's beak. wh.	63%	0.001	0.516	0.033	0.000	0.083	0.998
1999 Cuvier's beak. wh.	86%	0.999	0.772	0.691	0.859	0.999	0.824
2000 Cuvier's beak. wh.	100%	0.000	0.000	0.000	0.000	0.000	0.999
2003 Cuvier's beak. wh.	100%	1.000	1.000	0.000	0.000	0.000	0.000
2006 Cuvier's beak. wh.	100%	0.000	0.000	0.000	1.000	0.000	0.000
1986 Blue whale	100%	1.000	0.000	0.000	1.000	1.000	1.000
1987 Blue whale	85%	1.000	0.949	0.997	0.973	0.706	0.919
1988 Blue whale	100%	1.000	0.000	0.000	0.999	0.000	1.000
1989 Blue whale	95%	0.820	0.820	0.985	0.999	0.886	0.893
1990 Blue whale	100%	1.000	1.000	1.000	1.000	1.000	1.000
1998 Blue whale	77%	0.999	0.323	0.707	0.348	0.993	0.995
1999 Blue whale	56%	1.000	0.998	0.365	0.015	0.148	0.348
2000 Blue whale	100%	0.000	1.000	1.000	1.000	0.000	0.000
2003 Blue whale	99%	1.000	0.358	0.438	1.000	0.548	0.397
2006 Blue whale	47%	1.000	0.379	0.418	0.657	0.002	0.999
1986 Dwarf sperm wh.	71%	0.296	0.998	0.994	0.639	0.068	0.136
1987 Dwarf sperm wh.	97%	0.132	0.329	1.000	0.126	0.311	1.000
1988 Dwarf sperm wh.	81%	1.000	1.000	1.000	1.000	1.000	1.000
1989 Dwarf sperm wh.	80%	0.001	0.004	1.000	0.003	0.006	0.004
1990 Dwarf sperm wh.	74%	1.000	1.000	0.943	0.998	0.987	1.000
1998 Dwarf sperm wh.	54%	0.012	0.998	0.997	0.999	0.001	0.827
1999 Dwarf sperm wh.	64%	0.073	0.030	0.030	1.000	0.119	0.999
2000 Dwarf sperm wh.	90%	0.000	0.999	0.666	0.000	0.000	0.014
2003 Dwarf sperm wh.	85%	0.980	0.596	0.999	0.589	0.016	1.000
2006 Dwarf sperm wh.	92%	0.383	0.918	1.000	0.631	0.856	0.618
1986 Killer whale	71%	0.994	0.538	0.986	0.983	0.490	0.990
1987 Killer whale	78%	0.000	0.222	0.649	0.000	0.292	0.780
1988 Killer whale	71%	0.999	0.999	0.536	0.998	0.998	0.998
1989 Killer whale	61%	0.061	0.137	0.439	0.999	0.007	0.999

Table 4. Summary results from GAM models with data separated by individual years.
Continued.

Year + Cetacean Taxon	DevExp	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets
1990 Killer whale	81%	1.000	1.000	1.000	1.000	1.000	1.000
1998 Killer whale	27%	0.211	0.999	0.980	0.396	0.159	0.300
1999 Killer whale	91%	0.985	0.871	0.993	0.995	0.793	0.973
2000 Killer whale	59%	0.216	0.997	0.098	1.000	0.997	0.053
2003 Killer whale	95%	1.000	0.998	0.995	0.987	1.000	1.000
2006 Killer whale	7%	0.999	0.800	1.000	1.000	0.999	0.771
1986 Mesop. beak. wh.	53%	0.071	1.000	0.010	0.097	0.189	0.009
1987 Mesop. beak. wh.	41%	0.999	0.001	1.000	0.027	0.043	0.005
1988 Mesop. beak. wh.	83%	0.682	1.000	0.839	0.875	0.818	0.814
1989 Mesop. beak. wh.	76%	0.000	0.025	0.011	0.000	0.019	0.000
1990 Mesop. beak. wh.	9%	0.091	0.999	0.994	1.000	1.000	1.000
1998 Mesop. beak. wh.	28%	0.266	0.253	0.997	0.084	0.999	0.453
1999 Mesop. beak. wh.	39%	0.081	0.137	0.999	0.471	0.061	0.225
2000 Mesop. beak. wh.	4%	1.000	0.999	0.998	0.999	1.000	0.316
2003 Mesop. beak. wh.	41%	1.000	0.027	0.501	0.084	0.999	0.999
2006 Mesop. beak. wh.	78%	0.999	0.192	0.042	0.001	0.343	1.000

Table 5. Summary results from GAM models built with all years of data except 2003. Models explain the indicated percent of deviance in the cetacean data. P-values for smoothed functions of yellowfin tuna metrics indicate whether each metric is important in explaining each taxon. Darker shades of green indicate higher levels of significance ($p < 0.001$ is darkest). “D”, “S”, and “L” signify dolphin, school, and log fishing, respectively. “CPUE” = metric tons of catch per day of fishing effort. “Sets” = number of times the nurse-seine net was set in pursuit of tuna. Taxonomic information as in Table 1.

Taxon	DevEx	R-sq	GCV	D_CPUE	S_CPUE	L_CPUE	D_Sets	S_Sets	L_Sets	Year
Eastern spin. dolph.	18%	0.06	0.55	0.015	0.628	0.992	0.997	0.516	0.037	0.070
Wb. spin. dolph.	56%	0.42	0.04	0.121	0.543	0.018	0.994	0.999	0.034	0.867
Offsh. spot. dolph.	16%	0.15	1.08	0.000	0.992	0.000	0.008	0.010	0.998	0.341
Coastal spot. dolph.	44%	0.19	0.57	0.000	0.542	0.833	0.000	0.019	0.209	0.004
Off. spot. + east. spin.	29%	0.18	0.88	0.000	0.658	0.992	0.000	0.000	0.001	0.267
Off. spot. + wb. spin.	22%	0.02	0.24	0.177	0.412	0.232	0.217	0.265	0.097	0.245
Striped dolphin	6%	0.07	2.00	0.992	0.039	0.163	0.017	0.995	0.205	0.308
Risso's dolphin	14%	0.14	0.87	0.350	0.018	0.369	0.103	0.059	0.468	0.032
Offsh. comm. dolph.	19%	0.15	1.23	0.003	0.022	0.998	0.165	0.088	0.282	0.000
Short-finned pilot wh.	17%	0.10	0.50	0.996	0.227	0.000	0.116	0.001	0.994	0.703
Bottlenose dolphin	15%	0.13	1.64	0.032	0.555	0.993	0.310	0.000	0.244	0.000
Rough-tooth. dolph.	12%	0.03	0.72	0.136	0.998	0.750	0.435	0.317	0.172	0.570
Sperm whale	21%	0.12	0.65	0.462	0.260	0.043	0.999	0.000	0.996	0.004
Bryde's whale	9%	0.04	0.66	0.544	0.999	0.724	0.998	0.077	0.999	0.000
Cuvier's beaked wh.	9%	0.07	0.49	0.998	0.354	0.175	0.534	0.094	0.468	0.224
Blue whale	33%	0.19	0.31	0.408	0.232	0.389	0.364	0.090	0.998	0.000
Dwarf sperm whale	27%	0.24	0.71	0.069	0.491	0.033	0.224	0.593	0.029	0.965
Killer whale	4%	0.00	0.42	0.383	0.591	0.996	0.243	0.998	0.480	0.564
Mesop. beaked wh.	12%	0.11	0.69	0.023	0.088	0.997	0.166	0.281	0.018	0.074

FIGURES

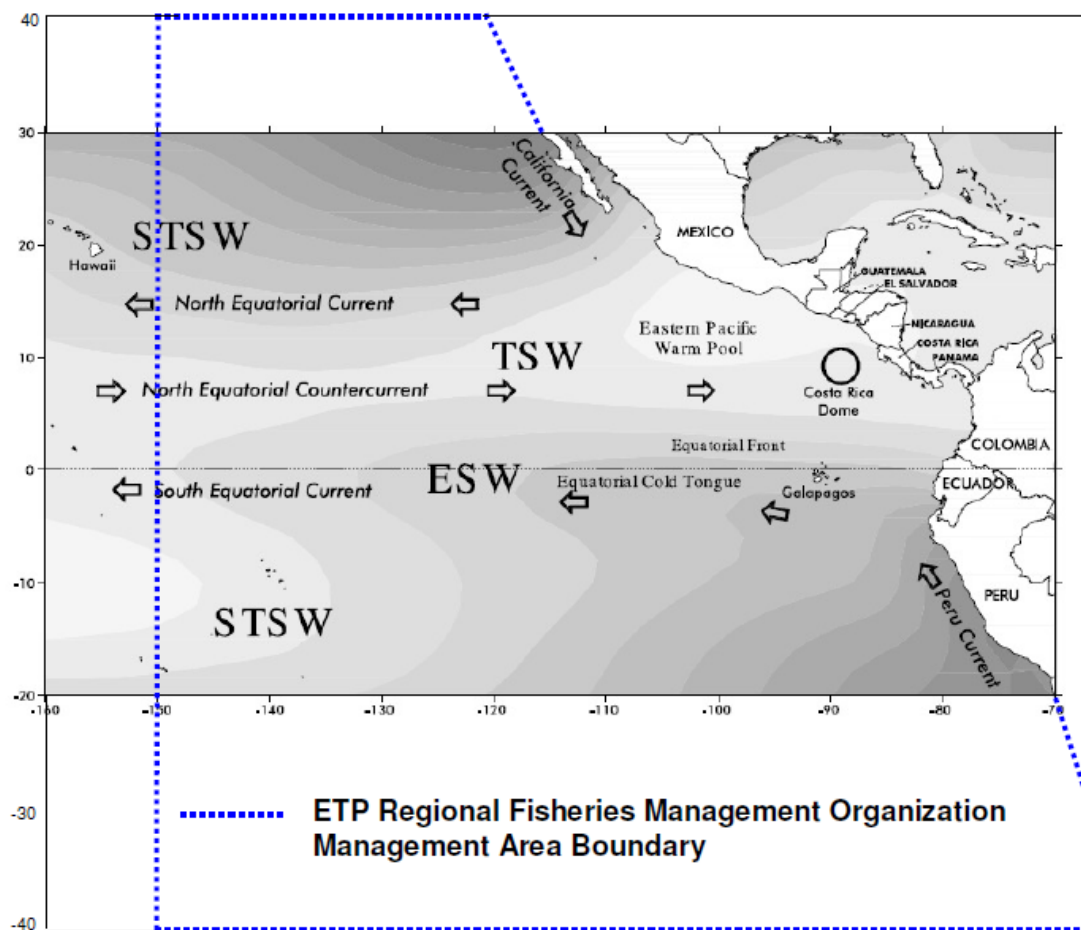


Figure 1. Schematic diagram of surface water masses and currents in the ETP. STSW = Subtropical Surface Water. TSW = Tropical Surface Water. ESW = Equatorial Surface Water. Shading represents mean sea surface temperature (darker = colder). The blue dotted line is the boundary that applies to the ETP Regional Fisheries Management Organization (the Inter-American Tropical Tuna Commission), which is responsible for the conservation and management of marine resources in the region bounded by 150°W, 40°N, 40°S, and the coasts of the Americas. Adapted from Figure 2 in Fiedler and Talley (2006).

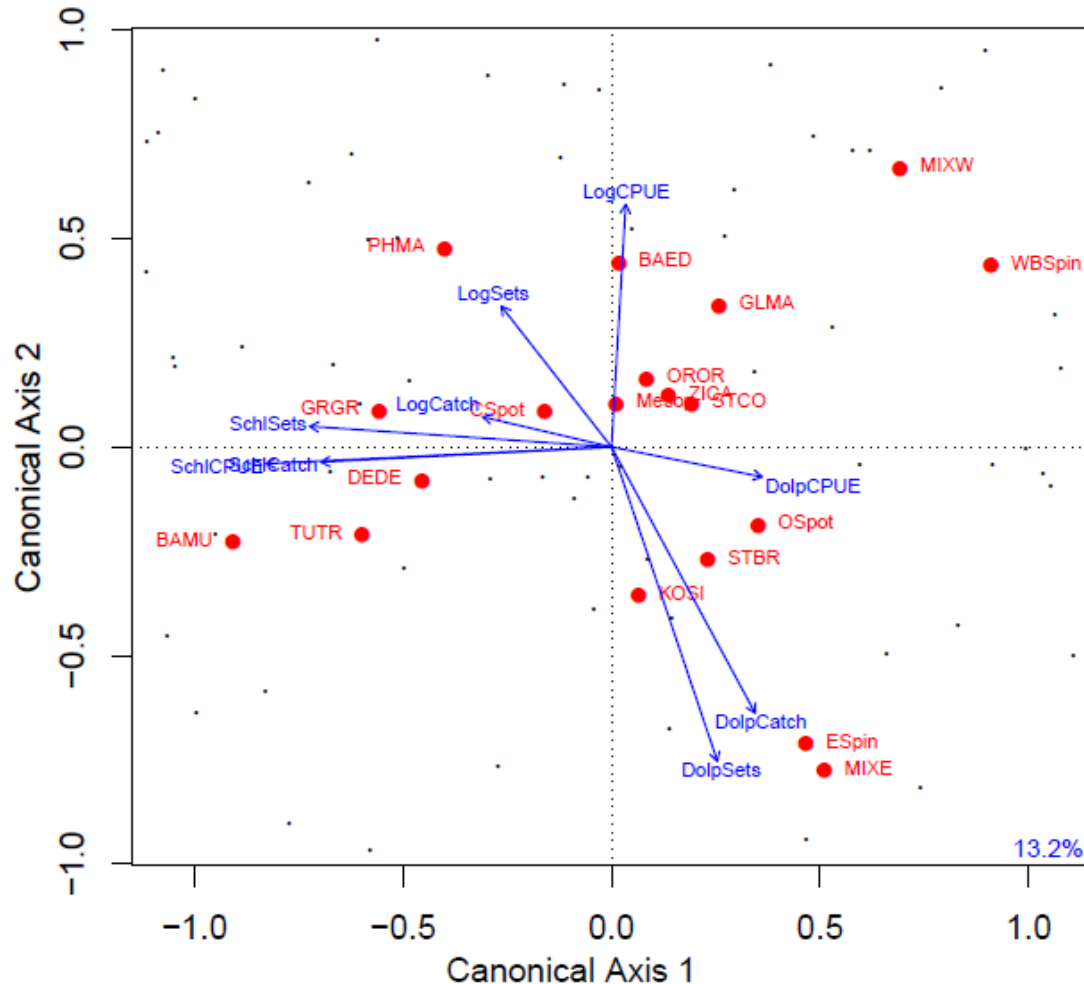


Figure 2. Relationships between tuna fishery metrics and sightings per hour for cetacean taxa as revealed by canonical correspondence analysis (CCA) with all data aggregated temporally into one group (climatological view). The CCA biplot contains grid cells as black points, yellowfin tuna fishery metrics as predictors in blue, and cetacean taxa in red. Predictors include – for dolphin, school, and log fishing methods – “Catch” (metric tons of catch), “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort, where effort is number of days fished). The predictors explain 13.2% of the variance in the cetacean data. The horizontal axis is canonical axis 1; the vertical axis is canonical axis 2. Values along the bottom and left sides correspond to cetacean axis scores. Taxonomic abbreviations as in Table 1.

Figure 3. Relationships between tuna fishery metrics and sightings per hour for cetacean taxa as revealed by canonical correspondence analysis (CCA) with data aggregated temporally by El Niño Southern Oscillation (ENSO) phase. The CCA biplot contains grid cells as black points, yellowfin tuna fishery metrics as predictors in blue, and cetacean taxa in red. The predictors explain 10.6–14.8% of the variance in the cetacean data. The horizontal axis is canonical axis 1; the vertical axis is canonical axis 2. Abbreviations of tuna predictors as in Figure 2. Taxonomic abbreviations as in Table 1

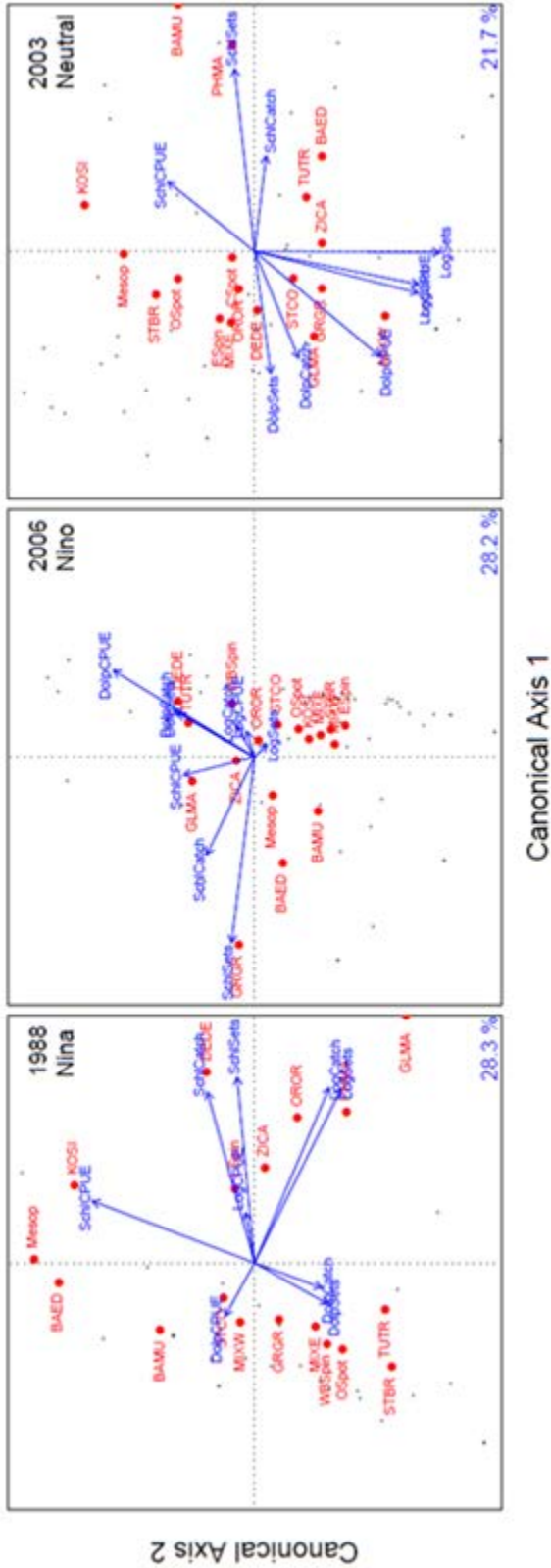


Figure 4. Relationships between tuna fishery metrics and sightings per hour for cetacean taxa as revealed by canonical correspondence analysis (CCA) for one example year for each El Niño Southern Oscillation (ENSO) phase. These example years had the highest explained variance of the years associated with each ENSO phase. The CCA biplot contains grid cells as black points, yellowfin tuna fishery metrics as predictors in blue, and cetacean taxa in red. The predictors explain 21.7-28.3% of the variance in the cetacean data. The horizontal axis is canonical axis 1; the vertical axis is canonical axis 2. Abbreviations of tuna predictors as in Figure 2. Taxonomic abbreviations as in Table 1.

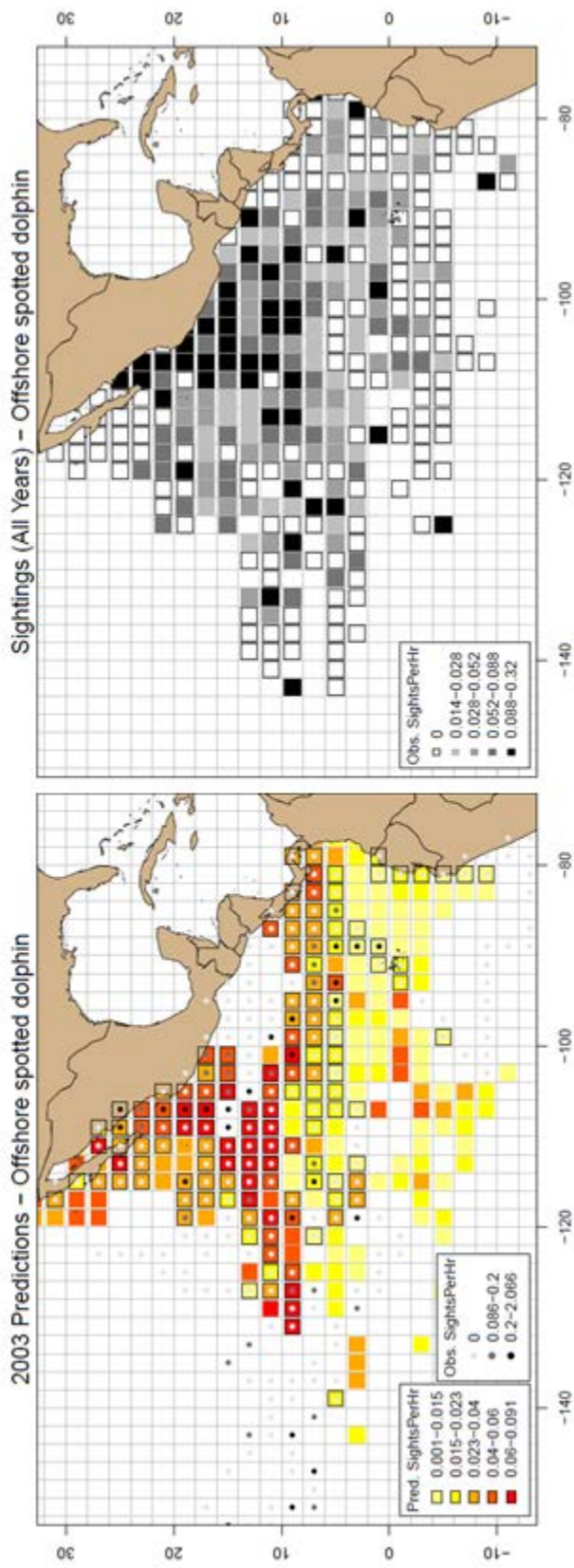


Figure 5. Model predictions (left) for the number of sightings per hour for pure schools of offshore spotted dolphins (*Stenella attenuata*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

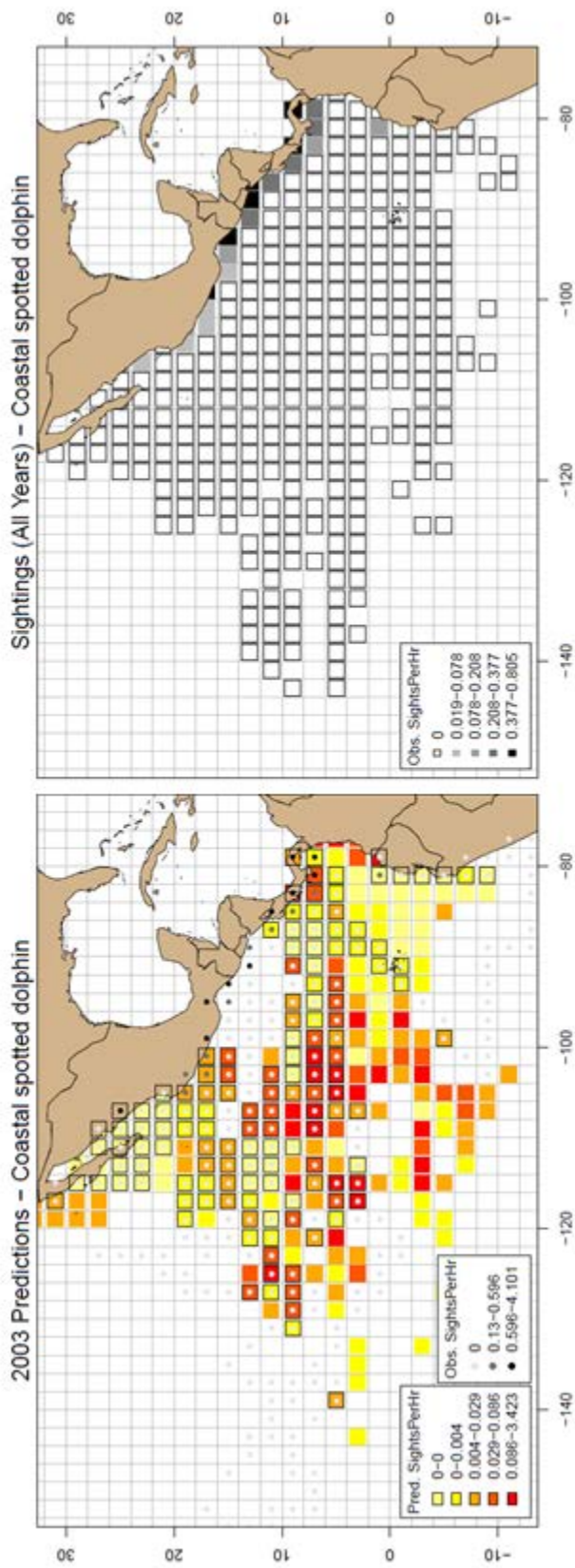


Figure 6. Model predictions (left) for the number of sightings per hour for coastal spotted dolphins (*Stenella attenuata graffmani*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a red dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate a reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

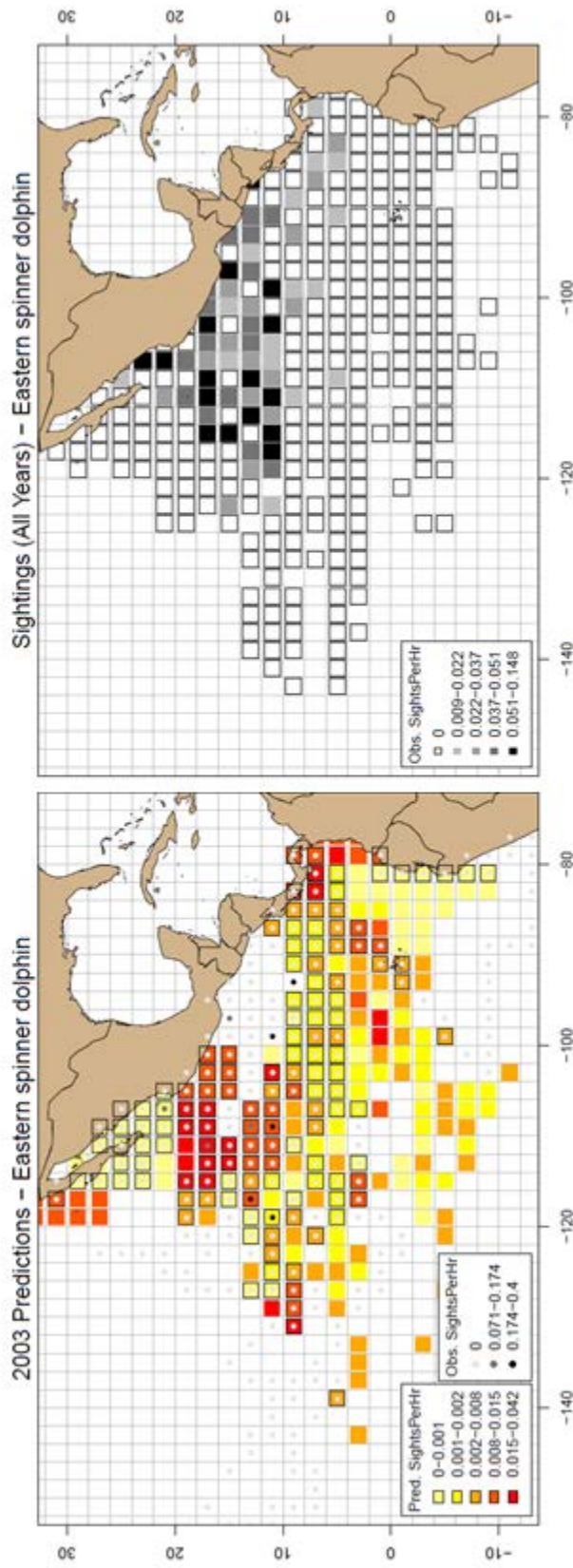


Figure 7. Model predictions (left) for the number of sightings per hour for eastern spinner dolphins (*Stenella longirostris orientalis*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a red dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and black dots on orange cells also indicate a reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

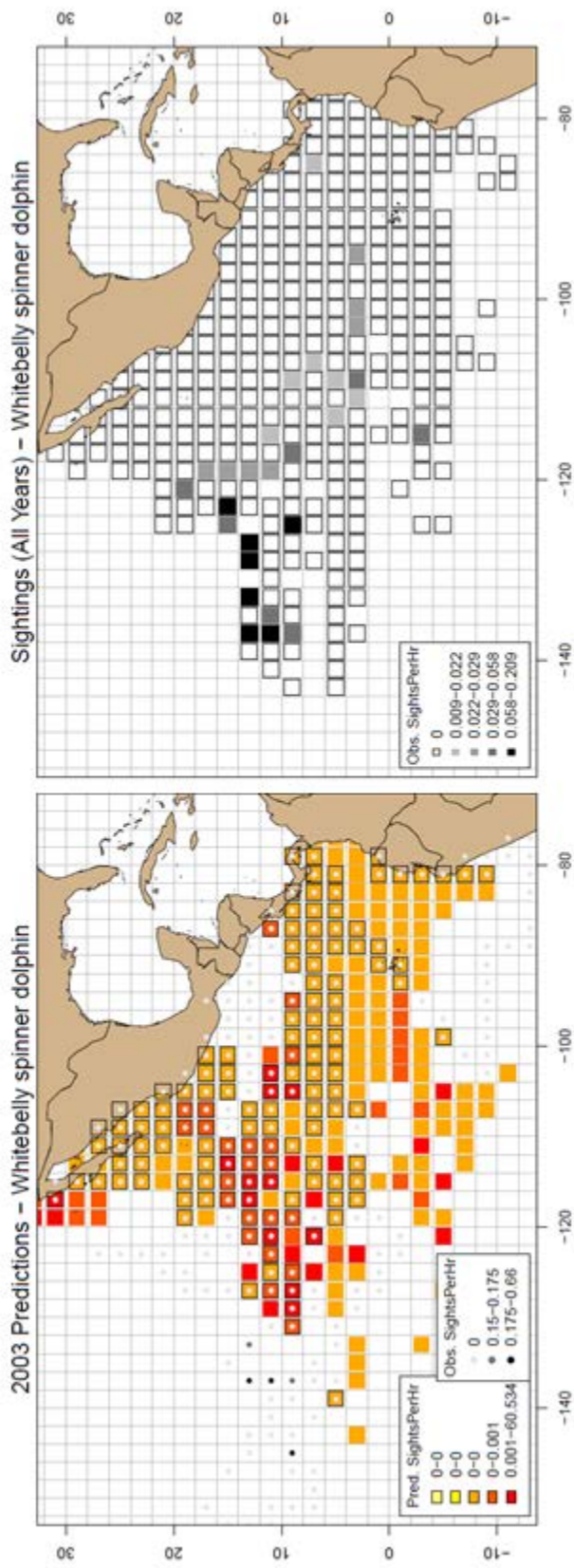


Figure 8. Model predictions (left) for the number of sightings per hour for whitebelly spinner dolphins (*Stenella longirostris*) *longirostris*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

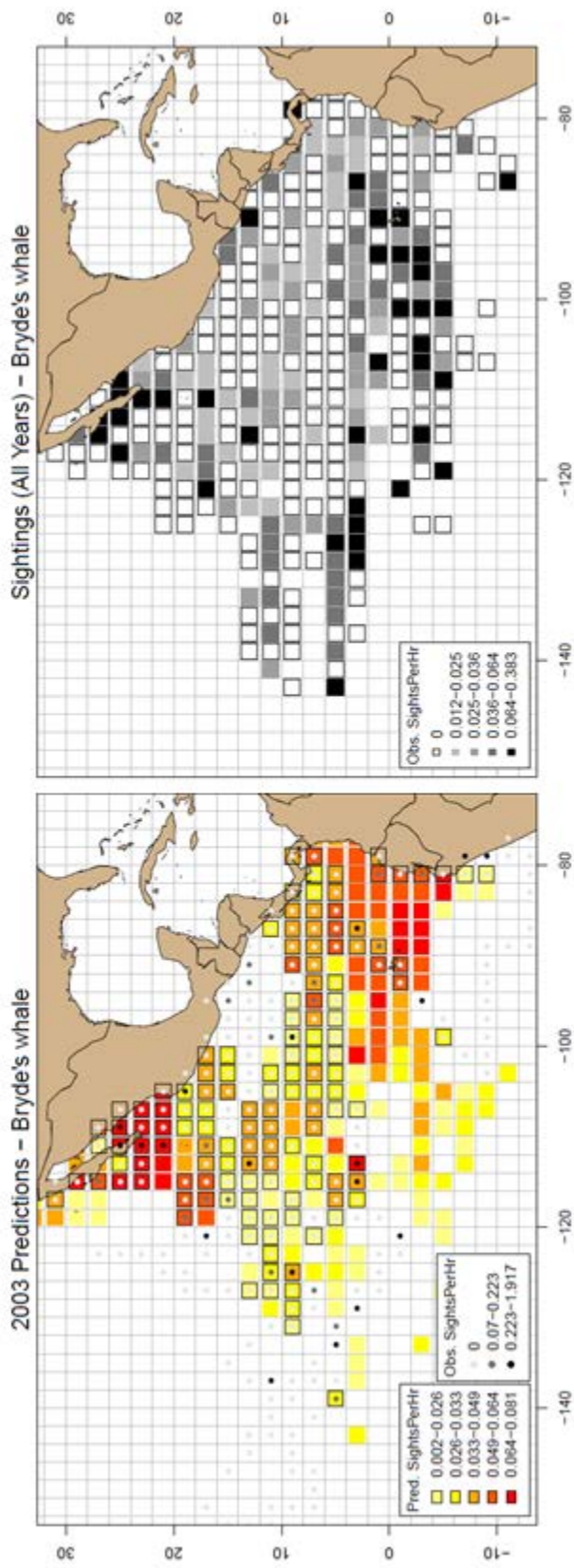


Figure 9. Model predictions (left) for the number of sightings per hour for Bryde's whales (*Balaenoptera edeni*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

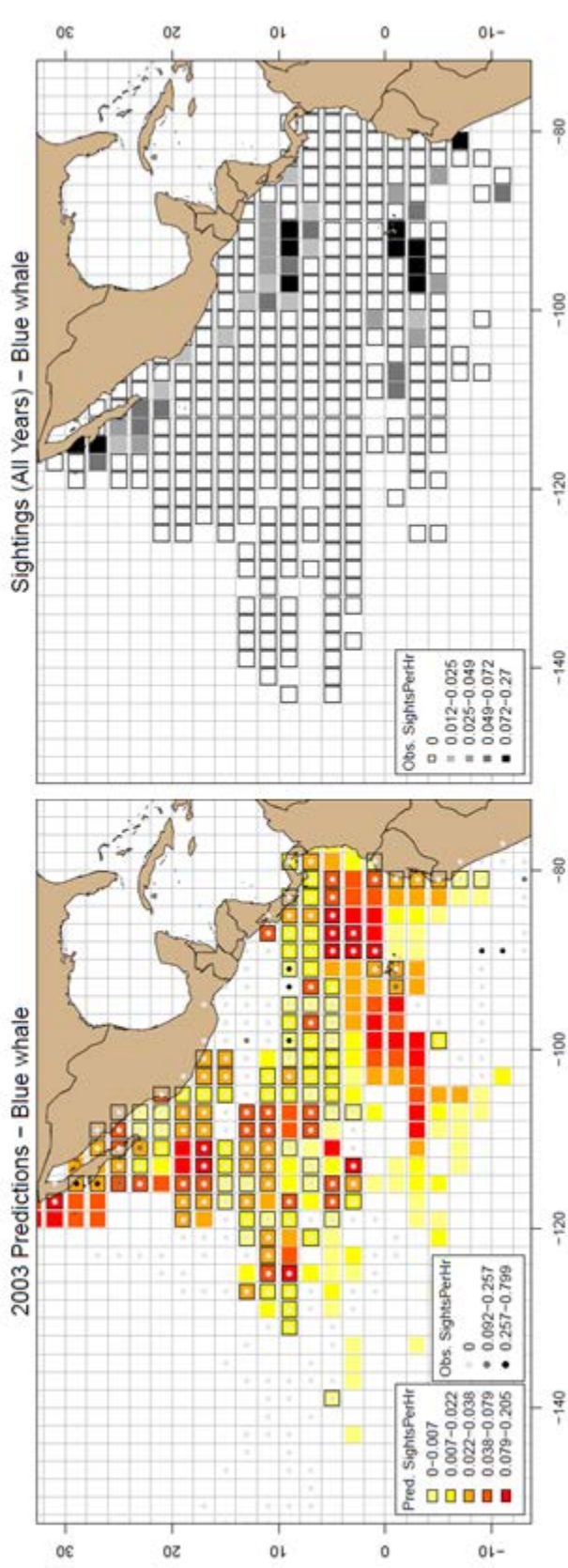


Figure 10. Model predictions (left) for the number of sightings per hour for blue whales (*Balaenoptera musculus*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

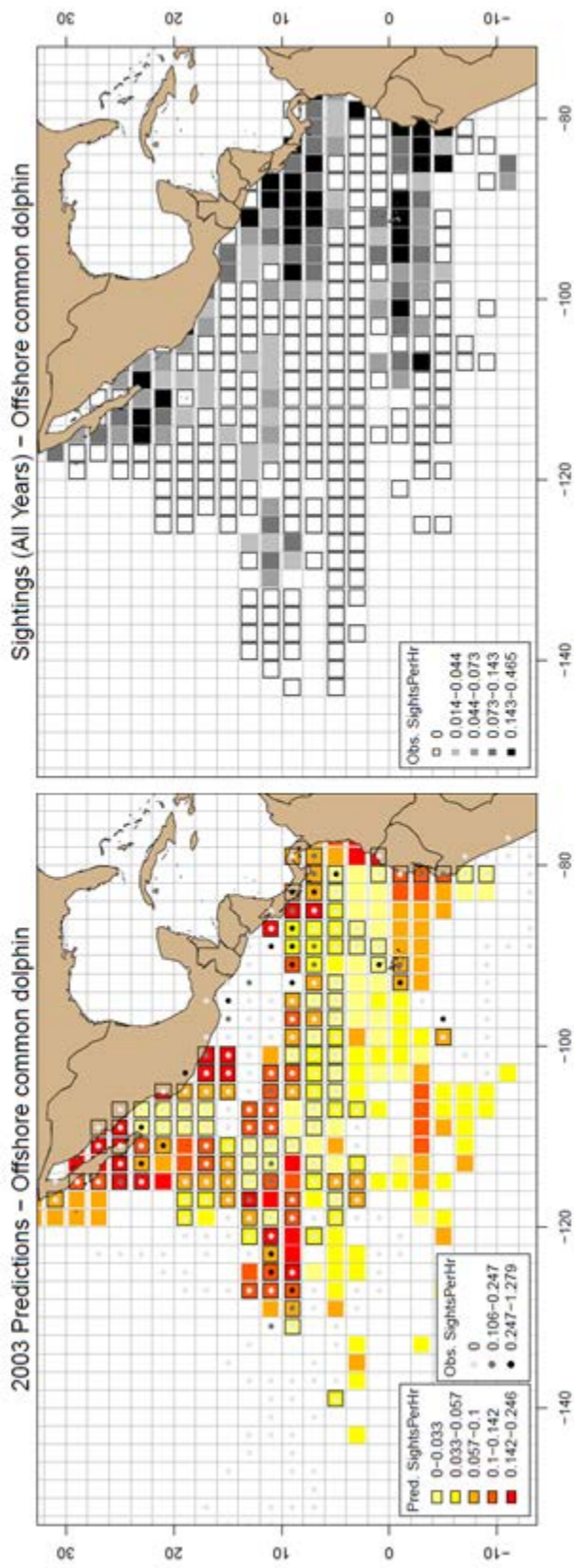


Figure 11. Model predictions (left) for the number of sightings per hour for offshore common dolphins (*Delphinus delphis*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a red dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate a reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

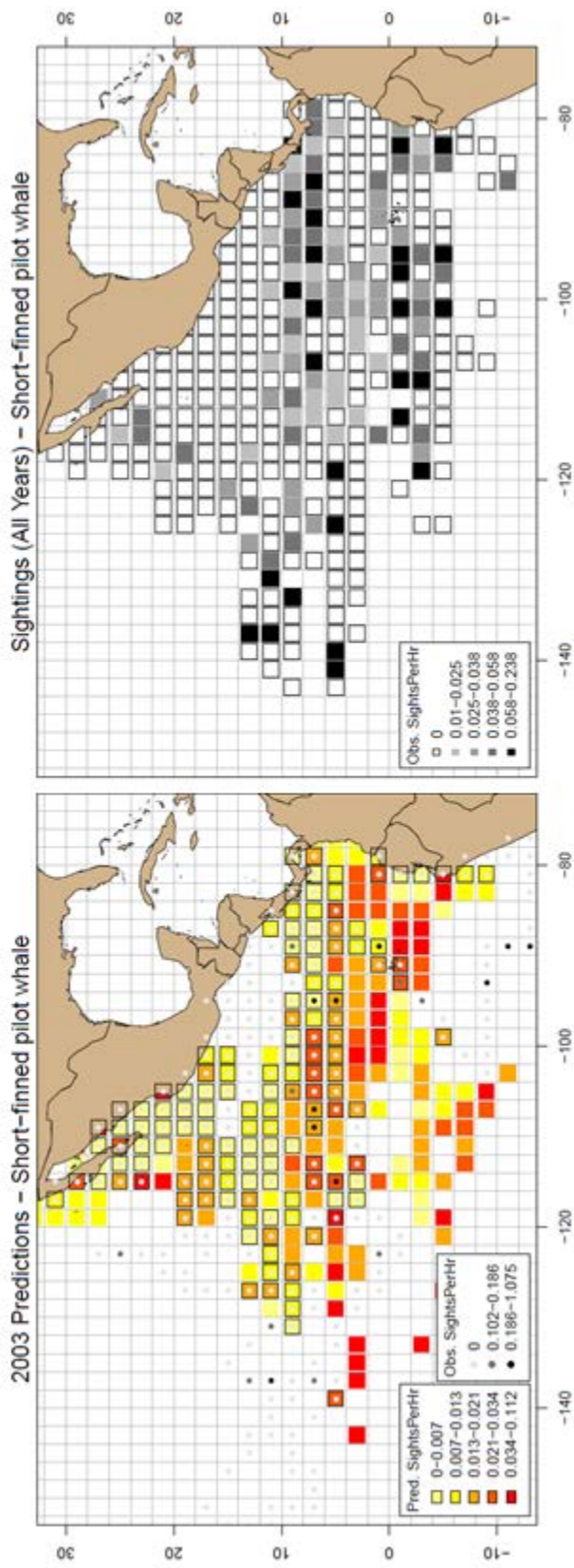


Figure 12. Model predictions (left) for the number of sightings per hour for short-finned pilot whales (*Globicephala macrorhynchus*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

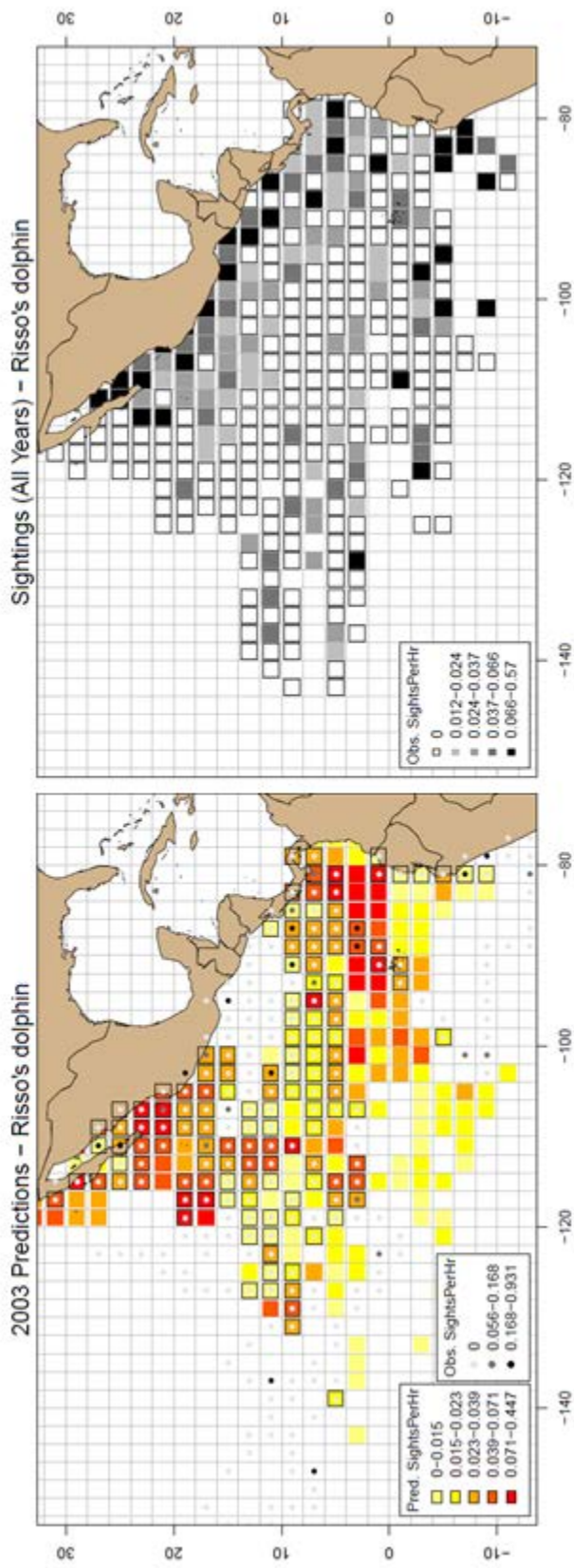


Figure 13. Model predictions (left) for the number of sightings per hour for Risso's dolphins (*Grampus griseus*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

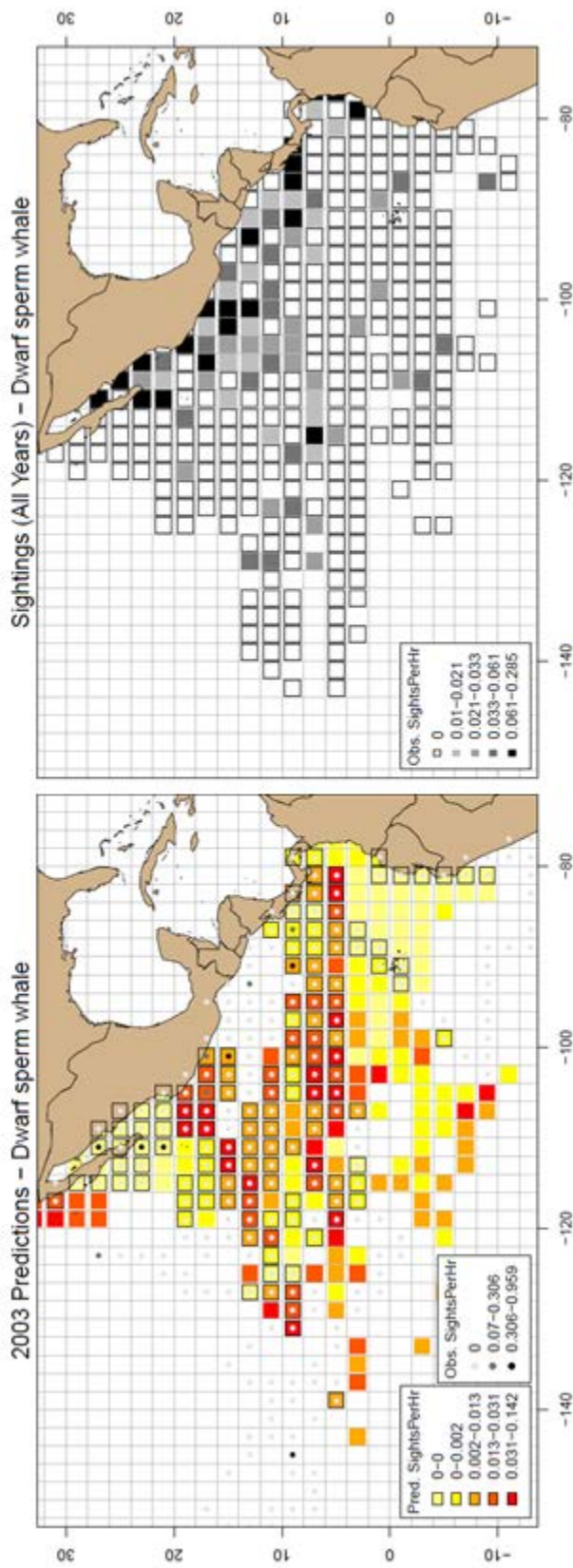


Figure 14. Model predictions (left) for the number of sightings per hour for dwarf sperm whales (*Kogia sima*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

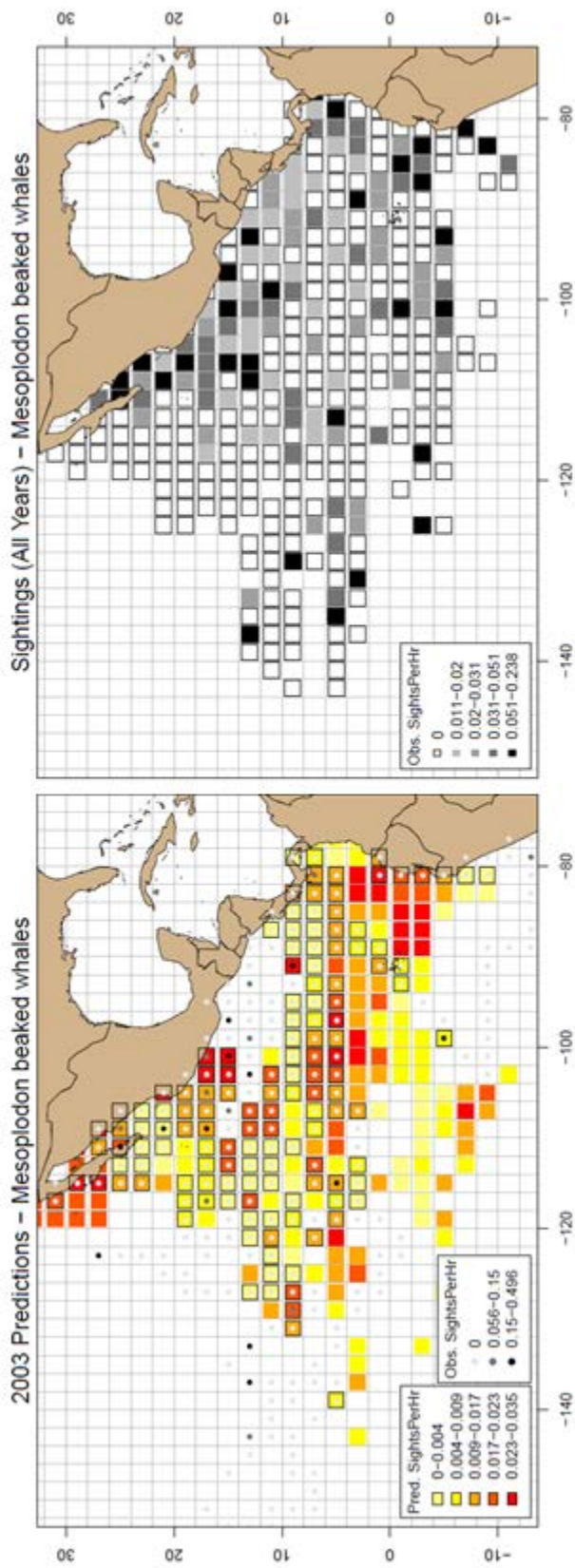


Figure 15. Model predictions (left) for the number of sightings per hour for beaked whales in the genus *Mesoplodon* (*Mesoplodon* spp.). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a red dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate a reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

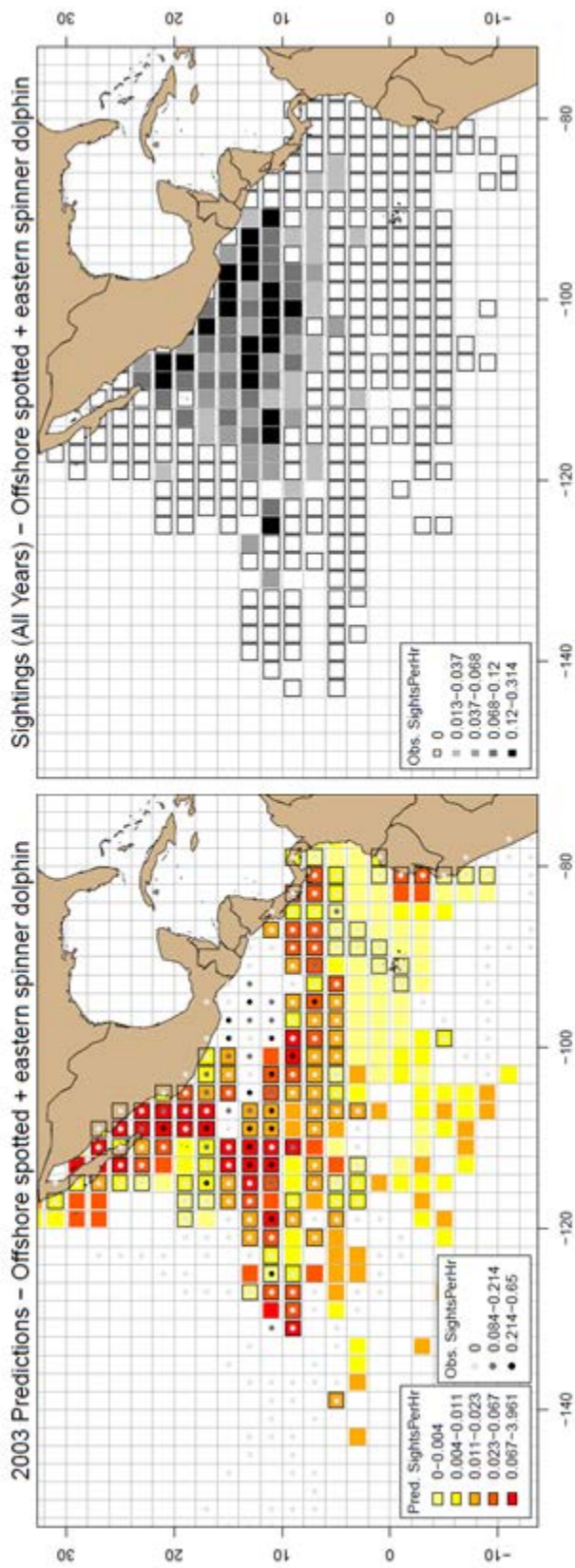


Figure 16. Model predictions (left) for the number of sightings per hour for mixed schools of offshore spotted and eastern spinner dolphins (*Stenella attenuata* and *S. longirostris orientalis*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

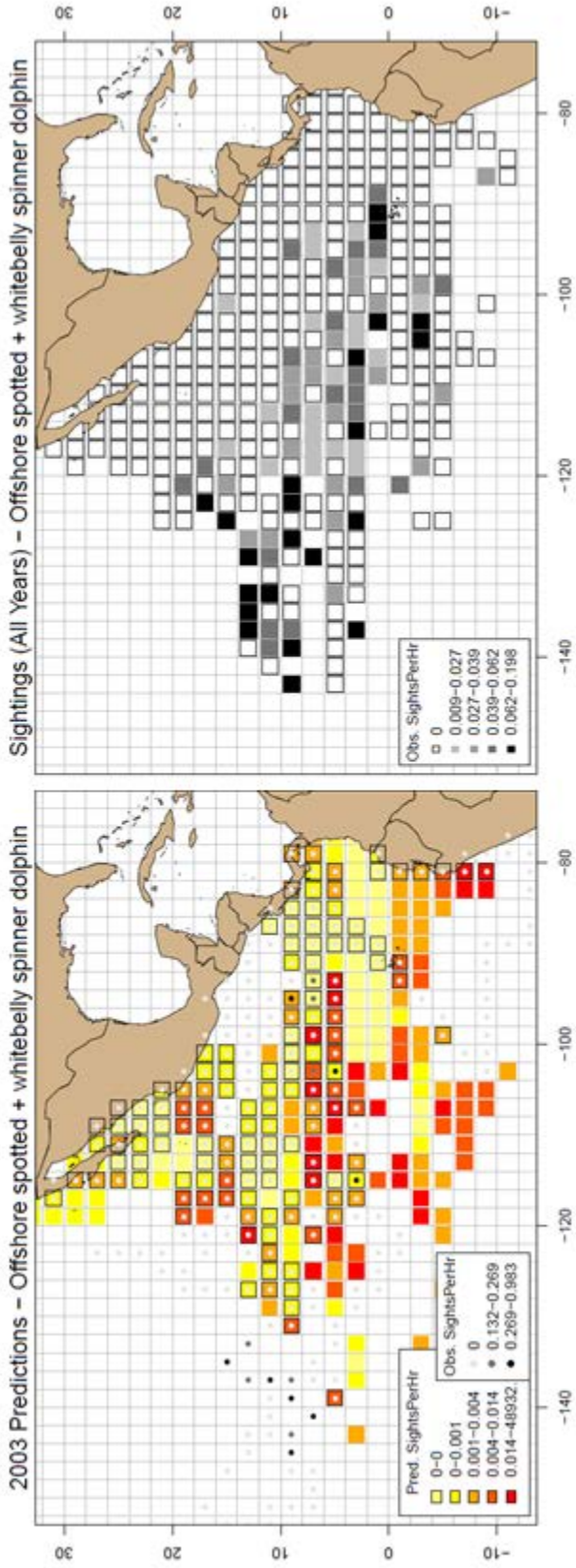


Figure 17. Model predictions (left) for the number of sightings per hour for mixed schools of offshore spotted and whitebelly spinner dolphins (*Stenella attenuata* and *S. longirostris longirostris*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

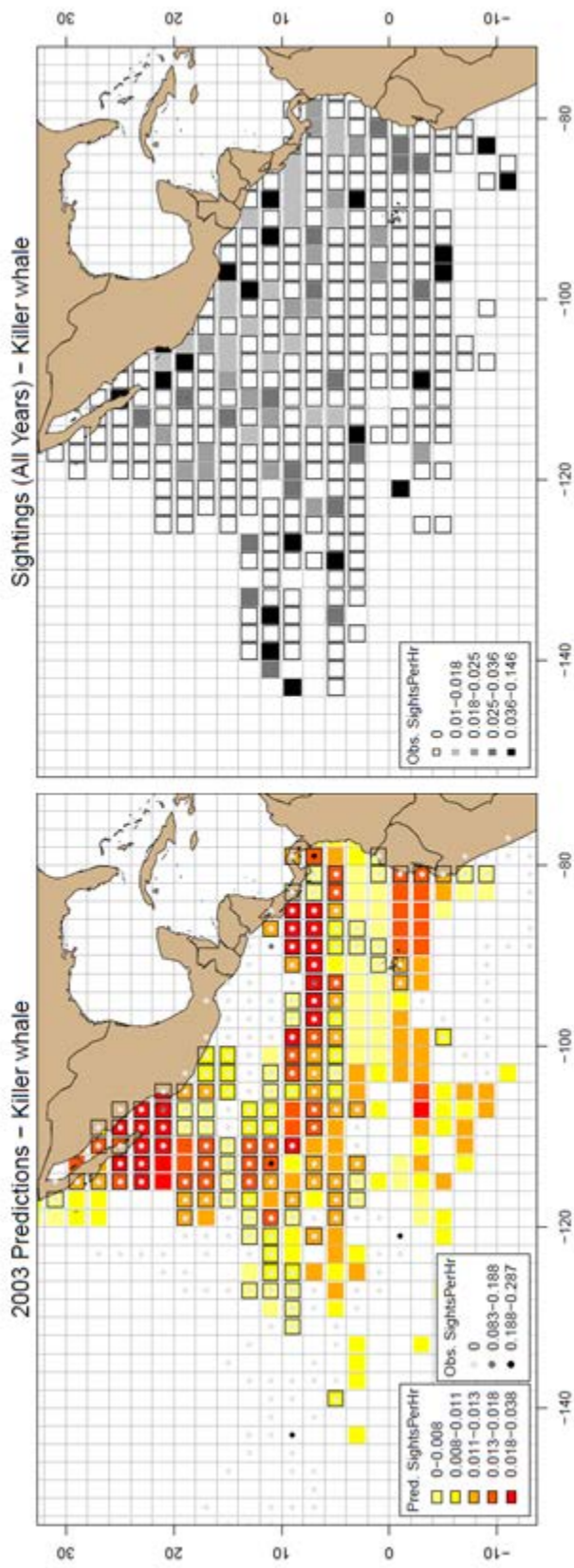


Figure 18. Model predictions (left) for the number of sightings per hour for killer whales (*Orcinus orca*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

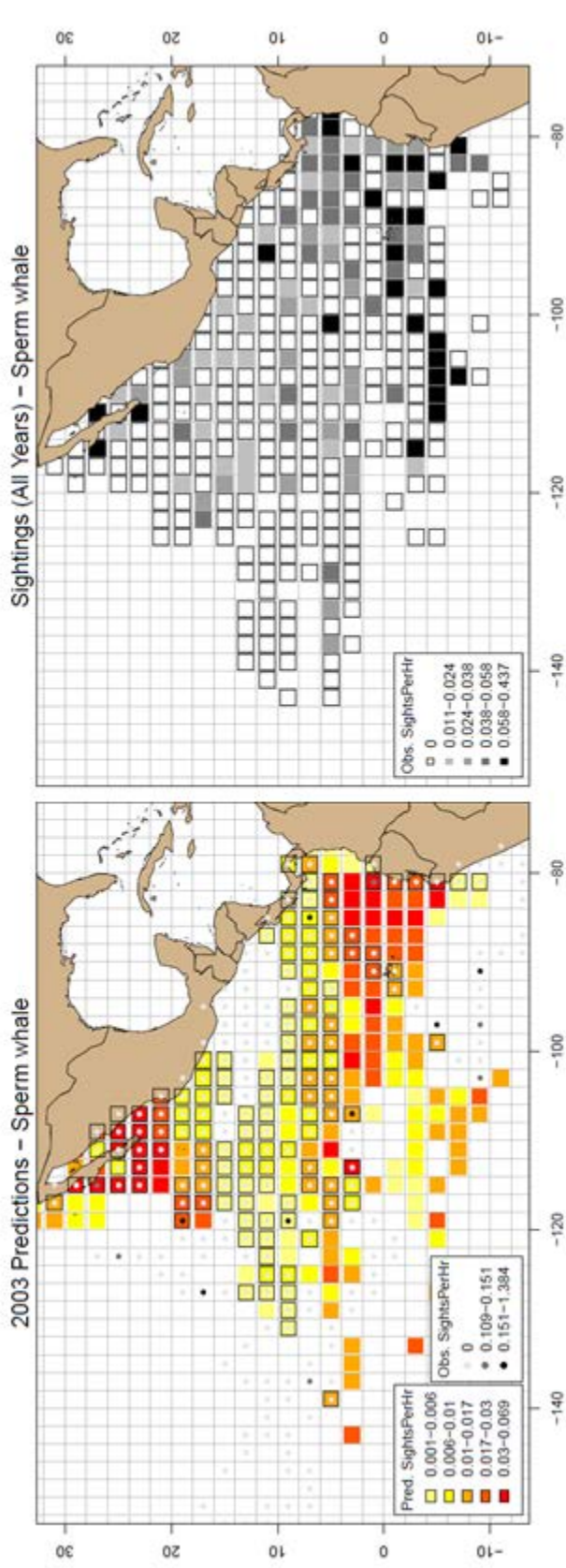


Figure 19. Model predictions (left) for the number of sightings per hour for sperm whales (*Physeter macrocephalus*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

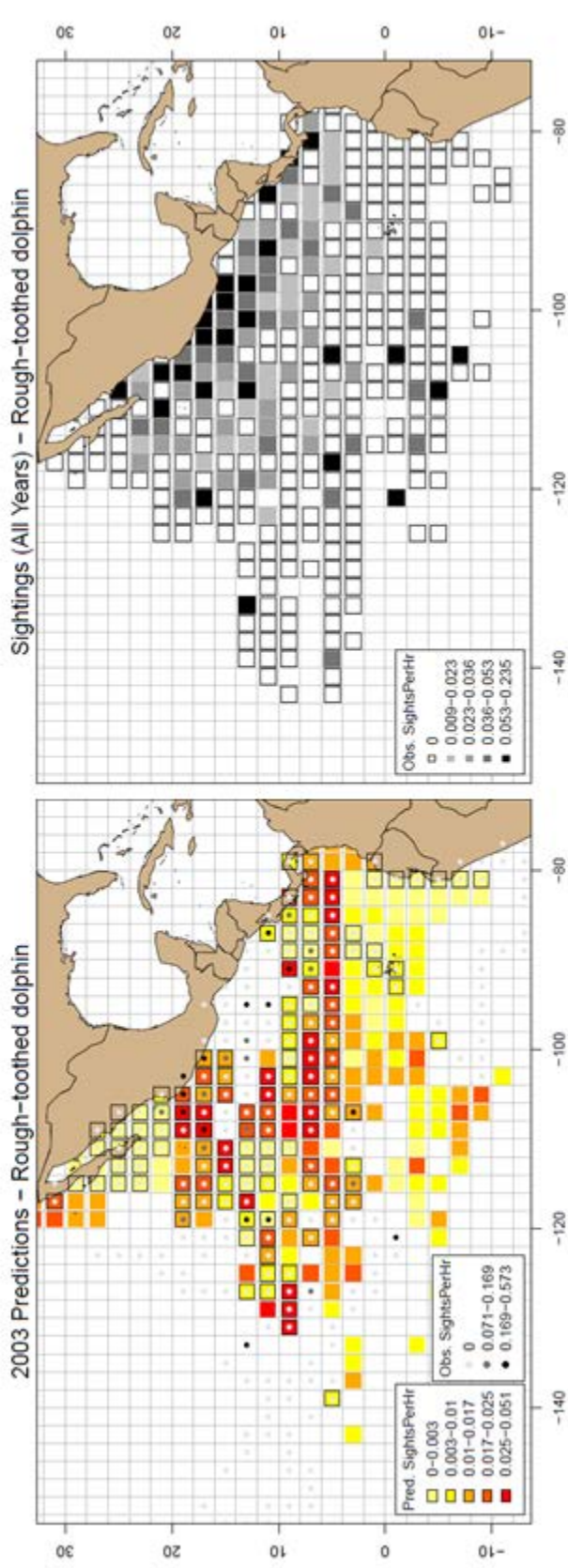


Figure 20. Model predictions (left) for the number of sightings per hour for rough-toothed dolphins (*Steno bredanensis*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

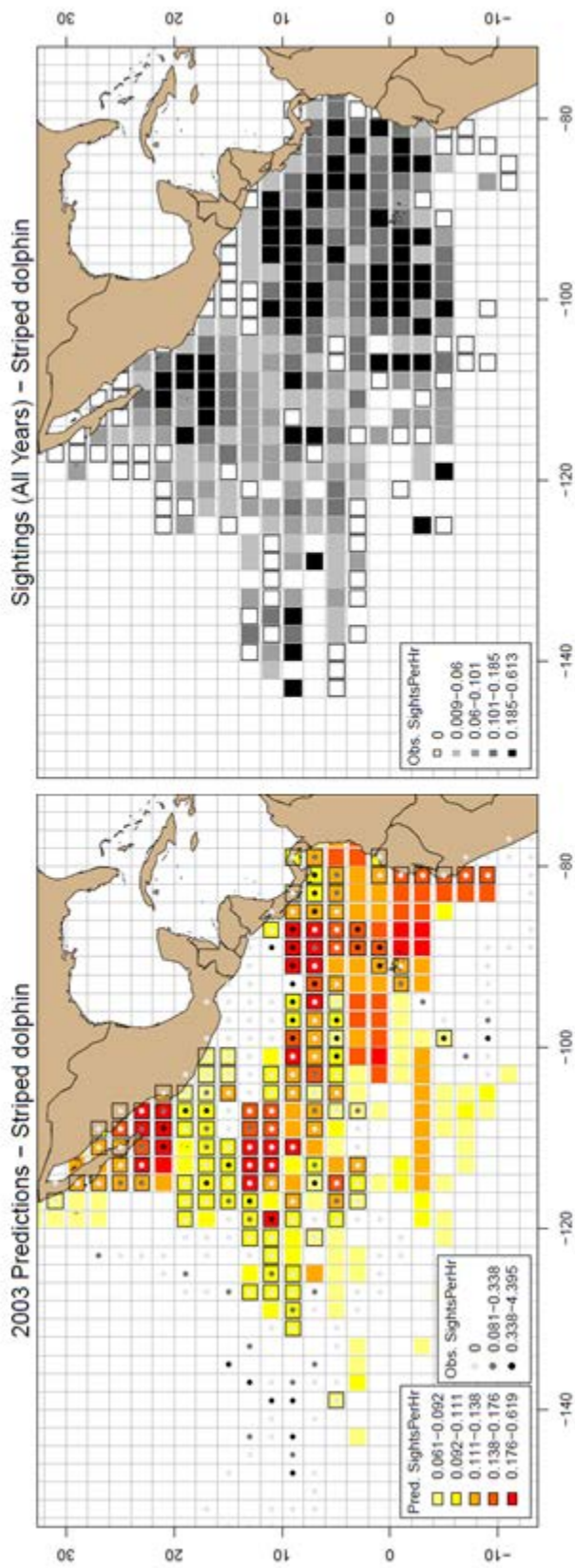


Figure 21. Model predictions (left) for the number of sightings per hour for striped dolphins (*Stenella coeruleoalba*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

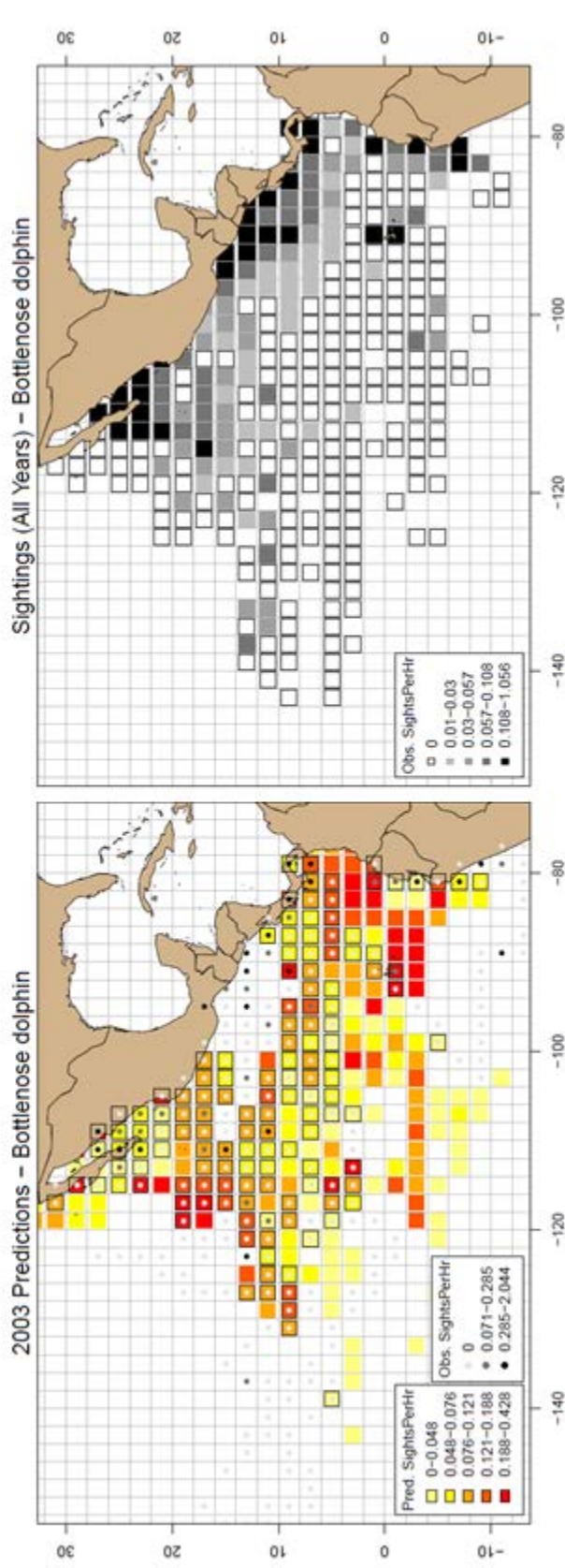


Figure 22. Model predictions (left) for the number of sightings per hour for bottlenose dolphins (*Tursiops truncatus*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

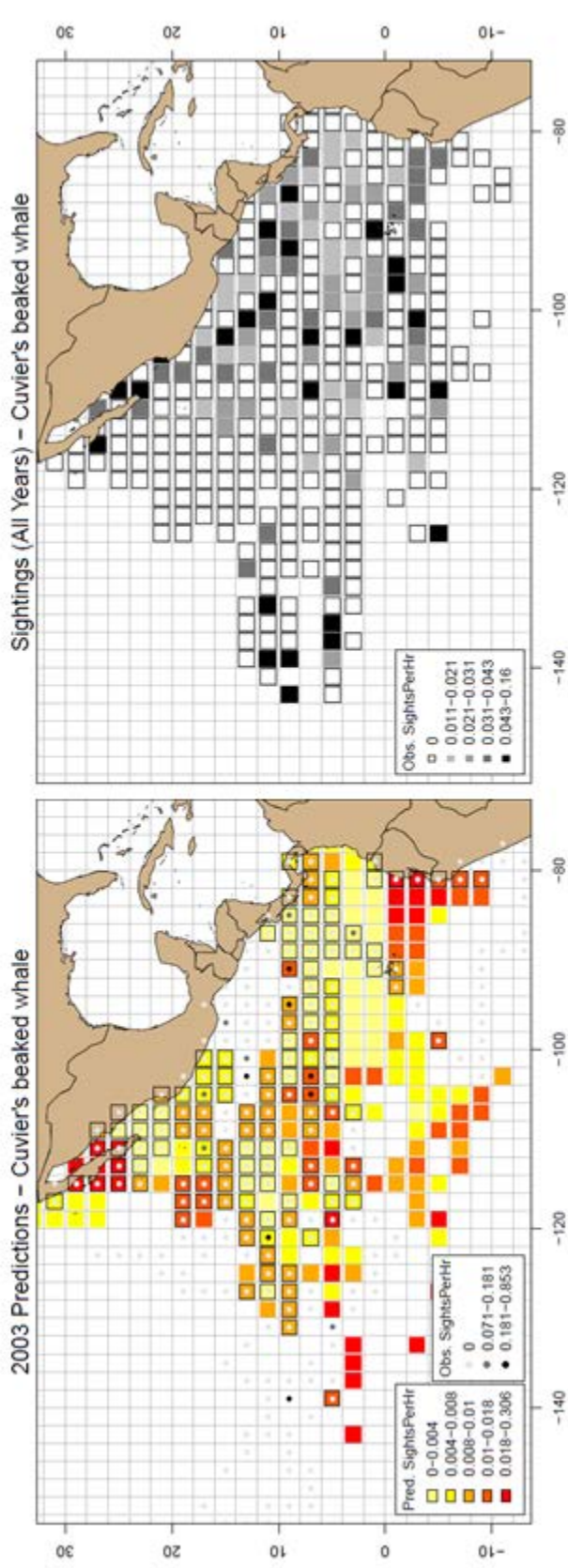


Figure 23. Model predictions (left) for the number of sightings per hour for Cuvier's beaked whales (*Ziphius cavirostris*). Grid cells outlined in black highlight locations of overlapping tuna purse-seine fishery effort and cetacean survey effort. Red to orange cells indicate relatively high predicted values; black and dark gray dots indicate relatively high observed values. Yellow cells indicate low predicted values; light gray dots indicate low observed values. Qualitatively, an ideal match of predictions to observations is represented by a black dot on a red cell (high sighting rate) or a light gray dot on a yellow cell (low sighting rate). Dark gray dots on red cells and dark gray or black dots on orange cells also indicate reasonable agreement. The observed number of sightings per hour across all survey years (right) provides context for the geographic range and historical sighting rate for this taxon. Cells outlined in black highlight locations with survey effort but no sightings. Observed sightings in 2003 alone may be relatively low, but comparing red to orange areas on the left with black to gray cells on the right provides a sense of how well the model generally captures areas with historically high and low sighting rates.

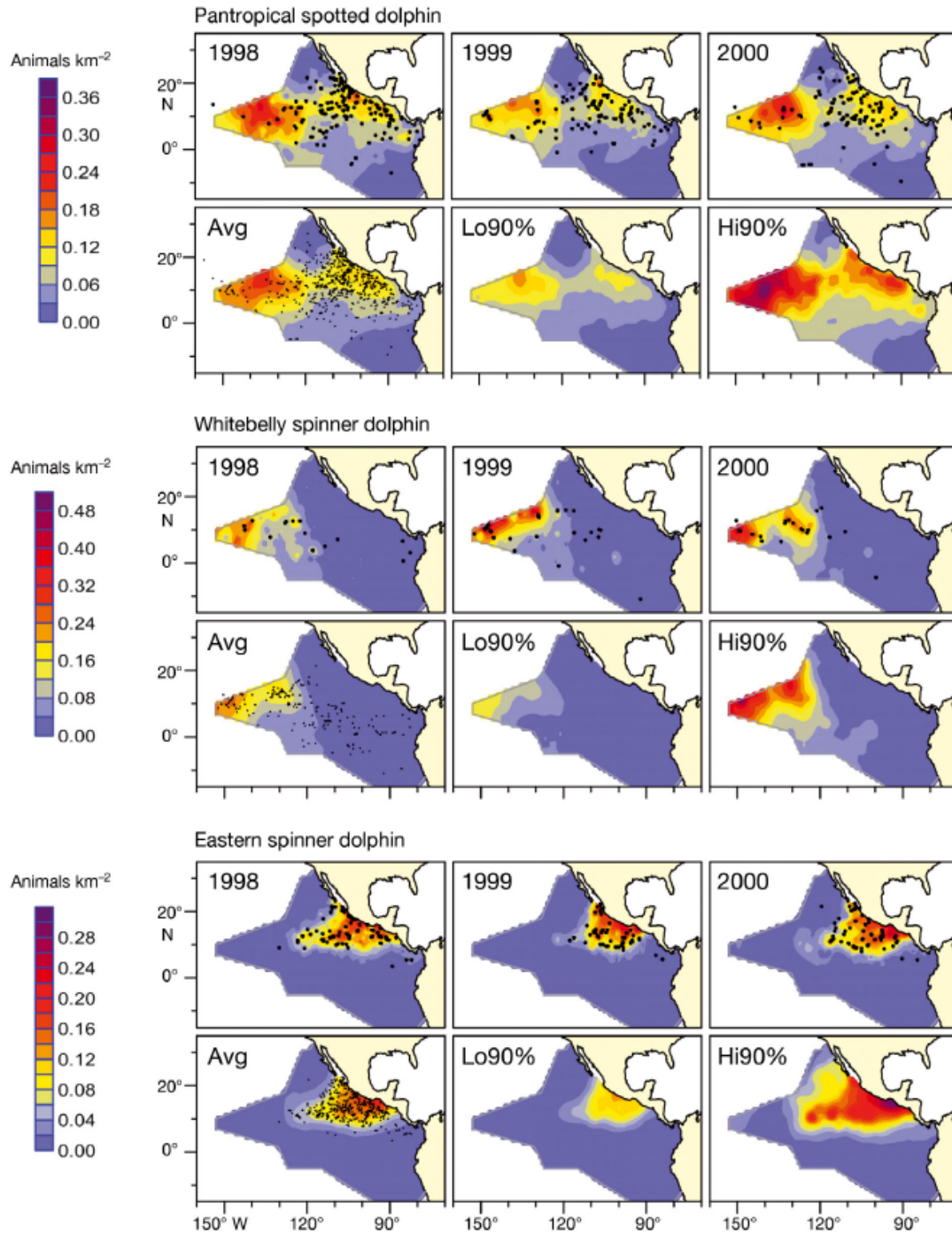


Figure 24. Modeled species densities for pantropical spotted dolphin (offshore spotted dolphin + coastal spotted dolphin), whitebelly spinner dolphin, and eastern spinner dolphin. Models were built with environmental predictor variables. Panels show 3 sample years, the multi-year average, and 90% confidence limits. Dots are observed sighting locations for each time period. Figure from Forney *et al.* 2012.

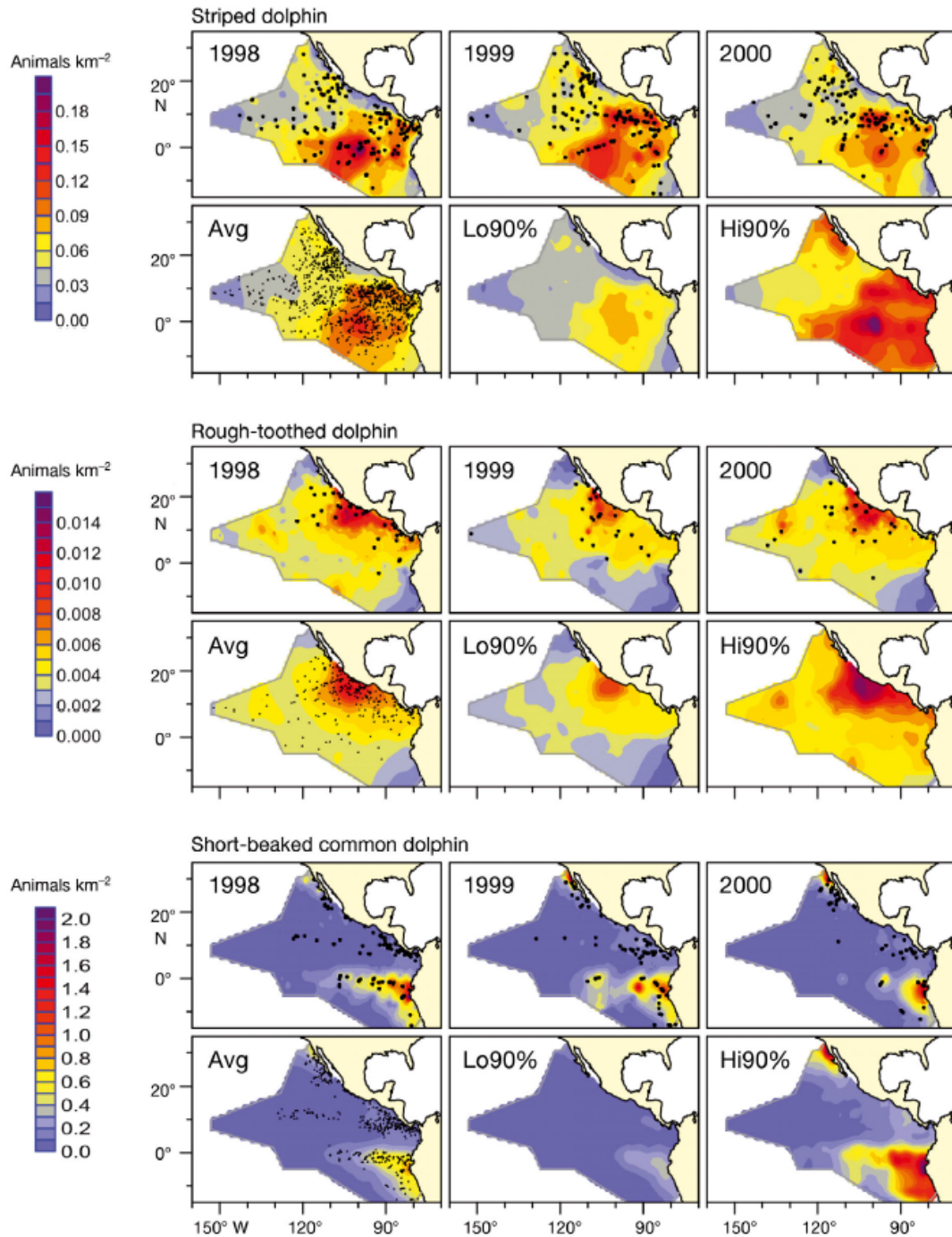


Figure 25. Modeled species densities for striped dolphin, rough-toothed dolphin, and short-beaked common dolphin (offshore common dolphin). Models were built with environmental predictor variables. Panels show 3 sample years, the multi-year average, and 90% confidence limits. Dots are observed sighting locations for each time period. Figure from Forney *et al.* 2012.

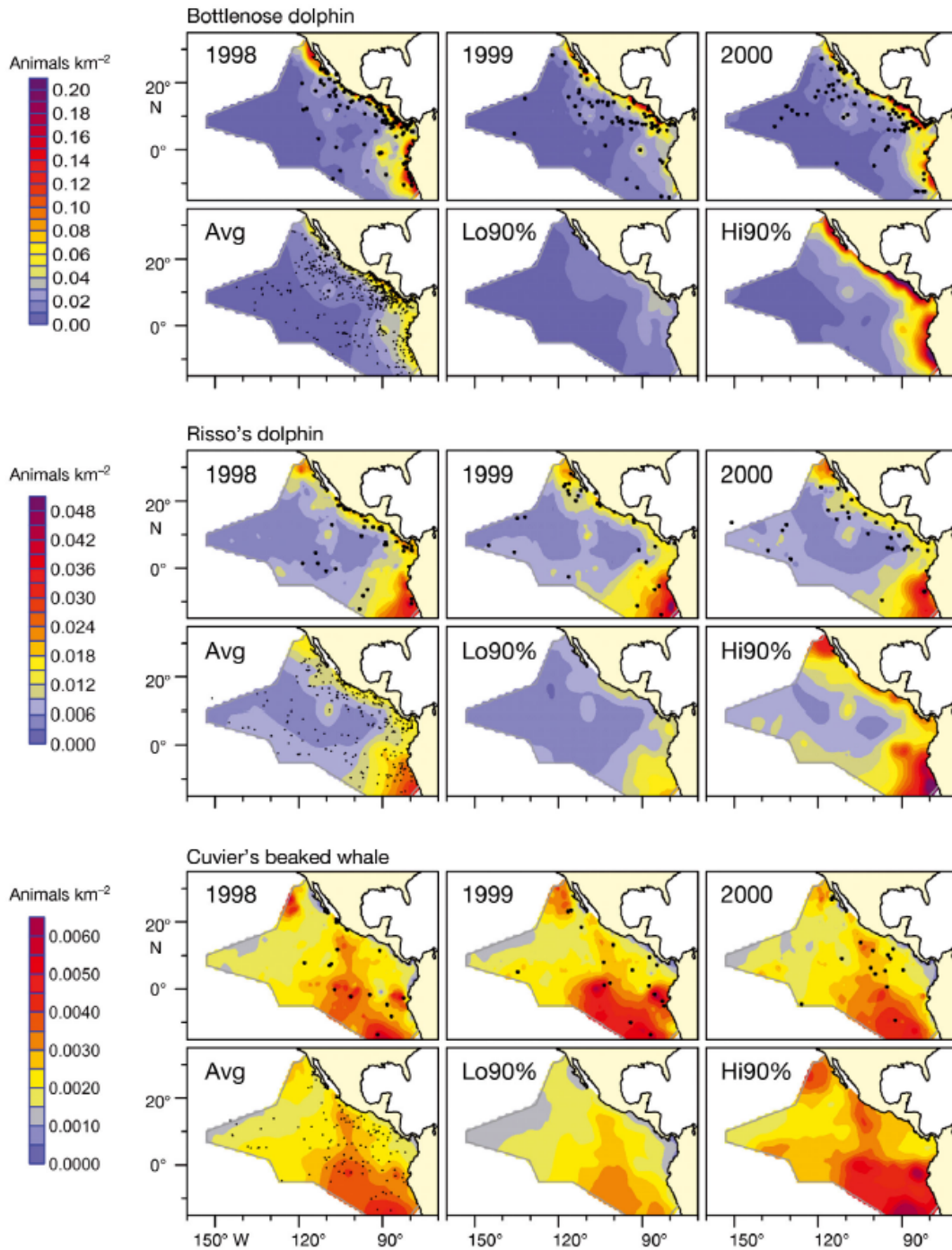


Figure 26. Modeled species densities for bottlenose dolphin, Risso's dolphin, and Cuvier's beaked whale. Models were built with environmental predictor variables. Panels show 3 sample years, the multi-year average, and 90% confidence limits. Dots are observed sighting locations for each time period. Figure from Forney *et al.* 2012.

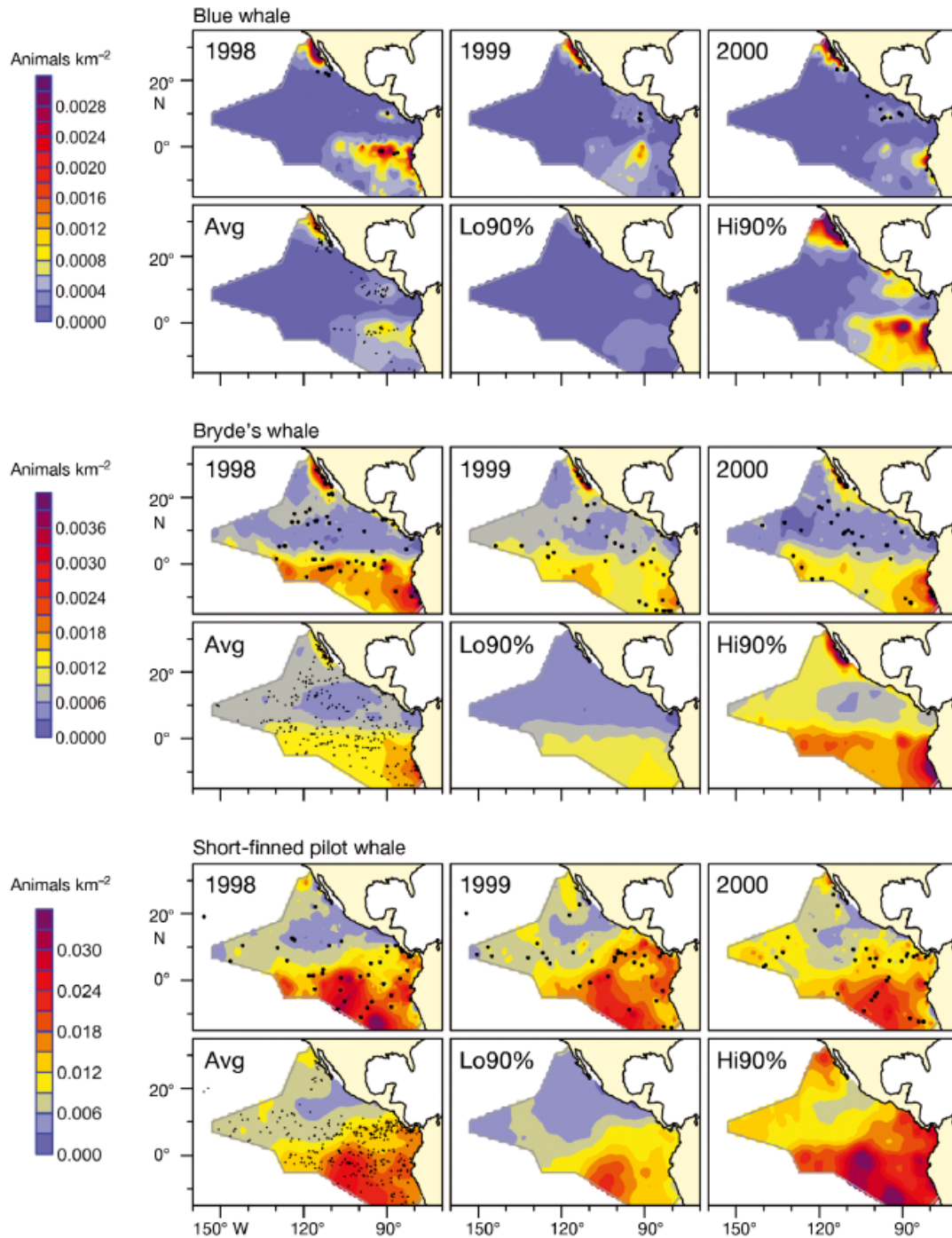


Figure 27. Modeled species densities for blue whale, Bryde's whale, and short-finned pilot whale. Models were built with environmental predictor variables. Panels show 3 sample years, the multi-year average, and 90% confidence limits. Dots are observed sighting locations for each time period. Figure from Forney *et al.* 2012.

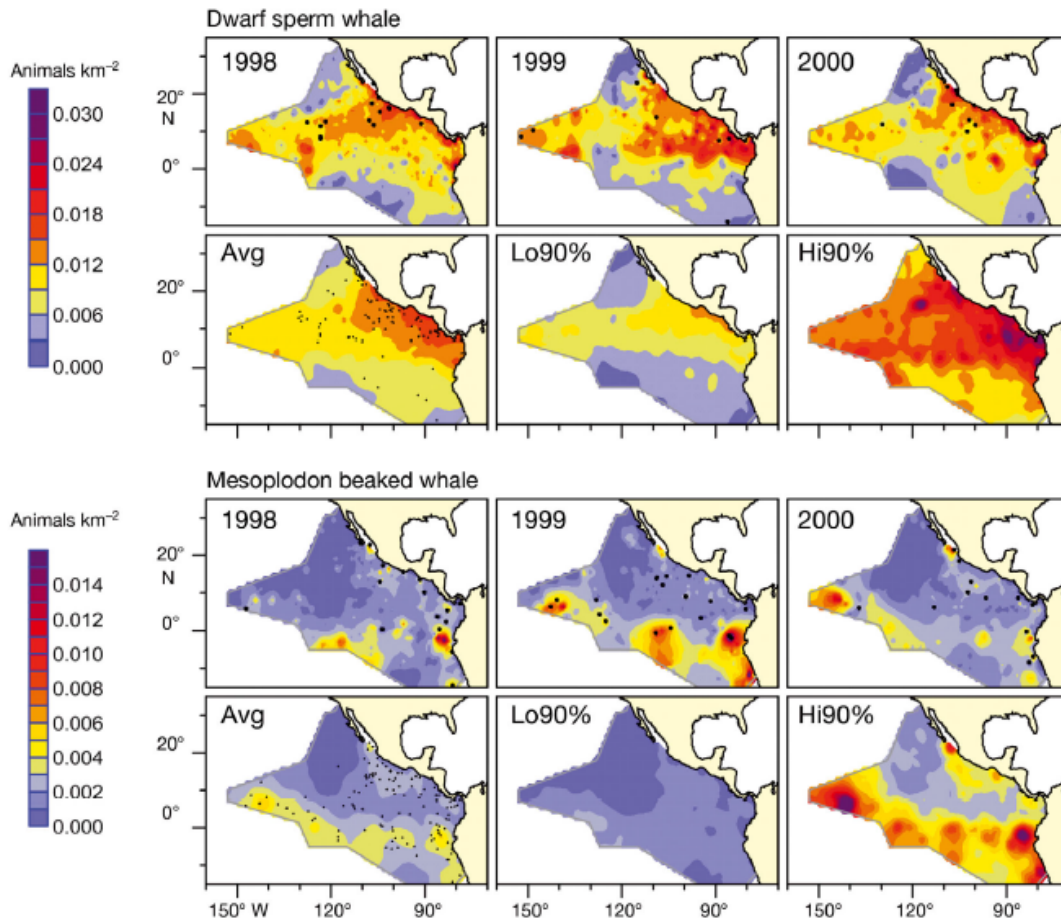


Figure 28. Modeled species densities for dwarf sperm whale and mesoplodont beaked whales. Models were built with environmental predictor variables. Panels show 3 sample years, the multi-year average, and 90% confidence limits. Dots are observed sighting locations for each time period. Figure from Forney *et al.* 2012.

APPENDIX 1

Canonical Correspondence Analysis Histograms

Results from canonical correspondence analysis (CCA) using all data aggregated temporally into one group (climatological view). Predictor variables are yellowfin tuna fishery metrics; the response is the number of sightings per hour for each of 19 cetacean taxa. Frequency histograms (transformed to percentages) of Axis 1 and 2 scores for each taxon mostly reveal unimodal relationships, thus validating a primary assumption of CCA. Taxonomic abbreviations as in Table 1.

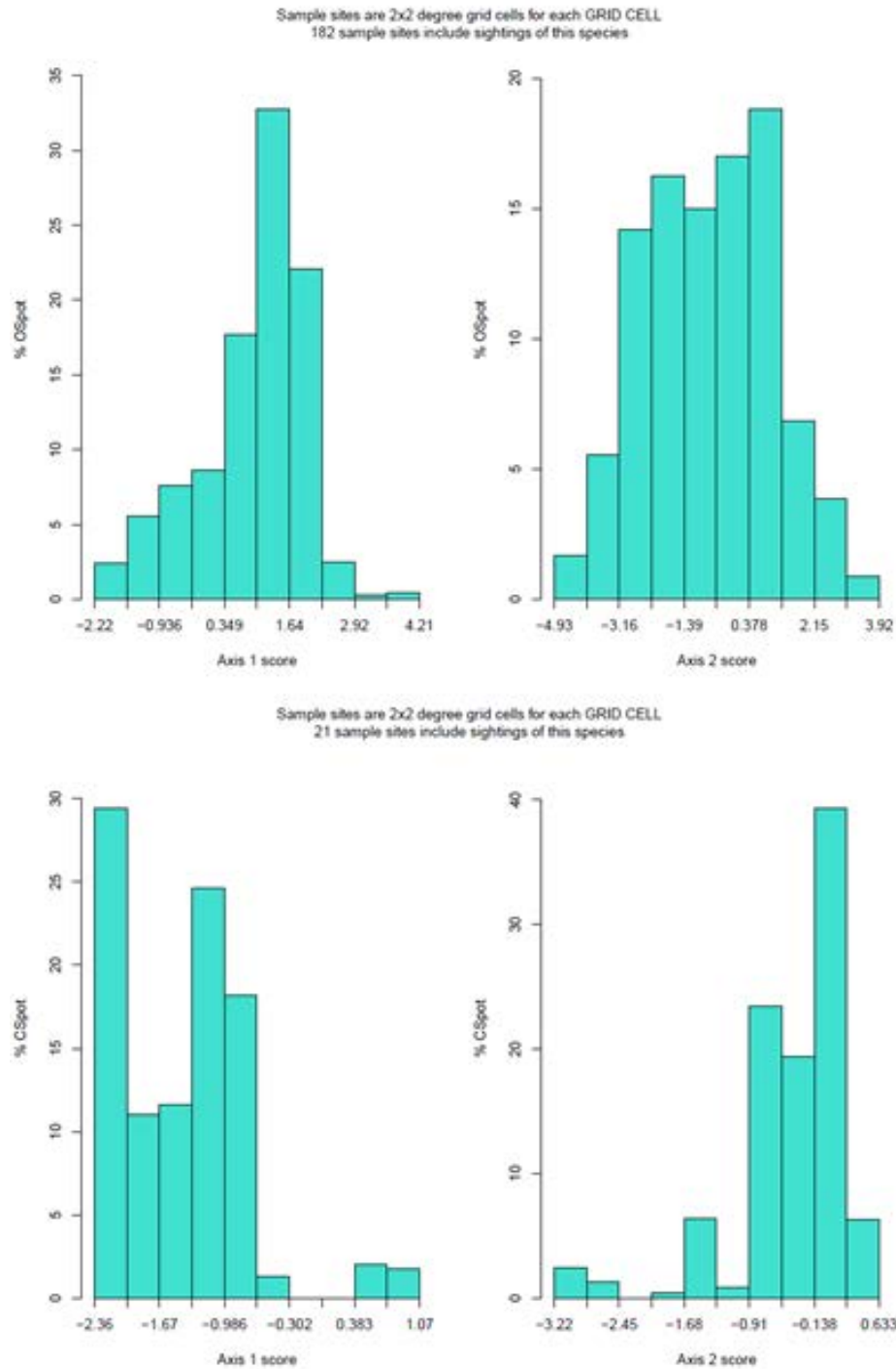


Figure A1.1. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for offshore spotted dolphins (“OSpot”; top) and coastal spotted dolphins (“CSpot”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

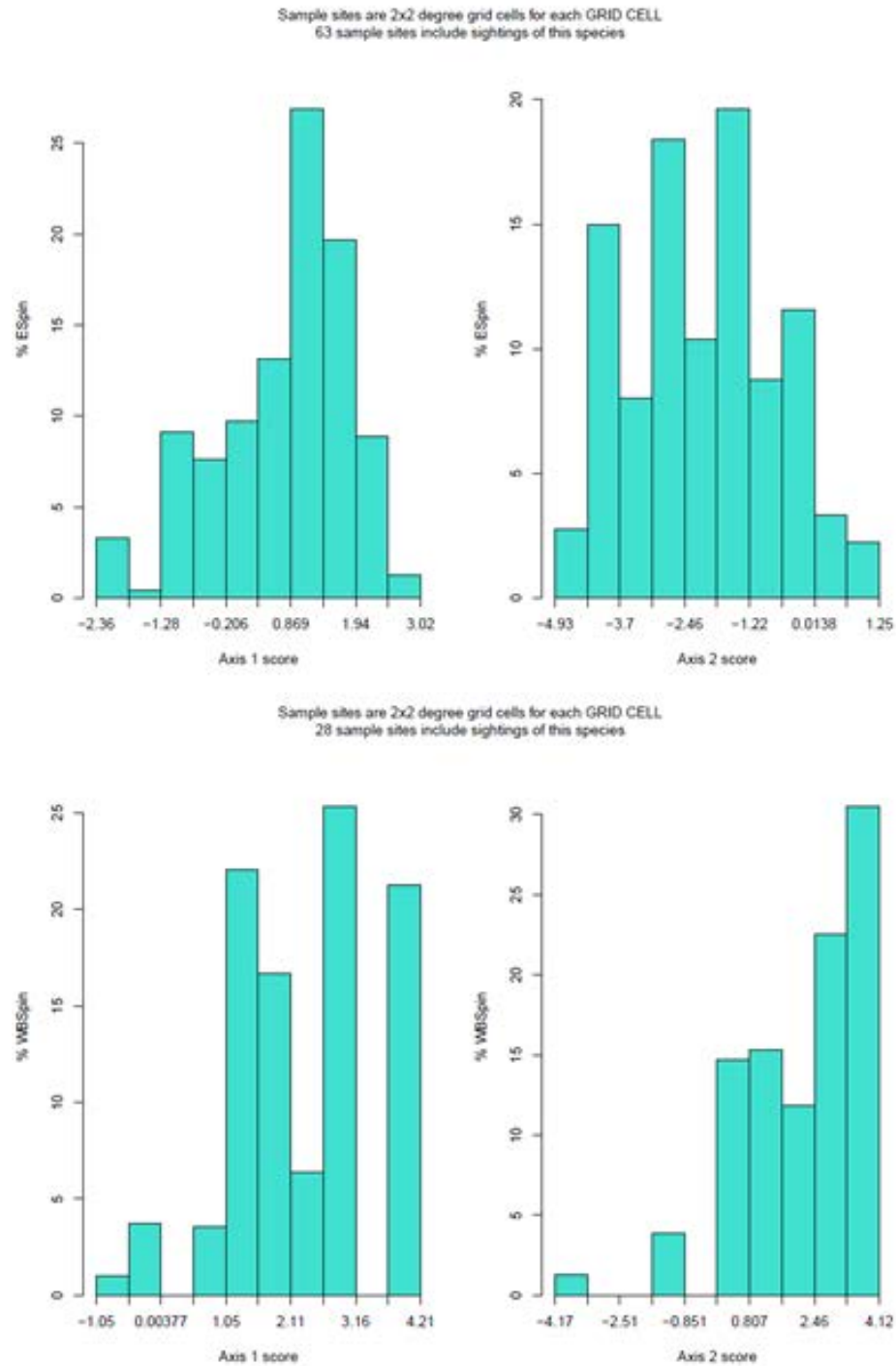


Figure A1.2. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for eastern spinner dolphins (“ESpin”; top) and whitebelly spinner dolphins (“WBSpin”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

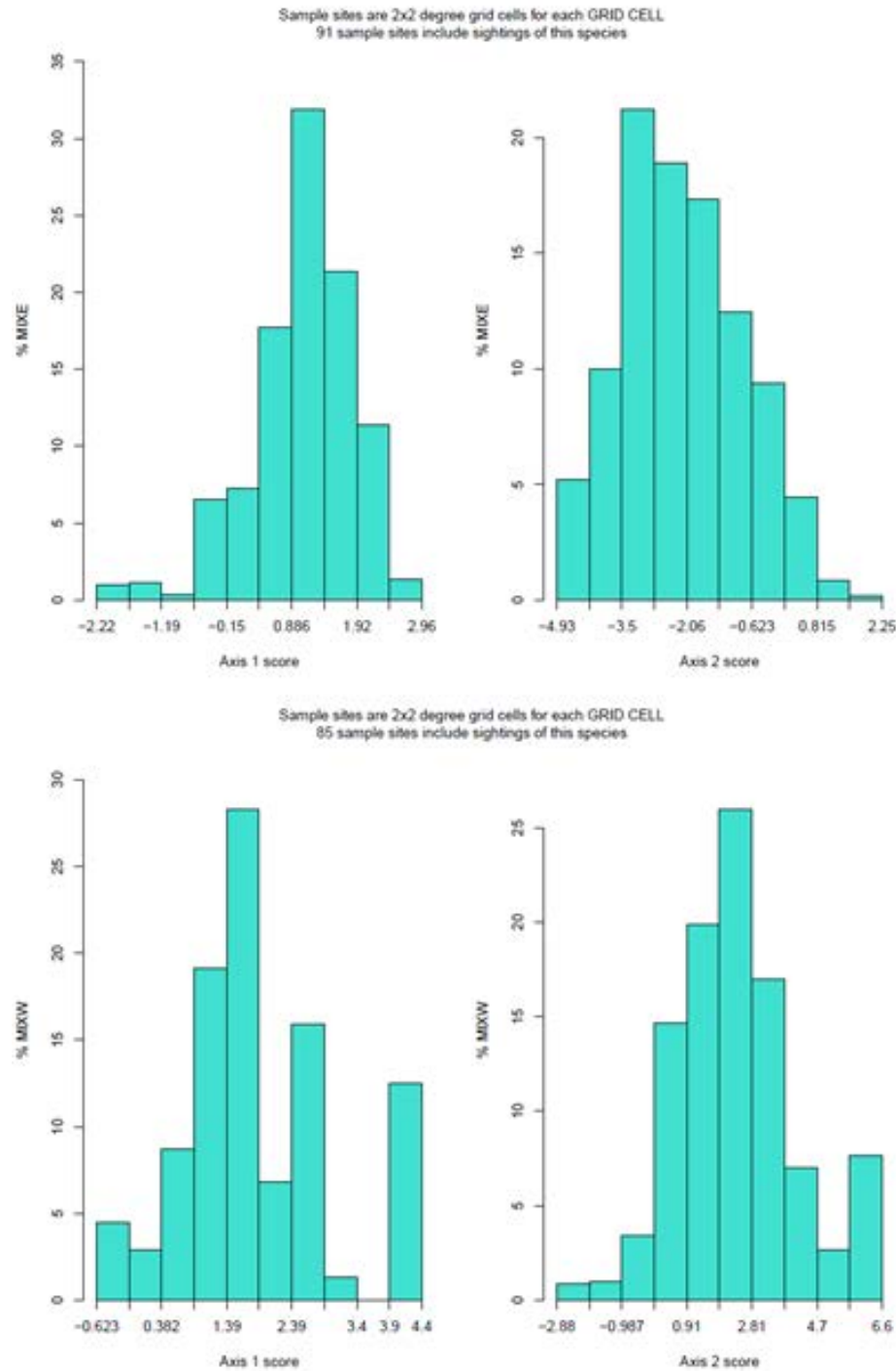


Figure A1.3. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for mixed schools of offshore spotted and eastern spinner dolphins (“MIXE”; top) and mixed schools of offshore spotted and whitebelly spinner dolphins (“MIXW”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

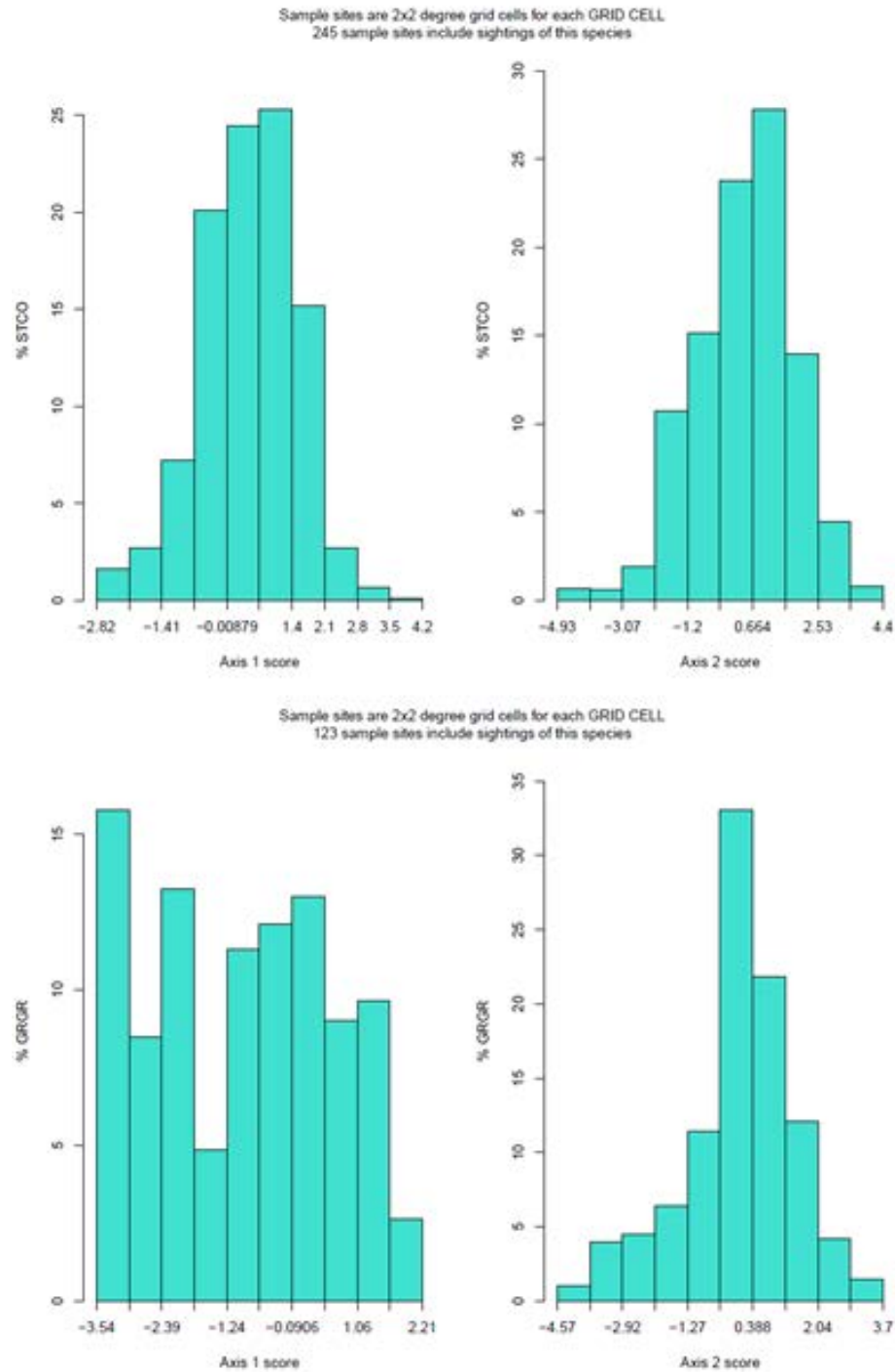


Figure A1.4. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for striped dolphins (“STCO”; top) and Risso’s dolphins (“GRGR”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

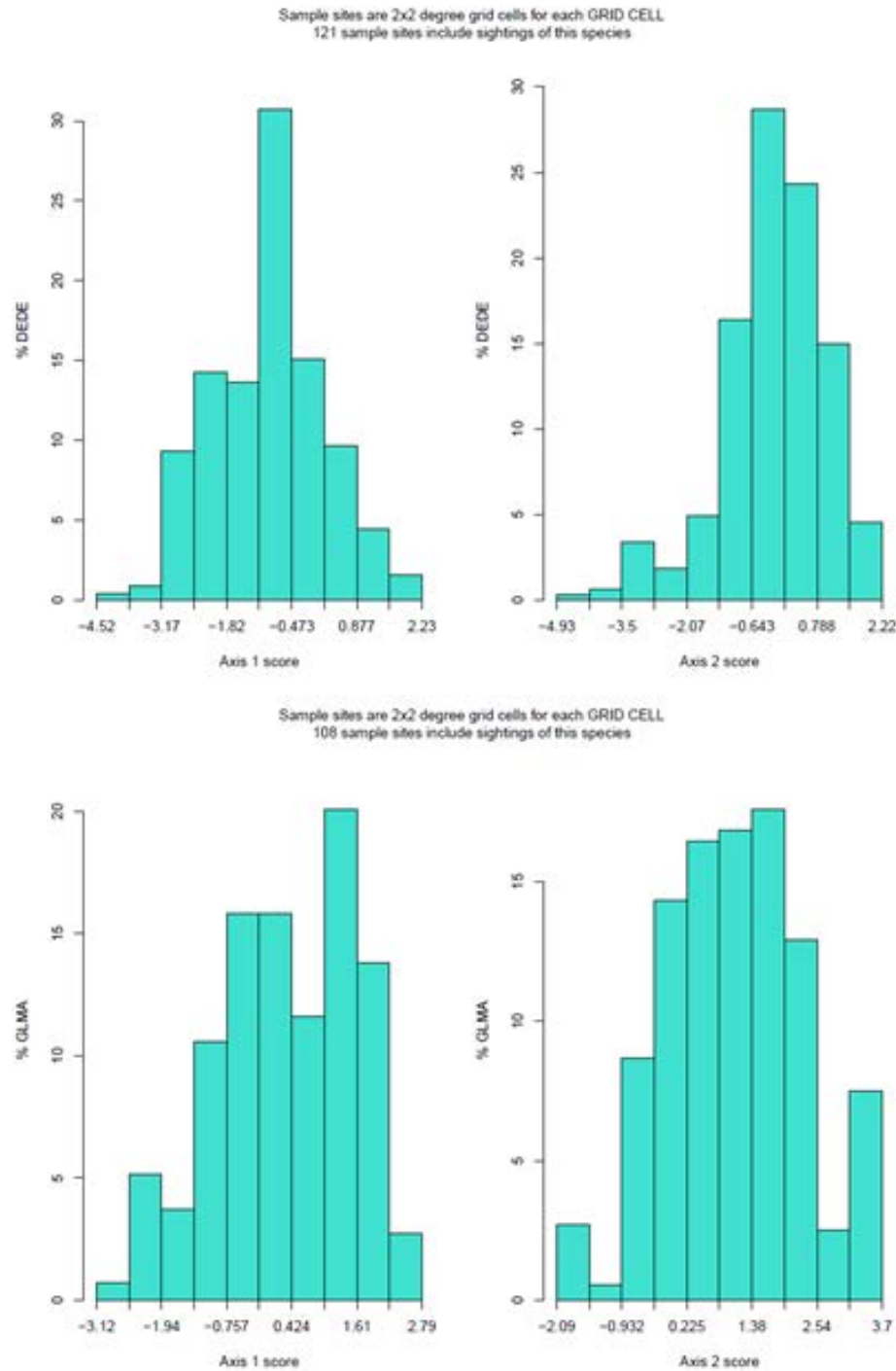


Figure A1.5. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for offshore common dolphins (“DEDE”; top) and short-finned pilot whales (“GLMA”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

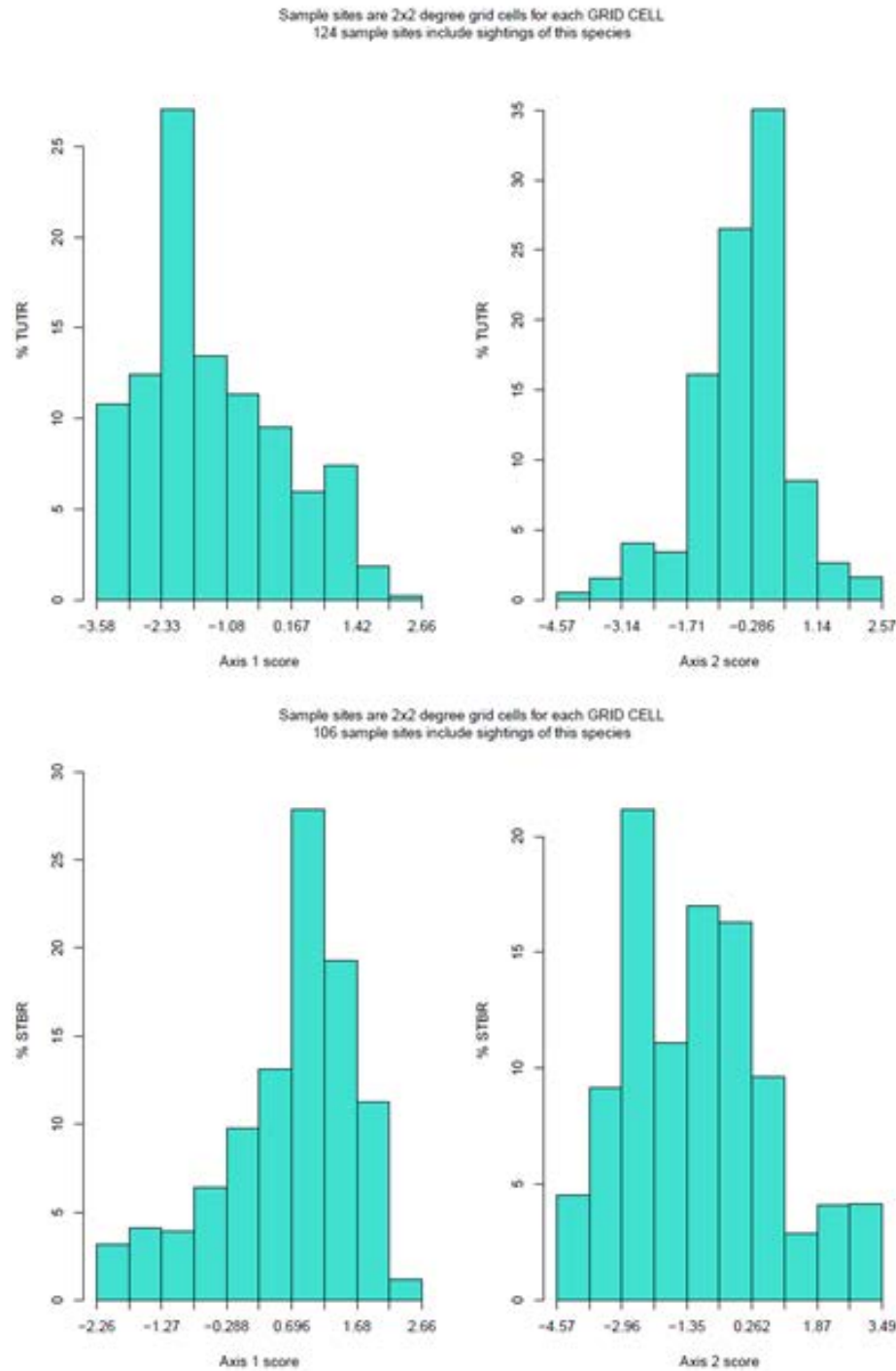


Figure A1.6. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for bottlenose dolphins ("TUTR"; top) and rough-toothed dolphins ("STBR"; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

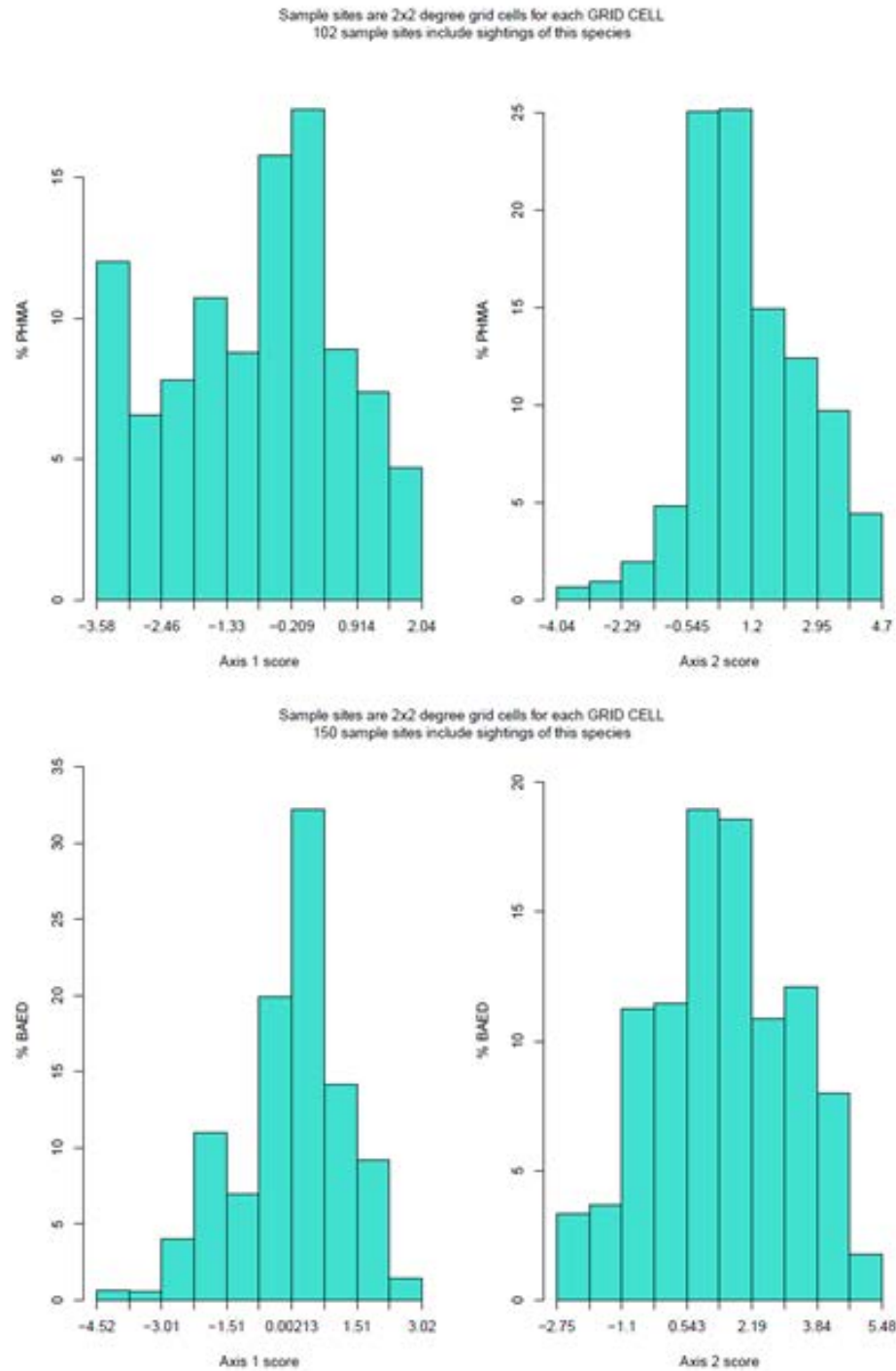


Figure A1.7. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for sperm whales (“PHMA”; top) and Bryde’s whales (“BAED”; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

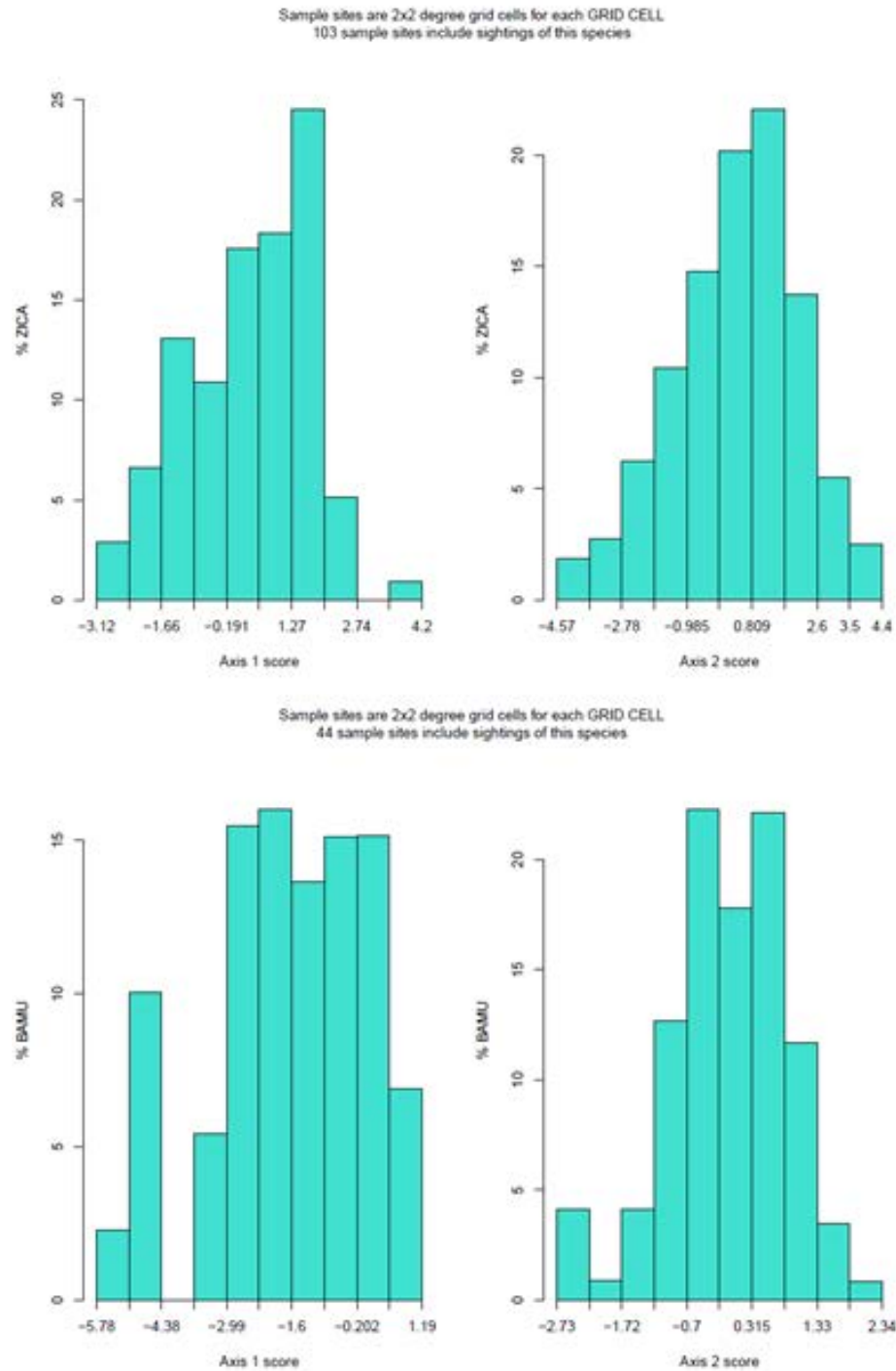


Figure A1.8. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for Cuvier's beaked whales ("ZICA"; top) and blue whales ("BAMU"; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

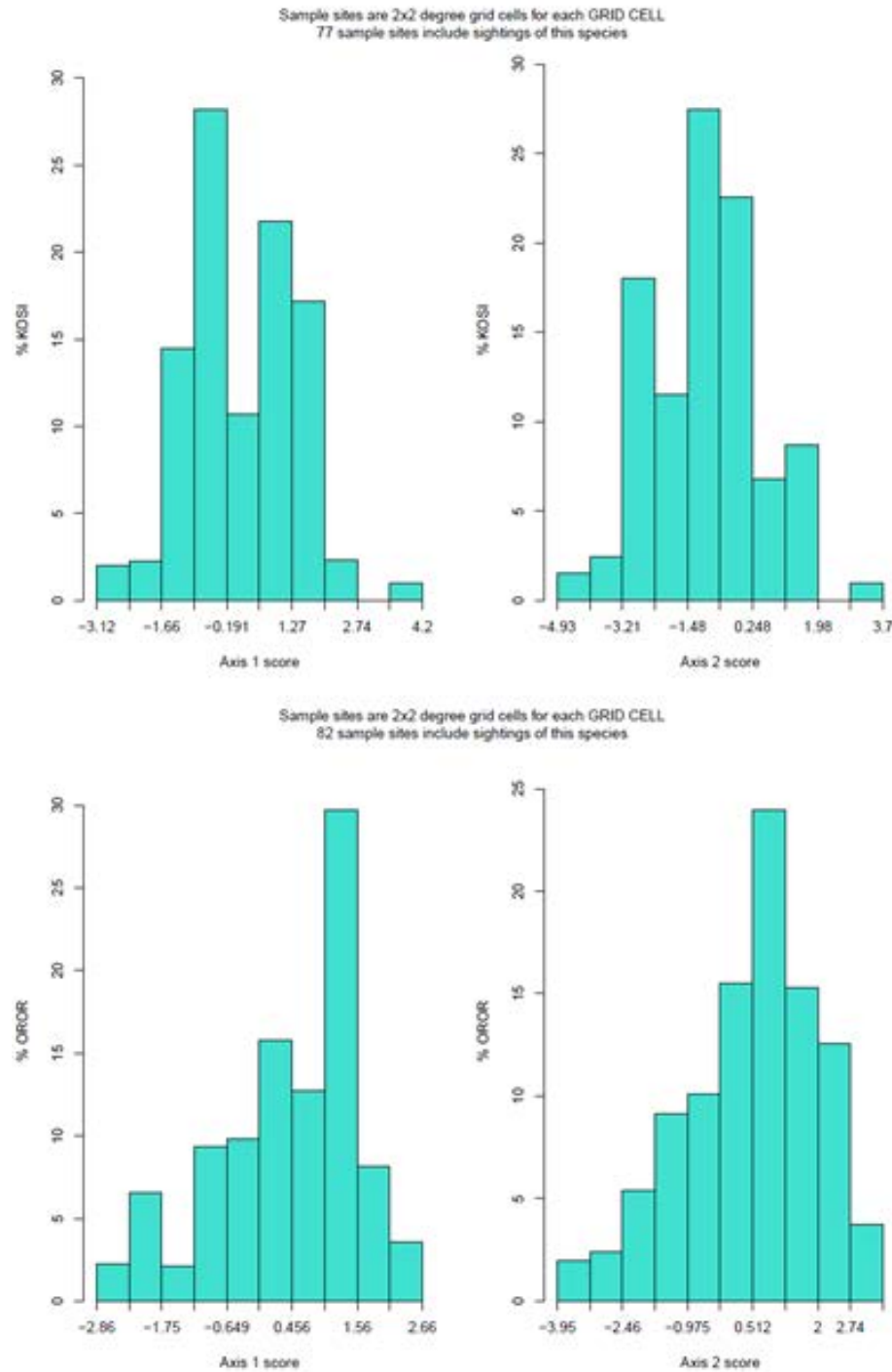


Figure A1.9. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for dwarf sperm whales ("KOSI"; top) and killer whales ("OROR"; bottom). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

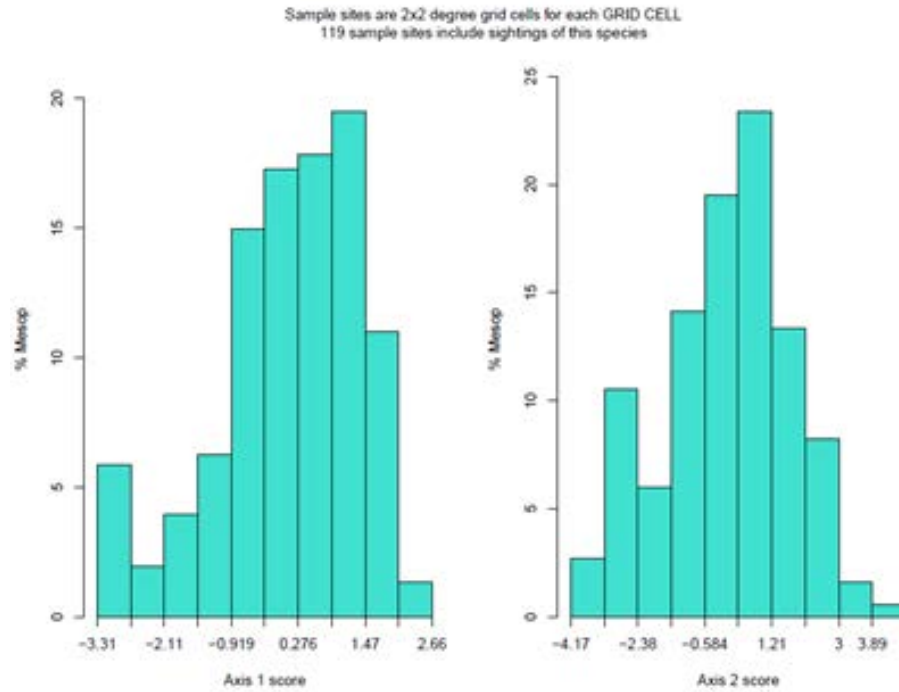


Figure A1.10. Frequency histograms (transformed to percentages) of canonical Axis 1 and 2 scores for mesoplodont beaked whales (“Mesop”). Results from canonical correspondence analysis relating cetacean sightings per hour to yellowfin tuna fishery metrics, with data aggregated temporally into one group (climatological view). Taxonomic abbreviations as in Table 1.

APPENDIX 2

Canonical Correspondence Analysis Variance Explained Plots

Results from canonical correspondence analysis (CCA) using all data aggregated temporally into one group (climatological view). Predictor variables are yellowfin tuna fishery metrics; the response is the number of sightings per hour for each of 19 cetacean taxa. Plots show the percent of variance in a given taxon's data explained by each of the first four canonical axes. Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4. Bar height indicates total variance explained by these axes.

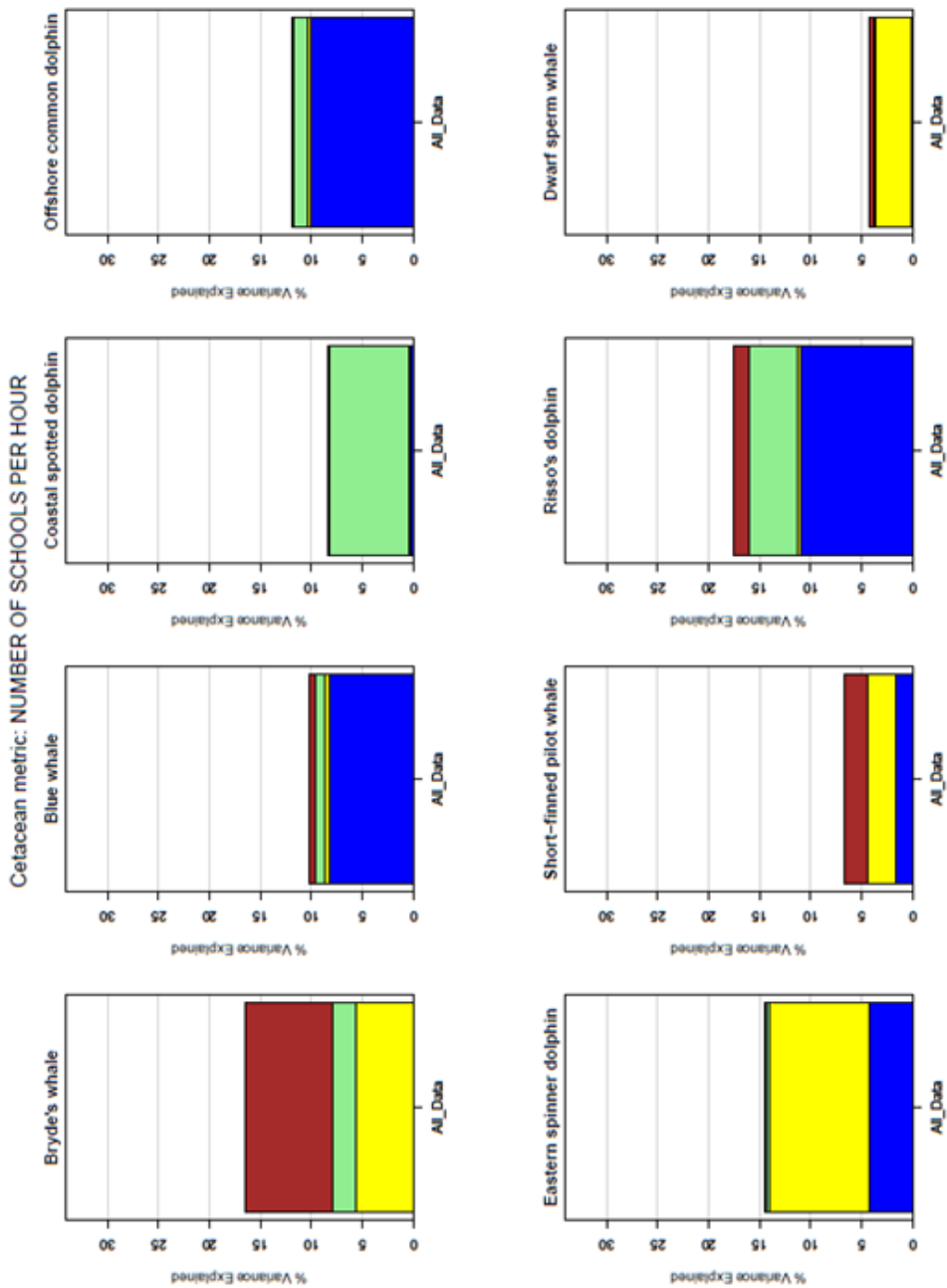


Figure A2.1. Results from canonical correspondence analysis using all data aggregated temporally into one group (climatological view). Predictor variables are tuna fishery metrics; the response is the number of sightings per hour for each of 19 cetacean taxa. Plots show the percent of variance in a given taxon's data explained by each of the first four canonical axes. Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4. Bar height indicates total variance explained by these axes.

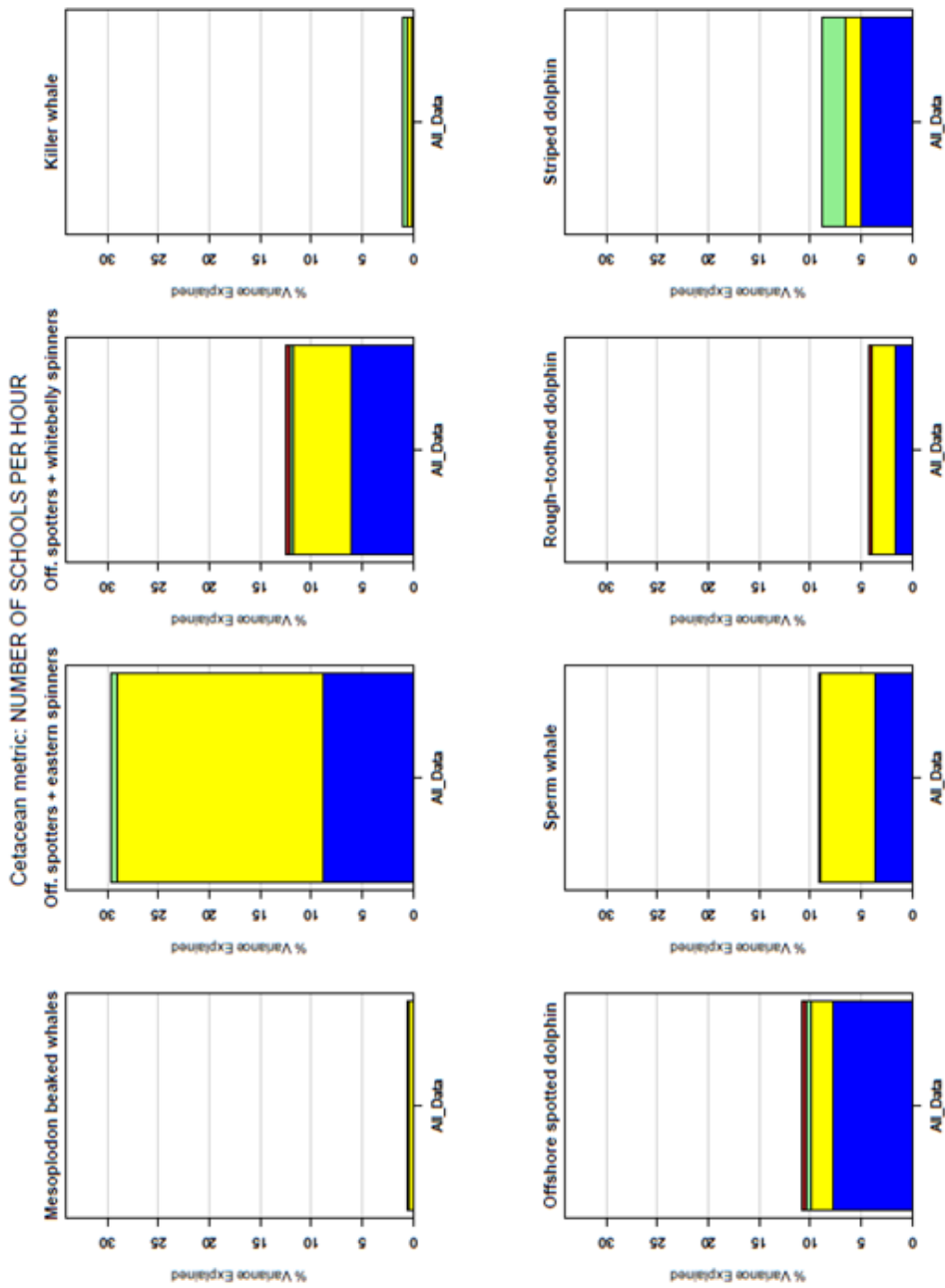


Figure A2.2. Results from canonical correspondence analysis using all data aggregated temporally into one group (climatological view). Predictor variables are tuna fishery metrics; the response is the number of sightings per hour for each of 19 cetacean taxa. Plots show the percent of variance in a given taxon's data explained by each of the first four canonical axes. Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4. Bar height indicates total variance explained by these axes.

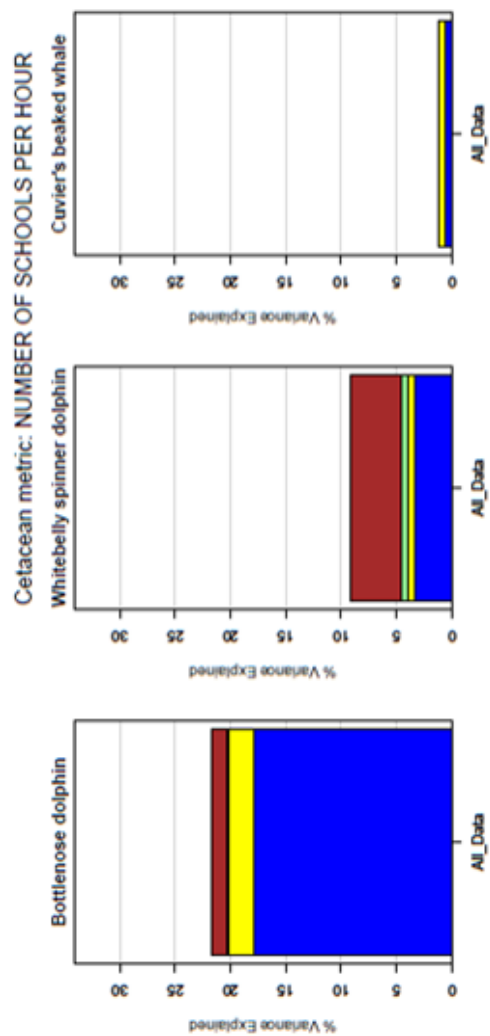


Figure A2.3. Results from canonical correspondence analysis using all data aggregated temporally into one group (climatological view). Predictor variables are tuna fishery metrics; the response is the number of sightings per hour for each of 19 cetacean taxa. Plots show the percent of variance in a given taxon's data explained by each of the first four canonical axes. Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4. Bar height indicates total variance explained by these axes.

APPENDIX 3

Generalized Additive Model Plots

Results from generalized additive models using yellowfin tuna fishery metrics as predictors and the number of sightings per hour for a given cetacean taxon as the response. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort, metric tons of catch per day of fishing).

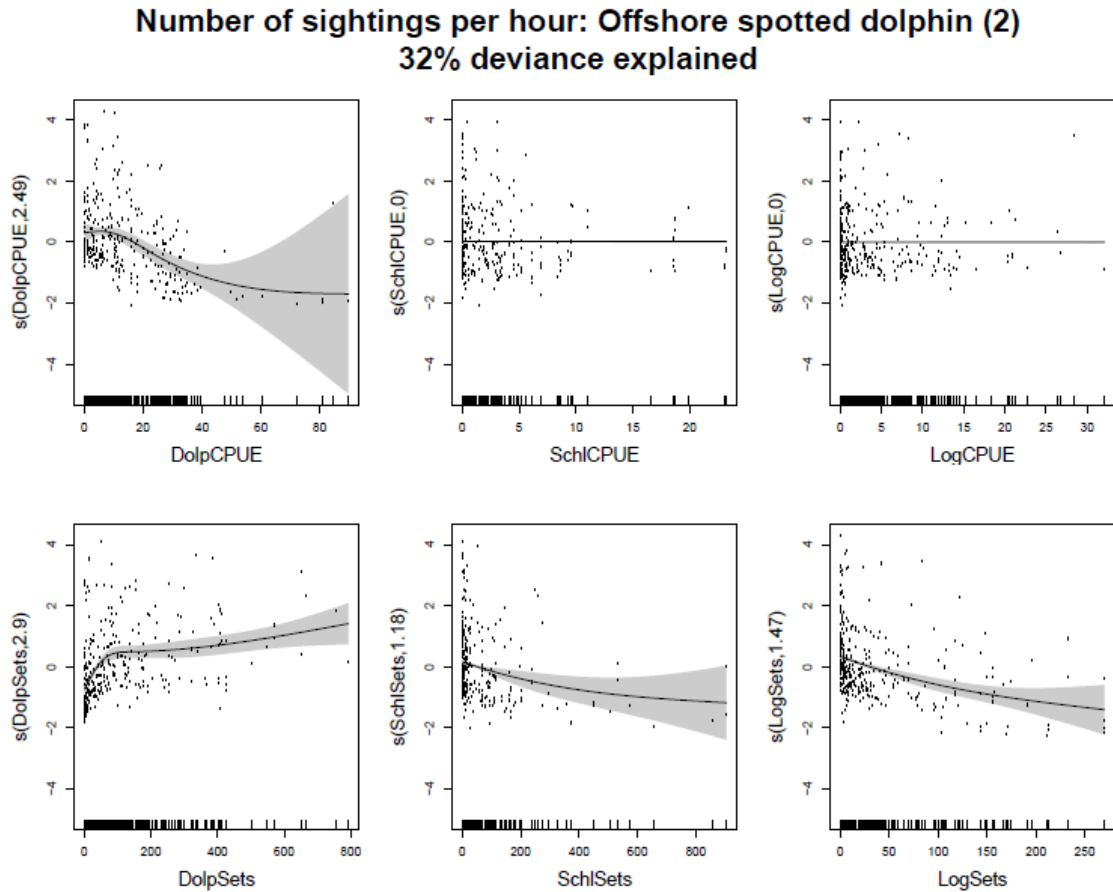


Figure A3.1 Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for offshore spotted dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

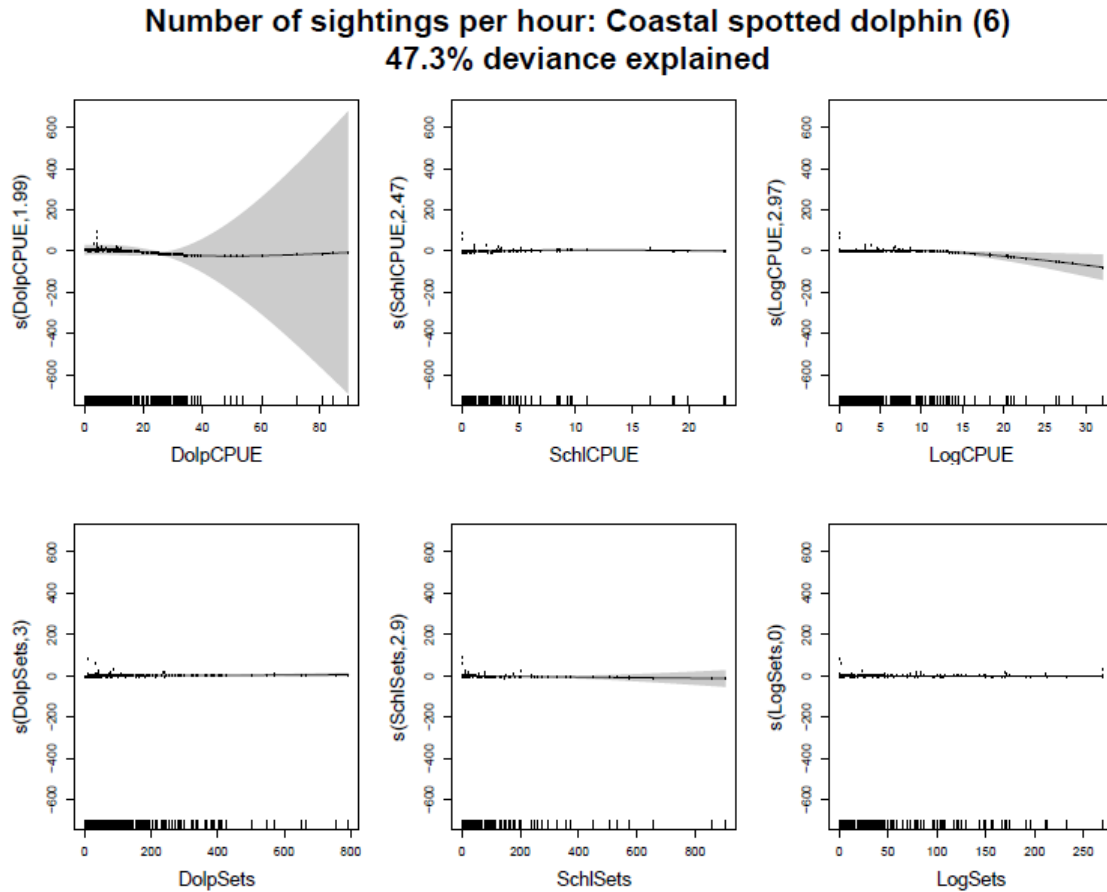


Figure A3.2. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for coastal spotted dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

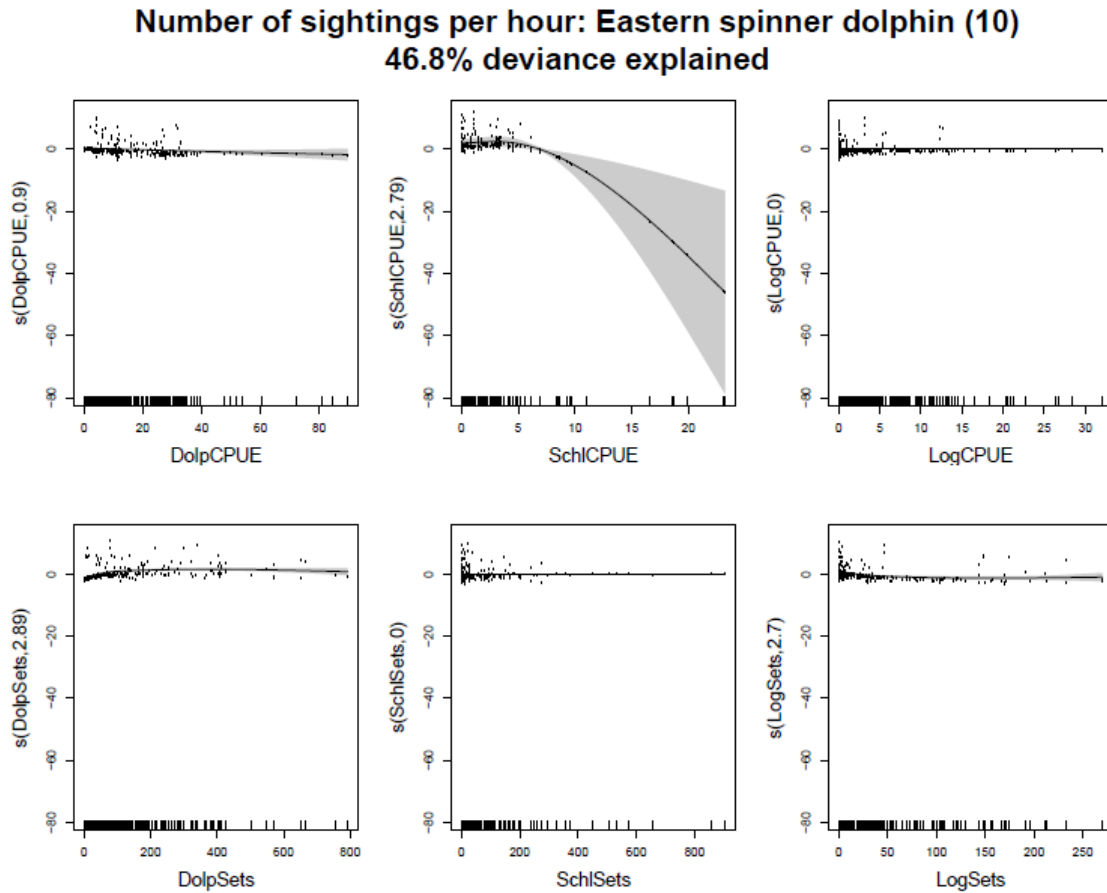


Figure A3.3. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for eastern spinner dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

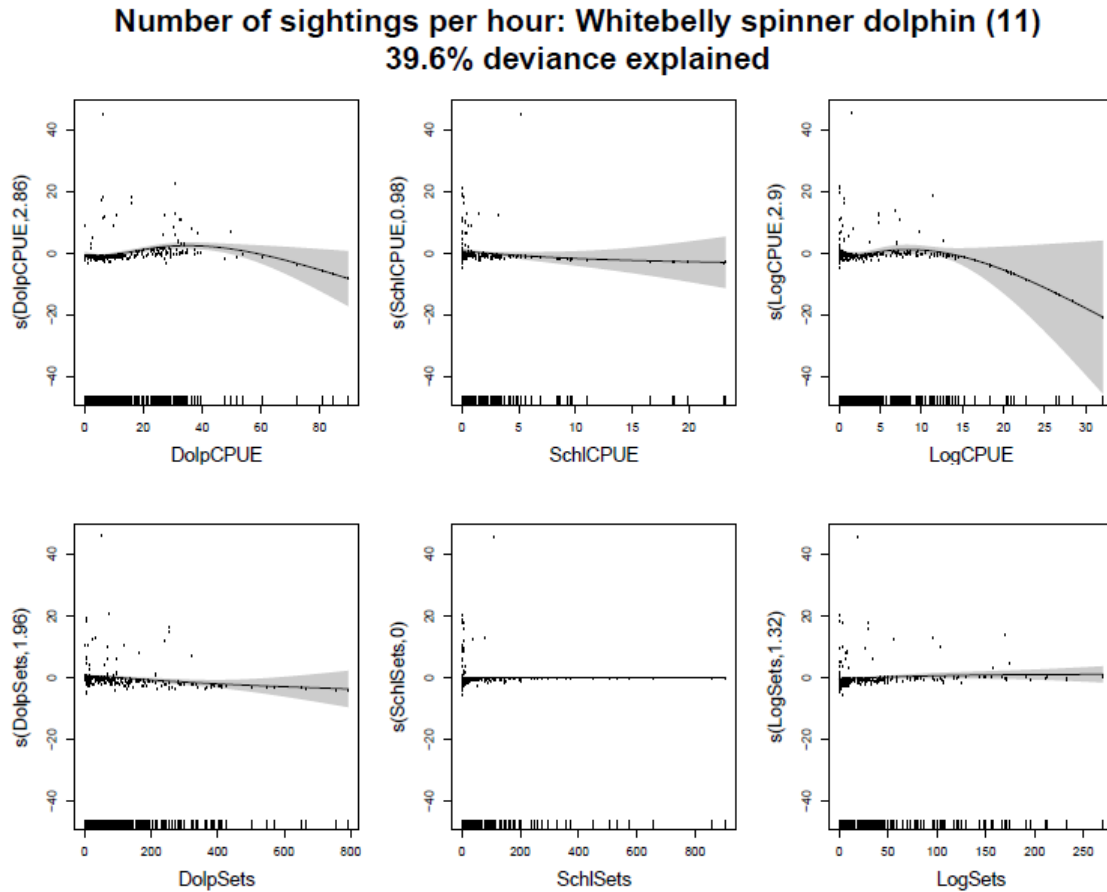


Figure A3.4. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for whitebelly spinner dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

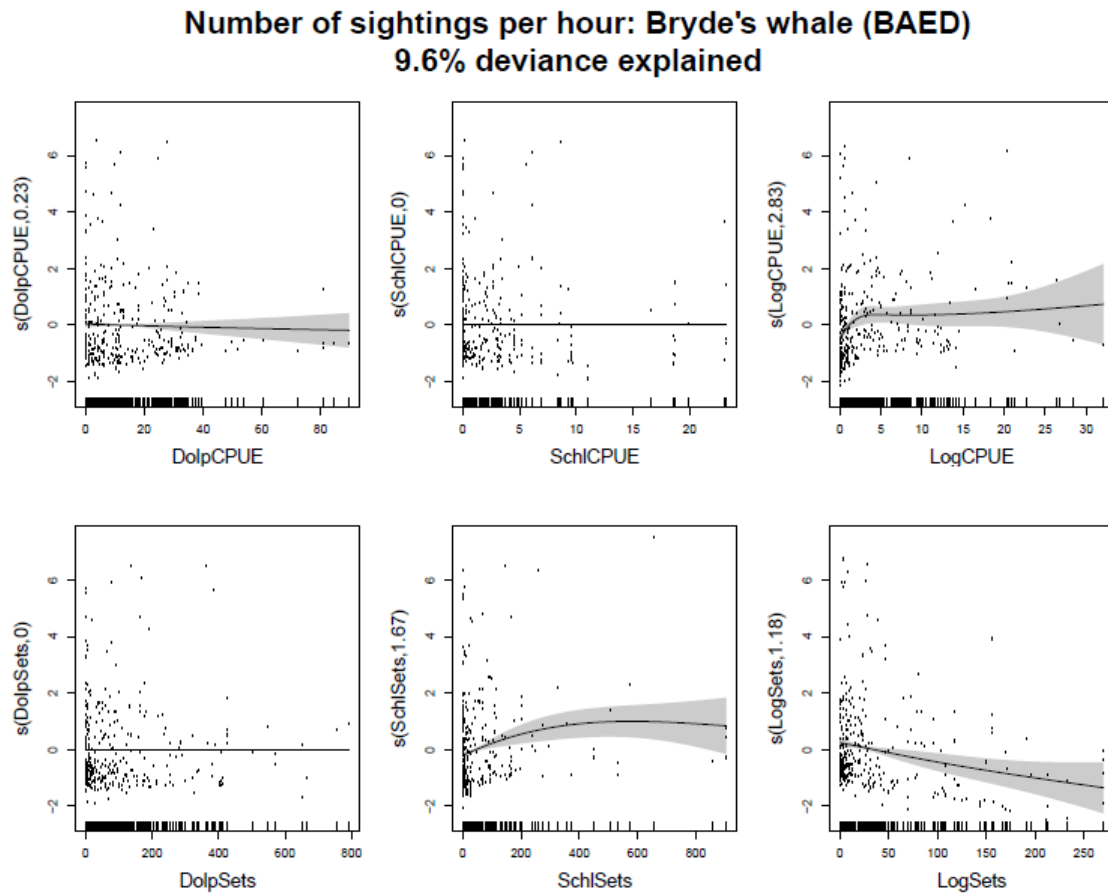


Figure A3.5. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for Bryde's whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

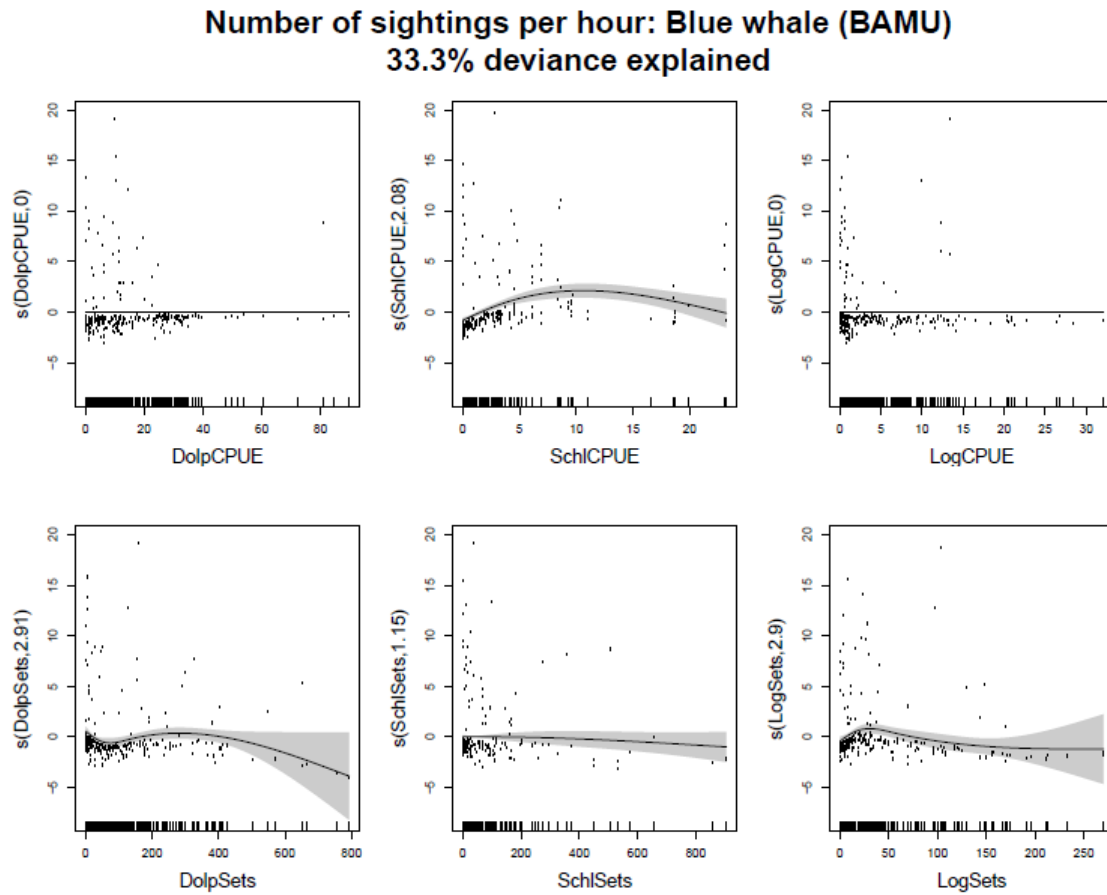


Figure A3.6. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for blue whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

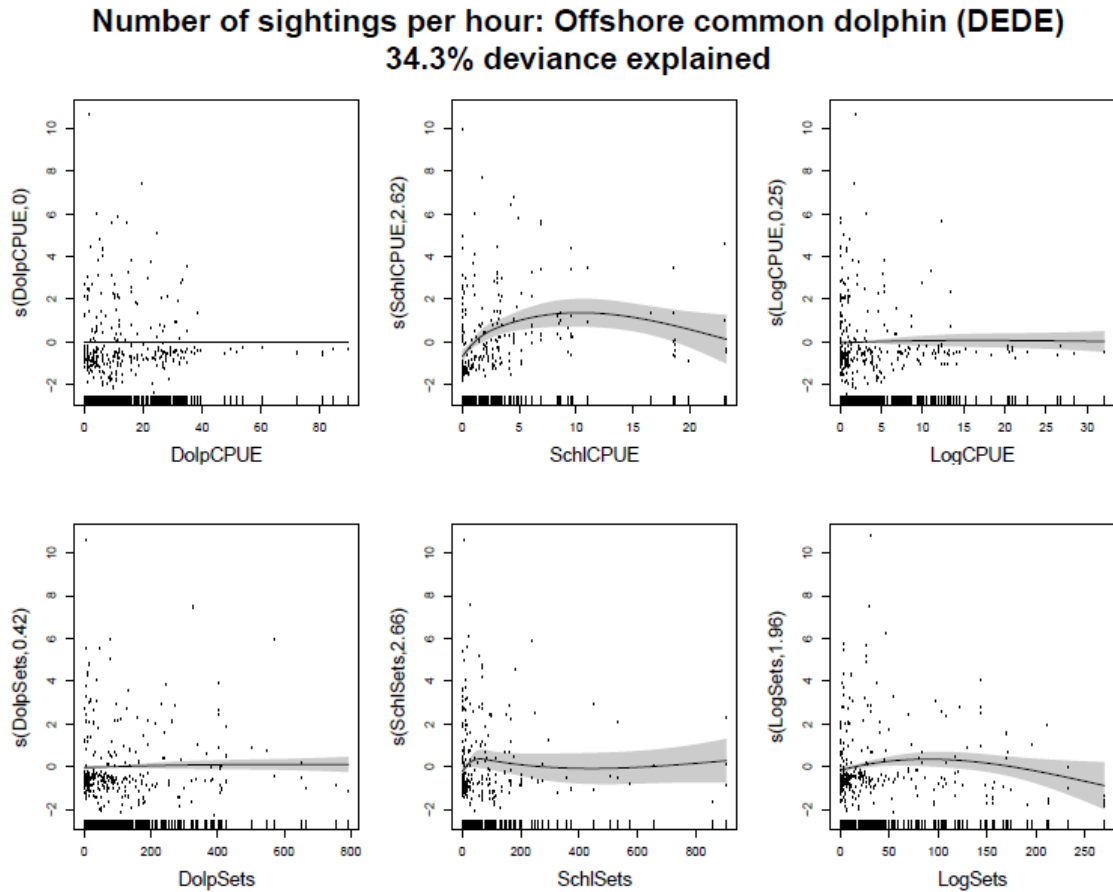


Figure A3.7. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for offshore common dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

Number of sightings per hour: Short-finned pilot whale (GLMA)
17.6% deviance explained

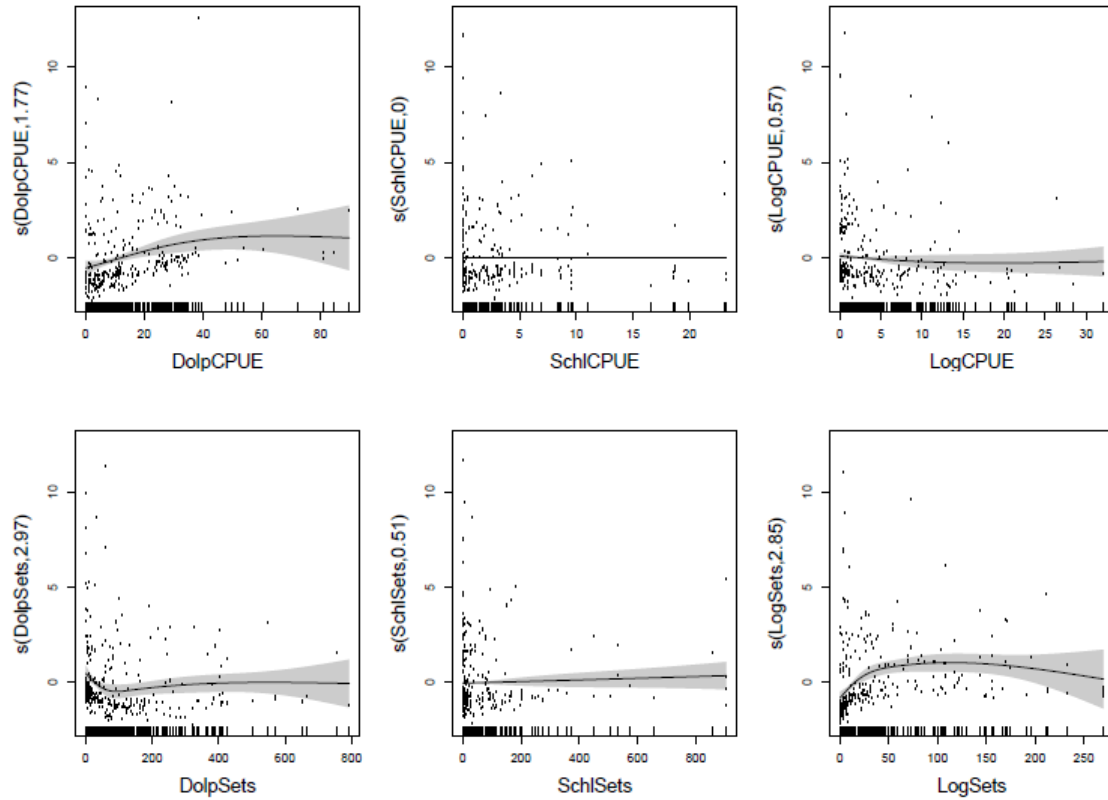


Figure A3.8. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for short-finned pilot whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

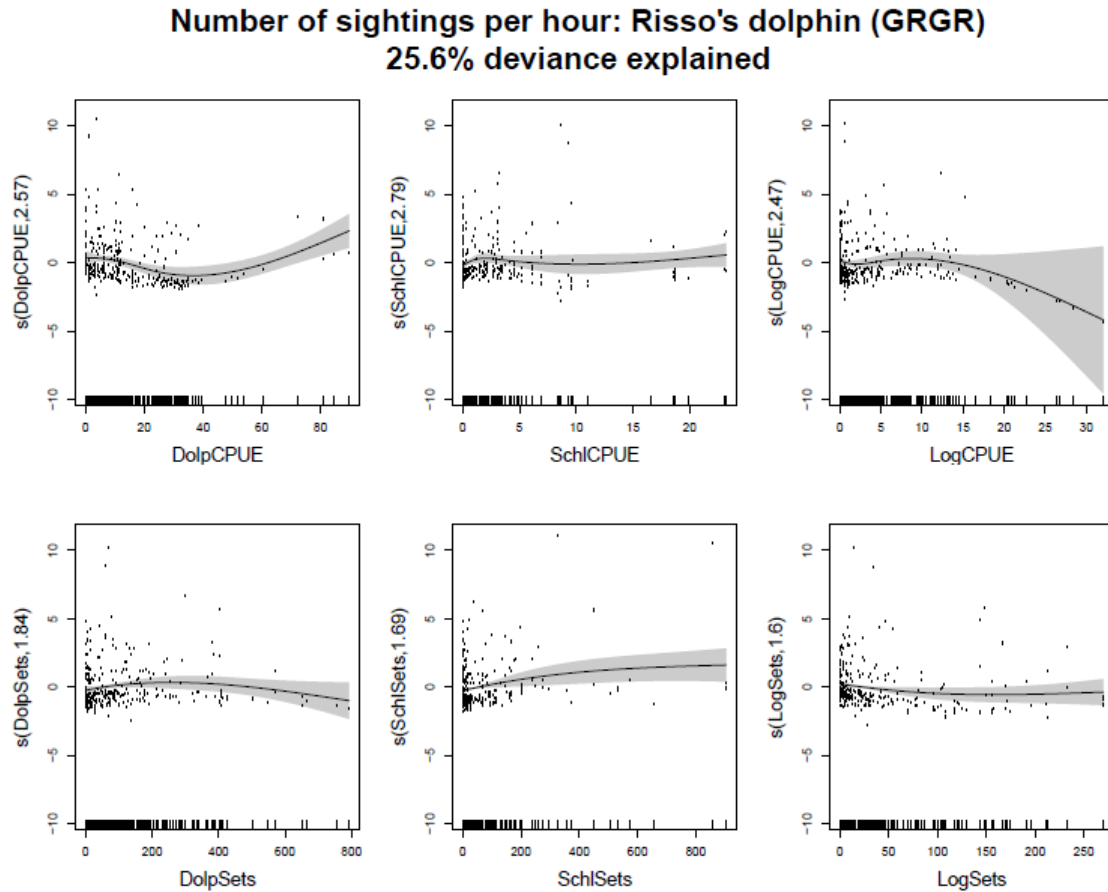


Figure A3.9. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for Risso's dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

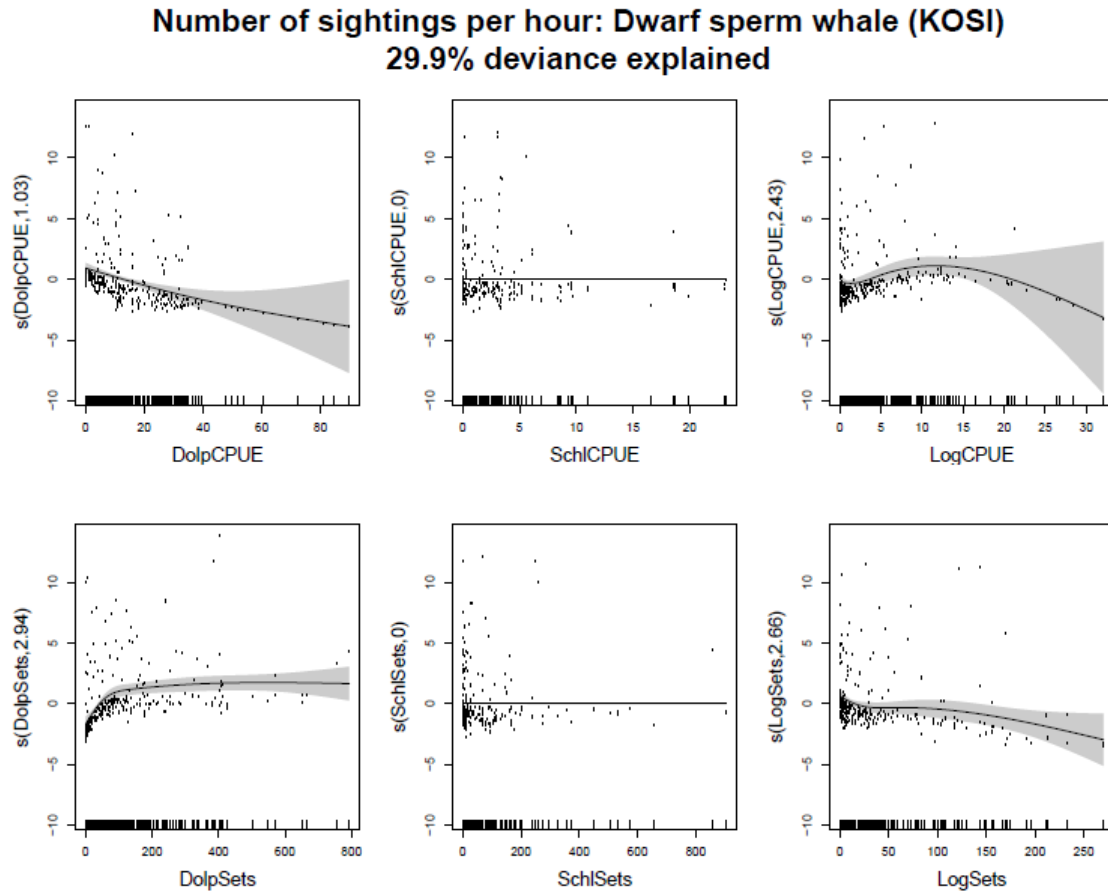


Figure A3.10. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for dwarf sperm whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

Number of sightings per hour: Mesoplodon beaked whales (Mesop)
14.3% deviance explained

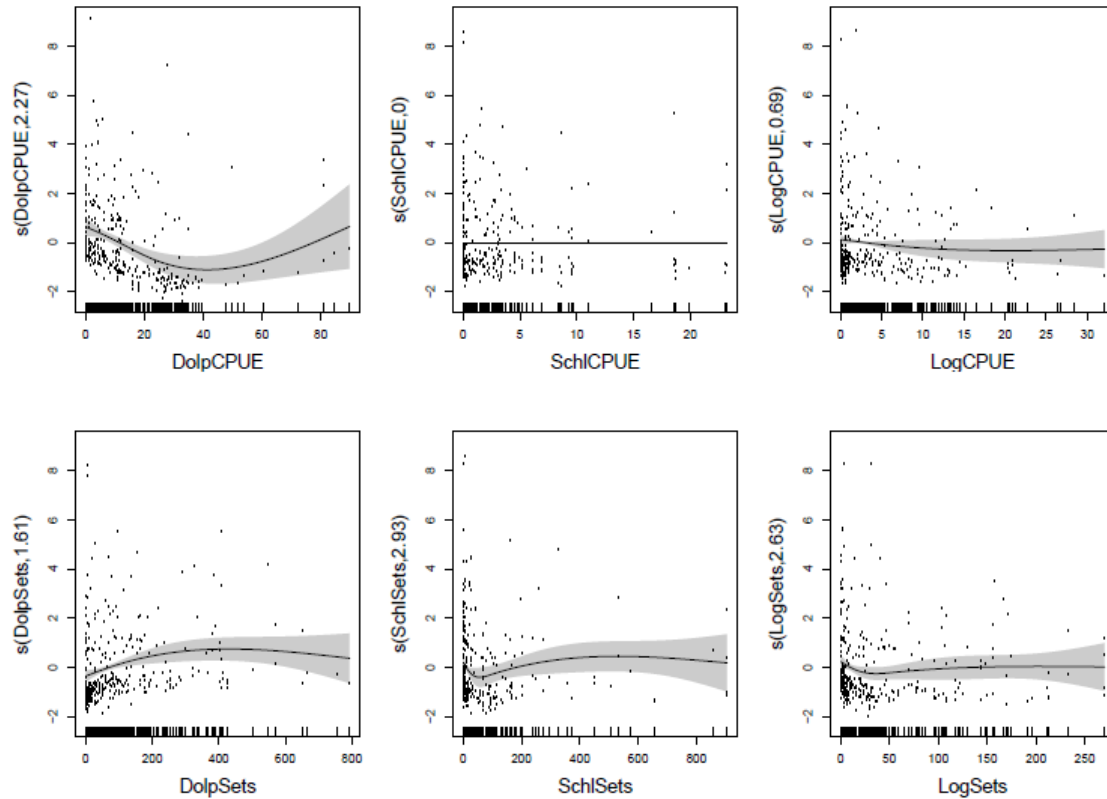


Figure A3.11. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for mesoplodont beaked whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

Number of sightings per hour: Offshore spotters + eastern spinners (MIXE)
55.6% deviance explained

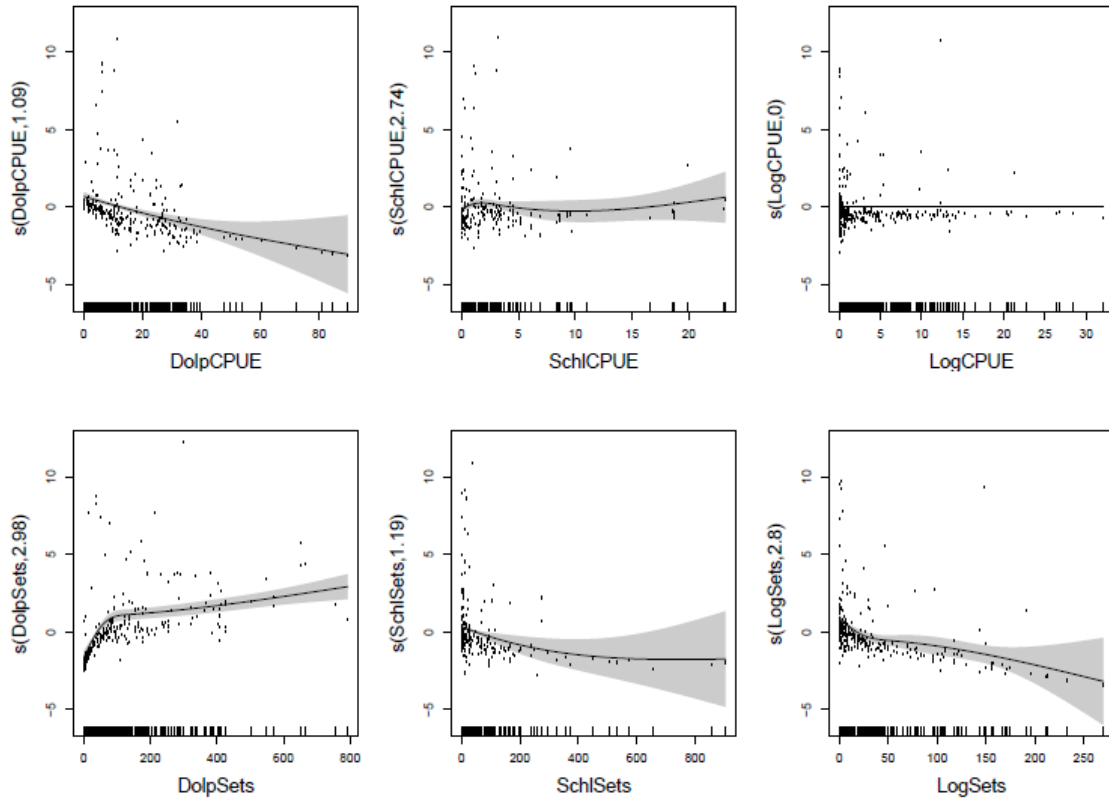


Figure A3.12. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for mixed schools of offshore spotted and eastern spinner dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

**Number of sightings per hour: Offshore spotters + whitebelly spinners (MIXW)
28.8% deviance explained**

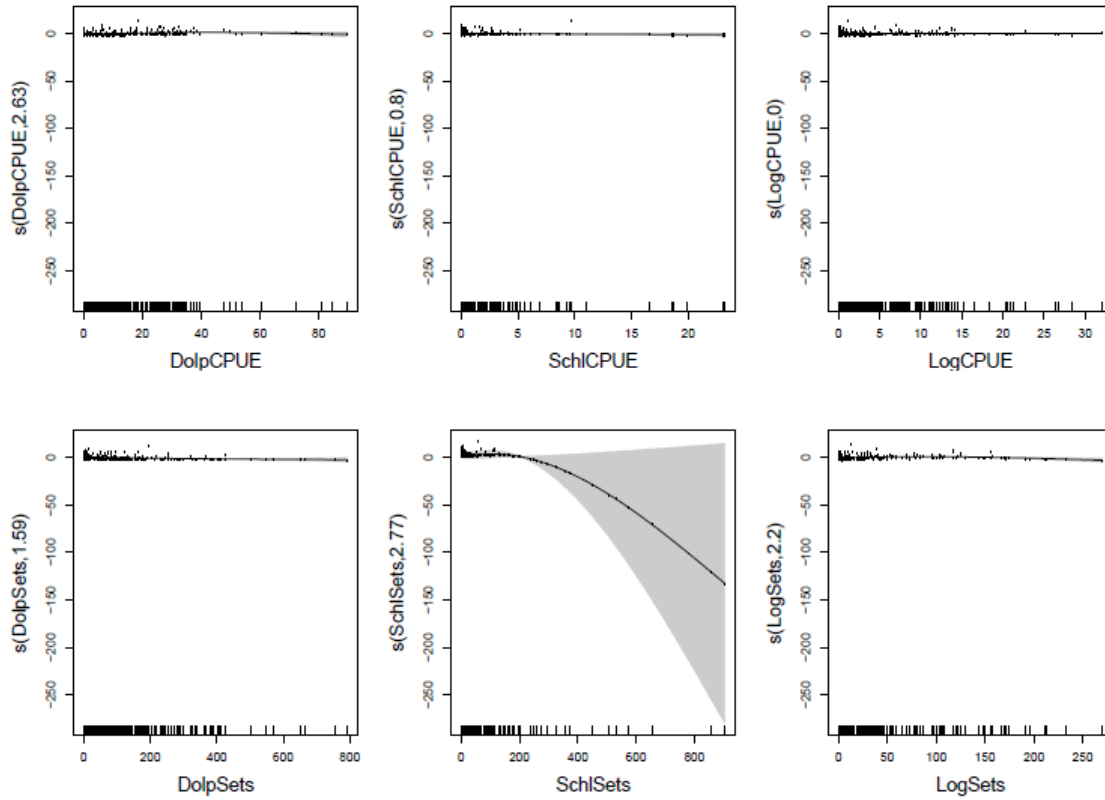


Figure A3.13. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for mixed schools of offshore spotted and whitebelly spinner dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

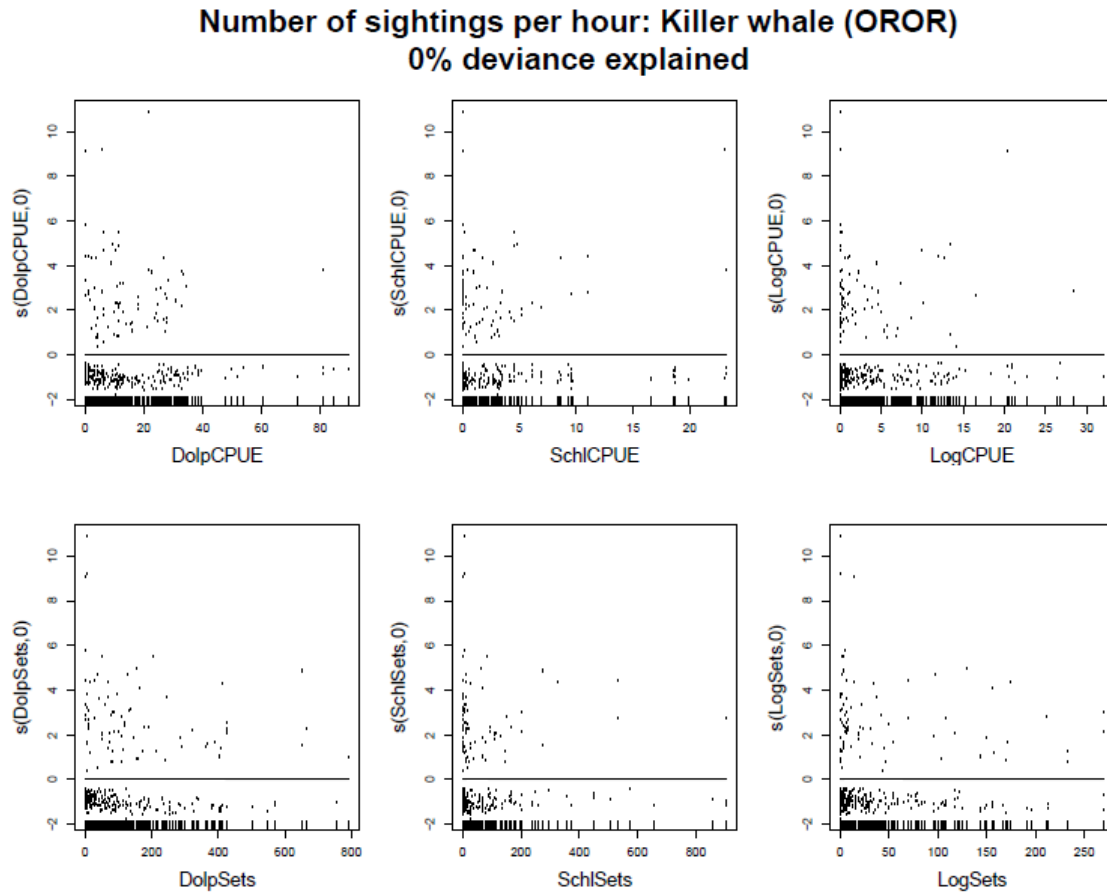


Figure A3.14. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for killer whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

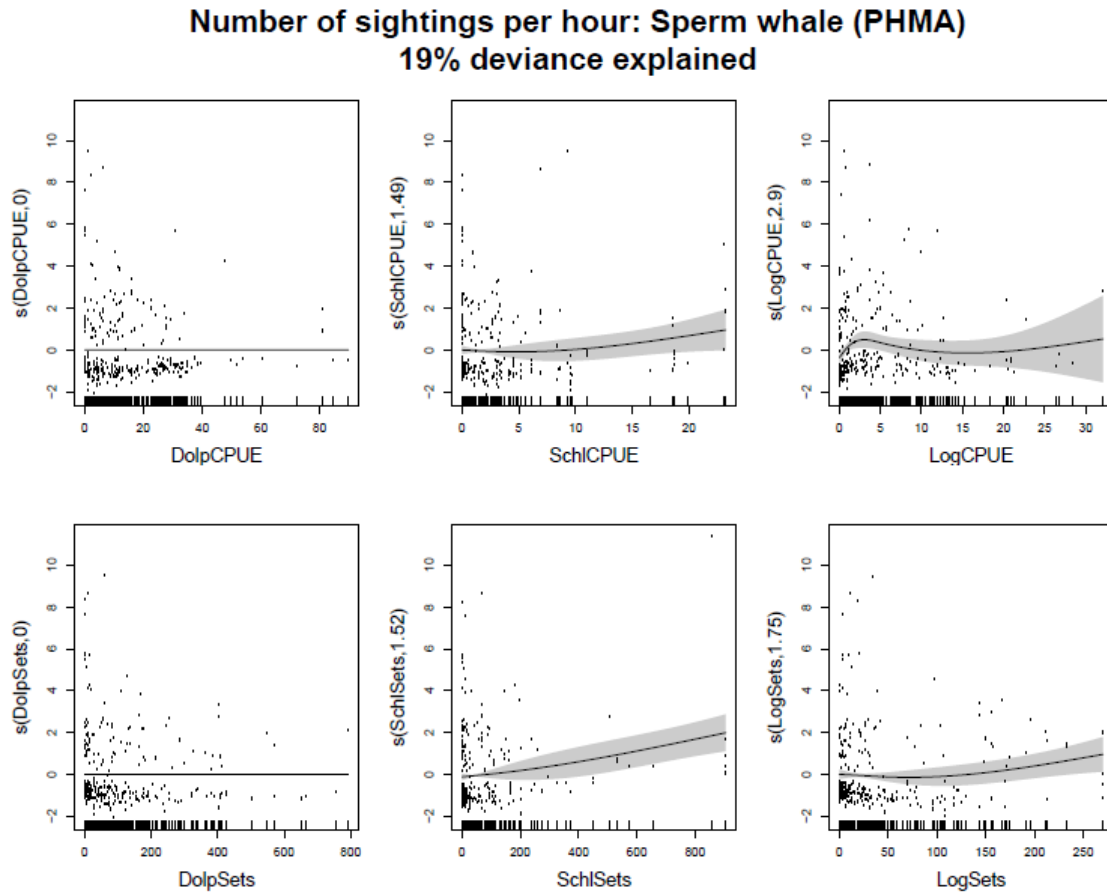


Figure A3.15. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for sperm whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

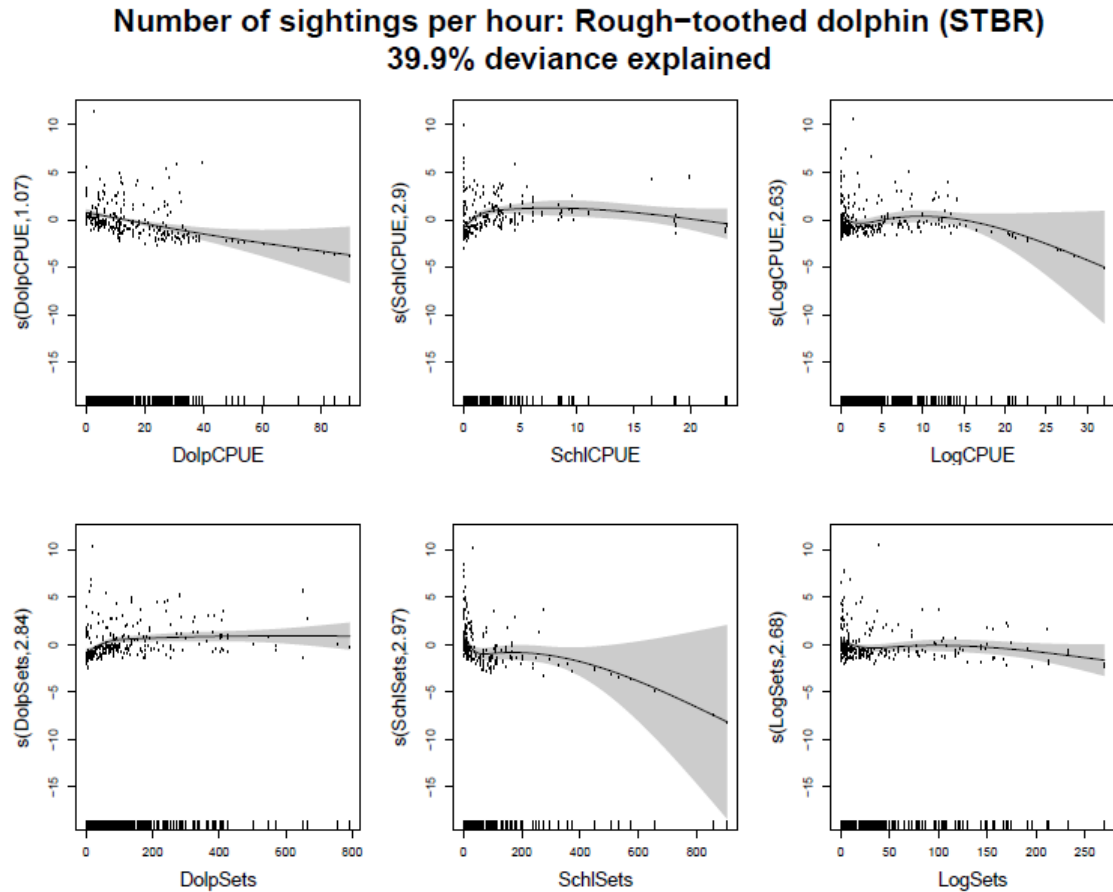


Figure A3.16. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for rough-toothed dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

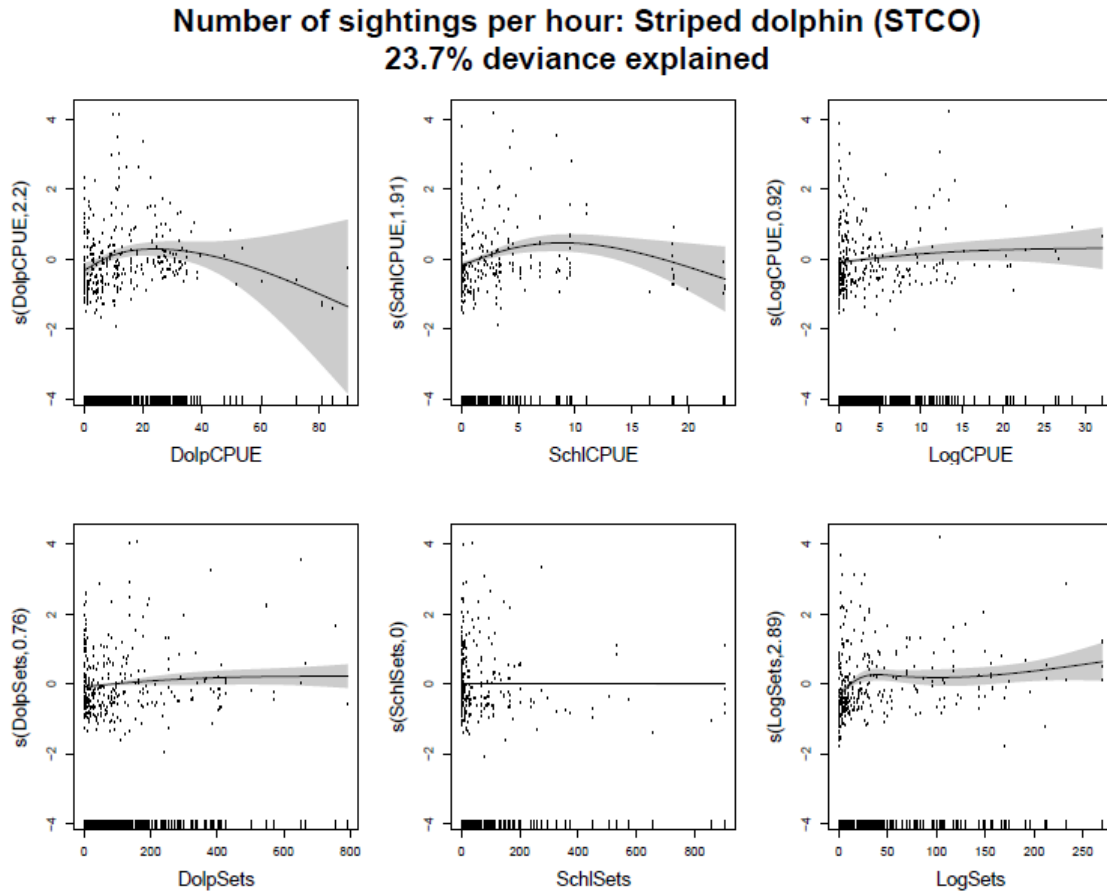


Figure A3.17. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for striped dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

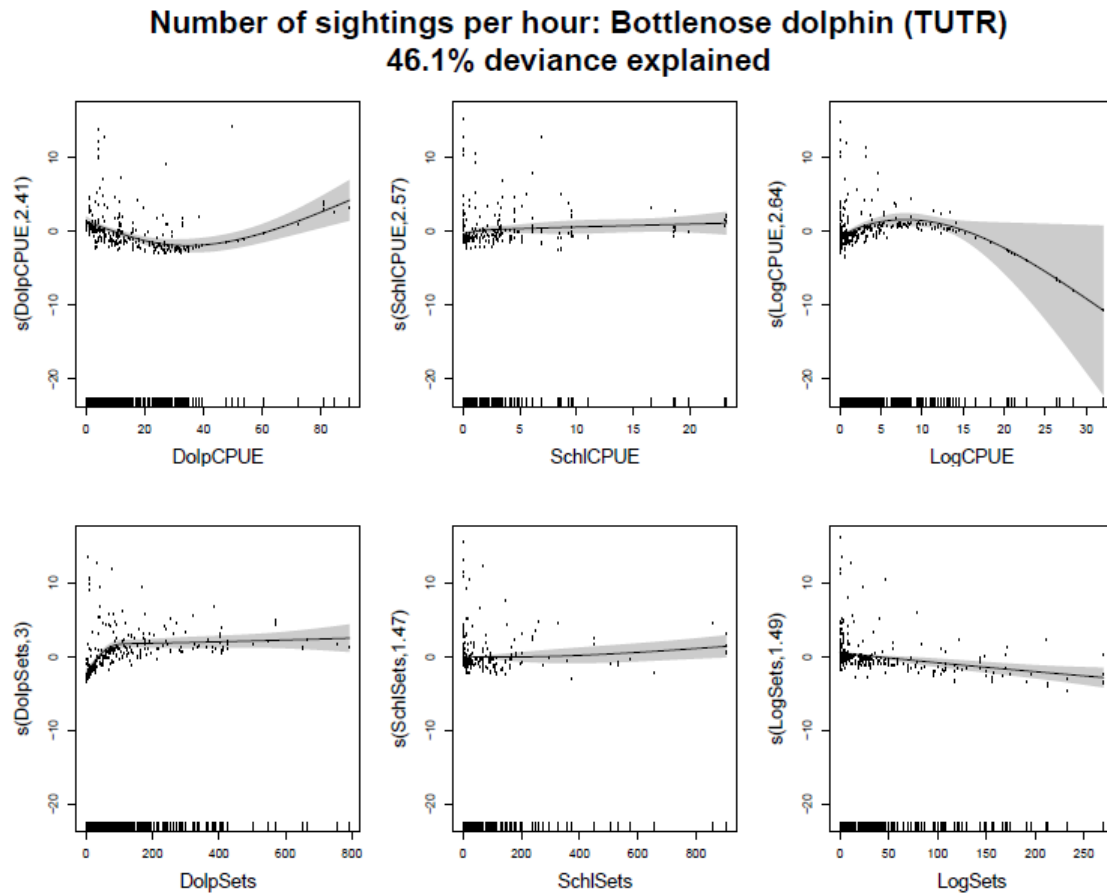


Figure A3.18. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for bottlenose dolphins as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

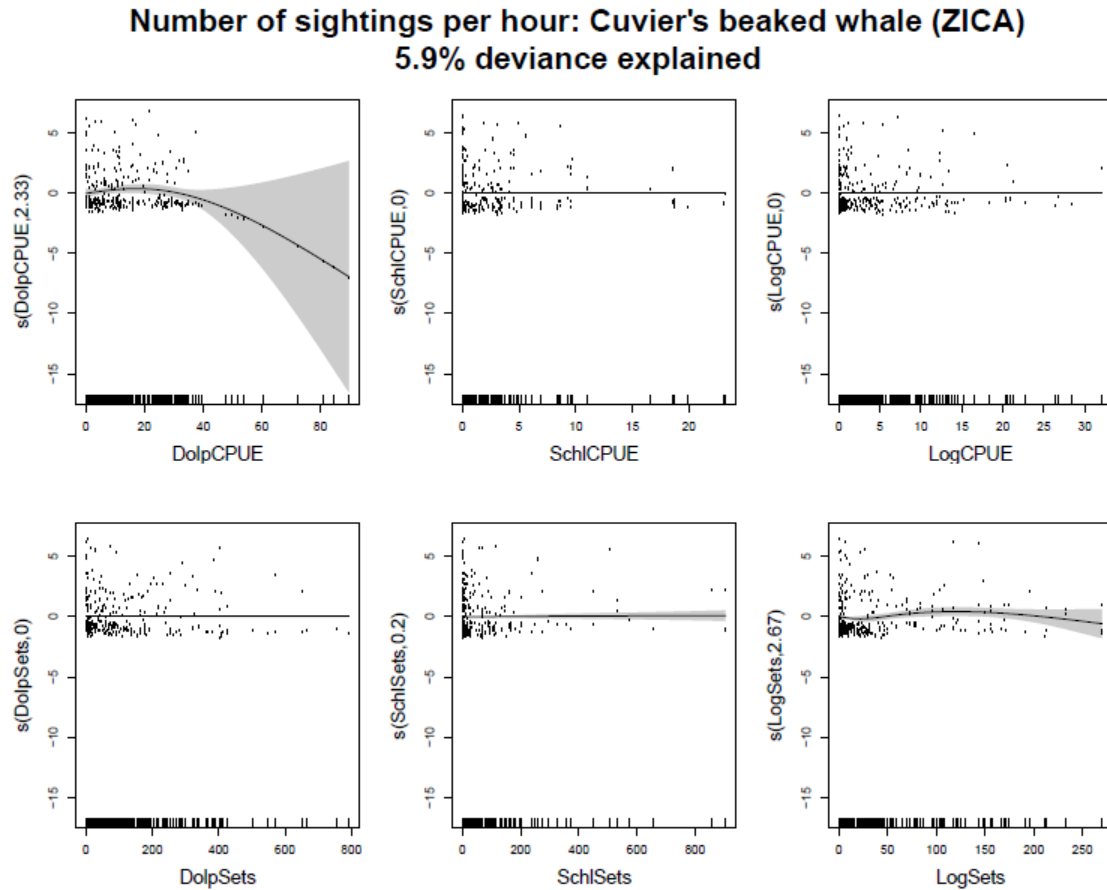


Figure A3.19. Results from generalized additive models with yellowfin tuna fishery metrics as predictors and sightings per hour for Cuvier's beaked whales as the response variable. Predictors include – for dolphin, school, and log fishing methods – “Sets” (number of sets of the purse-seine net), and “CPUE” (catch per unit of effort = metric tons of catch per day of fishing). Points are residuals; gray shading is the estimated 95% confidence interval; the rug plot (vertical lines along the x-axis) shows the distribution of data. Taxonomic information as in Table 1.

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CHAPTER 3

Bayesian inference and assessment for rare-event bycatch in marine fisheries: a drift gillnet fishery case study

ABSTRACT

Fisheries bycatch is a global threat to marine megafauna. Environmental laws require bycatch assessment for protected species, but this is difficult when bycatch is rare. Low bycatch rates combined with low observer coverage may lead to biased, imprecise estimates when using standard ratio estimators. Bayesian model-based approaches incorporate uncertainty, produce less volatile estimates, and enable probabilistic evaluation of estimates relative to management thresholds. Here, we demonstrate a pragmatic decision-making process that uses Bayesian model-based inferences to estimate the probability of exceeding management thresholds for bycatch in fisheries with <100% observer coverage. Using the California drift gillnet fishery as a case study, we: 1) model rates of rare-event bycatch and mortality using Bayesian Markov chain Monte Carlo estimation methods and 20 years of observer data, 2) predict unobserved counts of bycatch and mortality, 3) infer expected annual mortality, 4) determine probabilities of mortality exceeding regulatory thresholds, and 5) classify the fishery as having low, medium, or high bycatch impact using those probabilities. We focus on leatherback sea turtles (*Dermochelys coriacea*) and humpback whales (*Megaptera novaeangliae*). Candidate models included Poisson or zero-inflated Poisson likelihood, fishing effort, and a bycatch rate that varied with area, time, or regulatory regime. Regulatory regime had the strongest effect on leatherback bycatch, with the highest levels occurring prior to a regulatory change. Area had the strongest effect on humpback bycatch. Cumulative bycatch estimates for the 20-year period were 104-242 leatherbacks (52-153 deaths) and 6-50 humpbacks (0-21 deaths). The probability of exceeding a regulatory threshold under the U.S. Marine Mammal Protection Act

(Potential Biological Removal) of 0.113 humpback deaths was 0.58, warranting a “medium bycatch impact” classification of the fishery. No PBR thresholds exist for leatherbacks, but the probability of exceeding an anticipated level of 2 deaths per year, stated as part of a U.S. Endangered Species Act assessment process, was 0.0007. The approach demonstrated here would allow managers to objectively and probabilistically classify fisheries with respect to bycatch impacts on species that have population-relevant mortality reference points, and declare with a stipulated level of certainty that bycatch did or did not exceed estimated upper bounds.

INTRODUCTION

Rare Events in Ecology and Management

Rare events can be ecologically important when they have high impacts (e.g., dispersal events, catastrophic weather, or disease) or accumulate to levels that affect wildlife populations or human decision-making (e.g., ship strikes of whales, shark attacks on humans, or sightings of endangered species). However, inferring ecological parameters from rare-event data is challenging. The sample sizes typically required to estimate them with reasonable precision are quite large (Dixon et al. 2005, Amande et al. 2012). The data are commonly, though not always, overdispersed, often with more zeros than expected for conventional statistical distributions, and thus violate model assumptions (Cunningham and Lindenmayer 2005, Lewin et al. 2010, Webley et al. 2011). For instance, the Poisson distribution is useful for modeling count data, but its requirement for equal mean and variance is often violated by rare-event data. Despite these challenges, natural resource managers often must make inferences about rare events to inform their decisions (e.g., Rojas-Bracho et al. 2006).

Numerous approaches have been developed to deal with the analytical challenges posed by rare-event data. Most fall into the category of using mixture models consisting of one or more count and binomial processes (e.g., zero-inflated or hurdle models) to cope with the many-zeros problem (e.g., Ver Hoef and Jansen 2007, Lewin et al. 2010, Barlow and Berkson 2012, Okamura et al. 2012). Precision can sometimes be improved by utilizing ancillary information in the form of informative Bayesian priors, modified sampling designs (e.g., stratification), covariate-based prediction models, or additional data sets that inform the same process of interest (e.g., Dixon et al. 2005). All of these strategies can be accommodated by a Bayesian approach.

Bayesian methods emphasize probabilistic inference and posterior distribution summaries, which facilitate full and transparent communication of uncertainty (Ellison 1996, Wade 2000). Because of these features, Bayesian methods have a substantial history of application in the life sciences, ranging from human health and biomedical research (Manton et al. 1989, Richardson and Gilks 1993, Cai et al. 2010) to wildlife population dynamics and stock assessments (McAllister et al. 1994, Punt and Hilborn 1997, McAllister and Kirkwood 1998, Maunder et al. 2000, Maunder and Starr 2001, Hoyle and Maunder 2004, Amstrup et al. 2010, Jay et al. 2011). Given the high levels of uncertainty associated with rare-event problems and the importance of quantifying management error, Bayesian statistics provide a transparent method for estimating the probability of Type I (falsely inferring an effect) and Type II (failing to identify an important effect) error (Maunder et al. 2000, Ludwig et al. 2001, Hoyle and Maunder 2004).

Fisheries Bycatch

Bycatch (the incidental capture of non-target species in fisheries operations) remains a major global threat to marine megafauna, including sea turtles, marine mammals, and seabirds (Dayton et al. 1995, Lewison et al. 2004, Read et al. 2006, Wallace et al. 2010, Croxall et al. 2012). The U.S. has enacted a series of laws, including the Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA), which require assessment of bycatch impacts on legally protected species (Moore et al. 2009). Assessment is more difficult in practice than in principle because bycatch of some species is such a rare event (McCracken 2004, Amande et al. 2012).

The characteristics of rare-event bycatch pose estimation challenges. First, protected megafauna are typically not targeted; in fact, fishers in many countries have incentives not to catch these species (e.g., avoidance of damaged gear, legal fines, and increased fishery regulation). Thus, the number of animals caught is relatively low. Second, bycatch is recorded by scientific observers on board fishing vessels, but deploying observers on every fishing trip is typically cost-prohibitive. Thus, in most U.S. fisheries, observer coverage is less than 20%; in many it is less than 5% (Moore et al. 2009). Low bycatch rates combined with sparse observer coverage may lead to unacceptably low precision and severe bias in bycatch estimates (McCracken 2004, Amande et al. 2012, Carretta and Moore 2014).

Ratio estimators are commonly used to extrapolate bycatch estimates as the product of an observed bycatch rate (e.g., number of catches per observed fishing set or trip) and total effort in a fishery (e.g., number of sets or trips); however, they are not suitable when observer coverage or bycatch rates are relatively low. When applied in

such cases, commonly observed zeros result in under-estimates of zero bycatch, while those events observed by chance result in implausibly high estimates. For example, in the California drift gill net fishery (DGN fishery) off the west coast of the U.S., after 11 years (1999-2009) without a single observed sperm whale (*Physeter macrocephalus*) interaction (observer coverage ranging from 13.0% to 22.7% annually), two sperm whales were observed entangled in 2010 (Carretta et al. 2010), resulting in a ratio-based estimate of 16 deaths or serious injuries for the year. In reality, total bycatch probably was not as high as 16 in 2010 and not zero for all 11 of the previous years.

The issues with rare-event bycatch, including chance volatility in single-year estimates, are not just a statistical abstraction; they present managers with real problems related to MMPA and ESA regulations. To reduce the bias associated with single-year estimates, NMFS typically uses 5-year means in its assessments. This approach offers some improvement, but it is *ad hoc* and does not necessarily provide an adequate solution (Carretta and Moore 2014). In particular, it does not transparently communicate the uncertainty in single-year estimates, which may still be taken at face value by stakeholders. This problem arose recently when the 2010 sperm whale estimate was cited in a lawsuit against the U.S. National Marine Fisheries Service (NMFS) as evidence that regulatory thresholds were being exceeded (Center for Biological Diversity 2012). Such conclusions could have considerable, unnecessary impacts on the fishery, and they could be avoided with less volatile estimates.

Model-based approaches can reduce the volatility of bycatch estimates. There are several recent examples of using GLM-based mixture (e.g., zero-inflated) models to improve bycatch estimates (Pradhan and Leung 2006, Minami et al. 2007, Cambie 2011,

Winter et al. 2011). Bayesian methods are also particularly well suited for these problems (e.g., Gardner et al. 2008, Sims et al. 2008) and have been used to estimate bycatch of some protected species, including the vaquita (*Phocoena sinus*) (Gerrodette and Rojas-Bracho 2011), Hector's dolphins (*Cephalorhynchus hectori*) (Davies et al. 2008), and New Zealand fur seals (*Arctocephalus forsteri*) (Thompson et al. 2013). These methods more fully integrate uncertainty and are quite useful for producing less volatile bycatch estimates; however, they could be taken a step further to inform decision-making. Here, we propose a pragmatic decision-making process that uses Bayesian model-based inferences to classify the probability of protected species bycatch exceeding regulatory thresholds or other reference points in fisheries with less than 100% observer coverage.

In this paper, we use fisheries observer data to: 1) model rates (per unit of fishing effort) of rare-event bycatch and mortality (some animals are released alive but others die) for protected species; our models view observed bycatch counts as random variables, accounting for both observation error (imperfect detection of bycatch given incomplete observer coverage) and biological process error (true annual variation), 2) use those inferred rates to predict unobserved counts of bycatch and mortality, given a specified level of fishing effort, 3) infer expected annual mortality, given the data and a specified level of fishing effort, 4) determine probabilities of expected annual mortality falling within certain ranges defined by regulatory thresholds, and 5) classify a fishery into a category of low, medium, or high bycatch impact using the above probabilities. In this classification system, placing a fishery into a higher impact category when in fact the level of impact is low would be analogous to a Type I error. Assigning a lower impact category when in fact bycatch impacts are high would be analogous to a Type II error.

We demonstrate our approach using the DGN fishery as a case study. Rare-event bycatch has been observed in this fishery for numerous protected species, including leatherback sea turtles (*Dermochelys coriacea*), loggerhead sea turtles (*Caretta caretta*), short-finned pilot whales (*Globicephala macrorhynchus*), humpback whales (*Megaptera novaeangliae*), sperm whales, and beaked whales (Family Ziphiidae) (HMSMT 2012). We analyze data for leatherback sea turtles and humpback whales as representative examples of endangered species regulated under the ESA and MMPA, respectively.

METHODS

California Drift Gillnet Fishery History and Data

The DGN fishery has existed since the late 1970s, operating primarily from August through December and targeting large pelagic species such as thresher shark (*Alopias vulpinus*) and swordfish (*Xiphias gladius*). Effort in the fishery has declined over time according to California Department of Fish and Game (CDFG) vessel logbook data (Table 1, Figure 1) (Hanan et al. 1993). NMFS has maintained an observer program since 1990 to monitor marine mammal bycatch pursuant to the MMPA (Barlow 1989). The observer data provide details of fishing effort including the date, latitude and longitude coordinates, target and bycatch species caught, and condition of bycatch. From 1990 through 2009, there were 8,152 observations, with mean observer coverage of 15.6% per year (Table 1). There were 24 observed leatherback takes (a “take” is a single bycatch event), 13 of which resulted in mortality and one (“unknown”) that we conservatively assumed to also be fatal (Table 2). There were 0-5 observed leatherback takes per year in 1990-1999, none in 2000-2008, and 1 in 2009 (Table 2). There were 3

observed humpback takes, none of which resulted in death. The maximum number of leatherbacks or humpbacks ever observed entangled at one time was 1.

The gear type used in this fishery is a long, large-mesh net (approximately 1800 m length with 35.6 cm mesh), which fishers deploy offshore at dusk and retrieve at dawn (PFMC 2011). One iteration of this process is referred to as a “set.” Based on similarity among DGN sets in gear, technology, methods, and soak time, we treat the set as the basic unit of fishing effort (a conventional unit in bycatch analyses). Some physical variability in net characteristics (length, mesh size, depth) exists but has not been found to be a significant driver of bycatch variation (Julian and Beeson 1998). Since 1997, all nets have been equipped with acoustic pingers (to deter odontocetes) and 36-foot net extenders to reduce marine mammal bycatch.

Previous studies suggest that the amount, location, and timing of fishing effort are the most significant drivers of bycatch variation in this fishery, at least for leatherbacks (Julian and Beeson 1998, NMFS 2000, Benson et al. 2007). In 2001, NMFS implemented a time-area fishery closure (NMFS 2001) with an objective to limit leatherback bycatch to 9 takes and 6 deaths over a 3-year period (NMFS 2000). Annually, from August 15 through November 15 (“closure period” or “closure months”), the DGN fishery is prohibited from operating in the Pacific leatherback conservation area (“closure area”), comprised of state and federal waters from Point Conception (near Monterey Bay, California) north to 45 degrees latitude in Oregon (Figure 1) (NMFS 2001). This regulation targeted a time-area combination where most historical leatherback bycatch (18 takes) was observed (Figure 1). For our analysis, we classified all sets and takes as to whether they occurred inside or outside of the area or months delimited by the seasonal

closure (Table 1, Figure 1). For the unobserved sets, we used the CDFG logbook data (1990-2009) which contain dates and locations of fishing effort at the CDFG block level (typically 10-arcminute square blocks on a latitude-longitude grid).

Modeling Rare-Event Bycatch in the DGN Fishery with a Bayesian Approach

We explored models that could account for potential time-area differences in bycatch rates. Models varied with respect to available spatial and temporal covariates, functional form, and number of estimated parameters (Tables 3, 4).

For a single species (e.g., leatherbacks), we used a Poisson likelihood function to model the stochastic dependence of x_i , the number of observed takes in year i , on θ , the per-set take rate parameter, and n_i , the number of observed sets in year i :

$$f(x_i|\theta, n_i) = e^{-\theta n_i} \frac{(\theta n_i)^{x_i}}{x_i!}, \quad (1)$$

where $\theta n_i = \lambda_i$ is the Poisson rate (mean) parameter. Previous studies have also used the Poisson distribution to model bycatch (NMFS 2004, Pradhan and Leung 2006, Gardner et al. 2008, Murray 2009, 2011) because it can characterize data in which each observation has a high probability for a zero count, a small probability for a count of one, and an infinitesimal probability for a count of two or more. The DGN fishery data have these Poisson characteristics plus one more: a mean per-set take rate (2.944×10^{-3}) roughly equal to the variance (2.936×10^{-3}). A strong positive correlation between the numbers of observed takes and sets per year (Pearson's $r=0.672$; $p=0.001$; Figures 1, 2) supports including the number of sets in the model. We assume statistical independence of all sets and takes.

We modeled the number of observed deaths, w_i , with a binomial likelihood function which quantifies the stochastic dependence of w_i on x_i and a conditional mortality parameter, q (i.e., given a take of this species occurs, the probability that the animal dies):

$$f(w_i | x_i, q_s) = \frac{x_i!}{w_i!(x_i - w_i)!} q^{w_i} (1 - q)^{x_i - w_i}. \quad (2)$$

To estimate q for each species, we followed Chapter 2 in (Gelman et al. 2004) in specifying a flat prior of $Beta(1, 1)$ which yields a posterior distribution of the form $Beta(1 + w_{all}, 1 + x_{all} - w_{all})$, where w_{all} and x_{all} are the respective numbers of deaths and takes in all years of the data. For leatherbacks, $w_{all} = 14$ deaths and $x_{all} = 24$ takes; for humpbacks, $w_{all} = 1$ death and $x_{all} = 4$ takes (the fisher-reported mortality is conservatively treated as a take for purposes of estimating the conditional mortality rate for humpbacks). Thus, for the posterior of q in our analyses, we used $Beta(15, 11)$ for leatherbacks and $Beta(2, 4)$ for humpbacks. Appendix A contains more theoretical background on our Bayesian modeling approach for interested readers.

Candidate models are outlined in Table 3. In M1 (simple model), the bycatch rate θ is constant across all locations and times, such that expected annual observed bycatch (λ_i) varies simply with the number of observed fishing sets (n_i). For M1r (regulation model), θ differs for pre- and post-regulation periods (i.e., 1990-2000 and 2001-2009). In M2 (area model), M3 (time model), M4 (area-time interaction model), and M5 (area and time model), θ varies across different time-area combinations defined by the closure limits (Table 1). The binary area variable, a , indicates whether effort occurred inside or outside the area defined by the closure (whether or not the closure was in effect that year)

(in M2, M4, M5). The binary time variable, t , indicates whether or not effort occurred during the closure months of August 15 through November 15 (again, irrespective of whether it was a closure year) (in M3, M4, M5). Model M2 describes area-only differences in θ . Model M3 describes season-only differences in θ . For model M4, θ differs for sets inside the closure area and season from those conducted either outside the closure area or season. Finally, M5 allows for a unique θ for each combination of being in or out of the closure area or season. Regulation versions of M2-M5 (e.g., M2r) were not tested because the binary regulation variable r would be confounded with a and/or t , and there are not enough observed takes in post-regulation years (takes = 1) to fit overly complex models.

We included zero-inflated Poisson (ZIP) versions of each model to allow for the possibility that some effort may occur in time periods (e.g., post-regulation) or time-area combinations with no exposure to bycatch risk. A mixture of effort where a portion (p) is exposed to bycatch risk at Poisson rates (i.e., animals are present) and the other portion ($1 - p$) has no exposure to the risk (i.e., animals are not present) will result in more zeros and higher variance than predicted by the Poisson distribution. The ZIP likelihood function,

$$f(x_i|\theta, n_i) = pe^{-\theta n_i} \frac{(\theta n_i)^{x_i}}{x_i!} + (1 - p)0, \quad (3)$$

is simply an extension of the Poisson likelihood function (Eqn. 1). M1z, M2z, M3z, M4z, and M5z add ZIP parameters ($p_0 - p_3$) to their parent models to allow the degree of zero-inflation to vary across time-area categories (Table 3). For example, we hypothesize a

higher probability of zero bycatch for effort occurring outside the closure area than inside.

We used WinBUGS to implement Bayesian Markov chain Monte Carlo (MCMC) methods for model estimation (Lunn et al. 2000). WinBUGS uses the Gibbs sampling algorithm to sample from the posterior distributions of parameters. We used the R statistical environment with packages R2WinBUGS and Coda to interface with WinBUGS (Lunn et al. 2000, R Core Team 2013). Flat priors were specified for all parameters (Table 3). All 20 years of NMFS observer data were included in the estimation process. MCMC runs consisted of 200,000 iterations, including a burn-in of 50,000, and 3 chains. Convergence of chains onto stable estimates was confirmed using the diagnostic statistic \hat{R} and trace plots of parameter estimates over MCMC iterations.

To select the best model, we used the Deviance Information Criterion (DIC), a Bayesian measure of model fit that includes a penalty factor for the number of parameters (Spiegelhalter et al. 2002). Low DIC values are preferred to high DIC values. Models with DIC values within 1-2 points of the lowest value deserve consideration (Spiegelhalter et al. 2002). We selected models M1r and M2 as the best models for leatherbacks and humpbacks, respectively (see Results).

Predicting Total Takes, Total Mortality and Expected Annual Mortality

The Poisson rate parameters $\lambda_i = \theta n_i$ and $m_i = \lambda_i q$ are the expected annual takes and deaths, respectively, given fishing effort n_i , and where q is the conditional mortality rate for takes.

For each species, we generated posterior distributions for m_i and posterior predictive distributions (PPDs, estimated distributions of unobserved bycatch or mortality

counts given the estimated posterior for θ and a specified level a fishing effort; see Appendix A) for x_i (observed takes), $y_i - x_i$ (unobserved takes), y_i (total takes), w_i (observed deaths), $z_i - w_i$ (unobserved deaths), and z_i (total deaths), using the following simulation steps (model details in Table 3; parameter estimates in Table 4): (1) Calculate $\theta_{pre-reg.}$ and $\theta_{post-reg.}$ for leatherbacks (M1r was the best leatherback model; see Results), and $\theta_{outside}$ and θ_{inside} for humpbacks (M2 was the best humpback model), using random draws from the posteriors for β_0 and β_1 . (2) For year i , calculate a mean $\lambda_{i,e}$, where $e =$ observed, unobserved, or total sets in year i , i.e., $\lambda_{i,e} = \sum_{r=0}^1 \theta_r n_{i,r,e} f_{i,r,e}$ for leatherbacks and $\lambda_{i,e} = \sum_{a=0}^1 \theta_a n_{i,a,e} f_{i,a,e}$ for humpbacks, where f is the fraction of sets in a data classification. (3) Calculate $m_i = \hat{q} \lambda_{i,e}$ for each level of effort, where the value \hat{q} is drawn from the posterior of q . (4) Draw a value of $y_i - x_i$ from $Poisson(\lambda_{i,e=unobs.})$. (5) Calculate y_i by adding the true value of x_i to $y_i - x_i$. (6) Draw a value of $z_i - w_i$ from $Binomial(y_i - x_i, \hat{q})$. (7) Calculate z_i by adding the true value of w_i to $z_i - w_i$. (8) Draw a value of x_i and w_i , from $Poisson(\lambda_{i,e=obs.})$ and $Binomial(x_i, \hat{q})$, respectively (for comparison of model predictions with real data). (9) Repeat previous steps 10,000 times for year i to generate the PPDs. (10) Repeat previous steps for each year, 1990-2009. (11) Repeat steps 1-3 to calculate m_{future} for a hypothetical future year. For this, we use the average number of sets from the most recent 5-year period in the data (2005-2009), assuming this reasonably estimates the level of effort that would probably occur in near future years given the capacity (boats, permits, gear, etc.) and recent activity in the fishery. This simulation allowed us to recreate the 20-year history of the fishery in terms of observed, unobserved, and total bycatch and mortality (Figures 3, 4).

Comparison to Ratio Estimators

For fisheries with <100% observer coverage, ratio estimators are commonly used to estimate total bycatch and mortality (e.g., Julian and Beeson 1998, Carretta et al. 2004, Amande et al. 2012). The annual set-level bycatch rate for species s , r_s , is estimated as total observed bycatch divided by the total number of observed sets for the year.

Multiplying this by the total number of sets fished for the year, \hat{D} , generates the estimate of total bycatch (Carretta et al. 2004). The variance for total bycatch is $\sigma_m^2 = \hat{D}^2 \sigma_r^2$, where σ_r^2 is the variance estimate for the set-level bycatch rate. Following (Carretta et al. 2004), this may be obtained by resampling individual fishing trips (each containing one or more sets) from the dataset to construct a nonparametric bootstrap distribution for r_s from which the variance is calculated. For comparison to the Bayesian model-based approach presented here, we calculated ratio estimates for total takes and total mortality for both leatherbacks and humpbacks (Table 5, Figures 3, 4). Our calculations vary slightly from those reported by Julian and Beeson (1998) and Carretta et al. (2004) due to slight differences in our estimates of total fishing effort.

Comparing Expected Annual Mortality to Policy Thresholds

We compared the posterior distributions of m_{future} for each species to relevant policy thresholds. For humpbacks, the thresholds are prescribed by the MMPA. For the stock affected by the DGN fishery (California/Oregon/Washington stock), the maximum cumulative number of allowable deaths or serious injuries each year from *all* anthropogenic sources, or Potential Biological Removal (PBR), is 11.3 (this estimate applies to 2010-2012) (Carretta et al. 2010). Based on its annual interactions with a stock of marine mammals, a fishery can be classified as Category I (mortality $\geq 50\%$ of the

PBR level, i.e., frequent incidental mortality, or “high bycatch impact”), Category II (1% of the PBR level < mortality < 50% of the PBR level, i.e., occasional incidental mortality, or “medium bycatch impact”), or Category III (mortality \leq 1% of the PBR level, i.e., rare or no known incidental mortality, or “low bycatch impact”). We superimposed these classification thresholds (1% of PBR or 0.113 humpbacks per year and 50% of PBR or 5.65 humpbacks per year) onto the posterior distribution of m_{future} and calculated the probability that the DGN fishery would fall into each of the categories in future years. PBR is not used to manage sea turtles; however, Incidental Take Statements contained within Biological Opinions pursuant to the ESA essentially serve as *de facto* take limits (provided the stated take levels are associated with a no-jeopardy finding in the Biological Opinion). In this sense, NMFS “authorized” a maximum of 6 leatherback deaths in a 3-year period in 2000 (NMFS 2000). We evaluated the probability of m_{future} for leatherbacks exceeding 2 deaths per year.

RESULTS

Model Selection

Models M1r (simple model with regulation variable) and M1z (simple model with ZIP parameters corresponding to pre- and post-regulation) had the lowest DIC values for leatherbacks (Table 4); we favored M1r because of its simpler model structure (no zero-inflation) and its better fit to the data (M1z underestimated observed takes for pre-2001 years). There was little support for the next best models (M1, M2z, and M2), for which DIC values were 6-10 points higher. Model choice for humpback whales was less clear, owing to limited information in the dataset (only 3 observed takes). Models M2, M2z, M4, and M4z had the lowest DIC values, followed within 1-3 DIC points by M1, M1z

and M1r. We favored M2 (area model) for its simpler structure and because it captured the effect of area suggested by the observer data (all 3 humpback takes occurred outside the closure area).

In most cases, the addition of ZIP parameters did not substantially decrease the DIC value; ZIP models typically had DIC values within 0-2 points of their non-ZIP counterparts (Table 4). One exception was M1z for leatherbacks, which yielded a 6 point improvement over M1. However, the same decrease was achieved by M1r, which separated pre- and post-regulation periods without the addition of ZIP parameters. For most ZIP models, the ZIP parameter estimates were roughly equal across data classifications, suggesting a simpler model could have been specified with a θ parameter that varies and ZIP parameter p that remains constant. We specified and tested such models, but they were not well-supported (i.e., DIC values were too high) and they did not change results. Similarly, we tested models that held θ constant and let p vary across data classifications; again, we observed no improvements.

Based on model M1r for leatherbacks, the estimate of $\beta_0 = -5.6$ (Table 4, posterior mean) corresponds to a pre-regulation bycatch rate of $\theta = e^{\beta_0} = 0.0037$ takes per set. The estimate of $\beta_1 = -2.6$ corresponds to a post-regulation bycatch rate of $\theta = e^{\beta_0 + \beta_1} = 0.0003$, which suggests the per-set bycatch rate was more than ten times higher before the 2001 regulation was implemented. Based on model M2 for humpback whales, $\beta_0 = -7.8$ corresponds to $\theta = 0.0004$ for effort outside the closure area, while $\beta_1 = -800$ corresponds to θ being effectively zero for effort inside the closure area.

Predictions for Leatherback Turtles

Data and predictions for *observed* leatherback takes from model M1r show a distinct drop in takes after 2000 (Figure 3a). The upper limit of the 99% prediction interval (the prediction and credible intervals we describe are one-tailed) had a maximum of 8 takes in pre-regulation years and 2 takes in post-regulation years (Figure 3a). It was higher than the actual number of observed takes for all but one year. The median predictions ranged from 0 to 3 takes per year and appeared to fit the data well.

M1r predictions for total takes, total mortality, and expected annual mortality generally decreased from 1990 to 2000 (Figures 3b, 3c, 5a) -- reflecting a steady decline in fishing effort over that time period (Table 1). The upper limit of the 99% prediction interval during this time ranged annually from 13 to 36 for takes and from 9 to 25 for mortality; the upper limit of the 99% credible interval ranged from 7.4 to 21.6 for expected annual mortality. After 2000, predictions for all three quantities were close to zero. Pre-regulatory ratio estimates (Table 5) were much more volatile than our model-based estimates, ranging from zero in years when no bycatch was observed (even though some may well have occurred) to values considered rather unlikely by our model estimates (e.g., in 1992, 1995) (Figures 3b, 3c).

Based on the predicted mode across 20 years, the most probable cumulative number of leatherback takes in this fishery was 141 ($\bar{x} = 163$; 95% prediction interval [PI] = 104-242), with 88 of those resulting in mortality ($\bar{x} = 94$; 95% PI = 52-153).

Predictions for Humpback Whales

Data and predictions for *observed* humpback whale takes from model M2 remained relatively steady through time (Figure 4a). The upper limit of the 99%

prediction interval had a maximum of 2 takes in both pre- and post-regulation periods. It was higher than the true number of observed takes in all but 1 year (Figure 4a). The median prediction was zero for all years.

M2 predictions for total takes, total mortality, and expected annual mortality decreased slightly from 1990 to 2000 (Figures 4b, 4c, 5c). The upper limit of the 99% prediction interval over this time ranged annually from 4 to 6 for takes and from 2 to 3 for mortality; the upper limit of the 99% credible interval ranged from 1.1 to 2.0 for expected annual mortality. After 2000, predictions for all three quantities were similar but slightly closer to zero. The 3 years with observed takes had positive ratio estimates for takes; all other ratio estimates were zero (Figures 4b, 4c). There are no previously reported ratio estimates for humpback mortality, but (Julian and Beeson 1998) provided an estimate of *total takes* for 1994 (6 takes, CV=0.91).

The most probable cumulative number (the predicted mode) of humpback whale takes in this fishery over 20 years was 17 ($\bar{x} = 21$; 95% PI = 6-50), with 1 of those resulting in mortality ($\bar{x} = 6$; 95% PI = 0-21).

Comparing Expected Annual Mortality to Policy Thresholds

Posterior distributions for m_{future} are shown in Figures 5b and 5d. For leatherback turtles, the probability of m_{future} exceeding 2 deaths per year was 7.0×10^{-4} . For humpback whales, the probability that m_{future} was $\leq 1\%$ of the 2010-2012 PBR level (Category III) was 0.4198; the probability that it was between 1% and 50% of the PBR level (Category II) was 0.5802; the probability that it was $\geq 50\%$ of the PBR level (Category I) was 0. The cutoff threshold between Categories I and II (50% of PBR level, or 5.65 whales per

year) did not overlap with the posterior distribution and is therefore not shown in Figure 5d.

DISCUSSION

Estimating Rare-Event Fisheries Bycatch

When applied to fisheries with rare-event bycatch and low observer coverage, ratio estimators may provide misleading inference, with high levels of sampling variance generating a false appearance of catches ranging from zero in some years to alarmingly high values in others. Fisheries managers have recognized these issues and have sometimes used multi-year averages when assessing fisheries interactions for policy purposes. Pooling observer data from multiple years effectively reduces the volatility (sampling variance) of estimates associated with small numbers of observed takes, but pooling is an *ad hoc* strategy that leaves open questions as to how many of years of information should be pooled under different circumstances and may fail to address stakeholders' perceptions of low or high catches in individual years. The model-based Bayesian approach presented here achieves the same objective of reducing volatility through its formal use of all information contained in the time series, but it carries the added benefits of obviating arbitrary decisions about how many years of data to combine and enabling probabilistic inference for bycatch and mortality within a single year, conditional on the amount and known characteristics of fishing effort.

Modeling Conclusions

The purpose of this paper was to demonstrate a Bayesian model-based approach that uses rare-event bycatch data and minimal supporting detail on fishing effort to estimate bycatch, infer expected annual mortality, and evaluate the probability of

exceeding regulatory thresholds. We explored the importance of relevant covariates to account for broad scale differences in bycatch rates across regulatory regimes and time-area combinations, but causal inference was not our focus. Fully explaining variation in bycatch rates is important, but would require a richer dataset, including for example fishery-independent data on the habitat, range, migration, population structure, status, etc. for bycatch species (Eguchi et al. (in prep.)). In reality, the rare-event nature of bycatch typically limits evaluation of causal factors to simple models, since the associated small number of observed takes is difficult to fit to models with a large number of parameters. Our analysis suggested that the highest levels of leatherback bycatch occurred in years with higher levels of effort, and in years prior to regulatory implementation of the leatherback closure (decreased by an order of magnitude after the closure). For humpbacks whales, area was the strongest effect.

Management and Policy Applications

In our case study analysis of the DGN fishery, we expressed estimates of total bycatch and mortality for leatherbacks and humpbacks as PPDs (Figures 3b, 3c, 4b, 4c), which allowed us to quantify upper limits of the 99% prediction intervals for the estimates. These limits can be interpreted as upper bounds on the number of leatherbacks or humpbacks that are predicted to be incidentally caught or killed in a given year, and managers can declare with 99% certainty that total bycatch or mortality did not exceed that upper bound. It would be straightforward to evaluate other limits as well (e.g., obtain minimum estimates, or upper or lower limits for multi-year sums). We also presented median model predictions, which can be interpreted as point estimates of total bycatch or mortality and compared to ratio estimates (Figures 3b, 3c, 4b, 4c). Median model

predictions fluctuated with annual variations in fishing effort but otherwise varied over a narrower range than ratio estimates. This is due to the assumed model structure (i.e., bycatch rates that vary with regulatory regime or area, but not year) and our use of 20 years of data to estimate model parameters.

While estimates of total bycatch and mortality are important, regulatory reference points are based on limits to annual rates of mortality. The use of posterior distributions allows straightforward assessment of the probability that such limits (for a single year, or for multiple years combined) are exceeded. For humpbacks, we were able to make probability statements with respect to PBR-based thresholds used for MMPA fishery classification (Figure 5d). Using this approach, the DGN fishery might best be classified as a Category II fishery, since this is the most likely scenario given the data. If the model used for inference accurately represents the true data-generating process and parameter estimation is unbiased, the probability that the fishery should actually be classified in the low impact Category III (0.42) can be thought of as the probability of committing a Type I error (falsely inferring that bycatch impact is medium rather than low). Alternatively, if managers chose to classify the fishery as Category III, there would be a 0.58 probability of committing a Type II error (failing to recognize that bycatch impact is medium rather than low). A similar management model could potentially be implemented for sea turtles, though suitable population-relevant reference points for fisheries mortality would be needed to support this approach (Curtis and Moore 2013). This pragmatic approach for classifying fisheries bycatch impact would be novel for sea turtles.

Concluding Remarks

Bayesian model-based methods are well suited to analyze rare-event bycatch data for fisheries with <100% observer coverage. We have shown how inference of expected annual mortality could be used to evaluate the probability that regulatory thresholds are exceeded for a single protected species, providing examples for leatherback sea turtles and humpback whales. Future efforts should focus on generalizing the approach to inform multi-species or multi-fisheries bycatch management strategies. For example, one could use this approach to estimate the probability that bycatch exceeds a policy reference point for multiple species subject to bycatch. Given budgetary constraints for monitoring, approaches such as those employed here could help maximize the benefit of observer data for the protection of vulnerable marine species, while minimizing the cost of observer programs and the regulatory burden placed on fisheries.

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TABLES

Table 1. Summary of fishing effort in the California drift gillnet fishery, 1990-2009. The number of sets is shown for four time-area categories related to the leatherback sea turtle closure implemented in 2001 (O = Outside closure area; I = Inside closure area; N = Nonclosure period before August 15 and after November 15; C = Closure period from August 15 through November 15). Observed and unobserved sets are separated, with the level of observer coverage shown in the rightmost column. The mean observer coverage across all years was 15.6%.

Summary of California Drift Gillnet Fishery Sets, 1990-2009																
Year	Observed					Unobserved					Total					Observed
	O / N	I / N	O / C	I / C	Total	O / N	I / N	O / C	I / C	Total	O / N	I / N	O / C	I / C	Total	
1990	79	15	47	54	195	1405	214	1964	597	4180	1484	229	2011	651	4375	4.5%
1991	214	6	94	163	477	1413	121	1304	1263	4101	1627	127	1398	1426	4578	10.4%
1992	221	41	131	269	662	1204	311	1640	938	4093	1425	352	1771	1207	4755	13.9%
1993	294	74	44	350	762	1692	272	995	1931	4890	1986	346	1039	2281	5652	13.5%
1994	266	4	155	237	662	1218	29	1271	509	3027	1484	33	1426	746	3689	17.9%
1995	189	42	171	185	587	1204	167	1326	634	3331	1393	209	1497	819	3918	15.0%
1996	163	81	85	138	467	935	132	1252	603	2922	1098	213	1337	741	3389	13.8%
1997	249	41	246	212	748	1204	206	818	460	2688	1453	247	1064	672	3436	21.8%
1998	184	19	140	156	499	1187	27	913	333	2460	1371	46	1053	489	2959	16.9%
1999	178	0	302	48	528	584	0	1289	0	1873	762	0	1591	48	2401	22.0%
2000	181	2	223	38	444	643	0	779	87	1509	824	2	1002	125	1953	22.7%
2001	122	0	196	5	323	536	1	818	0	1355	658	1	1014	5	1678	19.2%
2002	165	4	204	0	373	605	0	695	0	1300	770	4	899	0	1673	22.3%
2003	119	0	176	0	295	523	10	605	0	1138	642	10	781	0	1433	20.6%
2004	124	0	82	0	206	402	0	414	0	816	526	0	496	0	1022	20.2%
2005	112	23	93	0	228	438	20	389	0	847	550	43	482	0	1075	21.2%
2006	130	14	139	1	284	630	1	438	0	1069	760	15	577	1	1353	21.0%
2007	63	0	95	0	158	320	9	511	0	840	383	9	606	0	998	15.8%
2008	53	4	89	0	146	448	0	466	0	914	501	4	555	0	1060	13.8%
2009	42	4	62	0	108	388	0	336	0	724	430	4	398	0	832	13.0%
Total	3,148	374	2,774	1,856	8,152	16,979	1,520	18,223	7,355	44,077	20,127	1,894	20,997	9,211	52,229	15.6%

Table 2. Summary of observed takes of leatherback sea turtles (DC) and humpback whales (MN) in the California drift gillnet fishery, 1990-2009. Time-area categories related to the leatherback sea turtle closure implemented in 2001 are shown (see Table 1 for definitions).

Summary of Observed Takes, 1990-2009				
Take #	Species	Year	Condition	Area / Time
1	DC	1990	Dead	I, C
2	DC	1991	Alive	I, C
3	DC	1992	Alive	I, C
4	DC	1992	Alive	I, C
5	DC	1992	Dead	I, C
6	DC	1992	Dead	I, C
7	DC	1992	Dead	O, N
8	DC	1993	Dead	I, C
9	DC	1993	Unknown	I, C
10	DC	1994	Alive	I, C
11	DC	1995	Alive	I, C
12	DC	1995	Dead	I, C
13	DC	1995	Dead	I, C
14	DC	1995	Dead	I, C
15	DC	1995	Dead	O, C
16	DC	1996	Dead	I, N
17	DC	1996	Dead	I, C
18	DC	1997	Dead	I, C
19	DC	1997	Dead	I, C
20	DC	1997	Alive	I, C
21	DC	1997	Alive	I, C
22	DC	1999	Alive	O, N
23	DC	1999	Alive	O, C
24	DC	2009	Alive	O, C
1	MN	1994	Alive	O, C
2	MN	1999	Alive	O, N
3	MN	2004	Alive	O, C

Table 3. Summary of models. In all models, x_i , the number of observed takes in year i , is modeled with a Poisson likelihood characterized by θ , the per-set take rate parameter, and n_i , the number of observed sets in year i . Fishing effort variables include r (2001 regulation), a (closure area), and t (closure time). Zero-inflated Poisson models (ZIP) include parameter p , indicating the proportion of sets subject to bycatch risk. Prior distributions are specified with large variances to make them flat and relatively noninformative.

Model Descriptions				
Model, Data Classifications	Likelihood	λ	θ	Prior Distributions
M1: simple all data in one group	$x_i \sim \text{Poiiss}(\lambda_i)$	$\lambda_i = \theta n_i$	θ	$\theta \sim \text{Gamma}(0, 100)$
M1z: simple, ZIP $r = 0$: pre-regulation years (1990-2000) $r = 1$: post-regulation years (2001-2009)	$x_i \sim \text{Poiiss}(\lambda_i)$	$\lambda_i = p_r \theta n_i$	θ	$\theta \sim \text{Gamma}(0, 100)$ $p_r \sim \text{Beta}(1, 1)$
M1r: regulation $r = 0$: pre-regulation years (1990-2000) $r = 1$: post-regulation years (2001-2009)	$x_i \sim \text{Poiiss}(\lambda_i)$	$\lambda_i = \theta_r n_i$	$\log(\theta_r) = \beta_0 + \beta_1 r_i$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 1$
M2: area $a = 0$: outside closure area $a = 1$: inside closure area	$x_{i,a} \sim \text{Poiiss}(\lambda_{i,a})$	$\lambda_{i,a} = \theta_a n_{i,a}$	$\log(\theta_a) = \beta_0 + \beta_1 a$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 1$
M2z: area, ZIP $a = 0$: outside closure area $a = 1$: inside closure area	$x_{i,a} \sim \text{Poiiss}(\lambda_{i,a})$	$\lambda_{i,a} = p_a \theta_a n_{i,a}$	$\log(\theta_a) = \beta_0 + \beta_1 a$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 1$ $p_a \sim \text{Beta}(1, 1)$
M3: time $t = 0$: outside closure months $t = 1$: inside closure months	$x_{i,t} \sim \text{Poiiss}(\lambda_{i,t})$	$\lambda_{i,t} = \theta_t n_{i,t}$	$\log(\theta_t) = \beta_0 + \beta_2 t$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 2$
M3z: time, ZIP $t = 0$: outside closure months $t = 1$: inside closure months	$x_{i,t} \sim \text{Poiiss}(\lambda_{i,t})$	$\lambda_{i,t} = p_t \theta_t n_{i,t}$	$\log(\theta_t) = \beta_0 + \beta_2 t$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 2$ $p_t \sim \text{Beta}(1, 1)$
M4: interaction $at = 0$: not within closure area OR months $at = 1$: inside both closure area AND months	$x_{i,at} \sim \text{Poiiss}(\lambda_{i,at})$	$\lambda_{i,at} = \theta_{at} n_{i,at}$	$\log(\theta_{at}) = \beta_0 + \beta_3 at$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 3$
M4z: interaction, ZIP $at = 0$: not within closure area OR months	$x_{i,at} \sim \text{Poiiss}(\lambda_{i,at})$	$\lambda_{i,at} = p_{at} \theta_{at} n_{i,at}$	$\log(\theta_{at}) = \beta_0 + \beta_3 at$	$\beta_j \sim \text{Norm}(0, 1000)$ $j = 0, 3$

Table 3. Summary of models. Continued.

Model Descriptions				
Model, Data Classifications	Likelihood	λ	θ	Prior Distributions
$at = 1$: inside both closure area AND months M5: all $(a, t) = (0, 0)$: not within closure area OR months $(a, t) = (1, 0)$: inside closure area; outside closure months $(a, t) = (0, 1)$: outside closure area; inside closure months $(a, t) = (1, 1)$: inside both closure area AND months	$x_{i,a,t} \sim Poiss(\lambda_{i,a,t})$	$\lambda_{i,a,t} = \theta_{a,t} n_{i,a,t}$	$log(\theta_{a,t}) = \beta_0 + \beta_1 a + \beta_2 t + \beta_3 at$	$p_{ad} \sim Beta(1, 1)$ $\beta_j \sim Norm(0, 1000)$ $j = 0, 1, 2, 3$
M5z: all, ZIP $(a, t) = (0, 0)$: not within closure area OR months $(a, t) = (1, 0)$: inside closure area; outside closure months $(a, t) = (0, 1)$: outside closure area; inside closure months $(a, t) = (1, 1)$: inside both closure area AND months	$x_{i,a,t} \sim Poiss(\lambda_{i,a,t})$	$\lambda_{i,a,t} = p_{a,t} \theta_{a,t} n_{i,a,t}$	$log(\theta_{a,t}) = \beta_0 + \beta_1 a + \beta_2 t + \beta_3 at$	$\beta_j \sim Norm(0, 1000)$ $j = 0, 1, 2, 3$ $p_{a,t} \sim Beta(1, 1)$

Table 4. Posterior parameter estimates and Deviance Information Criterion (DIC) of candidate bycatch models for leatherback turtles and humpback whales. θ is the mean per-set bycatch rate across all fishing sets in the dataset. For model M5z, $p_0 = p_{0,0}$ (see Table 3), $p_1 = p_{1,0}$, $p_2 = p_{0,1}$, $p_3 = p_{1,1}$.

Model	Posterior Parameter Estimates and Model Comparison															
	β_0		β_1		β_2		β_3		p_0		p_1		p_2		p_3	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
Leatherback Sea Turtles																
M1: simple	-5.6E+00	2.1E-01	-2.6E+00	1.3E+00					7.3E-01	2.0E-01	2.0E-01	1.6E-01			2.9E-03	5.9E-04
M1r: regulation	-7.2E+00	4.7E-01	2.4E+00	5.3E-01											2.9E-03	5.9E-04
M2: area	-6.2E+00	1.1E+00	2.4E+00	1.5E+00											3.0E-03	6.1E-04
M2x: area, ZIP	-7.2E+00	6.3E-01			1.8E+00	6.6E-01			5.1E-01	2.9E-01	5.0E-01	2.9E-01			2.9E-03	6.0E-04
M3: time	-6.2E+00	1.2E+00			1.8E+00	1.5E+00									3.0E-03	6.1E-04
M3x: time, ZIP	-7.0E+00	4.3E-01							5.0E-01	2.9E-01	5.0E-01	2.9E-01			2.9E-03	5.9E-04
M4: intxn	-6.1E+00	1.1E+00					2.4E+00	4.9E-01	5.1E-01	2.9E-01	5.0E-01	2.9E-01			3.0E-03	6.0E-04
M4x: intxn, ZIP	-7.7E+00	8.3E-01	1.2E+00	1.5E+00	6.7E-01	1.1E+00	2.4E+00	1.5E+00	5.1E-01	2.9E-01	5.0E-01	2.9E-01			3.0E-03	6.1E-04
M5: all	-6.7E+00	1.3E+00	1.2E+00	2.1E+00	7.4E-01	1.9E+00	1.1E+00	1.6E+00	5.1E-01	2.9E-01	4.9E-01	2.9E-01	4.9E-01	2.9E-01	2.9E-03	6.0E-04
M5x: all, ZIP	-6.7E+00	1.3E+00	1.2E+00	2.1E+00	7.4E-01	1.9E+00	1.0E+00	2.7E+00	5.1E-01	2.9E-01	4.9E-01	2.9E-01	4.9E-01	2.9E-01	2.9E-03	6.0E-04
Humpback Whales																
M1: simple	-8.3E+00	8.0E-01	4.2E-02	1.5E+00					5.3E-01	2.6E-01	5.6E-01	2.6E-01			3.7E-04	2.1E-04
M1r: regulation	-7.8E+00	6.3E-01	-8.0E+02	6.0E+02											3.6E-04	2.0E-04
M2: area	-6.8E+00	1.2E+00	-7.9E+02	6.0E+02											3.7E-04	2.2E-04
M2x: area, ZIP	-8.7E+00	1.3E+00							5.0E-01	2.9E-01	5.0E-01	2.9E-01			3.7E-04	2.2E-04
M3: time	-7.8E+00	1.7E+00			7.2E-01	1.5E+00									3.7E-04	2.1E-04
M3x: time, ZIP	-7.8E+00	6.3E-01			7.4E-01	2.1E+00			5.0E-01	2.9E-01	5.0E-01	2.9E-01			3.7E-04	2.2E-04
M4: intxn	-6.8E+00	1.2E+00					-8.0E+02	6.0E+02	5.0E-01	2.9E-01	5.0E-01	2.9E-01			3.7E-04	2.2E-04
M4x: intxn, ZIP	-8.6E+00	1.3E+00	-9.1E+02	6.3E+02	1.1E+00	1.5E+00	-8.0E+02	8.0E+02	5.0E-01	2.9E-01	5.0E-01	2.9E-01			3.7E-04	2.1E-04
M5: all	-7.7E+00	1.6E+00	-9.1E+02	6.3E+02	1.2E+00	2.1E+00	-3.8E+02	8.0E+02	5.0E-01	2.9E-01	5.0E-01	2.9E-01	5.0E-01	2.9E-01	3.7E-04	2.1E-04
M5x: all, ZIP	-7.7E+00	1.6E+00	-9.1E+02	6.3E+02	1.2E+00	2.1E+00	-3.8E+02	8.0E+02	5.0E-01	2.9E-01	5.0E-01	2.9E-01	5.0E-01	2.9E-01	3.7E-04	2.1E-04

Table 5. Ratio estimates calculated for total takes and mortality of leatherback turtles (also see Figures 3b and 3c), along with previously published (indicated by *) ratio estimates and coefficients of variation (Julian and Beeson 1998, Carretta et al. 2004). For 1996-1997, there were no ratio estimates published for total bycatch, only total mortality. For 1998-2002, there was no observed mortality and thus no estimate reported. Differences between our ratio estimates and those previously published are attributed to subtle differences in the estimates of total fishing effort. For years in which all observed takes resulted in mortality, the ratio estimates for total takes and total mortality are equal.

Summary of Ratio Estimates						
Year	Total Takes			Total Mortality		
	Ratio Estimate	Ratio Estimate*	CV*	Ratio Estimate	Ratio Estimate*	CV*
1990	22	23	0.97	22	23	0.97
1991	10	10	0.94	0	0	-
1992	36	29	0.46	22	15	0.65
1993	15	22	0.53	15	15	0.66
1994	6	6	0.91	0	0	-
1995	33	32	0.47	27	26	0.55
1996	15	-	-	15	25	0.63
1997	18	-	-	9	8	0.85
1998	0	-	-	0	-	-
1999	9	-	-	0	-	-
2000	0	-	-	0	-	-
2001	0	-	-	0	-	-
2002	0	-	-	0	-	-

FIGURES

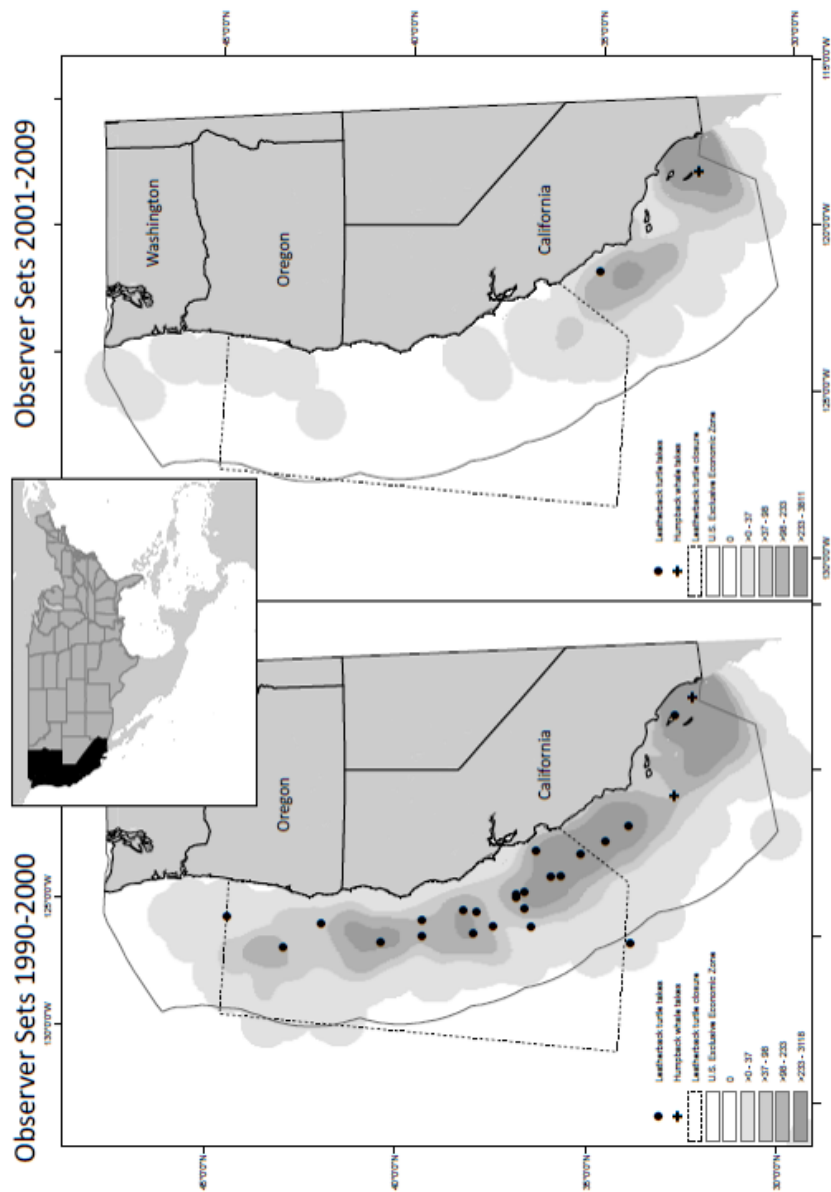


Figure 1. Maps of the California drift gillnet fishery before (1990-2000) and after (2001-2009) a time-area closure was implemented in 2001 to protect leatherback sea turtles (enclosed by the dashed line, effective August 15 - November 15 annually). Kernel density shading shows the average number of observed sets per 100 square nautical miles per year. Bycatch locations for leatherback sea turtles and humpback whales are indicated by dots and plus signs, respectively. Areas with higher concentrations of fishing effort have higher bycatch.

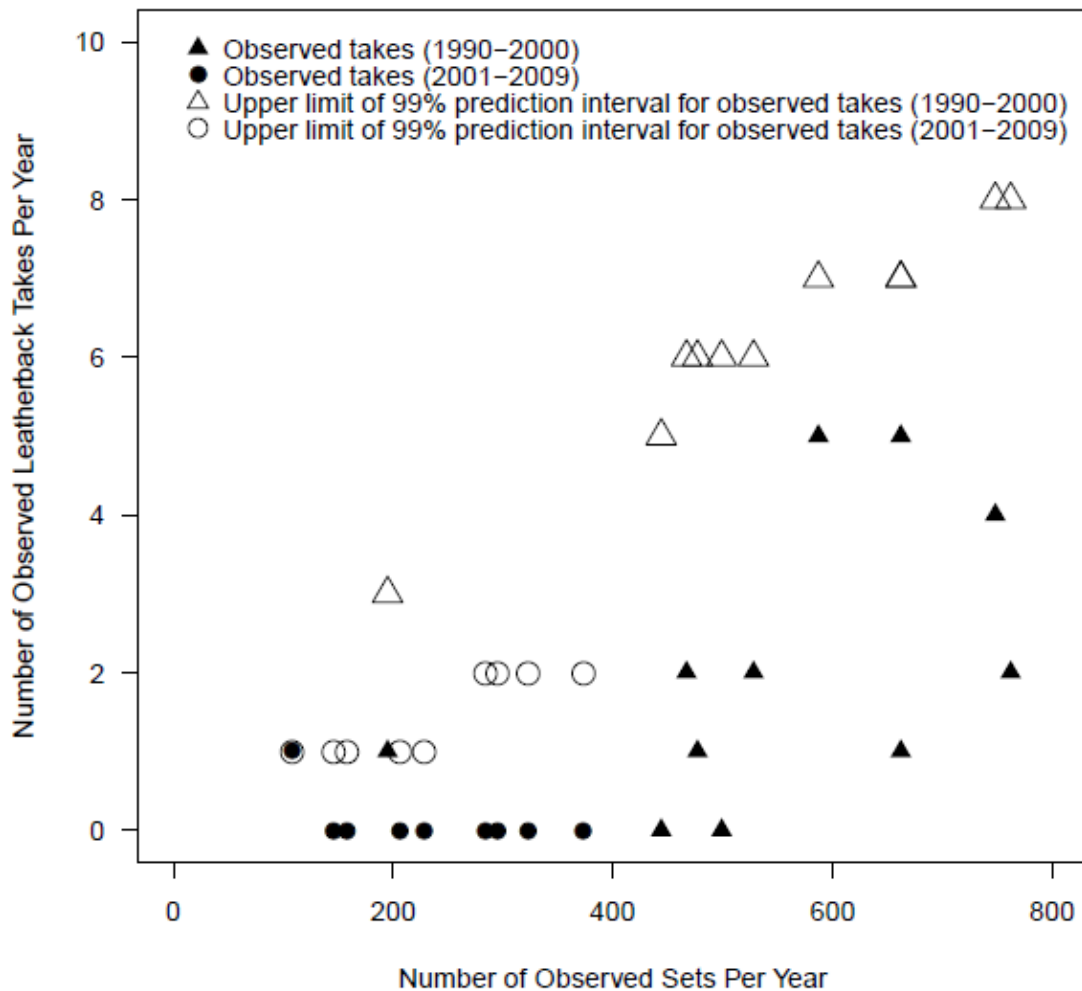


Figure 2. Scatterplot showing the relationship between the numbers of observed sets and leatherback sea turtle takes per year (Pearson's $r=0.672$; $p=0.001$). Observer data are indicated by closed symbols and model predictions by open symbols, with triangles and circles for pre- and post-2001 regulation time periods, respectively. Upper limits of the 99% prediction intervals were produced by model M1r (see Methods). Predictions were made for observed data only as a means of checking the model.

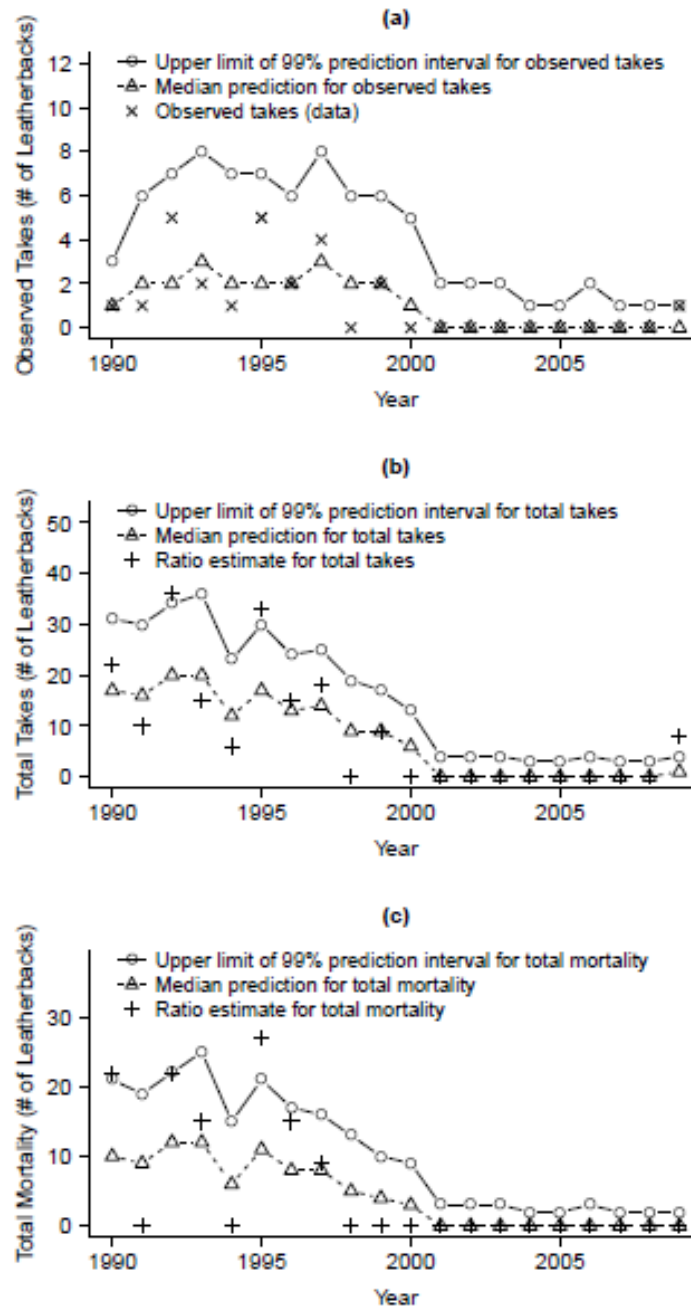


Figure 3. Model M1r predictions for the number of leatherback sea turtle takes in (a) the observed portion of fishing for each year, and (b) total fishing effort for each year. The upper limits of the 99% prediction intervals are indicated with circles and solid lines, the median predictions with triangles and dashed lines. The actual number of observed takes for each year is shown in (a), and ratio estimates are shown for comparison in (b). Model predictions and ratio estimates for total mortality are shown in (c).

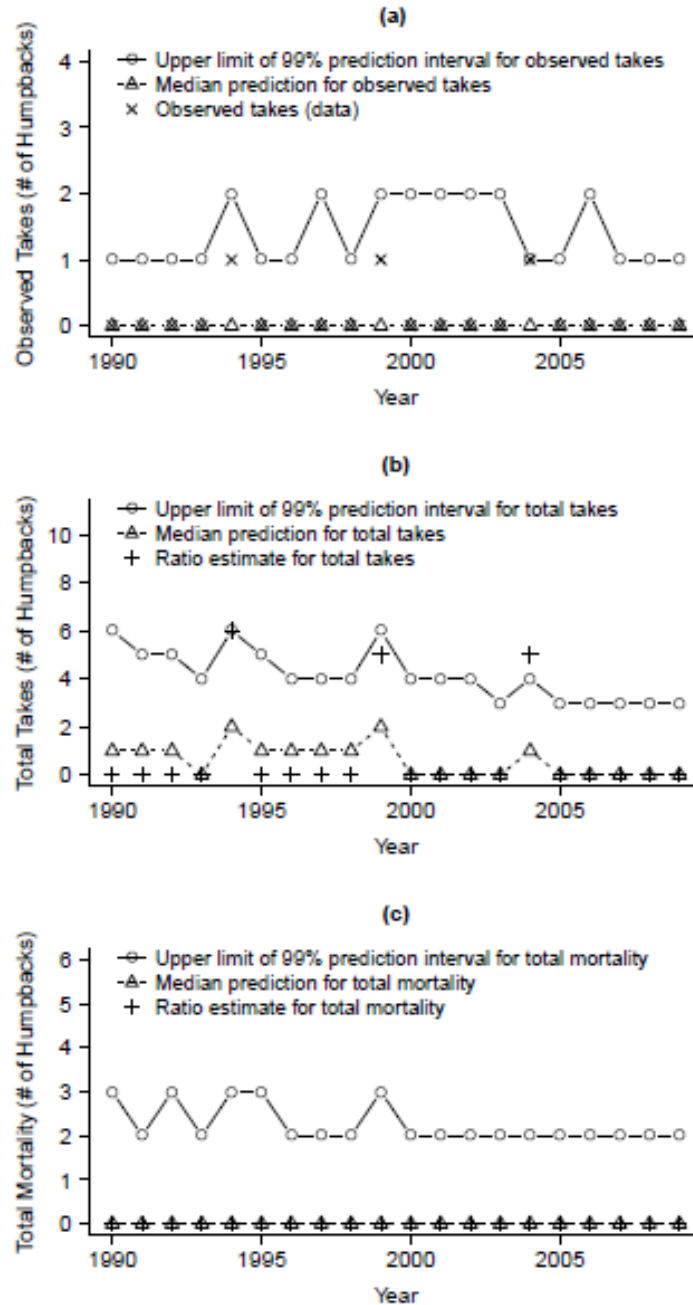


Figure 4. Model M2 predictions for the number of humpback whale takes in (a) the observed portion of fishing for each year, and (b) total fishing effort for each year. The upper limits of the 99% prediction intervals are indicated with circles and solid lines, the median predictions with triangles and dashed lines. The actual number of observed takes for each year is shown in (a), and ratio estimates are shown for comparison in (b). Model predictions and ratio estimates for total mortality are shown in (c).

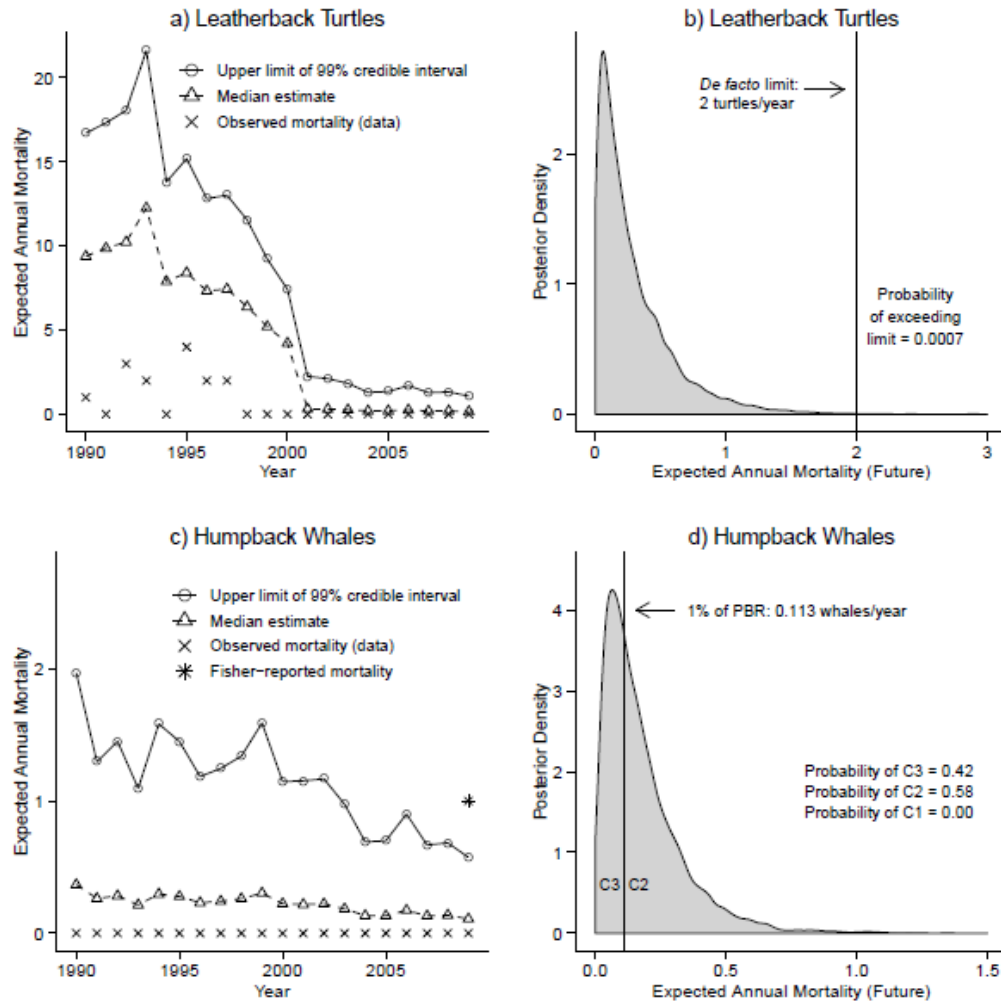


Figure 5. Model predictions for expected annual mortality (m_i , where i is year) for leatherback sea turtles (a; model M1r) and humpback whales (c; model M2). Observed and fisher-reported mortality are shown in (a) and (c) as benchmarks (note: observed data only represent 15.6% of fishing effort on average). In (b) and (d), expected annual mortality (m_{future}) is based on fishing effort for a hypothetical future year (1064 sets, the 2005-2009 average). In (d), a cutoff of 1% of the Potential Biological Removal (PBR) policy threshold for this population of humpback whales (0.113 whales per year) represents a decision point for classification of the fishery into either Category III (mortality \leq 1% of PBR) or Category II (1% of PBR < mortality < 50% of PBR). The *de facto* limit based on NMFS-authorized incidental mortality of leatherbacks is shown in (b).

APPENDIX A

Theoretical Basis for Estimating Rare-Event Bycatch Using a Bayesian Approach

For a single species (e.g., leatherbacks), we used a Poisson likelihood function to model the stochastic dependence of x_i , the number of observed takes in year i , on θ , the per-set take rate parameter, and n_i , the number of observed sets in year i :

$$f(x_i|\theta, n_i) = e^{-\theta n_i} \frac{(\theta n_i)^{x_i}}{x_i!}, \quad (\text{A.1})$$

where $\theta n_i = \lambda_i$ is the Poisson rate (mean) parameter. Previous studies have also used the Poisson distribution to model bycatch (NMFS 2004, Pradhan and Leung 2006, Gardner et al. 2008, Murray 2009, 2011) because it can characterize data in which each observation has a high probability for a zero count, a small probability for a count of one, and an infinitesimal probability for a count of two or more. The DGN fishery data have these Poisson characteristics plus one more: a mean per-set take rate (2.944×10^{-3}) roughly equal to the variance (2.936×10^{-3}). A strong positive correlation between the numbers of observed takes and sets per year (Pearson's $r = 0.672$; $p = 0.001$; Figures 1 and 2) supports including the number of sets in the model. We assume statistical independence of all sets and takes.

We used a conjugate gamma prior distribution for θ :

$$p(\theta) \propto e^{-\beta\theta} \theta^{\alpha-1}, \quad (\text{A.2})$$

which constrains θ to be positive. After applying Bayes' rule, the posterior density,

$$p(\theta|n_i, x_i) \propto f(x_i|\theta, n_i)p(\theta) \quad (\text{A.3})$$

$$\propto e^{-(\beta+n_i)\theta} \theta^{\alpha+x_i-1}, \quad (\text{A.4})$$

is also a gamma distribution, $\text{Gamma}(\alpha+x_i, \beta+n_i)$, with a form that suggests interpreting α and β as the prior numbers of observed takes and sets from previous years, respectively, before observing the current year's sample of x_i takes in n_i sets.

Following this interpretation, a noninformative prior could be specified by assigning $\alpha = 0$ and $\beta = 0$, yielding

$$p(\theta) = \theta^{-1}, 0 < \theta < \infty, \quad (\text{A.5})$$

which is diffuse and improper (does not integrate over the support). This prior reflects ignorance about θ before observing the data, and places the greatest weight on values near zero. The resulting posterior,

$$p(\theta|n_i, x_i) \propto e^{-\theta n_i} \theta^{x_i-1}, \quad (\text{A.6})$$

bears formal similarity to the likelihood function, but now summarizes reasonable beliefs about θ in light of the current observation of x_i . The posterior mean, $\mu_{\theta} = \frac{x_i}{n_i}$, and variance, $\sigma_{\theta}^2 = \frac{x_i}{n_i^2}$, are formally identical to the maximum likelihood estimator and variance of the maximum likelihood estimator of θ in the classical Poisson model, but are subject to a different interpretation under the Bayesian paradigm.

To specify an informative prior, we could assign $\alpha = x_p$ and $\beta = n_p$, where x_p and n_p are the respective numbers of observed takes and sets in all previous years p :

$$p(\theta) \propto e^{-\theta n_p} \theta^{x_p-1}. \quad (\text{A.7})$$

The corresponding posterior,

$$p(\theta|n_i, x_i) \propto e^{-\theta(n_p+n_i)} \theta^{x_p+x_i-1}, \quad (\text{A.8})$$

has a mean $\mu_{\theta} = \frac{x_p+x_i}{n_p+n_i}$ and variance $\sigma_{\theta}^2 = \frac{x_p+x_i}{(n_p+n_i)^2}$.

The posterior predictive distribution (PPD) for the number of unobserved takes, $y_i - x_i$, is derived from the Poisson likelihood function and the posterior for θ :

$$p(y_i - x_i | N_i, n_i, x_i) = \int_{\theta} p(y_i - x_i | \theta, N_i - n_i) p(\theta | n_i, x_i) d\theta, \quad (\text{A.9})$$

where y_i and N_i are the total (observed + unobserved) numbers of takes and sets in year i , respectively. This is a negative binomial distribution, $Negbin(\alpha + y_i - x_i, \frac{\beta + n_i}{N_i - n_i})$, where α and β are again the numbers of observed takes and sets from all previous years (Gelman et al. 2004). This PPD reflects posterior uncertainty in θ and in unobserved experience. Adding x_i produces a PPD for y_i . Whereas a posterior distribution supports inference about a parameter in the likelihood function (in our case, θ , a bycatch rate), a posterior *predictive* distribution supports predictive statements about the output of the likelihood function (in our case, $y_i - x_i$, the unobserved bycatch count). A PPD may be specified for any amount of fishing effort based on past numbers of observed sets and takes, regardless of whether the effort occurred in the past or has yet to occur in the future. This assumes that the same probability model holds under different years and conditions, which seems reasonable given that the distribution of these rare-event takes over 20 years appears to follow a Poisson distribution. The PPD can be used to produce range or point estimates of bycatch for the specified level of effort.

To model the number of observed deaths, w_i , we specify a binomial likelihood function which quantifies the stochastic dependence of w_i on x_i and a conditional mortality parameter, q (i.e., given a take of this species occurs, the probability that the animal dies):

$$f(w_i|x_i, q_s) = \frac{x_i!}{w_i!(x_i-w_i)!} q^{w_i} (1-q)^{x_i-w_i}. \quad (\text{A.10})$$

A noninformative, conjugate prior of $Beta(1,1)$ for q results in a posterior distribution of the form $Beta(1+w_p, 1+x_p-w_p)$ (Chapter 2 in (Gelman et al. 2004)). Over 20 years, $w_p = 14$ deaths and $x_p = 24$ takes for leatherbacks, and $w_p = 1$ death and $x_p = 4$ takes for humpbacks (the fisher-reported mortality is conservatively treated as a take for purposes of estimating the conditional mortality rate for humpbacks). Throughout our analyses, we use the posteriors $Beta(15, 11)$ for leatherbacks and $Beta(2, 4)$ for humpbacks.

The PPD for the number of unobserved deaths, $z_i - w_i$, can be constructed using $Binomial(PPD \text{ for } y_i - x_i, q)$. Adding w_i to this distribution produces a PPD for z_i , the total number of deaths for that species in year i .

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CONCLUSION

The goal of this dissertation was to apply theoretical concepts (ecosystem services, indicators, and trade-offs) of ecosystem-based management (EBM) to oceanic ecosystems. These ecosystems are incredibly important for supporting people around the world, and they need more holistic management if we expect them to provide services for a growing global population. The work accomplished in this dissertation has provided new insights related to ecosystem services, indicators, and trade-offs. All of these are important to the EBM goals of implementing management strategies that incorporate the needs of humans, manage anthropogenic influences, and are adaptive over time with continued scientific input. The findings show promise for EBM in oceanic ecosystems, and particularly for the eastern tropical Pacific (ETP).

This research has laid the foundation for several future studies that will continue to push EBM forward in the oceanic commons. Related to ecosystem services in the ETP, the importance of sport fishing (mostly for billfishes and tunas) to local economies should be further studied. There were only a few recent reports available on the economic impacts of this activity in a few of the major Latin American locations known for attracting anglers. The estimated value for the three major locations combined was \$1.2 billion per year, which was almost half of our estimated value for the commercial fishery. There is a perception among anglers that commercial fishing negatively impacts their experience, and this would be an interesting idea to test. This is part of a broader question – how does the use of one ecosystem service (e.g., commercial fisheries) impact the availability of another (e.g., recreational fishing)? A starting point might be to determine the degree of overlap in the fished populations. Similarly, a rich but complex area of

research would be to investigate how each unit of fishing impacts biodiversity and carbon storage in the ocean. With respect to the value of biodiversity in the ETP, it would be interesting and important to study both the existence value of cetaceans, seabirds, and marine turtles through surveys (e.g., contingent valuation surveys), and also the direct use value through surveys of eco-tourists throughout the region. The reason for doing this type of research would be to better understand the users and stakeholders of the ETP, other than commercial fisheries. Ideally, all of the stakeholders would be involved in setting overarching goals for the region.

The research on indicators in this dissertation demonstrated that tuna fishery metrics can be used to predict cetacean densities in the ETP. This was an exciting result in itself, and it also gives us confidence that we can apply the approach to seabirds and larval fishes, for which we have similar long-term datasets. The ability to predict densities of these three taxa using fishery metrics in future years would facilitate monitoring of upper trophic levels, which would be a powerful tool for EBM.

The chapter on informing protected species bycatch management is currently in press with *Ecological Applications*. There is potential to apply the approach to other species and fisheries, and the general methods are applicable to other natural resource problems.

This research has relied upon the use of long-term datasets that have been maintained over decades. These datasets are invaluable and will continue to be instrumental in understanding linkages among species, oceanographic habitats, and human activities as we examine them with new perspectives that are relevant to EBM for the oceans.