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**The Predator's Dilemma:
Investigating the responses of seabirds to changes in the
abundance and distribution of small pelagic prey**

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Abstract

The Predator's Dilemma: Investigating the responses of seabirds to changes in the abundance and distribution of small pelagic prey

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Understanding relationships between predators and their prey is a central question in ecology and ecosystem management. For seabirds, relationships between food availability and breeding success and survival are typically non-linear. Reduced food availability has been identified as a potential threat to seabirds and other central place foragers (CPFs), especially in regions where large commercial fisheries target forage fish. For CPFs, food availability can be defined in terms of abundance, accessibility, concentration, and distance from the colony. The design of effective conservation responses depends on understanding the effects of changes in food availability on foraging success. The goal of this research was to strengthen understanding of the effects of changes in various aspects of prey availability on the foraging success of seabirds and other CPFs. A spatially-explicit individual-based foraging model (IBFM) was developed, guided by the foraging ecology of two seabird species, the Peruvian Booby (*Sula variegata*) and Guanay Cormorant (*Phalacrocorax bougainvillii*). The prey field in the IBFM was derived from geostatistical simulations of the distribution of Peruvian anchoveta (*Engraulis ringens*) based on acoustic survey data representing contrasting foraging conditions. Seabird tracking data were partitioned into different movement modes to guide simulation of movement processes. Decision rules in the IBFM were informed by analysis of foraging site selection by Peruvian Boobies and Guanay Cormorants in terms of the abundance and depth distribution of their prey. The effects of different assumptions about search strategies used by seabirds to locate

ephemeral prey patches were explored in the IBFM. The IBFM was then used to investigate the effects of changes in the abundance and distribution of prey on the foraging success of Peruvian Boobies and Guanay Cormorants. The results highlight the importance of the depth distribution of prey for surface-foraging seabirds, and provide insights into differences in the vulnerabilities of the two seabird species to changes in the abundance and distribution of their prey. More broadly, the results have implications for the potential effectiveness of marine protected areas and other fisheries management strategies in safeguarding the foraging success of CPFs in the context of environmental variability that affects the distribution of prey.

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List of Abbreviations

AIC	Akaike's information criterion
AICc	Akaike's Information Criterion corrected for small samples
ARS	area-restricted search
CCW	cold coastal waters
Chl <i>a</i>	chlorophyll <i>a</i>
CPF	central place forager
CPUE	catch per unit effort
ENSO	El Niño Southern Oscillation
ESDU	elementary sampling distance unit
GPS	global positioning system
GRT	gross registered tonnage
HCS	Humboldt Current system
HMM	hidden Markov model
IBFM	individual-based foraging model
IMARPE	Instituto del Mar de Perú
MCMC	Monte Carlo Markov chain
MPA	marine protected area
MVT	marginal value theorem
NASC	nautical area scattering coefficient
REML	restricted maximum likelihood
R/V	research vessel
SST	sea surface temperature
TDR	time depth recorder
dbar	decibar
g	gram
kHz	kilohertz
m	meters
nm	nautical mile
sec	seconds
t	metric ton

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Dedication

To my father, Henry Marlow Boyd

“... for dappled things — ...

For rose-moles all in stipple upon trout that swim;

Fresh-firecoal chestnut-falls; finches' wings ...”

(Excerpted from “Pied Beauty” by Gerard Manley Hopkins (1877))

Introduction

Background

Understanding relationships between predators and the abundance and distribution of their prey is a central question in theoretical and conservation ecology, and for ecosystem approaches to natural resources management. Holling (1959) argued that the relationship between prey densities and prey consumption per predator should be non-linear, and stimulated research on the mechanisms that underpin these relationships. For seabirds, Cairns (1987) hypothesized that the non-linear relationships between prey availability and response indicators such as breeding success and adult survivorship would be sensitive over different ranges of food availability, and that species would respond differently, depending on their ability to adjust foraging behavior within time constraints. Cury et al. (2011) analyzed the relationship between prey abundance in seven ecosystems and breeding success in 14 species of seabird, and found a similar asymptotic relationship for all species. In contrast to Cairns' (1987) hypothesis, Cury et al. (2011) also found similar scaling for all species, with the threshold at which breeding success began to decline from the asymptote falling close to the long-term mean of prey abundance. Based on these results, Cury et al. (2011) recommended that ecosystem approaches to fisheries management maintain forage fish biomass greater than one third of the maximum long-term biomass to ensure the sustainability of predator-prey interactions.

Seabirds exploit variable resources in dynamic ecosystems, and have therefore evolved foraging and life history strategies to cope with this variability (Lack 1968, Ricklefs 1990, Weimerskirch 2002, Furness 2007, Weimerskirch 2007). The generality of the relationship between prey abundance and seabird breeding success suggests that it is derived from functional responses and life history trade-offs characteristic of seabirds (Cury et al. 2011).

Seabirds and other central place foragers (CPFs), such as pinnipeds, return to a specific location between foraging trips. These spatial constraints imply that CPFs are especially vulnerable to localized depletion or broad-scale shifts in the distribution of food resources. Colony-based empirical studies have shown that, over some ranges in prey availability, seabirds are able to mitigate the relationship between prey availability and reproductive success through variation in foraging effort (Piatt et al. 2007). For example, parent birds may increase time spent away from the colony on foraging trips in response to reduced food availability, thus buffering breeding success through 'compensatory strategies' (e.g. Kitaysky et al. 2000). However, at lower ranges of food availability, adults are no longer able to compensate, and adopt 'fixed

foraging effort strategies', in which time away from the colony remains relatively constant despite reduced food availability, leading to reduced breeding success (e.g. Croll et al. 2006). As proposed by Cairns (1987), the threshold between compensatory and fixed strategies may differ among species (and among populations of the same species), and is generally assumed to reflect trade-offs between breeding success and adult survival within overall time or energetic constraints (Croxall et al. 1999).

Seabirds are often operating close to time and energy constraints during the breeding season (Ashmole 1963). Failure to increase foraging effort in response to reduced prey availability may indicate that birds are operating close to time or energy constraints (e.g. Masman et al. 1989). For all CPFs, there is likely to be an upper constraint beyond which individuals cannot increase foraging effort any further. Within these constraints, breeding adults also need to balance investment in reproduction with investment in their own survival (Burke and Montevecchi 2009). Seabirds are long-lived with maximum life spans of 12 to 60 years depending on species (Schreiber and Burger 2002). When foraging conditions are poor, adults may abandon breeding efforts to avoid jeopardizing their own survival and still have good lifetime reproductive success. Thus, long-lived species, such as seabirds, generally favor survival of adults over that of their dependent offspring in a given year (Stearns 1992). Indicators of breeding success and adult survival are therefore expected to be sensitive over different ranges of prey availability (Cairns 1987). The ability of adults to adjust their foraging effort in response to variation in foraging conditions may be critical to breeding success and ultimately population persistence (Ashmole 1963). The implication of this type of life-history strategy is that population growth rates are highly sensitive to changes in adult mortality (Russell 1999).

Many seabird species are at risk of extinction (IUCN 2011). Seabirds face a wide range of threats, including habitat modification and invasive species at breeding sites, over-harvesting, incidental mortality in fisheries and competition with fisheries, pollution, disease, and climate change (Schreiber and Burger 2002, Grémillet and Boulinier 2009). Threats to seabirds, especially incidental mortality in fisheries, are increasing at faster rates than for any other group of birds (BirdLife International 2004, Butchart et al. 2004).

Reduced food availability due to competition with fisheries has also been identified as a major threat to a number of globally threatened or near-threatened seabird species, especially in regions where large commercial fisheries target forage fish that are also important for seabirds (Duffy et al. 1984, Becker and Beissinger 2006, Crawford et al. 2006). There are also growing concerns about the potential impacts of climate change on food availability (Croxall et al. 2002,

Schreiber and Burger 2002, Furness 2007). There has been long-standing debate about whether seabird populations are regulated in a density-dependent manner through competition for food (see Birkhead and Furness 1984 for an overview). Lack (1954, 1966) argued that bird populations were regulated through competition for food, mostly outside the breeding season, but this is difficult to demonstrate for seabirds. Ashmole (1963) suggested that seabirds in the tropics, and possibly higher latitudes, may be limited by food during the breeding season. Birt et al. (1987) found evidence of prey depletion around colonies of Double-crested Cormorants (*Phalacrocorax auritus*), which feed on relatively sedentary benthic fish (see also Elliott et al. 2009). Lewis et al. (2001) found that mean foraging trip durations were positively correlated with colony size, and that the per capita population growth rates of Northern Gannets (*Morus bassanus*) in Britain and Ireland declined with increasing population size.

Overall, there is little evidence of stability in seabird populations, and much evidence of large-scale changes in numbers (Birkhead and Furness 1984). Exogenous changes in food availability are probably an important factor impacting seabird populations (Birkhead and Furness 1984, Croxall and Rothery 1991). Jahncke et al. (2004) successfully predicted the growth in populations of guano-producing seabirds in the northern Humboldt Current system from 1925 to 1955 as a function of increasing primary productivity and hence biomass of small pelagic forage fish. Large-scale changes in the population sizes of several species are correlated with climate variability (Birkhead and Furness 1984). There is evidence of severe declines in the breeding success and populations of seabirds in upwelling systems during oceanographic anomalies, with food availability assumed to be the key mechanism (Crawford and Shelton 1978, Crawford and Jahncke 1999, Thayer and Sydeman 2006).

While food availability is assumed to be correlated with food abundance, it also reflects the ease with which a species can locate and capture prey (Cairns 1987). For CPFs, food availability can be defined in terms of abundance, accessibility, and distance from the colony or central place (Boyd 1999). A further aspect of food availability is the concentration of prey (for example, prey may be clustered in a few aggregations or dispersed throughout the prey field (see Bertrand et al. 2004b)). These aspects of prey availability can be consequential — population dynamics and ecosystem models that focus on prey abundance alone may not fully explain the responses of seabird populations. For example, in the northern Humboldt Current system (HCS), population dynamics and ecosystem models based on abundance tend to perform well overall, but underpredict the negative effects of severe oceanographic anomalies (e.g. Jahncke et al. 2004, Taylor et al. 2008). Abundance may be a good proxy for prey availability in most years, but the

explanatory power of abundance may be over-estimated if low abundance is correlated with reduced accessibility during severe anomalies. For example, Jahncke et al. (2004) developed an ecosystem model with anchoveta abundance estimated based on oceanographic variables and allocated between fisheries, seabirds, and other predators. The model performed well overall, explaining about 94% of the variation in seabird numbers between 1925 and 2000, but underestimated the severe reduction in seabird population estimates during the 1957-58 and 1965 El Niño events. Taylor et al. (2008) developed a dynamic ecosystem model (Ecopath with Ecosim) of the HCS over an El Niño Southern Oscillation (ENSO) cycle. The model performed well overall, but failed to reproduce the substantial observed decline in seabird populations and slow recovery following El Niño. Taylor et al. (2008) concluded that seabirds were probably more affected by changes in the accessibility of anchoveta associated with changes in fish distribution than by changes in the biomass of anchoveta. In contrast to these abundance-focused models, Muck and Pauly (1987) developed a model of anchoveta consumption by seabirds with emphasis on prey availability and competition among seabirds and with fisheries. Accessibility of anchoveta to seabirds was assumed to be a function of the horizontal and vertical spatial overlap between predator and prey, and the concentration or dispersion of anchoveta. However, these variables were assumed to be related to sea-surface temperature (SST), so that the final model is a function of abundance and SST only. During the strong 1957-58 El Niño event, the model indicated a gradual decline in relative anchoveta biomass, but a sharp reduction in accessibility, leading to a sharp reduction in the availability of anchoveta to seabirds and a corresponding reduction in relative seabird biomass.

The design of effective conservation and management strategies for species threatened by reduced food availability depends on how foraging success and ultimately population dynamics are affected by changes in different aspects of food availability. Some aspects of food availability are more amenable to management action than others (for example, abundance versus accessibility, distance, and concentration). This raises the question of whether and how management actions can achieve changes in abundance sufficient to offset changes in accessibility and spatial configuration that lie beyond management control. The broad goal of the research presented in this dissertation was therefore to strengthen understanding of the effects of changes in different aspects of food availability on the foraging success of seabirds and other CPFs.

Despite the acknowledged importance of other aspects of food availability, most empirical studies have focused on prey abundance as the independent variable. In short-term datasets,

the different aspects of prey availability are often confounded, and cannot be disaggregated using methods based on correlation analysis. For example, Piatt et al. (2007) summarized availability in five years of data on forage fish from targeted acoustic surveys in terms of prey densities. Long-term studies rarely benefit from targeted data collection on prey availability to CPFs, and instead rely on the output of fisheries stock assessments and/or data from fisheries or stock surveys. For example, Cury et al. (2011) matched data on seabird breeding success from long-term studies of 14 species with data on the abundance of their main prey species, mostly generated from fisheries stock assessments. However, stock assessment outputs typically do not include information on changes in the spatial configuration of forage fish and their accessibility to CPFs. Furthermore, differences in the sampling strategies between seabirds and fisheries or stock surveys, in terms of size/age class and space, often frustrate efforts to match seabird responses with these data sources (Croxall 1987, Hunt et al. 1991, Montevecchi 1993). The northern Humboldt Current system, the focal region for this dissertation, benefits from acoustic survey data covering the range of the northern stock of anchoveta dating back to 1983 (Gutiérrez et al. 2007). It is one of only a few systems with long-term datasets on forage fish suitable for analysis of different aspects of prey availability and seabird populations. Other systems include regions covered by acoustic surveys of forage fish, such as the Benguela Current system (Crawford 2007), or acoustic krill surveys, such as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises (Abraham and Sydeman 2004), and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) surveys (Reid et al. 2005).

Given these limitations, a different research approach was adopted here. An Individual-based Foraging Model (IBFM), a mechanistic model of the foraging trips of CPFs, was developed and used to investigate the effects of changes in various aspects of food availability on foraging success. The IBFM was developed using a short-term dataset comprising global positioning system (GPS) data on the movement patterns of two species of seabirds, the Peruvian Booby (*Sula variegata*) and Guanay Cormorant (*Phalacrocorax bougainvillii*), and data on the abundance and distribution of their main prey, Peruvian anchoveta (*Engraulis ringens*), from a targeted acoustic survey. The IBFM was developed and tested using these contemporaneous data on foraging patterns and foraging conditions during one breeding season, and then applied to similar data for a second breeding season characterized by contrasting foraging conditions. A key advantage of this approach was that the abundance, accessibility, and spatial configuration of prey from the contrasting years could be disaggregated and recombined in novel prey fields that isolated changes in different aspects of prey availability. Using the mechanistic IBFM, it

was then possible to simulate seabird foraging patterns based on each of the novel prey fields in order to explore the effects of changes in each of these aspects of prey availability in isolation.

Study system and species

Study system

The focal system for this research is the northern Humboldt Current upwelling system (HCS) off the western coast of South America. Of the four eastern boundary current systems, the northern HCS is characterized by its high productivity and pronounced variability at multiple scales (Chavez et al. 2008). The continental shelf is relatively narrow and steep, with the Andes to the east and the Peru-Chile ocean trench to the west, but broadens to up to 150 km in northern and central Peru (Bruland et al. 2005). In terms of major current systems, a key driver of the northern HCS is the poleward Peru Undercurrent which stems from the Equatorial Undercurrent. The Peru Undercurrent flows over the broad shelf in northern and central Peru, collecting key nutrients such as silicates, nitrates, and iron. This is the major source of the nutrient-rich upwelled waters that support the high productivity of the northern HCS (Brink et al. 1983, Strub et al. 1998). As with other eastern boundary current systems, dominant alongshore wind stress sets up offshore Ekman transport at the surface, stimulating the upwelling of deeper waters. A key feature of the HCS underlying its high productivity is that it is relatively close to the equator, so that intensive and near-continuous upwelling is produced without high wind-induced turbulence (Bakun and Weeks 2008).

The HCS is characterized by several distinct water masses (Bertrand et al. 2004a, Swartzman et al. 2008). In particular, recently-upwelled cold coastal waters (CCW) are characterized by low salinity, high nutrients, and relatively large phytoplankton and zooplankton, and favor anchoveta. In contrast, subtropical surface waters are characterized by high salinity, low nutrients, relatively small phytoplankton, and favor sardine. The distribution of these water masses is highly variable and is a function of basin-scale oceanographic forcing and wind stress (Bertrand et al. 2008b). Anchoveta is strongly associated with the cold coastal waters. As anchoveta populations increase, anchoveta densities tend to increase within this suitable habitat rather than expand beyond it (Bertrand et al. 2004a). In the vertical dimension, anchoveta is limited by the oxycline, which is relatively shallow in the HCS (Bertrand et al. 2008a).

There is growing awareness that climate variability at multiple scales plays an important role in the structure and functioning of marine ecosystems (Chavez et al. 2008). Climate variability leads to changes in ocean circulation patterns and hence in the availability and distribution of nutrients, phytoplankton, zooplankton, and small pelagic fish, which in turn influences the

population dynamics of upper trophic-level species. Recent studies have highlighted the effects of centennial-scale variability in the HCS (e.g. Gutiérrez et al. 2008). Major ecosystem reorganization at the centennial scale overwhelms variability on the multidecadal scale (Chavez et al. 2008). Centennial scale regime shifts, such as the one that occurred around 1820 at the end of the little ice age, have seen the HCS transformed from a relatively low productivity system to the current regime, characterized by a shallow and intense oxygen minimum zone, high primary productivity, and abundant small pelagic fish, with both anchoveta and sardine favored (Gutiérrez et al. 2008). In contrast, multidecadal oscillations in the HCS are epitomized by shifts in the dominance of anchoveta and sardine (Chavez et al. 2003, Alheit and Niquen 2004, Alheit 2007). On a multidecadal scale, the cool regime ('La Vieja') is associated with a shallow thermocline, increased nutrient supply, and high productivity, and is favorable to anchoveta. The warm regime ('El Viejo') is associated with the opposite, and is favorable to sardine. The HCS experienced a warm regime from the early-1970s, and then switched to a cool regime in the mid- to late-1990s (Chavez et al. 2003, Chavez et al. 2008).

Inter-annual variability in the HCS is driven by trade-wind anomalies that drive basin-scale oceanic forcing and variation in patterns of westward-propagating Rossby Waves and eastward-propagating Kelvin Waves (Bertrand et al. 2008b). Rossby Waves tend to reduce sea-surface height along the Peruvian coast and raise the thermocline, thus compressing surface waters. This leads to a horizontal expansion of the CCW over the continental shelf, such that the distribution of anchoveta is broad and shallow. Anchoveta is also relatively abundant in this context, as upwelling brings nutrients from below the thermocline to the surface, enhancing the productivity of both phytoplankton and zooplankton. In contrast, Kelvin Waves tend to increase sea surface height, deepen the thermocline, and lead to intrusion of subtropical surface waters unfavorable to anchoveta. El Niño events are associated with an accumulation of Kelvin Waves, whereas La Niña events are associated with a relaxation in the number and intensity of Kelvin Waves (Bertrand et al. 2008b). During El Niño events, pockets of CCW are restricted to areas of persistent deep upwelling, often close inshore. Anchoveta takes refuge in these pockets, and is often distributed deeper in the water column and is therefore less accessible to surface foragers. While upwelling persists, it no longer brings nutrient-rich water from below the thermocline, but instead recycles the nutrient-depleted waters above the thermocline. The productivity of the system and the abundance of anchoveta is reduced. However, there are indications that the collapse in anchoveta abundance during El Niño events may have been overstated (Bertrand et al. 2004a). Anchoveta may be able to locate and occupy pockets of suitable habitat within otherwise unfavorable conditions. Stocks in inshore pockets may not be

detected by acoustic survey vessels, but their existence can be inferred from stock recovery rates after El Niño events.

The Peruvian anchoveta fishery mainly targets the largest and most productive stock off northern and central Peru, and is one of the largest single species fisheries in the world (Fréon et al. 2008). The industrial anchoveta fishery started to develop in the 1950s, following the collapse of the California sardine fishery, and expanded rapidly for the first 20 years (Chavez et al. 2008). A strong El Niño event occurred in 1957/58. There was a severe reduction in seabird populations (Fig. 0.1), but the fishery was still in the early stages of development and the impacts on landings were limited (Fig. 0.1). However, in the early 1970s, a combination of overfishing and a severe El Niño event in 1972/73 was blamed for a collapse in anchoveta stocks (Muck 1989). Anchoveta stocks recovered slowly under several changes of management regime. The fishery is now partitioned into two seasons, with closures designed to protect the stocks during the main spawning periods in winter and summer (Chavez et al. 2008). The stock off northern and central Peru is currently managed under a constant escapement rule of 5 million tons of spawning stock biomass (Fréon et al. 2008), recently increased to 7 million tons, and landings have shown considerable stability given the inherent variability of the system (Fig. 0.1).

While there have been substantial advances in understanding the possible effects of directional climate change on upwelling systems, such as the northern HCS, several questions remain (Fréon et al. 2009). Global models show a reduction in upwelling within 15 degrees of the equator, which would include the northern HCS (Sarmiento et al. 2004). Vecchi et al. (2006) argued that the trade wind system which drives basin-scale oceanographic forcing may weaken as the poles warm more rapidly than the tropics. However, Bakun (1990) argued that upwelling will intensify due to increased alongshore wind stress. Models at finer spatial scales may be necessary to predict coastal upwelling effectively (Fréon et al. 2009).

Stratification may increase as surface waters warm more rapidly than deeper waters (Bopp et al. 2001, Schneider et al. 2007). This would be expected to lead to reduced nutrient input into the euphotic zone and reduced primary productivity (Behrenfeld et al. 2006), but may be mitigated in nearshore waters by enhanced upwelling (Fréon et al. 2009). This combination of effects could lead to an expansion of warmer, stratified, nutrient-poor surface waters dominated by relatively small phytoplankton and favorable to sardine in offshore regions, together with the persistence of cooler nutrient-rich waters characterized by relatively large phytoplankton and

zooplankton and favorable to anchoveta in areas of enhanced upwelling near shore (Fréon et al. 2009).

Within these broad distributional shifts, the locations of optimal habitat may also change. Bakun (1990) hypothesized that successful recruitment of species with pelagic larvae depends on a favorable combination of three essential processes: enrichment of nutrient supply, concentration of larvae and their prey, and retention of larvae and recruits in the nursery areas. Enhanced upwelling near shore could increase nutrient supply, but at the cost of disruption of the food supply to larvae through increased turbulence, and offshore transport of larvae through advection. The altered balance between the three essential processes at different locations could lead to shifts in the location of optimal habitat (Fréon et al. 2009).

It is also unclear how climate change will interact with natural climate variability, such as the El Niño Southern Oscillation (ENSO) and multidecadal oscillations (Fréon et al. 2009). Some studies indicate more severe and/or more frequent El Niños as a result of global warming (e.g. Timmermann et al. 1999, Hansen et al. 2006), while others argue that the evidence is inconclusive (IPCC 2007).

The HCS provides a unique opportunity for the research presented in this dissertation. Questions about predator responses to prey are best addressed in systems in which several species with contrasting ecological characteristics depend mainly on a single prey species or type (Reid et al. 2005, Furness 2007). Upwelling systems are dominated by relatively few species at the mid-trophic level. In the HCS, anchoveta is important for a wide variety of seabirds, predatory fish, and marine mammals, including the Peruvian Booby and Guanay Cormorant (Duffy 1983a). Upwelling systems, especially the HCS, are highly dynamic on inter-annual and inter-decadal scales (Chavez et al. 2003), facilitating the study of species' responses to variability. The northern HCS is also one of the best monitored large marine ecosystems in the world (Chavez et al. 2008). In particular, the abundance and distribution of anchoveta, which supports one of the largest single-species fisheries in the world, are tracked through regular acoustic surveys (Gutiérrez et al. 2007).

Study species

The focal seabird species for this research, the Peruvian Booby (*Sula variegata*) and Guanay Cormorant (*Phalacrocorax bougainvillii*), are both endemic to the northern HCS and forage primarily on anchoveta. Based on archeological and historical data, populations of seabirds in the northern HCS have varied widely, reflecting variability in the HCS at multiple scales

(Nelson 1978). During severe oceanographic anomalies, breeding may fail, adults may abandon colonies, and substantial adult mortality may occur (Nelson 1978, Duffy 1983b).

In the early 1950s, seabird populations in the northern HCS were probably higher than at any other time in the 20th Century (see Nelson 1978 for a detailed discussion of methods for estimating the population sizes of guano birds). The increase in populations from 1925 to 1955 has been attributed to a long-term increase in primary productivity and anchoveta biomass (Jahncke et al. 2004). Since 1955, population trends for the two focal species have been strikingly different (Fig. 0.1, Jahncke 1998, Goya 2000, Weimerskirch et al. 2010). The population of Guanay Cormorants peaked at around 21 million in 1954, declined sharply during the 1957/58 El Niño event and again during the 1965 El Niño event, and has averaged around 2 million birds since then (Fig. 0.1, Jahncke 1998). The Guanay Cormorant is now listed as Near Threatened on the IUCN Red List of Threatened Species (IUCN 2011). In contrast, populations of Peruvian Boobies have been comparatively stable from the mid-1950s to present, at around 2 million birds. The decline in seabird populations since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (Jahncke et al. 2004), but it remains unclear why populations of Guanay Cormorants have failed to recover following severe oceanographic anomalies whereas populations of Peruvian Boobies have remained comparatively stable.

Peruvian Booby

The Peruvian Booby is a member of the family Sulidae, comprising gannets and boobies, and most closely related to the cormorants and darters, in the order Pelecaniformes (del Hoyo et al. 1992). The species has a core range between 6-10°S and around 13°S, corresponding to the main spawning grounds of the northern stock of anchoveta (del Hoyo et al. 1992). Colonies may number up to 750,000 pairs. Among sulids, the Peruvian Booby is highly productive, with a modal clutch size of three eggs (compared to one or two for most congenics) and much higher breeding success than any of the other boobies, in the order of 63% (del Hoyo et al. 1992, Nelson 2005). Age at first breeding is two to three years (Nelson 2005). Nelson (2005) states that there are no reliable data on juvenile mortality but estimates it at 50%, and adult mortality at 10% in normal years and as high as 90% in El Niño years.

The Peruvian Booby feeds predominantly on anchoveta in cold coastal waters, usually close inshore, but occasionally beyond 80 km offshore (Nelson 2005). Foraging is mainly diurnal, with foraging trip durations from 2 to 12 hours. The sulids are plunge divers, foraging in the upper surface waters, using wing propulsion once underwater. The Peruvian Booby often forages in flocks with Guanay Cormorants and other seabirds (Murphy 1936, Duffy 1983a). It is not

thought to be dependent on interactions with other seabirds or subsurface predators for location or capture of prey (Nelson 2005).

Guanay Cormorant

The Guanay Cormorant is a member of the family Phalacrocoracidae, the cormorants and darters, in the order Pelecaniformes. The Guanay Cormorant has a more extensive core breeding range from 2.5-33°S. The population was estimated at 3.7 million individuals in 1996 (Zavalaga and Paredes 1999). Compared to most seabird families, many of which lay single-egg clutches, cormorants are highly productive, with the Guanay Cormorant laying a modal clutch of three eggs. Age at first breeding is probably two years (Nelson 2005). No data are available on breeding success or juvenile mortality, but adult mortality is unlikely to be higher than 10-15% in normal years (Nelson 2005).

As with the Peruvian Booby, foraging is mainly diurnal. Peruvian Boobies and Guanay Cormorants often forage together in large foraging flocks (Murphy 1936, Duffy 1983a). In contrast to Peruvian Boobies, Guanay cormorants are pursuit-divers, diving from the surface and then using their webbed feet to dive once underwater, achieving mean maximum depths of 33.9m (n = 27) in one previous study (Zavalaga and Paredes, 1999).

Research framework

Data

For the research presented in this dissertation, data on the distribution of anchoveta comprise acoustic survey data collected by RV 'Olaya' off Grupo Pescadores (~11.77°S) in December 2008 and December 2009 (Fig. 0.2). Data on the movement patterns of Peruvian Boobies comprise high-resolution (1 second) GPS tracking data collected at Isla Guañape Sur (~8.56°S) in December 2007, and at Grupo Pescadores in December 2008. Some individuals were also instrumented with time-depth recorders (TDRs). Data on the movement and diving patterns of Guanay Cormorants comprise lower-resolution (> 30 seconds) GPS tracking data and TDR data collected at Grupo Pescadores in December 2008.

Data were collected by the Peruvian Institute for Marine Research (IMARPE), the French National Center for Scientific Research (CNRS), and the French Institute for Research and Development (IRD), under the umbrella of the research project 'Top Predators as Indicators of Exploited Marine Ecosystems' (TOPINEME) funded by the French National Research Agency (ANR).

Individual-based foraging model (IBFM)

The broad goal of the research presented in this dissertation was to strengthen understanding of the effects of changes in various aspects of food availability on the foraging success of seabirds and other CPFs. This goal was addressed by developing an individual-based model (Grimm and Railsback 2005) designed to strengthen understanding of the processes that underpin the foraging patterns of CPFs foraging on schooling prey.

Design of the IBFM was guided by optimal foraging theory and informed by the foraging ecology of Peruvian Boobies and Guanay Cormorants. In optimal foraging models (MacArthur and Pianka 1966), optimal foragers use a set of decision rules to maximize or minimize a specific objective function, such as net energy gain or foraging trip duration, while foraging on a patchy resource environment. The attributes of the resource environment are variable. For example, the resource value and spatial configuration of patches may vary, and patches may be constantly renewed or become depleted. Foragers are defined by a set of characteristics, and subject to a set of constraints. In central place foraging models (Orians and Pearson 1979), foragers must return to a specific location at the end of each foraging trip. Other characteristics or constraints may relate to movement processes, or the information available to searching foragers on the location and resource value of patches. A foraging trip involves a series of decisions or strategies: the decision to forage, search strategies, patch or prey selection, patch residence time, and time to satiation (see Hart 1993). An objective of optimal foraging models is to identify the set of decision rules that will enable individual foragers to optimize their objective function given their characteristics and constraints, and the attributes of the resource environment. For example, Ford et al. (2007) developed an optimal foraging model for Black-legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound, Alaska, to investigate questions about the location and spacing of colonies. In contrast, the objective of the IBFM is to assess the effects of changes in the attributes of the resource environment on performance indicators, given a set of species characteristics, decision rules, and constraints. Individual performance is measured in terms of indicators that relate to the objective functions attributed to optimal foragers, such as foraging success, foraging trip duration, and net energy gain (see Schoener 1971).

Key processes and interactions in the IBFM are informed by analysis of observed data on the resource environment, seabird movement processes, and patch selection. The resource environment is simulated based on acoustic survey data on the distribution of anchoveta. The movement processes of individual foragers are informed by analysis of GPS tracking data. Patch selection and patch residence time are informed by analysis of foraging site selection

based on GPS tracking data, TDR data, and acoustic survey data. Performance indicators include foraging trip duration and foraging success. Foraging trip durations and maximum distance from the colony of simulated seabirds can be compared to observed data.

Objectives and hypotheses

Chapter I: resource environment

Seabird tracking data used in the analysis of foraging site selection and to define movement processes in the IBFM are spatially-continuous, whereas data on the distribution of anchoveta were derived from systematic, transect-based acoustic surveys. The objective of Chapter I was therefore to generate simulated prey fields of the spatial distribution of anchoveta over the entire foraging region as the basis for analysis of foraging site selection and as an input to the IBFM.

This was achieved by structural analysis of the spatial distribution of anchoveta based on acoustic survey data for 2008 and 2009, followed by geostatistical simulation of the distribution of anchoveta to a set of grid cells encompassing the foraging region. Simulations based on the 2008 survey data were used as an input to the analysis of foraging site selection (see Chapter III below). Simulations based on data for both 2008 and 2009, representing contrasting foraging conditions, were used as an input to the IBFM (see Chapters IV and V below).

Chapter II: movement processes

In the IBFM, individual foragers have different behavior modes (such as outbound travel, foraging, and return travel). CPFs often follow area-restricted search patterns in which long-distance travel is indicated by fast, directed movement patterns, and searching behaviors are indicated by slower, more sinuous movement patterns. In the IBFM, behavior modes are characterized by different movement processes. The objective of Chapter II was to define movement processes associated with different behavior modes.

For the regular, high-resolution GPS data for Peruvian Boobies, this was achieved by partitioning tracks into different movement modes using a hidden Markov model (HMM). Estimates of movement parameters for different movement modes were then used to inform the movement processes of simulated seabirds in the IBFM. However, this approach was not appropriate for the more irregular and lower-resolution GPS data for Guanay Cormorants. In the IBFM, fast, directed movement processes were used to simulate movement patterns during travel and broad-scale search behavior modes. A simple partitioning method indicated that the flight speeds of Guanay Cormorants during fast movement modes were similar to those of

Peruvian Boobies. The two species therefore follow the same movement processes during travel and broad-scale search behavior modes in the IBFM. Movement patterns during foraging and fine-scale, area-restricted search were not simulated explicitly in the IBFM.

Chapter III: patch selection and patch residence time

The objective of Chapter III was to define rules on patch selection and patch residence time for the IBFM. This chapter also provided an opportunity to test the hypotheses that patch selection is a function of prey availability at a location (specifically, a multiplicative function of prey abundance and accessibility); and patch residence time (here measured in terms of the number of dives or total duration of dives at a location) is a function of prey availability at a location.

For both Peruvian Boobies and Guanay Cormorants, patch selection and patch residence time were investigated by overlaying data on the location of diving behavior for each species on geostatistical simulations of the spatial distribution of anchoveta based on acoustic survey data for 2008, and developing appropriate resource selection functions in terms of the relative abundance and depth distribution of anchoveta.

Chapter IV: search strategies

The IBFM requires rules on the search strategies and information used by CPFs to locate prey resources. However, direct data on the information and cues used by Peruvian Boobies and Guanay Cormorants are not available. The objective of Chapter IV was therefore to explore the effects of different rules on information and navigation in the IBFM.

Weimerskirch et al. (2010) hypothesized that Guanay Cormorants tend to orient their outbound headings in line with the direction of returning birds, whereas Peruvian Boobies mainly depend on network foraging. Chapter IV explores two hypotheses relating to these search strategies: the effectiveness of search strategies is sensitive to population densities (specifically, search strategies are less effective when population densities are low); and the value of information depends on foraging conditions (specifically, information is more valuable when foraging conditions are poor).

The effectiveness of search strategies based on orientation of outbound headings in line with the direction of returning birds and network foraging was explored by running IBFM simulations with sets of rules representing these strategies (separately and combined), for a range of different seabird population densities. The value of information was investigated by comparing performance indicators from IBFM simulations with full information (i.e. both search strategies and high population densities) and versus simulations with no information and with perfect

information (i.e. assuming an 'optimal' forager with complete information on the spatial distribution of prey resources), based on prey fields representing contrasting foraging conditions.

Chapter V: Effects of changes in different aspects of prey availability

The objective of Chapter V was to address the primary research question for this dissertation, concerning the effects of changes in various aspects of prey availability on the foraging success of CPFs foraging on schooling prey. The following specific hypothesis was tested: the foraging success of Peruvian Boobies and Guanay Cormorants foraging on anchoveta depends on the depth distribution and spatial configuration of prey as well as abundance (see Taylor et al. 2008).

The 2008 and 2009 acoustic survey data reveal contrasting foraging conditions in terms of the regional abundance, depth distribution, distance from the coast, and concentration of anchoveta (see Chapter I). To investigate the above hypothesis, a series of novel prey fields were created by disaggregating and recombining the abundance, accessibility, and spatial configuration aspects of geostatistical simulations based on these data. (For example, the regional abundance for 2008 was combined with the depth distribution and spatial configuration for 2009.) IBFM simulations for Peruvian Boobies and Guanay Cormorants were then run over each of these prey fields, and regression trees were used to assess the relative importance of various aspects of prey availability on foraging performance indicators.

As noted above, populations of Guanay Cormorants have exhibited a substantial decline since 1954 from around 21 million to 2 million birds, while populations of Peruvian Boobies have been comparatively stable at around 2 million birds (Jahncke 1998, Goya 2000, Weimerskirch et al. 2010). The general decline in seabird populations since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (Jahncke et al. 2004), but the differences in population trajectories for the two species remains unexplained. Various hypotheses are available, including differences in diet specialization, flight proficiency, dive capacities, and search strategies (Furness and Ainley 1984, Furness and Tasker 2000). The pursuit-diving Guanay Cormorant is capable of reaching greater depths than the plunge-diving Peruvian Booby, but this should increase prey availability. There are some suggestions that Guanay Cormorants may require denser prey schools than the Peruvian Boobies for effective foraging (e.g. Nelson 1978). Analysis in Chapter III indicated different foraging site selection patterns between the two species in terms of the abundance and depth distribution of prey. In Chapter V, the IBFM was used to explore the hypothesis that differences in patch selection can lead to

differences in expected foraging success when prey availability is low. The effects of various search strategies were investigated in Chapter IV.

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Figures

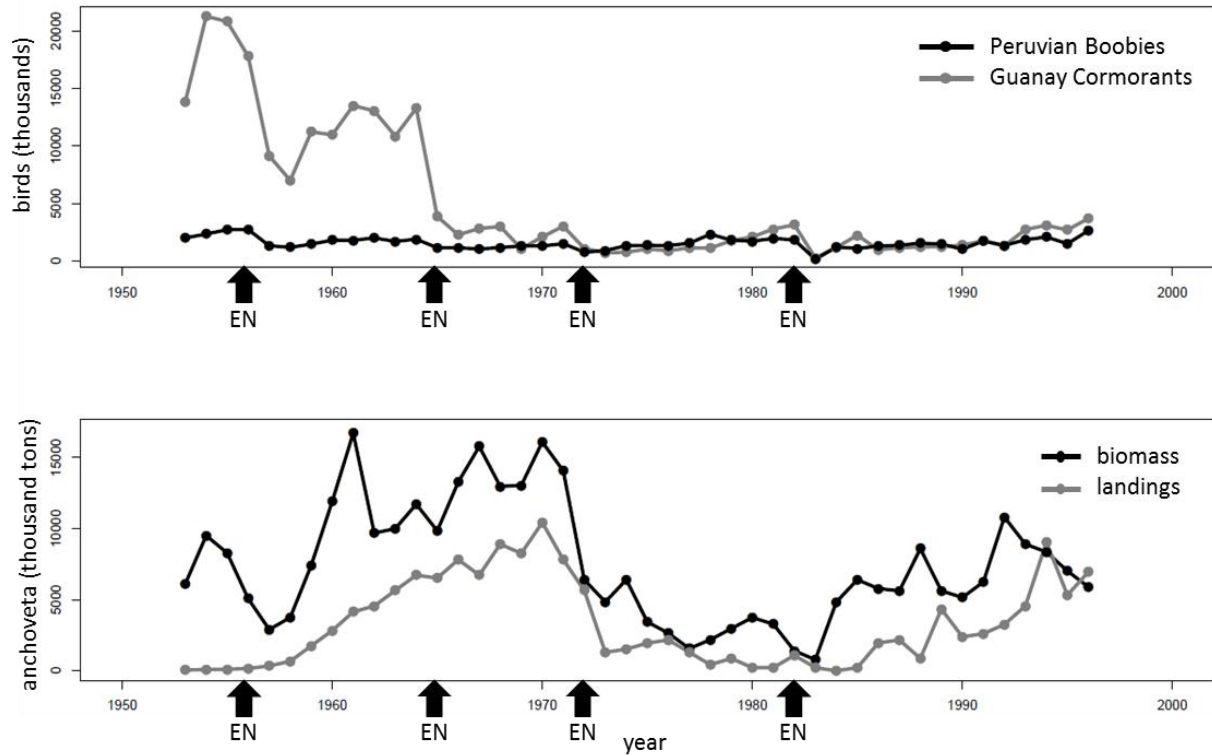


Figure 0.1. Estimated average population sizes of Peruvian Boobies and Guanay Cormorants (upper panel). Estimated average biomass and landings of anchoveta (lower panel). Major El Niño (EN) events are indicated. Data source: Jahncke 1998.

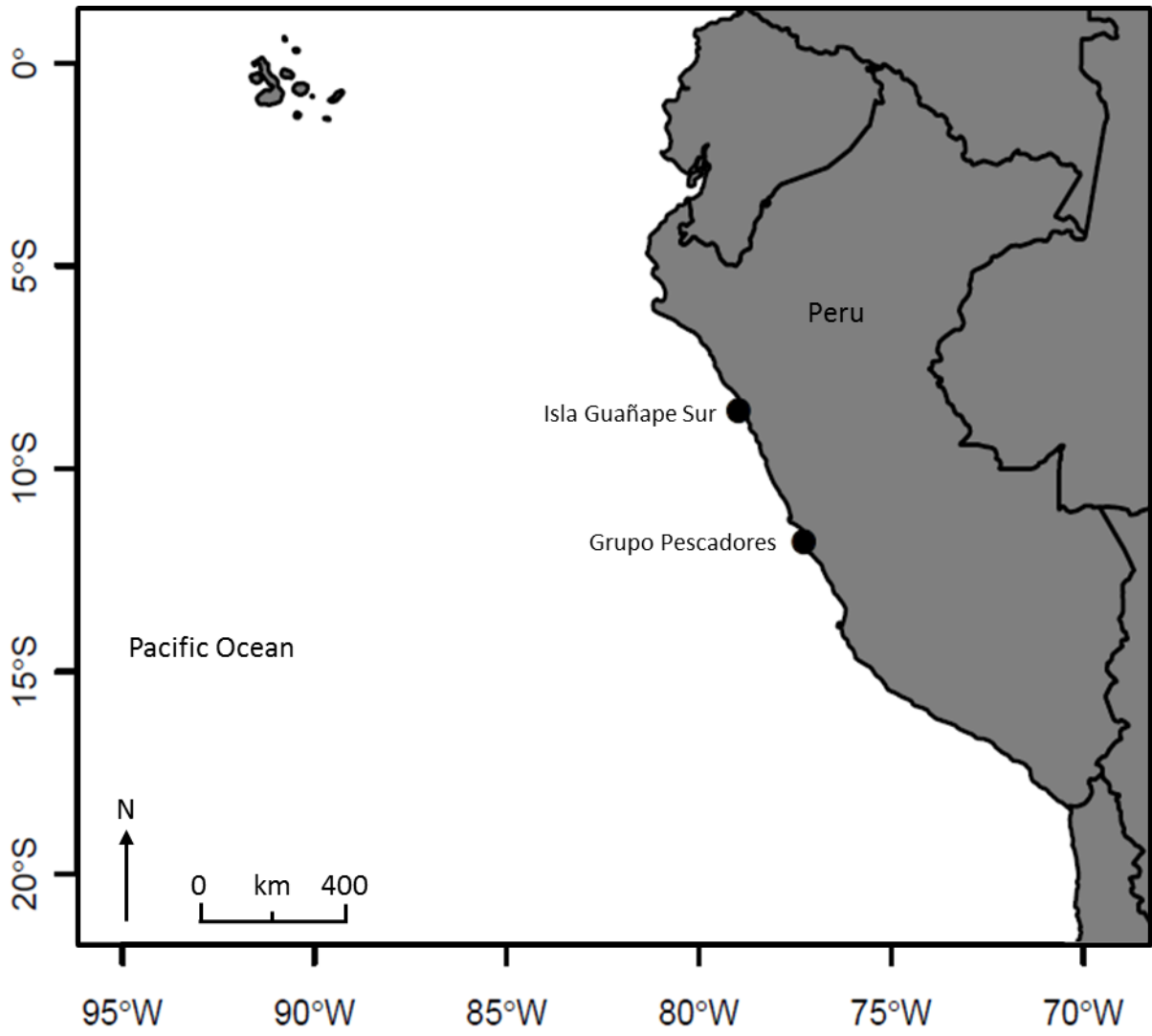


Figure 0.2. Coast of Peru with study sites indicated by black points.

Chapter I: Simulating the distribution of Peruvian anchoveta

Introduction

Analyzing predator-prey relationships is challenging for species foraging in marine environments, as both predators and prey are often highly mobile and difficult to monitor (Torres et al. 2008). Technologies such as global positioning system (GPS) data loggers have provided new opportunities to generate spatially-continuous data on the movement patterns of marine foragers, such as seabirds and pinnipeds (Wilson et al. 2002). In contrast, data on the distribution of their prey, such as aggregations of schooling fish, are typically limited to discrete locations or linear transects. For the purposes of integrated analysis of foraging patterns, observations of marine foragers could be matched to the nearest observation of their prey, or data on the prey could be interpolated to the entire study region. Here, the second approach is preferred because it provides a basis for simulating prey fields for the individual-based foraging model (IBFM) presented in Chapter IV. Standard interpolation methods, such as kriging, smooth over the patchiness in fish distributions (Gimona and Fernandes 2003) that may be an influential feature underlying foraging strategies (Weimerskirch et al. 2005). In this chapter, a methodology based on geostatistical simulation for generating representations of the distribution of Peruvian anchoveta (*Engraulis ringens*) is developed and applied. The geostatistical simulations honor the patchiness observed in acoustic survey data and represent the uncertainty in the interpolation process directly. These simulations form the basis for analysis of foraging site selection and the individual-based foraging model in later chapters.

Distribution of anchoveta

Peruvian anchoveta occurs in the Humboldt Current system off the coasts of Peru and northern Chile (Mathisen 1989). Off Peru, anchoveta stocks are concentrated close to shore, at distances between 20 and 100 nm from the coast, depending on the year (Simmonds et al. 2009). Stocks are strongly associated with recently-upwelled nutrient-rich cold coastal waters (CCW), characterized by sea-surface temperatures in the range 15-19°C and salinity in the range 34.80-35.05 (Bertrand et al. 2004a, Swartzman et al. 2008). In the vertical dimension, the distribution of anchoveta is limited by the oxygen minimum zone (Bertrand et al. 2010). When anchoveta stocks are high relative to the volume of CCW, densities increase in favorable areas rather than expand beyond the CCW habitat (Bertrand et al. 2008). In most years, the CCW spread in a broad shallow layer over the continental shelf, and support abundant anchoveta. In contrast, during warm water anomalies, CCW may be restricted to isolated pockets associated with

persistent upwelling, and anchoveta may occur at greater depths due to the increased depth of the oxycline (Bertrand et al. 2004a).

Within this CCW habitat, the distribution of anchoveta is less well-defined, but is probably directly associated with the availability and distribution of prey, in particular large zooplankton such as euphausiids and large copepods, rather than abiotic variables, such as sea-surface temperature (SST) (Bertrand et al. 2004a, Bertrand et al. 2008, Espinoza and Bertrand 2008). Zooplankton in turn feed on phytoplankton, but the peaks of abundance in phytoplankton and zooplankton communities are spatially separate, so the relationship between anchoveta and chlorophyll concentration is probably indirect (Espinoza and Bertrand 2008). Sub-mesoscale physical processes associated with the shelf break, such as internal waves, may also concentrate plankton into patches, enhance the availability of plankton to anchoveta, and thus influence the spatial distribution of anchoveta (Bertrand et al. 2008).

As with other small pelagic fish species, the distribution of anchoveta within suitable habitat is characterized by nested aggregation structures (Fréon and Misund 1999). Anchoveta exhibits strong schooling tendencies, and schools may form clusters of schools within broader aggregations (Bertrand et al. 2008). Both factors — the strong association of stocks with particular water masses, and the formation of aggregations — lead to a high degree of patchiness in the distribution of schooling fish.

The distribution of suitable habitat and the distribution of schooling fish within suitable habitat are both likely to be characterized by spatial autocorrelation (i.e. observations close together may be more similar than observations farther apart). Spatial autocorrelation may be induced in response to an underlying spatially-autocorrelated variable, such as habitat suitability, or be inherent, reflecting the innate aggregative behaviors of schooling fish (see Kissling and Carl 2008). The expectation of spatial autocorrelation in the distribution of anchoveta implies the need for a geostatistical approach to structural analysis and inference (Rivoirard et al. 2000).

Likelihood-based geostatistics

Geostatistics refers to the field of statistics in which the measured variable of interest depends on an underlying spatially-continuous process (Diggle and Ribeiro 2007). Classical geostatistics is distribution-free — it does not require that the dependent variable follows a known parametric distribution (Roa-Ureta and Niklitschek 2007). In contrast, likelihood-based geostatistics requires an explicit assumption about the distribution of the dependent variable (Diggle et al. 1998). There are several advantages to the likelihood-based approach over classical

geostatistics for structural analysis of spatial processes and parameter estimation (Ecker 2003). Specifically, the likelihood-based approach may reveal structural relationships in the data that are not apparent using classical techniques. For example, in linear models, likelihood-based geostatistics allows for simultaneous estimation of all model parameters, whereas classical geostatistics typically involves a stage-based approach to parameter estimation. The availability of a likelihood function also enables the use of likelihood profiles to investigate parameter uncertainty, and likelihood-based information criteria, such as Akaike's Information Criterion (AIC) (Burnham and Anderson 2002), for model comparison and selection. However, these analytical advantages depend on specific assumptions about the distribution of the variable of interest and how well the assumed distribution function approximates the true distribution of the variable of interest (see Matheron 1978, Isaaks and Srivastava 1989).

Conditional geostatistical simulation

Within geostatistics, kriging refers to a set of methods for spatial interpolation and prediction (Cressie 1990). Kriging generates a prediction of a spatial variable at unobserved locations by minimizing the variance in the predicted values and thus tends to smooth over local variability or patchiness (Gimona and Fernandes 2003). One approach to incorporating the patchiness that may be important for foraging seabirds in the IBFM and other applications is to use nested models (e.g. Maravelias et al. 1996). Another is to use geostatistical simulation (Goovaerts 1997, Chiles and Delfiner 1999).

As with kriging, conditional geostatistical simulations are designed to respect observed values at observed locations, and reproduce the statistical properties and spatial patterns of the sample data. However, in contrast to kriging, geostatistical simulation involves generating one or more possible realizations of a spatial variable by sampling from the spatial signal process and residual variance at each location. Over many iterations, geostatistical simulation thus samples from the full range of variability at each location, and each individual realization honors the patchiness in the observed data (Goovaerts 1997). This is demonstrated in Figure 1.1 which shows a simulated Gaussian random field. An 'observed' dataset was extracted from this simulated dataset, following a pattern designed to resemble a systematic transect-based survey. This 'observed' dataset was then used to predict values at all points corresponding to the underlying simulated dataset by kriging, and to generate a conditional geostatistical simulation. To minimize estimation error, the Gaussian random field was simulated without residual error, and the parameters used to simulate the Gaussian random field were used for both kriging and conditional simulation.

Model structure

Geostatistical methods require a model of the spatial distribution of the target stock. The distribution of small pelagic fish is often characterized by gaps in the area occupied and strong localized peaks in abundance (Petitgas 1993, Rivoirard et al. 2000), presenting challenges for modeling (Ciannelli et al. 2008). The appropriate model structure for the simulation of schooling fish depends on an understanding of the processes that structure their distribution. As discussed above, gaps in the distribution of anchoveta may be attributable to the strong association of anchoveta stocks with particular water masses and/or aggregative behaviors within suitable habitat. Areas of unsuitable habitat within a region would point towards a model structure in which the distribution of suitable habitat is modeled as one process, and densities within suitable habitat are modeled as another. The conventional approach to modeling gaps in the distribution of fish stocks is consistent with this scenario. A two-stage model structure is developed, in which the presence/absence process (first stage) is treated as separable and independent from the process explaining non-zero densities (second stage) (Maunder and Punt 2004, Walline 2007). However, if all habitat within the region is suitable, and aggregative behaviors are responsible for gaps in the distribution, then the appropriate model structure would model zero and non-zero values as an integrated process (see Roa-Ureta and Niklitschek 2007). Consistent with this latter scenario, Woillez et al. (2009) developed an integrated approach by modeling the distribution of schooling fish as a truncated Gaussian random field. Woillez et al. (2009) modeled the presence/absence process in terms of the truncation point, and the relative abundance of fish where present as values above the truncation point, in an integrated framework.

In December 2008, observed data indicate that anchoveta was broadly distributed throughout the survey area with some gaps in the distribution. This pattern is consistent with the assumption that the on-shelf area covered by the acoustic survey mostly encompassed acceptable habitat for anchoveta, and that gaps in the distribution are most likely attributable to the aggregative behavior of anchoveta within suitable water masses. In 2009, the observed data indicate larger gaps in the distribution, with anchoveta occurring both near shore and close to the shelf break. While this distribution could reflect gaps in suitable habitat, the presence of anchoveta both near shore and close to the shelf break suggests that suitable CCW also occupied the shelf area of the study region in this year, and that larger areas of suitable habitat were unoccupied due to comparatively low regional abundance (Bertrand, S. pers. comm.). Thus, the observed distribution of anchoveta in both 2008 and 2009 points towards an integrated modeling approach.

Chapter objective and summary of methods

The objective of this chapter was to generate simulated prey fields of the spatial distribution of anchoveta over the entire foraging region as the basis for analysis of foraging site selection and as an input to the IBFM. As noted above, the observed distribution of anchoveta in both 2008 and 2009 points towards an integrated modeling approach. However, the integrated modeling approach developed by Woillez et al. (2009) involves a non-parametric transformation process (Gaussian anamorphosis), and does not fit within the likelihood-based approach. This method is therefore inconsistent with the likelihood-based approach used in other chapters. Therefore, the integrated modeling approach developed by Woillez et al. (2009) was adapted to fit within a likelihood-based approach, by assuming a parametric transformation and estimating the truncated Gaussian random field within a likelihood-based framework. The performance of this new method for modeling the horizontal distribution of schooling fish was then compared with a two-stage model based on (a) indicator simulation (classical geostatistics) followed by a linear model (likelihood-based); and (b) a binomial model followed by a linear model (both stages likelihood-based). Conditional geostatistical simulation was then used to simulate the horizontal distribution for 2008 based on each method. The performance of each method was assessed in terms of how well it reproduced the sample statistics and spatial pattern of the 2008 survey data. The method which performed best for the 2008 data was then applied to the 2009 data. A separate model was used to simulate the vertical distribution of schooling fish in both 2008 and 2009. In this case, a linear model within the likelihood-based framework was estimated, and conditional geostatistical simulation was again used to generate multiple realizations of this process. Figure 1.2 provides a summary of methods used to model the horizontal and vertical distribution of anchoveta.

Data

The data comprise acoustic back-scattering from anchoveta derived from survey transects conducted by the Instituto del Mar del Perú (IMARPE) on the R/V "Olaya". Surveys took place over 2-5 December 2008 and 4-7 December 2009. Both surveys followed the Peruvian coastline from approximately 11.4°S to 12.2°S, covering the foraging region of tracked seabirds from colonies at the island group of Pescadores. (For the purposes of this analysis, the northernmost transect for 2008 was excluded so that the coverage of the two surveys overlapped more closely.)

The survey design was systematic, based on parallel, equally-spaced, onshore-offshore transects approximately 10 km apart (Fig. 1.3). The eastern end of each transect was near shore, while the

western end of most transects fell within the shelf break approximately 60 km from the coast, with every third transect continuing beyond the shelf break to cover the observable range of anchoveta. Sampling effort therefore differed between the on-shelf and off-shelf area. For the purposes of this analysis, the study region was restricted to the on-shelf area covered by the survey. (The movements of all tracked seabirds in 2008 and 2009 fell well within the shelf break and the study region.)

Acoustic data were collected using a calibrated Simrad scientific echosounder (EK60) operating at 120 kHz. The acoustic data were processed by the IMARPE, using Echoview acoustic postprocessing software (SonarData, Hobart, Tasmania, Australia). Acoustic backscatter was identified to species based on known backscattering characteristics, cross-validated by biological samples taken from mid-water trawls during the survey. Only backscatter attributed to anchoveta was used in this analysis.

The data were processed in two ways. First, the nautical area scattering coefficient (NASC) attributed to anchoveta was computed from the mean volume backscattering strength over 1 nm transect segments (elementary sampling distance units, ESDUs). (See MacLennan et al. (2002) for definitions.) Second, a school detection algorithm was used to identify relatively homogeneous regions of acoustic backscatter. The ESDU output was used as the basis for modeling relative abundance, and the output of the school detection algorithm for modeling the depth distribution of aggregations of anchoveta. For each identified aggregation, the height and mean depth were estimated and used to calculate the upper depth limit of the aggregation. (All depths refer to depths below the echosounder (i.e. depths are measured from 3.4m below the sea surface). No adjustment is made for possible vessel avoidance by anchoveta.)

In December 2008, anchoveta was fairly broadly distributed from near shore to the shelf break, with some gaps in the distribution (Fig. 1.3). Anchoveta was more patchily distributed in December 2009, with larger gaps in the distribution. In both years, the distributions of acoustic densities in the study region were characterized by high proportions of zero values (approximately 40% of the total in 2008 and 60% in 2009).

The conditional abundance of anchoveta (i.e. abundance of anchoveta where it occurred) was lower during the warm anomaly of 2009 than in 2008. In both years, the distribution of non-zero acoustic densities was strongly right-skewed. Following log-transformation, the non-zero acoustic densities followed a Gaussian-like distribution, but with few observations in the lower

tail in 2008 (Fig. 1.4). This may be representative of the true distribution of anchoveta, or may reflect sampling error.

The upper depth limits of aggregations detected in 2008 were mainly distributed in the upper surface waters (95% of aggregations had estimated upper depth limits less than 10.47m below the echosounder), probably reflecting a shallow oxycline (Bertrand et al. 2010). In 2009, aggregations were deeper (95% of aggregations had estimated upper depth limits less than 20.34m below the echosounder), and more broadly through the water column (Fig. 1.5).

Methods

Geostatistical estimation

A geostatistical model (following Diggle and Ribeiro, 2007) may comprise a trend surface, a spatial signal process, and additional non-spatial or residual variance:

$$Y_i \sim \sum_{j=1}^J \beta_j D_{ji} + S_i + \varepsilon_i \quad 1.1$$

where Y is a random variable observed at a set of sampling locations $i = 1 \dots N$; D_{ji} are measured spatial coordinates or environmental covariates, $j = 1 \dots J$; β_j are the corresponding parameters; S_i is an underlying spatial signal process (assumed to follow a specific parametric distribution in likelihood-based geostatistics); and ε_i are independent and identically distributed with zero mean and non-spatial variance τ^2 , and capture residual variance in measured values given $S(x)$, such as measurement error or variance at a finer scale than the minimum distance between locations.

The theoretical variogram is used to characterize spatial dependence in $S(\cdot)$ (Diggle and Ribeiro 2007):

$$V(x, x') = \frac{1}{2} \text{Var}[S(x) - S(x')] \quad 1.2$$

In the stationary and isotropic case, this simplifies to:

$$V(h) = \sigma^2 [1 - \rho(h)] \quad 1.3$$

where σ^2 is the variance of the spatial signal process (i.e. the 'partial sill'), which is constant in the stationary case; $\rho(h)$ is the correlation function; and h is the absolute Euclidean distance between two locations, x and x' . Isotropy implies that spatial continuity is similar in all directions. Stationarity here refers to second-order stationarity, and implies that the mean is

constant for all locations ($\mu(x) = \mu$ for all x), and that the covariance depends only on the absolute distance between two locations ($Cov[S(x), S(x')] = \gamma(x, x') = \gamma(h)$.)

The correlation function is usually chosen from a range of standard families which are known to be positive definite, but are otherwise sufficiently flexible to meet the needs of geostatistical data (Diggle and Ribeiro 2007). Desirable properties for correlation functions include that they decrease monotonically with $\rho(0) = 1$ and $\rho(h) \rightarrow 0$ as $h \rightarrow \infty$ that allows for varying degrees of smoothness in the underlying spatial process. For this analysis, a correlation function from the flexible two-parameter Matérn family was used:

$$\rho(h) = \{2^{k-1}\Gamma(\kappa)\}^{-1}(h/\phi)^k K_\kappa(h/\phi) \quad 1.4$$

where $\phi > 0$ is a scale parameter which indicates the distance at which correlation approaches zero; $\kappa > 0$ is a shape parameter which determines smoothness, most notably influencing the behavior of the function near the origin; and $K_\kappa(\cdot)$ denotes a modified Bessel function of order κ .

While the shape parameter, κ , can be estimated in linear models within the likelihood-based framework, it is often poorly identified. Diggle and Ribeiro (2007) therefore recommend selecting values of κ from a limited set. Here, models were estimated for two discrete values of κ with contrasting smoothness: $\kappa = 0.5$ (equivalent to the exponential correlation function) and $\kappa = 1.5$.

Spatial coordinates and environmental covariates

Where the distribution of schooling fish is related to environmental covariates, such as SST and chlorophyll concentration, incorporating these covariates in the model may improve prediction. However, for the purposes of interpolation, environmental covariates must be measurable at all prediction points. Unfortunately, in this case, complete data layers for SST and chlorophyll concentration are only available at coarse temporal and spatial scales, due to frequent cloud cover during the sampling periods, and may not be representative of conditions at the time of the survey. An alternative to treating SST and chlorophyll concentration as covariates is to use spatial proxies, such as latitude and longitude. In this study, given that the coastline does not run directly North-South, bathymetry may provide a better proxy than latitude or longitude for environmental processes that are fairly continuous alongshore, but exhibit more rapid turnover in the offshore dimension. Spatial coordinates and bathymetry (sampled from the GEBCO_08 30 arc-second grid, www.gebco.net) were therefore included in the structural analysis presented below.

Anisotropy

Spatial autocorrelation may be isotropic or anisotropic. However, in this case, the survey design was not suitable for detecting anisotropy. Analysis of anisotropy is therefore not included in the structural analysis presented below.

Models 1 and 2: two-stage models for relative abundance

For the first stage of the two-stage models, the data were transformed into a binary vector using the indicator function:

$$I(x) = \begin{cases} 0, & \text{if the acoustic signal for anchoveta at location } x \text{ is } 0 \\ 1, & \text{if the acoustic signal for anchoveta at location } x \text{ is } > 0 \end{cases}$$

Model 1a: indicator simulation

Indicator simulation is a non-parametric method derived from classical geostatistics. In indicator simulation, each point is simulated using indicator kriging (Goovaerts 1997). For each simulation point, the conditional distribution is derived from a weighted sum of values at neighboring locations:

$$\hat{p}(x_0) = \sum_{i=1}^N \omega_i(x_0) \cdot I(x_i) \quad 1.5$$

The weights, ω_i , are computed to minimize the prediction variance, $Var\{\hat{p}(x_0) - p(x)\}$, where $p(x)$ is the global proportion of positive signals, subject to the unbiasedness condition, $\sum_{i=1}^n \omega_i = 1$. In ordinary kriging, based on the assumptions of an unknown but constant mean and a known variogram, the weights are given by the linear equation system:

$$\begin{pmatrix} \omega_1 \\ \vdots \\ \omega \\ m \end{pmatrix} = \begin{pmatrix} \gamma(x_1, x_1) & \cdots & \gamma(x_1, x_n) & 1 \\ \vdots & \ddots & \vdots & \vdots \\ \gamma(x_n, x_1) & \cdots & \gamma(x_n, x_n) & 1 \\ 1 & \cdots & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} \gamma(x_1, x_0) \\ \vdots \\ \gamma(x_n, x_0) \\ 1 \end{pmatrix} \quad 1.6$$

where m is a Lagrange multiplier used to honor the unbiasedness condition when minimizing the prediction variance.

The variogram was estimated by constructing an empirical indicator variogram, $\hat{V}(h)$:

$$\hat{V}(h) = \frac{1}{n_h} \sum_{(x, x') \in n_h} [I(x) - I(x')]^2 \quad 1.7$$

where n_h is the number of pairs in a distance bin for distance class h .

A theoretical variogram was then fitted to the empirical indicator variogram using weighted least squares with weights $w_h = n_h / h^2$ (i.e. greater weights were given to points that are close together, as well as to bins that have a larger number of contributing pairs).

Model 2a: binomial model

In likelihood-based geostatistics, the appropriate model for presence/absence data is the binomial model. The binomial model is based on the assumption that the spatial signal process takes the form of an underlying Gaussian random field which is transformed into a probability field through the inverse logit function. The response variable is assumed to follow a binomial distribution based on the probability field:

$$E(Y_i) = p_i; \quad p_i = \frac{e^{\eta_i}}{(1+e^{\eta_i})} \quad 1.8$$

where p_i is the probability of a positive signal; and η_i is the linear predictor:

$$\eta_i \sim \sum_{j=1}^J \beta_j D_{ji} + S_i + \varepsilon_i \quad 1.9$$

In likelihood-based geostatistics, the variogram model is fitted to the distances between each pair of points (x, x') with parameters estimated using maximum likelihood. The integral which defines the likelihood function can be expressed as an expectation with respect to the distribution of \underline{S} :

$$L(\theta, \psi) = E[\prod_{i=1}^n f_i(y_i | S, \theta)] \quad 1.10$$

where θ represents the parameters which determine the conditional distribution of \underline{Y} given \underline{S} , and ψ denotes the parameters defining the distribution of \underline{S} . Monte Carlo maximum likelihood estimation (Christensen 2004) was used to estimate the variogram because, in the case of generalized linear spatial models, the s_i are not independent and hence Equation 1.10 is a high-dimensional integral for which conventional methods of integration often fail (Diggle and Ribeiro 2007). For any set of values for θ and ψ , it is possible to simulate the corresponding distribution of S . If this process is repeated many times, then the likelihood can be approximated by:

$$\hat{L}(\theta, \psi) = \frac{1}{J} \sum_{j=1}^J [\prod_{i=1}^n f_i(y_i | S_j, \theta)] \quad 1.11$$

where J here is the total number of simulations.

Monte Carlo Markov Chain (MCMC) simulation provides a more efficient method to achieve this than independent random sampling (Diggle and Ribeiro 2007). The parameters for the variogram model can then be estimated based on the approximated likelihood function.

To investigate spatial trends, models were fitted with no trend (i.e. constant mean), trend as a linear function of the spatial coordinates (i.e. latitude and longitude), and trend as a linear function of bathymetry. Model estimation was conducted in the R (R Foundation for Statistical Computing, Vienna, Austria) using the package `geoRglm`. However, model comparison in the binomial model is not straightforward because estimates of the likelihood for different models are derived from different approximations. Therefore, as in indicator simulation, the simplest model, without trend, was used as the basis for conditional simulations.

Model 1b and 2b: linear model

The distributions of the non-zero acoustic densities are truncated at zero and highly right-skewed (Fig.1.4). In likelihood-based geostatistics, this type of distribution can be fitted using a linear model following Box-Cox transformation (Box and Cox 1964). Maximum likelihood estimation was used to fit models with no trend, trend as a linear function of the spatial coordinates, and trend as a linear function of bathymetry. Models were therefore fit with the Box-Cox parameter, λ , estimated simultaneously with other parameters and fixed at 0 (indicating a lognormal transformation). Model estimation was conducted in the R package `geoR`. All models were then compared using AIC.

Model 3: integrated model for relative abundance

Wouillez et al. (2009) developed an alternative approach to two-stage models for modeling distributions with a high proportion of zero observations. Working within a classical geostatistics framework, Wouillez et al. (2009) used a non-parametric Gaussian anamorphosis to transform the observed distribution to a truncated standard Gaussian random field. This approach was adapted here to fit within a likelihood-based framework. For the non-zero densities, the same Box-Cox distribution was assumed as in Models 1b and 2b, and a parametric transformation was used to transform these values into standard Gaussian space. Second, the scaling parameter, ϕ , was estimated using maximum likelihood estimation. This differs from the method followed by Wouillez et al. (2009) who computed ϕ indirectly from the variogram of the truncated Gaussian based on the theory of Hermite polynomials.

The observed non-zero density distribution was transformed into a truncated Gaussian distribution with the truncation point set to allow for the observed proportion of zero values.

Let:

$$p_t = P(y = 0) \quad 1.12$$

then:

$$p'_i = p_t + [p_{obs,i} * (1 - p_t)] \quad 1.13$$

$$z_i = \Phi^{-1}(p'_i) \quad 1.14$$

where p_t is the percentile of the truncation point; $p_{obs,i}$ is the probability point of each observed non-zero data point assuming a lognormal distribution; p'_i is the probability point of the transformed data, z_i , in standard Gaussian space; and Φ is the cumulative distribution function of the standard Gaussian distribution.

The transformed variable was assumed to follow an isotropic standard Gaussian random field with mean vector $\underline{\mu} = (0,0)$, spatial variance $\underline{\sigma}^2 = (1,1)$, and residual variance $\tau^2 = 0$, as in Equation 1.1 (i.e. no spatial trend was included in the model and the spatial signal process was modeled by the Gaussian random field). The first two assumptions derive from the transformation into standard Gaussian space, together with the assumption of a constant mean, which greatly simplifies the modeling approach. The third assumption derives from the finding that the residual variance is poorly identified in the maximum likelihood estimation of truncated Gaussian random fields (De Oliveira 2005). Tests using simulated datasets with known parameters indicated that the assumption of $\tau^2 = 0$ is necessary for effective maximum likelihood estimation of ϕ . Given these assumptions, the restricted maximum likelihood (REML) estimator simplifies to:

$$LL_{REML}(\phi) = -0.5\{n \cdot \log(2\pi) + \log|\mathbf{R}_\phi| + \log\{\text{sum}(\mathbf{R}_\phi^{-1})\} + (\underline{Z}'\mathbf{R}_\phi^{-1}\underline{Z})\} \quad 1.15$$

where n is the number of observations; \mathbf{R}_ϕ is the covariance matrix of the Gaussian random field computed from the covariance function, $\gamma(h) = \sigma^2\rho(h)$; and \underline{Z} is the vector of transformed values, z_i . (See Diggle & Ribeiro (2007) for derivation of the REML estimator for the full model.)

The maximum likelihood estimate of the scaling parameter, ϕ , was obtained by minimizing the negative log of the REML likelihood function. The function to estimate ϕ was written in R, and the R function `optim` used to minimize the negative of the REML likelihood function.

Model 4: Linear model for the depth distribution of aggregations

The depth distribution of aggregations is also assumed to be a realization of a continuous non-zero random variable, and was analyzed using a linear model within the likelihood-based framework. Several aggregations occurred at the same horizontal location, but at different depths in both 2008 and 2009. There were 20 sets of duplicate coordinates over a total of 1,562 identified aggregations in 2008 and 43 sets of duplicate coordinates over a total of 1,230 aggregations in 2009. Multiple observations at the same location are not supported in geostatistics. Options for resolving this issue include removing all but one duplicate, taking the mean value at duplicate locations, or jittering the coordinates. Here, the coordinates were jittered.

Maximum likelihood was used to fit models with no trend, trend as a linear function of the spatial coordinates, and trend as a linear function of bathymetry. Model estimation was conducted in the R package *geoR*. As with the conditional acoustic densities, the distribution of the upper depth limit of aggregations is truncated at zero and right-skewed (Fig. 1.5). The Box-Cox parameter, λ , was estimated simultaneously with other parameters and fixed at 0 (indicating a lognormal transformation) and at -0.5 (indicating an inverse square root transformation). All models were then compared using AIC.

Geostatistical simulation

Simulation points

For both the analysis of foraging site selection and the IBFM, simulated prey fields should comprise a set of grid cells, each with data on the availability and distribution of prey at each location. A regular hexagonal grid was therefore generated encompassing the study region. The resolution of the grid cells is such that the distance between the center points of neighboring cells is 2 km, slightly longer than the 1 nm ESDUs. The center points of these grid cells comprise the prediction points for simulation of acoustic densities. Each hexagonal grid cell represents an area rather than a linear transect, but, assuming isotropy at local scales, the density for the area represented should be proportional to the density along any linear transect segment. There was no need to estimate this relationship because subsequent analysis was based on relative rather than absolute abundance.

Models 1 and 2: two-stage models for relative abundance

Model 1a: indicator simulation

Sequential indicator simulation (Goovaerts 1997) was used to simulate the presence/absence of anchoveta. This method involves ordering all simulation points randomly, and at each point in

turn (a) identifying all observed data and previously simulated values within a given neighborhood, (b) computing the conditional distribution for each simulation point using indicator kriging, and (c) drawing a simulated indicator value from this conditional distribution. This process was repeated 100 times to generate 100 indicator simulations. Each simulation is different because the order in which the values were simulated and the random seed was different.

Model 2a: binomial model

One hundred conditional geostatistical simulations were conducted based on the selected binomial model. For each simulation, conditional geostatistical simulation was used to generate the linear predictor, η_i at all simulation points, based on the maximum likelihood parameter estimates. 110,000 simulations were run, with 10,000 simulations removed for burn-in, and every 100th simulation saved thereafter. The results were back-transformed using the inverse link function to give the predicted probability of presence of anchoveta, p_i , at each location i for each saved simulation. Finally, a binary value for each location was drawn from the Bernoulli distribution with probability p_i . Simulations were generated using the R package `geoRglm`.

Model 1b and 2b: linear model

The selected second stage model was used to generate conditional geostatistical simulations of the conditional density of anchoveta. As the model is for conditional (non-zero) densities, values were only simulated at locations where the first-stage simulation indicated presence of anchoveta. A different first-stage simulation was used as a mask for each second-stage simulation. Two sets of 100 conditional geostatistical simulations were generated, one for each first stage model. Conditional geostatistical simulations were generated using the R package `geoR`.

Model 3: integrated model for relative abundance

For the integrated model, the first step in the simulation process was to generate values in standard Gaussian space for locations with observed zeroes. Geostatistical simulation was used to simulate values for these 'missing' data, conditional on the transformed observed non-zero data and the model of spatial dependence based on the estimated scaling parameter, ϕ . To achieve this, iterative conditional simulations were generated, with simulated values that fell at or below the truncation point added to the observed data after each iteration until no missing values remained. (In 2008, two transects crossed, leading to overlapping ESDUs with zero and non-zero densities, likely reflecting changes in the distribution of anchoveta between the time the two transects were conducted. Given the assumption of no residual variance, this presents

problems during the conditional simulation stage as simulated values conditioned on the nearby observed non-zero data do not fall at or below the truncation point. To resolve this, it was necessary to remove two points with zero densities from the simulation.) This process was repeated 100 times to generate 100 partially-simulated datasets. Each partially-simulated dataset was then used as the basis for one conditional geostatistical simulation to all the simulation points. The final set of conditional simulations was generated using the R package *geoR*. Following this approach, the final set of 100 conditional simulations to the simulation points was conditioned on the observed non-zero data and the locations of the zero observations only (i.e. imputed values were not treated as data). The results were then back-transformed using the inverse of the transformation procedure described above (Equations 1.12-1.14).

Model 4: Linear model for the upper depth limit of aggregations

The selected linear model for the upper depth limits of aggregations was used to simulate the depth distribution of anchoveta aggregations for all grid cells. In contrast to the analysis of acoustic densities which was based on ESDUs, the depth model was based on data for individual anchoveta aggregations. The transition from individual aggregations to 2 km grid cells represents a change in support between estimation and prediction. This was addressed through conditional geostatistical simulation (Bivand et al. 2008). For the analysis of foraging site selection, the independent variable for the depth component is based on the depth distribution of aggregations at each location and requires an estimate of the mean and the variance of the upper depth limits of aggregations in each grid cell. A set of approximately 25 fine-scale points was therefore generated within each grid cell. 100 conditional simulations were then generated to each of these fine-scale points. The R package *geoR* uses a global neighborhood for prediction, but this is computationally demanding for a set of over 45,000 points. Conditional simulations were therefore generated in the R package *gstat*, with the neighborhood set equal to ϕ . The mean and the variance of the upper depth limits of simulated aggregations in each grid cell were then computed for each conditional simulation.

Comparison of models 1, 2 and 3 for relative abundance

The performance of the methods was compared in terms of (i) reproduction of sample statistics (indicated by the percentage of zero values, and the means and empirical cumulative distribution functions of the non-zero densities); and (ii) reproduction of the spatial pattern in the observed data (indicated by boxplots derived from empirical variograms for each

conditional simulation, overlaid with the empirical variogram computed from the observed data).

For the presence/absence process, simulation tests were also used to investigate the capacity of each method to predict presence/absence. The locations of the observed data and the simulation points were combined into a single grid. A binary prey field was then simulated to this grid using a binomial geostatistical model. All points with simulated probability greater than 0.4 (corresponding to the percentage of non-zero values in the observed data) were considered occupied. The simulated values at the locations of the observed data were then extracted and used to fit models using each of the three methods. Finally, 100 conditional simulations were generated to the simulation points for each method. It was then possible to compare the results of the conditional simulations for each method to the simulated 'truth'. (This test was conducted on simulated datasets, so that the 'true' values as simulation points would be known. An alternative approach would be to remove observations from the observed data and compare the ability of the different models to predict these data. However, the results would depend on whether single data points or entire transects were removed. The simulation-based approach used here gives clearer insight into the ability of each model to predict data throughout the region where data were not observed.)

Results

Model comparison and selection

Spatial vs non-spatial models

For the likelihood-based models, alternative models were compared using AIC when possible. AIC was not used for model comparison in the binomial model because the estimated likelihood depends on an approximation of the likelihood function. For the integrated model and the linear models for non-zero densities and depth distributions, AIC indicated that spatial models have greater support than non-spatial models (Tables 1.1, 1.2, and 1.3).

Correlation function

For the integrated model and the linear models for non-zero densities and depth distributions, AIC also indicated that the Matérn correlation function with smoothness parameter $\kappa=0.5$ (i.e. the exponential correlation function) had similar or greater support from the data than the Matérn correlation function with smoothness parameter $\kappa=1.5$ (Tables 1.1, 1.2, and 1.3). For the indicator simulation, the fits of the two correlation functions were compared to the indicator variogram by eye. The difference was marginal. The exponential correlation function was therefore selected for all models used for geostatistical simulation.

Box-Cox transformations

In the second-stage model for non-zero densities for 2008 data, the likelihood profile for the Box-Cox parameter, λ , indicated that it is close to 0 (equivalent to the lognormal transformation). AIC indicated similar levels of support for models with λ estimated and fixed at 0 (Table 1.1). Geostatistical simulations were therefore based on the lognormal transformation, and a lognormal distribution was also assumed for the integrated model.

In the model for depth distributions based on 2008 data, the likelihood profile for λ indicated that it is close to -0.5 (equivalent to an inverse square-root transformation). AIC also indicated that models with the inverse square-root transformation have greater support than equivalent models with the lognormal transformation (Table 1.3). However, qq-plots for the 2008 data (Fig. 1.6) showed that, while the inverse square root transformation provides a better fit overall, the lognormal transformation provides a better fit to the data at the lower end of the distribution (i.e. shallow depths). As the distribution of shallow depths is probably more important for foraging site selection by surface-foraging and diving seabirds, the lognormal transformation was selected over the inverse square-root.

In the model for depth distributions based on 2009 data, the likelihood profile for λ indicated that it lies between 0 and 1. As AIC indicated greater support for former over the latter, the lognormal transformation was selected.

Spatial trends

Non-linear models:

Model comparison based on AIC is not possible for indicator simulation as this is not a likelihood-based approach. The simplest model, without a spatial trend component, was therefore used for geostatistical simulations.

As noted above, the estimated likelihood in the binomial model depends on an approximation of the likelihood function. Convergence of MCMC simulations used when fitting the binomial model was also questionable, reflecting the lack of information available to estimate spatial dependence in binary data. Differences in AIC between models were small and varied with the random seed (results not shown). The simplest model, without a spatial trend component, was therefore selected.

No spatial trends were estimated in the integrated method.

Linear models:

In the second-stage model for non-zero densities for 2008 data, AIC indicated support for the model with spatial trend as a linear function of the spatial coordinates. This model was therefore used as the basis for the conditional simulations.

In the model for depth distributions for 2008 data, AIC indicated weak support for the model with spatial trend as a linear function of the spatial coordinates. Leave-one-out cross-validation indicated negligible difference in the prediction capacity of models with and without trend. Similarly, qq-plots on sets of 10 pilot simulations indicated negligible difference in the statistical properties of the residuals for models with and without trend. The simpler model without trend was therefore selected as the basis for conditional simulations.

In the model for depth distributions for 2009 data, AIC indicated stronger support for the model with spatial trend as a linear function of the spatial coordinates. Leave-one-out cross-validation and qq-plots on test simulations did not contradict AIC, so the model with trend was used as the basis for conditional simulations.

Comparison of simulation results for models 1, 2 and 3 for relative abundance

Presence/absence

All three methods performed fairly well in terms of reproducing the observed percentage of locations occupied by anchoveta, although the integrated model tended to under-estimate the area occupied by the stock (Table 1.4).

However, in simulation tests, indicator simulation and the integrated model performed better than the binomial model at predicting absence when the 'truth' was absence and presence when the truth was presence (Table 1.5).

In terms of reproduction of the spatial pattern, while indicator simulation is the only one of the three methods specifically designed to reproduce the indicator variogram, the integrated model performed almost as well (Fig. 1.7). In contrast, the binomial model performed notably less well than the other two models at reproducing spatial autocorrelation at shorter distances.

Figure 1.8 highlights the marked contrast in spatial patterns generated by each method. Indicator simulation leads to the most consolidated pattern, the integrated model to a slightly more fragmented pattern, and the binomial model to a much more fragmented pattern.

Non-zero densities

Comparison of the means, medians, and empirical cumulative distribution functions of the simulated non-zero acoustic densities with the observed non-zero data indicated that the three methods performed similarly in reproducing the sample statistics in log-space (see Table 1.4 for comparison of means). However, following back-transformation into the original data space, the means of simulations for both two-stage models are positively biased compared to the sample mean, while the integrated model exhibits less bias and is more precise (Fig.1.9). All three models simulated values in the upper tail of the lognormal distribution, beyond those that occur in the observed data. However, the integrated model simulated fewer and less extreme values. While the percentage of extreme values is small, this extrapolation probably explains the positive bias in the two-stage models.

In terms of the spatial pattern of non-zero acoustic densities, comparison of simulation results prior to back-transformation with the empirical variogram did not reveal any substantial differences in the performance of the three models (Fig. 1.10). It is worth noting that spatial autocorrelation is more influential at shorter distances, so this is the most important area of variogram.

Zero and non-zero densities combined

In terms of reproduction of the sample statistics, the issues noted for non-zero densities following back-transformation do not disappear when zero and non-zero densities are combined (Table 1.4).

All three models for acoustic densities reproduced the major hotspots and coolspots in the observed data (Fig.1.11). However, differences can be detected in the pattern generated by the three methods. Most notably, the integrated model generally simulated low values (if any) in areas where the survey returned zero values, whereas the two-stage models simulated relatively high values in these areas in some simulations. (Note that the simulation points do not coincide exactly with the survey locations, so non-zero values are possible in an area where the survey did not indicate presence of anchoveta.) Comparison of simulation results with the empirical variogram suggest that the spatial pattern simulated by the integrated method reproduces the spatial pattern in the observed data more closely than either of the two-stage models (Fig. 1.12).

Simulation results for the depth model

Figure 1.13 shows the predictions of the depth distribution of aggregations for 2008 and 2009, in terms of the mean probability that the upper depth limit of aggregations is less than 7.5m below the echosounder.

Discussion

Comparison of methods

Reproduction of sample statistics

The analysis presented above indicates that all three methods performed fairly well in terms of reproducing the percentage of the survey region occupied by anchoveta, although the integrated model tended to underestimate the area occupied by the stock (Table 1.4). However, the performance of the methods differed in terms of reproducing the sample statistics for the non-zero densities (Fig. 1.9), and hence for the zero observations and non-zero densities combined (Table 1.4). For the two-stage models, the divergence between statistics for the observed data and simulated values is linked to the assumption, based on structural analysis, that the non-zero densities followed a lognormal distribution. The integrated model followed the same assumption, but the variance in simulated values was lower, which limits the divergence between the mean of observed data and simulated values following back-transformation into the original data space. The lower variance in the integrated method is explained by differences in the way that spatial dependence is modeled, and by the assumption in the integrated method that non-spatial variance is negligible. There is greater inherent spatial structure in the integrated model, which tends to reduce the variance in simulated values. In the integrated method, simulated values close to the edges of patches are correlated with neighboring values that are less than the truncation point. In contrast, spatial autocorrelation between zero and non-zero densities is not incorporated in the two-stage models, as information on the location of observed zeroes is not used in simulating non-zero densities. The assumption that non-spatial variance is negligible in the integrated method may not be appropriate in all contexts, but probably contributed to the effective reproduction of sample statistics in this case.

Reproduction of spatial pattern

The purpose of the geostatistical simulations presented here was to generate multiple realizations of the spatial distribution of anchoveta consistent with observed data, as the basis for spatial analysis of the foraging patterns of their predators. As discussed above, conditional

geostatistical simulation is designed to respect observed data at data locations, but nevertheless, there are differences in the spatial patterns generated by the three methods.

With regard to subsequent analysis of foraging patterns, reproduction of the spatial pattern of the presence/absence process is the priority, as this process underpins the patchiness of prey resources which is likely to be important for seabirds. Indicator simulation and simulation based on the integrated model performed similarly in terms of reproducing the indicator variogram (Fig. 1.7). The binomial model performed notably less well than the other two models at reproducing spatial autocorrelation at shorter distances. (Given that spatial autocorrelation is more influential at shorter distances, this is the most important area of variogram). This may be attributable to the additional assumptions associated with the binomial model. In indicator simulation, each point is simulated based on a simple distance-weighted average of observed and previously simulated points. In contrast, the binomial model is based on the assumption of an underlying Gaussian random field which is transformed through the inverse logit function into a probability field. The additional information encapsulated in this assumption does not seem to improve prediction capacity. Instead, it seems to dilute the information available from the observed data, and thus undermines accuracy. This effect is most notable close to observed data points, as the value of the information in the observed data decreases with distance (Fig. 1.7).

Simulation based on the binomial model led to a more fragmented spatial pattern than simulations based on indicator simulation or the integrated model (Fig. 1.8). This is attributable to the final step of the binomial simulation process, in which an indicator value is drawn independently for each location based on the simulated spatially-dependent probability field. This simulation step would be appropriate for species that do not have inherent aggregative tendencies beyond the scale of the unit of analysis. However, it is less appropriate for species, such as anchoveta, that exhibit inherent aggregative behaviors at multiple scales (Bertrand et al. 2004b). For such species, presence/absence at a location is not independent of presence/absence at neighboring locations, even after the underlying probability of occurrence is taken into account.

When the two components of the two-stage models were combined, all three methods reproduced the major 'hotspots' and 'coolspots' in the observed data (Fig. 1.11). However, there were also differences in the spatial pattern generated by the different approaches. A notable strength of the integrated model was that it generally simulated low values (if any) in areas where the survey returned zero values, whereas the two-stage models simulated relatively high

values in these areas in some simulations. This difference reflects the different structures of the methods. In the two-stage models, all points with simulated presence are treated as equal in the second stage model. No information is passed from the first stage on the probability of occurrence at a location. In contrast, this information is available throughout the simulation process in the integrated model.

Summary

In summary, the integrated model outperformed the two-stage models overall, in terms of the reproduction of the sample statistics for the zero and non-zero densities combined, and the spatial pattern of the presence/absence process and the zero and non-zero densities combined. It also falls within the framework of likelihood-based geostatistics, and is thus consistent with the statistical approaches applied elsewhere in this dissertation. This modeling approach was therefore selected as the basis for subsequent analyses, and applied to the 2009 acoustic survey data.

Comparison of the distribution of anchoveta at Grupo Pescadores in December 2008 and 2009

The conditional simulation results based on the integrated method are consistent with observed data in showing a much reduced area occupied by anchoveta in 2009 compared to 2008. Figure 1.14 highlights the broad distribution of anchoveta in 2008 with areas of high abundance occurring across the study region. In contrast, anchoveta was less broadly distributed in 2009, with few areas of high abundance, mostly near shore, and some areas in the mid-shelf apparently unoccupied.

Conditional simulations are also consistent with the observed data in showing much reduced regional abundance in 2009 compared to 2008. The ratio of regional abundance in 2009 versus 2008 simulations is 0.083. However, conditional simulations also indicate that the anchoveta biomass which was found in the study region in 2009 was closer to the colony in 2009 than in 2008. In 2009, the average distance of anchoveta biomass from the colony, located at 11.775°S, 77.266°W, was 30 km compared to 46 km in 2008 (see Fig. 1.14).

The conditional simulation results are also consistent with the observed data in showing an increased average depth in 2009 compared to 2008. Figure 1.13 shows the depth distribution of anchoveta as relatively shallow throughout the study region in 2008, and deeper, with more spatial structure in 2009. In 2009, anchoveta was more likely to be more accessible to surface-foraging seabirds near shore than elsewhere in the foraging region.

Notation

$\underline{\beta}$	parameters corresponding to spatial coordinates and/or measured environmental covariates (D)
$\Gamma(\cdot)$	gamma function
$\gamma(\cdot)$	covariance function
ε	measurement error and/or process error at a finer-scale than the minimum distance between locations
η	linear predictor in the binomial model
θ	the parameters which determine the conditional distribution of the dependent variable, \underline{Y}_x given the spatial signal process, \underline{S}
$K_\kappa(\cdot)$	modified Bessel function of order κ
κ	shape or 'smoothness' parameter in the correlation function, $\rho(h)$
λ	Box-Cox parameter
μ	mean of the spatial signal process
$\rho(\cdot)$	the correlation function
σ^2	the variance of the spatial signal process, $S(x)$; the 'partial sill'
τ^2	the (non-spatial) residual variance of the measurement or fine-scale process error, ε ; the 'nugget'
Φ	the cumulative distribution function of the standard Gaussian distribution
ϕ	scale parameter in the correlation function, $\rho(h)$; the 'practical range' (where $\rho(h) = 0.05$)
ψ	the parameters defining the distribution of the spatial signal process, \underline{S} .
ω	weights used in weighted least squares estimation
D	spatial coordinates and/or measured environmental covariates
h	the absolute Euclidean distance between x and x'
$I(\cdot)$	indicator function
$L(\cdot)$	likelihood
m	Lagrange multiplier
n_h	number of pairs in a distance bin of the empirical variogram
n	number of observations
$P(\cdot)$	probability
p	probability of a positive signal
p_t	the percentile of the truncation point in the integrated model

$p_{obs,i}$	the probability point (quantile) of an observed positive data point in the integrated model
p'_i	the probability point (quantile) of a transformed data point in standard Gaussian space in the integrated model
R_ϕ	the covariance matrix of the Gaussian random field and is dependent on the scaling parameter, ϕ
$S(\cdot)$	spatial signal process
$V(\cdot)$	the variogram
\underline{X}	sampling locations
\underline{Y}	dependent variable
\underline{Z}	transformed dependent variable in the integrated model

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Tables

Table 1.1. Model comparison for the linear model for non-zero densities (models 1b and 2b); selected model in bold. (λ denotes the Box-Cox parameter.)

	parameters	number of parameters	Δ AIC	
			$\lambda = 0$	λ estimated
Non-spatial models:				
No trend (constant mean)	$\beta_0, \tau^2, [\lambda]$	2 [+1]	62	68
Spatial model, k=0.5 (k = 1.5):				
No trend (constant mean)	$\beta_0, \sigma^2, \phi, \tau^2, [\lambda]$	4 [+1]	7 (8)	9 (9)
Trend ~ spatial coordinates	$\beta_0, \beta_1, \beta_2, \sigma^2, \phi, \tau^2, [\lambda]$	6 [+1]	0(1)	1 (2)
Trend ~ bathymetry	$\beta_0, \beta_b, \sigma^2, \phi, \tau^2, [\lambda]$	5 [+1]	4 (5)	6 (6)

Table 1.2. Model comparison for the integrated model (model 3); selected models in bold.

	parameters	number of parameters	Δ AIC	
			2008 data	2009 data
Non-spatial model:				
No trend (constant mean)	NA	0	148.204	185.670
Spatial model, k = 0.5 (k = 1.5):				
No trend (constant mean)	ϕ	1	0 (48.133)	0 (59.415)

Table 1.3. Model comparison for linear models for the depth distribution (model 4); selected models in bold. (λ denotes the Box-Cox parameter.)

parameters	number of parameters	2008 data (ΔAIC)		2009 data (ΔAIC)	
		$\lambda = 0$	$\lambda = -0.5$	$\lambda = 0$	$\lambda = 1$
Non-spatial models:					
No trend (constant mean)	$\beta_0, \tau^2, [\lambda]$	884	734	730	1274
Spatial models, $k = 0.5$ ($k = 1.5$):					
No trend (constant mean)	$\beta_0, \sigma^2, \phi, \tau^2, [\lambda]$	124 (124)	1 (1)	0 (7)	381 (383)
Trend ~ spatial coordinates	$\beta_0, \beta_1, \beta_2, \sigma^2, \phi, \tau^2, [\lambda]$	121 (128)	1 (9)	1 (9)	362 (363)
Trend ~ bathymetry	$\beta_0, \beta_b, \sigma^2, \phi, \tau^2, [\lambda]$	123 (131)	1 (9)	1 (8)	376 (377)

Table 1.4. Reproduction of sample statistics for 2008 data. Proportion of non-zero observations in observed data, and the overall mean proportion of non-zero observations for each set of 100 geostatistical simulations (with interquartile ranges from individual simulations in parentheses). Mean of observed non-zero densities and overall mean for each set of 100 geostatistical simulations in log-space (standard deviation in parentheses). Mean of observed non-zero densities and overall mean for each set of 100 geostatistical simulations in the original data space (with interquartile ranges from individual simulations in parentheses).

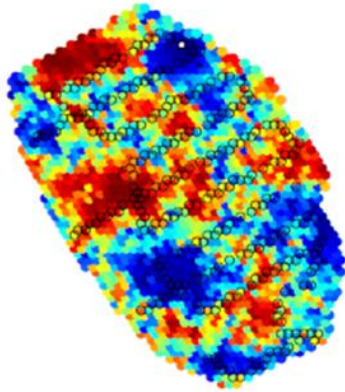
	proportion non-zero	non-zero densities (log-space)	zero and non-zero densities combined
observed data	0.606	4.97 (2.32)	861
Indicator simulation	0.597 (0.573-0.620)	4.94 (2.41)	1385 (994-1617)
Binomial model	0.597 (0.580-0.614)	4.92 (2.39)	1291 (958-1494)
Integrated model	0.579 (0.562-0.597)	5.00 (2.25)	879 (627-991)

Table 1.5. Capacity of candidate models to predict presence/absence based on simulated data. (pr(1) indicates the mean probability of presence.)

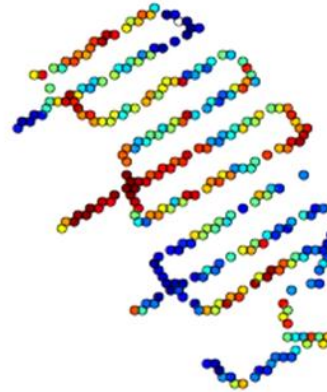
	pr(1)	pr(1) where truth=0	pr(1) where truth=1
The "truth"	0.63	0	1
Indicator simulation	0.64	0.39	0.78
Binomial model	0.65	0.49	0.74
Integrated model	0.65	0.39	0.81

Figures

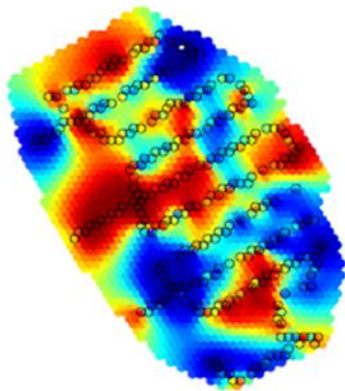
Simulated data



'Observed' data



Kriging output



Conditional simulation output

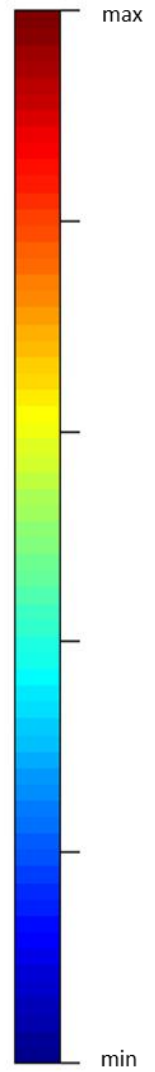
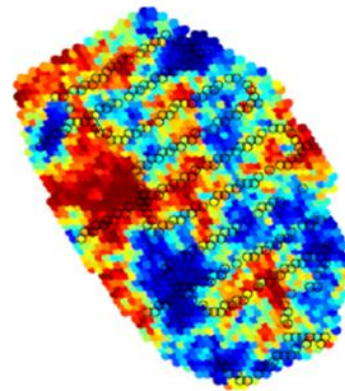


Figure 1.1. Comparison of kriging and conditional simulation outputs, based on 'observed' data extracted from a simulated Gaussian random field. (Plots are based on quantiles.)

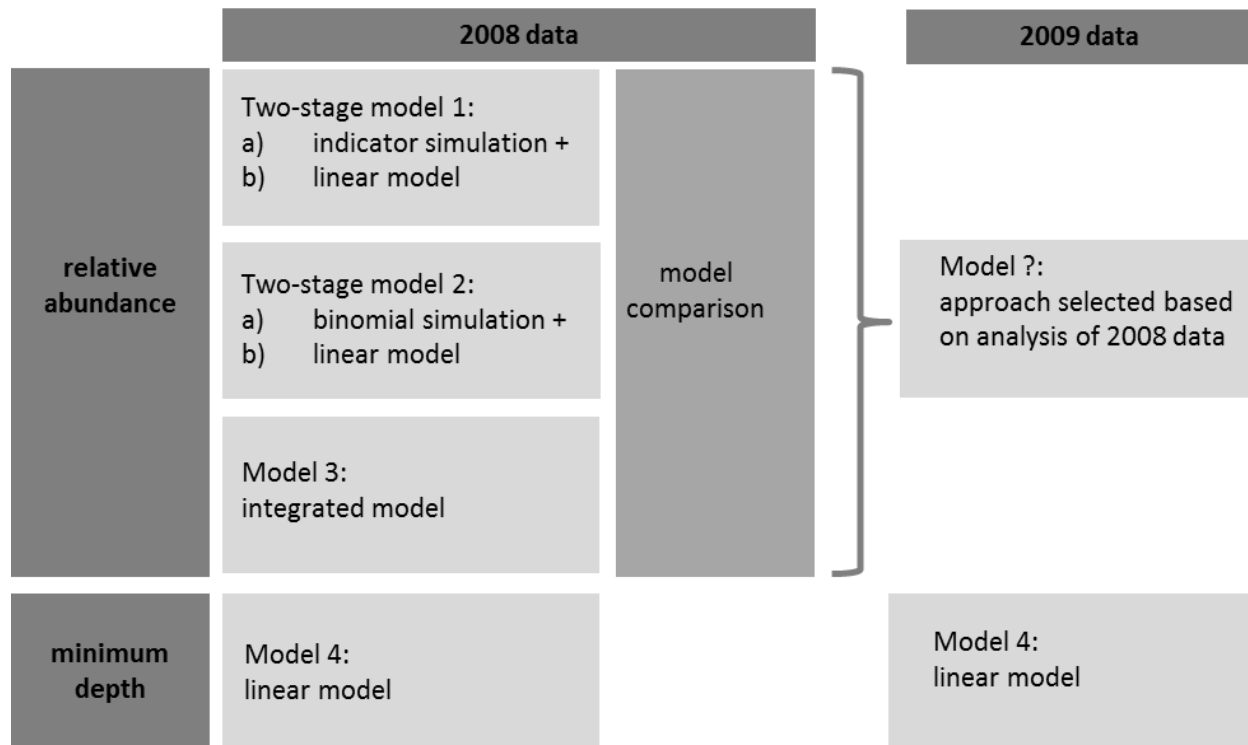


Figure 1.2. Summary of methods. (Models 1b and 2b are the same.)

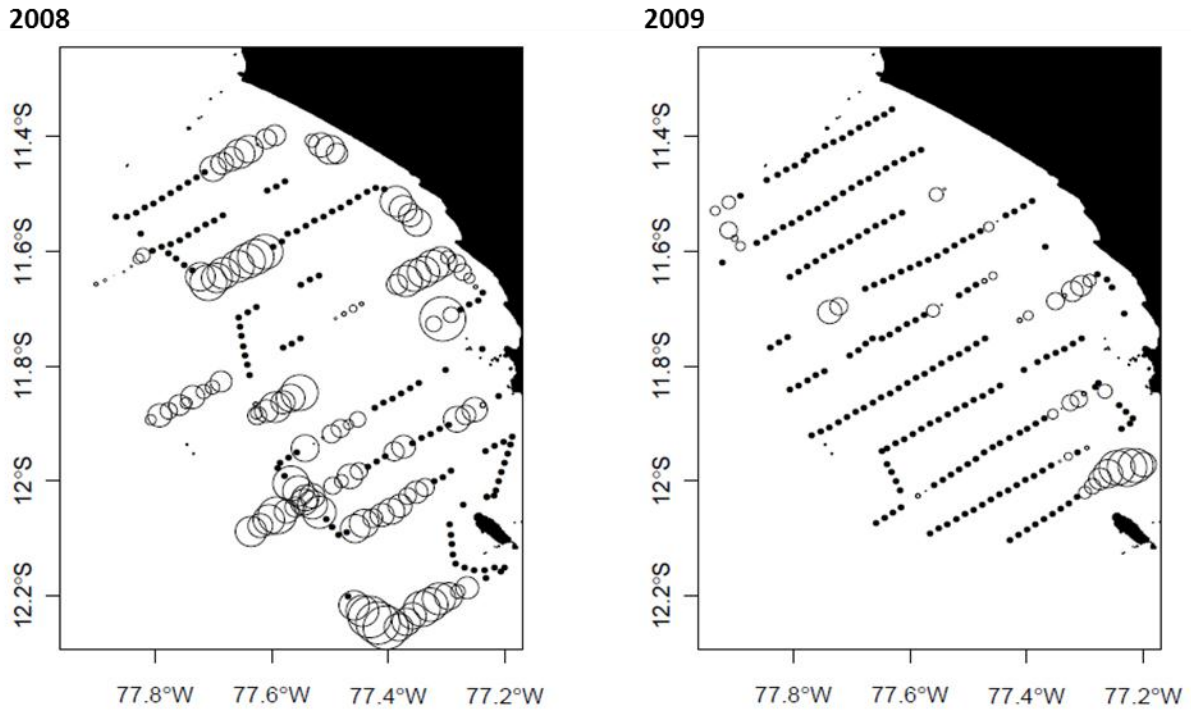


Figure 1.3. Map of the study region showing survey transects from 2008 and 2009. Elementary sampling distance units (ESDUs) are marked by points (zero values for anchoveta) and circles (positive values, diameter of the circles proportional to the logarithm of relative anchoveta abundance.)

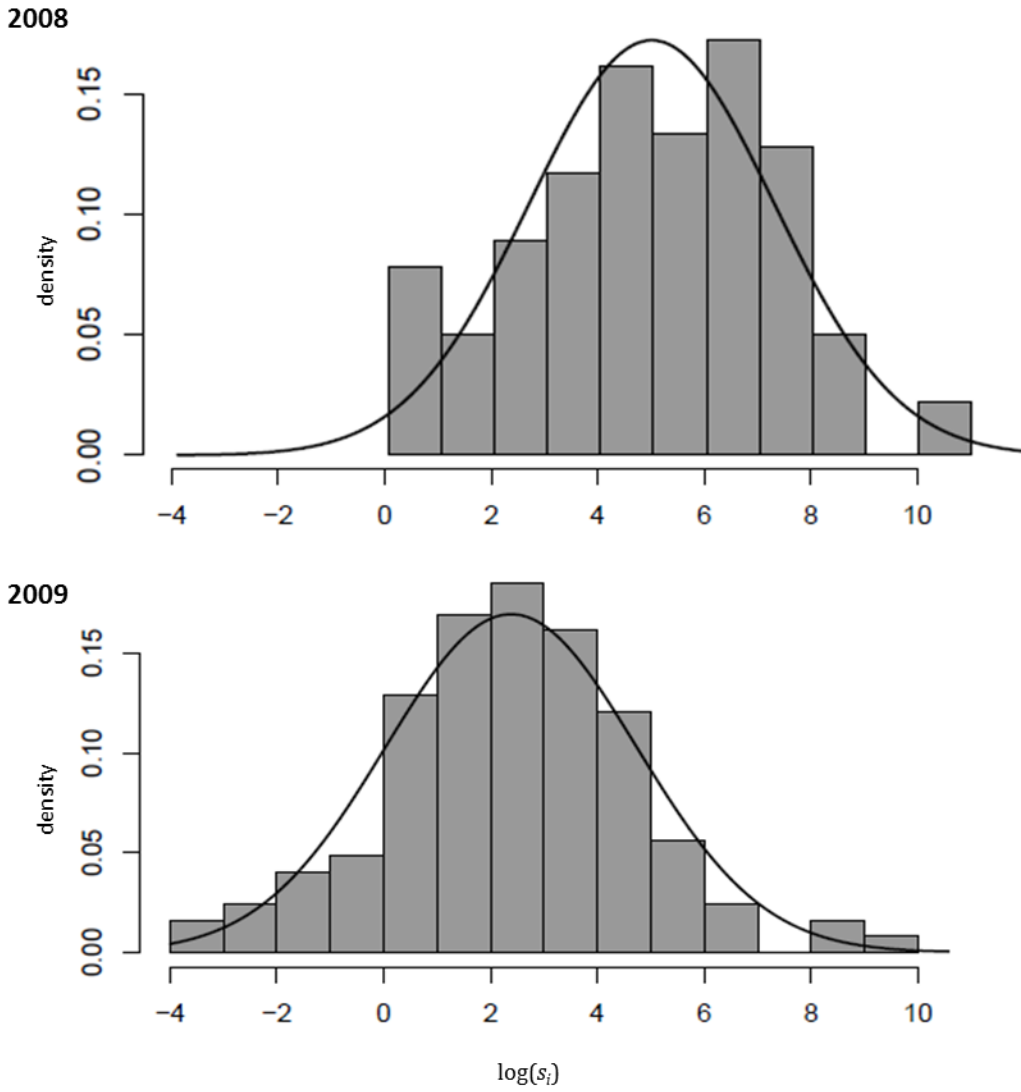
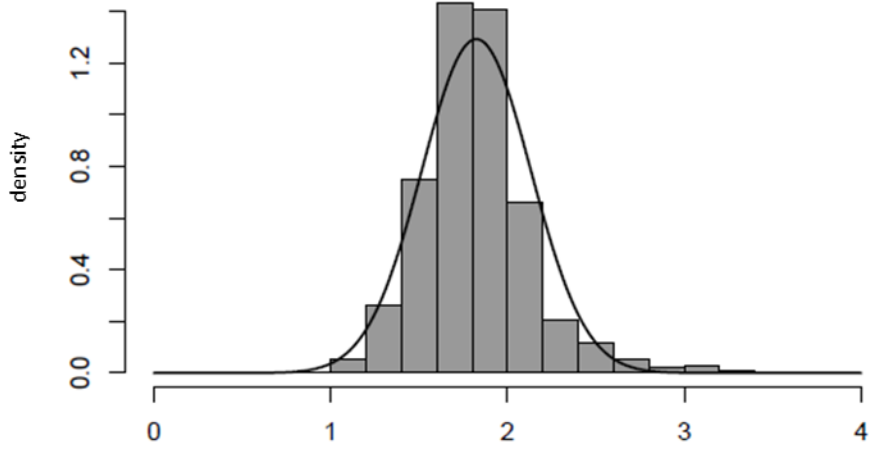


Figure 1.4. Histograms of the log of non-zero acoustic densities by ESDU for 2008 and 2009, with normal density distributions overlaid.

2008



2009

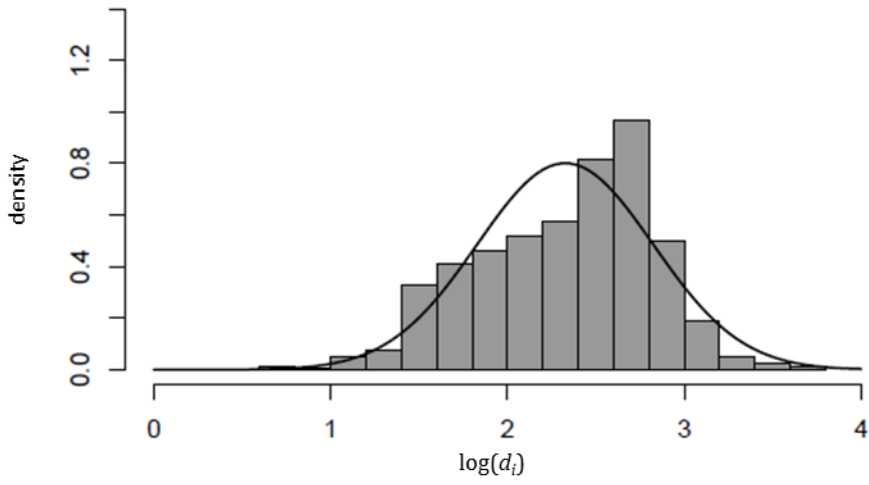


Figure 1.5. Histograms of the log of the upper depth limits of aggregations for 2008 and 2009, with normal density distributions overlaid.

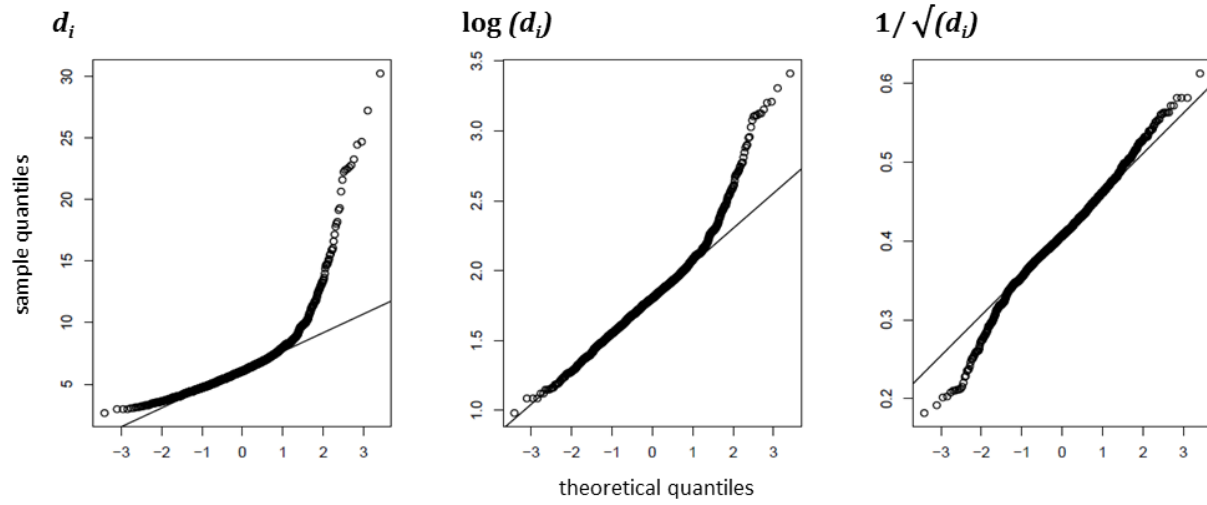
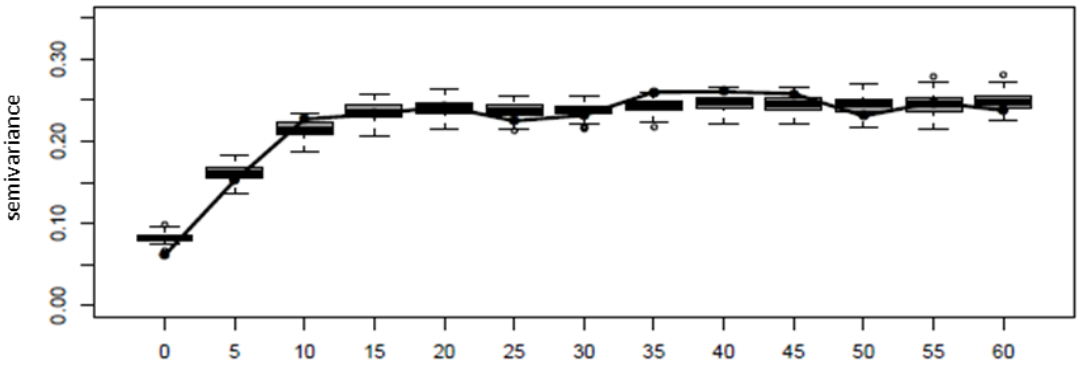
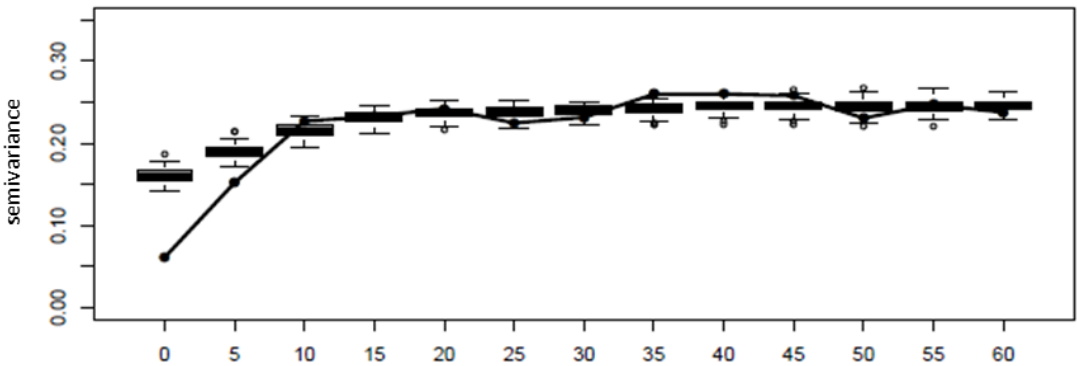


Figure 1.6. QQ plots of the upper depth limits of aggregations in 2008.

Indicator simulation



Binomial model



Integrated model

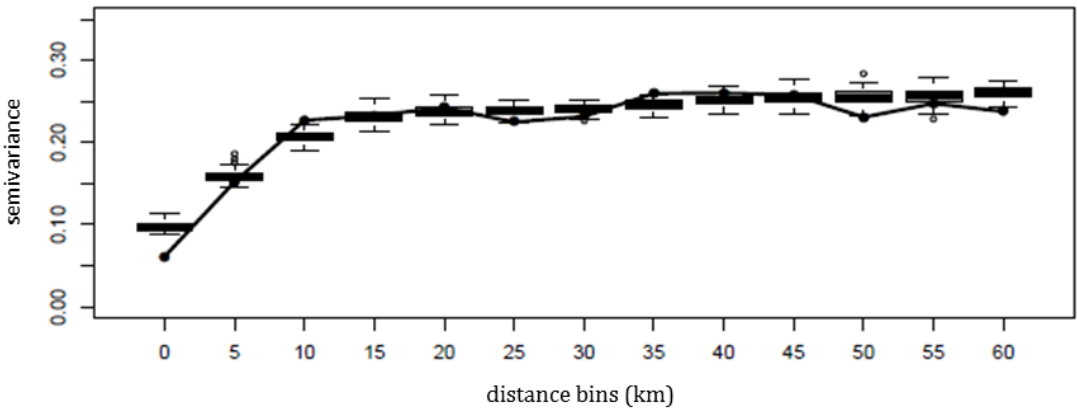
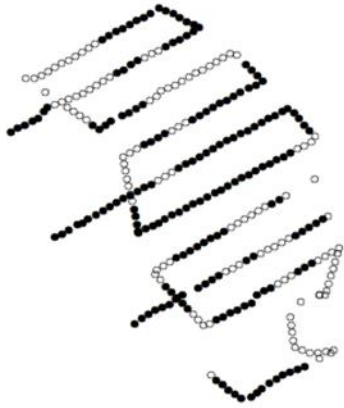


Figure 1.7. Reproduction of the spatial pattern of the presence/absence process in 2008. Box plots represent summaries of empirical indicator variograms computed from conditional simulation results. The black line represents the empirical indicator variogram for the observed data.

Observed data



Indicator simulation



Binomial model



Integrated model



Figure 1.8. Observed data and sample simulations for the presence/absence process in 2008. Black points indicate presence, white indicates absence.

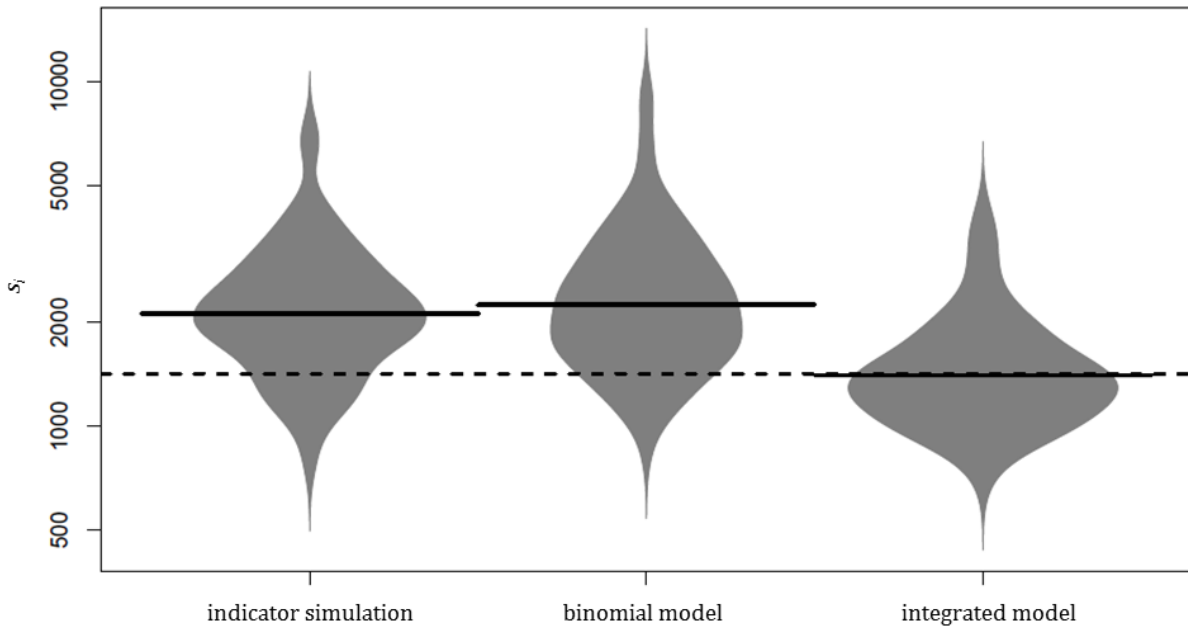
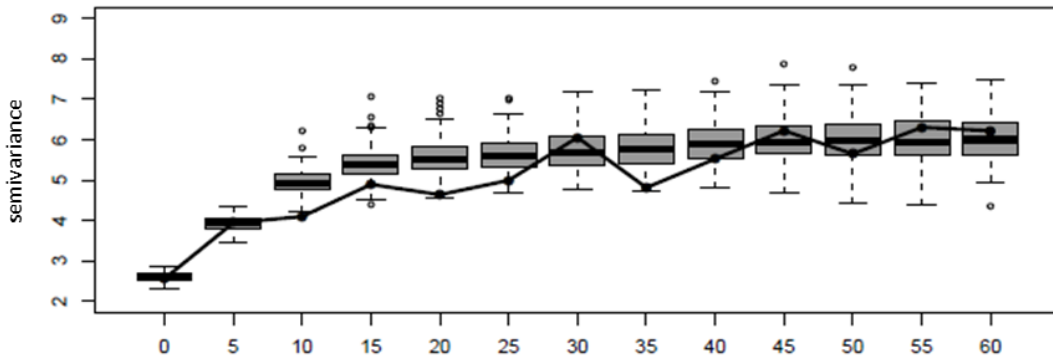
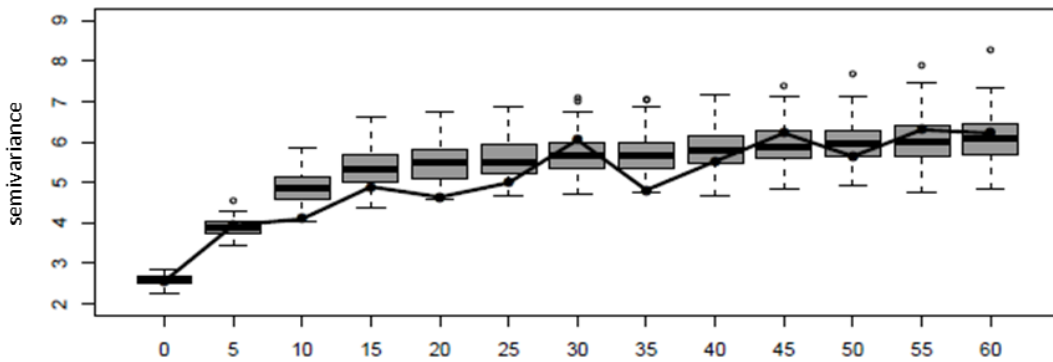


Figure 1.9. Comparison of the means of geostatistical simulations (non-zero values only) with the mean of the observed non-zero data (dashed line) in the original data space.

Indicator simulation



Binomial model



Integrated model

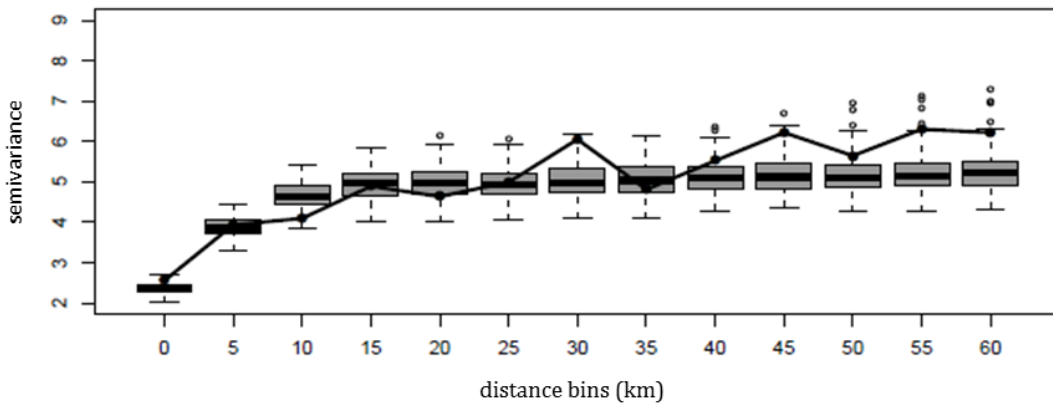


Figure 1.10. Reproduction of the spatial pattern of non-zero acoustic densities in log-space. Box plots represent summaries of empirical variograms computed from conditional simulation results. The black line represents the empirical variogram for the observed data.

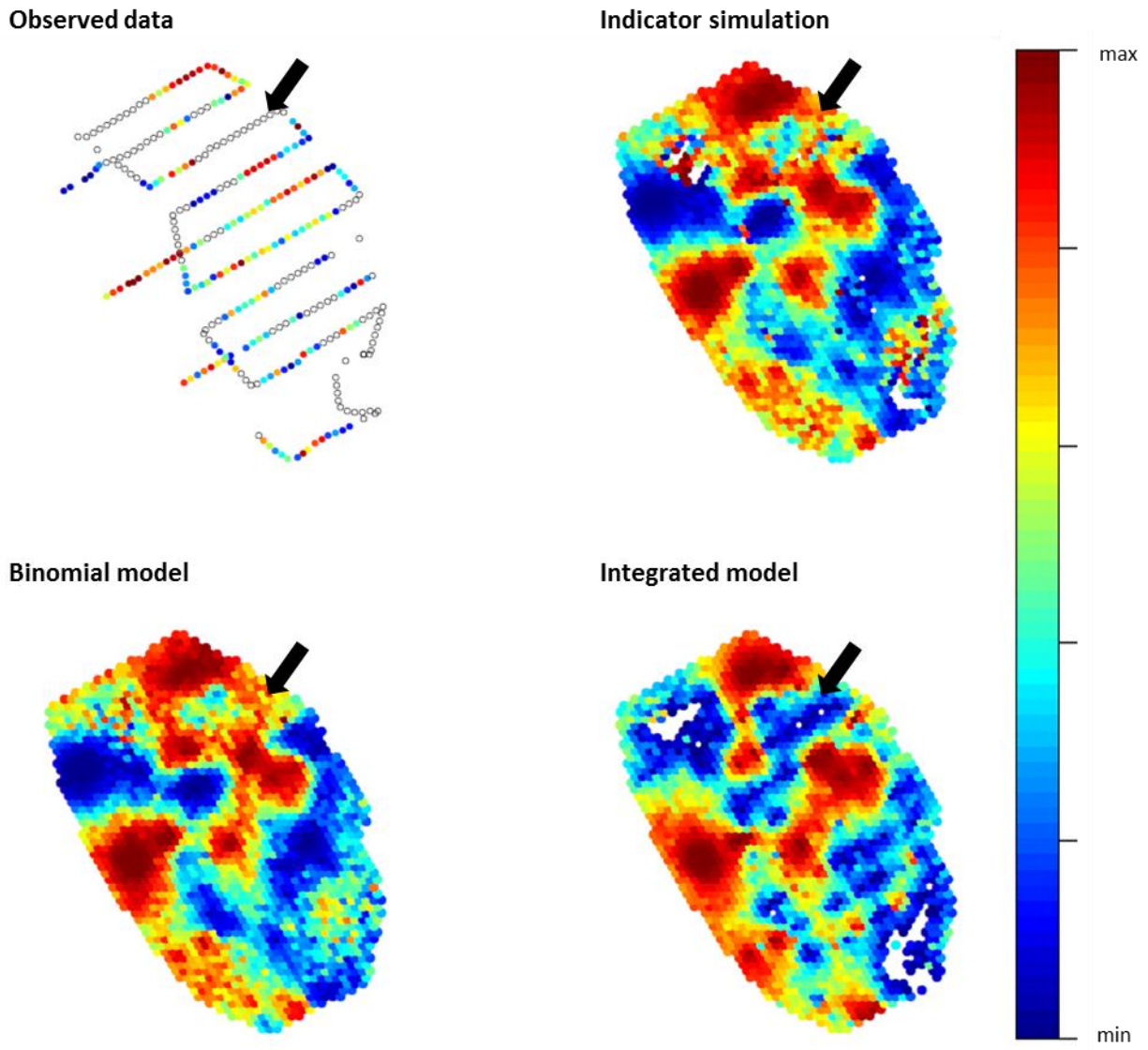
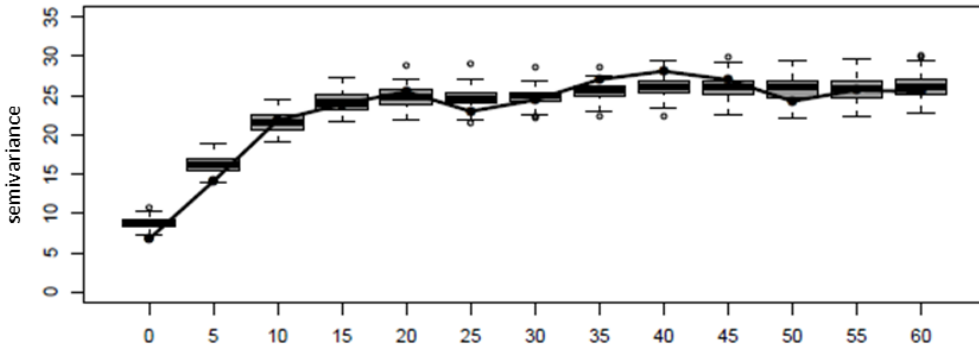
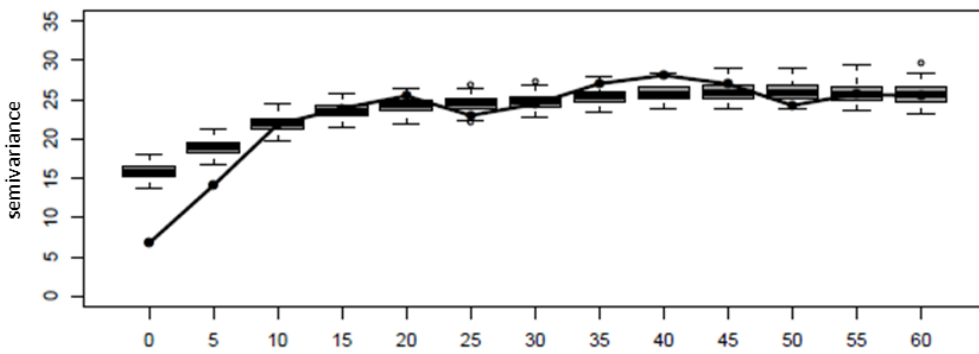


Figure 1.11. Observed data and means of conditional simulations in log-space. The arrows indicate an area where the survey returned zero values for anchoveta, and the integrated model generally simulates low values (if any), while the two-stage models may simulate relatively high values. (Plots are based on quantiles calculated for each set of simulations separately.)

Indicator simulation



Binomial model



Integrated model

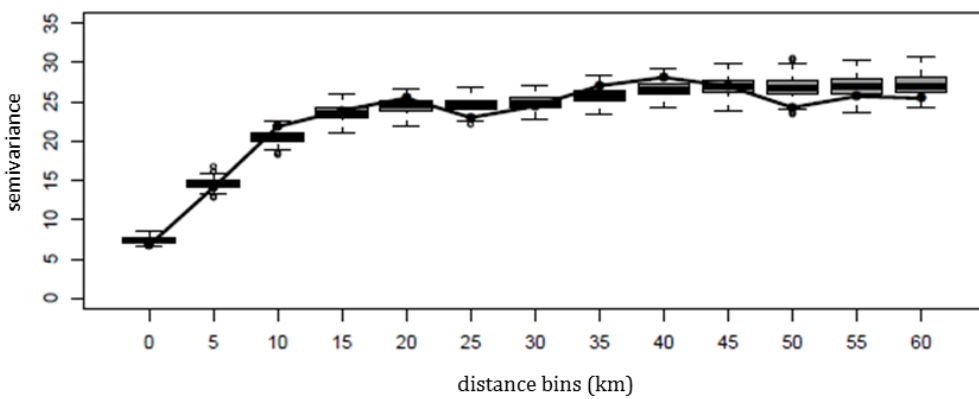


Figure 1.12. Reproduction of the spatial pattern of anchoveta. Box plots represent summaries of empirical variograms computed from conditional simulation results. The black line represents the empirical variogram for the observed data. Variograms are presented in log-space to facilitate comparison. All zero observations and simulated values were converted to a small value prior to log-transformation.

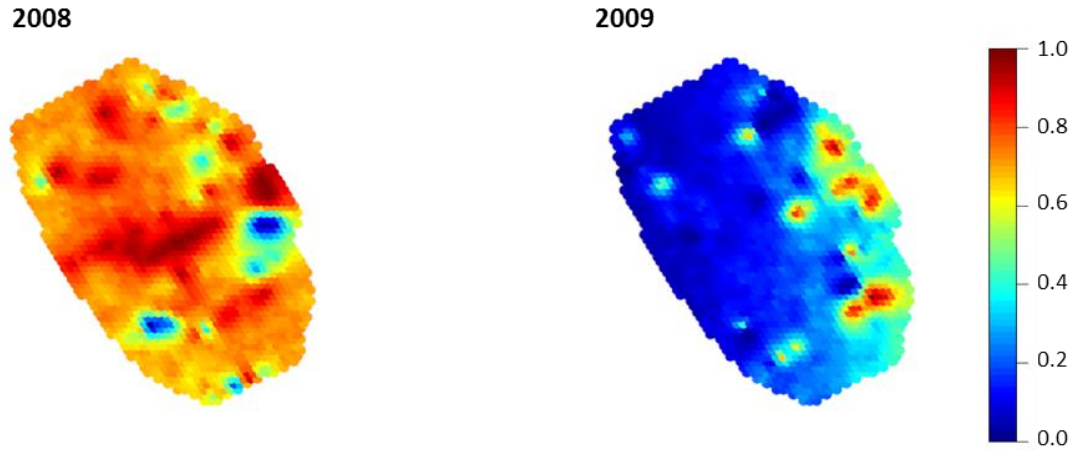
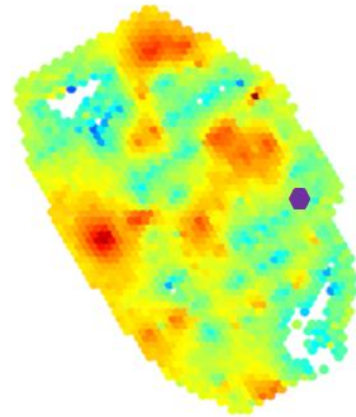
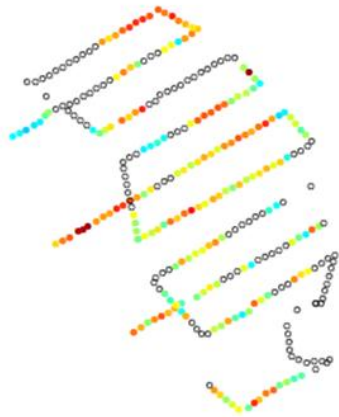
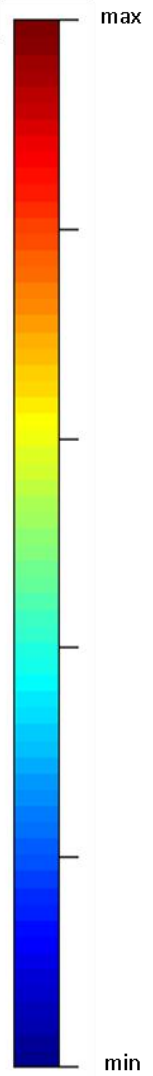
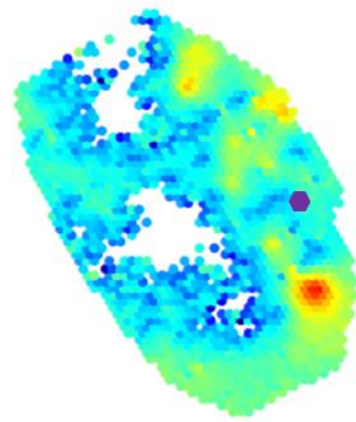
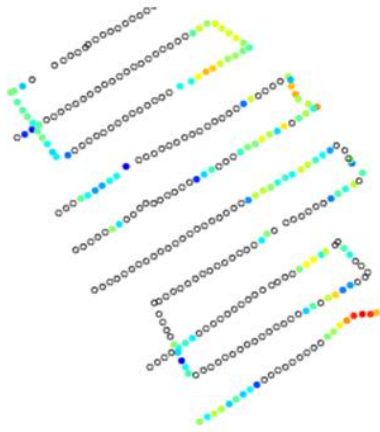


Figure 1.13. Mean probability that the upper depth limit of aggregations is less than 7.5 m based on conditional simulations. (The threshold of 7.5m was selected as indicative of the upper surface waters.)

2008



2009



observed data

integrated model

Figure 1.14. Observed data and means of conditional simulations of relative abundance for 2008 and 2009. (Classification is based on equal intervals and is the same for both years.) The colony is indicated by a purple hexagon in the simulation plots.

Chapter II: Analysis of the movement patterns of Peruvian Boobies

Introduction

Analysis of animal movement patterns can provide insights into interactions between animals and their environment (Schick et al. 2008). Movement processes (such as speeds and turning angles) are observable, and represent a response to the environment mediated by an individual's internal state or motivation, and bounded by its physiological capabilities (Nathan et al. 2008).

Seabirds and other foragers searching for patchily-distributed prey often exhibit area-restricted search (ARS) patterns, in which periods of relatively fast and directed movement associated with travel behavior are distinguished from slower more sinuous movement patterns associated with fine-scale searching and active foraging behavior (Kareiva and Odell 1987). Analysis of ARS patterns has been used to investigate the scales of interaction between seabirds and resources and identify foraging locations (e.g. Pinaud and Weimerskirch 2005, Fauchald and Tveraa 2006, Suryan et al. 2006).

Variation in time spent in different movement modes may be a response to variation in the foraging environment. Analysis of seabird movement patterns could provide insights into variation in foraging effort and foraging costs in response to changes in the environment. Here, a simple energetics-based model was developed to provide a conceptual framework for analyzing variation in time allocation within foraging trips. To be sustainable, the foraging trips of breeding seabirds must enable them to maintain their own body condition, provision young, and replace energy expended during foraging trips (Ydenberg 2007). Thus, over time,

$$\alpha T_f = E_b + e_t T_t + e_f T_f + E_p \quad 2.1$$

where daily energy intake is a function of time spent foraging per day (T_f) and energy intake per unit of time spent foraging (α); and daily energy expenditure comprises energy required to meet daily field metabolic requirements at the colony (E_b), additional energy required to compensate for energy expended during broad-scale search and travel ($e_t T_t$ where T_t is total time spent on broad-scale search and travel per day), additional energy required to compensate for energy expended during fine-scale search and foraging ($e_f T_f$), and energy used to provision young (E_p). All energy components (i.e. E_b , E_p , e_f , e_t) may be measured in terms of basal metabolic rate.

Changes in the abundance and distribution of prey may lead to changes in energy expenditure through changes in the broad-scale search and travel time required to locate food (T_t) and/or to changes in energy intake through changes in catch per unit effort or energy value per item captured (α , CPUE). There are two main ways in which birds can respond. They may increase foraging effort, for example increasing time spent foraging (T_f) to compensate for reduced CPUE or additional energy expenditure associated with increased broad-scale search and travel time. However, if they are operating close to time or energy thresholds and are unable to increase foraging effort, the energy invested in maintaining adult body condition or provisioning must be reduced. As long-lived species, seabirds are expected to adjust provisioning before compromising their own body condition and survival potential (Stearns 1992). For example, two separate studies found that Common Murre (*Uria aalge*) chicks fledged at low weights when prey was scarce, indicating reduced investment in provisioning (Piatt et al. 2007, Burke and Montevecchi 2009). Provisioning rates are influenced both by the amount of food delivered at the end of each foraging trip and the frequency of foraging trips (Boyd 1999, Pinaud et al. 2005, Costa 2008). For example, longer foraging trips by Yellow-nosed Albatross (*Thalassarche chlororhynchos*) led to reduced meal frequency, but no change in meal size, resulting in reduced provisioning rates (Pinaud et al. 2005).

Within the ARS framework, animal movement patterns can be modeled as a combination of random walks or movement modes characteristic of different behaviors. Hidden Markov models (HMMs) can be used to partition tracks into distinct movement modes. Morales et al. (2004) developed a series of models to partition the tracks of elk (*Cervus elaphus*) into one, two or three random walks. HMMs have also been used to partition tracks into distinct movement modes for caribou (*Rangifer tarandus*) (Franke et al. 2004), wolves (*Canis lupus*) (Franke et al. 2006), leatherback turtles (*Dermochelys coriacea*) (Jonsen et al. 2007, Bailey et al. 2008), and fishing vessels (Vermard et al. 2010, Walker and Bez 2010). This chapter presents the first application of an HMM to seabird movement patterns.

An HMM was developed to partition the tracks of Peruvian Boobies into multiple movement modes to inform the individual-based foraging model (IBFM) and investigate variation in time allocation within foraging trips. Following the ARS framework, fast, directed movement patterns are interpreted as indicative of travel or broad-scale search behaviors, and slow, sinuous movement patterns as indicative of fine-scale search or foraging behaviors (including resting on the water after diving). The tracks for Peruvian Boobies, recorded by high-resolution global positioning systems (GPS), are characterized by occasional gaps in the regular sequence

of GPS observations. These are shown below to correspond to diving behavior (see also Wanless 1993), and this information was incorporated in the HMM. The HMM provides estimates of movement parameters in different movement modes as the basis for simulating movement processes in the IBFM.

Variation in time spent in different movement modes was then explored to see whether this could provide insights into the processes underpinning variation in foraging effort by central place foragers. In particular, the extent to which seabirds adjust the amount of time spent foraging to compensate for variation in travel time was investigated to guide development of the IBFM. A series of models of time allocation was developed based on Equation 2.1, including a null model in which the amount of time spent in modes associated with fine-scale search and foraging is similar for all trips, a model in which time spent foraging increases as a function of time spent in travel or broad-scale search to compensate for additional energy expenditure, and models in which treatment effects allow for variation in energy invested in adult body condition or provisioning, or in energy gain per unit of time spent foraging. Each model was then compared in terms of how well it is supported by the HMM results.

Data

GPS instruments were fitted to breeding Peruvian Boobies at Isla Guañape Sur in 2007 and at Grupo Pescadores in 2008 (Fig. 2.1). These site/year combinations are considered separate treatments. In 2007, 35 individuals were successfully tracked using GPS (Gipsy GPS, Technosmart, Rome, Italy, 25-30g) recording at 1-second intervals, and 11 individuals in 2008. In both years, additional individuals were tracked at 2 second or 30 second intervals. The decision to use only tracks recorded at 1-second intervals was designed to maximize data consistency.

Each track was split into trips by excluding observations within a threshold distance (2 km) from the starting location of each track (Fig. 2.2). The distance threshold was based on examination of histograms of the distances of observations from the starting point of each track. At distances of up to 2 km, there are high densities of observations in all tracks, attributable to birds resting or milling about at or near the colony. Beyond 2 km, the density of observations drops off as birds are mostly traveling to or from foraging locations. This method is similar to that described by Boersma et al. (2009) for detecting the distance from the colony at which Magellanic Penguins (*Spheniscus magellanicus*) engage in foraging activity.

Trips were then filtered to exclude incomplete trips, trips where the bird spent the night or rested for 15 minutes or longer on land, trips with gaps in the GPS record greater than two

minutes, and trips of less than 15 minutes. (Trips with long resting periods or gaps in the GPS record would undermine parameter estimation for active birds, in particular estimation of transition parameters (see below).) For 2007, 33 trips by 28 individuals were included in the HMM; and for 2008, 28 trips by 11 individuals.

For species such as Peruvian Boobies, which may make one or more foraging trips per day, analysis of variation in foraging effort per day is more appropriate than analysis of variation per trip. For the analysis of variation in time allocation within foraging trips, the unit of analysis was therefore a 'complete foraging day'. Only data from individuals tracked from at least 7.30 am to 5.00 pm local time were included in this analysis. Birds may leave the colony earlier and return later than these cut-off times. However, birds on the nest at these times have most likely not yet embarked on a foraging trip or have returned for the night. Days on which the bird spent the night away from the colony and days with incomplete trips were excluded. For 2007, 11 complete foraging days were recorded, comprising 15 trips; for 2008, seven complete foraging days were recorded, comprising 14 trips.

Methods

Gaps in the GPS record

The 1-second GPS tracks were characterized by occasional gaps in the regular sequence of observations. The GPS cannot receive a satellite signal while the bird is submerged. These gaps may therefore be indicative of diving behavior. This hypothesis was tested using data from Isla Guañape Sur in 2007. In this year, 15 birds were fitted with both GPS and Time Depth Recorders (TDRs, G5, Cefas Technology, Lowestoft, UK, 3g; nominal resolution 0.03 dbar), providing independent data on diving activity for 19 foraging trips. TDRs are calibrated so that the pressure at sea-level is 0 dbar, but this calibration may drift over time. In this analysis, pressure greater than 1 dbar threshold (indicating a depth of 1m below the sea surface) is considered strongly indicative of dive activity. Applying this 1 dbar threshold can reduce measurement error associated with drift, and remove superficial bathing activity from the analysis. Overall, 0.1% of recorded GPS observations and 28.0% of missing GPS observations were associated with pressure greater than 1 dbar.

For each trip, gaps in the GPS record were identified and the maximum pressure recorded by the TDR during this interval was noted. In total, 402 gaps in the GPS record were identified. Of these, 277 (68.9%) coincided with pressure values greater than 1 dbar.

Hidden Markov model

Movement modes

In the HMM, a seabird is assumed to have a true, but unknown, movement mode at each observed location. This movement mode gives rise to an expected movement pattern (i.e. combination of distance to the next location and turning angle between locations), subject to process error. Observations of locations are here assumed to be measured without error, given the precision of modern GPS. In this application, the HMM was formulated with three true movement modes and one ‘pseudo-mode’. Based on the earlier finding that gaps in the GPS record are indicative of diving, this information was incorporated explicitly into the HMM. All observations with incomplete data were automatically assigned to the pseudo-mode (Mode 0), and no observations with complete movement data were assigned to this mode.

Three true movement modes were used, being the minimum necessary to capture the range of observed movement patterns. The HMM was initially developed with two true movement modes. A slow, sinuous mode, and a faster mode including both sinuous and directed movement patterns emerged. A third mode was therefore added, allowing three distinct movement modes to emerge: a slow sinuous mode (Mode A), a medium speed sinuous mode (Mode B), and a fast directed mode (Mode C). Together, Modes 0, A, and B are interpreted as indicative of fine-scale search and foraging behavior, while Mode C is interpreted as indicative of travel and broad-scale search behavior.

Model structure

In the HMM, the unobserved or hidden movement mode at each location is assumed to be the outcome of a stochastic Markov process, such that the probability distribution of the movement mode at time t depends only on the mode of observations at time $t - 1$ or $t + 1$ and not on any preceding or subsequent observations. The probability of each observation being in a specific movement mode can then be estimated based on the observed movement pattern.

Within a Bayesian framework, the probability of each observation being in a particular mode (e.g. mode x of M possible modes) depends on the likelihood of the data under each mode for each observation, on priors derived from the probable state of preceding and subsequent observations, and on the probability of switching among modes.

$$P(\text{mode}_t = x | D_t) = \frac{L(D_t | \text{mode}_t = x) P(\text{mode}_t = x)}{\sum_{m=1}^M L(D_t | \text{mode}_t = m) P(\text{mode}_t = m)} \quad 2.2$$

In this application, the likelihood of the data is the product of the likelihood for the observed distance traveled between times t and $t + 1$ (modeled using a Weibull distribution), and that for the observed turning angle between times t and $t + 1$ (modeled using a wrapped Cauchy distribution). These distributions were chosen because of their flexibility. The Weibull distribution is a continuous probability distribution, defined over the range 0 to ∞ , with a more flexible shape than the lognormal distribution (Johnson et al. 1995). The wrapped Cauchy is a symmetrical unimodal circular distribution, which converges on the uniform circular distribution when the persistence parameter $\rho \rightarrow 0$, and on a point distribution centered on the mean direction when $\rho \rightarrow 1$ (Fisher 1993). For all modes, the mean direction was assumed to be 0, so only ρ was estimated. There are therefore three movement parameters for each true movement mode (i.e. the scale and shape of the Weibull distribution and the persistence parameter for the wrapped Cauchy distribution). There are several constraints on the movement parameters. The scale and shape parameters must be greater than zero while the persistence parameters must fall within the range 0 to 1.

In addition to the movement parameters, the HMM includes transition parameters to define the matrix $P(m \rightarrow x)$. In this application the matrix is 4×4 (Table 2.1) with twelve free parameters, given that the transition parameters for each mode must sum to 1. For the purposes of investigating variation in time allocation within foraging trips among years, the propensity to switch between modes was allowed to vary by year by incorporating a fixed year effect on all transition parameters, while the parameters of the Weibull and wrapped Cauchy distributions for each mode were assumed to be time-invariant.

Model parameters were estimated using a forwards-backwards algorithm to compute the total likelihood of each observation with complete movement data. The model was run forwards, with priors for the movement mode of observation t based on the probability of movement modes at observation $t - 1$, and backwards, with priors for the movement mode of observation t based on the probability of movement modes at observation $t + 1$:

$$P_{forward}(mode_t = x) = \sum_{m=1}^M P(mode_{t-1} = m | D_{t-1}) \cdot P(m \rightarrow x) \quad 2.3$$

$$P_{backward}(mode_t = x) = \sum_{m=1}^M P(mode_{t+1} = m | D_{t+1}) \cdot P(x \rightarrow m) \quad 2.4$$

where $P(m \rightarrow x)$ is the probability of changing from mode m to mode x . The likelihood of each observation given the model is then computed as the sum of the joint likelihoods of the observation being in each mode, given the forwards and backwards priors, i.e.:

$$L(D_t|\underline{\theta}) = \sum_{m=1}^M L(D_t|mode_t = m).P_{forward}(mode_t = m).P_{backward}(mode_t = m) \quad 2.5$$

where $\underline{\theta}$ is a vector of model parameters determining the Weibull and wrapped Cauchy distributions as well as the transition parameters. The total likelihood for the HMM is the product of the likelihood over all observations.

Model evaluation and comparison

For high temporal resolution GPS data, subsampling may be advantageous to reduce noise to signal ratios and computational demands (Turchin 1998, Ryan et al. 2004). As mentioned above, in 2007, 15 birds were fitted with both GPS and TDR devices, providing independent data on diving activity for 20 foraging trips. To evaluate the subsampling intervals and modeling approach, these trips were subsampled at 2 second, 5 second, 10 second, 20 second, and 30 second intervals. The HMM was then applied to each dataset, and the observed distance and turning angle between each subsampled location were assigned to the most probable movement mode under the maximum likelihood parameter estimates. The model was implemented in AD Model Builder (ADMB Foundation, <http://admb-foundation.org>).

HMM results were considered consistent with observed data if at least one observation occurring during a dive recorded independently by TDR with a 1 dbar threshold (n = 344) was assigned to one of the modes associated with fine-scale search and foraging behavior (i.e. Modes 0, A or B). As a further test, dives were randomly repositioned within each trip, and consistency between the HMM results for the observed data and randomly-repositioned dives was tested. For the set of 344 observed dives, each dive was repositioned by drawing a new start time at random from a uniform distribution bounded by the start and end times of the trip. No changes were made to dive durations. This randomization process was repeated 100 times.

Once a subsampling interval had been selected, the HMM was run on the full dataset for 2007 and 2008, with and without fixed treatment effects on transition parameters. The models with and without treatment effects were then compared using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002).

Variation in time allocation within foraging trips

To provide context to the analysis of variation in time allocation within foraging trips, the maximum distance from the colony and foraging trip duration beyond the 2 km threshold were computed for all trips included in the HMM. The number of trips per day and total time spent away from the colony were also computed for all 'complete foraging days'.

To assess variation in time allocation within foraging trips, each observed location was assigned to the most probable movement mode under the maximum likelihood parameter estimates. For each trip, the numbers of observations assigned to modes indicative of fine-scale search and foraging behavior (i.e. Modes 0, A or B), versus the mode indicative of broad-scale search and travel behavior (i.e. Mode C) were then computed, and designated T_{slow} and T_{fast} respectively. Monte Carlo Markov chain (MCMC) simulations indicated that this partitioning was robust to parameter uncertainty (results not shown). Seven models were then applied to these results, assuming that errors between model predictions and observations are normal (Table 2.2). For comparison, variation in the number of dives per foraging day, using the number of gaps in the GPS record (N_{gap}) as a proxy for the number of dives, was also analyzed, using the same seven models and assuming a negative binomial distribution.

In the null model (Model 1), time spent in behaviors associated with fine-scale search and foraging (T_{slow}) is constant, consistent with fixed foraging effort. In Model 2, a treatment effect on the intercept allows for variation in fixed foraging effort among treatments. In Model 3, foraging effort may adjust to compensate for energy expended during variable broad-scale search or travel time (T_{fast}). Model 4 is similar to Model 3, but allows for additional inter-treatment variation in foraging effort. Model 5 allows for inter-treatment variation in the foraging effort required to compensate for time spent in broad-scale search and travel. The full model (Model 6) allows for inter-treatment variation in foraging effort required to compensate for time spent in broad-scale search and travel, and additional inter-treatment variation in foraging effort. The final model (Model 7) combines these treatment effects into a single parameter, applied to both the fixed and variable components. This model is consistent with inter-treatment variation in CPUE and variation in foraging effort to compensate for variable time spent in broad-scale search or travel mode. For all models that include T_{fast} as an explanatory variable, the data were assumed to be normally-distributed about the model predictions with constant variance. The different models were compared using Akaike's Information Criterion corrected for small samples (AICc).

Results

Hidden Markov model

The HMM performed best when applied to data subsampled at 2-, 5- or 10-second intervals based on evaluation against dives recorded independently by TDRs (Table 2.3). The HMM performed worst when applied to 1-second interval data. This may reflect a high noise to signal ratio in the 1-second data attributable to oversampling, as discussed by Turchin (1998). Based

on these results, the 10-second interval was selected for subsampling Peruvian Booby data, given the additional computational demands of working at 2- or 5-second intervals. A total of 344 dives were identified by TDR with a 1 dbar threshold. Of these dives, 272 (79.1%) were indicated by a gap in the GPS record during the dive. At the 10-second subsampling interval, the HMM assigned at least one observation to a mode indicative of fine-scale search or foraging (i.e. Mode 0, A or B) during 342 of 344 dives (99.42%). In comparison, when dives were randomly repositioned within trips, an average of 44 of 344 randomly-placed dives (12.8%) overlapped with an observation in Mode 0, A or B over the course of 100 simulations (range: 28-64 dives).

When the HMM was applied to data from both 2007 and 2008, the HMM with fixed treatment effects on transition parameters has greater support from the data than the HMM without treatment effects, as indicated by AIC ($\Delta AIC = 164.4$). Figure 2.3 shows the fit of estimated distance and turning angle distributions to observations assigned to different movement modes by the HMM. The estimates for different movement modes (Table 2.4) provide the basis for simulating movement patterns in the IBFM.

Variation in time allocation within foraging trips

Peruvian Boobies at Isla Guañape Sur in 2007 traveled farther from the colony and foraging trips were longer than for conspecifics at Grupo Pescadores in 2008 (Table 2.5). Most birds at Isla Guañape Sur in 2007 undertook one foraging trip per day, whereas most birds at Grupo Pescadores in 2008 undertook two trips per day. Nonetheless, birds at Isla Guañape Sur spent more time away from the colony per day than those at Grupo Pescadores.

Gaps in the GPS record indicate that Peruvian Boobies from Isla Guañape Sur in 2007 undertook about 25% more dives per day, but spent nearly twice as much time diving per day as conspecifics from Grupo Pescadores in 2008 (Table 2.5). Estimates of dive time are based on a count of the number of 'missing' 1-second locations from the raw GPS record. In some cases, the GPS may take a few seconds to recover the satellite signal once a bird resurfaces, so these values may present an over-estimate of the amount of time spent diving per day.

At the maximum likelihood estimates, HMM output indicates that birds at Isla Guañape Sur in 2007 spent an average of 79 minutes in movement modes indicative of fine-scale search and foraging (Modes 0, A and B) per day, and 132 minutes in the movement mode indicative of travel per day; whereas birds at Grupo Pescadores in 2008 spent an average of 35 minutes in modes indicative of fine-scale search and foraging, and 103 minutes in the mode indicative of

travel. While birds at Isla Guañape Sur traveled more than twice as far and foraging trips were more than twice as long as for birds at Grupo Pescadores (Table 2.5), they spent only a third more time travelling per day than birds at Grupo Pescadores because they averaged fewer trips per day. The HMM results indicate that time away from the colony was longer for birds at Isla Guañape Sur, in part, because they were spending more than twice as much time engaged in fine-scale search and foraging.

When foraging effort is measured in terms of the number of gaps in the GPS record (N_{gap}), the model with greatest support from the data, Model 3, is consistent with variation in the number of dives per day in response to variation in time spent traveling (Table 2.2). The data do not support any of the models that allow for treatment effects (i.e. Model 2 and Models 4-7). In other words, the data do not support the hypothesis of a change in CPUE or change in investment in provisioning or adult body condition between treatments.

However, when foraging effort is measured in terms of time spent in movement modes indicative of fine-scale search and foraging (T_{slow}), a different pattern emerges. Model 5, which includes treatment effects on the response to travel time, and Model 7, which includes a response to travel time and applies the same treatment effect to both the fixed and variable explanatory components, had the greatest support (Table 2.2). Model 7 is consistent with variation in foraging effort to compensate for variation in travel time and variation in CPUE, and has the simpler ecological interpretation of the two models.

Discussion

Modeling movement patterns

In this chapter, GPS tracks for Peruvian Boobies were partitioned into multiple random walks using an HMM. This is the first application of an HMM to the movement patterns of seabirds. The HMM partitioned the tracks of Peruvian Boobies in 2007 and 2008 into three distinct movement modes (Fig. 2.3). Mode A is a slow and sinuous mode (modal speed = 1.11 km/hour). It often, but not always, immediately follows a gap in the GPS record indicative of diving. This mode is interpreted as closely associated with diving for prey, including resting on the sea surface after diving. Mode B is also sinuous, but considerably faster (modal speed = 25.26 km/hour). This mode is consistent with birds in flight slowing down to search for prey or circling above a prey school. In contrast, Mode C is fast and directed (modal speed = 52.23 km/hour), consistent with broad-scale search and travel behaviors. Camphuysen (2011) reports on ship-based surveys in which the behaviors of Northern Gannets (*Morus bassanus*) in the North Sea were classified into 20 types of foraging behavior and 16 types of non-foraging

behavior. Commonly-observed behaviors included 'direct(ed) flight' and 'actively searching'. According to Camphuysen, "In the case of gannets, the difference between direct flight and searching for prey is obvious under field conditions. Travelling birds follow straight lines, with a fully stretched body and the bill pointing forward. Searching gannets have somewhat slower 'bouncing' wingbeat, they often look down, follow a more or less meandering path and/or circle over a given location. An incidental peer down into the sea by a bird otherwise clearly travelling was not recorded as 'searching'" (Camphuysen 2011, p. 63). Thus, the HMM partitioned the tracks of Peruvian Boobies into distinct movement modes consistent with observed movement patterns of sulids, although here travelling birds may also be engaged in broad-scale search. The HMM could be extended to allow for random effects at the day, individual, or trip level.

For Peruvian Boobies, joint analysis of GPS and TDR data showed that gaps in the GPS record were consistent with diving activity indicated in the TDR record. In this case, gaps in the GPS record are informative, and this information was incorporated directly into the HMM, rather than treated as measurement error. The HMM assigned GPS observations corresponding to diving activity to movement modes indicative of fine-scale search and foraging. These results compare favorably with efforts to identify the location of foraging activity by identifying regions of ARS using ARGOS tracking data (Robinson et al. 2007).

For large-bodied seabirds, information on foraging effort may be obtained directly by deploying multiple instruments on the same individual (as with the individuals jointly equipped with TDRs and GPS in this study). The method described here infers foraging behavior from movement patterns based on GPS data and provides a means to gain insights into time allocation during foraging trips for small-bodied birds that cannot support multiple instruments or when the cost of multiple instruments is a constraint. This adaptation could also be useful in the analysis of the movement patterns of other species where gaps in the GPS record provide information on behavior modes.

Variation in time allocation within foraging trips

Several studies have investigated variation in seabird foraging trip duration and colony attendance (e.g. Kitaysky et al. 2000, Davoren and Montevecchi 2003, Piatt et al. 2007), but relatively few have investigated time allocation within foraging trips (Lewis et al. 2004). Here, analysis of variation in time allocation within foraging trips was conducted for complete foraging days to allow for variation in foraging strategies among trips (see Weimerskirch et al. 1994). While this substantially reduces the sample size, the results demonstrate that this type of

analysis can provide insights into the processes underpinning variation in foraging effort by central place foragers.

Simple trip statistics indicate that the average maximum distance of foraging trips from the colony indicates that suitable foraging sites were farther from the colony for Peruvian Boobies at Isla Guañape Sur in 2007 than for conspecifics at Grupo Pescadores in 2008 (Table 2.5). Analysis of HMM results indicates that birds at Isla Guañape Sur in 2007 spent more time traveling per day than birds at Grupo Pescadores in 2008, despite undertaking fewer trips per day. Gaps in the GPS record indicate Peruvian Boobies at Isla Guañape Sur in 2007 undertook about 25% more dives per day than those at Grupo Pescadores in 2008 (Table 2.5). Analysis of HMM results indicates that birds at Isla Guañape Sur in 2007 spent more than twice as much time per day in movement modes indicative of fine-scale search and foraging than birds at Grupo Pescadores in 2008.

Based on the conceptual framework outlined above, two hypotheses are available to explain the greater foraging effort (i.e. number of dives and time allocated to fine-scale search and foraging) by Peruvian Boobies at Isla Guañape Sur in 2007. One hypothesis is that additional foraging effort was necessary to compensate for greater travel time. Green et al. (2010) found that, for the Australasian Gannet (*Morus serrator*), a close relative of the Peruvian Booby, flight is energetically expensive compared to resting at the colony. This implies that increased distances traveled during foraging trips must either be offset by increased energy intake or lead to reduced net energy gain. A second hypothesis is that the greater foraging effort observed at Isla Guañape Sur in 2007 was necessary to compensate for lower CPUE. Changes in CPUE may be an important component of variation in net energy gain from foraging but, unfortunately, for most marine predators, it is extremely challenging to collect data on CPUE.

The results of analysis of variation in the number of dives per day are consistent with the first hypothesis (i.e. a need to increase energy intake to compensate for increased energy expenditure while traveling). These findings are similar to those of Lewis et al. (2004) who investigated how foraging activity by Northern Gannets varied across trips with different durations, and found that dive rates were similar for trips with different durations. Unfortunately, no data are available for the present study to assess possible differences in prey capture rates per dive. However, for other plunge-diving sulids, prey intake has been linked to diving in at least 75% of cases (Hennicke et al. unpublished data cited in Ropert-Coudert et al. 2004), suggesting that the number of gaps in the GPS record may be a useful proxy for the number of prey captured. The longer dives undertaken by birds at Isla Guañape Sur in 2007

suggest that prey may have been deeper or otherwise harder to capture than at Grupo Pescadores in 2008.

The results of analysis of variation in the amount of time spent in movement modes indicative of fine-scale search and foraging per day are consistent with both hypotheses. After taking into account the need to increase energy intake to compensate for additional time spent in broad-scale search and travel, the additional time spent in fine-scale search and foraging suggests that birds at Isla Guañape Sur in 2007 found it harder to locate and target prey than birds at Grupo Pescadores in 2008.

Taken together, these results indicate that Peruvian Boobies at Isla Guañape Sur in 2007 needed to undertake more dives per day to compensate for increased energy expenditure during travel to and from foraging locations. Furthermore, they exerted greater foraging effort in terms of dive duration and time spent in fine-scale search and foraging. The population at Isla Guañape Sur in 2007 was considerably larger than that at Grupo Pescadores in 2008 (Weimerskirch, H., pers. comm.). Both the greater distances traveled and the additional foraging effort of birds at Isla Guañape Sur in 2007 may be a consequence of differences in the distribution and availability of prey between the two treatments and/or differences in colony size (see Lewis et al. 2001).

The analysis presented here demonstrates that analysis of movement patterns based on locational data can be tied to a simple energetics model (Equation 2.1) to investigate hypotheses about how seabirds adjust their foraging effort in response to variation in foraging conditions. This conceptual framework, and the analysis presented here, provide the basis for an integrated approach to the analysis of seabird foraging strategies in which identification of different behaviors is coupled with assessments of the costs of these activities in terms of time and energy (Wilson and Vandenabeele 2012).

Notation

α	rate of energy intake per unit of time spent foraging
β, γ, κ	parameters in models of variation in the structure of foraging trips
ρ	persistence parameter of the wrapped Cauchy distribution
$\underline{\theta}$	vector of model parameters, here parameters determining the Weibull and wrapped Cauchy distributions of all modes together with the transition parameters
D_t	the data at time t , i.e. the observed distance traveled between times t and $t+1$; and the observed turning angle between times t and $t+1$
E_b	energy required to meet daily field metabolic requirements at the colony
E_p	energy used to provision young
e_f	rate of energy expenditure during broad-scale search and travel
e_t	rate of energy expenditure during broad-scale search and travel
$L(\cdot)$	likelihood
M	number of possible modes
m	mode m
N_{gap}	the number of gaps in the GPS record
$P(\cdot)$	probability (prior or posterior)
$P_{backward}$	backwards prior
$P_{forward}$	forwards prior
T_f	time spent foraging per day
T_{fast}	total number of observations per foraging trip assigned to Mode C by maximum likelihood
T_{slow}	total number of observations per foraging trip assigned to Mode 0,A,or B by maximum likelihood
T_t	time spent on broad-scale search and travel per day
t	time step t
x	mode x
y	treatment y

Mode 0	'pseudo-mode' assigned to a time step with incomplete movement data (i.e. distance and/or turning angle), indicative of diving behavior
Mode A	slow, sinuous movement mode, indicative of fine-scale search and foraging behavior
Mode B	medium speed, sinuous movement mode, indicative of fine-scale search and foraging behavior
Mode C	fast and directed movement mode, indicative of broad-scale search and travel behavior

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Tables

Table 2.1. Transition parameters for the HMM.

From/To	Mode 0	Mode A	Mode B	Mode C	Total probability
Mode 0	pr (switch00)	pr (switch0A)	pr (switch0B)	pr (switch0C)	= 1
Mode A	pr (switchA0)	pr (switchAA)	pr (switchAB)	pr (switchAC)	= 1
Mode B	pr (switchB0)	pr (switchBA)	pr (switchBB)	pr (switchBC)	= 1
Mode C	pr (switchC0)	pr (switchCA)	pr (switchCC)	pr (switchCC)	= 1

Table 2.2. Models of variation in time allocation within foraging trips.

Model	Model	Number of parameters	N_{gap} ΔAIC_c	T_{slow} ΔAIC_c
1	$\sim \kappa$	2	1.81	4.18
2	$\sim \kappa_y$	3	4.11	1.52
3†	$\sim \kappa + \beta \cdot T_{\text{fast}}$	3	0.00	2.53
4	$\sim \kappa_y + \beta \cdot T_{\text{fast}}$	4	3.25	1.93
5	$\sim \kappa + \beta_y \cdot T_{\text{fast}}$	4	3.27	0.00
6	$\sim \kappa_y + \beta_y \cdot T_{\text{fast}}$	5	7.18	3.33
7††	$\sim \gamma_y \cdot (\kappa + \beta \cdot T_{\text{fast}})$	4	6.61	0.26

† Model 3 is a re-parameterization of Equation 2.1 in which $\kappa = \frac{1}{(\alpha - e_f)} \cdot (E_p + E_b)$; $\beta = \frac{e_t}{(\alpha - e_f)}$; and $T_{\text{fast}} = T_t$.

†† Similarly, Model 7 is a reparameterization and extension of Equation 2.1 in which $\gamma_y = \frac{(\alpha_0 - e_f)}{(\alpha_y - e_f)}$ where α_0 represents α in the baseline treatment.

Table 2.3. Evaluation of subsampling intervals. Model output was considered consistent with observed dives (identified by pressure greater than 1 dbar recorded by TDR) if one or more GPS observations during the dive were assigned to movement modes 0, A, or B.

Number of dives recorded	Number of dives with consistent model output					
	1 sec	2 sec	5 sec	10 sec	20 sec	30 sec
344	296	340	344	342	332	332
	84.05%	98.84%	100.00%	99.42%	96.51%	96.51%

Table 2.4. Movement parameters for different movement modes from the model with treatment effects on transition parameters. The scale parameter corresponds to the distance covered per minute measured over 10 second sampling intervals. CV refers to coefficient of variation

	distance (Weibull)		turning angle (wrapped Cauchy)
	scale (CV)	shape (CV)	persistence (CV)
Mode A	0.030 (0.010)	1.761 (0.013)	0.441 (0.022)
Mode B	0.519 (0.005)	2.479 (0.009)	0.377 (0.020)
Mode C	0.910 (0.001)	5.011 (0.004)	0.885 (0.001)

Table 2.5. Summary statistics for foraging trips and complete foraging days for Peruvian Boobies foraging from Isla Guañape Sur in 2007 and Grupo Pescadores in 2008.

	Isla Guañape Sur 2007	Grupo Pescadores 2008	p-value
Trip statistics (test):	(n = 33)	(n = 28)	
Mean maximum distance (Welch's t-test on log-transformed data)	44.69 km	19.67 km	3.14e-09
Mean foraging trip duration (t-test on log-transformed data)	170 minutes	65 minutes	1.16e-11
Day statistics (test):	(n = 11)	(n = 7)	
Mean number of dives (see Table 2.2)	39.3	31.6	
Mean time spent diving (t-test on log-transformed data)	4.97 mins	2.62 mins	0.051
Mean time away from colony (t-test on log-transformed data)	3.5 hours	2.3 hours	0.034
Number of trips per day:			
1 trip per day	63.64%	14.29%	
2 trips per day	36.36%	71.43%	
3 trips per day	0.0%	14.29%	

Figures

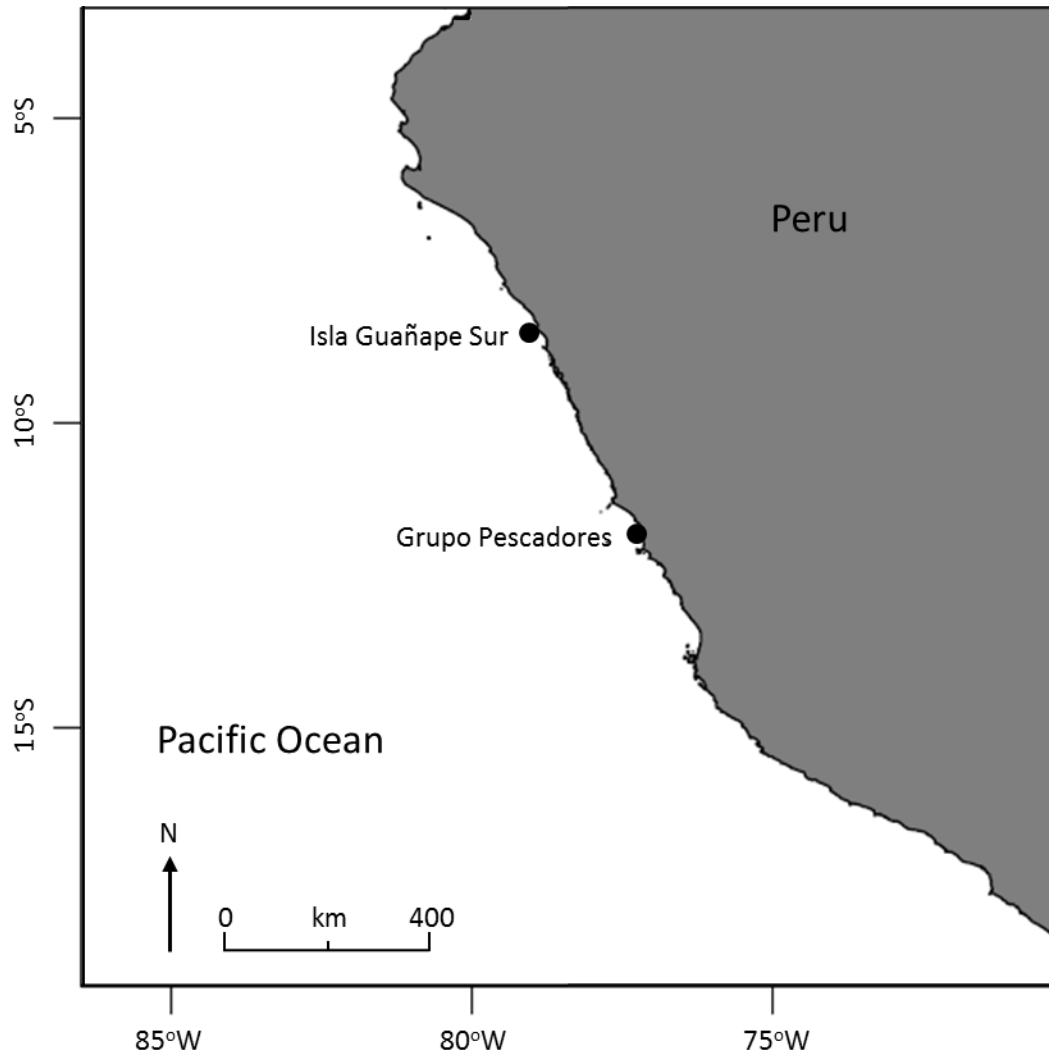


Figure 2.1. Coast of Peru with study sites indicated by black points.

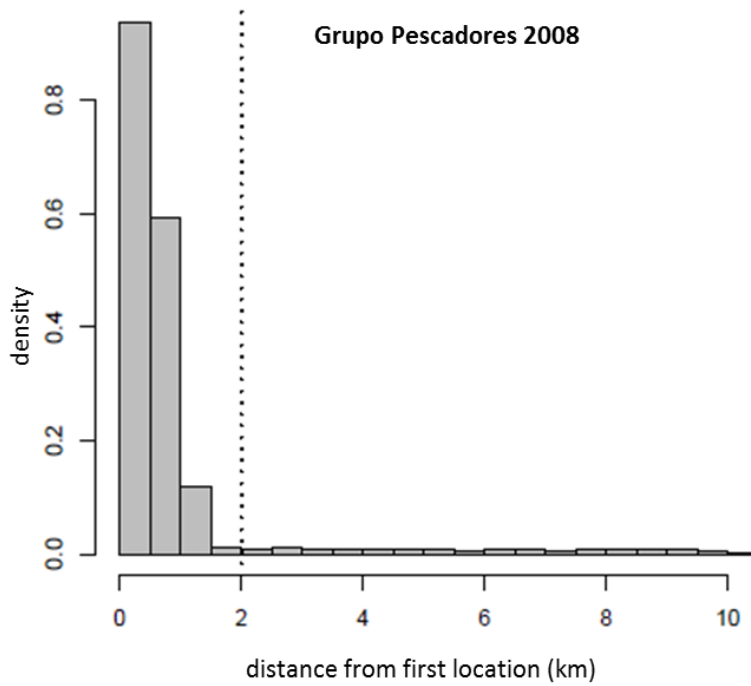
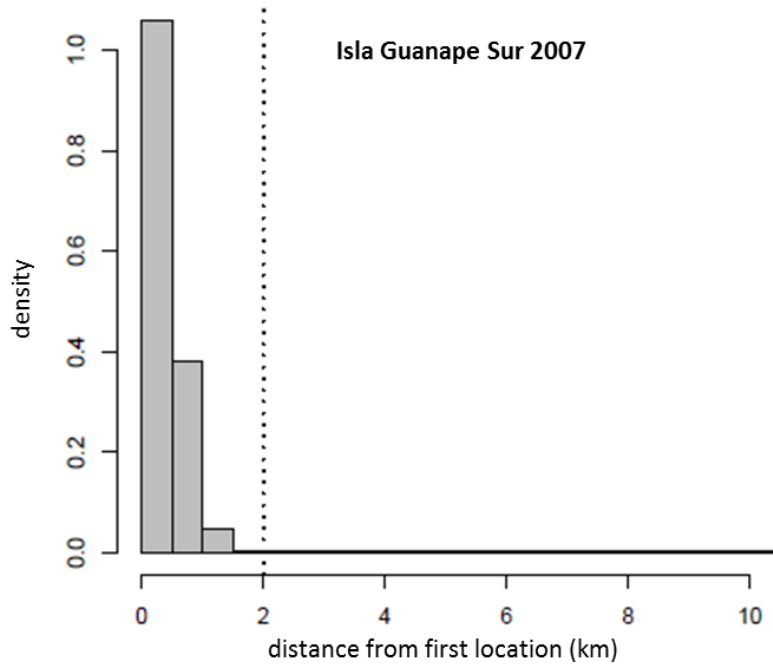
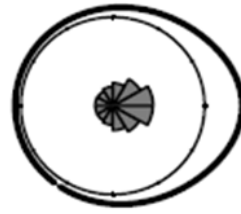
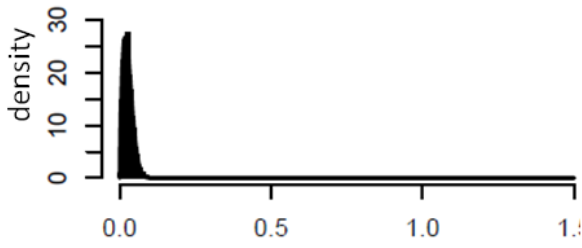
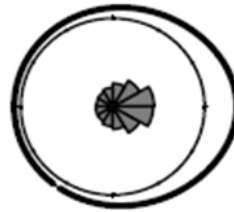
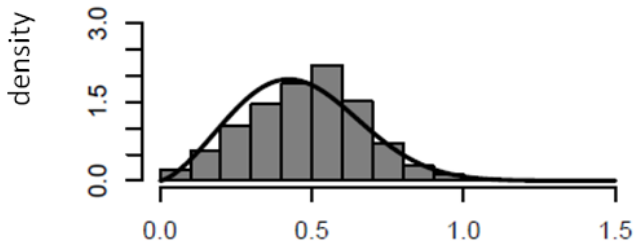


Figure 2.2. Histograms of frequency of observations by distance from the colony.

Slow mode (mode A)



Medium mode (mode B)



Fast mode (mode C)

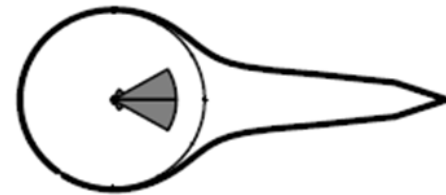
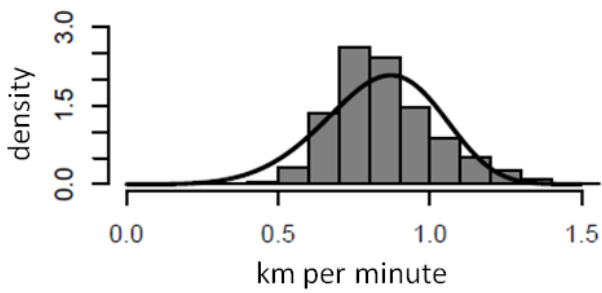


Figure 2.3. Observed and maximum likelihood-estimated distributions of distance travelled and turning angles in the slow (mode A), medium (mode B), and fast modes (mode C).

Chapter III: Foraging site selection by Peruvian Boobies and Guanay Cormorants

Introduction

Understanding the distribution patterns of species and the ecological processes underlying these patterns is a fundamental goal in spatial ecology (Levin 1992). These questions can be addressed by developing resource selection functions that predict the probability of a species' occurrence at a particular location as a function of resource attributes (Boyce et al. 2002). However, developing resource selection functions is challenging for species foraging in marine environments, as both predators and prey are often highly mobile and difficult to monitor (Redfern et al. 2006). New technologies, in particular global positioning system (GPS) data loggers, have enabled the collection of precise data on the locations of some marine species, especially central place foragers such as seabirds (Wilson et al. 2002). Location data have been mapped against remote-sensing data on environmental covariates and used to define foraging areas in terms of sea-surface temperature (SST), chlorophyll concentration, and other environmental variables (Redfern et al. 2006, Tremblay et al. 2009, Wakefield et al. 2009). Yet, in many cases, it is the relationship between predator and prey that is the process of interest. Models based on environmental covariates cannot provide information on this process if the distribution and attributes of prey are not effectively signaled by environmental covariates (Gremillet et al. 2008). Bertrand et al. (2004, 2005, 2008a, 2008b) have explored correlations between the movement patterns of fishing vessels and the spatial distribution of targeted fish stocks. Yet, to date, few studies have developed resource selection functions for marine predators based on the distributions and attributes of their prey.

This chapter presents a comparative analysis of foraging site selection by two species of seabird, the Peruvian Booby (*Sula variegata*) and Guanay Cormorant (*Phalacrocorax bougainvillii*), based on analysis of relationships between their movement patterns and the distribution of their main prey, Peruvian anchoveta (*Engraulis ringens*). Recent population trends for the two seabird species are strikingly different, with Guanay Cormorants exhibiting a substantial decline from around 21 million to 2 million birds since 1955, while populations of Peruvian Boobies have been comparatively stable at around 2 million birds (Jahncke 1998, Goya 2000, Weimerskirch et al. 2010). The analysis presented here provides insights into the comparative ecological niches of these two species, which often forage together in large foraging flocks, but have different foraging modes.

Zavalaga et al. (2010a) analyzed foraging site selection by Peruvian Boobies at Isla Lobos de Tierra and Isla Lobos de Afuera in northern Peru, in terms of bathymetry, SST, and chlorophyll *a* (Chl *a*) concentrations, as proxies for ocean productivity. They found that Peruvian Boobies foraged over the continental shelf or shelf break and that Chl *a* concentrations were significantly higher in foraging areas than expected from a random distribution, but that the SST of foraging areas was similar to that of available areas. The present study complements this prior research by analyzing foraging site selection by Peruvian Boobies directly in terms of the distribution of their prey.

In this chapter, patterns of foraging site selection by Peruvian Boobies and Guanay Cormorants were analyzed by overlaying data on the location of diving behavior for each species on geostatistical simulations of the spatial distribution of anchoveta based on acoustic survey data for 2008. Resource selection functions were then developed in terms of the relative abundance of anchoveta in the upper surface waters at visited locations. The factors that trigger foraging behavior by a seabird may differ from those that stimulate persistent foraging behavior at a location. To address this, a two-stage model was developed. The first-stage was designed to investigate the hypothesis that the probability that a bird engages in foraging behavior is a function of the relative abundance and depth distribution of prey at each location. The second-stage was designed to investigate the hypothesis that the persistence of foraging behavior at a location is also a function of the relative abundance and depth distribution of prey.

Data

The seabird tracking data used in the analysis of foraging site selection in this chapter are spatially-continuous, whereas data on the distribution of anchoveta were derived from acoustic survey transects. The objective of Chapter I was therefore to generate simulations of the spatial distribution of anchoveta over the entire foraging region as the basis for analysis of foraging site selection, and as an input to the individual-based foraging model (IBFM). This was achieved by establishing a set of regular hexagonal grid cells encompassing the foraging region of seabirds from Grupo Pescadores, Peru. Geostatistical simulations of the acoustic density and the depth distribution of anchoveta (specifically, the distribution of the upper depth limits of aggregations of anchoveta) were generated for each grid cell based on acoustic survey data for 2–5 December 2008. These simulations reproduced the spatial patterns and statistical properties of the observed data, and provide 100 sets of predictor variables for analysis of foraging site selection.

Analysis of resource selection based on animal movement patterns faces two associated methodological challenges. First, for any animal track, movement observations are inherently

clustered spatially, leading to uneven sampling effort. Here, this issue was addressed by binning movement observations into grid cells. Second, behavioral observations within trips are likely to be characterized by serial autocorrelation, which may exaggerate apparent preferences for some resources (Aarts et al. 2008). Treating individual trips as the sampling unit serves to reduce the effects of serial autocorrelation (Aebischer et al. 1993, Aarts et al. 2008). Here, this issue was addressed by defining all seabird observations belonging to the same trip within a grid cell as a sampling unit.

A further issue in presence-only studies, including many studies based on animal movement data, is the need to generate pseudo-absence data as a contrast to presence data (e.g. Torres et al. 2008). The method used here avoids this issue by contrasting cells in which diving occurred with cells visited by seabirds in which diving did not occur.

The data available for the two focal seabird species differ. For the Guanay Cormorants, 11 trips by 5 individuals during the period 1-5 December 2008 were recorded by GPS (MiniGPSlog, Earth and Ocean GPS, Kiel, Germany, 30g) recording at minimum intervals of 30 seconds, and by Time Depth Recorders (TDRs; G5, CEFAS Technology, Lowestoft, UK, 3g) recording at 1 second intervals. To construct the dependent variables for the foraging site selection model, TDR observations of greater than 1 dbar were used to identify diving activity. TDRs are calibrated so that the pressure at sea-level is 0 dbar, but this calibration may drift over time. The 1 dbar threshold used here (indicating a depth of 1m below the sea surface) is designed to reduce measurement error associated with drift, and to remove superficial bathing activity from the analysis. These observations were geo-referenced by interpolating the GPS data and matching the resulting track with the TDR record. For each trip, cells were identified as including diving behavior if at least one observation greater than 1 dbar occurred in a cell. For each of these cells, the total number of observations greater than 1 dbar was used to indicate the amount of time spent diving in each cell.

For the Peruvian Boobies, 13 trips by 6 individuals were recorded by high-resolution GPS (Gipsy GPS, Technosmart, Rome, Italy, 25-30g) recording at 1 second intervals, during the period 2-5 December 2008. As described in Chapter II, analysis of GPS and TDR data for Peruvian Boobies equipped with both instruments in 2007 showed that gaps in the GPS record were consistent with diving behavior indicated in the TDR record (see also Wanless 1993). For each trip, cells were identified as including diving behavior if at least one gap in the GPS data occurred in a cell. Interpolation between locations immediately before and after a gap was used to geo-reference gaps in the GPS data. While the total duration of gaps in the GPS data would

provide an indicator of the persistence of diving behavior for Peruvian Boobies similar to that used for Guanay Cormorants, the GPS may not recapture the satellite signal immediately when a bird resurfaces, and thus the duration of gaps may over-estimate dive duration. As an alternative, more reliable measure of persistent effort, the total number of distinct gaps was used as an indicator of the number of dives occurring in each cell in which at least one gap occurred. Given that plunge divers, such as the Peruvian Booby, must become airborne before diving again, dives in very quick succession are not feasible, and it is therefore likely that the GPS will have recovered the satellite signal before the bird dived again.

Methods

Likelihood functions

First stage

For both species, the probability that diving behavior occurs in a cell was modeled as a Bernoulli process (i.e. a binary stochastic process). Each sample (i.e. seabird observations belonging to the same trip within a grid cell as a sampling unit) was treated as a single Bernoulli trial, for which the likelihood function is:

$$L(p | k) = p^k \cdot (1 - p)^{(1-k)} \quad 3.1$$

where L indicates the likelihood function; p represents the probability that diving behavior occurs in a cell; and $k \in \{0, 1\}$ is an indicator function for whether or not diving behavior was observed in a cell.

Second stage

The number of gaps in the GPS record (indicative of the number of dives per cell) for the Peruvian Boobies, and the amount of time spent diving per cell for the Guanay Cormorants, were both assumed to follow a negative binomial distribution, with likelihood function:

$$L(N = n) = \frac{\Gamma(n + \vartheta)}{n! \Gamma(\vartheta)} \cdot \left(\frac{\vartheta}{\mu + \vartheta}\right)^\vartheta \cdot \left(\frac{\mu}{\mu + \vartheta}\right)^n \quad 3.2$$

where n is the number of gaps observed in a cell for the Peruvian Boobies or the number of TDR observations with pressure > 1 dbar for the Guanay Cormorants; Γ indicates the gamma function; $\mu \geq 0$ is the expected number of observations per sample; and $\vartheta \geq 0$ is a measure of dispersion in the number of observations among samples. A zero-truncated likelihood function was used in the case of the Peruvian Boobies because the second stage model was restricted to cells in which at least one dive occurred. For the Guanay Cormorants, the mean of n is much greater than for Peruvian Boobies (294 vs 4) because the dependent variable represents dive

duration rather than the number of dives. The difference between the zero-truncated and non-zero-truncated likelihood was therefore marginal (< 0.05 units of likelihood), so the simpler non-zero-truncated likelihood function was used instead.

Predictors

To test the hypothesis that seabird diving behavior is a response to relative abundance of prey in the upper surface waters, the predictor for all models was assumed to be a multiplicative function of the relative abundance of prey and the probability that the upper depth limit of prey aggregations was less than a threshold depth:

$$\eta_i \sim f\{s_i, P(d_i < \delta)\} \quad 3.3$$

where s_i is derived from the relative acoustic density at location i ; d refers to the upper depth limit of aggregations; and δ is an estimated scaling parameter.

Relationships between seabird responses and the relative abundance and distribution of their prey may be non-linear (Cairns 1987, Piatt et al. 2007). For Stage 1 models, non-linearities are incorporated by modeling the logistic function of the probability of diving behavior, such that:

$$p_i = \frac{e^{\eta_i}}{(1 + e^{\eta_i})} \quad 3.4$$

implying a symmetrical s-shaped curve between the probabilities 0 and 1 (although only part of that curve may correspond to available data).

For the negative binomial models, the predictor is linked to the likelihood function as follows:

$$\mu_i = e^{\eta_i} \quad 3.5$$

To accommodate a wider range of relationships, the contribution of the prey abundance component was modeled in three ways (Table 3.1): using a binary indicator for the presence/absence of simulated anchoveta at a location (e.g. Model 2), as a linear function in logit- or log-space of the simulated acoustic densities of anchoveta at a location (e.g. Model 3), and as a power function of the density of simulated anchoveta with estimated exponent (e.g. Model 4). The presence/absence model allows for a sharp threshold at a point consistent with the detection threshold in the acoustic survey, while the power function allows for greater flexibility in the shape of the response. The model for the depth component incorporates an estimated scale parameter, δ (Equation 3.3). Models were estimated for the abundance component, the depth component, and both combined (Models 6, 7, 8). A null model was also

estimated for comparison (see Table 3.1 for a list of all the models considered). Generalized additive models (Hastie and Tibshirani 1990) were not used because the predictors for all models are assumed to be multiplicative functions of the relative abundance of prey and the probability that prey aggregations occur in the upper water column (Equation 3.3).

Random effects

The seabird data are derived from multiple individuals, with one or more trips per individual. Pooling data across individuals (or, in this case, trips) is only appropriate if individuals do not differ (Aebischer et al. 1993). In this analysis, variation at the trip level was incorporated by developing a hierarchical model with trips treated as random effects. Null models with random effects by day and individual were also explored. The random effects (u_j in Table 3.1) were added to the predictors, implying that the expected probabilities or persistence of diving behavior are inherently higher or lower for some trips. The random effects were assumed to follow a normal distribution with zero mean and variance σ^2 . All models were estimated in the random effects module of AD Model Builder (ADMB Foundation <http://admb-foundation.org>). (It was necessary to convert zero abundances to the minimum non-zero abundance to estimate Model 4 and Model 8 with random effects. All models were fitted to this amended dataset.)

Model comparison

Uncertainty in the abundance and distribution of anchoveta were taken into account by using 100 conditional geostatistical simulations of the relative abundance and depth distribution of anchoveta to construct the independent variables. For each model, parameters were estimated accounting for all 100 geostatistical simulations by minimizing the negative logarithm of the average likelihood over all simulations:

$$NLL(\mathbf{D}|\underline{\psi}) = -\log\left\{\frac{1}{100}\sum_{i=1}^{100}L(\underline{D}_i|\underline{\psi})\right\} \quad 3.6$$

where $\underline{\psi}$ represents all model parameters. This objective function essentially treats each simulation as an alternative representation of the distribution of anchoveta, given that it is not known which simulation provides the closest representation to that encountered by the seabirds. For each species, the different models were then compared using Akaike's Information Criterion corrected for small samples AICc (Burnham and Anderson 2002).

For both species, the dependent variable is the probability of diving behavior, but the data sources on diving behavior were derived from different sources (i.e. gaps in the GPS record for Peruvian Boobies and TDR data for Guanay Cormorants). For this reason, data for the two

species were not combined into a single dataset, and parameters were not compared within the same model.

Results

Random effects

For all models, comparison of null models with and without random effects indicated support for random effects at the trip level (Table 3.1).

First stage

For both species, the model with greatest support from the data was the product of abundance raised to a power and the probability that upper depth limit of aggregations was less than an estimated threshold (Table 3.1, Model 8). This model is consistent with the hypothesis that seabird diving behavior is a response to the relative abundance of prey in the upper surface waters. Figures 3.1 and 3.2 compare observed and predicted probabilities of diving behavior in this model. Minimizing the negative log of the average likelihood (Equation 3.6) implies a better fit for simulations that are close to the average than those that are far from the average. This explains the looser fit of the selected model for both species as conditions move away from the average (indicated by the horizontal dotted lines in Figure 3.1). Specifically, the models tended to over-estimate the probability of patch selection at locations with high relative abundance or shallow depth distributions, and under-estimate the probability of patch selection at locations with low relative abundance or deeper depth distributions (see Figure 3.2).

For both species, the linear depth model (Model 5) received greater support than any of the abundance only models. For both species, the estimated scaling parameter, δ , in the selected model (Model 8) was fairly shallow, at 7.07m for Peruvian Boobies and 8.33m for Guanay Cormorants. This scaling parameter refers to the upper limits of aggregations in areas where birds are foraging, and should not be interpreted as a direct indicator of dive capacity (see Discussion). Comparison of the likelihood profiles for the scaling parameter in the selected models (Model 8, Fig. 3.3) indicates that the distribution of parameter estimates for the two species are different, and suggests that the Peruvian Boobies are selecting foraging locations with shallower prey than the Guanay Cormorants. Figure 3.2 shows that the probability of patch selection increases more steeply with reduced depth for Peruvian Boobies than Guanay Cormorants when aggregations are very shallow.

For both species, models based on relative abundance (Models 2-4) received greater support from the data than the null model (Model 1), with the most general model (Model 4) receiving

the most support. For both species, the estimated exponent in the selected model (Model 8) was close to 0, indicating a sharp increase in the probability of diving behavior at relatively low levels of abundance followed by a leveling off (Fig. 3.2). For any level of abundance, including patches with zero abundance, the probability of foraging behavior was slightly greater for Peruvian Boobies than Guanay Cormorants (Fig. 3.2).

Second stage

Results of the second-stage model indicate that the data do not provide evidence of a relationship between the persistence of diving behavior and the relative abundance and depth distribution of prey for either species. For the Peruvian Booby, the model for the number of dives per cell with greatest support from the data was the null model with random effects by trip (Model 1, Table 3.1). Likewise, for the Guanay Cormorant, the model for the total amount of time spent diving in a cell with greatest support from the data was also the null model with random effects by trip (Model 1). Figure 3.4 compares observed values with the expected value under the null model. Figure 3.5 shows histograms of the observed data together with the predicted distribution of values under the fitted model.

Discussion

In this chapter, a series of resource selection functions was developed to assess seabird foraging site selection in terms of various aspects of prey availability based on contemporaneous data on the movement patterns and foraging locations of Peruvian Boobies and Guanay Cormorants and the distribution of their main prey.

Previous efforts to compare the distributions of foragers with their prey resources have had mixed results (Swartzman and Hunt 2000). Several authors have emphasized the importance of scale in analyzing relationships between predators and prey (Hunt and Schneider 1987, Logerwell and Hargreaves 1996, Wakefield et al. 2009). The strength of association may be scale-dependent. In some cases, a close association has been detected at broad spatial scales reflecting physical oceanographic structure such as water masses, but not at the finer-scales corresponding to biological structure (Russell et al. 1992, but see also Redfern et al. 2008). Differences in the temporal and spatial resolution of data can undermine efforts to match foraging behavior to available prey (see Torres et al. 2008). In this study, the temporal and spatial resolution was set by the acoustic survey which took place over a four day period and was based on systematic transects approximately 10 km apart. The methodology used here allowed for uncertainty in the distribution of anchoveta, by averaging results over 100 conditional geostatistical simulations of anchoveta. While anchoveta schools are mobile, the

results suggest that the survey was able to capture features of the spatial distribution of anchoveta which were sufficiently consistent over the period of the survey to support a relationship with the foraging patterns of seabirds.

The set of resource selection functions developed here is based on a multiplicative function of the relative abundance of prey at each location and the accessibility of prey. Accessibility was defined in terms of the probability that prey biomass falls within a specific habitat envelope that is accessible to the predator. Both Peruvian Boobies and Guanay Cormorants are surface foragers. In this case, foraging site selection was assumed to be a function of prey abundance through the water column and the probability that prey biomass is found in the upper surface waters, defined in terms of a scaled depth distribution. This structure enabled analysis of the comparative importance of the abundance and depth distribution of prey in defining suitable foraging sites for these surface foragers. The structure could be adapted to capture the probability that prey is accessible to foragers with other types of constraints. For example a relevant resource selection function for large predatory fish such as tunas might be defined in terms of the probability that prey falls within a specific temperature or oxygen concentration envelope rather than depth distribution (see Lehodey et al. 2008).

The results for the first stage model highlight the importance of the depth distribution of anchoveta in foraging site selection by both Peruvian Boobies and Guanay Cormorants. The Peruvian Booby is a plunge diver, and forages close to the surface (up to 9m, Zavalaga et al. 2010b); while the Guanay Cormorant is a pursuit diver, capable of foraging at much greater depths (up to 74m, Zavalaga and Paredes 1999).

Results indicate that Guanay Cormorants are more likely than Peruvian Boobies to select foraging sites where prey occurs at moderate depths (Fig. 3.2). Nevertheless Guanay Cormorants preferentially select sites where prey is close to the surface. Prey capture may be facilitated where shallow fish schools can be trapped against the ocean surface by pursuit-divers attacking from below. For species that dive beneath prey, selection of foraging locations where prey is shallow is not inconsistent with dives recorded at greater depths.

The results for the first-stage model also suggest some differences in the response to the relative abundance of anchoveta. For both species, there is a sharp increase in the probability of diving behavior at relatively low levels of abundance followed by a leveling off (Fig. 3.2). For any level of abundance, the probability of foraging behavior is slightly greater for Peruvian Boobies than Guanay Cormorants (Fig. 3.2). This finding is consistent with the hypothesis that Guanay

Cormorants, which tend to forage in groups, require larger or denser aggregations for effective foraging than Peruvian Boobies (Nelson 1978).

The delta-AICc between the full model (Model 8) and the depth-only model (Model 5) is low (2.45) for Peruvian Boobies, suggesting weak support for the addition of the abundance component. It is higher (6.52) for Guanay Cormorants, suggesting that abundance may be more important for Guanay Cormorants than Peruvian Boobies.

No relationship was found between the persistence of diving behavior at a location and the relative abundance and depth distribution of prey for either species. There are several possible explanations for this result. For example, where anchoveta occurs at shallow depths and triggers diving behavior, it may occur at such high densities due to the aggregative nature of anchoveta that there is no clear relationship between the persistence of foraging effort and the abundance and depth distribution of prey. Instead, the duration of foraging bouts may depend on other factors which are not captured in the data, such as individual satiation, the structure of aggregations, and the presence of facilitators and competitors, which in turn may influence prey capture. In addition, some variability may be attributable to the cell-based structure of the analysis, in that the persistence of foraging effort in a cell may depend in part on how close a bird is foraging to the cell boundaries.

An understanding of predator aggregation patterns and the processes that lead to elevated trophic transfer is essential for marine ecosystem conservation planning (Hyrenbach et al. 2000, Hooker et al. 2011). Previous research has highlighted predictable spatial associations between seabirds and static or dynamic habitat features that serve to enhance prey availability (e.g. Yen et al. 2004). This study represents a missing link by analyzing foraging site selection directly in terms of the abundance and distribution of prey. The results indicate that processes that concentrate prey close to the surface need to be considered alongside those that enhance abundance. This finding is consistent with the results of several previous studies. For example, Hunt et al. (1998) found that Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) in the Aleutians foraged in areas where physical processes, such as tidally-driven upwelling and convergence, concentrated copepods and euphausiids near the surface. Vilchis et al. (2006) identified thermocline topography as a key feature influencing the abundance and distribution of seabirds, probably because of its effect on prey availability. Ribic et al. (2008) found that the spatial distribution of krill was related to bathymetric structure, and that different predators (seabirds and marine mammals) were associated with shallow and/or deep prey concentrations.

However, resource selection patterns may vary with foraging conditions. Central place foraging theory predicts that species should become more selective in terms of prey items or increase load sizes in response to reduced food availability (Orians and Pearson 1979). Burke and Montevecchi (2009) found that single prey-loading Common Murres (*Uria aalge*) were more selective when foraging conditions were unfavorable. In December 2008, anchoveta was broadly distributed through most of the foraging region for seabirds at Grupo Pescadores, and the depth distribution of anchoveta was relatively shallow (see Chapter I). The association between predators and prey may be stronger when prey availability is low or when prey is more patchily distributed. Hunt et al. (1991) also suggested that, if prey was sufficiently abundant in the patch, then birds would be able to find adequate food without seeking the best available patch. Vlietstra (2005) found that the spatial associations between Rhinoceros Auklets (*Cerorhinca monocerata*) and Pacific Loon (*Gavia pacifica*) and prey biomass were stronger on days when regional prey abundance was relatively low. Logerwell et al. (1998) also found that the association between Thick-billed Murres (*Uria lomvia*) and prey biomass was poor when prey variance was relatively low, suggesting that there is limited advantage to aggregating at slightly more profitable locations if prey distribution is fairly uniform.

In years when anchoveta is generally distributed deeper in the water column, central place foraging theory would predict that the shallow-diving Peruvian Boobies would be more strongly associated with shallow patches of prey. However, in the same context, the deeper-diving Guanay Cormorants would have the option of selecting prey at deeper depths. As a result, the contrast in estimated scaling parameters for the two species might be expected to increase when prey is distributed more deeply. Similar analyses should therefore be conducted for several years over which the abundance and distribution of anchoveta varies. Comparison of results across multiple years would provide further valuable insights into the comparative ecological niches of Peruvian Boobies and Guanay Cormorants, and ways in which the two species adapt resource selection patterns in response to changes in resource availability.

Notation

$\underline{\beta}$	vector of parameters for models of foraging site selection
$\Gamma(.)$	gamma function
δ	scaling parameter
η	predictor in the binomial and negative binomial models
μ	the expected number of gaps in the GPS data or dives in a cell
θ	dispersion parameter in the negative binomial distribution
σ^2	variance of the random effects, \underline{u}
$\underline{\psi}$	vector of model parameters
D	the data
d_i	upper depth limit of aggregations in a cell
$I(.)$	indicator function for the presence or absence of simulated anchoveta in a cell
i	cell or location index
j	foraging trip index
k	indicator function of whether or not diving behavior was observed in a cell
$L(.)$	likelihood
$NLL(.)$	negative log-likelihood
n	number of gaps in the GPS data or dives observed in a cell
$P(.)$	probability
p_i	probability that diving behavior occurs in a cell
s_i	relative acoustic abundance in a cell
\underline{u}	vector of random effects
z_i	probability that the upper depth limit of aggregations in a cell, d_i , is less than the estimated scaling parameter, δ ; $P(d_i < \delta)$

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Tables

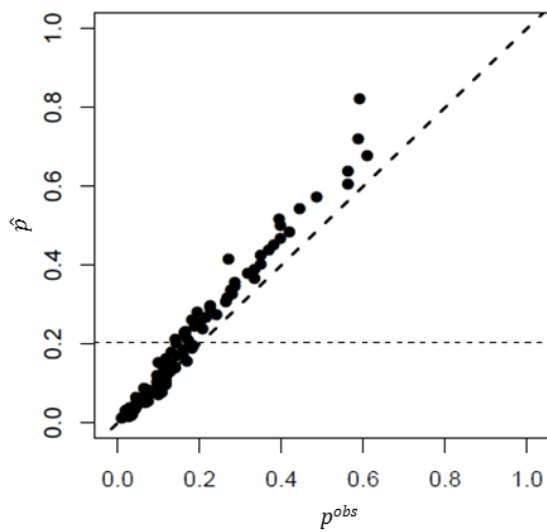
Table 3.1. Model comparison by delta-AICc for foraging site selection models with random effects at the trip-level. PEBOs refers to Peruvian Boobies and GUCOs to Guanay Cormorants. I refers to the indicator function on the presence or absence of simulated anchoveta; s refers to relative abundance of simulated anchoveta; z refers to the probability that the upper depth limit of simulated aggregations is less than an estimated scaling parameter; and u_j refers to the random effect for the j th trip.

Model		First stage			Second stage		
		no. of pars [†]	PEBOs	GUCOs	no. of pars [†]	PEBOs	GUCOs
0	$\eta_i = \beta_0$	1	67.99	47.57	2	23.54	17.89
1	$\eta_i = \beta_0 + u_j$	2	43.53	29.29	3	0.00	0.00
2	$\eta_i = \beta_0 + \beta_1 * I_i + u_j$	3	22.74	19.19	4	2.32	2.45
3	$\eta_i = \beta_0 + \beta_1 * s_i + u_j$	3	33.55	17.45	4	1.94	2.44
4	$\eta_i = \beta_0 + \beta_1 * s_i^{\beta_2} + u_j$	4	18.51	11.73	5	4.37	5.03
5	$\eta_i = \beta_0 + \beta_1 * z_i + u_j$	4	2.45	6.52	5	4.64	4.87
6	$\eta_i = \beta_0 + \beta_1 * I_i * z_i + u_j$	4	10.73	13.11	5	4.72	4.76
7	$\eta_i = \beta_0 + \beta_1 * s_i * + u_j$	4	26.90	18.19	5	4.37	5.08
8	$\eta_i = \beta_0 + \beta_1 * s_i^{\beta_2} * z_i + u_j$	5	0.00	0.00	6	6.89	7.47

† including scaling parameter, δ , and variance on random effects, σ^2

Figures

Peruvian Boobies



Guanay Cormorants

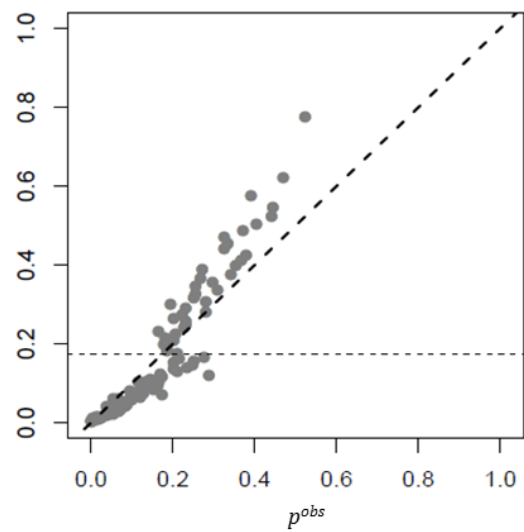


Figure 3.1. Observed versus predicted probability that diving behavior occurs in a cell for Peruvian Boobies and Guanay Cormorants, based on selected models (Model 8 for both species). Predicted probabilities (\hat{p}) are computed for each observation over the 100 geostatistical simulations; predicted probabilities are then grouped by quantile and compared to the mean observed value (p^{obs}) for the group. The horizontal dotted lines represent the mean of \hat{p} .

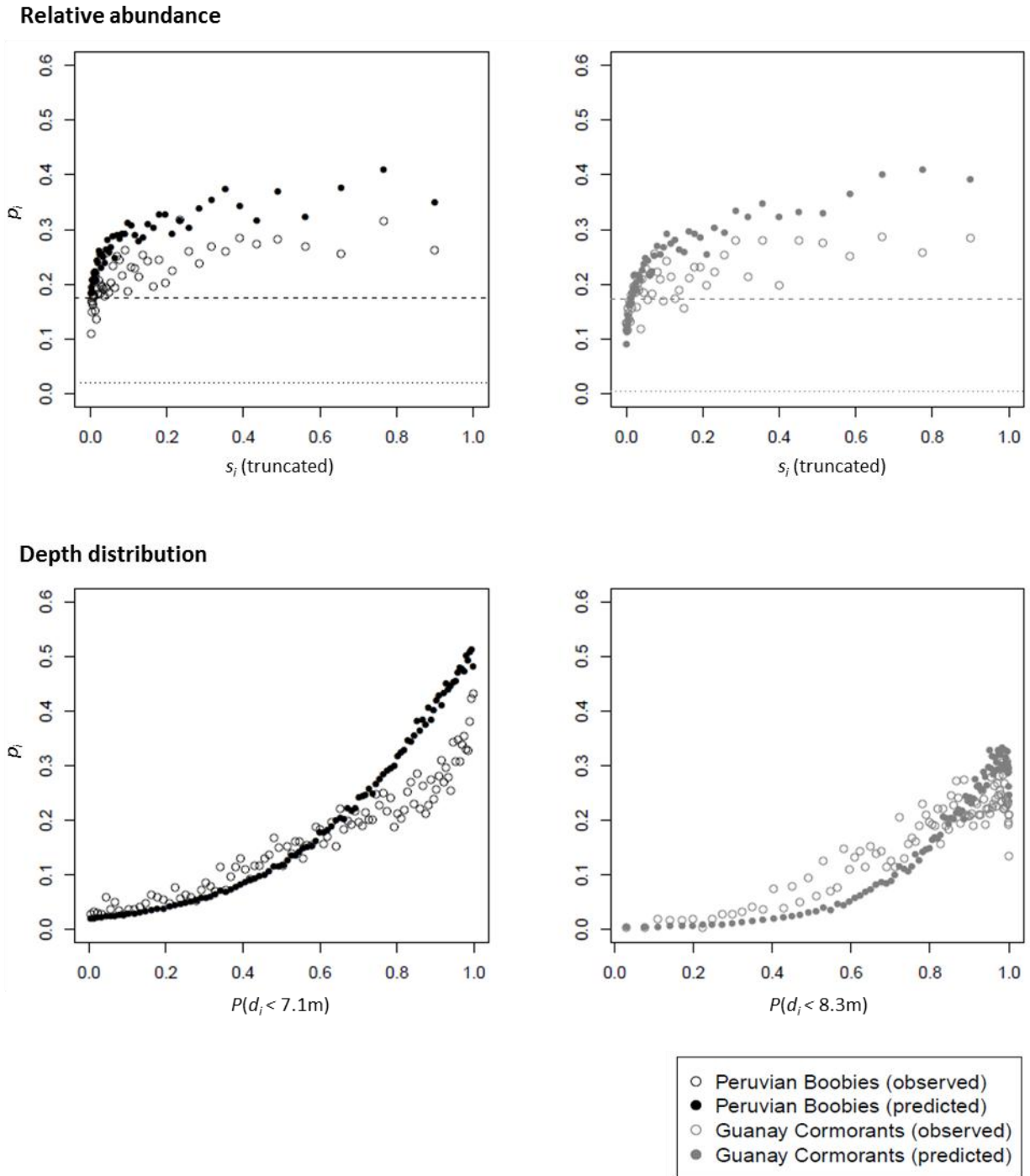
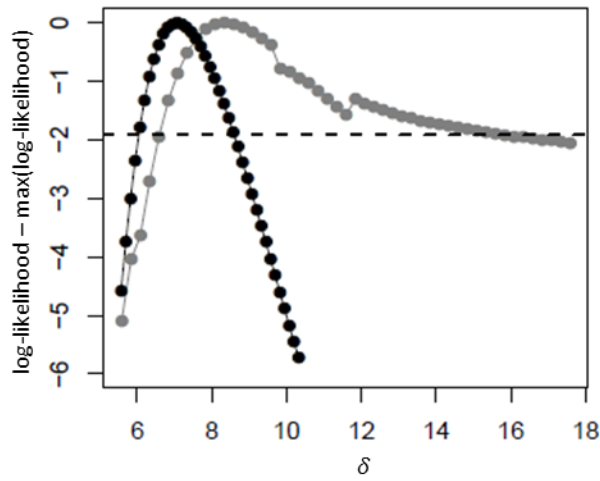


Figure 3.2. Comparison of observed and predicted probabilities of diving behavior as a function of relative abundance (s_i) and the probability that the upper limit of aggregations is less than the estimated scaling parameter. Dashed lines indicate the observed mean probability of patch selection for each species. Dotted lines indicate the probability of patch selection when abundance is 0.

Likelihood profiles for the minimum depth threshold (δ)



Standard deviation of the random effects (σ) vs δ for Guanay Cormorants

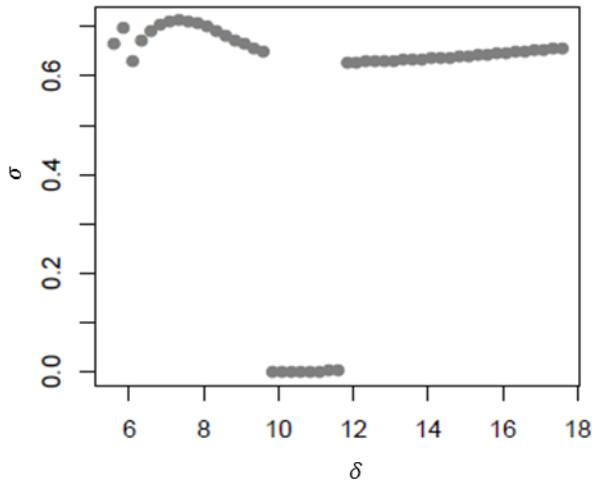


Figure 3.3. Likelihood profiles for the estimated scaling parameter (δ) for Peruvian Boobies (black) and Guanay Cormorants (grey), based on Model 8. The dashed line indicates the 95% confidence interval. Standard deviation of the random effects (σ) vs δ for the Guanay Cormorants, showing that variation in the random effects process underpins the reduction in the likelihood for $9.83 \leq \delta \leq 11.58$.

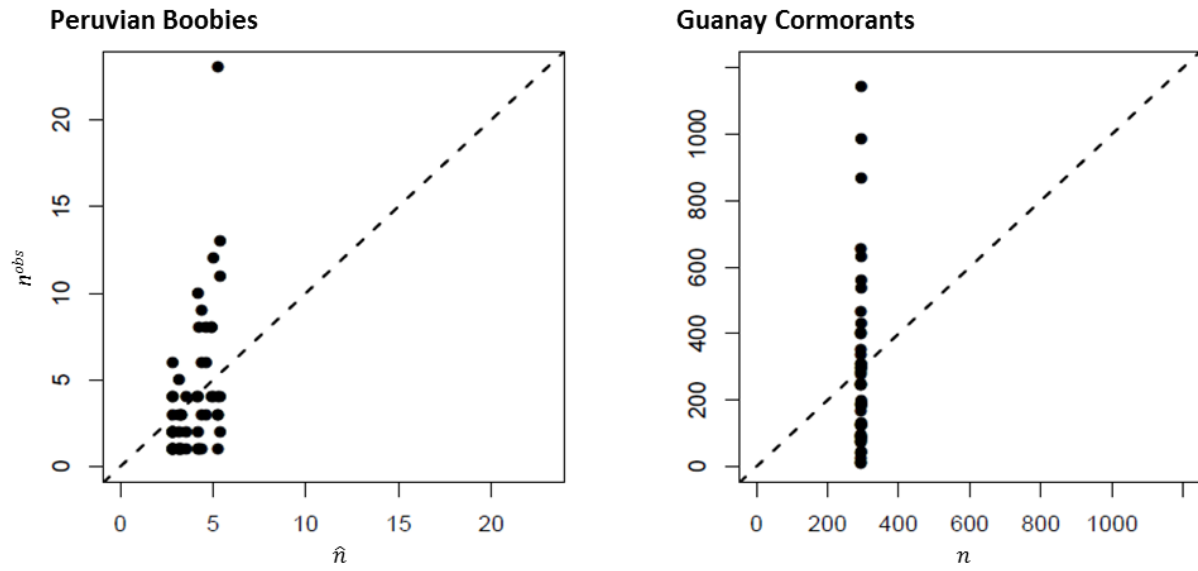
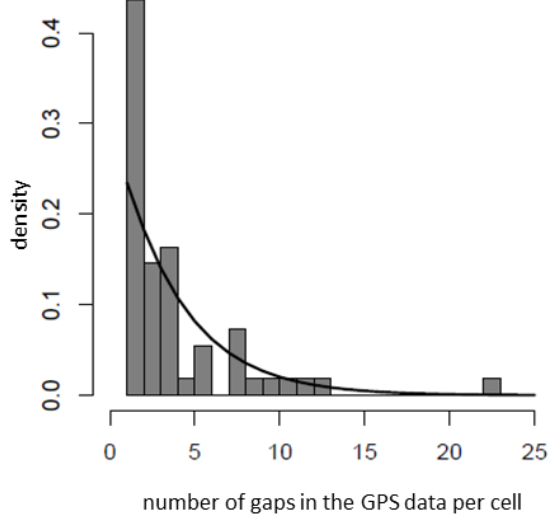


Figure 3.4. Predicted number of gaps in the GPS data per cell (\hat{n}) versus observed number (n^{obs}) for Peruvian Boobies, and predicted total dive duration per cell (\hat{n}) versus observed total dive duration (n^{obs}) for Guanay Cormorants, based on Model 1.

Peruvian Boobies



Guanay Cormorants

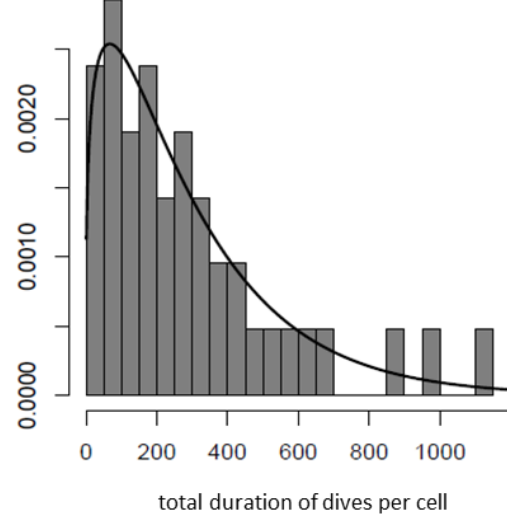


Figure 3.5. Histogram of number of gaps in the GPS data per cell for Peruvian Boobies and the total dive duration per cell (seconds) for Guanay Cormorants. The black lines show the fitted null model (Model 1 for both species).

Chapter IV: Sensitivity of search strategies used by seabirds to population densities and foraging conditions

Introduction

Major questions in foraging ecology concern the information foragers use to locate prey resources. Understanding how seabirds and other central place foragers (CPFs) locate prey at sea represents a key step in understanding how these species respond to changes in the abundance and distribution of prey resources (see Veit 1999).

Observation of seabird behavior and movement patterns has led to the development of several hypotheses for how CPFs locate patchy resources. When the distribution of prey is predictable over long time frames, individuals may develop long-term cognitive maps and exhibit site fidelity over relatively long time frames. In a review paper, Hunt et al. (1999) found that seabirds forage preferentially at locations where physical processes, such as fronts, generate predictable aggregations of prey. In a more recent review paper, Weimerskirch (2007) found that seabirds appear to have good knowledge of the location of areas of enhanced productivity, such as shelf edges, frontal zones, and upwelling, especially in temperate and polar systems.

When the distribution of prey is predictable over shorter time frames, individuals may use short-term recall. Davoren et al. (2003) found aggregations of prey for Common Murres (*Uria aalge*) that persisted for up to two weeks, and concluded that murres most likely use memory to locate these aggregations, at least on a coarse scale. Irons (1998) found that Black-legged Kittiwakes (*Rissa tridactyla*) exhibited foraging site fidelity over several days, and were able to time their foraging trips to coincide with daily tidal cycles (see also Hunt et al. 1998). Differences among individuals indicate the importance of learning and knowledge over information transfer. These findings support the hypothesis that kittiwakes learn and remember when and where to forage.

Information transfer at or near the colony has also been hypothesized (Wittenberger and Hunt 1985). Ward and Zahavi (1973) argued that birds departing from a colony may select any one of a wide range of outbound headings, and that information derived from the passage of birds between the colony and profitable foraging areas may facilitate navigation. Studies of several seabird species have suggested that such information streams may be important. Gaston and Nettleship (1981) found that the position of preferred feeding areas for Thick-billed Murres (*Uria lomvia*) could change within a single day, due to changes in patterns of ice distribution. Individuals departing the colony usually flew down to the sea and then departed in flocks from

there. Gaston and Nettleship (1981) hypothesized that outbound flocks could orient themselves by observing the flight paths of incoming flocks. Similarly, for Common Murres, Burger (1997) found that birds sitting on the ocean within a kilometer of nest sites appeared to have a clear view of the orientation of incoming flocks, and of successful adults carrying fish, and proposed that this zone acts as an information halo, where uninformed birds can obtain information on the location of their mobile, patchy prey. Davoren et al. (2003), also working with Common Murres, noted that specific commuting routes of murres to and from dense prey aggregations were obvious at sea.

Network foraging may be important when prey patches are highly mobile or ephemeral. Under this search strategy, individuals searching for prey also monitor the behavior of other individuals and converge on the location of individuals who are seen to find prey. Foraging models indicate that, when this foraging strategy is followed, the effective search area greatly exceeds the area a single individual can search alone (Buckley 1997, Grünbaum and Veit 2003). Camphuysen (2011) described how actively-searching Northern Gannets (*Morus bassanus*) in the North Sea dispersed individually, but responded immediately to the fine-scale search or foraging behavior of conspecifics, and argued that this response increased potential foraging opportunities for individuals.

In many cases, individuals may use a combination of search strategies. Review papers by Hunt et al. (1999) and Weimerskirch (2007) emphasize the importance of scale, suggesting that predictability may be higher at broad scales than at fine scales, so individuals may develop knowledge about areas of enhanced productivity at a broad scale, but use other search strategies to pinpoint prey patches at finer scales. For example, Davoren et al. (2003) concluded that Common Murres may use a combination of recall and information streams to locate prey on a broad scale, with network foraging at a finer scale.

The value of information derived from different search strategies depends on the distribution, predictability, and persistence of resource patches relative to foraging trip durations and the intervals between trips. For example, Hamer et al. (2001) found that Northern Gannets from two colonies in the North Atlantic differed in their foraging strategies, with individuals from Bass Rock in the North Sea exhibiting much higher site fidelity than those at Great Saltee in the Celtic Sea, and attributed the difference to less predictable prey distributions in the Celtic Sea. Preliminary findings reported by Weimerskirch (2007) suggested that predictability may be generally lower in tropical systems than in temperate or polar systems.

Long-term site fidelity is unlikely to play an important role in much of the Humboldt Current system because prey patches are ephemeral (Nelson 1978). Duffy (1983) found that many large groups foraging over shoals persisted for two to three hours or more, although in some cases, the birds formed a mosaic of smaller aggregations which persisted for only about 15 minutes. This rapid turnover indicates that short-term recall may also be of limited value. Individuals may gain more up-to-date information from the direction of birds returning from foraging. Weimerskirch et al. (2010) hypothesized that Peruvian Boobies and Guanay Cormorants breeding at the same colony and foraging on similar resources, nevertheless use different search strategies to locate available prey. According to this hypothesis, Guanay Cormorants form a raft at the sea surface whose orientation may indicate the direction of prey patches and guide the outbound heading of large groups or columns of individuals as they leave the raft. The raft itself may have evolved from the tendency of social birds such as Guanay Cormorants to bathe in large groups on leaving the colony (Weimerskirch et al. 2010). In contrast, Peruvian Boobies often leave the colony singly or in small groups, and may depend more on short-term recall and network foraging. For both species, foraging behavior and the flight directions of returning birds are either difficult to conceal or concealment would have limited benefit. Both orientation of outbound headings in line with the direction of returning birds and network foraging therefore draw on public information and do not depend on reciprocal altruism.

Questions have been raised about the population densities required to support search strategies based on public information, in particular information streams, and hence the possibility of Allee-type density dependence in declining populations (e.g. Ward and Zahavi 1973, Weimerskirch et al. 2010). These questions are challenging to address through field observations because of limitations in the ability to manipulate key variables, such as population densities and foraging conditions. In this context, models can provide a useful complementary tool to observational studies by exploring the consequences of changes in these variables (see, for example, Buckley 1997, Grünbaum and Veit 2003).

The research objectives in this chapter were to explore the effectiveness of search strategies under a range of population densities, and the value of the information generated given different foraging conditions. The chapter is focused on two strategies: the orientation of outbound headings in line with the direction of returning birds, and network foraging. Two hypotheses were investigated: search strategies are less effective when population densities are low, and information is more valuable when foraging conditions are poor (for example, characterized by comparatively low abundance and reduced accessibility). To investigate these

hypotheses, a spatially-explicit individual-based foraging model (IBFM) was developed and used to explore four scenarios. In Scenario A, individuals in the foraging model act independently, and do not benefit from any information from other individuals about the location of prey resources. In Scenario B, individuals orient their outbound headings in line with the direction of returning individuals. In Scenario C, individuals use network foraging. In Scenario D, individuals orient their outbound headings in line with the direction of returning individuals, and use network foraging. Short-term recall was not included in any of the scenarios. The analyses are not designed to prove or disprove either search strategy, but to explore the contribution of each strategy to search effectiveness under different conditions. The effectiveness and value of information are measured in terms of foraging success and foraging trip duration.

The analysis in this chapter is based on a single species, the Peruvian Booby (*Sula variegata*). However, the key findings are not specific to Peruvian Boobies, but rather have broader relevance to seabirds foraging on patchy and unpredictable prey.

Model structure

In ecology, mechanistic models are designed to strengthen understanding of complex systems by exploring whether and how individual processes, and interactions among them, generate patterns that correspond to those observed in nature. The IBFM is a mechanistic model designed to explore the processes that give rise to seabird foraging patterns.

The appropriate complexity of an individual-based model depends on the questions it is designed to address and the behavior that must be included for the model to perform satisfactorily, for example in reproducing key emergent patterns (Grimm and Railsback 2005). The IBFM is informed by data on the distribution of Peruvian anchoveta (*Engraulis ringens*) and the movement and foraging patterns of Peruvian Boobies. However, the IBFM is not intended to represent the full complexity of search strategies or replicate observed foraging patterns exactly. Several processes have been simplified in order to focus on the key processes of interest here (see Oreskes et al. 1994, Starfield 1997).

The IBFM has three main components: a prey field, individual foragers, and performance indicators. This section provides a description of these three components. Details of the specific scenarios evaluated in this chapter are presented in the Methods (below).

Prey field

The prey field in the IBFM is discrete, comprised of hexagonal grid cells, each with information on the abundance and depth distribution of prey resources within the cell. Hexagonal gridcells were chosen because the distance between the center points of neighboring cells is the same in all directions, which is a useful feature for modeling simple movement patterns between cells. (This type of movement pattern is not used in the current version of the IBFM, but hexagonal cells would support this option if required.) In this application, the spatial extent of the foraging region was set to encompass fine-scale acoustic survey data on Peruvian anchoveta collected in December 2008 and 2009. The global positioning system (GPS) tracks of all Peruvian Boobies and Guanay Cormorants recorded in December 2008 and 2009 fell well within this region (Fig. 4.1). The resolution (minimum diameter) of grid cells was set to 2 km to correspond with the resolution of the acoustic survey data processed to 1 nm linear transect segments. The location of the colony was based on the mean center of the first locations for the GPS tracks used in this analysis, specifically 11.77545°S, 77.26630°W.

Conditional geostatistical simulation was used to generate multiple equi-probable realizations of the prey field from acoustic survey data for anchoveta collected during December 2008 and December 2009 (see Chapter I). The two periods represent contrasting conditions in terms of the abundance and distribution of prey (Fig. 4.2). In 2008, anchoveta was broadly distributed with areas of high abundance throughout the foraging region. Anchoveta schools were also relatively shallow throughout the region. In contrast, in 2009, anchoveta was more concentrated, with few areas of high abundance, mostly near shore, and some areas of the mid-shelf apparently unoccupied. In comparison to 2008, anchoveta schools were generally deeper, with greater variability in the depth distribution.

Individual foragers

The IBFM fits well within the movement ecology paradigm developed by Nathan et al. (2008). This paradigm emphasizes the value of identifying different behavior modes as a key step towards a mechanistic, process-based approach to analyzing and modeling animal movement patterns. The paradigm has four components: internal state (what motivates the movement?), movement processes (how is the movement performed?), navigational capacity (when and towards what target is the movement performed?), and external factors (which external biotic and abiotic factors affect this movement and how?). Movement patterns in each behavior mode result from the combination of all four components. A key challenge is to identify the proximate

and ultimate drivers, such as environmental cues, that stimulate individuals to switch between behavior modes.

Behavior modes

In the IBFM, seabirds have two internal states: satiated and not satiated. Observed seabird foraging trips may be characterized as ‘commuting’ or ‘looping’ (Fig. 4.3; Weimerskirch et al. 2010). In commuting trips, individuals follow a particular heading from the colony to a foraging patch and then return directly to the colony from the patch in the same direction as they departed. In looping trips, individuals change direction more than once during the foraging trip, often feeding at several locations, and return to the colony from a patch in a different direction from the one in which they departed. The decision to commute or loop is likely to be made during the course of a trip (i.e. it is an emergent pattern) and may be based on each individual’s internal state (satiated or not satiated), the abundance and rate of depletion of patches in which foraging occurs, the expected abundance of other patches and expected time taken to locate another patch (Charnov 1976, Weimerskirch et al. 2010). However, data were not available to model this decision as a response to the prey field, so seabirds in the IBFM determine whether to follow a commuting or looping trajectory based on a single Bernoulli trial prior to departure. Here, the probability of a commuting trip was set at 40% for Peruvian Boobies, based on observed data (Weimerskirch et al. 2010).

The IBFM is based on discrete, fixed time steps. Here, the time step is 10 seconds, corresponding to the subsampling interval used in the analysis of the movement patterns of Peruvian Boobies (see Chapter II). At each time step, individual foragers may be in one of nine behavior modes (Figs 4.4 and 4.5): at the colony (Mode 0), outbound travel (Mode 1), foraging (Mode 2), broad-scale search (Mode 3) transit (Mode 4), following (Mode 5), homebound travel (Mode 6), returned (Mode 7), and failed (Mode 8). The foraging mode (Mode 2) may include fine-scale area-restricted search patterns and resting behavior associated with foraging. The following mode (Mode 5) is not used in this application. It could be used to model explicitly the long columns of birds marking the route from the colony to feeding areas, as described by Murphy (1936). These behavior modes do not correspond directly to the movement modes in Chapter II (see section on movement processes for further details).

On initialization, all foragers are unsatiated and at the colony (Mode 0). Each forager is allocated a departure time and decides whether to commute or loop. At departure, each forager selects an outbound heading and leaves the colony in outbound travel mode (Mode 1). On entering a new cell (i) in outbound mode (Mode 1), the forager decides whether to switch to

foraging mode (Mode 2) based on the probability of patch selection associated with the cell ($p_{patch,i}$). If it does not, it continues in outbound mode. On commuting trips, a forager that has switched to foraging mode (Mode 2) remains in the same cell for a number of time steps until it is satiated and returns directly to the colony in homebound travel mode (Mode 6). On looping trips, a forager that has switched to foraging mode (Mode 2) remains in the same cell for a number of time steps before either returning directly to the colony in homebound travel mode (Mode 6) if satiated, or if not, switching to search mode (Mode 3) and searching for another patch. On entering a new cell (i) in search mode (Mode 3), the forager decides whether to switch to foraging mode (Mode 2) based on the probability of patch selection associated with the cell ($p_{patch,i}$). If it does not, it continues in search mode. When a bird in homebound mode (Mode 6) reaches the colony, it has returned (Mode 7). If a bird moves beyond the bounds of the foraging region, it is logged as failed (Mode 8).

In scenarios with network foraging, a forager in outbound or search mode (Modes 1 or 3) that detects another individual in foraging mode (Mode 2) within a specified detection distance from its current location (r_{sea}) switches to transit mode (Mode 4) and travels directly towards the cell occupied by that individual (the target cell) (e.g. Fig. 4.5d). On entering any new cell (i) in transit mode (Mode 4), the forager decides whether to switch to foraging mode (Mode 2) while in that cell ($p_{patch,i}$). Thus, it may switch to foraging before reaching the target cell. If it does not, it continues in transit mode. If the bird does not switch to foraging on entering the target cell, it switches back to the mode it was in prior to switching to transit mode (either Mode 1 or Mode 3).

Information and navigation

Outbound headings:

The choice of outbound heading may be a significant factor influencing the time taken to locate a foraging patch, and may depend on the information available to foragers. Here, if foragers departing the colony have no information on the likely direction of available prey, the outbound heading is drawn at random from a uniform circular distribution. Alternatively, foragers may use the direction of returning foragers within a specified detection distance (r_{colony}) as an indicator of the likely direction of available prey, and orient their outbound headings accordingly. This would be consistent with individuals cueing off returning individuals or groups, or the emergence of 'compass rafts' (i.e. groups of outbound individuals aggregating near the colony and orienting themselves towards returning individuals or groups). For example, Weimerskirch et al. (2010) describe Guanay Cormorants forming compass rafts and

selecting an outbound heading in line with ‘the largest returning columns of cormorants’. In this chapter, in scenarios in which foragers use the direction of returning foragers to guide their outbound heading (Scenarios B and D), the compass is partitioned into twelve 30° segments (Fig. 4.6). When a bird is ready to depart, it assesses the number of returning birds in each segment within a set radius (r_{colony}), identifies the segment with the most returning birds, and then selects a heading within that segment.

Network foraging:

In scenarios with network foraging (Scenarios C and D), a forager in transit mode travels directly towards a cell occupied by an individual in foraging mode. If more than one individual in foraging mode falls within the forager’s detection distance (r_{sea}), the nearest individual is targeted.

Detection distances:

In the IBFM, foragers are assumed to be able to sense the abundance and depth distribution of prey within the cell they occupy, but are unable to perceive prey attributes in neighboring cells directly. However, as outlined above, birds may be able to detect prey indirectly over greater distances by monitoring the behavior of other foragers. In the IBFM, increasing detection distances beyond the distances over which individuals are able to detect other foragers (see Haney et al. (1992) for an assessment of the visual ranges of seabirds) provides a computationally-efficient mechanism for modeling large population densities implicitly. For example, when birds orient their headings in line with the direction of returning birds, the number of returning birds detected depends on the number of birds in the simulation and the detection distance. In the case of network foraging, the effective search area depends in part on the density of birds and in part on the detection distance. However, increasing detection distances does not compensate for the greater potential for a large population to sample all grid cells (see Discussion). Detection distances may be set higher for foragers at the colony (r_{colony}) than for foragers at sea (r_{sea}) to account for the high densities of foragers typically found close to the colony. In this chapter, the detection distances r_{colony} and r_{sea} are set at 12 km and 6 km respectively.

Boundary rules:

The foraging region is finite, and may be bounded by land or sea. In this application, the foraging region is bounded by land to the east of the colony, the shelf break to the west, and by sea elsewhere (Fig. 4.1). All observed seabird tracks fell well within the seaward boundaries, but in several cases, observed birds headed towards land and then turned to follow the coastline

north or south. Individuals in the IBFM that encounter the landward boundary similarly turn north or south to follow the coastline, whereas birds that move beyond the seaward boundaries are logged as failed (Mode 8).

Decision rules

In the IBFM, foragers have up to five non-deterministic decision rules: to commute or to loop, the choice of outbound heading, patch selection, patch residence time (i.e. the time spent foraging in each patch), and satiation time (i.e. the total amount of time spent foraging prior to returning to the colony). In this application, patch residence time and satiation time are fixed.

Patch selection:

The probability of patch selection ($p_{patch,i}$) is a function of the availability of prey in a cell. Patch selection is based on the observed probability that at least one dive occurs in a cell, as indicated by gaps in the GPS data (see Chapter II), as a multiplicative function of the relative abundance of anchoveta in a cell (s_i) and the probability that the upper depth limit of aggregations in a cell (d_i) is less than an estimated scaling parameter (δ) (see Model 8, Chapter III).

$$p_{patch,i} = \frac{e^{\eta_i}}{(1 + e^{\eta_i})} \quad 4.1$$

$$\eta_i \sim f[s_i, P(d_i < \delta)] \quad 4.2$$

For Peruvian Boobies, patch selection is parameterized as follows:

$$\eta_i \sim -3.533 + 3.298 \cdot s_i^{0.034} \cdot P(d_i < 7.472) \quad 4.3$$

For the purposes of the IBFM, this function was re-estimated using the objective function:

$$NLL(\psi|D) = -\sum_1^N \log\{L(\psi|D_i)\} \quad 4.4$$

where ψ represents all model parameters and D represents the data, and N is the total number of data points across all simulations. The objective function used in Chapter III treats each simulation as an alternative representation of the distribution of anchoveta. This leads to a better fit for simulations that are close to the average than for those that are far from the average. While this is appropriate for Chapter III, in the IBFM it would lead to poor prediction of foraging behavior in simulations that are far from the average, in particular over-prediction of foraging behavior under unusually favorable conditions. The objective function used here treats each simulation as an independent dataset, leading to better prediction of foraging behavior under conditions far from the average.

Satiation time and patch residence time:

In order to keep the model simple and focus on the key questions of information flows, the amount of time spent in foraging patches prior to satiation time (T_{satis}) is fixed. Satiation time is based on the total time spent per foraging trip in cells in which at least one dive occurs – approximately 23 minutes for Peruvian Boobies. This time period may include fine-scale search, foraging, and resting behaviors. Also to keep the model simple, foragers on commuting trips only forage in a single patch so that patch residence time is the same as satiation time ($T_{patch} = T_{satis}$), while foragers on looping trips always forage in two patches with the satiation time divided equally between them ($T_{patch} = T_{satis}/2$).

Movement processes

In the IBFM, movement processes that cover broad-scales are spatially-continuous and spatially-explicit, while fine-scale movement processes (i.e. fine-scale search and foraging) occur within a specific grid cell and are not modeled explicitly. To keep the model simple, and focus on the key questions of information flows, movement patterns are simplified in this application (Table 4.1). All broad-scale movement modes (Modes 1, 3, 4, 6) have fixed step lengths (i.e. distance covered per time step), based on the expected distance of fast, directed movement patterns estimated by a hidden Markov model (HMM) (see Chapter II). The outbound, transit, and homebound modes are fully directed (i.e. without turning angles). The outbound travel mode (Mode 1) is oriented towards the selected outbound heading, the directed travel mode (Mode 4) is directed towards the target cell (i.e. the cell in which a foraging seabird has been detected), and the homebound mode (Mode 6) is directed towards the colony. The broad-scale search mode (Mode 3) is simulated as a correlated random walk, with turning angles based on the persistence of fast, directed movement patterns estimated in the HMM (see Chapter II). This mode does not incorporate the slower, more sinuous movement patterns estimated in the HMM that are considered indicative of finer-scale area-restricted search type movement patterns.

Performance indicators

There is no explicit objective function in the IBFM because it is not an optimizing model. Nevertheless, foragers are assumed to pursue an underlying objective function, and performance indicators are identified that are relevant to this underlying objective function (see Schoener 1971 for a discussion of performance indicators for foraging strategies). It is assumed that the ultimate objective function of CPFs, as with other species, is to maximize lifetime fitness. In the context of central place foraging and provisioning (see Ydenberg 2007), it is assumed that the underlying objective function of CPFs is to minimize foraging trip duration

subject to the constraint of meeting basic metabolic requirements, provisioning young, and compensating for energy lost during foraging. Minimization of time spent searching for prey is important for CPFs during breeding (Cairns et al. 1990). The time spent on an individual foraging trip may be constrained to daylight hours in the case of diurnal foragers, by the need to feed young at regular intervals, and/or by increased chick or pup mortality for unguarded young. The young face increased risk of mortality if adults consistently fail to meet foraging and provisioning objectives within these time constraints. When adults cannot meet energy demands within time constraints, they are expected to reduce parental care and eventually abandon their young, given that long-lived species, such as seabirds, generally maximize lifetime fitness by favoring survival of adults over that of their dependent offspring in a given year (Stearns 1992).

This underlying objective function leads to two main performance indicators in the IBFM. The effectiveness of search strategies is measured in terms of foraging success and foraging trip duration. Foraging success is the inverse of failure. Birds are logged as failed if they fail to locate prey within the foraging region and leave the foraging region, or fail to return to the colony by the end of the simulation (see below). For foraging trip duration, the timer starts and ends when the forager is 2 km from the colony in outbound or homebound mode, corresponding to the 2 km threshold used to distinguish foraging trips in the observed data. To assess the value of information generated in the IBFM, simulation results based on different information scenarios can be compared with expected results under perfect information.

The IBFM also records information on whether an individual made a commuting or looping trip, the outbound heading and whether an individual used information from returning birds to guide this heading, the time and distance to the first patch, whether an individual used network foraging and whether this led to patch selection, the time spent in travel, search or foraging modes, and the maximum distance from the colony. This information is useful in understanding the mechanisms that underpin the results.

Methods

Scenarios

As outlined above, four scenarios are explored to investigate the effects of different rules governing the sources and transfer of information on time to first patch selection, based on data for Peruvian Boobies. In Scenario A, individuals do not benefit from any information about the location of resources; outbound headings are drawn from a uniform circular distribution. In Scenario B, individuals orient their outbound headings in line with the direction of returning

individuals. In Scenario C, individuals use network foraging. In Scenario D, individuals orient their outbound headings in line with the direction of returning individuals and use network foraging. Short-term recall was not included in any of the scenarios.

Contrasting foraging conditions

Each scenario was run on the same set of 10 simulated prey fields based on data for anchoveta from December 2008 and December 2009. These two periods represent contrasting conditions in terms of the abundance and distribution of prey, which translate into contrasting patterns for the probability of patch selection (p_{patch}) (Fig. 4.7).

Population densities

For Scenario A, there are no interactions among foragers. The scenario was run once over each simulated prey field, with 60 individuals in each case. Once interactions among foragers are introduced (in Scenarios B, C, and D), population densities at sea influence information flows in the model. For each of these scenarios, the IBFM was therefore run over each simulated prey field for a series of departure rates representing different population densities: individuals were scheduled to leave systematically every 4 minutes, 2 minutes, and 1 minute. The number of birds in each simulation is not intended to match that number of birds at the colony, as that would be extremely demanding computationally.

Peruvian Boobies are diurnal foragers, with individuals departing from first light onwards and returning to roost on land by dusk. For Scenarios B, C, and D, individuals were scheduled to depart the colony over a period of 12 hours. Analysis of results was based on individuals departing in the fourth hour after initialization, so that information builds up through individuals returning to the colony and/or through network foraging over the preceding three hours. Scheduled departures were continued after the fourth hour so that recorded individuals were not left in isolation. Each simulation was run until all recorded individuals had returned or left the foraging region, with a maximum duration of 12 hours.

Value of information

To assess the value of information generated in the IBFM, simulation results based on different information scenarios were compared with expected results under perfect information. The constraints of central place foraging imply that the probability of cell i being selected in the IBFM is a function of both $p_{patch,i}$ and the probability that a forager reaches a cell, which is a function of the cumulative probability of patch selection for all preceding cells. For any given prey field and outbound orientation, the expected failure rate and expected foraging trip

duration can be calculated for individuals that travel in straight lines from the colony and only forage in one cell, as follows:

$$P(\text{failure}) = \prod_1^M (1 - p_{\text{patch},i}) \quad 4.5$$

$$\begin{aligned} E(\text{foraging trip duration}) = & t_{\text{satis}} + 2t_{\text{patch},1} \cdot p_1 + \\ & 2t_{\text{patch},2} \cdot (1 - p_{\text{patch},1}) \cdot p_{\text{patch},2} + \\ & 2t_{\text{patch},3} \cdot (1 - p_{\text{patch},1}) \cdot (1 - p_{\text{patch},2}) \cdot p_{\text{patch},3} \dots \\ & + 2t_{\text{patch},m} \cdot \prod_1^{M-1} (1 - p_{\text{patch},M-1}) \cdot 1 \end{aligned} \quad 4.6$$

where M is the number of cells encountered in a straight line from the colony, and $t_{\text{patch},i}$ is the time taken to travel to cell i , multiplied by 2 to cover both the outbound and return journey. In calculating the expected foraging trip duration, it was assumed that a bird always selects the last patch available before leaving the foraging region. IBFM simulations were run for a population of 360 seabirds with outbound headings selected systematically from a uniform circular distribution for each of 10 geostatistical simulations based on data from 2008 and 2009. The probability of failure and expected foraging trip duration under no information were estimated by averaging over the results for all directions and all simulations for each year. The probability of failure under perfect information was taken as the minimum probability of failure among the 360 directions averaged over all simulations for each year. (Note that perfect information is used to select the optimal heading, but information does not change the probability of patch selection, $p_{\text{patch},i}$.) The expected foraging trip duration under perfect information was taken as the average minimum expected foraging trip duration over all simulations for each year. In the perfect information scenario, birds that seek to minimize the probability of failure and those that seek to minimize expected foraging trip durations do not follow the same outbound heading because expected foraging trip duration depends on the distribution of patch selection probabilities ($p_{\text{patch},i}$) in terms of distance from the colony, whereas the probability of failure depends on the product of patch selection probabilities, without reference to their distribution in terms of distance.

Results

Value of information

The value of information is greater in 2009 than in 2008. Table 4.2 indicates the value of information in the IBFM under different foraging conditions, by comparing the expected failure

rates and foraging trip durations of individuals with no prior information and with perfect information.

Perfect information reduces the probability of failure by $< 0.5\%$ in 2008 but $> 5\%$ in 2009. The value of perfect information in terms of reduced expected foraging trip duration is also greater in 2009. As a result, the expected foraging trip durations under perfect information are similar for 2008 and 2009 despite the differences in foraging conditions.

IBFM simulations corroborate these results. For both search strategies explored here (i.e. orientation of outbound headings and network foraging), the reduction in failure rates and foraging trip durations achieved in Scenario D (full information) is greater for 2009 than for 2008 (Fig. 4.8). The differences in simulation results between Scenario A (no information) and Scenario D are small in 2008. As a result, the effects of different search strategies are much clearer in simulations based on foraging conditions in 2009.

Orientation of outbound headings

Orientation of outbound headings in line with the direction of returning birds tends to concentrate outbound headings in directions associated with relatively high probabilities of patch selection close to the colony (Fig. 4.9). Higher population densities improve accuracy and precision, because larger populations sample the environment more effectively on initialization and information is built up more rapidly over time.

In 2009, orientation of outbound headings in line with the direction of returning birds leads to a reduction in failure rates, even at low population densities (Fig. 4.8). The effects on failure rates are less clear for simulations based on 2008 foraging conditions. In both years, the strategy of orienting outbound headings in line with returning birds reduces foraging trip durations (Fig. 4.8), with effects again occurring even at low population densities.

Network foraging

Under network foraging, birds move towards birds that are foraging. This tends to retain birds close to the colony where populations are more dense, reducing the maximum distance birds travel in comparison to scenarios without network foraging (Fig. 4.10). This effect increases with higher population densities.

In 2009, network foraging reduces failure rates, even at low population densities (Fig. 4.8). Again, the effects are less clear for 2008. The effect on foraging trip durations is apparent at higher population densities for 2009, but is limited for 2008.

Orientation of outbound headings and network foraging combined

Orientation of outbound headings appears to facilitate network foraging by increasing the densities of birds in profitable areas. The mean number of times a simulated bird encounters another individual foraging increases when birds are concentrated in one or a few directions through the orientation of outbound headings (Fig. 4.11). Furthermore, the percentage of encounters that leads to foraging in the target cell is higher under Scenario D because encounters are more likely to occur in an area with high foraging potential.

In the IBFM, the effects of increasing information to individuals are more evident when both search strategies are combined. Failure rates are lower under the combined strategy (Scenario D), than under either strategy in isolation (Scenarios B and C), especially at higher densities (Fig. 4.8). The combined strategies also lead to a reduction in both the mean and variance of foraging trip duration compared to scenarios with no information or with each strategy in isolation (Fig. 4.12).

Discussion

Effectiveness of search strategies under different population densities

The first hypothesis investigated in this chapter was that search strategies are less effective when population densities are low. IBFM simulations indicate that both search strategies investigated here — the orientation of outbound headings in line with the direction of returning birds and network foraging — are effective at reducing failure rates, even at low densities, in simulations based on 2009 foraging conditions. In 2008, failure rates were low even in the scenario without information (Scenario A), and the effects of different search strategies on failure rates are less clear.

Even with only a few individuals returning to the colony, the orientation of outbound headings in line with returning birds serves to prevent birds heading in directions where prey resources are scarce. Higher population densities lead to more accurate and precise targeting of available prey, but finding the optimal direction may not be necessary if areas with few prey resources are successfully avoided. Avoiding failure may be more important than minimizing expected foraging trip duration (see Caraco 1980). This result depends on the precise definition of the mechanism for orienting outbound headings. Birds must depart in line with the largest column of returning birds, as described by Weimerskirch et al. (2010), rather than in the mean direction of all returning individuals.

In the case of network foraging, several mechanisms may contribute to the reduction in failure rates. In the IBFM, network foraging retains birds close to the colony where populations are more dense, and this may have the effect of reducing failure rates even at low population densities. This may be considered a side effect of network foraging rather than its true function. As with the orientation of outbound headings, the mechanism is more efficient at higher population densities, but this is not necessary to reduce failure rates. In practice, given the spatial constraints faced by CPFs, other mechanisms might serve to retain birds close to the colony. For example, seabirds may have an expectation of the distance or time from the colony, before which they expect to locate prey. On reaching this point, individuals may turn rather than continue traveling away from the colony. This distance or time may be informed by short-term recall from previous trips with some level of error, as in scalar expectancy theory (Gibbon 1977, Giraldeau 1997). It was not necessary to build this type of mechanism into the IBFM because network foraging has a similar effect.

Higher population densities seem to be required for network foraging to lead to reduced foraging trip durations (Fig. 4.8). Network foraging serves to increase the effective search area covered by an individual. Grünbaum and Veit (2003) analyzed the effects of population densities on network foraging among Black-browed Albatross (*Thalassarche melanophrys*) using a combination of observed data and modeling. Their results suggest strong Allee-type density dependence in foraging success. Buckley (1997) developed a model to explore whether coloniality would lead to more rapid discovery of food patches by concentrating foragers in space and facilitating network foraging, compared to more dispersed breeding systems. Buckley (1997) found that, whenever feeding flocks are more conspicuous than food patches, searchers locate patches faster when they can monitor other foragers because the area of effective search is much greater than a single individual can search alone. Network foraging is therefore likely to be more effective at reducing search times when populations are high or when other mechanisms, such as the orientation of outbound headings through recall or the direction of returning birds, concentrate individuals in profitable areas.

In the IBFM, an additional mechanism associated with network foraging may contribute to increased search effectiveness. In the IBFM, under network foraging, birds in search mode switch from a fairly sinuous movement pattern to a more directed movement pattern when they detect another bird foraging. Relatively straight movement patterns represent efficient search strategies over broad scales when there is limited information on the location of available resources (Zollner and Lima 1999, Weimerskirch et al. 2007). In contrast, sinuous movement

patterns represent efficient strategies at finer scales, within an area where prey resources are known (or expected) to be available (Tremblay et al. 2007). For Peruvian Boobies, observed movement patterns over broad scales, including movements between patches, are relatively straight (see Fig. 4.3). This implies that the long-distance movement patterns of these seabirds may be better modeled as directed rather than correlated random walks. Unfortunately, this remains challenging at a population scale (see McClintock, 2012). Sinuous movement patterns, characteristic of area-restricted search, are localized and mostly associated with foraging. Unfortunately, the observed data do not reveal whether the relatively straight movement patterns are because birds are moving towards a specific location based on available information, or because birds with no information nevertheless select relatively straight movement patterns.

Comparison of search strategies

It would be inappropriate to compare the population densities required to ensure the effectiveness of network foraging with those necessary for effective orientation of outbound headings in the IBFM. While birds departing the colony may orient their outbound headings primarily by cueing off conspecifics, birds at sea may cue off conspecifics and other species that forage on anchoveta (Duffy 1983), and possibly fishing vessels. In order to keep the model simple, the version of the IBFM presented here focuses on a single species and colony, and thus does not capture the contribution of other species to network foraging. In addition, the choice of detection distance may affect the strength of results. For example, if the detection distance at the colony, r_{colony} , was reduced to 200m, high densities of birds would be necessary for effective information transfer at the colony. The size of prey schools may also influence detectability, both directly and indirectly, if large schools support large foraging flocks that can be detected at greater distances, but this is not incorporated in the current model.

Furthermore, the IBFM is not designed to prove or disprove either search strategy, and cannot be used to test the hypothesis that Guanay Cormorants depend more on information transfer at the colony than Peruvian Boobies. In open systems, similar observed patterns may be generated by several different mechanisms (Oreskes et al. 1994). Even if observed foraging patterns were reproduced with Guanay Cormorants orienting their outbound headings in line with the direction of returning birds and Peruvian Boobies depending on network foraging, this would support, but not demonstrate, the hypothesis of species-specific search strategies. As modeled here, the search strategy of orienting outbound headings in line with the direction of returning birds is consistent with individuals cueing off returning individuals or groups, and does not

require the emergence of ‘compass rafts’. The departure of Guanay Cormorants from compass rafts in line with the direction of returning birds points to the role of compass rafts as information mechanisms, but compass rafts could also act as an assembly or recruitment mechanism if foraging by Guanay Cormorants is facilitated by group foraging (see Evans 1982, Richner and Heeb 1996). Similarly, as noted above, the observed pattern of few birds traveling far from the colony (Fig. 4.1) could be an effect of network foraging or the result of birds turning when they reach an expected maximum distance from the colony based on short-term recall.

Value of information under different foraging conditions

The second hypothesis investigated in this chapter was that information is more valuable when foraging conditions are poor. The analytical results presented in Table 4.2 indicate that the value of information was greater in 2009, when anchoveta was more concentrated, with few areas of high abundance, and the anchoveta schools were generally deeper and more variable in depth. In contrast, the value of information was limited in 2008, when anchoveta was broadly distributed with areas of high abundance occurring throughout the foraging region, and anchoveta schools were relatively shallow. Table 4.2 shows that, when prey is broadly-distributed in all directions (as in 2008), information on directions to avoid have limited value. IBFM simulations corroborate these analytical results, and also indicate that the difference in time spent searching for prey with and without network foraging is limited when prey is broadly distributed (Fig. 4.8).

In the IBFM, simulated birds under Scenario D (oriented outbound headings and network foraging) with high population densities achieve foraging trip durations similar to those calculated for ‘optimal’ seabirds with perfect information. Under this scenario, the difference in mean failure rates and mean foraging trip durations between simulations based on 2008 and 2009 prey data is minimal, suggesting that information may play a role in mitigating poor foraging conditions.

The key mechanism underpinning these results is revealed by comparing selection patterns in simulations where birds have no prior information (as in Scenario A) with those in which birds do have access to information (as in Scenarios B, C, D). For a given simulated prey field, $p_{patch,i}$ is the same for each cell under all scenarios, so any differences in the values of p_{patch} in selected cells reflects changes in the probability that foragers reach cells with high probabilities of patch selection. If search strategies are effective at guiding foragers towards profitable areas, then we would expect to see a shift in the distribution of selected cells towards more profitable cells, even though there are no changes in p_{patch} .

Figure 4.13 shows the distribution of selected cells in terms of abundance, the depth distribution, and the estimated probability of patch selection. The plots for 2008 indicate limited change in the distribution of selected cells. In terms of abundance, in 2008, scenarios with information (Scenarios B, C, and D) do not lead to a clear shift towards cells with higher abundance, compared to the scenario without information (Scenario A). (For the abundance plots, the bimodal distribution reflects the high proportion of zero values in the observed data for anchoveta.) In contrast, in 2009, the scenarios with oriented outbound headings (Scenario B and D) lead to a shift towards cells with higher abundance, whereas the scenario with network foraging only (Scenario C) has limited effect. In terms of the depth distribution, in 2008, the only scenario that outperforms the scenario with no information (Scenario A) is the one with oriented outbound headings only (Scenario B). In comparison, the scenario with oriented outbound headings and network foraging (Scenario D) tends to retain the birds close to the colony so that they do not reach the cells where prey is more shallow. (Distributions for Scenario D are multimodal, reflecting the relatively small set of cells that is selected in each simulation in this scenario.) In contrast, in 2009, all three scenarios with information outperform the scenario without information (Scenario A), with the scenario with full information (Scenario D) performing best. In terms of the probability of patch selection ($p_{patch,i}$), in 2008, scenarios with information (Scenarios B, C, and D) do not lead to a clear shift in the distribution of selected cells. In contrast, in 2009, the scenario with full information (Scenario D) leads to a marked shift in the distribution of selected cells, indicating the combination of search strategies is effective in guiding birds to cells with higher selection probabilities. Figure 4.13 supports results presented elsewhere in this chapter that the effects of additional information are greater when foraging conditions are poor (as in 2009).

Hypotheses for a dynamic prey field

The effectiveness of both search strategies would be reduced in the context of a highly dynamic prey field in which favorable segments of the prey field shift rapidly, for example through fish movement patterns and/or depletion in areas with high densities of foragers. This dynamism would reduce the probability that a patch indicated by the direction of returning birds would be available by the time an outbound bird arrived. Depletion would also mitigate the value of information provided through network foraging. In the context of depletion through competition, Buckley (1997) found that concentration of individuals is favored when food patches are sufficiently large or short-lived for competition to be limited, while the dispersal of foragers is favored when patches are small or long-lived, such that they could provide resources over longer periods if competition is reduced. Krebs (1974) found that foraging flocks of Great

Blue Herons (*Ardea herodias*) only built up where foraging conditions were good. Piatt (1990) found evidence for a threshold effect in the response of Common Murres and Atlantic Puffins (*Fratercula arctica*) to spawning schools of capelin off Newfoundland, with thresholds varying by species and by prey availability. In the North Sea, Camphuysen (2011) found that Northern Gannet foraging flocks in the North Sea were typically short-lived, except when flocks formed in association with cetaceans which prevented prey from escaping to deeper waters. In the northern Humboldt Current system, Duffy (1983) found that small foraging flocks persisted for about 15 minutes, but many large groups foraging over shoals persisted for two to three hours or more. This suggests that prey were unable to escape predation, perhaps due to sub-surface predators including Guanay Cormorants or to a shallow thermocline, and that some foraging locations remained profitable for several hours despite the presence of large numbers of competing predators.

In the context of a dynamic prey field, the comparative effectiveness of the two strategies discussed here would depend on the scale and rate of change. Both the orientation of outbound headings and network foraging would lead to individuals heading in similar directions if segments of the prey field remain favorable over long periods, sufficient for individuals to make several foraging trips. The main difference is that information would build up more slowly under the short-term recall strategy. In contrast, short-term recall would have limited effectiveness and the direction of returning birds would provide more current information if favorable segments change rapidly relative to foraging trip durations and intervals between trips. This question could be investigated in the IBFM, using artificial prey fields with different rates of change at different scales.

In the context of a highly dynamic prey field, looping tracks would provide a mechanism for discovering new areas, catalyzing shifts in the distribution of outbound headings over time. Observations of compass rafts indicate that these tend to shift over time consistent with mobile patches and/or the depletion of some patches and discovery of others (Weimerskirch et al. 2010). This could be investigated in the IBFM by comparing the rate of change of the distribution of outbound headings in simulations with only commuting birds versus simulations with only looping birds.

The value of information generated by other birds raises the question of why an individual would leave the colony and scout for prey (as described by Murphy (1936)) when it could lounge around at the colony and wait for information to develop. The answer may lie in the depletion of prey close to the colony or hunger. Early birds might have lower expected foraging

trip durations at the expense of higher failure rates. This question could be addressed in the IBFM by investigating the evolution of foraging trip durations over time given different depletion rates. (This “scout-lounger” version of the IBFM would be named in honor of R.C. Murphy and in recognition of existing producer-scrounger models (Stephens et al. 2007).)

Notation

δ	scaling parameter
η	predictor in the binomial model for patch selection
ψ	vector of model parameters
D	the data
d_i	upper depth limit of aggregations in a cell
i	cell or location index
$L(.)$	likelihood
M	number of cells encountered in a straight line from the colony
N	total number of data points across all simulations
$NLL(.)$	negative log-likelihood
$P(.)$	probability
$p_{patch,i}$	patch selection probability, i.e. probability that diving behavior occurs in a cell
r_{colony}	detection radius for birds at the colony
r_{sea}	detection radius for birds at sea
s_i	relative acoustic abundance in a cell
T_{patch}	patch residence time
T_{satis}	satiation time
Mode 0	at the colony
Mode 1	outbound travel
Mode 2	foraging
Mode 3	broad-scale search
Mode 4	transit
Mode 5	following
Mode 6	homebound travel
Mode 7	returned
Mode 8	failed

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Tables

Table 4.1. Movement parameters for the IBFM.

Mode	Step lengths (km per hour) [†]	Turning angle
0 at colony	NA	NA
1 outbound travel	50	0; oriented by outbound heading
2 search	50	~ wrapped Cauchy (0, 0.886)
3 foraging	NA	NA
4 transit	50	0; directed towards target cell
6 homebound travel	50	0; directed towards colony
7 returned	NA	NA
8 out-of-bounds	NA	NA

[†] Step lengths (i.e. distance covered per time step) are rounded to the nearest km per hour.

Table 4.2. Probability of failure and expected foraging trip durations with and without perfect information.

	Probability of failure			Expected foraging trip duration (FTD)		
	no information	min. P(failure)	value of information	no information	min. E(FTD)	value of information
2008	0.41%	< 0.001%	0.41%	49.56 mins	36.13 mins	13.43 mins
2009	5.94%	0.21%	5.72%	54.34 mins	37.95 mins	16.40 mins

Figures

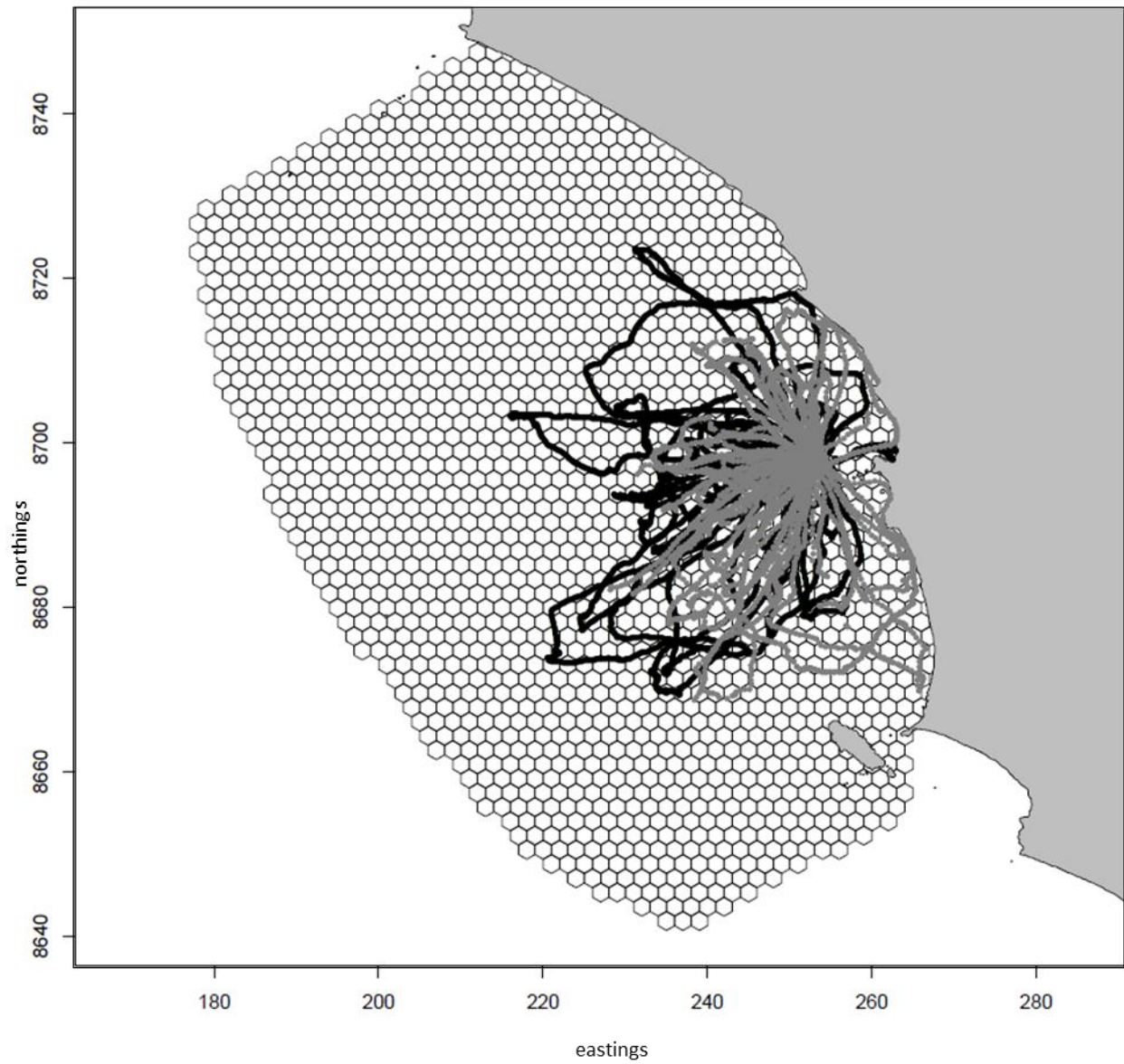
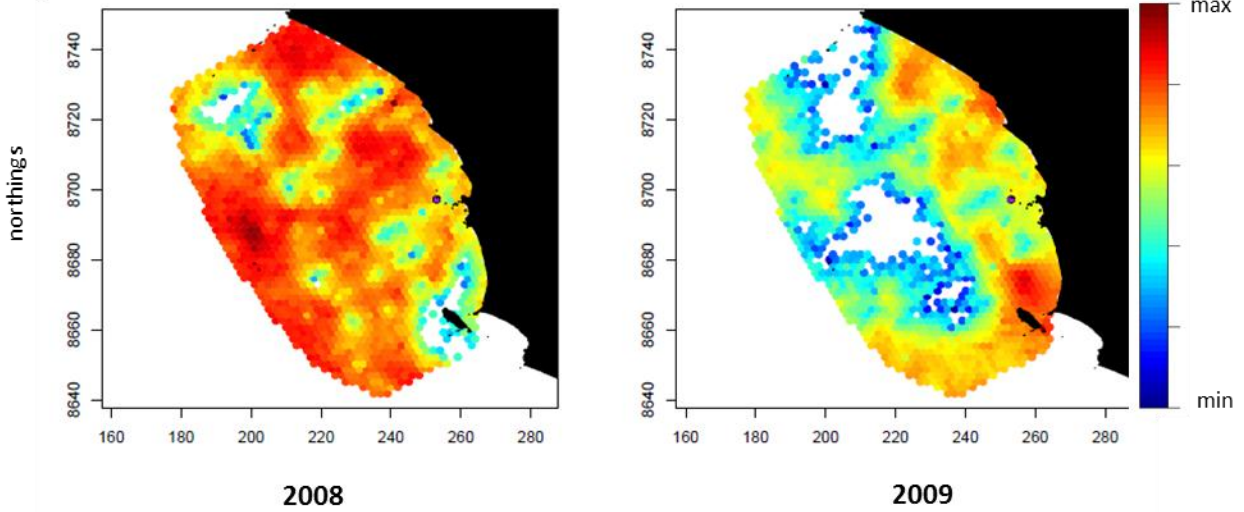


Figure 4.1. Extent of the foraging region showing observed tracks for Peruvian Boobies and Guanay Cormorants in 2008. Black points indicate Peruvian Boobies; grey points indicate Guanay Cormorants; pale grey indicates land.

Log of mean relative abundance



Mean probability that the upper depth limit of aggregations is less than 7.472 m

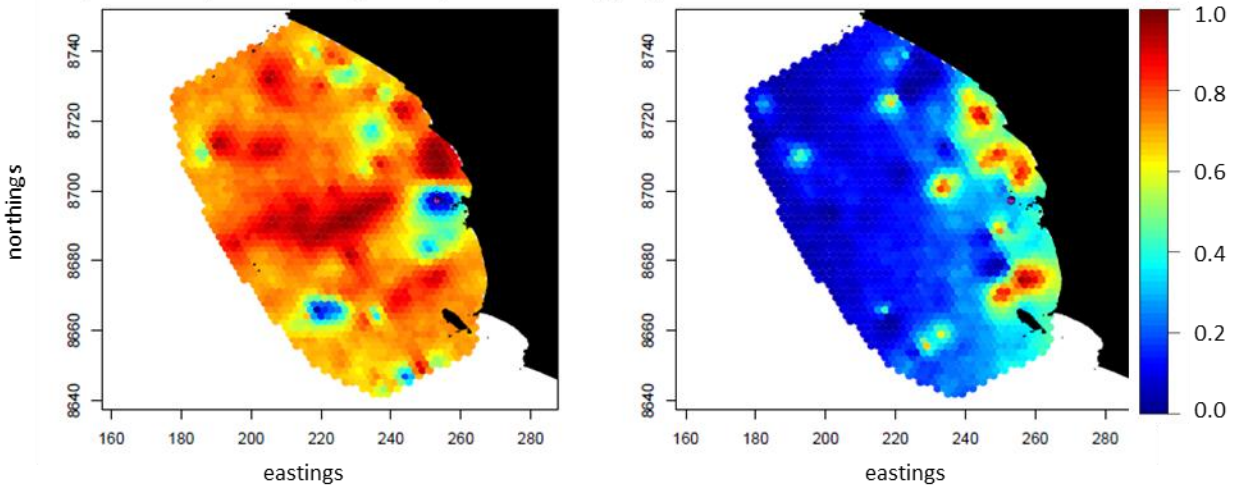


Figure 4.2. Contrasting foraging conditions in 2008 and 2009. Plots are based on conditional geostatistical simulations of acoustic survey data of anchoveta. In the patch selection decision rule for Peruvian Boobies, the scaling parameter for depth distributions is 7.472m. Classifications are based on equal intervals, with the same scale for both years. Land is indicated in black. The colony is indicated by a purple hexagon.

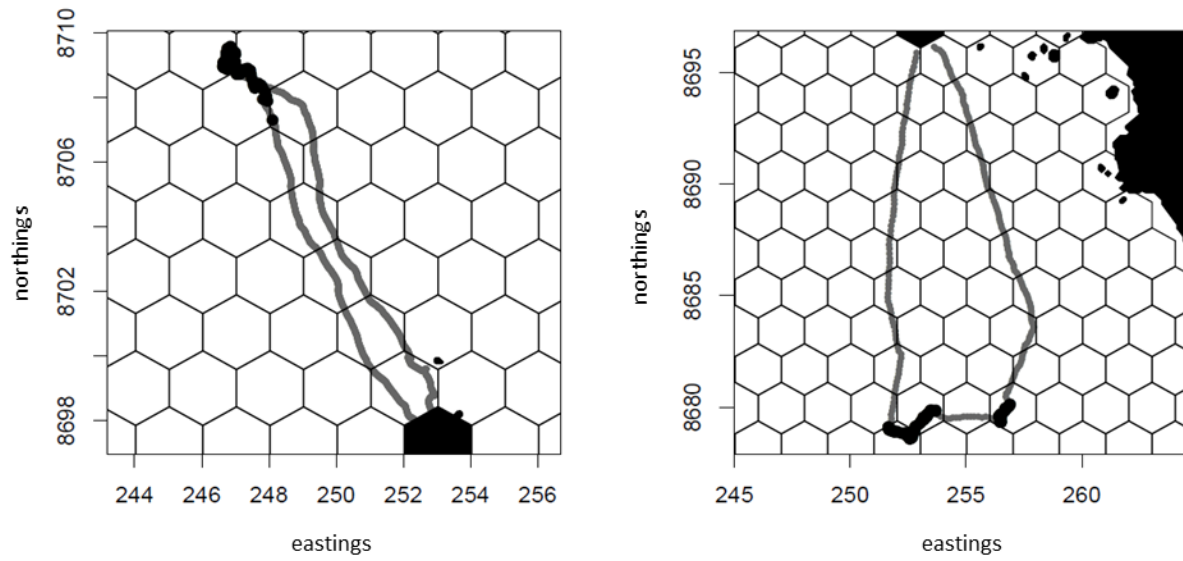


Figure 4.3. Examples of a commuting track (left panel) and looping track (right panel) by Peruvian Boobies. Black points indicate fine-scale search and foraging behavior as indicated by the hidden Markov model presented in Chapter II.

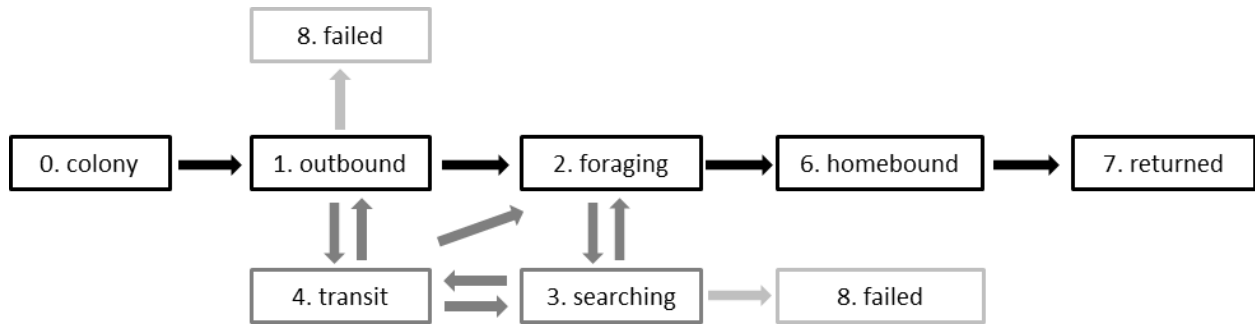


Figure 4.4a. Structure of foraging trips in the IBFM. All individuals pass through modes outlined in black.

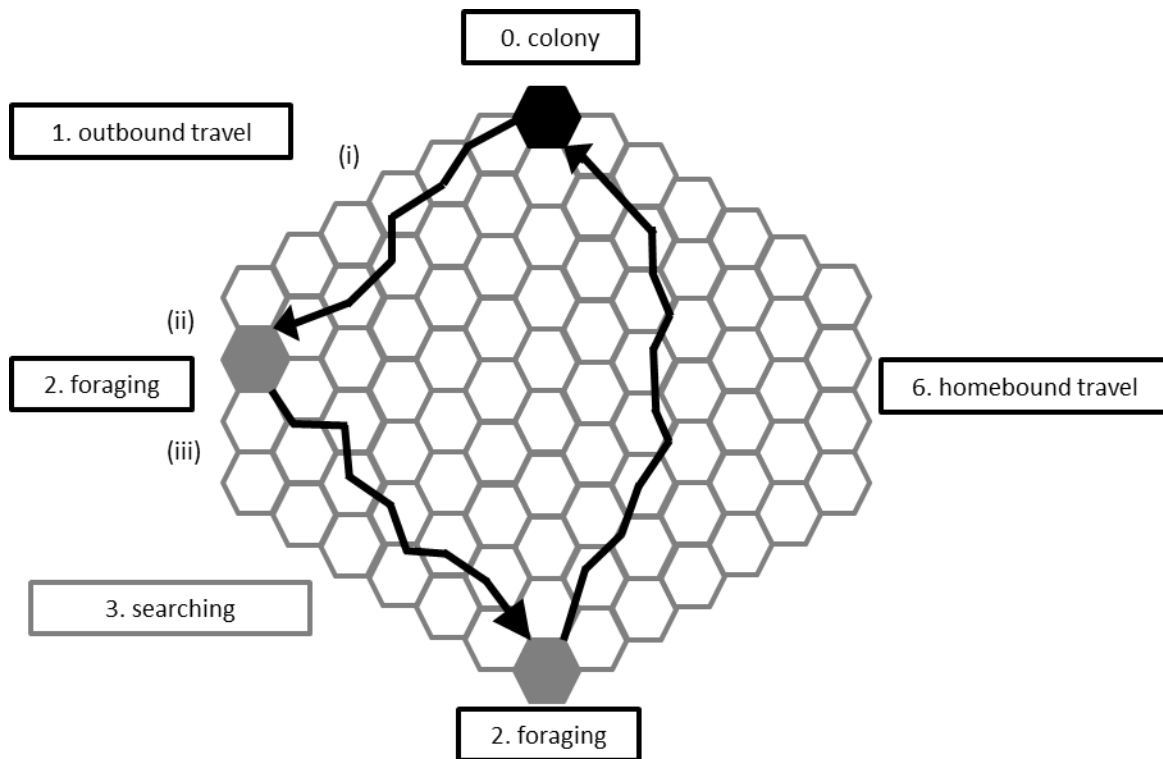


Figure 4.4b. Structure of foraging trips in the IBFM. (i) The forager selects an outbound heading and departs the colony in outbound travel mode (Mode 1). (ii) On entering a new cell, the forager decides whether to switch to foraging mode (Mode 2) while in that cell. While in a foraging cell, the individual monitors the amount of time spent in foraging mode (Mode 2). (iii) Once patch residence time is reached, it either switches to search mode (Mode 3) to search for another patch (looping trips, as shown here) or switches to homebound mode (Mode 6) and returns to the colony (commuting trips).

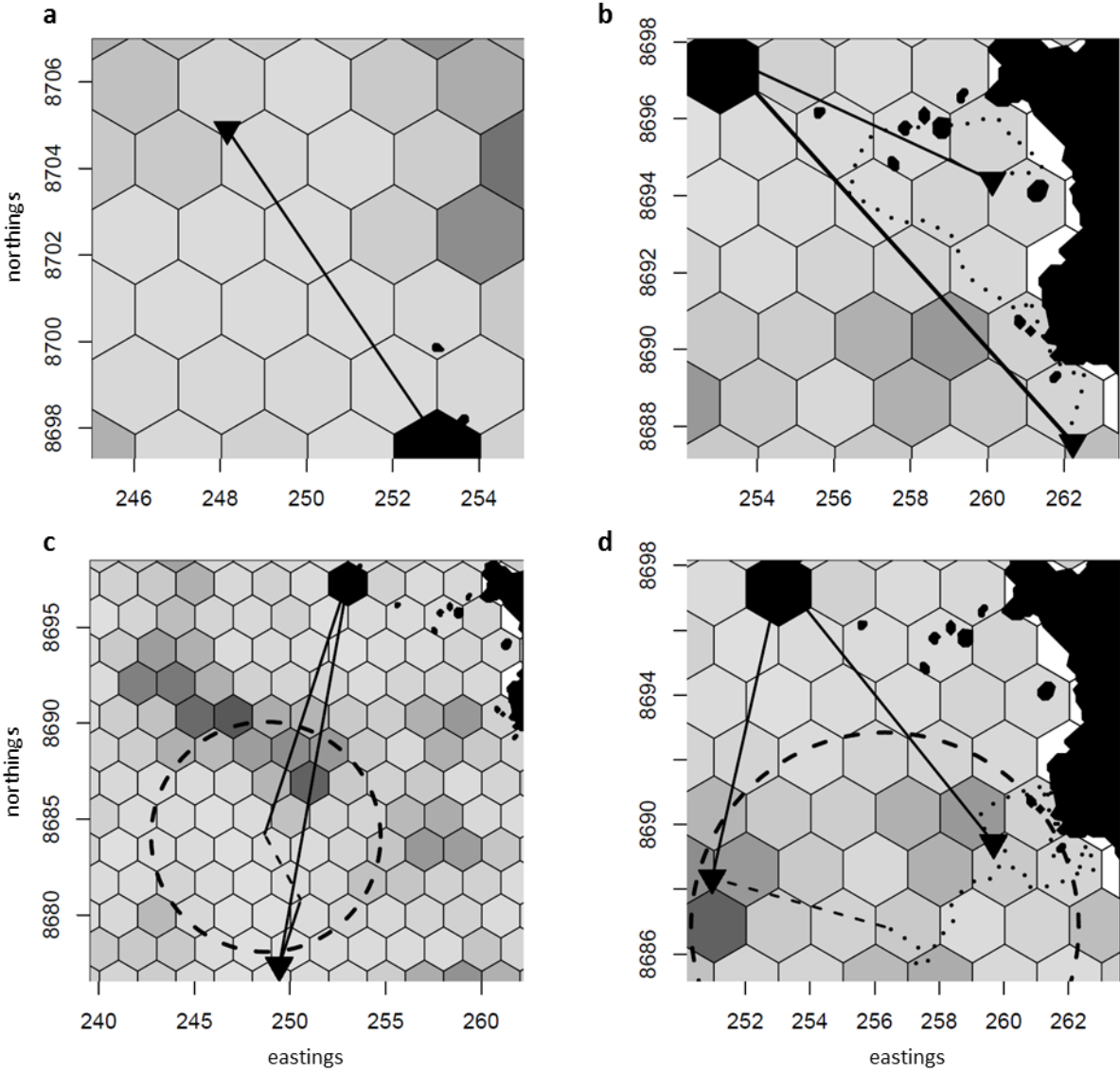


Figure 4.5. Examples of simulated tracks. a) commuting track without network foraging; b) looping track, without network foraging; c) commuting track with network foraging; d) looping track with network foraging. Outbound and homebound modes are shown as solid lines; search modes are shown as dotted lines; dashed lines indicate transit towards a foraging bird; circles indicate the detection distance for network foraging (6 km); foraging is indicated by black triangles; the colony is indicated by a solid black hexagon.

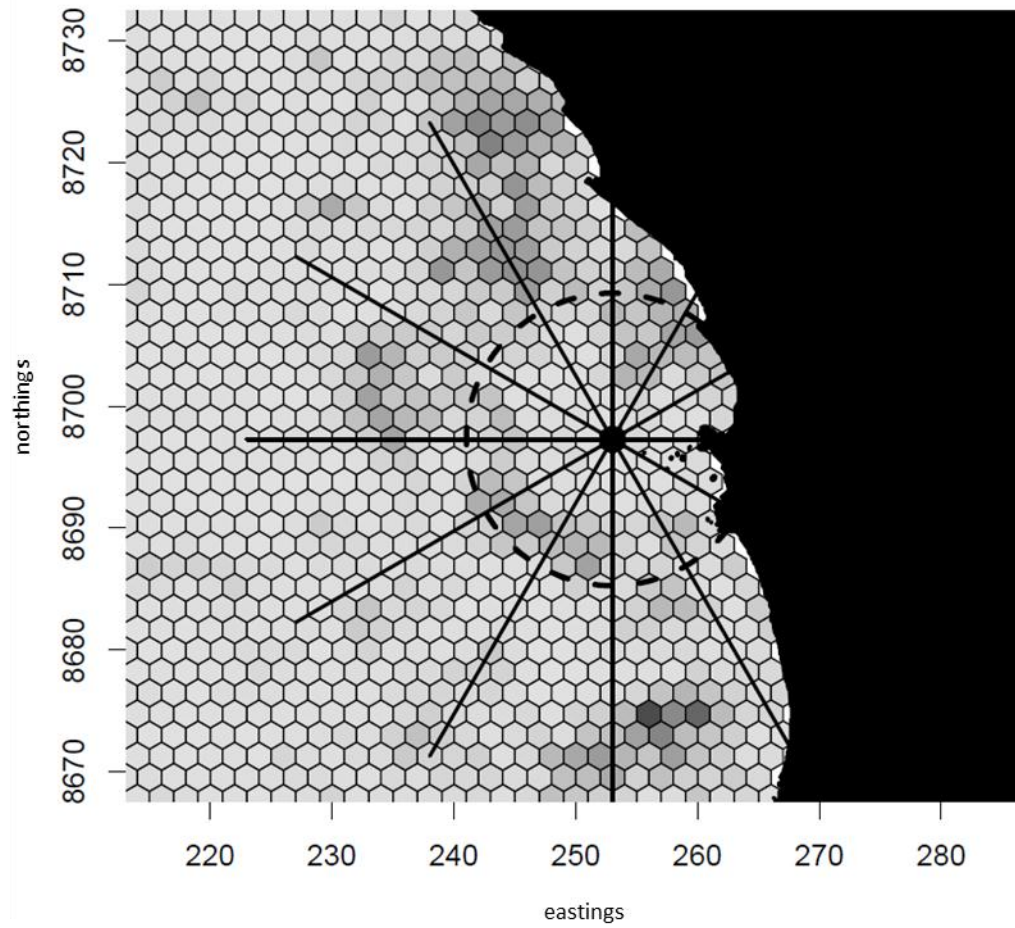


Figure 4.6. Simulated prey field showing segments for orientation of outbound headings. The circle indicates the detection distance from the colony (12 km).

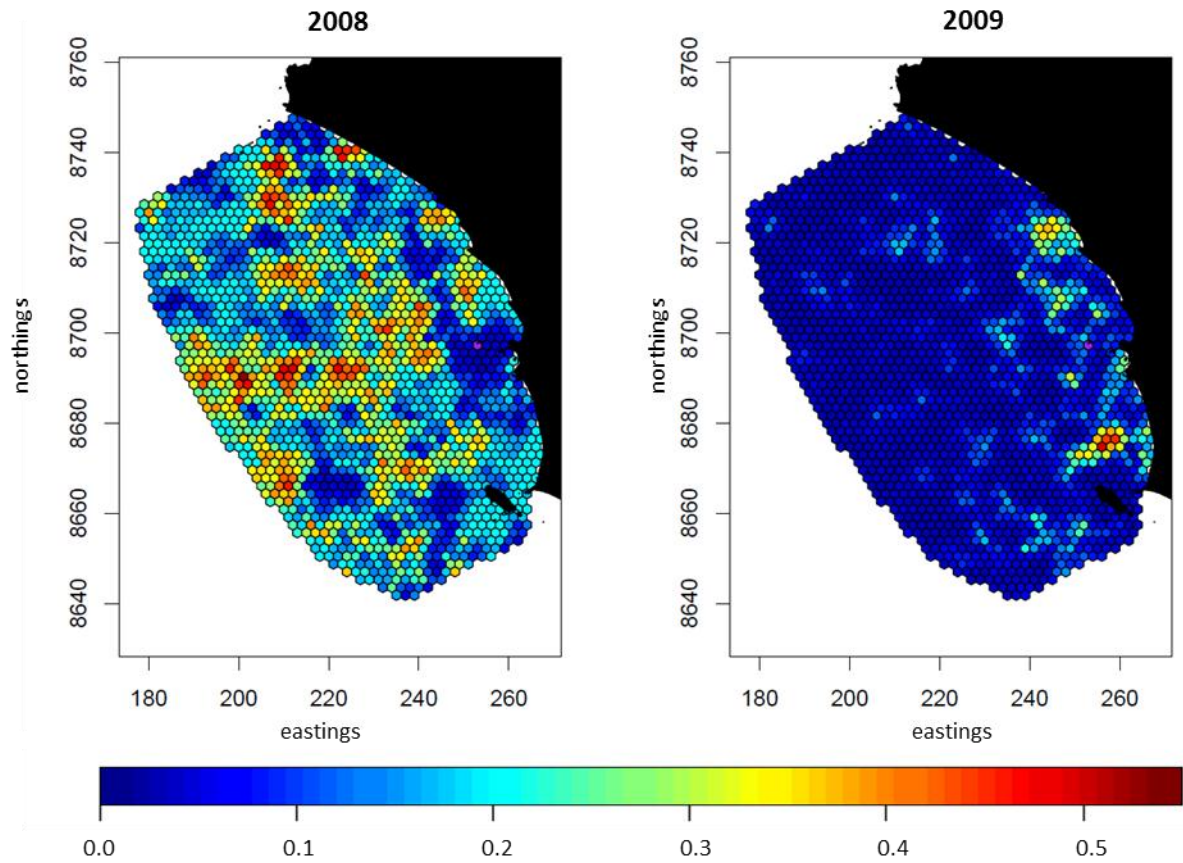
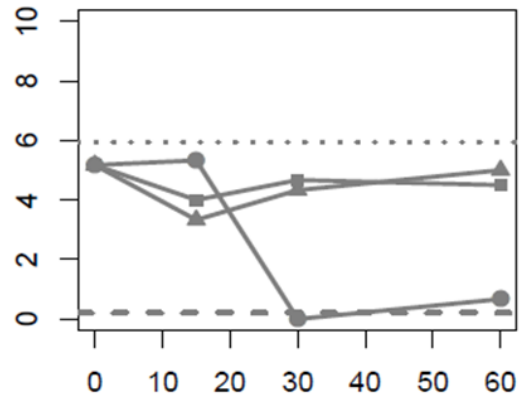
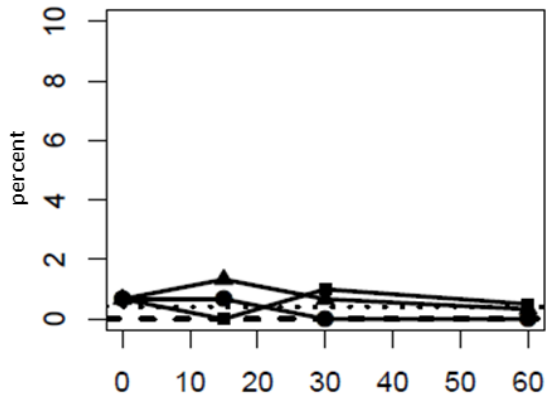


Figure 4.7. Sample simulated prey fields for 2008 and 2009. Irregular solid shapes indicate land; the colony is indicated by a purple hexagon.

Failure rates



Foraging trip duration

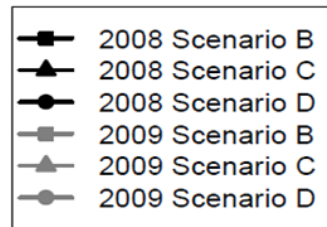
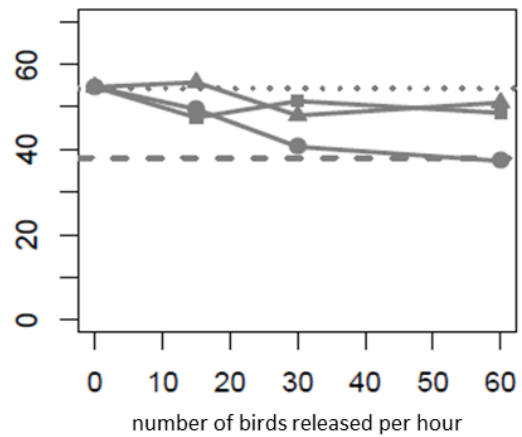
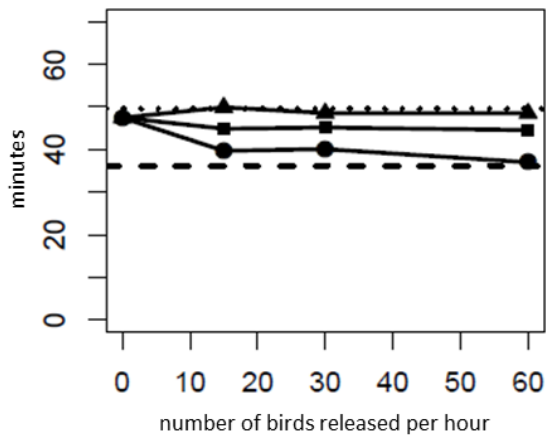
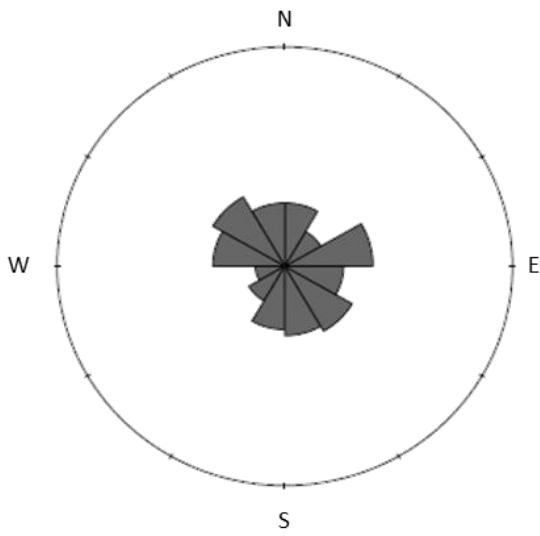
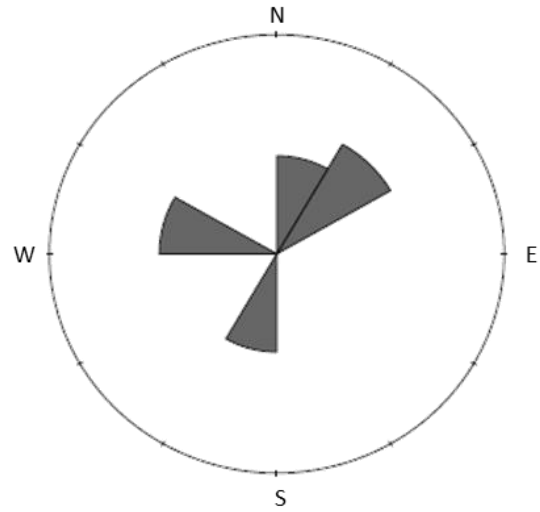


Figure 4.8. Mean failure rates and mean foraging trip durations under various information rules and population densities. Dotted lines indicate expected results for commuting trips with no information. Dashed lines indicate expected results for commuting trips with perfect information.

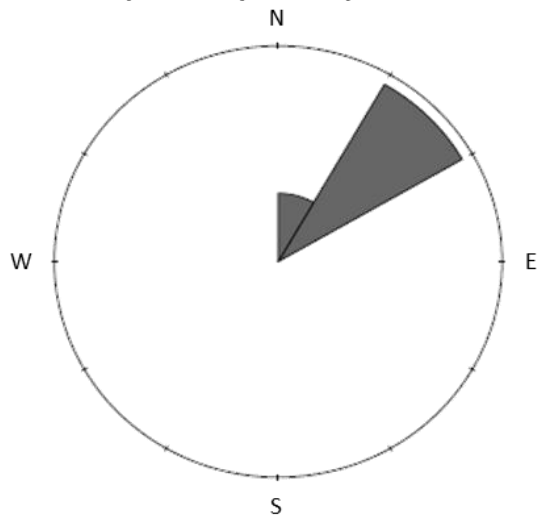
No orientation (60 birds per hour)



Orientation (15 birds per hour)



Orientation (30 birds per hour)



Orientation (60 birds per hour)

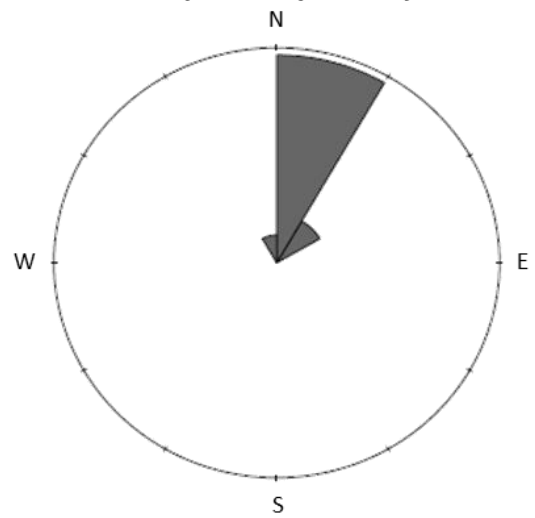


Figure 4.9. Distributions of oriented outbound headings for simulations with various population densities. Simulations are based on the 2009 prey field.

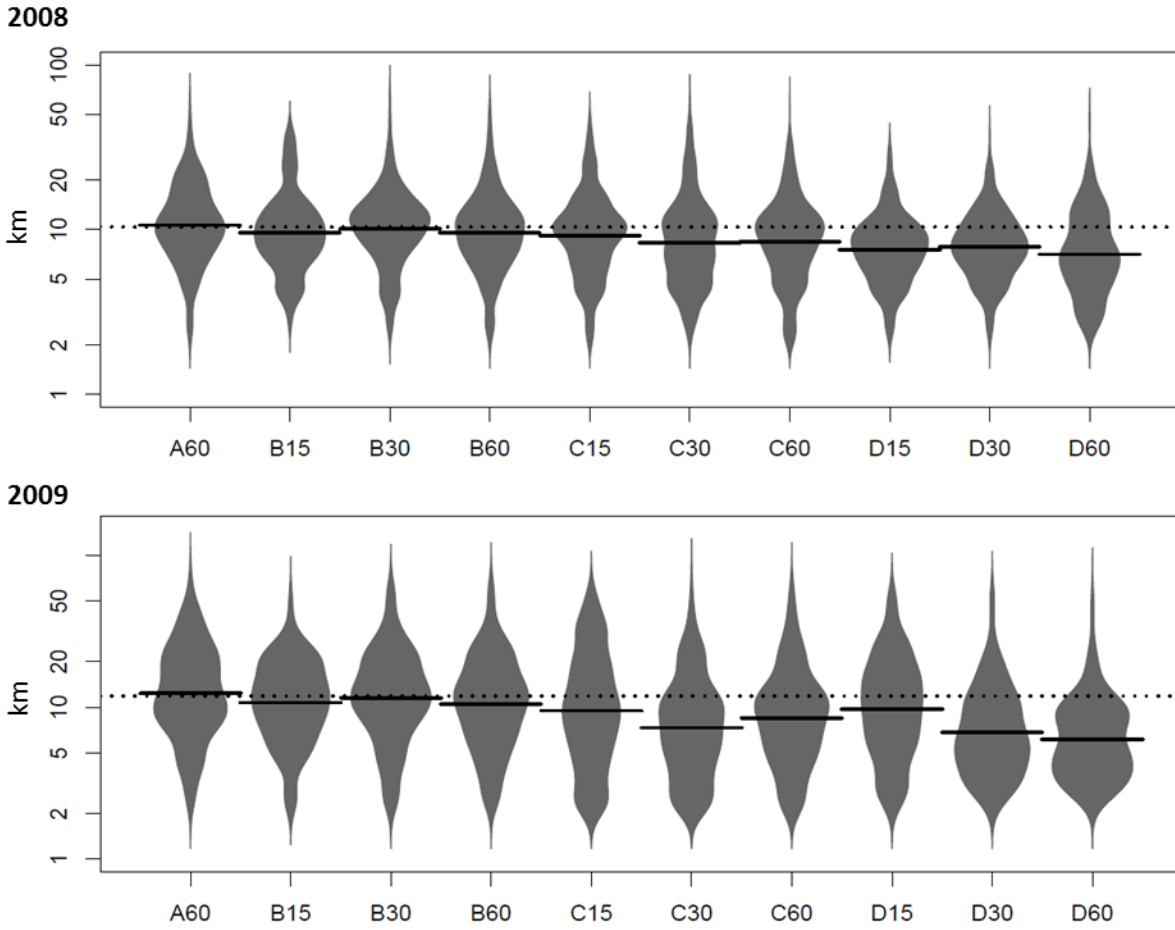
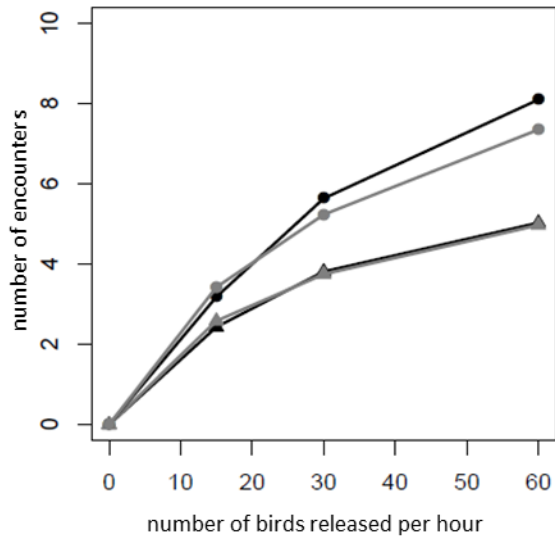


Figure 4.10. Beanplots of maximum distance under Scenarios A, B, C, and D. (A60 indicates Scenario A with 60 birds departing per hour.) The overall mean for each year is indicated by the dotted line; bars indicate the mean for each scenario and population density combination.

Mean number of encounters per individual



Mean percentage of encounters leading to foraging in the target cell

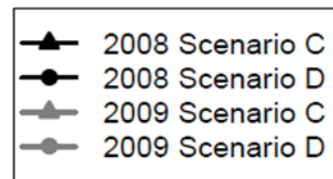
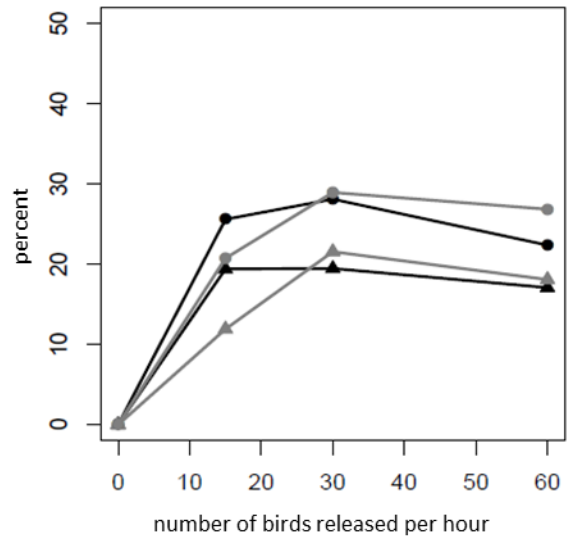


Figure 4.11. Network foraging. Mean number of encounters per individual and mean percentage of encounters leading to foraging in the target cell under various information rules and foraging conditions.

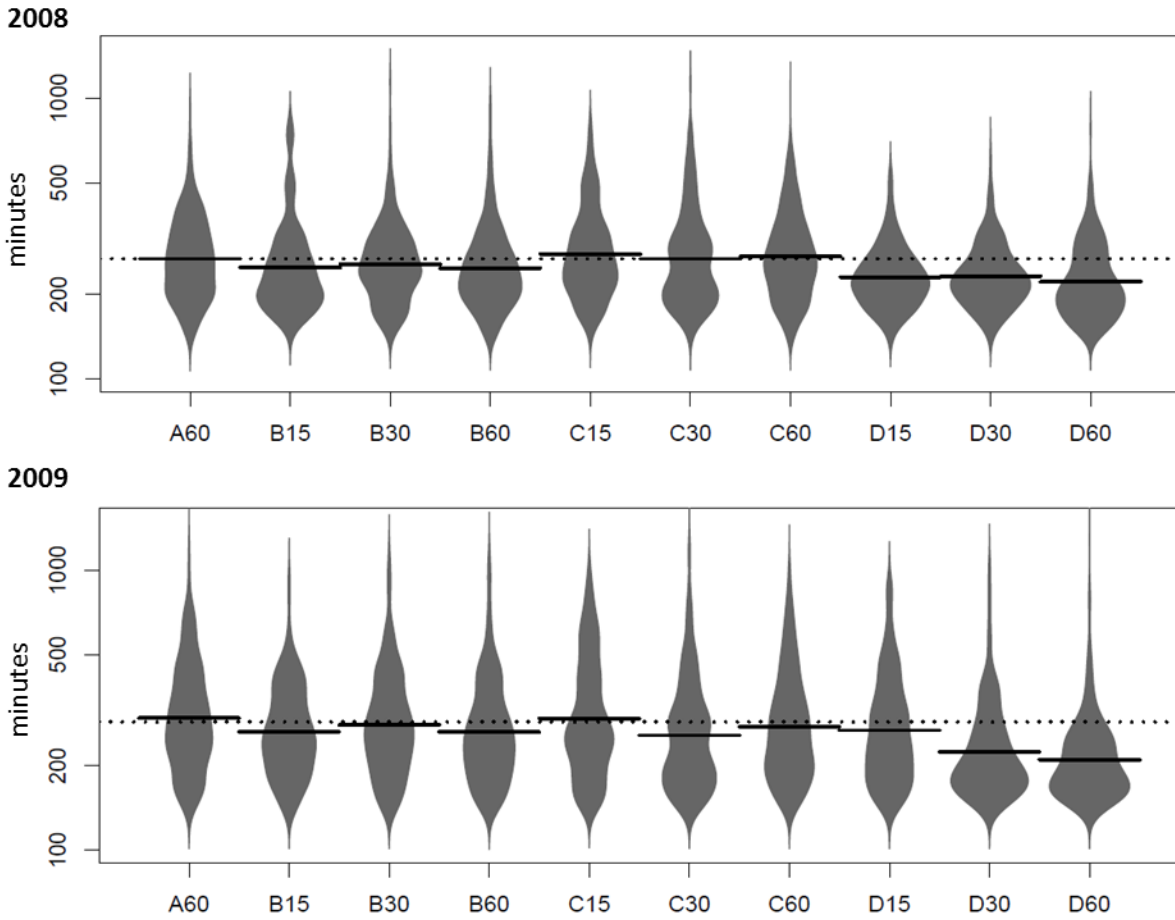


Figure 4.12. Beanplots of foraging trip durations under Scenarios A, B, C, and D. (A60 indicates Scenario A with 60 birds departing per hour.) The overall mean for each year is indicated by the dotted line; bars indicate the mean for each scenario and population density combination.

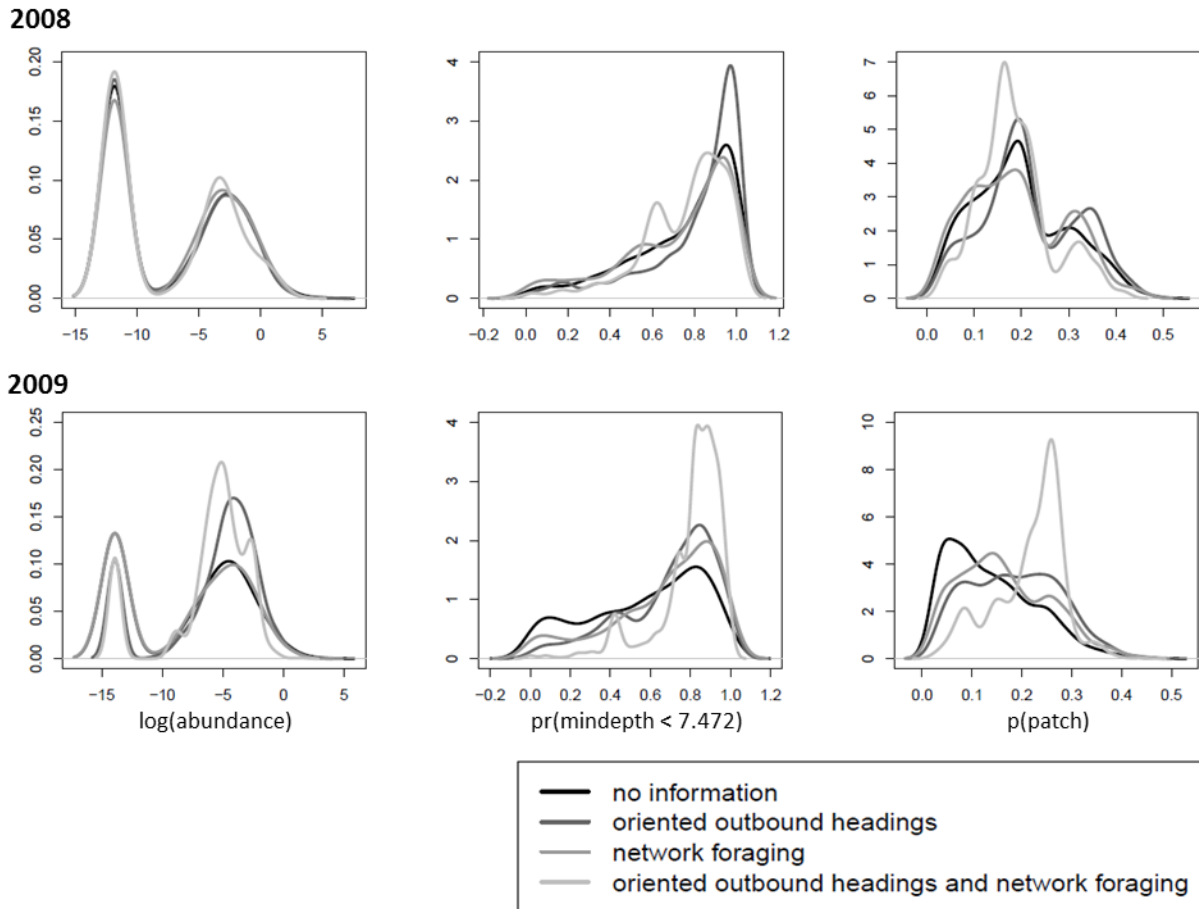


Figure 4.13. Selected cells in terms of abundance (left panel) and the depth distribution (center panel), and the estimated probability of patch selection (right panel) based on simulations for 2008 and 2009 under various information rules.

Chapter V: Effects of changes in the abundance and distribution of prey on the foraging patterns of Peruvian Boobies and Guanay Cormorants

Introduction

Seabirds, pinnipeds, and other central place foragers (CPFs) are especially vulnerable to reduced prey availability. CPFs return to a specific location, such as the breeding colony, between foraging trips (Orlans and Pearson 1979), and this restricts the potential for CPFs to respond spatially to changes in the availability and distribution of their prey. During the breeding season, seabirds may also be operating close to time and energy constraints (Ashmole 1963). Together, these constraints imply that the ability of adults to adjust their foraging effort in response to variation in foraging conditions may be critical to breeding success and ultimately population persistence (Ashmole 1963).

There is evidence of severe declines in the breeding success and populations of several species of seabirds in upwelling systems during oceanographic anomalies, with food availability assumed to be the main mechanism (e.g. Crawford and Shelton 1978, Crawford and Jahncke 1999, Jahncke and Goya 2000, Thayer and Sydeman 2006). Reduced food availability due to competition with fisheries has been identified as a major threat to a number of globally threatened or near-threatened seabird species, especially in regions where large commercial fisheries target forage fish that are also important for seabirds (Duffy et al. 1984, Becker and Beissinger 2006, Crawford et al. 2006, Furness 2007). There are also growing concerns about the potential impacts of climate change on food availability (Croxall et al. 2002, Schreiber and Burger 2002, Furness 2007).

While prey availability is usually correlated with abundance, other factors also influence the ability of predators to locate and capture prey (Cairns 1987). For CPFs, prey availability can be defined in terms of abundance, accessibility, and distance from the colony or central place (Boyd 1999). A further aspect of food availability is the concentration of prey. Prey may be clustered in a few large patches or aggregations, or widely dispersed in many small patches (see Davoren 2000, Bertrand et al. 2005). The design of effective conservation and management strategies for species threatened by reduced food availability depends on how foraging success, and ultimately population dynamics, is affected by changes in various aspects of food availability. Some aspects of food availability are more amenable to management action than others (for example, abundance compared to accessibility, distance, and concentration). It is therefore important to understand the effects of changes in various aspects of prey availability

on the foraging success of CPFs, in order to design strategies that will be effective in safeguarding foraging success in the context of competition with fisheries, oceanographic variability, and long-term climate change.

Empirical studies have provided valuable insights into the effects of changes in prey availability (usually measured in terms of abundance) on the foraging success of seabirds and other CPFs (e.g. Boyd 1999, Russell 1999, Davoren 2000, Kitaysky et al. 2000, Reid et al. 2005, Croll et al. 2006, Furness 2007, Piatt et al. 2007, Burke and Montevecchi 2009). However, empirical studies face challenges in separating out the effects of various aspects of prey availability. Long time-series with corresponding data on predator and prey are needed to separate out the several different components of prey availability, which are often correlated. However, there are relatively few long-term datasets available, and those that do exist mostly have data on the abundance of prey, but not the other aspects of prey availability mentioned here. For example, Cury et al. (2011) matched data on seabird breeding success from long-term studies of 14 species with data on the abundance of their main prey species, mostly generated from fisheries stock assessments. However, stock assessment outputs typically do not include information on changes in the spatial configuration of forage fish and their accessibility to CPFs. Furthermore, differences in the sampling strategies between seabirds and fisheries or stock surveys, in terms of size or age class and space, often frustrate efforts to match seabird responses with these data sources (Croxall 1987, Hunt et al. 1991, Montevecchi 1993).

In this context, mechanistic models can play a useful complementary role to empirical studies. In this chapter, the individual-based foraging model (IBFM) described in Chapter IV is used to explore the effects of changes in various aspects of prey availability on the foraging success of seabirds and other CPFs foraging on schooling prey. Specifically, the effects of changes in the abundance, accessibility, and the spatial configuration of prey resources on the foraging patterns of surface-foraging seabirds are investigated. Here, accessibility is approximated by the depth distribution of prey, and 'spatial configuration' refers to both the average distance of prey from the colony and the spatial concentration of prey, which are confounded in the data. The following hypothesis is tested: foraging success depends on the depth distribution and spatial configuration of prey as well as abundance.

As described in Chapter I, acoustic survey data for the region off Grupo Pescadores, Peru, in early December 2008 and 2009 reveal contrasting foraging conditions, in terms of the regional abundance, depth distribution, and spatial configuration of anchoveta (Figure 5.1). A series of novel prey fields was created by disaggregating and recombining the abundance, depth

distribution, and spatial configuration aspects of geostatistical simulations based on these data. Using the mechanistic IBFM, it was then possible to simulate seabird foraging patterns for each of the novel prey fields in order to explore the effects of changes in each of the various aspects of prey availability in isolation.

Two species were considered, the Peruvian Booby and the Guanay Cormorant, in order to gain insight into how differences in species characteristics influence the effects of changes in various aspects of prey availability. Both species forage primarily on anchoveta, and often forage together in large foraging flocks (Duffy 1983), but have contrasting flight energetics and diving capabilities (del Hoyo et al. 1992). Since the mid-1950s, Guanay Cormorants have exhibited a substantial decline from around 21 million to 2 million birds, while populations of Peruvian Boobies have been comparatively stable at around 2 million birds (Jahncke 1998, Goya 2000, Weimerskirch et al. 2010). The general decline in seabird populations in the northern Humboldt Current system (HCS) since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (e.g. Jahncke et al. 2004), but it remains unclear why populations of Guanay Cormorants have failed to recover following severe oceanographic anomalies whereas populations of Peruvian Boobies have remained comparatively stable. Various hypotheses are available to explain this response, including differences in diet specialization, flight proficiency, dive capacities, and search strategies (Furness and Ainley 1984, Furness and Tasker 2000). In particular, there is some evidence that the Guanay Cormorant may require denser prey schools than the Peruvian Booby for effective foraging (Nelson 1978). On the other hand, the pursuit-diving Guanay Cormorant is capable of reaching greater depths than the plunge-diving Peruvian Booby. Several researchers have found that surface feeders or shallow-diving seabirds are more vulnerable than deep divers to oceanographic change because of their more restricted foraging range within the water column (e.g. Oedekoven et al. 2001). Analysis of foraging site selection in Chapter III indicated that both Peruvian Boobies and Guanay Cormorants responded to a combination of abundance and the depth distribution of prey, but differences in parameter estimates indicated different selection patterns.

Methods

For the analyses presented in this chapter, the structure of the IBFM is as presented in Chapter IV Scenario D, with three modifications.

First, an additional mechanism has been incorporated to allow for depletion of prey resources by foraging seabirds and by the fishery. The acoustic surveys on which geostatistical simulations of prey fields were based took place over a period of several days, continuing

through the night, and thus may be assumed to average over depletion due to seabirds and the fishery. However, if depletion is not incorporated in the IBFM, a single patch of prey could sustain the entire colony through a day-long simulation. As a result, prey fields with a single accessible patch close to the colony might be considered more favorable than prey fields with many accessible patches a short distance farther away. This would undermine analysis of the effects of variation in foraging conditions, so for this reason, depletion is incorporated in the IBFM for the purposes of this analysis.

Second, the mechanism for determining outbound headings was modified to enable birds to adapt more rapidly to evolving foraging conditions given depletion.

Third, the detection distance for network foraging (r_{sea}) was reduced to 2 km. As discussed in Chapter IV, network foraging tends to retain individuals close to the colony. In this chapter, the detection distance was reduced, so that individuals forage at similar distances from the colony as observed in 2008, given simulated prey fields based on 2008 data.

Species

The differences in the representation of the two species in the IBFM are in decision rules relating to commuting vs looping behaviors, patch selection, and satiation time. For the purposes of this analysis, the IBFM is run separately for the two species — there are no inter-specific interactions.

Commuters vs loopers

In the IBFM, both species determine whether to follow a commuting or looping trajectory based on a single Bernoulli trial prior to departure. Here, the probability of a commuting trip was set at 40% for Peruvian Boobies and 60% for Guanay Cormorants based on observed data (Weimerskirch et al. 2010).

Patch selection

As in Chapter IV, patch selection is based on the observed probability that at least one dive occurs in a cell as a function of the relative abundance and depth distribution of anchoveta in each cell.

For Peruvian Boobies, patch selection is parameterized as:

$$\eta_i \sim -3.533 + 3.298 \cdot s_i^{0.034} \cdot P(d_i < 7.472) \quad 5.1$$

For Guanay Cormorants, patch selection is parameterized as:

$$\eta_i \sim -5.855 + 5.163 \cdot s_i^{0.019} \cdot P(d_i < 9.714) \quad 5.2$$

The differences in parameterizations for the two species imply that, for all levels of abundance in the upper surface waters, the probability of patch selection will be lower for Guanay Cormorants than for Peruvian Boobies. However, the estimated scaling parameter is deeper for Guanay Cormorants than Peruvian Boobies. Thus, Guanay Cormorants are able to access a greater share of the biomass distributed through the water column than Peruvian Boobies, unless prey is very shallow or very deep (see Fig. 5.2).

Satiation time

As in Chapter IV, the amount of time spent foraging prior to satiation, T_{satis} , is fixed, based on the total amount of time per foraging trip in cells in which at least one dive occurs. This is approximately 23 minutes for Peruvian Boobies and 54 minutes for Guanay Cormorants. For commuting birds, satiation time equals patch residence time. For looping birds of both species, the satiation time is divided equally between two patches.

Depletion

In this chapter, the main purpose of the IBFM is to explore the effects of changes in the abundance, depth distribution, and spatial configuration of prey resources on the foraging success of CPFs. Depletion by the focal species and other foragers may play an important role in this process. A depletion mechanism is therefore incorporated into the version of the IBFM used in this chapter. Each time a forager switches to foraging (Mode 2) in a cell, a fixed amount of biomass is removed from the upper surface waters. The relative abundance and depth distribution are then recalculated, as follows:

$$s'_{i,t} = s_{i,t} * z_{i,t} \quad 5.3$$

$$s'_{i,t+1} = s'_{i,t} - x \quad 5.4$$

$$s_{i,t+1} = s_{i,t} - x \quad 5.5$$

$$z_{i,t+1} = \frac{s'_{i,t+1}}{s_{i,t+1}} \quad 5.6$$

where $s_{i,t}$ refers to the relative acoustic abundance in cell i at time step t ; $z_{i,t}$ refers to the probability that the upper depth limit of aggregations is less than the estimated scaling parameter; and x refers to the amount of biomass removed. Relative abundance is not allowed to fall below zero. The mechanism assumes that anchoveta deeper in the water column do not

move into the upper surface waters to replace fish that have been removed. The patch selection probability is recalculated using Equation 5.1 or 5.2 as appropriate. The next bird to enter the cell bases its decision on whether or not to forage on the updated patch selection probability $p_{patch,i,t+1}$.

This mechanism may represent depletion by the modeled species or by other foragers in the system, especially CPFs from the same colony. The appropriate depletion rate is unknown. To test the sensitivity of results to different depletion rates, the model was run with depletion set to zero and at two contrasting rates, differing by two orders of magnitude: $x = 0.1$ and $x = 10$. (See Appendix V.1 for an explanation of how these rates were selected.)

To demonstrate the effects of depletion in the IBFM, 60 seabirds were released sequentially, following the same heading, and the effects of depletion on probabilities of patch selection through the course of the simulation were recorded. Figure 5.3 shows how the effects of depletion depend on initial relative abundance. When initial relative abundance is low, removing a fixed amount of biomass from the upper surface waters leads to a rapid decline of available biomass, and the probability of patch selection is reduced to minimum levels. Patches close to the colony with low patch selection probabilities (e.g. patches 1 and 2) were selected rarely. Patches with higher selection probabilities were selected more frequently, especially if close to the colony (e.g. patches 3 and 4).

Outbound headings

In Chapter IV Scenario D, departing birds selected an outbound heading from the compass segment with the largest number of returning birds. For this chapter, this mechanism was modified so that birds select a segment with probability proportional to the number of returning birds in each segment, within the same detection distance as previously (r_{colony}). This leads to a more dispersed distribution of outbound headings. In the context of a dynamic prey field undergoing depletion, this mechanism enables birds to adapt their outbound headings more rapidly as prey becomes depleted in a previously-favored direction.

Scenarios

Simulated prey fields based on data for 2008 and 2009 differ in terms of regional abundance (i.e. the total relative abundance over the simulated prey field), spatial configuration (both the concentration of prey and the average distance from the colony), and the depth distribution (Fig. 5.4).

To address the question of whether and how the foraging patterns of Peruvian Boobies and Guanay Cormorants change in response to changes in each of these three aspects of prey availability, novel prey fields were constructed by combining various aspects of geostatistical simulations based on acoustic survey data of anchoveta in December 2008 and 2009 (Table 5.1). Novel prey fields were coded as follows: A08 for regional abundance as in 2008, C08 for spatial configuration as in 2008, and D08 for depth distribution as in 2008, and likewise for 2009.

All C08 simulations were based on geostatistical simulations for 2008, and all C09 simulations were based on geostatistical simulations for 2009. The ratio of regional abundance in simulations based on 2009 data is 0.083 of the abundance in simulations based on 2008 data (Chapter I). For simulated prey fields in which the spatial configuration of 2008 was combined with the abundance of 2009 (e.g. A09.C08...), this ratio was used to downscale the relative abundance in each cell. Conversely, when the spatial configuration of 2009 was combined with the abundance of 2008 (e.g. A08.C09...), this ratio was used to upscale relative abundance.

Each simulation was then combined with a simulated depth distribution for the appropriate year (i.e. D08 or D09). As described in Chapter I, each geostatistical simulation of the depth distribution was generated separately from simulations of relative abundance, and contains an estimate for all cells in the prey field, including locations where no prey was encountered during the acoustic survey. For each scenario in Table 5.1, 100 simulated prey fields were generated, and the IBFM was run separately for each species on each simulated prey field.

Performance indicators

As in Chapter IV, the performance of simulated seabirds was measured in terms of foraging success or, conversely, failure rates (i.e. whether or not birds succeeded in locating prey, foraging, and returning to the colony without leaving the foraging region before dusk), as well as foraging trip duration and the maximum distance from the colony.

Regression trees were used to identify the independent variables (such as abundance, depth distribution, and spatial configuration) that are most important in predicting failure rates. Regression trees provide a non-linear, non-parametric method to partition a response variable into hierarchical subsets based on predictor variables (Ripley 1996). All possible splits in the response variable are identified and then evaluated using a 'goodness of split' criterion. Here, this criterion was based on deviance (i.e. the split which maximizes the reduction in unexplained deviance was accepted). This process was continued until the unexplained deviance could not be reduced further.

Regression trees are prone to over-fitting. Proposed splits may be validated using statistical tests. However, comparative boxplots/beanplots are presented rather than statistical tests and evaluation is left open given a lack of information on the scale of differences in failure rates that are ecologically-significant, and that the 'data' are simulation results.

Results

Comparison of simulated foraging trip statistics with observed data for 2008

IBFM simulation results for Peruvian Boobies and Guanay Cormorants based on simulated prey fields for 2008 (i.e. A08.C08.D08) are reasonably consistent with observed data for that year (Table 5.2). For both species, the mean foraging trip duration and maximum distance for simulated birds is closer to the observed values when depletion is included in the IBFM. Unfortunately, there are insufficient observed data from the acoustic survey period in 2009 to make any comparisons.

Figure 5.5 compares the mean directions of simulated outbound headings based on simulated prey fields for 2008 with the mean direction of observed birds in that year. The mean direction of outbound headings for observed birds in 2008 was 249° (approximately west-southwest) for Peruvian Boobies and 290° (approximately west-northwest) for Guanay Cormorants. For Peruvian Boobies the mean directions of simulated outbound headings are generally more northerly than the mean direction of the observed outbound headings. For Guanay Cormorants, the mean direction of simulated outbound headings is more in line with the observed mean direction, especially under the higher depletion rate.

Effects of changes in overall foraging conditions on foraging success and foraging trip duration

Comparison of simulation results for prey fields based on 2008 data versus 2009 data integrate the effects of changes in regional abundance, depth distribution, and spatial configuration. For both species, the failure rates are higher, foraging trip durations are longer, and the maximum distance from the colony is farther for simulations based on 2009 foraging conditions compared to 2008 (Table 5.2). Of the three performance indicators, failure rates are the most sensitive, and foraging trip durations are the least sensitive to changes in foraging conditions, even after taking into account that time spent foraging is fixed. Recorded birds have at least seven hours to locate prey, forage, and return to the colony before the end of the simulation. While a greater percentage of simulated birds failed to locate prey in 2009 within the modeled foraging region or within the time frame of the simulation, and were therefore logged as failed, birds that succeeded in locating prey aggregations in 2009 logged similar trip durations to simulated birds for 2008 (Fig. 5.6). This may reflect the specific spatial configuration of anchoveta in 2009 in

which increased depth and reduced abundance were coupled with reduced distance of average biomass from the colony. The remainder of this chapter therefore focuses on differences in failure rates as the key performance indicator.

Effects of changes in aspects of prey abundance and distribution on foraging success

The IBFM allows the effects of various aspects of the abundance and distribution of prey on foraging success to be disaggregated. For both species, and all three levels of depletion, the primary predictor for differences in failure rates identified by regression trees was the depth distribution (Fig. 5.7). For both species, and all depletion rates, failure rates were higher when prey was distributed deeper in the water column, as in 2009. With one exception, regional prey abundance was identified as a secondary or tertiary factor when prey was distributed more deeply. The exception was for Peruvian Boobies in simulations without depletion. Higher regional abundance, as in 2008, served to reduce the effect of deeper prey distributions, but did not eliminate the effect entirely. Spatial configuration, which integrates both the clustering of prey patches and the distance of prey from the colony, was identified as a secondary or third-level factor in several regression trees. In all cases where it was identified, the spatial configuration represented in simulations based on 2009 data, when prey was closer to the colony and more concentrated, favored foraging success. Boxplots provide further insight into the results of the regression trees (Fig. 5.8). In particular, they show that the effects of depth distribution and regional abundance increase with depletion.

Variation by species

When simulation results for both species are combined and species is included as a possible factor, species is identified as a factor in only one regression tree (Fig. 5.9). When prey is distributed deeply (as in 2009), but abundance is high (as in 2008) and there is no depletion in the IBFM, Guanay Cormorants have lower failure rates than Peruvian Boobies.

However, comparative beanplots based on results for simulations with deeper prey distributions (as in 2009) suggest that this relationship may change when abundance is low (as in 2009), especially when depletion is included in the model (Fig. 5.10). This split is not identified in the regression tree as the terminal nodes are too small to be split further.

Discussion

Modeling approach

The IBFM is a heuristic, mechanistic model, designed to strengthen understanding of a complex system by exploring whether and how individual processes, and interactions between them,

generate patterns such as those observed in nature. The combination of a mechanistic modeling framework with key components informed by analysis of observed data represents a new approach for investigating the effects of changes in various aspects of prey availability on the foraging patterns of CPFs.

Models are, by definition, a simplification of reality (see Walters 1986). The IBFM is a simplified model of a complex and dynamic natural system, and is not designed to be predictive (see Oreskes et al. 1994). To focus on the effects of changes in various aspects of the abundance and distribution of prey resources, several relevant factors have been suppressed or simplified. Nevertheless, the IBFM represents a useful tool for advancing understanding of the effects of various aspects of prey availability on the foraging success of CPFs.

Comparison of IBFM simulation results to observed data

Insights into the foraging behavior of CPFs may be gained by comparing model output with observed behavior.

Divergence between observed and simulated foraging trip statistics

For 2008 data, IBFM simulations lead to similar foraging trip durations and maximum distance from the colony to those observed, but in both cases, foraging takes place closer to the colony and trip durations are shorter in the IBFM than in the observed data (Table 5.2). Incorporating depletion into the IBFM leads to foraging trip statistics in closer alignment with the observed data. The effects of depletion are to ‘flatten’ the prey field over time, reducing the probability of patch selection in a halo close to the colony (see Ashmole 1963), so that birds start to look for foraging opportunities in other directions and progressively farther from the colony. One possible explanation for the divergence between observed foraging statistics and IBFM performance indicators is that depletion rates are underestimated. However, it is unlikely that the higher depletion rate underestimates depletion close to the colony. This rate is set at levels designed to approximate removals by the fishery, but the spatial pattern of exploitation by the fishery is expected to differ from that of seabirds, in part because fisheries operate from mainland ports, so would not be expected to concentrate around the colony, and in part because patch selection functions are expected to differ.

Another possible explanation is that network foraging has been over-estimated. As discussed in Chapter IV, network foraging tends to retain birds close to the colony where population densities tend to be higher. In this chapter, the distance over which network foraging occurs (r_{sen}) was reduced from 6 km to 2 km in order to limit this effect. Given the visual capacity of

seabirds (see Haney et al. 1992) and the high visibility of foraging flocks (Murphy 1936), it is unlikely that this represents an under-estimate. In the North Sea, Northern Gannets (*Morus bassanus*) responding to foraging individuals several kilometers away (Camphuysen 2011).

A third possible explanation is under-estimation of selectivity. Patch selection in the IBFM is informed by analysis of foraging site selection based on integrated analysis of seabird movement patterns and acoustic survey data. Data on seabird movement patterns are spatially continuous, and recorded at 1 second intervals for Peruvian Boobies and approximately 30 second intervals for Guanay Cormorants, while the acoustic survey data are derived from transects at approximately 10km intervals, recorded over a period of several days. The response variable (based on seabird movement patterns) is thus more precise than the predictor variables. Therefore, the predictor variables are probably characterized by measurement error due to differences in the temporal and spatial resolution of the two datasets. This implies that coefficients are likely to be under-estimated (Carroll 1983), leading to a shallower sigmoid curve for the estimated logistic function than the true function. This would lead to over-estimation of the probability of patch selection for patches with low true selection probabilities. If patches close to the colony have low true selection probabilities, this would lead to higher patch selection close to the colony in IBFM simulations compared to observed data.

Evaluation of the IBFM would be strengthened by comparing simulated and observed foraging trip statistics for 2009. Unfortunately, there are insufficient observed data for 2009 to compare foraging trip statistics between simulated and observed birds in 2009.

Performance indicators

Foraging trip durations and maximum distance

Foraging trip duration and maximum distance from the colony are widely used as indicators of foraging effort by CPFs (e.g. Boyd 1999, Grémillet et al. 2006, Hamer et al. 2007, Burke and Montevecchi 2009). These data are now relatively straight-forward to collect for most seabird species (Burger and Shaffer 2008, Wilson and Vandenberg 2012), but the results presented here show that these indicators do not always reflect variation in food availability or foraging effort.

Observers at Grupo Pescadores in December 2009 found fewer breeding adults and apparently poor breeding motivation compared to December 2008 (Tremblay, Y. pers. comm.). Acoustic survey data show that regional abundance of anchoveta was lower and the vertical distribution deeper in 2009 compared to the previous year. IBFM simulations based on acoustic survey data

for the two years show an increase in both foraging trip duration and maximum distance from the colony for 2009 compared to 2008 (Table 5.2), but the difference is small in simulations without depletion. In these simulations, foraging trip duration is the least sensitive indicator of those used here. This result probably reflects the specific spatial configuration of anchoveta in 2009 in which increased depth and reduced abundance was coupled with reduced distance of average biomass from the colony.

Limited differences in foraging trip duration and maximum distance do not imply that differences in foraging performance between the two years were negligible. In particular, catch per unit effort (CPUE) at foraging locations may have been lower in 2009 as a result of reduced local abundance and deeper depth distributions of prey. Variation in CPUE might lead to substantial variation in the net energy gained from foraging trips, despite limited differences in trip durations and maximum distance. Conversely, variation in CPUE may lead to similar energetic costs for trips with different durations and maximum distance (Obst et al. 1995).

These results highlight the value of collecting data on a range of indicators of foraging effort where possible. Data on the number, duration, and depth of dives, and energy expenditure while foraging can provide additional insights into variation in foraging effort (e.g. Croll et al. 2006, Grémillet et al. 2006); while data on food supplied to young, growth rates of young, and changes in adult body condition provide insights into net energy gain and the relationship with demographic parameters (e.g. Piatt et al. 2007). Birds may compensate for variation in food availability by adjusting trip frequency as well as foraging effort per trip (Boyd 1999). It is therefore essential to measure variation of foraging effort or performance over a fixed period of time, rather than just per trip. Colony attendance over time may also provide a better indicator of time budgets than individual trip durations (e.g. Harding et al. 2007).

Failure rates

In this analysis, the key performance indicator in the IBFM was foraging success or, conversely, failure rates. Birds that fail to locate prey within the foraging region and return to the colony by the end of the simulation were logged as failed. In the case of Peruvian Boobies and Guanay Cormorants, failure to return to the breeding colony at night could be taken as an indicator of failure, although this should be confirmed by observation. Data should be collected on birds that have not been handled to rule out the effects of handling (see Whidden et al. 2007).

Avoiding failure may be more important than minimizing trip duration (see Caraco 1980). This raises the question of what levels of failure rate are sustainable. Observed data for 2008 indicate

that individuals of both species tend to make two to three trips per day. Thus, if each pair is assumed to make approximately five trips per day, then a failure rate of 20% or above would lead to an expected failure rate of at least one trip per day. The question of thresholds highlights the importance of variance in failure rates, given that the probability that the failure rate exceeds any threshold is a function of both the mean and the variance (see Stephens and Charnov 1982). For example, in Figure 5.8, for Guanay Cormorants under higher depletion rates, the increased probability of failure rates greater than 20% between A08.D09 and A09.D09 is a function of the increase in both mean and variance of failure rates.

Failure rates are easier to measure in the IBFM than in the field. In practice, foraging success or failure may not be binary, but may rather be characterized by a spectrum from the complete failure to find prey to success in meeting all the energy requirements of adults and chicks. In this context, analysis of energy budgets and thresholds would provide further insight into variation in foraging success and the levels of failure rates that are sustainable.

Energetics

For some species, energetic constraints may become binding prior to time constraints. For example, Masman et al. (1989) removed food supplied to the nest by kestrels (*Falco tinnunculus*), and found that males kestrels increased energy expenditure up to levels considered maximal, while about half of available daylight still remained available for foraging. With additional data on foraging energetics, the IBFM could report results in terms of net energy gain, and be a useful tool for investigating the energetic implications of changes in prey availability (see Ellis and Gabrielsen 2002, Enstipp et al. 2006, Green et al. 2010). This would provide a more integrated approach to the analysis of variation in seabird foraging strategies in response to variation in prey availability, and the associated costs and benefits (Wilson and Vandenabeele 2012).

Effects of changes in various aspects of prey availability

The analysis presented in this chapter indicates that changes in the accessibility of prey, as in the change in the depth distribution of anchoveta off Grupo Pescadores between 2008 and 2009, can be a major factor driving the foraging success of Peruvian Boobies and Guanay Cormorants, supporting the hypothesis of Taylor et al. (2008). In this case, regression trees indicate that changes in accessibility were more important than changes in abundance. When prey is shallow in distribution (as in 2008), changes in regional abundance levels (as between 2008 and 2009 levels) have limited effects on foraging success. When prey is distributed more deeply (as in 2009), increasing regional abundance from 2009 to 2008 levels has a positive effect on foraging

success, but this is not sufficient to offset the effects of reduced accessibility entirely (Fig. 5.8). These results hold for both species and are robust to a wide range of depletion rates. The one exception is for Peruvian Boobies in simulations without depletion. In this case, the only factor identified was the depth distribution. Regional abundance was not identified as a factor even when prey distributions were deeper.

Overall, the spatial configuration of the prey field appears less important than the depth distribution and regional abundance (Fig. 5.7), but this may reflect the fact that two distinct aspects, the average distance of prey from the colony and the spatial concentration of prey, are confounded in the data. Where spatial configuration does play a role, the configuration encountered in 2009, when prey was more concentrated and closer to the colony, favors foraging success.

Variation by species

The decline in populations of guano-producing seabirds in the northern HCS since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (e.g. Jahncke et al. 2004), but it remains unclear why populations of Guanay Cormorants have failed to recover following severe oceanographic anomalies whereas populations of Peruvian Boobies have remained comparatively stable. In the IBFM simulations presented in this chapter, Guanay Cormorants perform better than Peruvian Boobies when regional abundance is high (as in 2008) but prey is distributed deeper in the water column (as in 2009) (Fig. 5.9). Simulation results suggest that this relationship changes when prey is deep, but less abundant (as in 2009) and subject to depletion (Fig. 5.10). (This change in comparative failure rates is more evident when higher depletion rates are used.)

In the IBFM, the differences in the way the two species are modeled are limited. Guanay Cormorants have longer patch residence times, but this should not lead to differences in failure rates. Guanay Cormorants are less likely to undertake looping trips than Peruvian Boobies, which should lead to lower failure rates. Any differences in failure rates that show Guanay Cormorants with higher failure rates than Peruvian Boobies must therefore be attributable to differences in patterns of foraging site selection. Figure 5.11 reveals the mechanism that leads to this change in comparative failure rates in the IBFM.

Recalling Equations 5.1 and 5.2, for any given abundance of prey in the upper surface waters, Guanay Cormorants have a lower probability of selecting a patch. However, the scaling parameter is deeper for Guanay Cormorants than for Peruvian Boobies. Thus, for a given level

of abundance through the water column, the comparative probability of patch selection depends on the depth distribution. If the distribution is shallow, then Peruvian Boobies will have a higher probability of patch selection than Guanay Cormorants. Conversely, Guanay Cormorants will have a higher probability of patch selection than Peruvian Boobies if prey is distributed deeper in the water column such that there is substantially more biomass accessible to Guanay Cormorants than to Peruvian Boobies (Fig. 5.11).

For both species, prey is depleted by removing a fixed amount of biomass from the upper surface waters. If prey is shallow, the probability of patch selection tends to decline more rapidly for Peruvian Boobies than for Guanay Cormorants as the number of successful foraging events increases, as they have less capacity to access prey deeper in the water column. (This probably explains the identification of regional abundance as a factor in the D08 branch of the regression tree for Peruvian Boobies under the higher depletion rate.) However, when all prey is distributed deeper in the water column, as in 2009, accessible biomass is low for both species. As this biomass is eroded through depletion, the probability of patch selection declines to the minimum for both species, which is lower for Guanay Cormorants than for Peruvian Boobies, given Equations 5.1 and 5.2. Hence, in the IBFM, even though the Guanay Cormorants can access prey deeper in the water column, they tend to fare worse than Peruvian Boobies when prey is deeper and regional abundance is low or subject to depletion.

Population sizes

This chapter is based on simulations with 60 individuals departing the colony every hour, for all scenarios. Interannual variation in the size of seabird colonies and in fishing effort was not included in this analysis, but could have substantial effects on foraging trip duration through competition. Similarly, a reduction in fishing effort would have implications for the higher depletion rate used here.

Depletion

As we have no information on the appropriate depletion rate, results are presented for simulations with no depletion, and with depletion set at a lower and higher rate, designed to approximate the effects of the seabird colony and the fishery (see Appendix V.1 for an explanation of how these rates were selected). Higher depletion rates compensate in part for the single species and limited population size included in the model. The major results presented here on the comparative importance of the depth distribution and abundance in explaining variation in foraging success for the two species in the model are robust to the different depletion rates included in the analysis.

However, depletion is obviously a complex process which is not captured fully by the mechanism used here. The mechanism used here implies that anchoveta deeper in the water column do not move into the upper surface waters to replace fish that have been removed. Data on the response of anchoveta to predation by seabirds, with and without the presence of sub-surface predators, would be useful to inform this aspect. Other species that forage on anchoveta, but with shorter foraging distances, such as Peruvian Pelicans (*Pelecanus thagus*) and Inca Terns (*Larosterna inca*), may intensify depletion close to the colony. The industrial purse-seine fishery for anchoveta, which operates from mainland ports, was also active in the area during the periods covered by the observed data and may have contributed to the depletion of forage fish in the foraging region. However, the spatial pattern of exploitation by the fishery likely differs markedly from seabirds, given that the fishery operates from mainland ports and would be expected to have different patch selection functions. The effects of depletion by the fishery would be better addressed by modeling the fishing fleet explicitly.

Adaptive foraging site selection

A further important caveat to the results presented in this chapter is that decision rules for foraging site selection were based on analysis of 2008 data when the distribution of anchoveta was relatively shallow. Insufficient data were available to estimate patch selection parameters separately for 2009. Consequently, the analysis here explores the effects of changes in the abundance and distribution of prey resources on Peruvian Boobies and Guanay Cormorants, assuming no change in decision rules. However, foragers may be expected to change decision rules, such as patterns of selectivity, in response to changes in prey availability. In particular, Guanay Cormorants may adapt to deeper prey distributions by foraging at sites where prey is distributed more deeply. The mean maximum dive depth of Guanay Cormorants during trips used in the analysis of foraging site selection was 14.6m (number of trips = 11) with a deepest dive of 23.8m, whereas Zavalaga and Paredes (1999) found a mean maximum dive depth of 33.9m with a deepest dive of 74m (number of individuals = 27). This potential highlights the importance of continuing to collect suitable data for the analysis of foraging site selection by Guanay Cormorants over a wide range of foraging conditions.

Further questions

Adaptive foraging strategies

Seabirds and pinnipeds have evolved in the context of climate variability and must have developed foraging strategies with the variation in prey availability that has occurred during evolutionary time (Furness 2007, Weimerskirch 2007). Adaptive foraging strategies may be

critical to species' future persistence in the context of fisheries and global change. A better understanding of these strategies, and the limits to their effectiveness is required to predict how seabirds and other CPFs might adapt to changes in food availability associated with fishing pressure and/or climate change. Conservation strategies should take these coping strategies into account. For example, a marine protected area (MPA) might encompass the foraging region used by a seabird colony in years when prey is close to the colony, but seabirds may forage well beyond that area in years when prey availability is low or even abandon the colony.

The responses of marine species to short-term variability may provide the best available indicator of responses to long-term change (Trathan et al. 2007, Grémillet et al. 2012). The IBFM could be used to assess the effectiveness of adaptive foraging strategies in maintaining foraging success in the context of current climate variability. Peruvian Boobies and Guanay Cormorants have contrasting flight and dive proficiencies. Peruvian Boobies have limited scope to increase foraging depths, compared to Guanay Cormorants, but are morphologically adapted for efficient flight (del Hoyo et al. 1992). As a result, the two species may follow different strategies to maximize net energy gain in response to changes in the abundance and distribution of prey resources. For example, in response to deeper prey distributions, Guanay Cormorants may adapt their patterns of foraging site selection to forage on prey at deeper depths, and thus mitigate the need for increased flight distances. In contrast, the shallower-diving but more aerodynamic Peruvian Boobies are probably unable to adapt patterns of foraging site selection in this way, and would be expected to travel farther in search of accessible prey. In the observed data and in the IBFM, adaptive decision rules on patch selection would be expected to reduce inter-annual variation in foraging trip durations for Guanay Cormorants compared to Peruvian Boobies. With suitable data, these hypotheses could be investigated using the IBFM. This research would be strengthened by additional data on the energetic costs of flight and diving to different depths for both species.

Effects of fisheries

The IBFM could also be used to address questions relating to the effects of fisheries on foraging success, and the potential effectiveness of fisheries management strategies. Competition with fisheries has been identified as a major threat to a number of globally threatened or near-threatened seabird species, especially in regions where large commercial fisheries target forage fish that are also important for seabirds (Duffy et al. 1984, Becker and Beissinger 2006, Crawford et al. 2006, Furness 2007). The IBFM provides a framework for spatially-explicit analysis of the effects of the industrial anchoveta fishery on CPFs. Given suitable data, it would be straight-

forward to incorporate the effects of fisheries explicitly in the IBFM, with fishing vessels modeled as CPFs. Similar data to those available for seabirds in this study on behavior modes, decision rules, and movement patterns could be extracted from vessel monitoring system data for fishing vessels. Data on anchoveta removals per set and the fuel and labor costs of fishing would also be useful. Fishing vessels would then interact with seabirds or other CPFs through the prey field. Additional information on the indirect effects of fishing activity on the availability of fish to seabirds would provide valuable context. For example, does fishing activity disrupt schools in such a way as to reduce or increase the availability of fish to seabirds? Further information on the movement patterns of fish would also be useful.

Effectiveness of fisheries management strategies

The ultimate goal for the IBFM is as a tool to support assessments of the effectiveness of proposed fisheries management strategies, such as reduced regional fishing effort or spatial closures, at safeguarding food availability to CPFs threatened by competition with fisheries, in the context of environmental variability and potentially climate change.

Pichegru et al. (2010) argue that even small closures can benefit African Penguins (*Spheniscus demersus*) foraging on small pelagic prey, but this raises questions about how effective spatial closures can be at maintaining prey availability within closed areas, given the mobility of fish stocks. The results presented in this chapter suggest that a fisheries management strategy that succeeded in maintaining high abundance levels in the foraging region (as in levels similar to 2008) during a severe oceanographic anomaly would mitigate the effects of reduced accessibility of prey for Peruvian Boobies and Guanay Cormorants due to increased depth distributions of prey associated with the vertical expansion of cold coastal waters (CCW), but might not be able to offset these effects entirely.

The IBFM could be used to explore the potential effects on seabird foraging success of different fisheries management strategies such as a reduction in regional fishing effort, permanent spatial closures, or flexible time-area closures. It could also be used to assess the costs of various strategies to fishing vessels, in terms of reduced catch or increased fishing trip durations.

Appendix V.1: Depletion rates

The computational demands of simulating all seabirds at a colony in the IBFM would be excessive. Therefore, a limited number of seabird foraging trips are simulated in the IBFM. When setting depletion rates, each simulated seabird may represent a share of all seabirds at the colony or even a share of seabirds and other anchoveta predators in the system. To test the sensitivity of results to different depletion rates, the IBFM was run with two contrasting rates: $x = 0.1$ and $x = 10$. These rates were selected to approximate the effects of the entire seabird colony, and the seabird colony if it also took as much anchoveta as the industrial fishery.

For simulations with 60 departures per hour and approximately 1.5 foraging events per trip, the total number of foraging events per day is 1,080. Weimerskirch et al. (2010) estimated that the colony at Grupo Pescadores comprised 190,000 breeding Guanay Cormorants and 15,000 breeding Peruvian Boobies in 2008. Based on figures compiled by Muck and Pauly (1987), the mean consumption of anchoveta per day was estimated as 0.167 kg for Peruvian Boobies and 0.274 kg for Guanay Cormorants (Table A.5.1). This gives a total estimated consumption per day of approximately 55t by these two species. This was increased to 60t per day to allow for non-breeding birds and other species. Divided by 1,080 simulated foraging events per day, this gives approximately 0.0556t per foraging event, or 2,778 fish assuming a mean weight of 20 g per anchoveta (Pauly et al. 1989).

Table A.5.1. Estimated daily consumption by breeding Peruvian Boobies and Guanay Cormorants at Grupo Pescadores in 2008.

	estimated population	mean adult weight	daily ration (% body weight) [†]	percent anchoveta in diet	anchoveta consumption per capita	total anchoveta consumption
Peruvian Boobies	15,000	1.28 kg	16.3%	80%	0.167 kg	2.504t
Guanay Cormorants	190,000	1.94 kg	14.7%	96%	0.274 kg	52.017t
Total	205,000					54.521t

† These are the lower estimates presented in Muck and Pauly (1987) based on metabolic equations.

For the fishing fleet, it was assumed that a fleet of 60 vessels makes one fishing trip per vessel per day. Average removals per vessel were assumed to be 100t per trip, based on an estimated 0.5t per gross registered tonnage (GRT) per trip (Csirke 1989) and 200 GRT per vessel (Murphy 1972), giving 6,000t per day. Divided by 1,080 simulated foraging events per day, this gives

5.56t per foraging event, or 277,778 fish. In the IBFM, these removals follow the same spatial pattern as foraging events by seabirds.

Conversion of fish to the nautical area-scattering coefficient (NASC) is based on the following equation (MacLennan et al. 2002):

$$\rho_a = s_A / (4\pi \cdot \sigma_{bs}) \quad \text{A.5.1}$$

where ρ_a is the number of targets per square nautical mile, s_A , and σ_{bs} is the backscattering coefficient estimated at 3e-06. The area of each grid cell is approximately 1 nm². This gives a NASC of 0.107 and 10.692 per event for the seabird colony and for the fishery respectively. These approximations are rounded to $x = 0.1$ and $x = 10$.

Notation

η	predictor in the binomial model for patch selection
σ_{bs}	backscattering coefficient
ρ_a	number of targets per square nautical mile
d_i	upper depth limit f aggregations in a cell
i	cell or location index
$P(.)$	probability
p_i	patch selection probability, i.e. probability that diving behavior occurs in a cell
r_{colony}	detection radius for birds at the colony
r_{sea}	detection radius for birds at sea
s_A	nautical area scattering coefficient, NASC
s_i	relative acoustic abundance in a cell
T_{satis}	satiation time
\underline{u}	vector of random effects
x	depletion rate
z_i	probability that the upper depth limit of aggregations in a cell, d_i , is less than the estimated scaling parameter, δ ; $P(d_i < \delta)$
A08	global abundance as in 2008
A09	global abundance as in 2009
C08	spatial configuration as in 2008
C09	spatial configuration as in 2009
D08	depth distribution as in 2008
D09	depth distribution as in 2009
Mode 0	at the colony
Mode 1	outbound travel
Mode 2	foraging
Mode 3	broad-scale search
Mode 4	transit
Mode 5	following
Mode 6	homebound travel
Mode 7	returned
Mode 8	failed

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Tables

Table 5.1. Construction of simulated prey fields representing various combinations of abundance, spatial configuration, and depth distributions, based on geostatistical simulations from 2008 and 2009.

	Abundance	Spatial configuration	Depth distribution
A08.C08.D08	2008	2008	2008
A09.C08.D08	2009	2008	2008
A08.C09.D08	2008	2009	2009
A08.C08.D09	2008	2008	2009
A08.C09.D09	2008	2009	2009
A09.C08.D09	2009	2008	2009
A09.C09.D08	2009	2009	2008
A09.C09.D09	2009	2009	2009

Table 5.2. Foraging trip statistics for Peruvian Boobies and Guanay Cormorants: observed data for 2008 and IBFM simulation results for 2008 and 2009. (Coefficients of variation shown in parentheses.)

Peruvian Boobies:

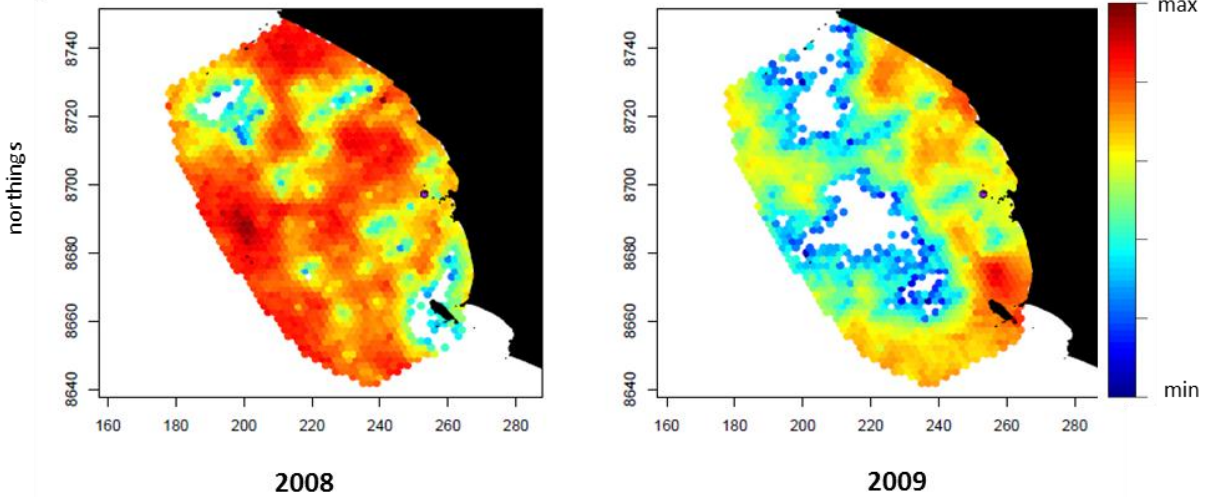
	2008					2009		
	observed	simulated				observed	simulated	
	(n = 13)	no depletion	lower depletion	higher depletion		no depletion	lower depletion	higher depletion
Mean failure rate	NA	0.33% (2.11)	1.50% (1.10)	1.17% (1.51)	NA	7.5% (0.66)	7.17% (0.45)	11.67% (0.33)
Mean foraging trip duration	65 mins (0.44)	47 mins (0.37)	49 mins (0.42)	56 mins (0.43)	NA	49 mins (0.52)	53 mins (0.53)	68 mins (0.45)
Mean maximum distance from colony	21 km (0.43)	13 km (0.56)	15 km (0.64)	17 km (0.61)	NA	17 km (0.91)	19 km (0.89)	27 km (0.65)

Guanay Comorants:

	2008					2009		
	observed	simulated				observed	simulated	
	(n = 11)	no depletion	lower depletion	higher depletion		no depletion	lower depletion	higher depletion
Mean failure rate	NA	0.17% (3.16)	0.50% (2.25)	1.00% (1.61)	NA	6.00% (0.63)	8.00% (1.09)	12.17% (0.47)
Mean foraging trip duration	83 mins (0.40)	69 mins (0.23)	72 mins (0.29)	86 mins (0.35)	NA	70 mins (0.32)	77 mins (0.36)	92 mins (0.29)
Mean maximum distance from colony	16 km (0.37)	9 km (0.70)	10 km (0.75)	16 km (0.72)	NA	12 km (1.23)	16 km (1.02)	24 km (0.74)

Figures

Log of mean relative abundance



Mean probability that the upper depth limit of aggregations is less than 7.472 m

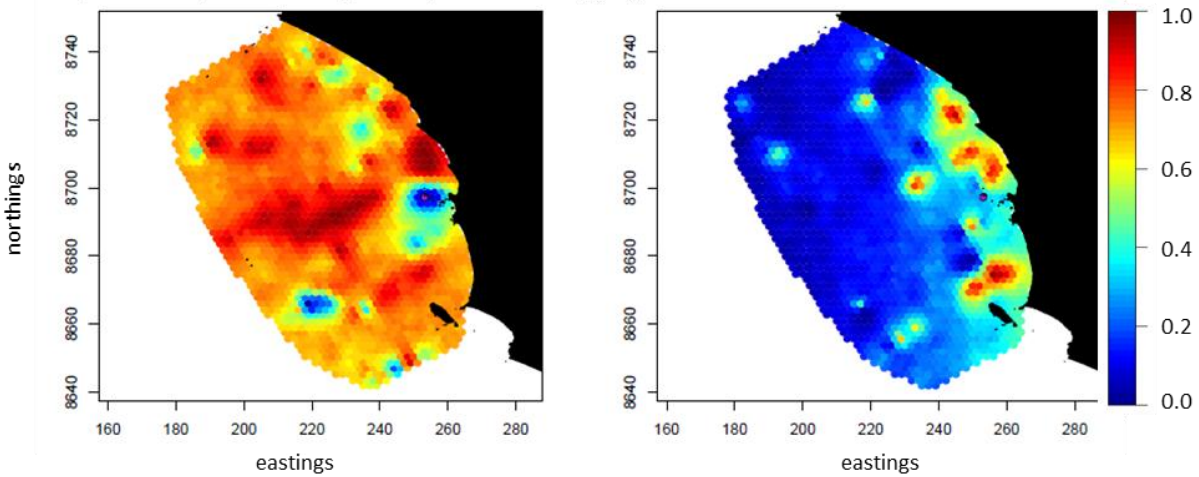
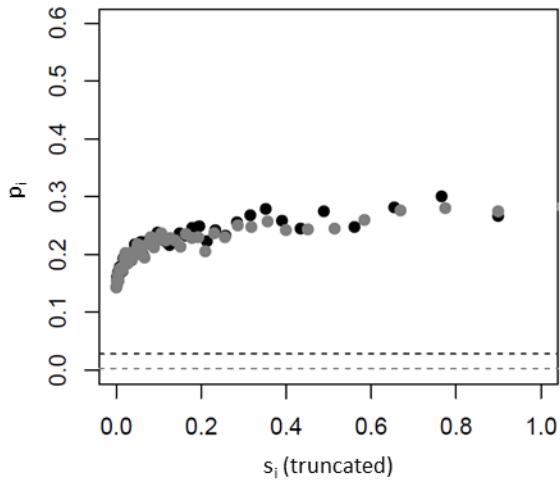


Figure 5.1. Contrasting foraging conditions in 2008 and 2009. Plots are based on conditional geostatistical simulations of acoustic survey data of anchoveta. In the patch selection decision rule for Peruvian Boobies, the scaling parameter for depth distributions is 7.472m. Classifications are based on equal intervals, with the same scale for both years. Land is indicated in black. The colony is indicated by a purple hexagon.

Relative abundance



Depth distribution

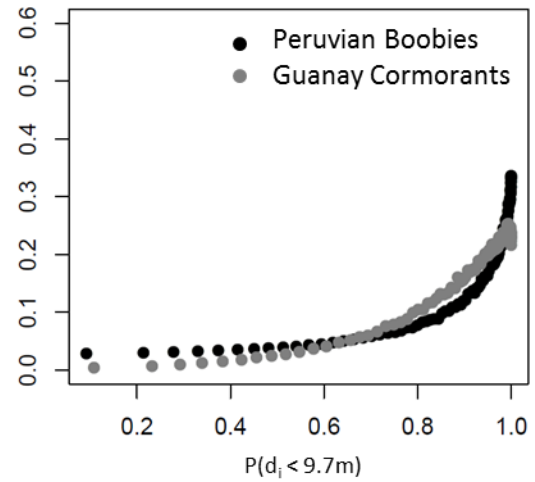


Figure 5.2. Comparison of predicted patch selection probabilities by Peruvian Boobies and Guanay Cormorants in the IBFM. Dashed lines indicate the probability of patch selection when abundance is 0. (The estimated scaling parameter differs for Peruvian Boobies and Guanay Cormorants, but for comparative purposes the horizontal axis refers to the estimated threshold for the Guanay Cormorant (9.7m) is used here.)

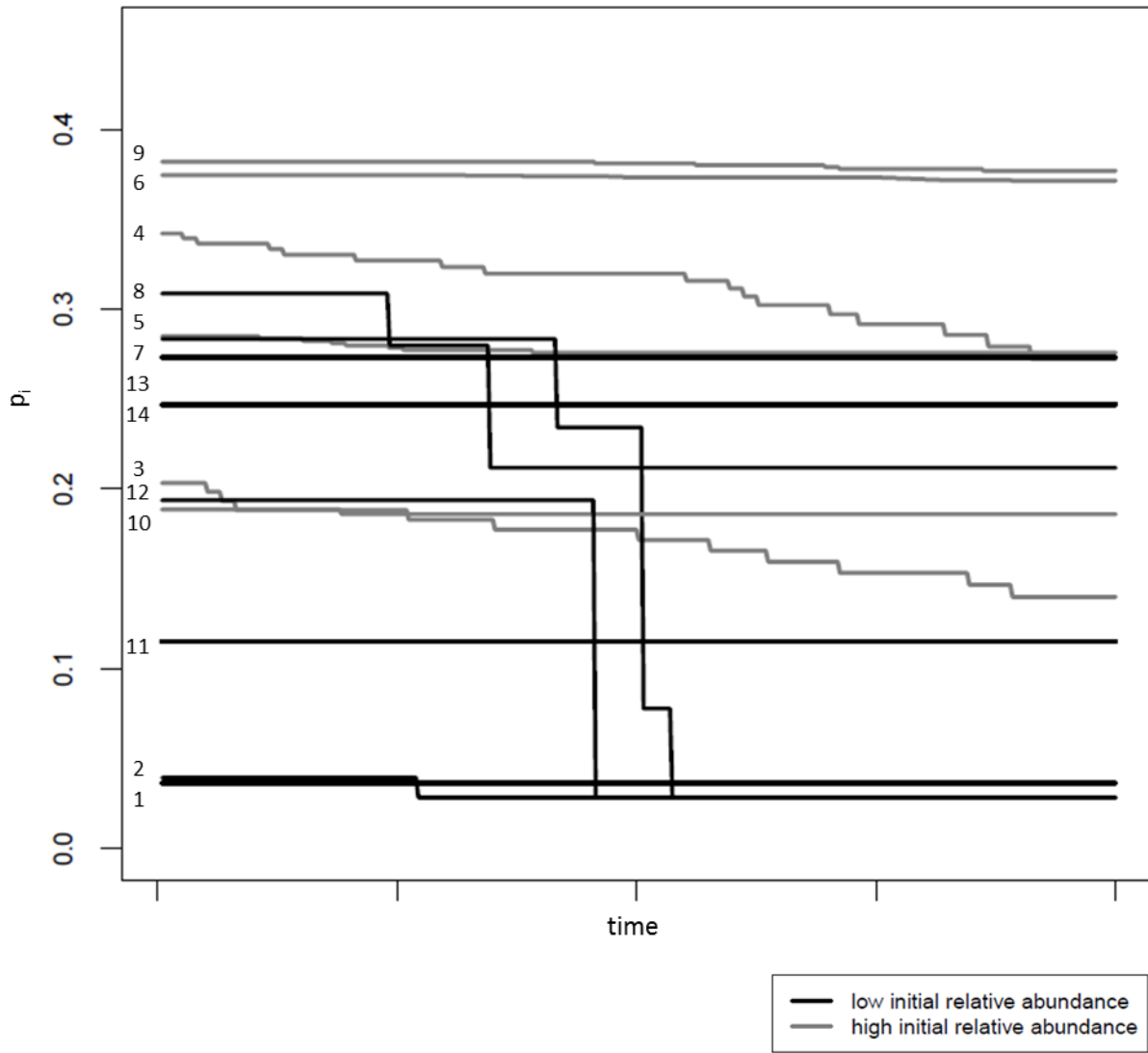


Figure 5.3. Effects of depletion on probabilities of patch selection over time, for patches with high and low initial abundance. In the IBFM, 60 seabirds were released sequentially, following the same heading, and the effects of depletion on probabilities of patch selection through the course of the simulation were recorded. Labels indicate the order in which patches are encountered by birds outbound from the colony.

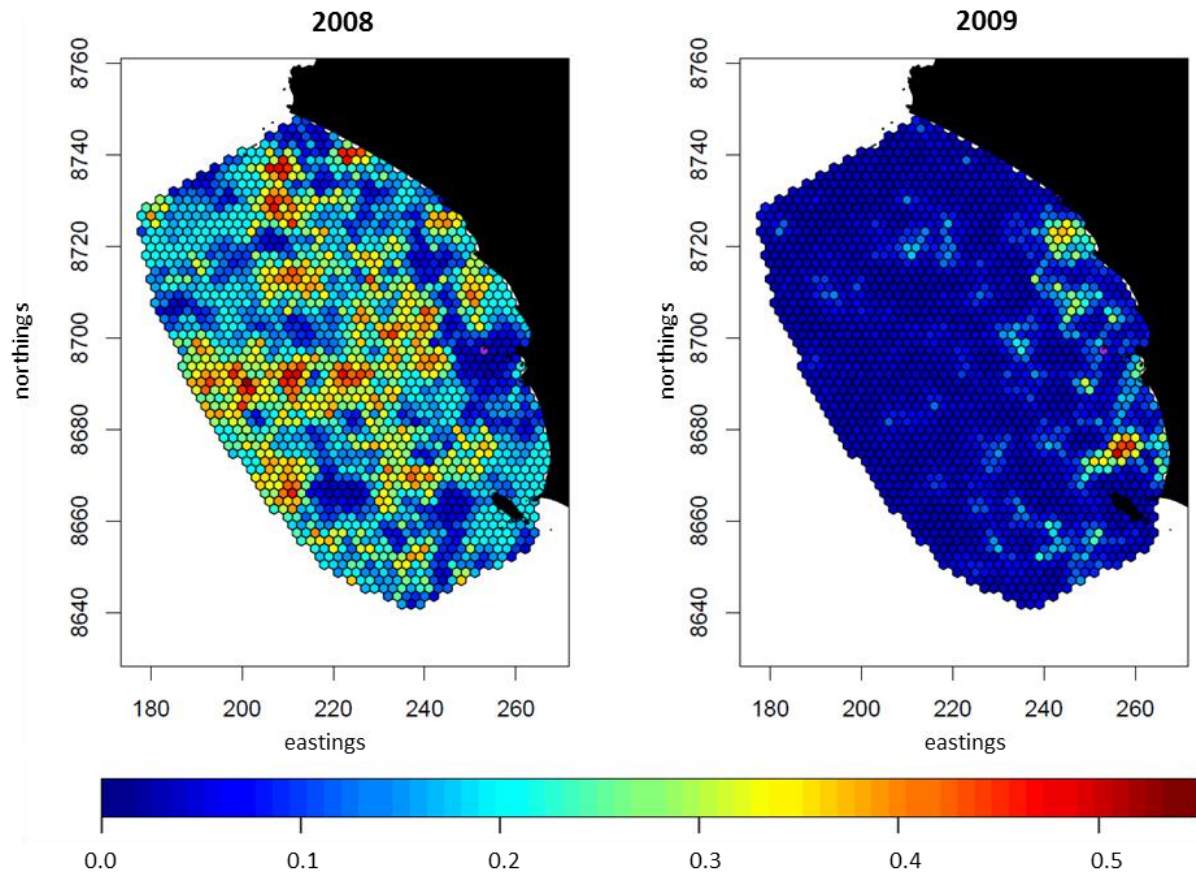
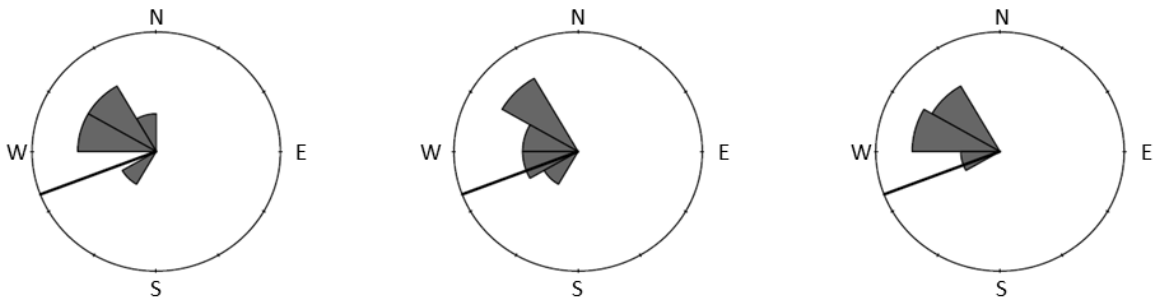


Figure 5.4. Sample distributions of the probability of patch selection for Peruvian Boobies in 2008 and 2009. Irregular solid shapes indicate land; the colony is indicated by a purple hexagon.

Peruvian Boobies



Guanay Cormorants

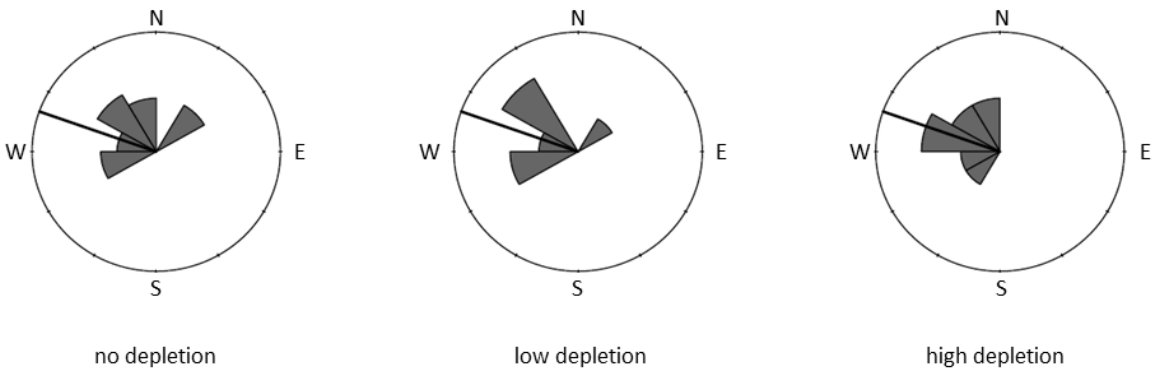
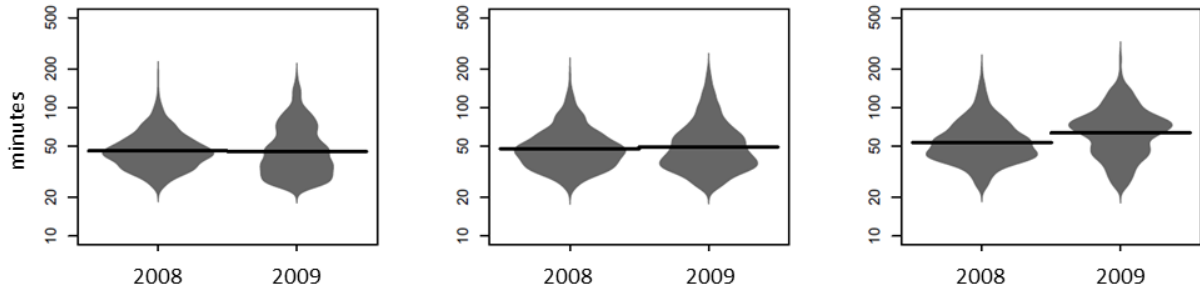


Figure 5.5. Rose diagrams of the mean directions of outbound headings in IBFM simulations. The mean direction of observed birds is shown as a solid line.

Peruvian Boobies



Guanay Cormorants

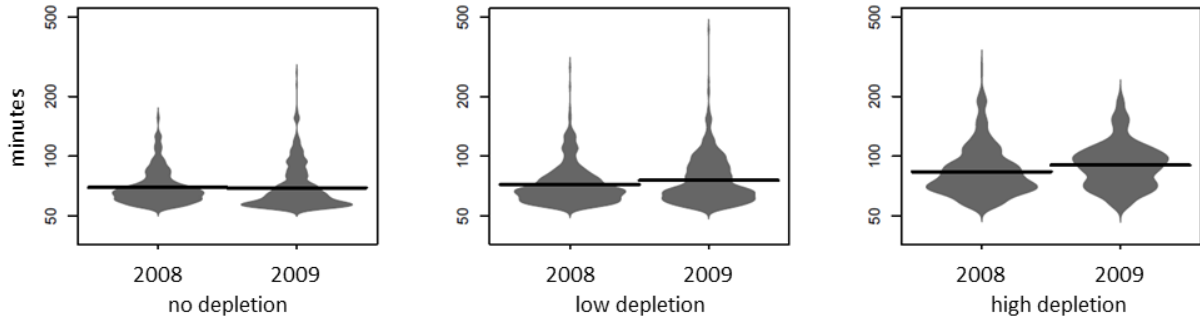
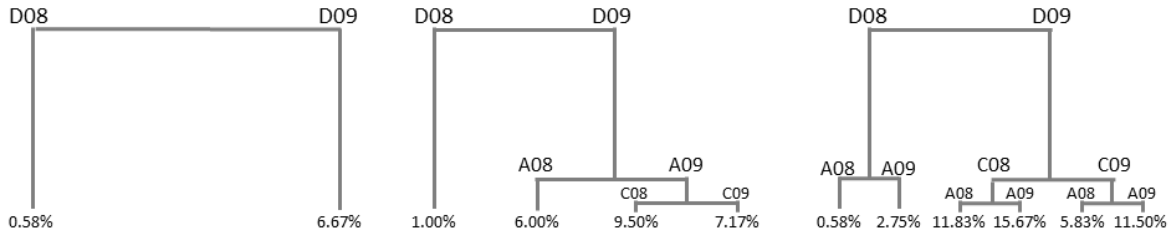


Figure 5.6. Beanplots of simulated foraging trip durations.

Peruvian Boobies



Guanay Cormorants

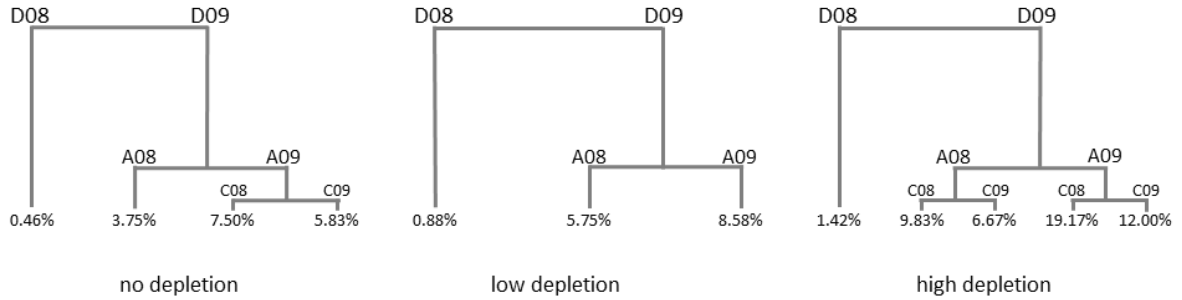
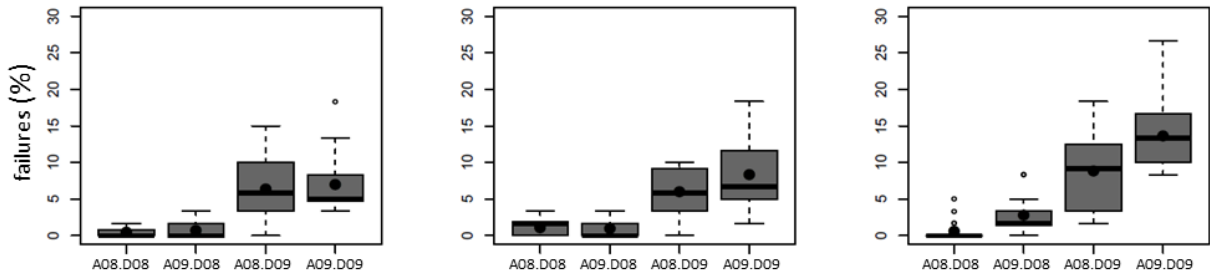


Figure 5.7. Regression trees for failure rates for Peruvian Boobies and Guanay Cormorants. A08 refers to regional abundance as in 2008; D08 refers to the depth distribution as in 2008; C08 refers to the spatial configuration as in 2008.

Peruvian Boobies



Guanay Cormorants

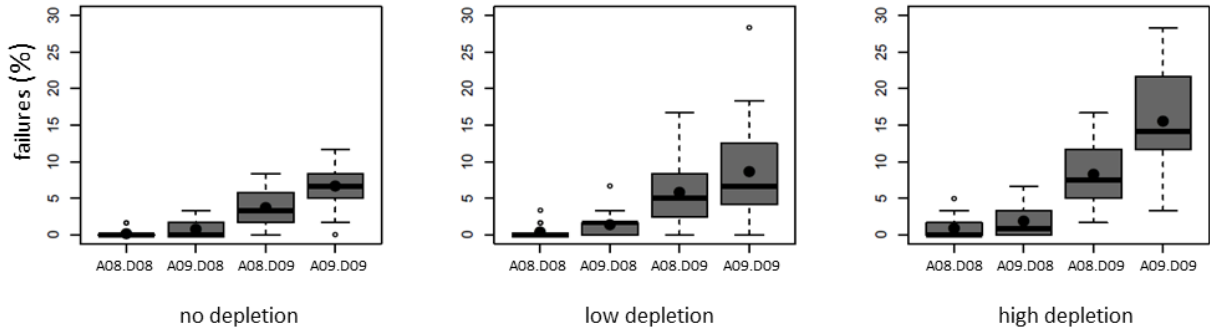


Figure 5.8. Boxplots of failure rates by depth distribution and regional abundance. Filled points indicate the mean for each group.

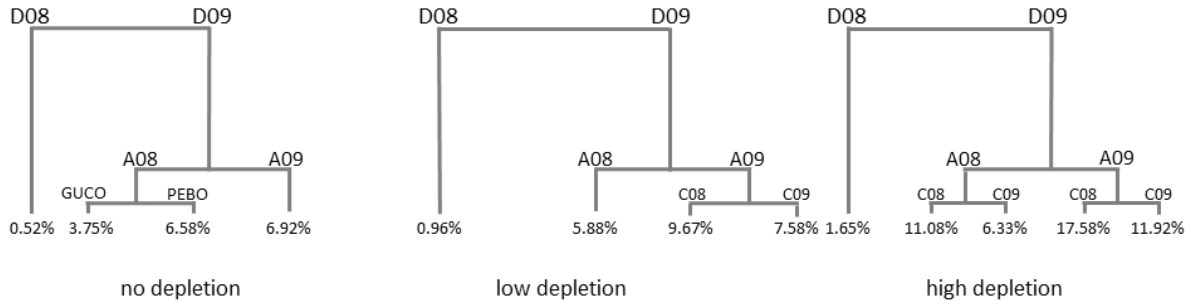
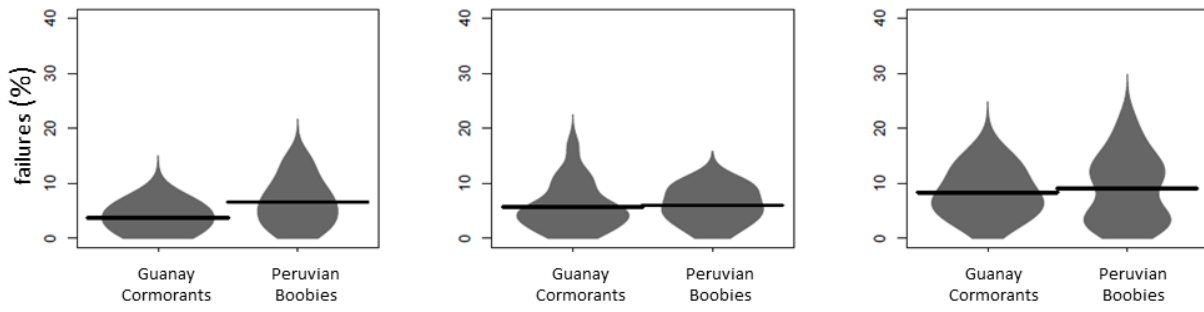


Figure 5.9. Regression trees for failure rates with species as a factor. Peruvian Boobies are abbreviated to PEBO and Guanay Cormorants are abbreviated to GUCO.

High regional abundance (as in 2008); deep depth distribution (as in 2009)



Low regional abundance (as in 2009); deep depth distribution (as in 2009)

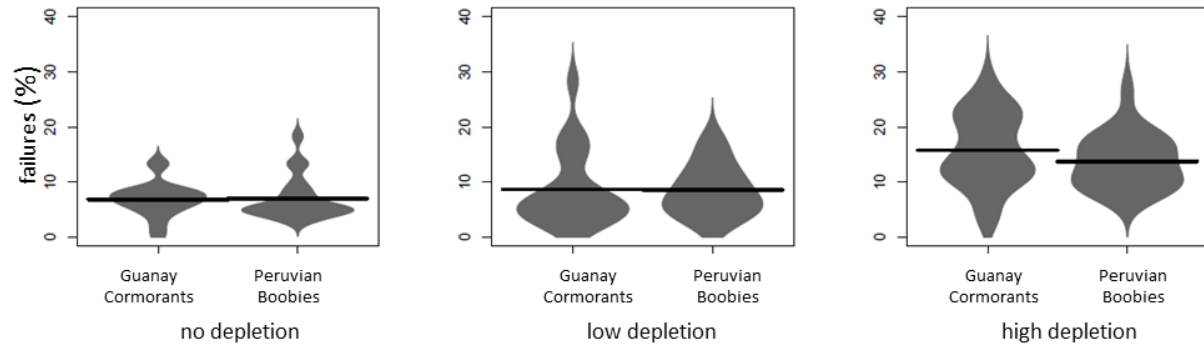
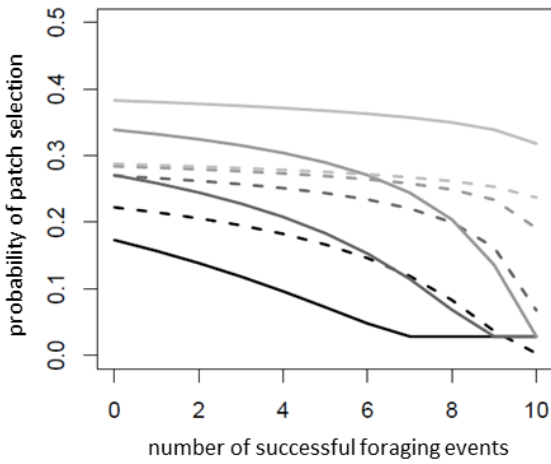


Figure 5.10. Beanplots showing differences in failure rates by species for 10 simulations based on 2009 depth distributions.

2008 depth distributions



2009 depth distributions

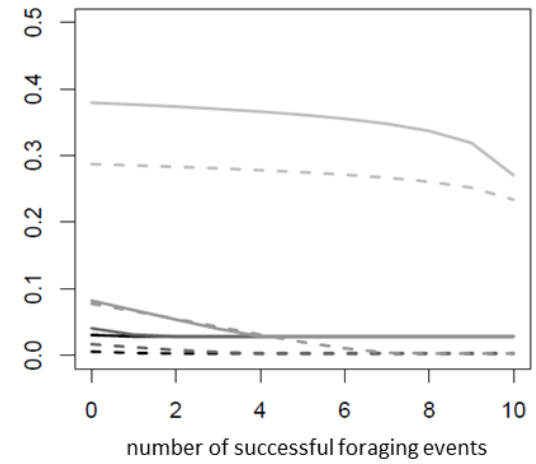


Figure 5.11. Changes in the probability of patch selection through depletion for Peruvian Boobies (solid lines) and Guanay Cormorants (dashed lines) for a single level of relative abundance and a series of depth distributions, based on quartiles of the depth distribution in 2008 (left panel) and 2009 (right panel). Darker shades indicate deeper depth distributions. The high rate of depletion is used here.

Discussion

Methodological developments

Individual-based model for central place foragers

In Chapters IV and V, an individual-based foraging model (IBFM) for central place foragers (CPFs) was developed and applied to data for two species of seabird foraging on schooling fish. The IBFM is a heuristic, mechanistic model, designed to strengthen understanding of a complex system by exploring whether and how individual processes and interactions between them generate patterns such as those observed in nature. Insights into the foraging behavior of CPFs may be gained by comparing model output with observed behavior.

The combination of a mechanistic modeling framework with key components informed by analysis of observed data represents a new approach for investigating the effects of changes in various aspects of prey availability on the foraging patterns of CPFs. As discussed in the Introduction, approaches based on correlation analysis are unable to disaggregate the various aspects of prey availability in short-term datasets, and suitable long-term datasets are limited to only a few systems around the world. A further advantage of the IBFM is that it is spatially-explicit, enabling investigation of the effects of various spatial fisheries management strategies, such as fixed or dynamic area closures. This type of exploratory investigation is not feasible using correlation analysis. However, it is important to emphasize that the IBFM is a simplified model of a complex and dynamic natural system, and is not predictive (see Oreskes et al. 1994). In particular, seabirds might be expected to adapt patterns of foraging site selection in response to changing foraging conditions, and this has not yet been incorporated in the model due to insufficient data.

The IBFM is flexible and adaptable, and could be reconfigured for other species. An increasing number of field studies generate data on the movement patterns of CPFs while foraging. The IBFM provides a framework for relating these movement patterns to simulated prey fields representing various scenarios for the abundance and distribution of prey. It could also be adapted to represent the foraging patterns of other CPFs (including fishing vessels). The IBFM could also be used to address a wide range of further questions (see below).

Likelihood-based approach to simulating the distribution of schooling fish

In Chapter I, a likelihood-based approach for geostatistical simulation of the patchy distributions of schooling fish based on acoustic survey data was developed and applied to anchoveta data for 2008. Geostatistical simulation is designed to generate simulated values of a

spatial variable at unobserved locations, while reproducing the spatial pattern (including patchiness) and statistical properties of the sample data. In the context of this research, a likelihood-based approach to geostatistics was preferred over distribution-free approaches, because it is more consistent with methods used for other research components.

Likelihood-based approaches have several advantages in terms of structural analysis, model selection, and parameter estimation, but require explicit assumptions about the distribution of the variable of interest. Currently, only a few parametric distributions are tractable in likelihood-based geostatistics. None of these distributions is able to reproduce the high proportions of zero observations characteristic of the distributions of schooling fish, together with the highly skewed distribution of non-zero densities. The conventional solution is to use a two-stage model structure (such as a binomial distribution for the presence/absence process, followed by a lognormal distribution for the conditional abundance process). As an alternative, Woillez et al. (2009) developed an integrated approach to simulating the spatial distribution of schooling of fish by modeling the abundance distribution as a truncated Gaussian random field following Gaussian anamorphosis. However, this approach is only semi-parametric and cannot be implemented within a likelihood-based framework. The approach developed here builds on that of Woillez et al. (2009), but uses a parametric transformation and estimates the parameters of the truncated Gaussian random field within a likelihood-based framework.

Geostatistical simulations using this approach were compared to those generated by two-stage models, based on (a) indicator simulation and (b) a binomial model. The approach developed here out-performed the alternative approaches overall, in terms of reproducing the spatial pattern of the presence/absence of anchoveta and the statistical properties of the observed data for 2008. The integrated approach also tended to simulate low values (if any) at locations where the survey returned zero values, whereas the two stage models were capable of simulating high values at these locations. This methodology could be applied to other schooling fish whose abundance distribution is characterized by high proportions of zero observations.

Hidden Markov model for animal tracks with informative gaps

Hidden Markov models (HMMs) have been used to partition tracks into distinct movement modes for a wide range of species (Morales et al. 2004, Franke et al. 2004, Franke et al. 2006, Jonsen et al. 2007). In Chapter II, global positioning system (GPS) tracks for Peruvian Boobies were partitioned into multiple random walks using an HMM solved with a forwards-backwards algorithm. This is the first application of an HMM to the movement patterns of seabirds.

In this case, the GPS tracks of Peruvian Boobies recorded at 1-second resolution were characterized by occasional gaps in the regular sequence of GPS observations. These were shown to be indicative of diving behavior (see also Wanless 1993). Rather than ignoring the gaps in the data sequence, an HMM was adapted to incorporate this information. This adaptation could be useful in the analysis of the movement patterns of other seabird species (especially where there are constraints on fitting individuals with both GPS and time depth recorders (TDRs)).

HMMs for animal movement patterns typically model these patterns as multiple correlated random walks. However, it is worth noting here that simulation of movement patterns in the IBFM highlights the prevalence of oriented random walks in the movement patterns of Peruvian Boobies and Guanay Cormorants (see also Boyd 1999). HMMs can be adapted to incorporate this type of movement pattern (McClintock et al. 2012), but this is computationally-intensive at the scale of the individual, let alone at the scale of the population.

Resource selection function for marine predators in terms of prey species

In Chapter III, a resource selection function was developed to assess foraging site selection in terms of various aspects of prey availability. Previous research on habitat selection in highly-mobile marine species has typically been based on remotely-sensed data on environmental covariates, such as sea-surface temperature (SST) and chlorophyll concentration, which may represent physiological constraints on the predator and/or proxies for the distribution of prey (Redfern et al. 2006, Tremblay et al. 2009, Wakefield et al. 2009). However, these models cannot provide information on responses of predators to changes in the distribution and attributes of prey that are not effectively signaled by changes in these environmental covariates. Here, contemporaneous data on the movement patterns and foraging locations of marine predators and the distribution of their main prey at appropriate spatial scales provided a unique opportunity to develop a resource selection function directly in terms of the distribution of prey.

The resource selection function developed here is a multiplicative function of the relative abundance of prey through the water column at each location and the accessibility of this prey. Accessibility is defined in terms of the probability that prey biomass falls within a specific habitat envelope within the water column that is accessible to the predator. Both Peruvian Boobies and Guanay Cormorants are surface foragers, so in this case, accessibility was defined in terms of the probability that prey is found in the upper surface waters, specifically the probability that the upper depth limit of prey aggregations is less than an estimated scaling

parameter. This structure enabled analysis of the comparative importance of the abundance and depth distribution of prey in defining suitable foraging sites for these surface foragers.

The basic structure of the resource selection function could be adapted to capture the probability that prey is accessible to foragers with other types of constraints. For example a relevant resource selection function for large predatory fish such as tunas might be defined in terms of the probability that prey falls within a specific temperature or oxygen concentration envelope rather than depth distribution.

Key findings

Importance of abundance and depth distribution of prey in foraging site selection

In Chapter III, the following hypotheses were tested for Peruvian Boobies and Guanay Cormorants foraging on anchoveta: patch selection is a function of prey availability at a location (specifically, a multiplicative function of prey abundance and accessibility); and patch residence time (here measured in terms of the number of dives or total duration of dives at a location) is a function of prey availability at the location. Accessibility of prey to surface-foraging seabirds was here defined in terms of the depth distribution of anchoveta.

Patch selection

The results for patch selection in 2008 indicate that Guanay Cormorants were more selective than Peruvian Boobies in terms of the abundance of prey. This corresponds with suggestions that Guanay Cormorants may require denser prey schools than Peruvian Boobies for effective foraging (e.g. Nelson 1978). The results also indicate that Guanay Cormorants were less selective than Peruvian Boobies in terms of the depth distribution of prey. This corresponds with well-established differences in the dive capacities of the two species (del Hoyo et al. 1992). The implications for foraging trip durations and foraging success were revealed in Chapter V.

However, the analysis highlights the importance of the depth distribution of anchoveta in foraging site selection for both Peruvian Boobies and Guanay Cormorants. Even though the Guanay Cormorant is capable of diving more deeply, foraging on prey at shallow depths may be more efficient if shallow fish schools can be trapped against the ocean surface by pursuit-divers attacking from below. (See Wilson et al. (2010) for a discussion of the energy efficiency of diving to different depths for seabirds.) For both species, the results of this analysis suggest that locations where prey is predictably found at shallow depths may be more important than locations where prey is predictably abundant. These results have implications for the design of spatial management strategies, such as fisheries closures or marine protected areas (MPAs).

Patch residence time

The data did not support a relationship between patch residence time and the relative abundance and depth distribution of prey for either species. One possible ecological explanation is that patch residence time may be influenced by factors such as individual satiation and the presence of facilitators and competitors, which are not captured in this dataset. These factors may be more ephemeral than the broad-scale pattern in the abundance and distribution of anchoveta which underlies patch selection.

Another possible technical explanation relates to the use of grid cells to define patches. This approach was used for consistency with the IBFM, but implies that a single foraging bout could be split between two or more patches. Defining a patch in terms of a given radius around the first dive location in each foraging bout would address this problem, but would be less consistent with the IBFM.

Influence of population densities and foraging conditions on the effectiveness of seabird search strategies and value of information

The two search strategies analyzed in Chapter IV were the orientation of outbound headings in line with the direction of returning birds, and network foraging. The following hypotheses were tested: the effectiveness of search strategies is sensitive to population densities (specifically, search strategies are less effective when population densities are low); and the value of information depends on foraging conditions (specifically, information is more valuable when foraging conditions are poor).

Influence of population densities on the effectiveness of search strategies

There are concerns that the search strategies used by seabirds may require high population densities to be effective, and may lead to Allee-type density dependence in declining populations (Ward and Zahavi 1973, Weimerskirch et al. 2010).

Analysis presented in Chapter IV indicates that both search strategies investigated here can be effective at reducing failure rates even at low population densities. Even with only a few individuals returning to the colony, orientation of outbound headings in line with returning birds acts to prevent birds heading in directions where prey resources are scarce. In the case of network foraging, several different mechanisms may contribute to this result. Network foraging has the effect of retaining birds close to the colony where populations are more dense, and this may lead to reduced failure rates in the IBFM, even at low population densities. Both search strategies become more efficient as population densities increase. Furthermore, the orientation

of outbound headings may facilitate network foraging by concentrating individuals and thus increasing population densities in profitable areas.

Influence of foraging conditions on the value of information

For both search strategies, IBFM results indicate that the value of information is greater when prey is more concentrated. Information on directions to avoid may have limited value, and individuals will spend less time searching for prey in the absence of information if prey is broadly-distributed in all directions. Logerwell et al. (1998) found that the association between Thick-billed Murres (*Uria lomvia*) with prey biomass was poor when prey variance was relatively low, suggesting that there is limited advantage to aggregating at slightly more profitable locations if prey distribution is fairly uniform. When the two strategies were combined, both the mean and the variance of failure rates were reduced. Changes in the variance of failure rates may be ecologically-significant because the probability of failure depends on the variance as well as the mean failure rate (see Caraco 1980 and Stephens et al. 2007).

Effects of changes in various aspects of prey availability on the foraging success of Peruvian Boobies and Guanay Cormorants

The broad goal of this research was to strengthen our understanding of the effects of changes in various aspects of food availability on the foraging success of seabirds and other CPFs. The following specific hypothesis was tested: the foraging success of Peruvian Boobies and Guanay Cormorants foraging on anchoveta depends on the depth distribution and spatial configuration of prey as well as abundance. An individual forager was considered successful if it succeeded in locating prey at one or more patches within the foraging region of the IBFM and returning to the colony within a set time frame.

The analysis presented in Chapter V indicates that changes in the accessibility of prey, as in the change in the depth distribution of anchoveta off Grupo Pescadores between 2008 and 2009, can be a major factor driving the foraging success of Peruvian Boobies and Guanay Cormorants, supporting the hypothesis of Taylor et al. (2008). In this case, the depth distribution of prey had greater effect on the biomass of prey that is accessible to surface foragers than regional abundance. Regression trees indicated that changes in accessibility were more important than changes in abundance. Changes in regional abundance levels (as between 2008 and 2009 levels) have limited effects on foraging success when prey is shallow (as in 2008). Increasing regional abundance from 2009 to 2008 levels has a positive effect on foraging success when prey is distributed more deeply (as in 2009), but this is not sufficient to offset the effects of reduced

accessibility entirely. These results hold for both species and are robust to a wide range of prey depletion rates.

These results suggest that a fisheries management strategy that succeeded in maintaining high abundance levels in the foraging region (as in levels similar to 2008) during a severe oceanographic anomaly would mitigate the effects of reduced accessibility due to increased depth distributions of prey associated with the vertical expansion of cold coastal waters (CCW), but might not offset these effects entirely.

Significance of differences in foraging site selection between Peruvian Boobies and Guanay Cormorants

Since the 1957/58 and 1965 El Niño events, the Guanay Cormorant has failed to recover to population sizes seen earlier in the 20th Century (Fig. 6.1), and is now listed as Near Threatened on the IUCN Red List of Threatened Species (IUCN 2011). In comparison, the population trajectory of Peruvian Boobies has been more stable over the same period (Fig. 6.1). The decline in seabird populations since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (e.g. Jahncke et al. 2004), but it remains unclear why populations of Guanay Cormorants have declined whereas those of Peruvian Boobies have remained comparatively stable.

IBFM simulations presented in Chapter V indicate that Guanay Cormorants have higher foraging success than Peruvian Boobies when prey is deeply distributed (as in 2009) but regional abundance is high (as in 2008). However, when regional abundance is reduced (as in 2009), this relationship starts to switch, especially when depletion is included in the model. This result is attributable to differences in patch selection based on the analysis of foraging site selection in Chapter III. Analysis of foraging site selection indicated that Guanay Cormorants were less selective than Peruvian Boobies in terms of the depth distribution of prey, but more selective in terms of the abundance of prey. As a result, the foraging success of Guanay Cormorants in the IBFM declines more rapidly than that of Peruvian Boobies when the abundance of prey in the upper surface waters is low.

An important caveat here is that decision rules for foraging site selection were based on analysis of 2008 data when the distribution of anchoveta was comparatively shallow. Given that Guanay Cormorants are capable of diving deeper, they may adapt to deeper prey distributions by foraging at sites where prey is distributed more deeply and thus mitigate the effects on foraging success shown here. This finding highlights the importance of continuing to collect suitable data

for the analysis of variation in foraging site selection over a wide range of foraging conditions. With data on patch selection under different foraging conditions, the IBFM could be used to explore the significance of adaptive decision rules in terms of foraging success.

Future work

Competition with fisheries has been identified as a major threat to a number of globally threatened or near-threatened seabird species, especially in regions where large commercial fisheries target forage fish that are also important for seabirds (Duffy et al. 1984, Becker and Beissinger 2006, Crawford et al. 2006, Furness 2007). As discussed in Chapter V, the IBFM provides a framework for spatially-explicit analysis of the effects of fisheries on CPFs and the potential effectiveness of fisheries management strategies at safeguarding the foraging success of CPFs in the context of environmental variability.

The IBFM could also be extended to address a wide range of additional questions. Questions relating to the effects of changes in prey availability on provisioning rates and breeding success would require an extension of the IBFM to incorporate variation in the frequency of foraging trips. The IBFM could then be linked to a population dynamics model to address questions of the effects of fisheries and fisheries management strategies on population persistence or recovery rates. Questions relating to the effects of climate change would require a biophysical oceanographic model to simulate the abundance and distribution of prey under different climate scenarios. With each extension, the IBFM would become more complex and data-demanding. Careful consideration therefore needs to be given to trade-offs between simplicity and complexity in addressing each question.

Provisioning rates and breeding success

Fundamental questions relate to the effects of changes in prey availability on provisioning rates and hence breeding success. For example, several researchers (e.g. Cairns 1987, Croxall et al. 1999, Piatt et al. 2007) have argued that the threshold at which breeding success starts to decline in response to reduced prey availability should vary among species as a result of inter-specific differences in foraging ecology, time and energy budgets, and the tradeoffs between breeding success and adult survival. Yet, Cury et al. (2011) found that this threshold fell close to the long-term mean of prey abundance for 14 species in seven ecosystems. The IBFM could be used to investigate whether differences in foraging ecology (such as patterns of foraging site selection) and time and energy budgets lead to differences in thresholds in provisioning rates for different species foraging in the same ecosystem and hence differences in breeding success. Provisioning

rates over time would also represent a more appropriate indicator for exploring the possible effects of conservation and management actions than foraging success during individual trips.

Trip frequency

Provisioning rates depend on the frequency of foraging trips. Foragers may respond to changes in the availability of prey by adjusting the frequency as well as the duration of foraging trips (Boyd 1999). For example, data for Peruvian Boobies at Isla Guañape Sur in 2007 indicate longer mean foraging trip durations but fewer trips per day than for conspecifics at Grupo Pescadores in 2008 (see Chapter II). The current version of the IBFM focuses on single foraging trips. To generate output in terms of provisioning rates, the first step would be to extend the IBFM to incorporate the decision to embark on a foraging trip, and hence variation in the frequency of foraging trips in response to changes in prey availability. This decision is likely a function of both internal and external factors, such as an individual's stomach fullness (or energy balance), stimulation by begging offspring (linked to offspring stomach fullness), and, for some species, the presence of the partner. (See Ropert-Coudert et al. 2004 for a foraging model based on stomach fullness, Phillips et al. 2009 for a discussion of how seabirds regulate provisioning effort, and Kitaysky et al. 2007 for a discussion of the role of the stress hormone, corticosterone). In the IBFM, the decision to forage could be based on an energetics model in which energy gained during a foraging trip is consumed, and the probability of departure is a function of remaining energy resources and the presence or absence of the partner. (Modeling multiple trips would also allow for short-term recall to be included in the IBFM as an additional information mechanism. For example, foragers could base their outbound heading on their previous return direction, rather than the direction of returning birds.)

The potential for a CPF to increase the frequency of trips (or conversely reduce colony attendance) will depend on how close the individual is operating to time and energy budgetary limits. In this study, prey fields were simulated based on observed data. However, it would be possible to generate artificial prey fields covering a wider range of foraging conditions. The results of IBFM simulations under different foraging conditions could then be compared to estimated time or energy thresholds for different species.

Time and energy budgets

Provisioning rates also depend on the amount of food delivered at the end of each foraging trip (Boyd 1999, Pinaud et al. 2005, Costa 2008). This depends in turn on other energy demands, the time spent foraging and catch per unit effort (CPUE). In theory, variation in patch CPUE could be modeled as a function of prey attributes at a patch (such as prey abundance or density, and

depth distribution). However, this would require data on variation in CPUE as a function of the prey attributes at a patch, which would be challenging to acquire (see Enstipp et al. 2007). It would also be useful to incorporate the effects of competition on CPUE, but again data would be challenging to acquire.

Analysis of provisioning rates might also benefit from incorporating additional sources of variation in foraging trip duration. Trip duration may vary as a function of variation in time to satiation and patch residence time, both of which were fixed in the current application. As discussed in Chapter II, the total time spent foraging (i.e. time to satiation) may vary as a function of energy supply (CPUE) and demand (to meet provisioning needs, maintain adult body condition, and replace energy expended during the foraging trip). In Chapter II, analysis of foraging trips by Peruvian Boobies from Isla Guañape Sur in 2007 and Grupo Pescadores in 2008 indicated that variation in time spent in fine-scale search and foraging was most plausibly explained by a combination of compensation for variation in energy expenditure during foraging trips and differences in CPUE. In the interests of simplicity, compensation for variation in energy expenditure during foraging trips was not included in the current version of the IBFM, as the effects would be proportional to travel time, which is the main source of variation in foraging trip duration in the current model. Variation in satiation time as a function of CPUE could be incorporated in the IBFM, but would require data on the relationship between CPUE and the local abundance and distribution of prey (see below).

Variation in patch residence time could be modeled by allowing depletion to occur continuously during a foraging bout. The simplest way to model variation in patch residence time would be to set a minimum threshold (in terms of the declining patch selection probability) which would trigger the forager to seek another patch (see also Krebs 1974). Alternatively, patch residence time could draw on the substantial literature based on Charnov's (1976) marginal value theorem (MVT) (see, for example, Nonacs 2001 and Hahn et al. 2005). In either case, the decision to commute or loop, which is currently pre-determined, would emerge as a consequence of a forager's decision to leave a patch before it is satiated. If the threshold approach was used, patch residence time would be expected to be shorter in scenarios with less prey available, and this might lead to an increased percentage of looping versus commuting trips, and hence longer expected foraging trip durations in scenarios with low prey availability. If the MVT approach was used, the effects would be less predictable as the spatial concentration of prey would play a role. An increase in the expected travel time between patches might lead to longer patch residence time.

Breeding success

To generate results in terms of breeding success, data and analysis on the relationship between provisioning rates and breeding success would also be required for each species, taking into account variation in the number and age of offspring and other factors.

Population persistence

Ultimately, we are interested in the effects of reduced prey availability and the potential effectiveness of fisheries management strategies on population persistence. Provisioning rates from the IBFM could be functionally linked to key demographic variables and, hence, a stage-structured population dynamics model for a more complete understanding of the relationship between prey availability and population persistence.

Given the pronounced variability in this system, a comparison of matrix population models before and after a management intervention (as per Oro et al. 2004) would be inadequate. Instead, an approach similar to that proposed by MacCall (1984) would be required. MacCall (1984) developed a simulation model for the Brown Pelican feeding on anchovy in the California Current system. Food availability was simulated assuming serial autocorrelation and a lognormal distribution over time. Breeding success was then modeled as a logistic function of food availability, while adult survivorship was fixed. Simulation results indicated that a steep logistic curve would generate high population variability, leading to the conclusion that the steepness of the relationship between breeding success and food availability would be very important in predicting fishery impacts. From these results, it can be inferred that, if the long-term mean of prey abundance lies above the intermediate point in the logistic function, then population variance would be reduced and individuals would be more consistently successful. The process of natural selection might therefore be expected to lead to the evolution of mechanisms that place the threshold defined by Cury et al. (2011) close to the long-term mean of prey abundance. Given the asymptotic functional form, there would be limited advantage to developing more efficient mechanisms, but less efficient mechanisms would rapidly increase the probability of species extinction in the long-term.

The IBFM could be used to investigate these mechanisms further. For example, a sequence of prey fields could be simulated representing the range of variability in a system. (For the northern Humboldt Current system (HCS), this could be informed by the series of coast-wide acoustic surveys conducted since 1983 (Gutiérrez et al. 2007)). For each breeding season, this would give a simulated snapshot of foraging conditions. IBFM simulations could then be used to generate provisioning rates corresponding to each simulated prey field. As above, data and

analysis on the relationship between provisioning rates and demographic parameters, in particular breeding success, juvenile survival (net of migration), and adult survival (net of migration), would be valuable.

Croxall and Rothery (1991) emphasize that the sensitivity of populations to food availability depends on both the sensitivity of demographic parameters to food availability and the sensitivity of population dynamics to demographic parameters. Breeding success is expected to be more sensitive to variation in prey availability than adult survival (Cairns 1987), but the population persistence of long-lived iteroparous species such as seabirds is likely to be more sensitive to adult survival than breeding success (Croxall and Rothery 1991, but see also Sandvik et al. 2012). Where adequate data are not available, Monte Carlo simulation of demographic variables based on appropriate non-linear functional forms between provisioning rates and demographic variables could be informative. Simulated sequences of demographic variables could then be used as inputs into a stage-structured population dynamics model to assess the probability of population persistence. This population dynamics model could be used to investigate the effects of fisheries and climate change on population persistence, and the potential effectiveness of conservation and management actions in increasing the probability of population persistence. It would also generate further insights into the mechanisms that could explain the consistent thresholds identified by Cury et al. (2011).

Potential effects of climate change

Important questions relate to the potential effects of climate change on the foraging success of CPFs under different climate scenarios (e.g. Furness 2007). In developing the IBFM, initial foraging conditions have been taken as given, based on geostatistical simulations derived from acoustic survey data of forage fish. To address these questions, it would be necessary to develop a model for the abundance and distribution of prey as a function of biophysical oceanographic processes. Different sets of prey fields could then be simulated corresponding to different climate change scenarios. IBFM simulations could then be run on these different sets of prey fields to investigate the potential effects of climate change on foraging success.

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Figures

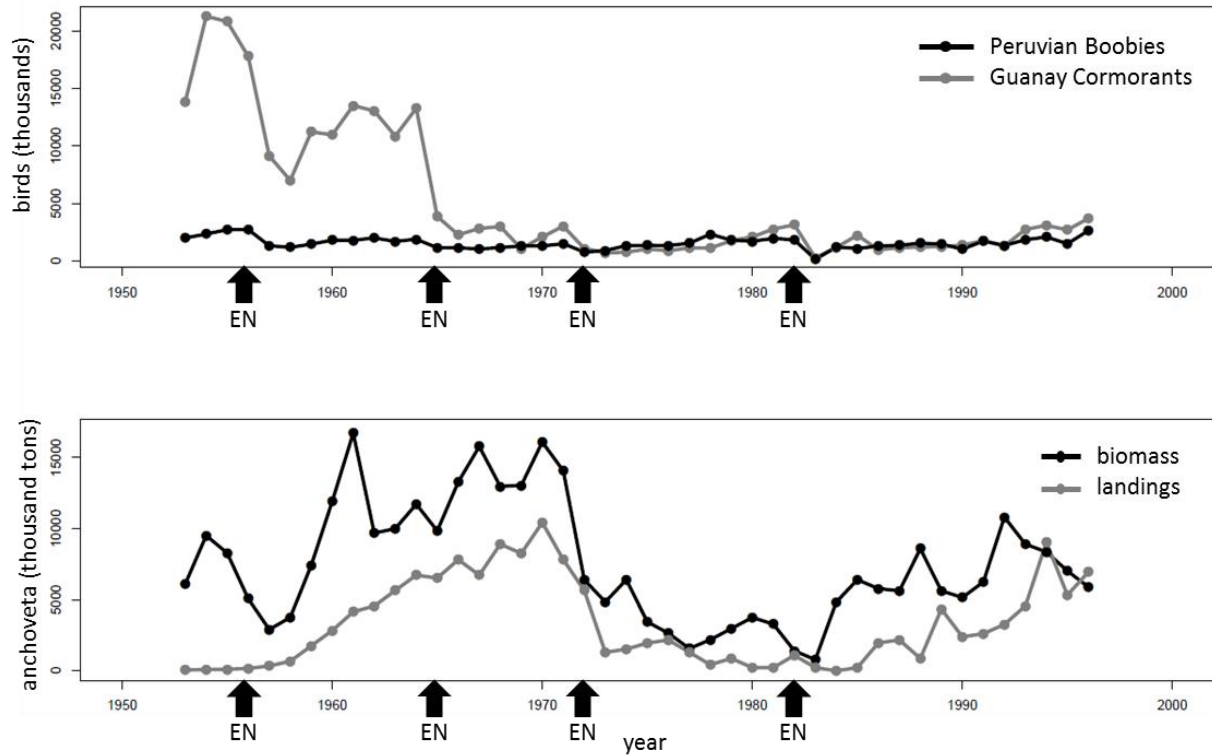
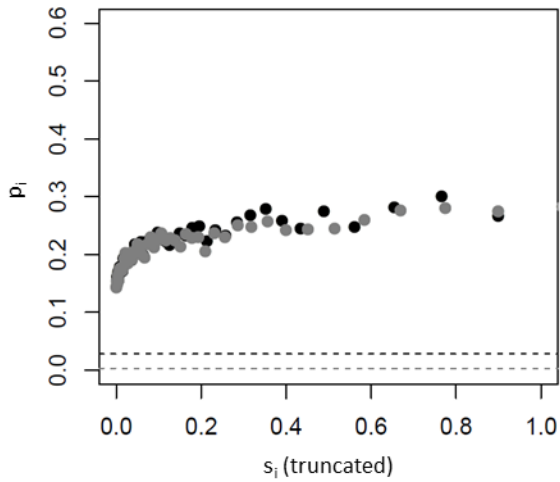


Figure 6.1. Estimated average population sizes of Peruvian Boobies and Guanay Cormorants (upper panel). Estimated average biomass and landings of anchoveta (lower panel). Major El Niño (EN) events are indicated. Data source: Jahncke 1998.

Relative abundance



Depth distribution

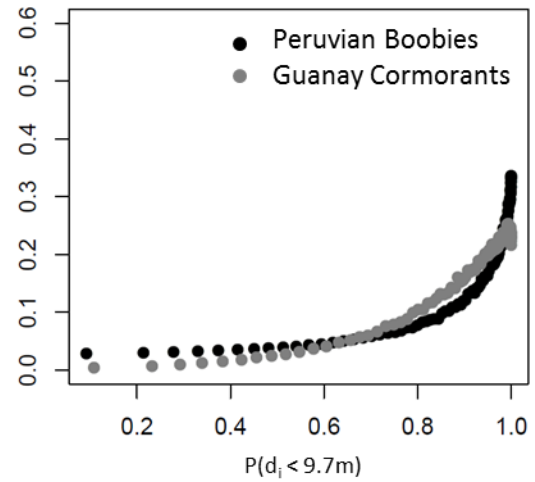


Figure 6.2. Comparison of predicted patch selection probabilities by Peruvian Boobies and Guanay Cormorants in the IBFM. Dashed lines indicate the probability of patch selection when abundance is 0. (The estimated scaling parameter differs for Peruvian Boobies and Guanay Cormorants, but for comparative purposes the horizontal axis refers to the estimated threshold for the Guanay Cormorant (9.7m) is used here.)

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