Living in the tropics: the foraging ecology
of the masked booby in the Pacific Ocean

Dissertation

in fulfilment of the requirements of
the degree of Dr. rer. nat.
at the Faculty of Mathematics and Natural Sciences
at Kiel University

Submitted by:

Miriam Lerma

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First examiner: Prof. Dr. Stefan Garthe

Second examiner: Prof. Dr. Hans-Rudolf Bork

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Abstract

Tropical regions represent half of the oceans on earth, yet our understanding of the ecological interactions in these areas lags far behind that for temperate or polar regions. By studying the foraging ecology of seabirds, ecological information about remote tropical regions can be obtained. However, in order to interpret the foraging ecology of seabirds, it is necessary to take account of local oceanography, inter-annual variations in environmental conditions at the colonies, and the sex and breeding stage of the birds.

In this study, I used the masked booby *Sula dactylatra* as a model species to analyze the effects of the aforementioned factors and their interactions on the foraging ecology of a pantropical distributed seabird. Fieldwork was conducted on two remote islands in the Pacific, Motu Nui and Clarion Island, during consecutive years (2016 and 2017 on Motu Nui and 2016, 2017 and 2018 on Clarion Island), using GPS, time-depth recorders, diet samples, and satellite data, and taking account of the sex and breeding stage of the individuals.

Masked boobies did not utilize the specific hydrographic features at Motu Nui and Clarion Island while foraging. Nor did they change their foraging behavior between years, likely because of relatively stable environmental conditions across years at both study sites. Notably, the El Niño event 2016 did not have a major effect on the environmental conditions at Clarion Island. While foraging trip parameters did not differ between sexes, isotopic signatures of females differed from those of males at Motu Nui. This suggests that, even when the sexes use the same areas, females may be feeding at a different trophic level than males. Foraging trip duration of birds at Motu Nui was affected by breeding stage: they foraged almost twice as long during incubation as during chick rearing. Masked boobies at Motu Nui foraged closer to their colony than those at Clarion Island, which was related to colony size but not to local environmental predictors such as chlorophyll-a concentration.

This study provides the first description of the foraging ecology of a seabird species at Motu Nui and Clarion Island, and demonstrates the value of local studies for providing information on underexplored pelagic areas. Similar to studies on the foraging ecology of tropical seabirds elsewhere, Motu Nui and Clarion Island seascape did not provide any specific areas where prey species accumulated. The unusual environmental stability around Motu Nui and Clarion Island, with no major inter-annual variations, may maintain local availability of the main prey species of masked boobies even between El Niño events, which may explain the observed consistency in foraging parameters across years. Consistent with previous studies, masked boobies showed few sex-specific differences in their foraging ecology. However, the difference in isotopic signatures between sexes is in contrast to previous reports that found no differences between male and female masked boobies, and therefore merits further investigations. Given that breeding stage affects foraging behavior, future studies should aim to use data from birds at the same breeding stage when comparing foraging parameters between sites or years. The results from this study confirm that seabirds from larger colonies are forced to travel further during foraging trips as a result of prey depletion closer to the colony due to continuous exploitation by a larger number of individuals.

In summary, this study corroborates that local oceanography, inter-annual variations in environmental conditions at the colonies, and the sex and breeding stage of the individual need to be considered when interpreting the foraging ecology of seabirds. The findings presented in this thesis are important for interpreting the foraging ecology of masked boobies and other tropical seabird species breeding on remote islands elsewhere. Moreover, they contribute to our understanding of complex food-webs in marine ecosystems, and are vital information for decision makers in marine spatial planning, management and conservation.

Zusammenfassung

Tropische Regionen machen die Hälfte der Ozeane der Erde aus, aber unser Verständnis der ökologischen Wechselwirkungen in diesen Gebieten bleibt weit hinter dem der gemäßigten oder polaren Regionen zurück. Durch Studien zur Ernährungsökologie von Seevögeln können ökologische Informationen über abgelegene tropische Regionen gesammelt werden. Für die Interpretation der Ernährungsökologie von Seevögeln müssen jedoch die lokale Ozeanographie, jährliche Schwankungen der Umweltbedingungen an den Koloniestandorten sowie das Geschlecht und die Brutzeitphase der Tiere berücksichtigt werden.

In der vorliegenden Arbeit wurde der Maskentölpel *Sula dactylatra* als Modellart ausgewählt, um den Einfluss der zuvor genannten Faktoren und ihrer Wechselwirkungen auf die Ernährungsökologie eines pantropischen Seevogels zu untersuchen. Die Feldarbeit wurde auf zwei abgelegenen Inseln im Pazifik, Motu Nui und Clarion Island, in aufeinanderfolgenden Jahren (2016 und 2017 auf Motu Nui und 2016, 2017 und 2018 auf Clarion Island) durchgeführt, mithilfe von GPS- und Zeit-Tiefe-Datenloggern, Nahrungsproben und Satellitendaten und unter Berücksichtigung des Geschlechts und der Brutzeitphase der Individuen.

Maskentölpel nutzten die spezifischen hydro-geografischen Merkmale um Motu Nui und Clarion Island nicht bei der Nahrungssuche. Zudem änderten sie ihr Ernährungsverhalten nicht zwischen den Jahren, was auf über mehrere Jahre relativ stabile Umweltbedingungen an beiden Standorten zurückzuführen sein könnte. Auffällig ist, dass das El Niño Ereignis von 2016 keine größere Auswirkung auf die Umweltbedingungen um Clarion Island hatte. Während sich in den Parametern der Nahrungssuchflüge keine geschlechtsspezifischen Unterschiede zeigten, unterschieden sich die Isotopensignaturen der Weibchen von denen der Männchen in Motu Nui. Dies deutet darauf hin, dass Weibchen, selbst wenn Individuen beider Geschlechter dieselben Gebiete nutzen, möglicherweise auf einem anderen trophischen Niveau fressen als Männchen. Die Dauer der Nahrungssuchflüge der Vögel von Motu Nui wurde durch die Brutzeitphase beeinflusst: sie suchten während der Inkubationsphase fast zweimal so lange nach Nahrung wie während der Kükenaufzucht. Maskentölpel von Motu Nui suchten näher an ihrer Kolonie nach Nahrung als Maskentölpel von Clarion Island, was von der Koloniegröße, aber nicht von lokalen Umweltindikatoren wie der Chlorophyll-a Konzentration, abhing.

Diese Studie liefert die erste Beschreibung der Ernährungsökologie einer Seevogelart von Motu Nui und Clarion Island, und zeigt die Bedeutung von lokalen Studien für die Bereitstellung von Informationen über weitgehend unerforschte pelagische Gebiete. Wie andere Studien zur Ernährungsökologie tropischer Seevögel bereits zeigten, bot auch die Meereslandschaft von Motu Nui und Clarion Island keine besonderen Gebiete, in denen sich Beutearten vermehrt aufhielten. Die ungewöhnlich stabilen Umweltbedingungen um Motu Nui und Clarion Island, ohne größere jährliche Schwankungen, könnte die lokale Verfügbarkeit der wichtigsten Beutearten der Maskentölpel sogar zwischen El Niño Ereignissen aufrechterhalten. Dies könnte die über mehrere Jahre beobachtete Beständigkeit bei Parametern der Nahrungssuche erklären. In Übereinstimmung mit früheren

Untersuchungen zeigten die Maskentölpel kaum geschlechtsspezifische Unterschiede in ihrer Ernährungsökologie. Die geschlechtsspezifischen Unterschiede in den Isotopensignaturen stehen jedoch im Gegensatz zu früheren Studien, in denen keine Unterschiede zwischen Maskentölpelmännchen und -weibchen festgestellt wurden, und sollten daher genauer untersucht werden. Da sich die Brutzeitphase auf das Ernährungsverhalten auswirkt, sollten künftige Studien darauf abzielen, Daten von Individuen in der gleichen Brutzeitphase zu verwenden, wenn Parameter der Nahrungssuche zwischen Standorten oder Jahren verglichen werden. Die Ergebnisse dieser Studie bestätigen, dass Seevögel aus größeren Kolonien dazu gezwungen sind, weitere Strecken bei der Nahrungssuche zurückzulegen. Dies ist auf die starke Abnahme der Beute in größerer Nähe zur Kolonie aufgrund der kontinuierlichen Nutzung durch eine größere Anzahl von Individuen zurückzuführen.

Insgesamt bestätigt die Studie, dass die lokale Ozeanographie, jährliche Schwankungen der Umweltbedingungen an den Koloniestandorten sowie das Geschlecht und die Brutzeitphase der Individuen bei der Interpretation der Ernährungsökologie von Seevögeln berücksichtigt werden müssen. Die Ergebnisse dieser Arbeit sind wichtig für die Auswertung von Daten zur Ernährungsökologie der Maskentölpel und weiterer tropischer Seevogelarten, die auf anderen abgelegenen Inseln brüten. Darüber hinaus tragen sie zu unserem Verständnis der komplexen Nahrungsnetze in marinen Ökosystemen bei und sind ausschlaggebende Informationen für Entscheidungsträger in mariner Raumplanung, Management und Naturschutz.

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Publications and contributions of authors

The chapters from this doctoral thesis are accepted for publication or in preparation for submission:

I. Foraging ecology of masked boobies (*Sula dactylatra*) in the world's largest 'oceanic desert'
Miriam Lerma, Juan Serratosa, Guillermo Luna-Jorquera, Stefan Garthe
Accepted for publication in Marine biology
ML, GL and SG experimental design; ML and JS collection of the data; ML analysis of the data, ML, JS, GL and SG commented and corrected the manuscript.

II. Foraging ecology of a marine top predator in the Eastern Tropical Pacific over 3 years with different ENSO phases
Miriam Lerma, José Alfredo Castillo-Guerrero, Salvador Hernández-Vázquez, Stefan Garthe
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ML, JACG, SHV and SG experimental design; ML collection and analysis of the data, ML, JACG, SHV and SG commented and corrected the manuscript.

III. Do masked boobies breeding within the oligotrophic gyre show sex-related differences in foraging ecology?
Miriam Lerma, Nina Dehnhard, Guillermo Luna-Jorquera, Christian C. Voigt, Stefan Garthe
In preparation for submission
ML, GL and SG experimental design; ML collection and analysis of the data; CCV and ML laboratory work; ML and ND writing of the manuscript; all authors commented and corrected the manuscript.

IV. Living in the tropics: inter-colony variations in foraging ecology of the masked booby
Miriam Lerma, Jose Alfredo Castillo-Guerrero, Salvador Hernandez-Vazquez, Guillermo Luna-Jorquera, Stefan Garthe
In preparation for submission
ML, JACG, SHV, GL and SG experimental design; ML collection and analysis of the data; all authors commented and corrected the manuscript.

Contents

1. General introduction

Background of the study

Tropical oceans are defined as areas between 23° north and 23° south of the equator (Figure 1.1) and with a sea surface temperature > 23° C for at least one season of the year (Ashmole 1971, Ballance & Pitman 1999). Tropical oceans support large populations of top predators including tuna, mammals, and seabirds (Ballance & Pitman 1999), as well as fisheries from many countries (Lluch-Belda *et al.* 2014, Booth *et al.* 2017, Cisneros-Mata *et al.* 2019). Although tropical oceans represent half of the open-water areas on earth, they remain poorly studied compared with temperate and polar regions. This is largely due to the complicated logistics associated with research in these areas (Ballance & Pitman 1999) and because research is generally skewed towards wealthier geographical locations (Reboredo-Segovia *et al.* 2020). This large knowledge gap limits our understanding and hampers our interpretation of food-web structures and changes affecting many of these ecosystems. Tropical seabird species, however, offer opportunities to collect information from many of these underexplored regions.
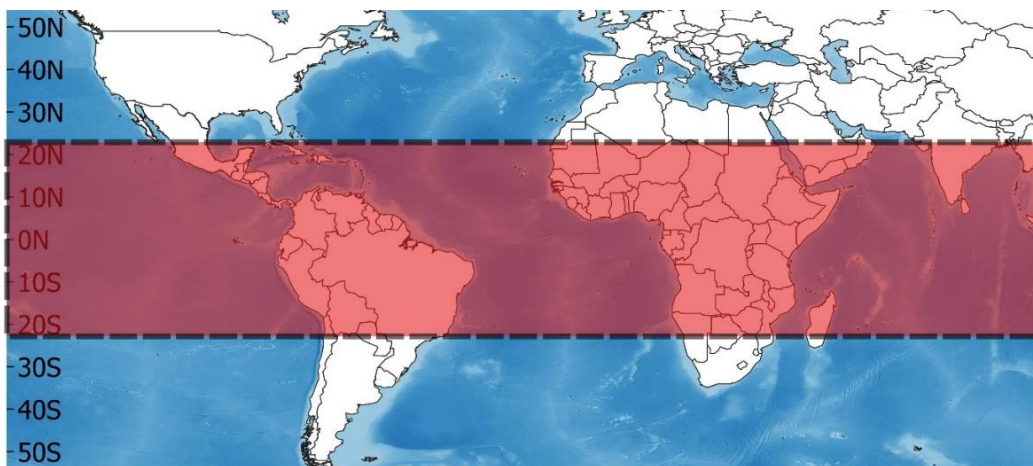
Figure 1.1. Tropical waters (in red) are defined as those between 23° north and 23° south of the equator.

Seabirds operate at the apex of marine food webs and are thus affected by trophic processes with environmental constraints, and can therefore be used to monitor marine ecosystems (Boyd & Murray 2001, Durant *et al.* 2009, Velarde *et al.* 2019). Studies of various aspects of seabird foraging ecology, such as diet, activity patterns, foraging movements, and feeding habitat selection, have substantially increased our knowledge of tropical areas. Observations of the foraging ecology of seabirds has provided information on places where fish accumulate (Parsons *et al.* 2008), changes in the abundance and distribution of fish stocks (Barrett & Krasnov 1996, Kitaysky *et al.* 2000), and early predictors of the effects of environmental variations on fish stocks (Velarde *et al.* 1994, 2004). Seabird foraging ecology has thus helped us to observe oceanographic changes affecting ecosystem

functions through time (Ainley *et al.* 1995, Weimerskirch *et al.* 2003, Gonzáles-Solís & Shaffer 2009) and has improved our understanding of ecosystem functions and food-web structure (Cairns 1992, Fowler 1999), thus providing vital information for inclusion in planning, management, and conservation recommendations to decision makers (Velarde *et al.* 2019). However, many gaps in our understanding of the factors affecting the foraging ecology of seabirds need to be clarified to allow seabirds to be used as proper indicators (Parsons *et al.* 2008).

Seabird foraging ecology can be affected by (1) local environmental conditions, (2) inter-annual environmental variations, (3) sex, and (4) the breeding stage of the sampled individuals. Prey abundance and distribution differ according to local oceanographic conditions and seabird foraging ecology adapts to such conditions (Shaffer *et al.* 2003, Garthe *et al.* 2007). Typically, environmental variations between years occur and seabirds adapt to prevailing environmental conditions affecting their prey availability (Burger & Piatt 1990, Croxall *et al.* 1999, Harding *et al.* 2007, Péron *et al.* 2012). Furthermore, seabird populations comprise heterogeneous groups, composed of individuals of different sexes and in different breeding stages, with both sex (González-Solís *et al.* 2000, Lewis *et al.* 2002, Pinet *et al.* 2012, Owen *et al.* 2013, Pichegru *et al.* 2013) and breeding stage having been shown to affect their foraging ecology (Cherel *et al.* 2008, Hipfner *et al.* 2013, Navarro *et al.* 2014). Although the factors affecting foraging are traditionally evaluated separately, increasing evidence suggests that these factors can interact, and that they merit further investigation (Figure 1.2; Ishikawa & Watanuki 2002, Cherel *et al.* 2008, Navarro *et al.* 2014, Ismar *et al.* 2017). Consideration of the factors affecting foraging will prevent the collection of biased information, and is essential to avoid misinterpretation of the results, such as underestimation or overestimation of the areas used by seabirds. Studies aimed at understanding the mechanisms underlying foraging patterns thus contribute to the scarce information in this field of research, as well as being of pivotal importance for the design and application of conservation management plans.
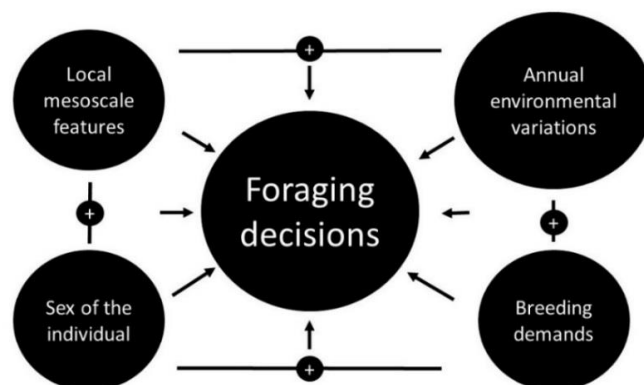
Figure 1.2. Main factors affecting foraging decisions by seabirds, and their possible interactions.

Study species

The masked booby (*Sula dactylatra*) is a seabird species that is widely distributed across the tropics (Nelson 1978, Steeves *et al.* 2005). Numerous studies have reported foraging data for masked boobies (Weimerskirch *et al.* 2009b, Young *et al.* 2010b, Kappes *et al.* 2011, Sommerfeld *et al.* 2013, Oppel *et al.* 2015, Poli *et al.* 2017), allowing comparisons among different localities. Masked boobies also continue to breed even during periods of reduced prey availability (Nelson 1978), thus enabling inter-annual differences in their foraging ecology to be tested under different conditions. Masked boobies are sexually dimorphic (Figure 1.3), with females being larger than males (Nelson 1978), and both parents share breeding responsibilities by taking turns to incubate and feed their chick (Nelson 1978). Collectively, these characteristics make masked boobies an ideal species in which to test the effects of local conditions, environmental variability, sex, and breeding stage, as well as some of the interactions among these parameters, on the foraging ecology of a marine top predator. Moreover, boobies often regurgitate food when disturbed, thus facilitating the study of their diet (Barrett *et al.* 2007), they are large enough (~2 kg) to carry tracking devices, and are more tolerant to manipulation than many other pelagic tropical seabirds (Marchant & Higgins 1990).

Figure 1.3. Masked boobies. Female, left, and male, right.

Study areas

Fieldwork was carried out at Clarion Island in the North Pacific Ocean and Motu Nui in the South Pacific (Figure 1.4). Clarion Island is the most-distant island in the Pacific Ocean belonging to Mexico (Figure 1.4). The island measures 6.4 × 9.7 km and reaches a height of > 305 m (Brattstrom 2015). The vegetation is dominated by grasses and short herbaceous plants (Wanless *et al.* 2009), but also includes areas of low shrubs and small trees up to 2.5 m high (Brattstrom 2015). I visited Clarion Island in January 2016, March 2017, and March 2018.

Motu Nui is located at the southwest of Rapa Nui (also known as Easter Island), which is the most distant island in the Pacific Ocean belonging to Chile (Figure 1.4). This islet has an area of 3.9 ha and is covered with grass and surrounded by sea-cliffs. I visited Motu Nui in October and November 2016, and in November 2017.
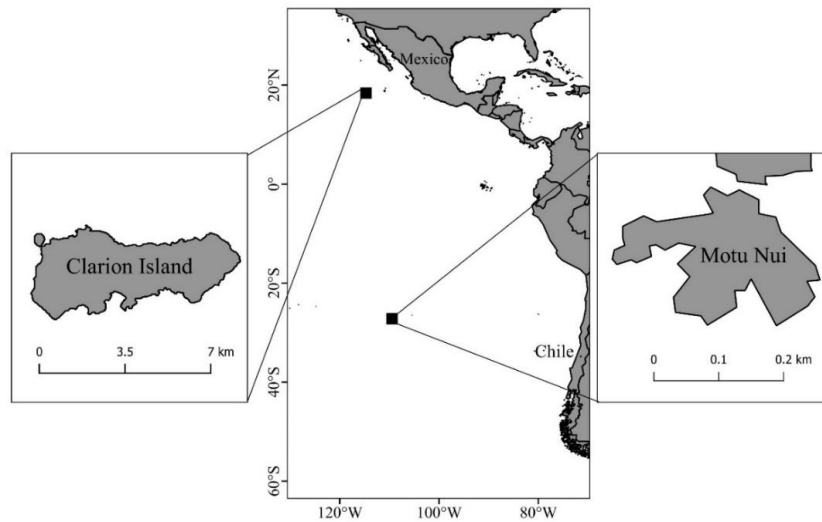
Figure 1.4. Locations of Clarion Island and Moto Nui in the Pacific Ocean.

Methods

Numerous methods can be used to assess the foraging ecology of seabirds, of which the most cost-effective include the deployment of electronic tracking devices (Weimerskirch 2007), collection of diet samples (Barrett *et al.* 2007), and use of stable isotopes (δ^{13}C and δ^{15}N) (Hobson 1999, Bearhop *et al.* 2004). The information obtained from these methods, coupled with satellite data, allows us to measure the relevant oceanic parameters (Poli *et al.* 2017, Santos *et al.* 2019) to further our understanding of the foraging ecology of seabirds.

In this study, I used the following techniques:

• Short-term deployment of tracking devices including global positioning system (GPS) and time-depth recorders (TDRs) (Figure 1.5). GPS data gives positions that can be used to infer spatial habitat use in the horizontal plane, while TDRs provide information on vertical habitat use.

• Diet samples from individuals that spontaneously regurgitated food from the proventriculus.

• Stable isotope (δ^{13}C and δ^{15}N) levels measured in whole blood samples, to provide insights into the trophic position and diet of seabirds.

• Satellite data on chlorophyll-a concentration (CHL) and sea surface temperature (SST) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor carried onboard NASA's Aqua satellite, as local and inter-annual environmental predictors.

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Figure 1.5. Attachment of GPS and TDR devices to the central rectrix feathers of a masked booby using waterproof tape.

Objectives
To examine the factors affecting the foraging ecology of masked boobies, as a model marine predator.
I aimed to investigate:
• The use of local oceanographic features by masked boobies in two colonies in the Pacific Ocean

• The effect of inter-annual environmental variations on the foraging ecology of masked boobies

• The effects of sex and breeding stage on the foraging ecology of masked boobies.

To achieve these aims:

- **Chapter 2:** I investigated the foraging ecology of masked boobies at Motu Nui in relation to local environmental conditions, using tracking and diet data coupled with environmental variables. I discuss the foraging behavioral adaptations of masked boobies to local oceanographic conditions at Motu Nui.
- **Chapter 3:** I analyzed the foraging ecology of masked boobies at Clarion Island in relation to inter-annual differences in environmental conditions. I used tracking and diet data coupled with environmental variables, considering three different phases of El Niño. I discuss the effects of these phases of El Niño on the foraging ecology of the species and on the local oceanographic conditions.
- **Chapter 4:** I investigated the effects of sex and breeding stage (incubation vs chick rearing period) on the foraging ecology of this seabird species at Motu Nui, using tracking, diet, and stable isotope data. I discuss the interactions of sex and breeding stage with the foraging ecology of masked boobies.
- **Chapter 5:** I review the foraging ecology of masked boobies as a species by comparing data collected as part of the current study with data from previous studies of masked boobies throughout their breeding range. I compare foraging parameters and diet, and discuss the effects of productivity and colony size on the foraging ecology of this species

CHAPTER 2.

2.   Foraging ecology of masked boobies in the world's largest oceanic desert

2.1. Abstract

The South Pacific Gyre has the most hyper-oligotrophic waters in the world and is considered the largest 'oceanic desert'. Rapa Nui (Easter Island), located within the South Pacific Gyre, is a breeding ground for masked boobies, which are seabirds with a foraging range that effectively confines them within the gyre. I examined the foraging ecology of this species in the gyre by attaching GPS and time-depth devices to chick-rearing adult birds (9 and 14 birds in 2016 and 2017, respectively) and by collecting regurgitates (18 and 15 samples in 2016 and 2017, respectively). In addition, I compared the birds' foraging ecology between years. Masked boobies travelled in various directions, dived at unspecific locations, and explored areas < 110 km from the colony. Local environmental conditions were not significantly different between years, and differences in foraging parameters (maximum foraging range, trip duration, and dive depth) were greater among individuals than between years. The foraging characteristics of masked boobies suggest that resources were ephemerally distributed around the colony, with similar abundances across years. Under these conditions, travelling to unspecific locations may increase the area covered and the probability of prey encounter. The spatial and temporal consistencies in environmental conditions explain the uniformity of foraging parameters between years. The ability of masked boobies to exploit ephemerally distributed resources in seascapes like Rapa Nui may help to explain its pan-tropical distribution.

2.2. Introduction

Optimal foraging theory suggests that predators make foraging decisions that optimize energy intake with minimal energy investment, thus maximizing energetic gain (Charnov 1976, Pyke *et al.* 1977, Louzao *et al.* 2014). In the tropical marine environment, prey can be concentrated in areas of enhanced primary productivity (high chlorophyll-a concentration (CHL) and lower sea-surface temperature (SST)) (Ballance *et al.* 2006), and seabirds may travel directly to these areas where prey encounters are likely to be higher (Weimerskirch 2007, Assali *et al.* 2017). However, the South Pacific Gyre may be an especially challenging region for seabirds. This region has the most hyper-oligotrophic superficial waters in the world (Claustre *et al.* 2008) and is considered to be the world's largest 'oceanic desert' (Morel *et al.* 2010). The gyre covers an area of 37 million square kilometers (Longhurst *et al.* 1995, Reintjes *et al.* 2019), with Rapa Nui, also known as Easter Island, located at its center. While some seabird species breeding within the gyre, such as petrels, travel thousands of kilometers to forage at fronts with high productivity (Clay *et al.* 2017), other species with smaller foraging ranges still manage to forage and breed successfully within the gyre (Jaramillo *et al.* 2008, Flores *et al.* 2014). Little is currently known about how seabirds adapt to survive in this tropical, low-

productivity environment, and how they modify their foraging strategies to fulfill their energetic requirements.

The masked booby preys mainly on flying fish and squid throughout its range but consumes other prey families according to localities (Nelson 1978, Priddel *et al.* 2005, Asseid *et al.* 2006, Weimerskirch *et al.* 2009b, Young *et al.* 2010a). Masked boobies forage by plunge diving, and have been reported at a maximum distance of 367 km from the colony (Asseid *et al.* 2006), meaning they are effectively confined within the gyre while breeding. Seabird species inhabiting low-productivity areas like Rapa Nui are expected to spend long periods searching for food because prey abundances are lower and more unpredictable than in productive areas (Ashmole 1971, Longhurst & Pauly 1987, Jaquemet *et al.* 2005). The waters around Rapa Nui have low variability in terms of CHL and SST at a mesoscale level (Testa 2014), and hence may not provide appropriate physical features for prey accumulation within the birds' foraging range. However, Rapa Nui forms part of the Easter Seamount, comprising large seamounts that can reach > 3000 m above the surrounding seafloor (Rodrigo *et al.* 2014). Seamounts support a wide diversity of fish and other potential prey species, and may thus act as a resource patch (Riotte-Lambert & Matthiopoulos 2020) providing enhanced foraging opportunities for marine top predators (Ballance *et al.* 1997, Pitcher *et al.* 2007, Clark *et al.* 2010). Seamounts can therefore be critical foraging areas for seabirds in the food-stressed environment of oligotrophic oceans (Pitcher *et al.* 2007).

Tropical regions typically experience variable environmental conditions (Hamer *et al.* 2002). During periods of lower productivity, which affect prey abundance, seabirds may forage further and for longer periods (Burger & Piatt 1990, Harding *et al.* 2007), use different areas to forage (Péron *et al.* 2012), or switch prey species and size (Burger & Piatt 1990, Croxall *et al.* 1999). However, conditions within the gyre are less well known than for other oceanographic regions (Mannocci *et al.* 2014, Clay *et al.* 2017, Reintjes *et al.* 2019), and levels of variability of environmental conditions are poorly known (Testa 2014). It is possible that masked boobies may adjust their foraging movements and diet between years if considerable environmental variation occurs (Nelson 1978, Sommerfeld *et al.* 2015). However, adjustments in their foraging movements and diet can be costly, because spending more time foraging during poor years increases absence times from the nest, potentially leading to deferred reproduction, lower growth rates, and higher chick mortality (Quillfeldt & Masello 2013, Guillemette *et al.* 2018).

With around 70 breeding pairs, the masked booby is the most numerous of the few native species on Rapa Nui (Jaramillo *et al.* 2008). It has a predictable presence on the island and is large enough to carry tracking devices that can be used to research their foraging strategies. These characteristics make the masked booby an ideal species for determining (1) if foraging incidents occur in relation to static marine features like seamounts in Rapa Nui, and (2) if the birds' foraging ecology remains consistent between years based on environmental characteristics. I expected that (1) masked boobies would travel directly to seamounts reducing foraging times, with lower variability in foraging behavior than if prey

patches were unknown (Sommerfeld *et al.* 2013, Patrick *et al.* 2014, Oppel *et al.* 2015), and (2) that their foraging parameters would adapt to inter-annual environmental conditions.

2.3 Materials and methods

Data collection

Rapa Nui is the highest point of the Easter Seamount chain, reaching > 400 m above sea level (Rodrigo *et al.* 2014). Moai and the Pukao are the closest seamounts to Rapa Nui, reaching > 2000 m above the sea floor, with summits at 261 and 623 m depth respectively (Rodrigo *et al.* 2014). Seamounts produce local turbulence and recirculation patterns that promote the entry of nutrients at relatively shallow depths, thus enhancing the primary productivity at Rapa Nui (Testa 2014). The seamounts at Rapa Nui are considered important marine conservation spots due to their diversity of fish (Friedlander *et al.* 2013), and are used sporadically by local fishermen (Mecho *et al.* 2019).

Data were collected at Motu Nui (109.4° W, 27.2°S) a 3.9 ha islet covered with grass and surrounded by sea-cliffs, located southwest of Rapa Nui. On Motu Nui, masked boobies nest in areas free from grass on the top of the islet and on the cliffs. Similar to Rapa Nui, Motu Nui has introduced species including the Argentine ant (*Linepithema humile*) and the Chimago caracara (P*halcoboenus chimango*), which can be potential predators of seabird chicks and eggs (Luna *et al.* 2018). There were 56 breeding pairs of masked boobies in 2016 and 77 breeding pairs in 2017.

The foraging movements of masked boobies were studied by attaching GPS CatLog-S devices sealed in a heat-shrink epoxy casing (3.7 x 2.2 x 0.8 cm, Catnip Technologies, Hong Kong) to nine chick-rearing birds (3 females and 6 males) in October and November of 2016 and to 14 chick-rearing birds (8 females and 6 males) in November of 2017. Chicks from tagged birds were covered with down and weighed 0.4–2.1 kg, and were thus estimated to be 1–8 weeks old (Priddel *et al.* 2005). Eight and 12 of the tracked birds in 2016 and 2017, respectively, were simultaneously equipped with time–depth recorders (TDRs; CEFAS Data Storage Tags G5+, Cefas Technology, UK). Two of the TDR devices had large sensor variations and were excluded from further analyses.

The GPS devices were programmed to record time, latitude, and longitude every 4 min, and the TDRs to record pressure data every second, and temperature every minute at 12 bits. The GPS devices weighed 26 g and the TDR devices weighed 6.5 g; given that masked boobies weighed 1.8–2.6 kg, the total weight was < 3% of the body mass threshold for attached devices (Wilson & McMahon 2006, Vandenabeele *et al.* 2012). The individuals were captured at their nest using a hand net from approximately 1 m. The loggers were attached on top of the three central tail feathers using waterproof adhesive TESA tape. All individuals were released back to their nest after attaching the devices. Birds were captured between 07:00 and 10:00 h and between 16:00 and 19:00 h to avoid the hottest time of the day. The total handling time during capture and recapture did not exceed 10 min.

Diet samples were collected opportunistically from masked boobies that regurgitated spontaneously as a result of our presence in the colony, or during tagging efforts. Eighteen regurgitated samples were collected in 2016 and 15 in 2017. Due to the digested state of the samples and a lack of information on Rapa Nui fish species, fish and squid in regurgitates were identified to family level using a Pacific fish guide (Fischer *et al.* 1995) and a site-specific fish guide (Randall & Cea 2010). Notably, although regurgitates provide a useful and non-invasive method for obtaining valuable information about seabird feeding ecology, the presence of different prey items in the diet may vary due to different intrinsic digestion rates (Barrett *et al.* 2007).

Regarding local environmental predictors, data on chlorophyll-a concentrations (CHL) and sea surface temperature (SST) were derived from monthly composites with a resolution of 0.025 ° (approx. 2.5 km) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor carried onboard NASA's Aqua satellite, and bathymetry (BATH) data from ETOPO[1], 0.017 °. The names and coordinates of the nearby seamounts were obtained from Rodrigo *et al.* (2014). Average environmental conditions were extracted using the raster data of BATH, CHL, and SST inside a radius of 120 km (maximum range of a masked booby from Rapa Nui with an error threshold) using the function 'extract' in the R package 'raster'.

Data processing

Tracking and diving data were processed using R 3.5.2. Foraging trip parameters including maximum foraging trip distance, total distance travelled, and trip duration were calculated after running the function 'tripSplit' provided by Lascelles *et al.* 2016. The maximum foraging trip distance was measured at the most distant point in a straight line from the colony. Total distance travelled was the sum of the distance between consecutive fixes from departure to return to the colony. Trip duration was the total time between departure and return to the colony. Foraging trips were considered as soon as the bird left a 1.5 km radius from the colony, because I observed flying fish leaving the water and masked boobies foraging in the vicinity of the colony. Although short trips may include birds bathing (Granadeiro *et al.* 2018), the presence of diving events in the vicinity of the colony demonstrated that these areas were also used as foraging grounds.

Using GPS data at 4 min intervals, foraging behavior during the foraging trips was classified using the speed and turning angle from successive locations with value delimiters of 0.60–3.14 radians (high turn) and 0–12 km h-1 (low speed). Value delimiters for speed and turning angle were based on the Expectation Maximization binary Clustering (EMbC) algorithm (Garriga *et al.* 2016), and were within the thresholds used for other sulids (Mendez *et al.* 2017). Regarding diving data, a zero offset correction was applied for surface drift in the pressure sensor, and only dives deeper than 0.5 m were considered as true dives. I acknowledge that this threshold may omit shallow dives (Hagihara *et al.* 2011), but a larger threshold identified 21% more records as dives by including false dives due to noise or

activities such as sitting on the water surface. Mean and maximum dive duration (s), mean and maximum diving depth (m), and diving rate (dives h^{-1}) were calculated per individual trip.

Diving and foraging locations are not necessarily the same; dives may reflect attempts to capture prey, whereas foraging locations reflect searching behavior (Bennison *et al.* 2017). Because of this dissimilarity, foraging and diving activities during the foraging trips were tested for matches in time and space. First, the locations were grouped into 'events' considering at least three successive locations (an area-restricted search approach; see Mendez et al. 2017). The locations falling within a 10 min range were then merged and assigned a median latitude and longitude as a central location. Finally, the locations were matched. False positives (foraging locations but no dives) may occur if boobies capture prey on the wing (Weimerskirch *et al.* 2005), in which case TDRs will fail to record dives, while false negatives (dives not matching foraging locations) may arise from opportunistic foraging events (Montevecchi *et al.* 2009), in which case the ability of a classification based on speed and turning angles is limited for identifying foraging behavior. Due to the associated error in each technique, foraging and diving events were tested separately. A radius of 10 km around each seamount was created and diving and foraging events within this radius were classified as 'close to seamount', while others were classified as 'far from seamount'. Distance from the seamounts was calculated for each dive and each foraging event using the R package 'geosphere'.

Statistical analyses

I tested if seamounts affected masked boobies' foraging behavior by applying linear mixed-effects models. Diving rate was used as dependent variable, seamount use or not use were used as factors, with the birds' identity as random factor. I determined if foraging or diving events were more likely to occur in the immediacies of the seamounts using chi-square analysis to compare dive and foraging events classified as 'close to seamount' vs 'far from seamount'. I evaluated the variability of individuals' foraging behavior by analysis of variance with foraging or diving parameters as dependent variables and the birds' identity as a fixed factor. Individual consistencies in foraging parameters were further investigated using the individual as a random intercept in the R package 'rptR'. This package calculates variances between and within individuals and produces a value between 0 and 1, with values closer to 1 representing higher consistency and values closer to 0 representing lower consistency (Stoffel *et al.* 2017, Courbin *et al.* 2018, Grecian *et al.* 2018).

Inter-annual differences in foraging trip parameters were examined using linear mixed-effects models with foraging (maximum foraging range, trip duration, total distance travelled) and diving parameters (mean diving depth, mean diving duration, dive rate) as dependent variables, year as a fixed factor, and birds' identity as a random factor to account for pseudo-replication. The models were fitted using the 'lme' function in the R package 'nlme'. Model selection was performed using a likelihood ratio test. There was no significant difference in foraging or diving parameters between the sexes ($P > 0.05$), and information for

both sexes was therefore pooled. Residuals were plotted against fitted values, and there was no obvious deviation from the assumption of normally distributed and homogeneous residuals. To test if similar areas were used during both years, the Bhattacharyya coefficient (BA) was extracted using the function 'overlap' in the R package 'ctmm' based on the GPS data (Calabrese *et al.* 2016). The BA is a measure of similarity between two probability distributions, which gives the overlap in the kernel density estimates (Winner *et al.* 2018). The overlap between years was calculated by analysis of similarity (ANOSIM) with BA using the R package 'vegan'. I compared the number of prey items by year using chi-square tests. The results are shown untransformed, and values for foraging parameters are given as mean ± standard deviation.

2.4. Results

A total of 123 foraging trips were recorded from 23 individual masked boobies (Figure 2.1). Nests were monitored every day during the tagging period of 4–6 days and no bird showed signs of discomfort associated with the devices, such as making frequent contact with the devices or increased preening activities.
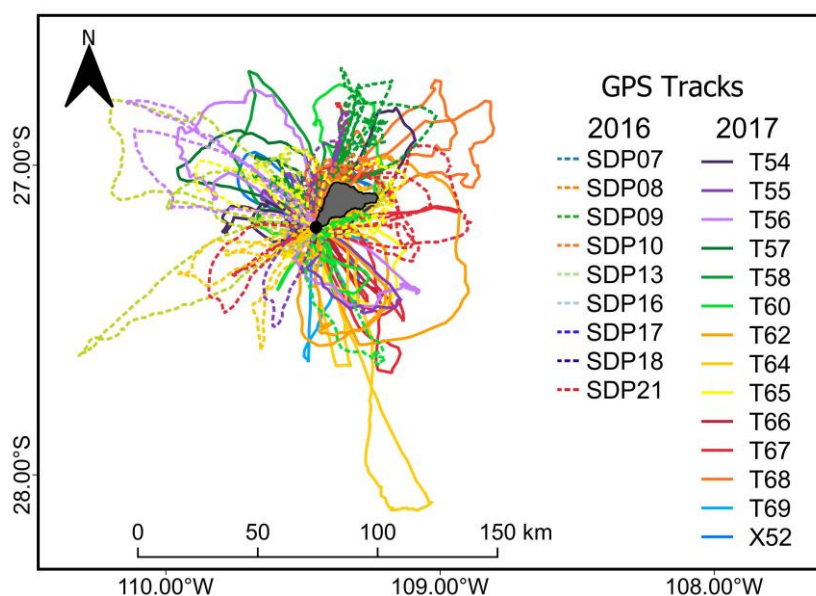
Figure 2.1. Foraging trips of individual masked boobies at Rapa Nui during the breeding seasons of 2016 (n = 9, dashed lines) and 2017 (n = 14, solid lines). Black dot indicates the location of the masked booby colony.

Individuals performed an average of 1.64 ± 0.48 trips per day. The mean maximum distance from the colony was 31.9 ± 21.5 km, mean foraging trip duration was 3.4 ± 2.1 h, and the mean total distance travelled during a foraging trip was 80.6 ± 54.2 km. Diving information was obtained from 18 individuals. Most dives occurred at the surface below 2 m

(59%) and lasted < 2 s (49%). The deepest dive was 6 m and the longest time submerged was 10 s. Regurgitates contained 3.7 ± 3.2 items from 1.5 ± 0.8 prey families. Considering the total number of prey items collected, flying fish dominated the diet (Figure 2.2).
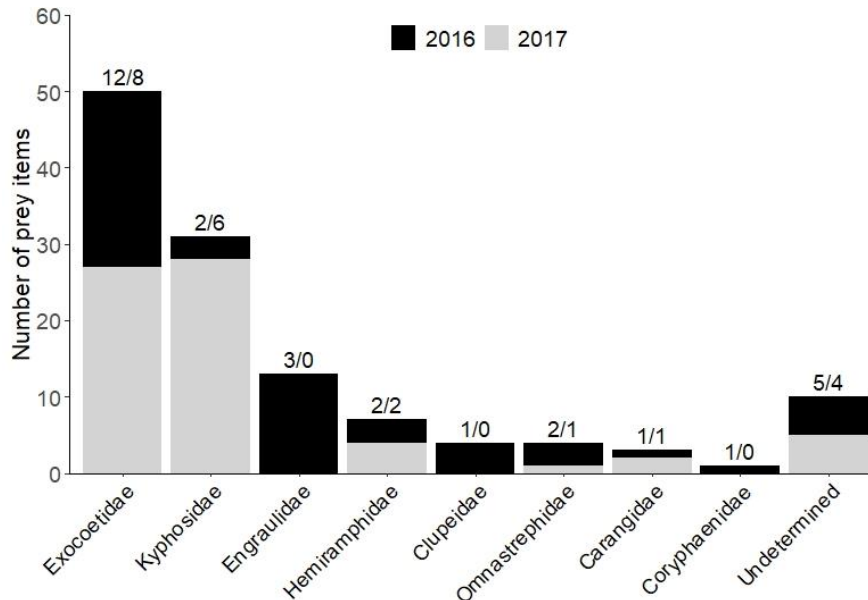
Figure 2.2. Prey species in regurgitates from masked boobies at Rapa Nui during the breeding seasons of 2016 (18 regurgitates, 56 prey items) and 2017 (15 regurgitates, 67 prey items). Families identified include Exocoetidae (flying fish), Kyphosidae (sea chub), Engraulidae (anchovy), Hemiramphidae (halfbeaks), Clupeidae (sardines), Omnastrephidae (squid), Carangidae (jacks), and Coryphaenidae (dolphinfish). The number of regurgitates that contained the prey item are presented above the bars and correspond to regurgitates of 2016/2017.

Foraging and dive events (n = 554) matched in 32% of all events (true positives), while 44% of all foraging events (n = 495) showed no dives (false positives) and 23% of all dive events (n = 497) did not match foraging events (false negatives). Foraging (χ^2_{494} = 467, P = 0.80) and dive events (χ^2_{496} = 466, P = 0.82) were not significantly related to seamounts (Figure 2.3). Dive rates ($F_{1, 95}$ = 0.27, P = 0.60) did not differ significantly between trips within or outside the immediacies (< 10 km) of seamounts. Only 28 of the 495 foraging events (searching behavior), and 31 of the 497 total dive events (attempts of capturing prey) occurred in the immediacies of seamounts (Figure 2.3).
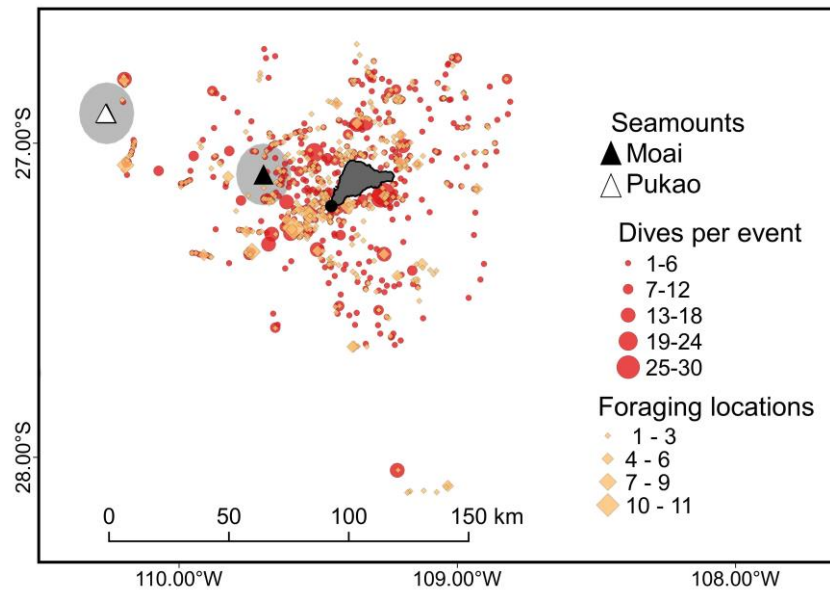
Figure 2.3. Diving (n = 497, red circles) and foraging events (n = 495, yellow diamonds) of tracked masked boobies at Rapa Nui. Triangles: seamounts; grey circles: area of influence of the seamounts; size of the symbol: number of dives or foraging locations per event; black dot: colony.

Foraging and diving parameters varied between individuals, with significant inter-individual differences in maximum distance from the colony, trip duration, mean dive duration, dive depth, and diving rate (Table 2.1). Individuals' dive depths and durations were repeatable, but the maximum distance from the colony, trip duration, and diving rate were not (Table 2.1).

Table 2.1. Analyses of foraging and diving parameters of chick-rearing masked boobies breeding at Rapa Nui in 2016 (GPS = 9, TDR = 6) and 2017 (GPS = 14, TDR = 12) showing inter-annual, inter-individual, and intra-individual comparisons

Parameter	Inter-annual		Inter-individual		Intra-individual
	Statistic	P	Statistic	P	Statistic
Maximum distance	$F_{1,\,21} = 0.39$	0.54	$F_{22,\,100} = 1.78$	**0.03**	0.09 ± 0.07
Trip duration	$F_{1,\,21} = 0.03$	0.87	$F_{22,\,100} = 2.22$	**< 0.01**	0.17 ± 0.10
Total distance	$F_{1,\,21} = 0.21$	0.65	$F_{22,\,100} = 1.70$	**0.04**	0.08 ± 0.07
Dive duration	$F_{1,\,16} = 0.15$	0.70	$F_{17,\,68} = 3.04$	**< 0.01**	0.43 ± 0.14
Diving depth	$F_{1,\,16} = 1.43$	0.25	$F_{17,\,68} = 2.88$	**< 0.01**	0.41 ± 0.15
Diving rate	$F_{1,\,16} = 2.76$	0.12	$F_{17,\,68} = 2.43$	**< 0.01**	0.13 ± 0.09

Within the foraging range of masked boobies, the water depth was 2.9 ± 0.5 km, CHL was of 0.02 ± 0.01 mg m^{-3} in both years, and SST was 22.2 ± 0.4 °C in 2016 and 21.6 ± 0.2 °C in 2017 (Figure 2.4). There were no significant differences in foraging and diving parameters between 2016 and 2017 (Table 2.1), and the areas used by masked boobies overlapped between years (BA range at 50% UD: $0.53 - 0.99$; ANOSIM R = 0.01, P = 0.10; BA range at 95% UD: $0.53 - 0.99$; ANOSIM R = 0.01, P = 0.09). The main prey items in both years were flying fish, but the birds' diet was more diverse in 2016 than in 2017, with the inclusion of anchovies (Engraulidae), sardines (Clupeidae), and dolphinfish (Coryphaenidae) (Figure 2.2). Sea chubs (Kyphosidae) were more important in 2017, occurring in six regurgitates with 4.6 ± 2.4 prey items, compared with two regurgitates with 1.5 ± 0.7 prey items in 2016. Nevertheless, the prey items in the diet were homogeneous between years ($\chi^2_8 = 2.50$, P = 0.96).
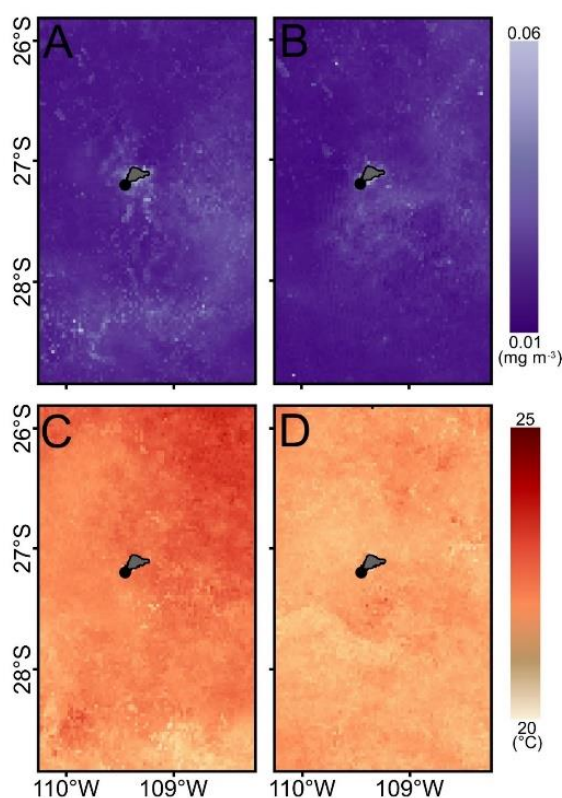
Figure 2.4. Chlorophyll-a concentrations at Rapa Nui in November 2016 (A) and 2017 (B), and sea surface temperatures in November 2016 (C) and 2017 (D). Black dot indicates the study area.

2.5. Discussion

The results of this study provide novel information on the foraging behavior of a seabird species in the South Pacific Gyre. The diving parameters were similar to previous reports on diving depths and durations acquired for the species at Clipperton Island (Weimerskirch *et al.*

2009b) and Phillip Island (Sommerfeld *et al.* 2013). Masked boobies at Rapa Nui made more trips per day (1.6 trips per day) than birds from St. Helena and Ascension Island (0.4–1.0 trips per day; Oppel *et al.* 2015), possibly related to the fact that foraging trips of masked boobies from Rapa Nui were similar to or shorter than those of masked boobies' from the other colonies. Interestingly, foraging trips of masked boobies would be expected to be shorter in colonies where water productivity was higher, and should thus reflect the possibilities of prey encounter. However, although the CHLs at St. Helena and Ascension Island were 0.07 and 0.08 mg m^{-3}, respectively (Oppel *et al.* 2015), foraging trips were similar to or longer (3.4 and 11.4 h) and further (41 and 78 km) than those at Rapa Nui, where the CHL was 0.02 mg m^{-3}. Similarly, masked boobies on Clipperton Island performed further and longer foraging trips on average (103 km and 8.9 h) in waters that were 10 times more productive (CHL 0.20 mg m^{-3}) (Weimerskirch *et al.* 2008) than at Rapa Nui.

The larger foraging ranges reported in other studies could be related to greater inter- or intra-specific competition at other sites. Masked boobies in the South Atlantic foraged closer to smaller colonies compared with larger colonies (Oppel *et al.* 2015). Accordingly, masked booby colonies on St. Helena (500 individuals), Ascension (4600 individuals) (Oppel *et al.* 2015), and Clipperton Island (120 000 individuals) (Weimerskirch *et al.* 2008) were larger, supporting the idea that larger colonies might experience high levels of intra-specific competition, resulting in longer foraging ranges (Lewis *et al.* 2001). Similar to land deserts, Rapa Nui supports small populations of generalist predators (Ashmole 1963, Cook 1997, Ayal 2007). The masked booby colony was ~70 breeding pairs, and no other large plunge divers, except tropicbirds, occur regularly in the area. The shorter foraging trips of masked boobies from Rapa Nui may thus reflect the low level of competition that occurs in small colonies.

The main prey item of masked boobies was flying fish, coinciding with results throughout their distributional range (Nelson 1978, Asseid *et al.* 2006, Weimerskirch *et al.* 2009b, Young *et al.* 2010b, Kappes *et al.* 2011). The diet of masked boobies at Rapa Nui included species such as anchovies and sea chubs, which were not reported in previous studies. The difference in supplementary prey species included in the diet of masked boobies must reflect the fact that geographically separated populations of seabirds are exposed to different environmental and ecological conditions (Garthe *et al.* 2007, Castillo-Guerrero *et al.* 2016).

Foraging strategy

I hypothesized that seamounts may attract foraging seabirds at Rapa Nui because of their increased food supply (Morato *et al.* 2010); however, contrary to my expectations, masked boobies did not appear to use seamounts. Similarly, red-footed boobies (*Sula sula*) did not preferentially forage over seamounts in the Mozambique Channel (Weimerskirch *et al.* 2005), though the use of seamounts appears to differ among seabird species (Pitcher *et al.* 2007, Clay *et al.* 2017). Masked boobies do not feed on primary producers, and there is a natural delay between the primary producers and fish (Suryan *et al.* 2012). Seamounts may thus not

concentrate the prey items that boobies are searching for, and may even have the opposite effect, given that flying fish are offshore specialist species that prefer low-productivity waters (Churnside *et al.* 2017, Lewallen *et al.* 2018).

In contrast, the foraging behavior of masked boobies in the hyper-oligotrophic waters of Rapa Nui showed that their prey was not predictably distributed or associated with static environmental features. This was demonstrated by the fact that foraging parameters differed both between and within individuals. I also found that an individual bird might make several trips on the same day following different behaviors and travelling to different places, in accordance with previous findings that showed low foraging-site fidelity in tropical seabirds (Weimerskirch 2007, Kappes *et al.* 2011, Hennicke & Weimerskirch 2014, Soanes *et al.* 2016, Oppel *et al.* 2017). Flying fish shoals are highly unpredictable (Oxenford *et al.* 1995); travelling to the same area is thus of limited value to masked boobies, and it may be more efficient to search in different locations. Other animals facing unpredictable resources move without any specific direction, but then travel directly when they see something of interest (Venter *et al.* 2017). This seems to reflect the behavior of masked boobies searching for a prey patch, subsurface predators, or conspecifics. The ephemeral distributions of flying fish are further supported by the techniques used by fishermen, who change locations both within and between days to catch flying fish in the Caribbean (Oxenford *et al.* 1995) and at Rapa Nui (Pau Hito, Rapa Nui fishermen, pers. comm.). Exploring new areas benefited fishermen facing stochastic systems (O'Farrell *et al.* 2019). Similarly, an explorative approach may be the dominant searching strategy used by seabirds in oligotrophic waters like Rapa Nui, and may allow the masked booby population to maintain a foraging range < 110 km radius.

Inter-annual comparisons

There were some differences in the proportion of prey families included in the diet of masked boobies between years. Between-year differences in seabird diets are often associated with environmental conditions that affect prey distribution and abundance (Burger & Piatt 1990, Croxall *et al.* 1999). However, the environmental conditions at Rapa Nui were similar during both years. Although our present understanding of prey abundances is limited by a lack of information, the differences in supplementary prey species included in the diets between years may merely be an effect of the birds' opportunistic behavior. Flying fish occur in patchily distributed shoals that are very difficult to predict in space and time (Oxenford *et al.* 1995), and birds may prevent interruptions to their food supply by opportunistically including other prey species (MacArthur & Pianka 1966, Giraldeau 2008). For example, masked boobies included small sea chubs, an inshore fish of which juveniles may occur offshore amongst drifting flotsam and algae (Randall & Cea 2010).

The foraging and diving parameters of the masked boobies were similar in both study years. Similarly, petrels, as other tropical seabird inhabiting the South Pacific Gyre, showed no inter-annual differences in their foraging parameters (Clay *et al.* 2017). The consistent foraging parameters and relatively stable environmental conditions around Rapa Nui suggest

that there was no need for the birds to change their foraging behaviors under these conditions. Flying fish may occur in the region throughout the year because they do not generally make long-distance migrations, and they have short generations (1–2 years) and small home ranges of < 500 km^2 (Lewallen *et al.* 2018). Masked boobies form associations with tuna species during foraging (Au & Pitman 1986), and tuna may occur in the area because of the presence of flying fish and because of the suitable sea conditions around Rapa Nui for some tuna species, including moderate SST and low surface CHL (Teo *et al.* 2007). However, detailed information on the distributions of flying fish and tuna is lacking, largely because data on the quantitative distributions of oceanic pelagic species is difficult and expensive to collect (Oxenford *et al.* 1995, Churnside *et al.* 2017, Lewallen *et al.* 2018). Nonetheless, masked booby foraging parameters suggest that prey availability is regular and stable, otherwise their energy reserves would be depleted and they would avoid breeding, which is demonstrably not the case. The evidence suggests that masked boobies breed on Rapa Nui throughout the year, and have done so since at least 1904 (Marin & Caceres 2010, Flores *et al.* 2014).

Peaks in productivity are often associated with an increase in food availability, which plays a significant role in the time of breeding for many seabirds (Hamer *et al.* 2002). However, tropical areas tend to have a weak productivity peak (Weimerskirch 2007). Year-round breeding of several tropical seabirds may thus be due to the stable but short year-round availability of food, which offers multiple breeding opportunities throughout the year, but for only a limited number of breeding pairs (Reynolds *et al.* 2014, Tarburton 2018). It is therefore worth speculating that the year-round breeding of masked boobies in Rapa Nui may be another adaptation to hyper-oligotrophic conditions, by diluting the peak of food demands and potentially allowing more birds to coexist in the same breeding grounds than if they all bred at the same time.

2.6. Conclusions

The current study provides the first description of the foraging ecology of a plunge-diving seabird species in the hyper-oligotrophic waters of the South Pacific Gyre. The results suggest that the foraging strategies of masked boobies were influenced by the distributions of flying fish at a distance < 110 km from the coast. The locations of foraging trips indicated that travelling to a specific location, such as seamounts, may be of little value to masked boobies in Rapa Nui. The stability of the environmental conditions around Rapa Nui means that the birds' foraging behavior remains similar between years, implying similar prey abundances. These results show that masked boobies can adapt to a wide range of oceanographic conditions, including the hyper-oligotrophic waters of the South Pacific Gyre, thus demonstrating the flexible characteristics of this species, which may in turn explain its wide distribution throughout the tropics.

CHAPTER 3.

3.   Foraging ecology of a marine top predator during 3 different ENSO-phases in the Eastern Tropical Pacific

3.1. Abstract

The El Niño Southern Oscillation (ENSO) is a recurrent climatic pattern with important ecological consequences for seabirds due to its impacts on the abundance and distribution on food resources. I investigated the effects of ENSO phases on the foraging ecology of a marine top predator at Clarion Island in the Eastern Tropical Pacific using GPS and time-depth recorder data and regurgitates from incubating masked boobies during 3 consecutive years. Foraging locations were recorded in 2016 (El Niño, one female, three males), 2017 (neutral; six females, nine males), and 2018 (La Niña; eight females, ten males). Local sea surface temperature (SST) and chlorophyll-a concentration (CHL) within the birds' foraging range were compared among the 3 years. Regurgitates were collected opportunistically from 25 and 31 incubating adults in 2017 and 2018, respectively. Average local CHL and SST were similar among years (mean SST 25 °C; mean CHL 0.10 and of 0.09 mg m^{-3} in January and March, respectively). Masked boobies travelled a maximum of 66 ± 34 km from the colony. The maximum trip duration was 7.7 ± 3.4 h and total distance travelled during a foraging trip was 164 ± 73 km, with no sex- or year-related differences. Masked boobies mainly caught flying fish, but their diet also included one squid and six other fish families. In contrast to previously reported changes in foraging ecology of seabirds, masked boobies at Clarion Island seemed to be unaffected during El Niño, because the local oceanography was relatively unperturbed by ENSO oscillations.

3.2. Introduction

The El Niño-Southern Oscillation (ENSO) is a dominant driver of inter-annual variabilities in the physical and biogeochemical states in the Pacific. Its warm phase, El Niño, is perhaps the most important climatic anomaly in the Eastern Tropical Pacific (McPhaden *et al.* 2006, DiLorenzo & Miller 2017), causing wide-scale ecological disturbances in the region (DiLorenzo & Miller 2017). The intensity and frequency of El Niño events are currently increasing as a result of human-accelerated climate change (Walther *et al.* 2002, Cai *et al.* 2014) and are unlikely to be accounted for solely by natural variability (Trenberth & Hoar 1997). Increases in the frequency of El Niño events are predicted to lead to decreased ocean productivity, altered food web dynamics, and shifts in species distributions (Walther *et al.* 2002, Hoegh-Guldberg & Bruno 2010, DiLorenzo & Miller 2017). Changes in the availability and distribution of fish species may impact the prey availability for top predators like seabirds, with consequences for their behavior, physiology, and demography (Vargas *et al.* 2006, Grémillet & Boulinier 2009, Oro 2014, Champagnon *et al.* 2018). Seabirds are currently the most threatened group of birds (Croxall *et al.* 2012) and conservation actions that anticipate the effects of climate change on their populations are required (Monahan & Fisichelli 2014). However, predicting the effects of global warming on seabirds is

complicated by gaps in knowledge for many remote tropical regions (Oro 2014), and there is thus a need for local studies to obtain information on the reactions of seabird species to local and wide-scale environmental oscillations (Jenouvrier 2013, Oro 2014).

Seabirds may respond to changes in availability of their main prey by switching the targeted prey species (Ancona *et al.* 2012) and adjusting their foraging behavior (Harding *et al.* 2007, Elliott *et al.* 2008, Castillo-Guerrero *et al.* 2016). During periods of lower productivity, which affect prey abundance, seabirds may forage further and for longer periods (Burger & Piatt 1990, Harding *et al.* 2007) and switch prey species and size (Burger & Piatt 1990, Croxall *et al.* 1999). Seabird species differ in terms of their behavioral plasticity (Gilmour *et al.* 2018), and although relatively plastic species continue to breed during El Niño events, less-plastic species may experience dramatic population collapses (Ribic & Ainley 1997, Quillfeldt & Masello 2013, DiLorenzo & Miller 2017, Wingfield *et al.* 2018). Masked boobies represent an ideal species for documenting the effects of El Niño events in a tropical marine predator. This species is large enough to carry tracking devices, continues breeding even during El Niño events (Nelson 1978), and individuals may adjust their foraging movements and prey items according to availability (Nelson 1978, Sommerfeld *et al.* 2015).

Notably, masked boobies are sexually size dimorphic, with females being 16% heavier and 2% larger than males (Sommerfeld *et al.* 2013). Some seabird species with size dimorphism have shown sex-specific foraging strategies during periods of reduced food availability (Ishikawa & Watanuki 2002). However, previous studies of masked boobies found no evidence of sex differences in foraging parameters (Weimerskirch *et al.* 2009b, Young *et al.* 2010b, Kappes *et al.* 2011, Oppel *et al.* 2015, Poli *et al.* 2017), though males in some colonies had lower diving rates and dived less deeply than females (Weimerskirch *et al.* 2009b, Sommerfeld *et al.* 2013). Foraging segregation between sexes may occur only under specific circumstances, e.g. when environmental conditions are poor and food becomes scarce (Castillo-Guerrero & Mellink 2011, Paiva *et al.* 2017, Miller *et al.* 2018). It is therefore important to explore the influence of climate on the foraging ecology of both sexes in seabirds, in order to highlight demographic heterogeneities with potential consequences for population dynamics (Oro *et al.* 2010, 2018, Patrick & Weimerskirch 2014).

In this study, I obtained tracking and diving data and collected and analyzed diet samples from masked boobies in order to describe the foraging ecology of this species under different environmental regimes (in relation to ENSO phases), and to evaluate the influence of wide-scale environmental conditions on local oceanography and foraging segregation between the sexes. I hypothesized that masked boobies would forage further and for longer periods during periods of lower productivity (which affect prey abundance), and may switch prey species and size. I also considered that sexual segregation in foraging would occur during periods of lower productivity (e.g. during El Niño), whereas foraging differences between sexes would be less evident during periods of average or high productivity (e.g. neutral or La Niña years).

3.3. Methods

Data collection

Revillagigedo Archipelago is a Mexican-designated marine protected area in the Eastern Tropical Pacific Ocean (CONANP 2017, DOF 2017), and is within an area vulnerable to marine heat waves (Frölicher & Laufkötter 2018, Smale *et al.* 2019). Clarion Island is the most remote island of the archipelago, with breeding populations of several species of birds, including the ground-nesting, piscivorous masked booby. Clarion Island (18°21'7.53"N, 114°43'18.61"W), which lies 985 km west of the Mexican mainland and 710 km southwest of the Baja California peninsula, includes a breeding colony of around 100 pairs of masked boobies (Wanless *et al.* 2009, Almanza-Rodríguez 2019).

I visited Clarion Island for 30-day periods in January 2016, March 2017, and March 2018, respectively. Tracking data were collected opportunistically from incubating birds using i-gotU Loggers (i-gotU GT-120: Mobile Action, Taiwan) in 2016 (four females and four males), and CatLog-S Loggers (Catnip Technologies, Hong Kong, China) in 2017 (six females and nine males) and 2018 (eight females and ten males) (Figure 3.1). Incomplete trips (departure or return from/to the nest not registered) and gaps in the tracking data while at sea occurred in 2016 (1–82 min), 2017 (1–13 min), and 2018 (1–8 min) due to battery failure of the GPS devices. Incomplete trips were excluded from the analyses, and trips with gaps were included to estimate foraging trip parameters (Figure 3.1). The GPS devices were programmed to record time, latitude, and longitude every 1 min in 2016 and 4 min in 2017 and 2018. Twenty-one of the birds with GPS devices were also equipped with time-depth recorders (TDRs; model G5+, Cefas Technology, UK), but only six birds had identifiable dives in 2017 and one in 2018. The TDR devices were programmed to record pressure data every 1 s on 12 bits.
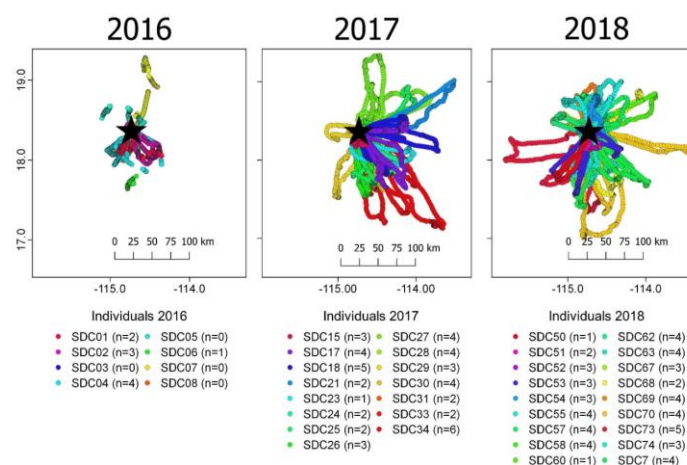
Figure 3.1. All tracking data collected in 2016, 2017, and 2018. Dots represent tracking positions, each color represents a different individual, and n indicates the number of trips completed by that individual. Star represents the colony. Incomplete trips are presented in the figure but were not included in the analyses

Individuals were captured at their nest by hand or using a hand net from a distance of 1 m. The sex of the individuals was determined by size and vocalization; females are bigger and have a rough voice, whereas males are smaller and have a high-pitched voice (Nelson 1978). The devices were attached using TESA tape on top of the three central tail feathers. The GPS devices, including the waterproof heat-shrink casing, weighed 22–30 g and the TDR devices weighed 6.5 g. The masked boobies weighed 1.4–2.6 kg, and the combined devices therefore did not exceed the recommended 3% weight threshold for attached devices (Wilson & McMahon 2006). The total handling time never exceeded 10 min to minimize distress to the birds as a result of the tagging process. Individuals were captured at night from 19:00 to 03:00 h to prevent sunstroke to the birds and to avoid potential predation of eggs and chicks by common ravens (*Corvus corax*) and snakes (*Masticophis anthonyi*). Among the 37 tracked individuals, 16 lost their eggs during the tracking period. However, the loss of eggs was not exclusive to tagged individuals: from 62 nests monitored in 2017, 14 eggs hatched and 12 of the 14 chicks died (Almanza-Rodríguez 2019).

Diet samples were collected opportunistically in 2017 and 2018 if the bird regurgitated spontaneously as a result of our presence in the colony or during tagging. The whole regurgitate was placed in an individual plastic bag and weighed, and each prey item was later removed from the bag, photographed, and identified to family level, based on Pacific fish guides (Fischer *et al.* 1995). Diet was described based on 'numerical frequency', defined as the number of items from a given prey family in relation to the total number of prey items (Alonso *et al.* 2018).

Environmental data on chlorophyll-a concentration (CHL) and sea surface temperature (SST) were downloaded from Aqua MODIS, NPP, 0.025 degrees, Pacific Ocean Lon+/-180, monthly composites, from the ERDDAP database. CHL and SST are influenced by ENSO (DiLorenzo & Miller 2017) and are considered to be good proxies for seabirds' prey availability (Kappes *et al.* 2010, Paiva *et al.* 2017). A circle of radius 180 km (maximum range of a masked booby from Clarion Island with an error threshold) was created around Clarion Island, and the CHL and SST within the circle were extracted using the function 'extract' in the R package 'raster'. Using the extracted data for CHL and SST, I calculated the mean and standard deviation for each variable within the maximum foraging range for the breeding seasons in 2016, 2017, and 2018 (Figure 3.2 and 3.3). In addition, the Oceanic Niño Index (ONI) was used to classify the year as El Niño, La Niña, or neutral.
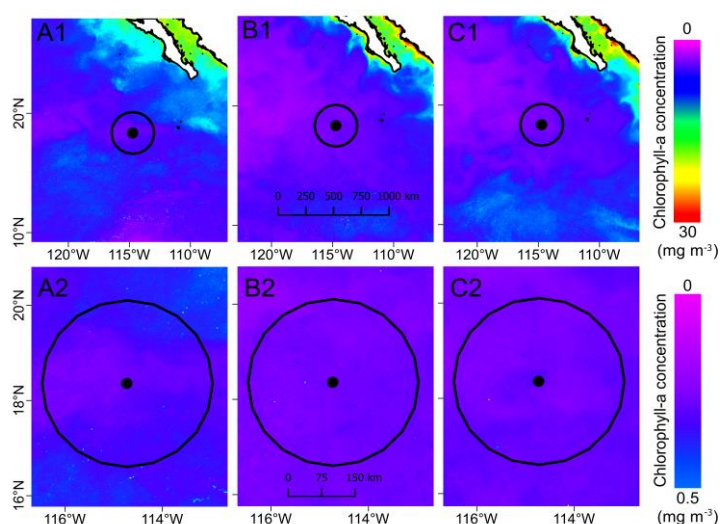
Figure 3.2. Chlorophyll-a concentration (CHL, mg m^{-3}) in the Eastern Tropical Pacific (upper panels) and at Clarion Island (lower panels) in January 2016 (A1 & A2), March 2017 (B1 & B2), and March 2018 (C1 & C2). Black dot indicates study area; circle represents area used to extract mean and standard deviation of CHL.
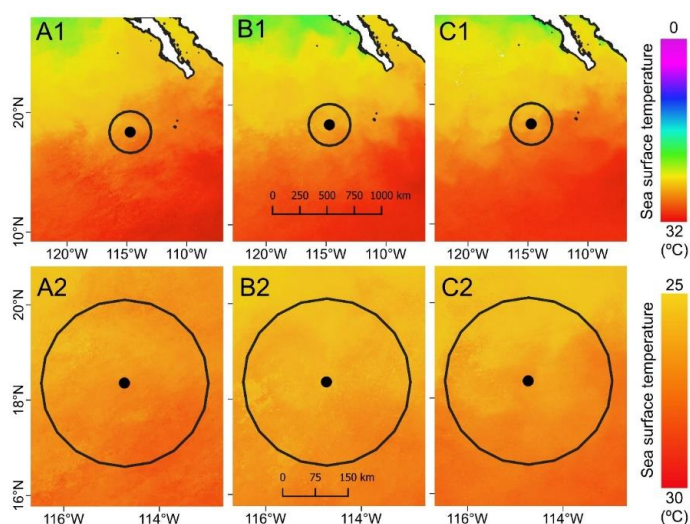
Figure 3.3. Sea surface temperature (SST, ºC) in the Eastern Tropical Pacific (upper panels) and at Clarion Island (lower panels) in January 2016 (A1 & A2), March 2017 (B1 & B2), and March 2018 (C1 & C2). Star indicates study area; circle represents area used to extract mean and standard deviation of SST.

Data processing

Tracking data were processed in R 3.6.2. GPS fixes included multiple trips from a single bird. To obtain information on the foraging parameters per individual trip, all GPS fixes were analyzed using the function 'tripsplit' in the package 'IBA'. This function calculates the maximum distance from the colony, total distance travelled, and the trip duration for each

individual trip (Lascelles *et al.* 2016). The maximum distance from the colony was measured as the most distant point in a straight line from the colony, total distance travelled was the summed distance between consecutive fixes from departure to return to the colony, and trip duration was the total time between departure and return to the colony. For the TDR data, a zero offset correction for surface drift was applied, and only dives deeper than 0.5 m were considered as true dives.

For tracking data in 2017 and 2018, foraging behavior was determined based on the speed and turning angles from successive locations during the foraging trips using a clustering algorithm (Garriga *et al.* 2016). Value delimiters of 0.18–3.14 (high turn) and 0–20 km h^{-1} (low speed) were used to identify foraging behavior and were within thresholds applied in other sulids (Mendez *et al.* 2017). Using the foraging locations, kernel estimation of the utilization distribution (UD) of core (50%) and general (95%) areas were delimited using the function 'kernelUD' in the R package 'adehabitatHR' (Calenge 2006). The reference bandwidth was used (0.10–0.13), and the Bhattacharyya coefficient (BA) was calculated. BA is a measure of similarity between two probability distributions, indicating the overlap in kernel density estimates, and can range from 0 (no overlap) to 1 (identical UD).

Statistical analyses

Inter-annual differences in CHL and SST were analyzed using one-way analysis of variance with year as factor. Differences in foraging parameters between sexes and years were analyzed using linear mixed-effect models in the R package 'nlme' with maximum distance from the colony, total distance travelled, and trip duration as response variables, respectively. Residuals were plotted against fitted values and there was no obvious deviation from the assumption of normality and homoscedasticity of residuals. Year, incubation status (maintained and losing eggs), and sex were included as fixed factors, as well as the two-way interactions year × incubation status and year × sex. All models included individual bird identity as a random factor to avoid pseudo-replication. The significance of the factors was tested by comparing models with and without interactions and fixed factors. Comparisons were made using likelihood ratio tests using the 'anova' function.

The overlap between sexes and years (2017 and 2018) was calculated by analysis of similarity (ANOSIM) with BA on the 95% and 50% UD using the R package 'vegan'. I compared the number of prey items by year and sex, respectively, using chi-square tests. Statistics were performed in R 3.6.2 and maps were produced using QGIS 3.4. The results are presented as mean ± standard deviation.

3.4. Results

The environmental conditions within the foraging range of masked boobies (< 180 km) during the 3-year study period (2016–2018) showed an average CHL concentration of 0.09 ± 0.02 mg m^{-3} and average SST of 26.3 ± 1.3 °C. Average local CHL and SST did not differ

significantly among years (CHL: $F_{1,1}$ = 2.12, P = 0.38, SST: $F_{1,1}$ = 0.61, P = 0.58) (Figure 3.2 and 3.3). Based on the ONI, January 2016 was an El Niño phase (ONI 2.5), March 2017 was El Niño-neutral (ONI 0.1), and March 2018 was a La Niña phase (ONI −0.6) (Figure 3.4). During the three tracking periods, the mean SST was 25 °C and the mean CHLs were 0.10 and 0.09 mg m^{-3} during January and March, respectively. The conditions within the foraging range of the masked boobies thus remained stable and did not coincide with the expected ENSO conditions.
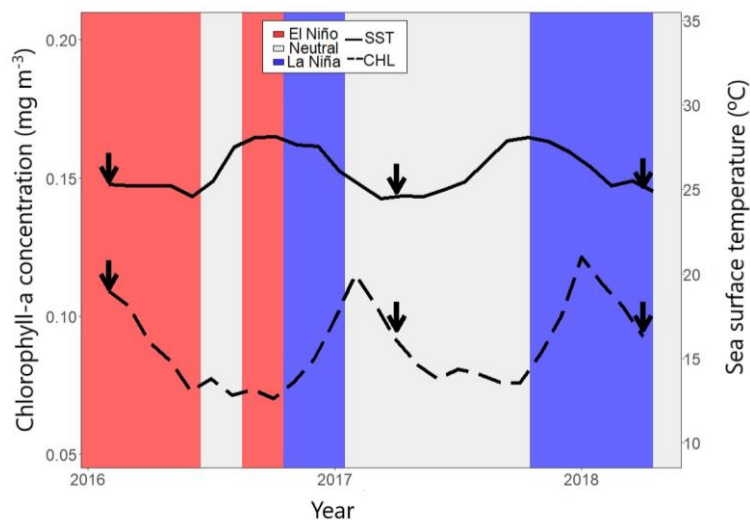
Figure 3.4. Time series of monthly mean chlorophyll-a concentration (CHL, dashed) and sea surface temperature (SST, line) within the maximum foraging range (180 km) for masked boobies from January 2016 to April 2018. Background corresponds to the Oceanic Niño Index (ONI), which classifies conditions as El Niño (index ≥ +0.5, indicating that the East-Central Tropical Pacific is warmer than usual), La Niña (index ≤ −0.5, indicating that the region is colder than usual), and El Niño-neutral (index −0.5 to +0.5). Arrows indicate tracking periods in January 2016, March 2017, and March 2018

Tracked birds were observed during the tagging period of 4 days and no individual showed signs of discomfort associated with the devices, such as frequent touching the device or increased preening activities. I obtained 115 tracks from the 37 birds leaving the island to go to sea. There were no significant differences in foraging trip parameters among birds in relation to incubation status (maintaining or losing the egg), sex, or the three tracking periods (January 2016, March 2017, and March 2018) (Figure 3.5) and there were no significant interactions between the factors (Table 3.1). The areas used for foraging by masked boobies were similar between sexes and years (2017 and 2018) (BA range at 50% UD: 0.11–0.99, ANOSIM R = -0.15, P = 0.96; BA range at 95% UD: 0.10–0.99, ANOSIM R = -0.16, P = 0.95).
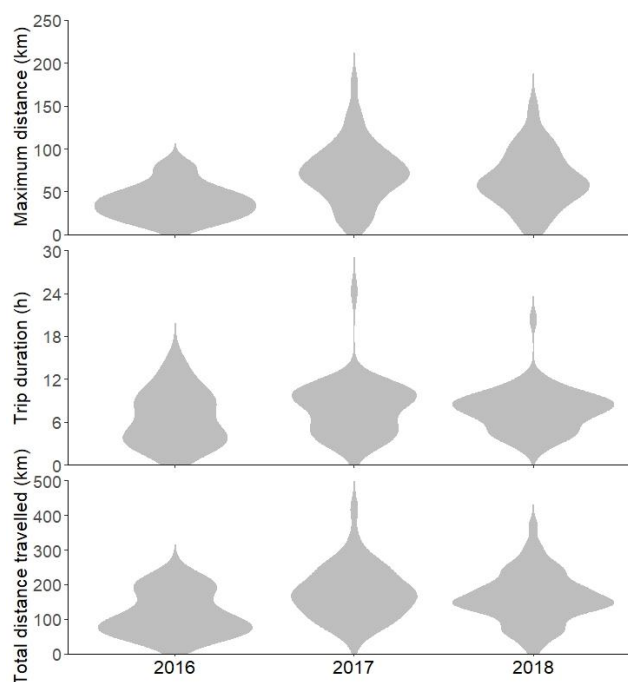
Figure 3.5. Foraging trip parameters of masked boobies at Clarion Island during the breeding seasons in 2016 (birds = 4, trips = 10), 2017 (birds = 15, trips = 47), and 2018 (birds = 18, trips = 58).

Table 3.1 Effects of year (2016, 2017, and 2018), sex (female and male), incubation status (keeping or losing egg), and their interactions on foraging trip parameters in masked boobies at Clarion Island, based on linear mixed-effect models with individual as random intercept

		Maximum distance	Trip duration	Total distance travelled
Year	$F_{1,4}$	0.49	0.04	0.32
	P	0.49	0.84	0.57
Sex	$F_{1,5}$	1.62	2.22	1.60
	P	0.20	0.14	0.21
Incubation status	$F_{1,6}$	2.66	< 0.01	2.09
	P	0.10	0.97	0.15
Sex × year	$F_{1,7}$	0.79	1.25	0.26
	P	0.37	0.26	0.61
Year × incubation status	$F_{1,7}$	1.16	2.62	1.27
	P	0.27	0.11	0.26

Of the 18 diving devices deployed on individuals in 2017 and the three in 2018, only seven recorded identifiable dives, while the other devices had no clear dives or showed large pressure variations that prevented the identification of dives. Among all dives, 66% lasted ≤ 3 s and 82% were ≤ 2 m depth. The deepest dive was 5.5 m and the longest 13 s. No statistical comparisons of diving parameters were possible due to the limited number of recorded dives.

Regurgitates from 25 individuals in 2017 (14 females and 11 males) and from 31 individuals in 2018 (14 females and 17 males) were collected, comprising 186 individual prey items. The numerically dominant prey family for both female and male masked boobies in 2017 and 2018 was flying fish (Figure 3.6). Regurgitates contained an average of 3.5 ± 2.1 prey items (range 1–13 items) from 1–3 families. The prey items in the diet were homogeneous between years ($\chi^2_7 = 4.96$, P = 0.66) and sexes ($\chi^2_7 = 2.96$, P = 0.89).
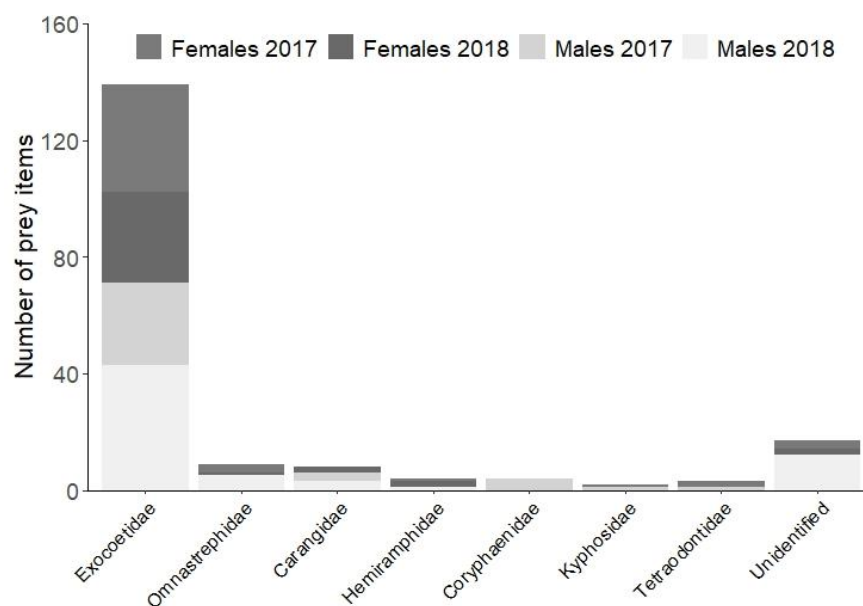
Figure 3.6. Prey families in regurgitates from masked boobies collected at Clarion Island in 2017 (14 females, 11 males) and 2018 (14 females, 17 males). Families identified in the regurgitates included Exocoetidae (flying fish), Omnastrephidae (squid), Carangidae (jacks), Hemiramphidae (halfbeaks), Coryphaenidae (dolphinfish), Kyphosidae (sea chub), and Tetraodontidae (pufferfish).

3.5. Discussion

Despite the limited number of samples, this study provides novel evidence for the foraging ecology of masked boobies at Clarion Island during consecutive years. I expected that masked boobies would show different foraging strategies in response to changes in the availability and distribution of their food resources; however, despite these assumptions, no significant ENSO effects were detected at Clarion Island.

Peaks in CHL and lower SST in the first trimester of the year mirrored the peaks from the California Current (Lluch-Cota 2000, Valencia-Gasti *et al.* 2015) and demonstrated the influence of this current at Clarion Island. However, the CHL peaks in the coastal part of the California Current reached 1.8 mg m^{-3} (Lluch-Cota 2000), compared with a maximum of only 0.1 mg m^{-3} in the present study. The low influence of the California Current may be caused by the distance between Clarion Island and the coastal upwelling resulting in a weakened effect on productivity, such that the island maintains low-productivity waters that are less susceptible to ENSO-related environmental oscillations. The unusual environmental stability around Clarion Island, with no major inter-annual variations, may thus maintain stable local availability of the main prey species of masked boobies between ENSO phases, which may explain the consistent foraging parameters of masked boobies across years.

El Niño affects the abundance and distribution of fish species that depend on upwelling, such as anchovies and sardines (Velarde *et al.* 2004, Ancona *et al.* 2012, Quillfeldt & Masello 2013, Champagnon *et al.* 2018), and is thus especially challenging for seabirds adapted to prey on these small pelagic species. Nazca boobies (*Sula granti*) and blue-footed boobies (*Sula nebouxii*) in the Galapagos were reported to be affected by El Niño (Anderson 1989), probably because they depend on fish species such as anchovies, herring, and sardines (Ancona *et al.* 2012, Tompkins *et al.* 2017). In contrast, red-footed boobies (*Sula sula*) and frigatebirds (*Fregata minor*), which prey on flying fish and squid (Schreiber & Hensley 1976, Young *et al.* 2010a), remained unaffected during El Niño (Anderson 1989), suggesting that El Niño may not represent an additional pressure for seabird species in low-productivity warm waters, such as masked boobies, that prey on flying fish. This may also help to explain why seabirds inhabiting higher productivity areas are more severely affected by El Niño than those in low-productivity areas (Ribic & Ainley 1997, Quillfeldt & Masello 2013, DiLorenzo & Miller 2017). Masked boobies in the current study inhabited a low-productivity area and preyed mainly on flying fish and squid, which may show increased abundances in warm and low-productivity waters (Lluch-Belda *et al.* 2014, Churnside *et al.* 2017, Doubleday & Connell 2018).

Consistent with previous studies on masked boobies, I found no significant difference between females and males in terms of maximum distance from the colony, trip duration, or total distance travelled (Weimerskirch *et al.* 2009b, Young *et al.* 2010b, Kappes *et al.* 2011, Oppel *et al.* 2015, Poli *et al.* 2017). Some previous studies found differences between the sexes in relation to diving depths and rates (Weimerskirch *et al.* 2009b, Sommerfeld *et al.* 2013); however, although previous studies reported no problems with detecting and analyzing dives for masked boobies (Sommerfeld *et al.* 2015), our current devices failed to record enough diving events for statistical analysis. The failure of the devices to record the diving behavior of masked boobies could be because the birds were catching their prey on the wing, when subsurface predators flush flying fish or squid to the surface or out of the water (Davenport 1994, Muramatsu *et al.* 2013). Masked boobies are likely to catch prey on the wing because they form associations with tuna species during foraging (Au & Pitman 1986), and albacore (*Thunnus alalunga*), yellow-fin (*T. albacares*), and bigeye (*T. obesus*) tuna,

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some of which also consume flying fish (Lacerda *et al.* 2017, Chagnon *et al.* 2018, Lewallen *et al.* 2018), all occur in the waters surrounding the Revillagigedo Archipelago. I recommend using accelerometers (Sommerfeld *et al.* 2015) or videography (Machovsky Capuska *et al.* 2011) in future studies to investigate the diving behavior of masked boobies.

Foraging trip parameters from tracked birds that lost their eggs and remained to defend their territory/sit on their nest were similar to those for birds that kept their eggs. Losing eggs may influence the bird's behavior at sea, because non-breeding boobies move over larger distances than breeding boobies (Kohno *et al.* 2019). However, considering that masked boobies may lay second clutches within a period of 28–83 days (Priddel *et al.* 2005), tracked masked boobies that lost their eggs did not modify their foraging behavior because they may continue to be tied to the nest site. An alternative explanation is that non-breeding seabirds presumably disperse in response to changes in food availability and prevailing local conditions (Dingle & Drake 2007, Newton 2012), and there were no dramatic changes in the prevailing local conditions at Clarion Island. Thus, breeding and non-breeding birds may share foraging grounds year-round, due to the local environmental stability at Clarion Island.

It is necessary to apply caution when interpreting the current results, given that some sex-related foraging differences may have been overlooked. However, the present findings suggest that females and males from Clarion Island did not differ, at least in terms of the foraging parameters measured in the present study. Although there were some differences in prey species included in the diet between years and sexes, flying fish were consistently the main prey item for both sexes and in both years. Moreover, the maximum distance from the colony (177 km) travelled by masked boobies from Clarion Island was shorter than that travelled by masked boobies from Clipperton (245 km) (Weimerskirch *et al.* 2009b), Phillip Island (231 km) (Sommerfeld *et al.* 2013), and Isla Muertos (232 km) (Poli *et al.* 2017). Masked boobies from less-densely populated colonies forage closer to the colony due to reduced intra-specific competition (Oppel *et al.* 2015). The small colony size (100 breeding pairs) and apparently stable prey availability at Clarion Island were thus associated with low levels of competition, and a consequent lack of sexual foraging segregation.

Although there were no clear effects of ENSO on the local oceanography and foraging behavior of masked boobies at Clarion Island, detailed information on foraging behavior taking account of dynamic oceanographic features such as currents and fronts (Spear *et al.* 2001, Cox *et al.* 2016, Poli *et al.* 2017), and with a larger sample size are needed. Moreover, the lack of response of masked boobies to El Niño does not mean that this seabird may not suffer from its consequences in other respects or at other colonies. Long-lived species such as masked boobies are expected to prioritize their own survival and future fecundity over individual breeding events (Drent & Daan 1980), and although El Niño may have no obvious effect in terms of their foraging behavior, it may have unseen impacts on their breeding participation or reproductive success (Dorward 1962, Priddel *et al.* 2005). Brown boobies (*Sula leucogaster*) ceased breeding at Isla San Jorge (Mellink 2003) and experienced reproductive failure and adult mortality at Christmas Island (Schreiber & Schreiber 1989) in response to El Niño, whereas there was no evidence of any survival effects on brown boobies

at Johnston Atoll (Beadell *et al.* 2003). Different effects on seabird behavior, physiology, and demography among colonies are likely to be related to the different local oceanographic conditions of the islands.

3.6. Conclusions

Contrary to my hypothesis, masked boobies did not travel further from their colony, or switch their prey items between sexes and years. The tropical pelagic ecosystem at Clarion Island remained environmentally stable, which may explain why the foraging ecology of masked boobies did not differ between years. The waters around Clarion Island did not follow the general ENSO-related patterns, showing that the general area around Clarion Island is less influenced by upwelling processes compared with coastal or other pelagic areas, where the effects are more dramatic. The similar foraging parameters of female and male masked boobies likely reflected low competition for food resources. I acknowledge that these conclusions are based on a limited number of samples and that further long-term studies should be carried out to investigate the effects of ENSO on integrated aspects of breeding and at additional colonies. Nevertheless, these results provide novel information on the foraging ecology of a seabird in the Eastern Tropical Pacific, which appears to be unaffected by ENSO phases.

CHAPTER 4.

4. Do masked boobies breeding within the oligotrophic gyre show sex-related differences in foraging ecology?

4.1. Abstract

Sexual segregation of foraging occurs in some species and populations of boobies (Sulidae), but it is not a general pattern. Sexual segregation in boobies may be an effect of food competition due to breeding stage pressures or to variations in food resources between locations. In this study, I examined sex-related foraging segregation in relation to breeding stage in masked boobies within the oligotrophic South Pacific Gyre. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of whole blood samples was carried out in four female and six male incubating masked boobies, and four female and six male chick-rearing birds. Nineteen of these birds were also tracked using GPS recorders and a total of 11 regurgitate samples were collected opportunistically. There were sex-related differences in whole blood stable isotope signatures: $\delta^{13}C$ levels in the blood were significantly less depleted in female than in male masked boobies, particularly during incubation. $\delta^{15}N$ blood levels were higher in females than males, regardless of the breeding stage. However, there were no differences in foraging trip parameters or diet between females and males. Both sexes traveled further and for longer while incubating than while rearing chicks. These results suggest that there are no sex-related differences in foraging trip parameters in masked boobies. The differences in $\delta^{15}N$ and $\delta^{13}C$ signatures between females and males may be caused by inconspicuous differences in foraging behaviors or by differences in body conditions linked to breeding.

4.2. Introduction

Sexual segregation is a widespread behavioral and ecological phenomenon among animal taxa (Wearmouth & Sims 2008). In many birds species, females and males differ in terms of their spatio-temporal distribution, at-sea behavior, and feeding ecology (Catry *et al.* 2005). Among boobies (*Sula* spp.), females are persistently larger than males (Nelson 1978), and this notable reversed sexual size dimorphism has frequently been associated with differences in foraging behavior and diet within this taxonomic group. Sex-related foraging differences in boobies may involve the use of different areas for foraging (Weimerskirch *et al.* 2006, Stauss *et al.* 2012), or different diving depths (Lewis *et al.* 2002, Weimerskirch *et al.* 2006, Zavalaga *et al.* 2007), diets (Zavalaga *et al.* 2007, Miller *et al.* 2018), or trophic levels (Young *et al.* 2010b, González-Medina *et al.* 2017).

However, contrasting results have been found within the Sulidae, making it difficult to interpret the persistence of sex-related patterns in foraging ecology among boobies. For example, female brown boobies (*Sula leucogaster*) foraged further from their colonies than males at Clipperton Island and at Raine Island (Gilardi 1992, Miller *et al.* 2018), while no sexual differences were noted in the same species foraging in the Gulf of California (Castillo-Guerrero *et al.* 2016). Similarly, no sex-related foraging differences were found in other

boobies, including red-footed (*Sula sula*) (Lewis *et al.* 2005), Abbott's (*Sula abbotti*) (Hennicke & Weimerskirch 2014), and Peruvian boobies (*Sula variegata*) (Weimerskirch *et al.* 2012), and in most colonies of masked boobies (*Sula dactylatra*) (Kappes *et al.* 2011, Oppel *et al.* 2015, Machovsky-Capuska *et al.* 2016, Poli *et al.* 2017).

Likewise, female and male brown boobies (Young *et al.* 2010b) and blue-footed boobies (Young *et al.* 2010b, González-Medina *et al.* 2017) had different δ^{13}C and δ^{15}N signatures, whereas no sexual differences in isotope levels were found in red-footed (Young *et al.* 2010b), blue-footed (Weimerskirch *et al.* 2009b), brown (Weimerskirch *et al.* 2009b, Navarro *et al.* 2014), or masked boobies (Young *et al.* 2010b, Mancini *et al.* 2013). These contrasting results in terms of foraging ecology among species and colonies of boobies suggest that sexual differences in foraging are flexible and might reflect local food abundance and availability.

It is possible that lower food availability might promote foraging segregation between sexes, while normal or high food availability might reduce such differences (Ishikawa & Watanuki 2002). However, the apparently conflicting results regarding foraging segregation in masked boobies may also be a consequence of the fact that previous work has focused mainly on detecting sex-related foraging differences either during incubation or during chick rearing, without considering possible interactions between sex and breeding stage. In seabirds, the switch from incubating to chick provisioning triggers pronounced changes in foraging behavior (Hipfner *et al.* 2013, Navarro *et al.* 2014), and seabirds rearing chicks may perform short trips to assure a regular food load to prevent reduced chick growth (Shoji *et al.* 2015), whereas incubating seabirds are free to forage further. Sexual differences during discrete breeding stages have been reported in various tropical seabirds in the Mozambique Channel (Cherel *et al.* 2008), at Christmas Island (Navarro *et al.* 2014), and even in temperate seabirds such as northern gannets (*Morus bassanus*) (Ismar *et al.* 2017). Sex-related foraging differences may therefore be an effect of constraints imposed by breeding, in interaction with local food availability.

Understanding the differences between sexes during different stages of breeding is important, because dissimilarities in fitness or survival rates caused by differential exposure of males and females to different conditions or threats may lead to an imbalanced sex ratio, with population dynamic consequences (Phillips *et al.* 2005, Harrison *et al.* 2011, García-Tarrasón *et al.* 2015, Gianuca *et al.* 2019). Furthermore, understanding the persistence of foraging behaviors among members of a population improves the ability to manage areas in relation to seabird life stages (Oppel *et al.* 2018).

Masked boobies are an ideal species to test for the effects of sex and breeding stage on foraging and diet in an environment with little food resources. Females and males are easy to differentiate: females are bigger and have a rough voice, whereas males are smaller and have a high-pitched voice (Nelson 1978, Sommerfeld *et al.* 2013). In contrast with most temperate areas, where breeding occurs synchronously (Hamer *et al.* 2002), masked boobies may breed throughout the year (Marin & Caceres 2010, Flores *et al.* 2014), offering a unique opportunity

to study foraging behavior and diet of incubating and chick-rearing birds simultaneously. Masked boobies breed in an area of low productivity in the South Pacific Gyre (Morel *et al.* 2010, Reintjes *et al.* 2019), which allows the occurrence of sexual foraging differences under food pressure to be tested. The current study used tracking technology and stable isotope analyses to test the hypothesis that masked boobies display sex-related foraging differences in a seascape with limited food resources, and that these sex-related foraging differences are related to constraints imposed by breeding. I expected females to travel further from the colony (Miller *et al.* 2018), dive deeper due to their larger size (Sommerfeld *et al.* 2013), and consequently have different isotopic signatures in their blood compared with males. I also considered that sexual segregation in foraging would occur during periods of increased breeding demands (e.g. during chick rearing), whereas foraging differences between sexes would be less evident during incubation.

4.3. Methods

Data collection

Rapa Nui (also known as Easter Island) is located in the middle of the South Pacific Gyre. The South Pacific gyre has oligotrophic waters characterized by low zooplankton biomass and low nutrient concentrations (Reid *et al.* 1978, Moraga *et al.* 1999, Reintjes *et al.* 2019), which are often associated with low food resources (Longhurst & Pauly 1987). The fish fauna of Rapa Nui is considered to be extremely impoverished, but with a similar abundance and biomass of fish compared with analogous isolated, high-latitude islands (Randall & Cea 2010, Friedlander *et al.* 2013). Masked boobies at Rapa Nui breed on Motu Nui (109.4° W, 21.2°S), a small (3.9 ha) rock islet located in the southwest of Rapa Nui. The masked booby colony consisted of 56 breeding pairs in 2016, including 32 incubating and 24 chick-rearing pairs.

Fieldwork consisted of 4-day visits twice a month between October and November 2016. Random nests containing incubating and chick-rearing individuals were selected and studied simultaneously. Included nests contained one or two eggs, or one chick. The chicks from tagged birds were covered with down and weighed 0.4–2.1 kg, giving an estimated chick age of 1–8 weeks (Priddel *et al.* 2005). Individuals were captured at their nests by hand or using a hand-net from a distance of 1 m to deploy the tracking devices. Devices (see below) were attached to the three central rectrix feathers using TESA tape, and retrieved after 4–6 days. During manipulation, the individuals were weighed, measured and the sex was determined by size and vocalizations. The total manipulation time did not exceed 10 min.

GPS loggers (model: CatLog-S, weight: 26 gr, dimensions: 3.7 x 2.2 x 0.8 cm) and time-depth recorders (TDRs; model G5+, weight: 6.5 gr, Cefas Technology, UK) were deployed to record foraging trip parameters. The GPS loggers recorded time, latitude, and longitude every 4 min and the TDR devices were programmed to record pressure data every 1 s. Masked boobies weighed 1.6–2.6 kg, and the weight of the devices was thus below the 3% acceptable body mass threshold for seabirds (Vandenabeele *et al.* 2012). Tracking and diving data were processed in R 3.5.2. Foraging trip parameters of trip duration, maximum distance

from the colony, and total distance were obtained using the function "tripsplit" in the package "marine IBA" (Lascelles *et al.* 2016). The maximum foraging trip distance was measured as the most distant point in a straight line from the colony. Trip duration was the total time between departure and return to the colony. Total distance travelled was the sum of the distance between consecutive fixes from departure to return to the colony. Foraging trips were considered as soon as the bird left a 1.5 km radius from the colony, because flying fish were observed leaving the water and masked boobies were seen foraging in the vicinity of the colony. Regarding the TDR data, a zero offset correction for surface drift was applied, and only dives deeper than 0.5 m were considered as true dives to account for noise on the recordings.

Habitat use was quantified using the function 'kernelUD' in the R package 'adehabitatHR' based on the GPS locations (Calenge 2006). Kernel estimations of the utilization distribution (UD) in the core (50%) and wider (95%) areas were delimited using the reference bandwidth (0.10–0.13). The Bhattacharyya coefficient (BA) was used to calculate the overlap in areas used according to sex and breeding stage. BA is a measure of similarity between two probability distributions, which gives the overlap in kernel density estimates and can range from 0 (no overlap) to 1 (identical UD). This method has been proved to be useful for detecting spatial overlap in seabirds (Winner *et al.* 2018, Dehnhard *et al.* 2019).

Diet samples were collected opportunistically from masked boobies that regurgitated spontaneously in response to our presence in the colony or during tagging efforts. A total of 11 regurgitated samples were collected (Table 4.1). Fish and squid were identified to family level using a Pacific fish guide (Fischer *et al.* 1995) and a site-specific fish guide (Randall & Cea 2010). The number of times that a given prey family occurred in relation to the total number of items was presented as the 'numerical frequency' (Alonso *et al.* 2018).

Table 4.1. Sample sizes of female and male masked boobies at Rapa Nui during the incubation and chick-rearing periods

	Incubation		Chick-rearing	
	Female	Male	Female	Male
Stable isotope whole blood samples	4	6	4	6
GPS deployment	4	6	3	6
TDR deployment	3	3	2	4
Regurgitates	4	3	1	3

Whole blood samples were collected from the brachial vein of individual birds during device recovery, using a 25 G needle and non-coated capillary tubes (Table 4.1). The samples were placed on glass microscope slides and transported to the lab (Bugoni *et al.* 2008). Dry whole blood samples (0.2–0.6 mg) from masked boobies were scraped from the slides and placed in tin cups. The isotope signatures of all the samples were analyzed at a single facility in the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. The values were

expressed in delta notation as the deviation from international standards (in air nitrogen for nitrogen and V-PDB for carbon) according to the equation $\delta X = [(R_{sample}/R_{standar})-1] \times 1000$, where X is ^{13}C or ^{15}N and R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. $\delta^{13}C$ levels indicated the foraging regions and feeding preferences, because $\delta^{13}C$ is enriched in inshore compared with offshore food webs (Cherel & Hobson 2007) and may reflect differences between plankton and benthic primary productions (Hobson *et al.* 1994). $\delta^{15}N$ provided a useful proxy for determining the trophic position of the organism (Bearhop *et al.* 2004, Inger & Bearhop 2008), because levels increase by 3 ‰–5 ‰ with each successive trophic level (DeNiro & Epstein 1981, Hobson & Clark 1992).

To confirm the low productivity of the waters surrounding Rapa Nui, data on chlorophyll-a concentration (CHL) and sea-surface temperature (SST) were downloaded from ERDAAP from November 2016 with a resolution of 0.025 ° (approx. 2.5 km) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor carried onboard NASA's Aqua satellite. Average environmental conditions were extracted using the raster data for CHL and SST within radii of 50 km (core) and 100 km (wider area), using the function 'extract' in the R package 'raster'. CHL and SST have been proven to be good proxies for seabird prey availability (Kappes *et al.* 2010, Paiva *et al.* 2010).

Statistical analyses

The degree of sexual dimorphism among Sulids differs (Nelson 1978), and sexual size dimorphism between female and male masked boobies at Rapa Nui was therefore calculated by analysis of variance (ANOVA) using body mass or wing length as dependent variables, and sex, breeding stage, and their interaction as factors.

Foraging trip parameters were examined using linear mixed-effects models with foraging and diving parameters (maximum foraging range, trip duration, total distance travelled, dive depth, and dive duration) as dependent variables, sex, breeding stage, and their interaction as fixed factors, body mass as a covariate to account for differences in mass among the individuals (Weimerskirch *et al.* 2009b, Sommerfeld *et al.* 2013), and bird ID as a random factor to account for pseudo-replication. The models were fitted using the 'lme' function in the R package 'nlme'. An analysis of similarity (ANOSIM) was run to test if similar areas were used by both sexes and breeding stages, with the BA using the R package 'vegan'.

Isotope levels were examined by ANOVA with the isotopic values ($\delta^{15}N$ and $\delta^{13}C$) as dependent variables, and sex, breeding stage, and their interaction as fixed factors. Regression analysis was performed to determine the effect of body mass on the isotopic values in females and males separately, but the difference was not significant ($P > 0.05$) and they were therefore not included in the model. Prey composition in the diet was compared between sexes and breeding stages, respectively, using χ^2 tests. The results are given as mean ± standard deviation.

4.4. Results

Mean body mass differed significantly between females and males, particularly during chick-rearing ($F_{1,14} = 5.36$, P = 0.03). Females were on average 21% heavier than males during chick rearing and 9% heavier during incubation (Figure 4.1). Although females were on average 1.7% larger in terms of wing length (females 46.7 ± 1.1 cm, males 45.9 ± 1.3 cm), there was no significant difference in wing length between sexes ($F_{1,15} = 1.64$, P = 0.22), breeding stages ($F_{1,15} = 0.34$, P = 0.57), or their interaction ($F_{1,15} = 0.04$, P = 0.85).
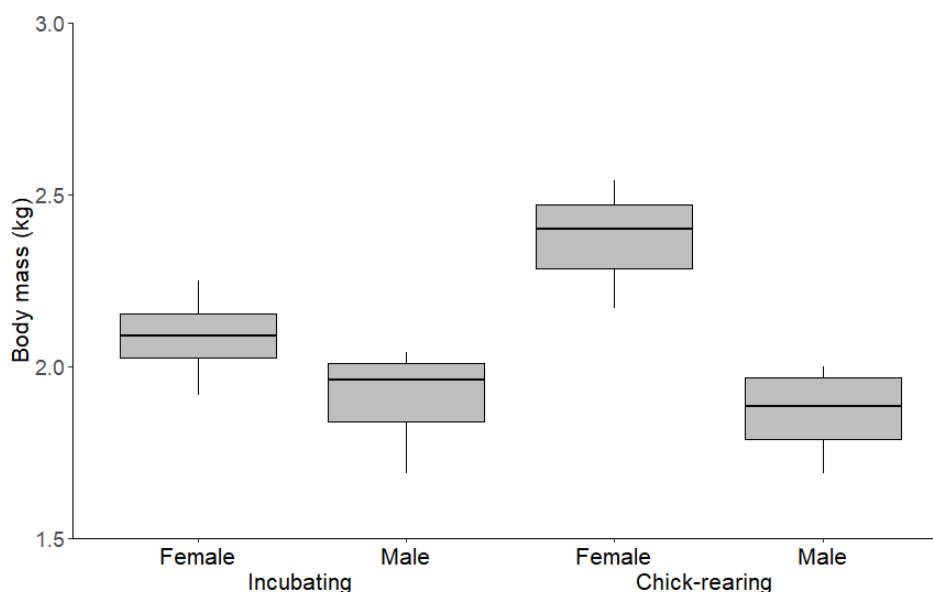
Figure 4.1. Body masses of female and male masked boobies during incubation and chick-rearing at Rapa Nui.

The average CHL was 0.02 ± 0.01 mg m^{-3} and average SST was 22.2 ± 0.3 °C in both the core (50 km) and wider (100 km) areas. A total of 34 trips were recorded from incubating birds (12 trips from 4 females, 22 trips from 6 males) and 61 from chick-rearing birds (16 trips from 3 females, 45 trips from 6 males) (Figure 4.2).

Foraging trip parameters differed significantly between breeding stages but not between sexes, and the interaction was not significant (Table 4.2). On average, birds travelled 46% further and 52% longer during incubation than during chick rearing (maximum distance from the colony, 42.3 ± 31.4 km vs 29.8 ± 22.0 km; trip duration, 4.5 ± 2.9 h vs 2.9 ± 2.1 h, respectively) (Figure 4.3). However, there were no significant differences in the areas used between and within females and males during the incubation and chick-rearing periods (50% UD BA: 0.09–0.99, ANOSIM R = −0.17, P = 0.94; 95%UD BA: 0.09–0.99 ANOSIM R = −0.17, P = 0.97).
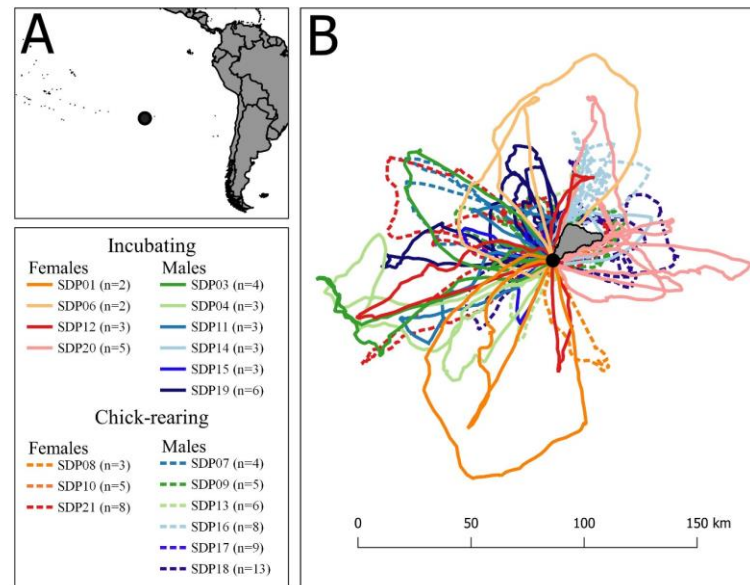
Figure 4.2. Rapa Nui location in the Pacific Ocean (A). GPS tracking data (B) for female and male masked boobies during incubation and chick rearing at Rapa Nui. Black dot shows location of masked booby colony.

Based on the recorded dives during incubation (3 females, 3 males) and chick rearing (2 females, 4 males), there were no significant differences in diving depth and duration (Table 4.2). Body mass did not correlate with diving depth in females ($r^2 = 0.26$, $P = 0.08$) or males ($r^2 = 0.05$, $P = 0.31$). The mean dive depth was 1.78 ± 1.1 m and the mean duration was 2.8 ± 1.5 s.

Table 4.2. Analyses of sex, breeding stage, and their interaction on foraging and diving parameters in masked boobies at Rapa Nui

Parameter	df	Interaction		Sex		Stage	
		F	P	F	P	F	P
Maximum distance	14	0.67	0.42	1.29	0.28	12.62	< 0.01
Trip duration	14	0.03	0.87	1.32	0.27	11.95	< 0.01
Total distance	14	0.42	0.53	1.36	0.26	13.57	< 0.01
Diving depth	8	0.35	0.57	1.42	0.27	0.66	0.44
Diving duration	8	0.46	0.51	5.01	0.06	0.15	0.70

$\delta^{13}C$ levels in the blood were significantly higher in female than in male masked boobies, particularly during incubation ($F_{1,16} = 5.86$, P = 0.03) (Figure 4.3). $\delta^{13}C$ levels were not significant different between females and males ($F_{1,16} = 3.23$, P = 0.09) and breeding stage ($F_{1,16} = 0.19$, P = 0.66). $\delta^{15}N$ levels were higher in females than in males ($F_{1,16} = 8.99$, P < 0.01) (Figure 4.3), regardless of breeding stage ($F_{1,16} = 0.35$, P = 0.56) or the interaction ($F_{1,16} < 01$, P = 0.92).
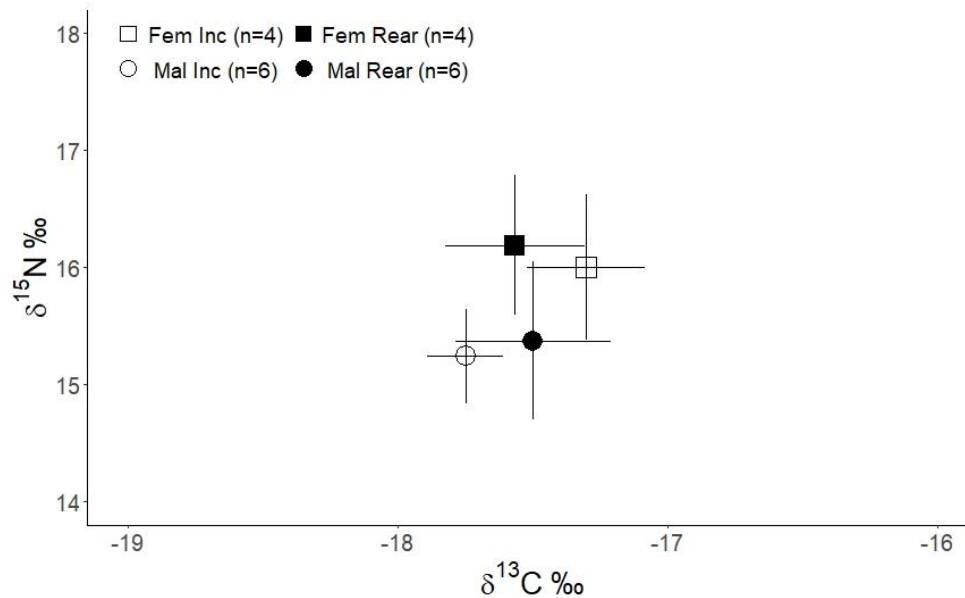
Figure 4.3. Sex-specific blood isotope levels ($\delta^{13}C$ & $\delta^{15}N$) in incubating and chick-rearing masked boobies at Rapa Nui. Shown as mean ± standard deviation.

The main prey item in regurgitates from masked boobies was flying fish (Figure 4.4). Anchovies only occurred in the diet of incubating birds, and sardines only in chick-rearing birds. The females' diet included jacks, while males included sardines, dolphinfish, and halfbeaks (Figure 4.4). Nevertheless, the prey items were homogeneous between the sexes ($\chi^2_8 = 4.67$, P = 0.79) and breeding stages ($\chi^2_8 = 6.00$, P = 0.64).
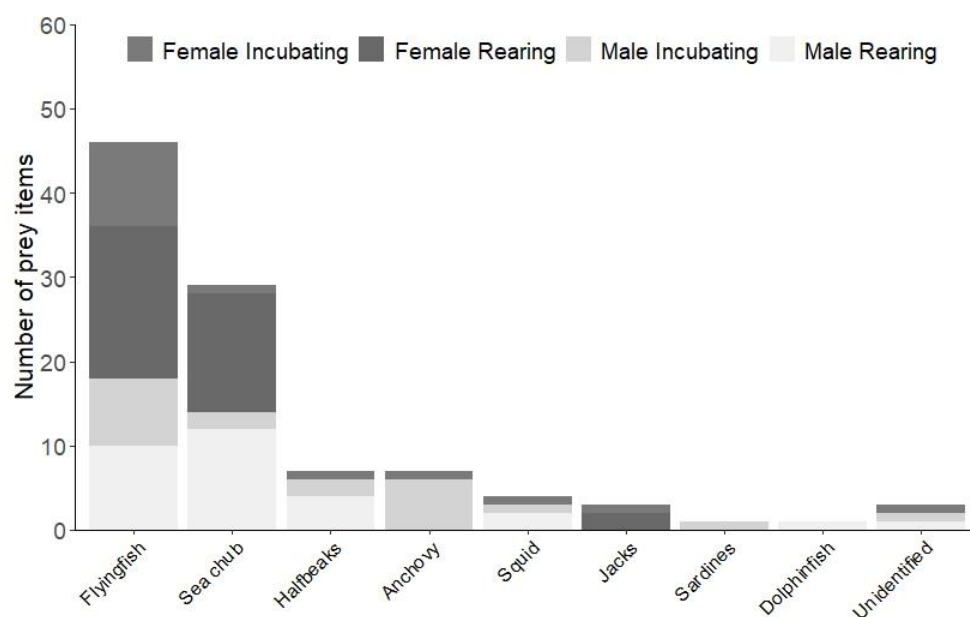
Figure 4.4. Prey items in diet of incubating female (birds=4, items=10) and male (birds=3, items=10) and chick-rearing female (birds=1, items=2) and male (birds=3, items=9) masked boobies at Rapa Nui. Families identified included flying fish (Exocoetidae), sea chub (Kyphosidae), halfbeaks (Hemiramphidae), anchovy (Engraulidae), squid (Omnastrepidae), jacks (Carangidae), sardines (Clupeidae), and dolphinfish (Coryphaenidae).

4.5. Discussion

The observation that masked boobies at Rapa Nui travelled further and longer during the incubation period coincided with the results of other studies of masked boobies (Oppel *et al.* 2015, Poli *et al.* 2017). Optimal foraging theory suggests that predators make foraging decisions that optimize energy intake with minimal energy investment (Charnov 1976, Pyke *et al.* 1977, Louzao *et al.* 2014), hence the energy investment of travelling further in incubating birds must have some advantages. The environmental conditions at Rapa Nui were similar in the core and wider areas, indicating that incubating and chick-rearing birds experienced similar environmental conditions. Although our interpretations are limited by a lack of information on food abundance, it is possible that areas closer to the colony are subject to greater depletion of food resources by individuals from the colony (Birt *et al.* 1987, Oppel *et al.* 2015), while this effect is reduced further from the colony. Chick-rearing birds may perform short trips to assure a regular food load to prevent reduced chick growth (Shoji *et al.* 2015), whereas incubating birds are free to forage further. More-distant areas, which offer less competition for food resources, may thus only be accessible to incubating individuals that are not constrained by the demands of breeding.

δ^{13}C levels act as tracers for foraging regions and feeding preferences. Although the current results may suggest that (1) incubating females were feeding in more-inshore waters or (2) they were feeding on benthic trophic webs, neither of these was supported by the analyses of diet and foraging parameters. Both sexes preyed on similar species, and contrary

to expectation, females travelled further (though not significantly further) from the colony than males. The fact that the $\delta^{13}C$ results did not coincide with the tracking data suggests that both parents were using similar areas, but females may have been targeting specific prey species, particularly during incubation. Female nutritional requirements may play an important role in sex-specific foraging behaviors (Lewis *et al.* 2002, Xavier & Croxall 2006), given that egg-laying is a demanding period for females (Nager *et al.* 2001), and females probably need to meet or recover from the nutritional requirements associated with egg production and laying (García-Tarrasón *et al.* 2015). The consumption of different prey items between females and males, particularly during incubation, coincides with the results for monomorphic Australasian gannets (*Morus serrator*) (Ismar *et al.* 2017) and dimorphic Magellanic penguins (*Spheniscus magellanicus*) (Raya Rey *et al.* 2012).

The current results showing higher $\delta^{15}N$ values in females than males were in contrast to the results from Palmyra Atoll (Young *et al.* 2010b), Albrolhos Island, Atol das Rocas, and Fernando de Noronha (Mancini *et al.* 2013), which found similar isotopic values in both sexes of masked boobies. The $\delta^{15}N$ values suggest that females tended to forage slightly more on prey at a higher trophic position than males (Bearhop *et al.* 2004, Inger & Bearhop 2008); however, the differences in $\delta^{15}N$ were very small (0.7 ‰), indicating that the diets were not from totally different trophic levels (3 ‰–5 ‰ per trophic level; DeNiro and Epstein 1981, Hobson and Clark 1992), but rather included different proportions of similar prey species. The different $\delta^{15}N$ values between females and males was in accord with the results from temperate Sulids, such as Australasian (*M. serrator*) (Ismar *et al.* 2017) and northern gannets (*M. bassanus*) (Stauss *et al.* 2012), and tropical Sulids such as blue-footed boobies (*S. nebouxii*) (González-Medina *et al.* 2017). However, the pattern was opposite in gannets and blue-footed boobies, with males having higher $\delta^{15}N$ levels than females. These differences may reflect differences in the trophic food webs among these species and colonies, and in the nutritional content of the available food items. Unfortunately, information on the nutritional content of seabird food items is lacking and the food webs at the different colonies are unknown, thus limiting our interpretation of the results.

Alternative hypothesis explaining the differences in $\delta^{13}C$ and $\delta^{15}N$ values rely on the premise that these measurements are primarily determined by the diet of the consumers. Although this is largely true (Hobson 1993, Cherel *et al.* 2005, Parnell *et al.* 2013), isotope levels may also be affected by physiological and biochemical factors, which are rarely taken into account and tested. Breeding is one of the most challenging periods for birds (Moreno 1989), with both physical and physiological effects (Drent & Daan 1980). Although the wing lengths of female and male masked boobies differed by ~2% at Clipperton (Weimerskirch *et al.* 2009a), Phillip Island (Sommerfeld *et al.* 2013), and in the current study, chick-rearing females were 14% heavier than males at Clipperton, 16% heavier at Phillip Island, and 21% heavier at Rapa Nui, while the difference in body mass was only 9% during incubation. Body condition is reduced during incubation in many seabirds (Gaston & Powell 1989, Monaghan *et al.* 1989, Croll *et al.* 1991, Dearborn 2001, Bauch *et al.* 2010), and female Sulids may be more severely affected than males (Velando & Alonso-alvarez 2003, González-Medina *et al.*

2017). This suggests that females may be in poorer body condition during incubation than while rearing chicks. If so, rather than indicating sex-related differences in foraging ecology, the different isotopic signatures between the sexes in this study may reflect differences in the physiological states of individuals, which in turn affect isotopic fractionation (Williams *et al.* 2007, Cruz *et al.* 2012, Swan *et al.* 2020).

Accordingly, changes in body mass in masked boobies coincided with the pattern of δ^{13}C blood levels. The lower body mass of females during incubation may reflect investment in the egg, and the higher δ^{13}C levels measured during this stage may be caused by increased lipid mobilization after egg laying, to recover their body mass (DeNiro & Epstein 1977, Bond & Jones 2009). Although there was no apparent relationship between δ^{13}C blood levels and body mass, this may be because body mass does not provide an adequate picture of the bird's physiological condition (Hovinen *et al.* 2019), and further studies are needed using plasma metabolites, such as triglycerides (González-Medina *et al.* 2020). Regarding δ^{15}N, females may have had higher values than males because of specific sex-related metabolic differences. The greater acquisition of nutritional reserves by females may help to satisfy and compensate for the demands of gonad growth and egg production, and as a body-reserve buffer for the rest of the breeding season (Petersen 1955, Moreno 1989). Better female body condition was associated with higher breeding success in other members of the Sulidae, and the physiological state of females may influence the blood levels of δ^{15}N (González-Medina *et al.* 2017, 2020). However, information on the physiology of seabirds during breeding is lacking, and more studies are needed to investigate its relationship with stable isotope values.

4.6. Conclusions

The present study provides the first investigation of the sex-specific foraging ecology of masked boobies at different breeding stages. Interestingly, although Rapa Nui is an oligotrophic area with potentially low food resources, which could promote foraging segregation, there were no obvious foraging differences between the sexes. Birds of both sexes consistently foraged further away and for longer periods during incubation compared with chick rearing, but there was no evidence of sexual segregation in terms of foraging trip parameters or diet. However, there were some clear results, including the findings that δ^{13}C sex-related differences interacted with breeding stage, and that females had different δ^{15}N signatures than males. This study demonstrates that foraging trip parameters do not differ between the sexes in masked boobies, even in oligotrophic waters. However, further studies focusing on the effects of physiological processes on stable isotope signatures in wild birds are needed to understand the reasons for the variations in δ^{13}C and δ^{15}N within this population.

CHAPTER 5.

5.   Inter-colony variations in foraging ecology of masked boobies

5.1. Abstract

The masked booby is a pantropical seabird species that exhibits different foraging parameters throughout its distributional range. These differences may be linked to the environmental conditions in specific areas, or to density-dependent processes affected by colony size. I investigated the effects of environmental conditions and colony size on the foraging ecology of masked boobies at three breeding colonies and compared the results with previous studies from other colonies. I recorded foraging locations of birds from Clarion Island in the eastern North Pacific (n=17), and Motu Nui (n=14) and Motu Motiro Hiva (n=3) in the eastern South Pacific. Diving information was obtained from Clarion Island (n=7) and Motu Nui (n=8), and regurgitates were opportunistically collected from 19 and 8 incubating birds on Clarion Island and Motu Nui, respectively. Foraging parameters of masked boobies across their distributional range were obtained from the literature and analyzed in relation to environmental satellite data. Foraging parameters were not related to local environmental conditions; however, maximum distance from the colony and total distance travelled during a foraging trip increased significantly with increasing colony size throughout the range. These results support the "Ashmole hypothesis", which states that larger colonies force seabirds to travel further during foraging trips as a result of prey depletion due to continuous exploitation by a larger number of individuals. Notably, this study found that masked boobies inhabit areas of low productivity, and I speculate that this is related to the presence of their preferred prey (flying fish) and to fewer competitive interactions with sympatric species.

5.2. Introduction

Seabirds have evolved numerous foraging strategies to enable them to obtain food in the marine environment. These strategies include species-specific prey preferences and the use of open ocean versus coastal habitats (Shealer 2002, Lescroël & Bost 2005, Quillfeldt *et al.* 2011). For example, some Sulid species, such as gannets, inhabit temperate areas, whereas others, such as boobies, inhabit tropical areas. The tropical species include coastal species, like blue-footed and brown boobies, and pelagic species, such as red-footed and masked boobies (Nelson 1978). However, although the foraging behavior of gannets is relatively well-understood, boobies foraging in tropical areas, particularly pelagic species inhabiting remote locations, have been less frequently studied largely due to the complicated logistics associated with research in these areas (Ballance & Pitman 1999) and because research is generally skewed towards wealthier geographical locations (Reboredo-Segovia *et al.* 2020).

Tropical areas have a lower resource base for tropical marine biota (Shealer 2002) and are less productive than their temperate counterparts (Longhurst & Pauly 1987). However, physical forces create different levels of productivity in the tropics (Fielder 1992, Claustre &

Maritorena 2003). Differences in local environmental conditions may thus explain the differences in diets between seabird populations (Lewis *et al.* 2003, Tremblay & Cherel 2003, Garthe *et al.* 2007, Castillo-Guerrero *et al.* 2016), and may also explain the differences in foraging parameters between pelagic booby populations (Kappes *et al.* 2011, Oppel *et al.* 2015, Mendez *et al.* 2017). In general, seabird species inhabiting less productive areas are expected to spend longer searching for food because their prey is more difficult to find (Jaquemet *et al.* 2005) or catch (Giraldeau 2008), while searching and capture times will be shorter in more productive areas with a higher abundance of prey. Nevertheless, the effect of productivity gradients on the foraging ecology of a single tropical seabird species remains poorly explored.

In contrast, extensive evidence suggests that foraging range is affected by colony size. Larger colonies deplete food resources in the immediate vicinity of the colony more notably, forcing individuals to forage further and for longer periods (Birt *et al.* 1987, Lewis *et al.* 2001, Elliott 2009). This phenomenon, known as "Ashmole's hypothesis", has been demonstrated in numerous seabird species (Corman *et al.* 2016, Jovani *et al.* 2016, Bolton *et al.* 2019), including pelagic boobies (Kappes *et al.* 2011, Oppel *et al.* 2015, Mendez *et al.* 2017). However, although the productivity gradient and colony size appear to be straightforward factors responsible for differences in foraging ranges among seabirds, it has been difficult to separate their effects from the environmental conditions of the colonies. For example, although foraging differences between colonies of masked boobies were attributed to colony size, the effect of productivity gradients was considered to be important but not tested.

Increasing literature on the foraging ecology of seabirds provides an opportunity to analyze the factors driving the differences within some tropical seabird species at a larger scale (Bolton *et al.* 2019). Masked boobies represent an ideal species for distinguishing between the effects of productivity gradient and colony size on the foraging ecology of a tropical seabird. Masked boobies are widely distributed in the tropics, covering different productivity gradients. This seabird species preys mainly on flying fish and squid (Nelson 1978, Priddel *et al.* 2005, Young *et al.* 2010b), but may also prey on other species such as halfbeaks (Hemiramphidae) (Weimerskirch *et al.* 2009a, Kappes *et al.* 2011), dolphinfish (Coryphaenidae) (Weimerskirch *et al.* 2009a), and tuna (Scombridae) (Asseid *et al.* 2006, Weimerskirch *et al.* 2009a). Masked booby colonies are vast and differ in size (Nelson 1978) and their foraging parameters also vary, with a maximum distance from the colony of 75 km (Young *et al.* 2010b) up to 360 km (Asseid *et al.* 2006). In the current study, I aimed to (i) compare the foraging ecology of masked boobies inhabiting the North Pacific (Clarion Island) and the South Pacific (Motu Nui), and (ii) use information from the literature to assess the effects of productivity gradients and colony sizes on the foraging ecology of masked boobies throughout their range. I expected that masked boobies would travel further from their breeding colonies and dive deeper and longer in (i) less productive and (ii) larger colonies. I also expected to find variations in their diet in relation to productivity gradients.

5.3. Methods

Data collection

Fieldwork was carried out on Clarion Island, Motu Nui, and Motu Motiro Hiva. Clarion Island (18°21'7.53"N, 114°43'18.61"W) is part of the Revillagigedo Archipelago, Mexico, and Motu Nui (27°12'4.19"S, 109°27'11.27"W) and Motu Motiro Hiva (26°28'S, 105°21'42.0"W) belong to Rapa Nui, Chile. Clarion Island was visited for 30-day periods in March 2017 and March 2018, Motu Nui was visited for 4-day periods twice a month in October and November 2016 and November 2017, and Motu Motiro Hiva was visited for a 3-day period in November 2016. Birds in the three colonies were tracked using GPS recorders (CatLog-S; Catnip Technologies, Hong Kong, China). The GPS recorders were programmed to record time, latitude, and longitude every 4 min. The same birds that were equipped with GPS devices were also equipped with time-depth recorders (TDRs; model G5+; Cefas Technology, UK). The TDRs were programmed to record pressure data every 1 s. The masked booby breeding colonies were estimated to include 100 pairs on Clarion Island (Wanless *et al.* 2009, Almanza-Rodríguez 2019), 77 pairs on Motu Nui, and 86 pairs on Motu Motiro Hiva.

Individuals were captured at their nest using a hand net from a distance of 1 m. The devices were attached on top of the three rectrix feathers using water-resistant tape. The GPS devices, including the waterproof heat-shrink casing, weighed 22–30 g and the TDR devices weighed 6.5 g. The masked boobies weighed 1.4–2.6 kg, and the total mass of both devices was therefore below the 3% acceptable body mass threshold for seabirds (Vandenabeele *et al.* 2012). Individuals were released back to the nest after a maximum of 10 min handling time, and were subsequently monitored on a daily basis during the tagging period.

Tracking data were processed in R 3.6.2. To obtain foraging parameters per individual trip, all GPS fixes were analyzed using the function 'tripsplit' in the package 'IBA'. This function calculates the foraging parameters of maximum distance from the colony, total distance travelled, and trip duration for each individual trip (Lascelles *et al.* 2016). The maximum distance from the colony was measured as the most distant point in a straight line from the colony, total distance travelled was the summed distance between consecutive fixes from departure to return to the colony, and trip duration was the total time between departure and return to the colony. For the TDR data, depth values were corrected on each tag based on sensor sensitivity, and only dives deeper than 0.5 m were considered as true dives. Maximum dive duration (s), maximum diving depth (m), and diving rate (dives h^{-1}) were calculated per trip for each individual.

During fieldwork, diet samples were collected opportunistically if birds regurgitated as a result of our presence in the colony or during tagging. The whole regurgitate was placed in an individual plastic bag and weighed, and each prey item was later removed from the bag, photographed, and identified to family level, based on Pacific (Fischer *et al.* 1995) and local fish guides (Randall & Cea 2010). Diet was described based on numerical frequency, defined

as the number of items from a given prey family in relation to the total number of prey items (Alonso *et al.* 2018).

Literature review

For comparison with previous studies, information was extracted from studies on masked boobies throughout their range (Figure 5.1). Information included tracking (maximum distance, trip duration, and total distance travelled), diving (maximum dive duration, maximum dive depth, and dive rate), and diet information (numerical frequency by family level). If diet information was not presented as numerical frequency at family level, it was calculated based on the level of information provided by the study. Studies from Lobos de Tierra (Jahncke & Goya 2000) and Galapagos (Anderson 1989) did not consider the separation between masked booby (*Sula dactylatra)* and Nazca booby (*Sula granti)* (Pitman & Jehl 1998), and are likely from Nazca not masked boobies (Figueroa 2004, Tompkins *et al.* 2017), thus were excluded from our analyses.
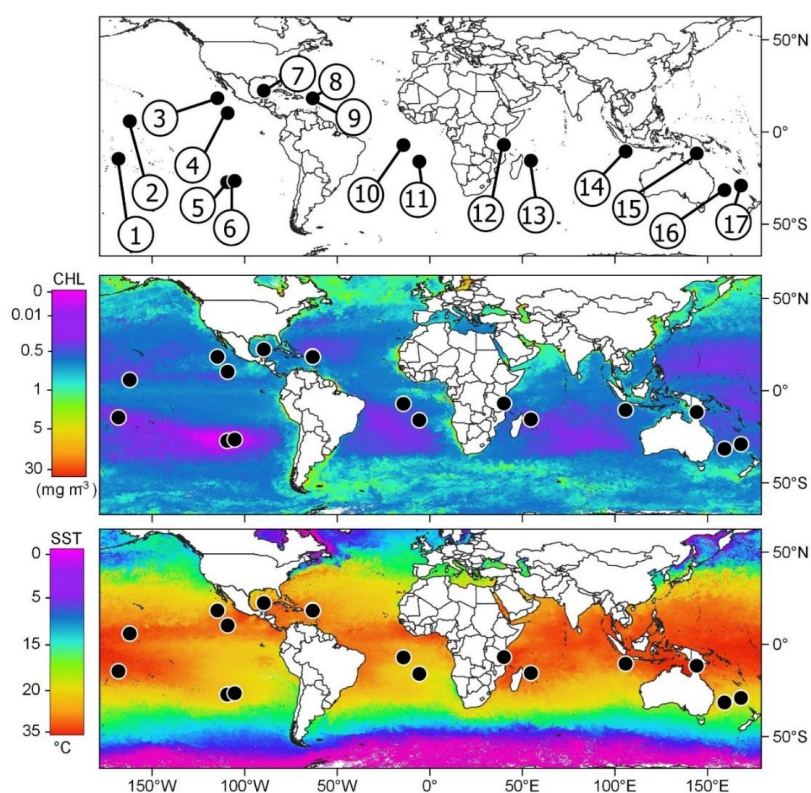
Figure 5.1. Global environmental variables at masked booby colonies. CHL: chlorophyll-a concentration, SST: sea surface temperature. Points represent tracking, diving, or diet studies. Numbers in the upper figure are ordered by latitude: 1, Rose Atoll; 2, Palmyra Atoll; 3, Clarion Island; 4, Motu Nui; 5, Clipperton Island; 6, Motu Motiro Hiva; 7, Isla Muertos; 8, Sombrero Island; 9, Dog Island; 10, Ascension Island; 11, Saint Helena; 12, Latham; 13, Tromelin; 14, Christmas Island; 15, Raine Island; 16, Lord Howe Island; 17, Phillip Island

Environmental data

Satellite measurements of ocean color provide a means of quantifying ocean productivity on a global scale (Behrenfeld *et al.* 2006). Environmental data such as chlorophyll-a concentration (CHL) and sea surface temperature (SST) are accessible throughout the ERDDAP database, and are frequently used as indicators of abundance and distribution of seabirds' prey (Kappes *et al.* 2010, Paiva *et al.* 2010). Monthly composites from January to December 2018 for CHL were downloaded from Aqua MODIS, NPP, 0.025 degrees, Pacific Ocean Lon+/-180, and for SST from Pathfinder, Night, Global, 0.0417 degrees.

The maximum distance from the colony per colony information was extracted from the literature, otherwise a 120 km foraging range was used based on the suggested maximum range of masked boobies (Oppel *et al.* 2018). A circle around each colony was created using the corresponding maximum range. The means and standard deviations of CHL and SST inside the circle for each site were calculated using the function 'extract' in the R package 'raster' (Figure 5.1). Importantly, the mean and standard deviation per colony were only used as an approximation of the conditions at the islands, and did not reflect the environmental conditions when the studies were performed. Environmental data were processed in R 3.6.2 and maps were produced using QGIS 3.4.

Statistical analyses

Inter-colony differences in CHL and SST data between Clarion Island and Motu Nui were analyzed by one-way analysis of variance (ANOVA) with colony as a factor. Differences in foraging ecology between Clarion Island and Motu Nui were analyzed using linear mixed-effect models in the R package 'lme4'. Foraging trip parameters (maximum distance from the colony, total distance travelled, and trip duration) and diving parameters (dive depth, dive duration, and dive rate) were used as response variables. Most previous studies found no differences in foraging parameters between female and male boobies (Young *et al.* 2010b, Kappes *et al.* 2011, Oppel *et al.* 2015, Poli *et al.* 2017), but I nevertheless included sex in the analyses. Initial models included colony (Clarion Island and Motu Nui) and sex as fixed factors, and the interaction colony × sex. Insignificant interactions and factors were eliminated by backward selection comparing the models using likelihood ratio tests with the 'anova' function (Peck-Richardson *et al.* 2018). Because different years were included in the analyses and birds performed more than one single foraging trip, both year and individual bird identification were included as random effects in all models. Residuals were plotted against fitted values and there were no obvious deviations from the assumption of normality and homoscedasticity of residuals. In addition, I compared the mass of regurgitates between colonies using two-way ANOVA with regurgitate mass as the response variable and colony (Clarion Island and Motu Nui), sex, and year as fixed factors, and the interactions colony × year and colony × sex. Notably, the presence of different prey items in the diet and the mass of the regurgitates may vary due to different intrinsic digestion rates (Barrett *et al.* 2007), but the digestion rate can be assumed to be similar between the colonies.

Inter-colony differences in local environmental variables (CHL and SST) within the masked boobies' distributional range were analyzed by one-way ANOVA, respectively, with colony as a factor. For comparisons with previous studies, models were compared using Akaike information criteria (AIC) weights and final models were selected based on minimizing the AIC. Initial models included the foraging parameters (maximum foraging range, trip duration, or total distance travelled) as response variables colony size (number of pairs), island area (km^2), mean and standard deviation of CHL (CHLm and CHLsd, respectively), and mean and standard deviation of SST (SSTm and SSTsd, respectively) as factors. Colony size, island area, and CHLm were log-transformed for normalization of the data. Diving information was only reported in the current and two other studies (Weimerskirch *et al.* 2008, Sommerfeld *et al.* 2015), and no statistical comparisons were therefore made. Diet comparisons included the proportion of flying fish as a response variable, and CHLm, CHLsd, SSTm, and SSTsd as factors. Colony size was not included in the diet analyses due to insufficient information (Schreiber & Hensley 1976, Harrison *et al.* 1983, Balber *et al.* 1995).

5.4. Results

Comparison between Clarion Island and Motu Nui

Tracking data were obtained for 52 trips from 17 incubating birds on Clarion Island, 48 trips from 14 incubating birds on Motu Nui, and 3 trips from 3 chick-rearing birds on Motu Motiro Hiva. Masked boobies from Clarion Island foraged further and for longer than those from Motu Nui (maximum distance from the colony: 68.5 ± 33.6 km and 33.4 ± 25.6 km, total distance from the colony: 168.0 ± 73.1 km and 86.4 ± 65.7 km, trip duration: 7.8 ± 3.4 h and 3.4 ± 2.4 h, respectively) (Table 5.1). The local environmental conditions at Clarion Island were 3.3 °C warmer ($F_{1,22} = 21.94$, $P < 0.01$) and 0.06 mg m-3 more productive ($F_{1,22} = 112.6$, $P < 0.01$) compared with Motu Nui (Table 5.2). Motu Motiro Hiva was excluded from these analyses because of the limited number of samples (n=3).

Table 5.1. Model comparisons of foraging parameters of masked boobies breeding on Clarion Island (GPS = 17, TDR = 7) and Motu Nui (GPS = 14, TDR = 8). The effects of colony, sex, and the interaction were compared by likelihood ratio tests with one degree of freedom (χ^2 test). All analyses include year and individual bird identification as random factors

	Colony		Sex		Colony × sex	
	χ^2	P	χ^2	P	χ^2	P
Maximum distance	14.25	< 0.01	2.14	0.14	1.85	0.17
Trip duration	18.29	< 0.01	1.60	0.20	0.12	0.72
Total distance travelled	13.30	< 0.01	1.85	0.17	1.34	0.24
Diving depth	7.03	< 0.01	3.37	0.07	2.32	0.12
Diving duration	6.46	0.01*	3.10	0.08	2.70	0.10
Diving rate	1.70	0.19	1.02	0.31	1.68	0.20

Table 5.2. Environmental conditions around masked boobies' colonies calculated using a buffer with maximum distance from the colony

Island	Lat	Lon	Max (km)	SST (ºC)	CHL x10^2 (mg m-3)	BATH (km)
Clarion	18.36° N	114.73° W	107[1]	26 ± 1	10 ± 2	3.6 ± 0.3
Motu Nui	27.2° S	109.45° W	176[1]	23 ± 2	3 ± 1	2.8 ± 0.5
Motiro Hiva	26.47° S	105.36° W	62[1]	23 ± 2	3 ± 1	2.7 ± 0.7
Clipperton	10.3° N	109.2° W	245[2]	28 ± 1	17 ± 5	3.6 ± 4.7
Phillip	29.02° S	167.57° E	258[3]	22 ± 2	13 ± 6	2.7 ± 0.8
Palmyra	5.52° N	162.04° E	75[4]	29 ± 1	10 ± 4	2.9 ± 0.8
Latham	6.54° S	39.56° W	364[5]	28 ± 1	21 ± 5	1.2 ± 1.7
Ascension	14.18° S	7.56° W	310[6]	26 ± 1	12 ± 3	3.4 ± 0.5
St. Helena	5.46° S	16° W	340[6]	22 ± 2	11 ± 4	4.3 ± 6.3
Tromelin	15.33° S	54.31° E	120[7]	27 ± 2	9 ± 4	4.4 ± 0.5
Muertos	22.4° N	89.7° W	232[8]	27 ± 2	38 ± 8	0.8 ± 1.4
Dog Island	18.27° N	63.25° W	120[7]	27 ± 1	11 ± 2	2.1 ± 2.1
Sombrero	18.58° N	63.42° W	120[7]	27 ± 1	11 ± 2	2.8 ± 2.4
Lord Howe	31.50° S	159.07° E	120[7]	21 ± 2	20 ± 11	2.7 ± 1.0
Raine Island	11.58° S	144.03° E	120[7]	27 ± 2	28 ± 0.3	0.9 ± 1.1
Rose Atoll	14.58° S	168.16° W	120[7]	28 ± 1	3 ± 1	5.0 ± 0.4
Christmas	10.52° S	105.63° E	120[7]	27 ± 1	15 ± 7	1.8 ± 1.1

Lat: latitude; Lon: longitude; Max: maximum distance from the colony; SST: sea surface temperature; CHL: chlorophyll-a concentration; BATH: water depth. Superscript in maximum range refers to 1- this study; 2- (Weimerskirch *et al.* 2009a); 3- (Sommerfeld *et al.* 2013); 4- (Young *et al.* 2010b); 5- (Asseid *et al.* 2006); 6- (Oppel *et al.* 2015); 7- (Oppel *et al.* 2018); 8- (Poli *et al.* 2017). Values presented are mean ± SD.

Sixteen and 12 of the same birds that were equipped with GPS devices on Clarion Island and Motu Nui, respectively, were also equipped with time-depth recorders, but only 7 birds on Clarion Island and 8 on Motu Nui had identifiable dives. At Clarion Island, 57% of the devices failed to record diving events or had large variations that prevented the identification of dives, whereas only 33% of devices from Motu Nui did not show clear dives. Based on the recorded dives, individuals from Clarion Island dived deeper and for longer than those from Motu Nui, but the diving rates were similar at both colonies (Table 5.2 & Table 5.3).

Table 5.3. Diving parameters of masked boobies throughout their range

Island	Dives, n (total)	Dive depth (m)	Dive duration (s)	Dive rate (dives/h)	Refs
Clarion Island	7 (3338)	2.6 ± 0.4	3.6 ± 0.5	3.5 ± 1.1	1
Motu Nui	8 (2828)	1.4 ± 0.6	2.1 ± 0.7	4.9 ± 3.6	1
Clipperton	18 (1244)	2.2 ± 1.1	2.9 ± 1.3		2
Phillip Island	131 (744)	2.8 ± 1.5		4.5 ± 3.5	3

Dives indicated as number of individuals (n) and total number of recorded dives in parentheses. Refs: 1, this study; 2, Weimerskirch *et al.* 2009; 3, Sommerfeld *et al.* 2013. Values presented as mean ± standard deviation.

Flying fish was the main prey item of masked boobies at both Clarion Island and Motu Nui (Figure 5.3). Other prey families were common to both colonies, including squid, sea chubs, and halfbeaks, while anchovies were found exclusively on Motu Nui and pufferfish exclusively on Clarion Island (Figure 5.3). The mean regurgitate mass was 164 ± 104 g, with no significant differences between sexes ($F_{1,\ 22} = 0.23$, P = 0.63), seasons ($F_{1,\ 22} = 0.10$, P = 0.76), or colonies ($F_{1,\ 22} = 1.53$, P = 0.20), and no significant interactions (P > 0.05).
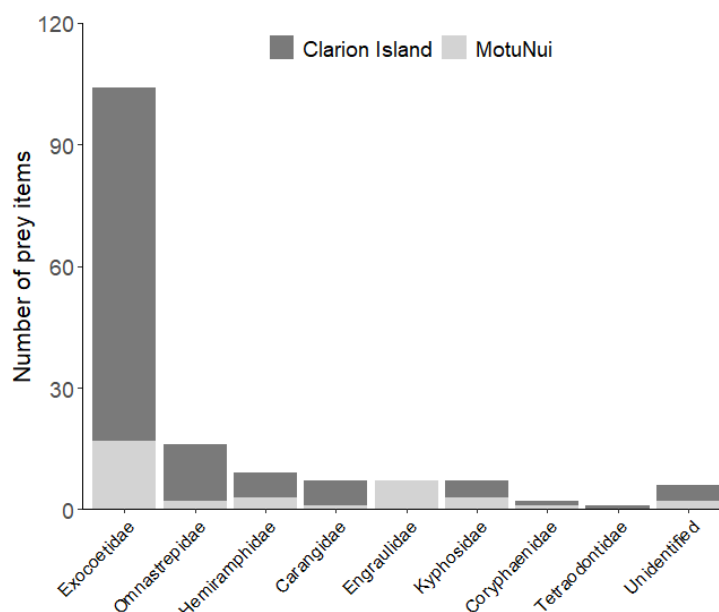
Figure 5.3. Prey species in regurgitates from incubating masked boobies (*Sula dactylatra*) at Clarion Island (n = 123 prey items) and Motu Nui (n = 36 prey items). Families identified in the regurgitates include Exocoetidae (flying fish), Omnastrephidae (squid), Hemiramphidae (halfbeaks), Carangidae (jacks), Engraulidae (anchovies), Kyphosidae (sea chubs), Coryphaenidae (dolphinfish), and Tetraodontidae (pufferfish).

Comparison throughout distributional range

Local environmental conditions at masked booby colonies differed significantly in terms of CHL ($F_{16, 187} = 37.55$, $P < 0.01$) and SST ($F_{16, 187} = 32.72$, $P < 0.01$) (Table 5.1, Figure 5.4). Among the 17 colonies included in the analyses (Figure 5.1), 29% had CHL concentrations < 0.01 mg m^{-3} and 71% were < 0.10 mg m^{-3} (Figure 5.4).
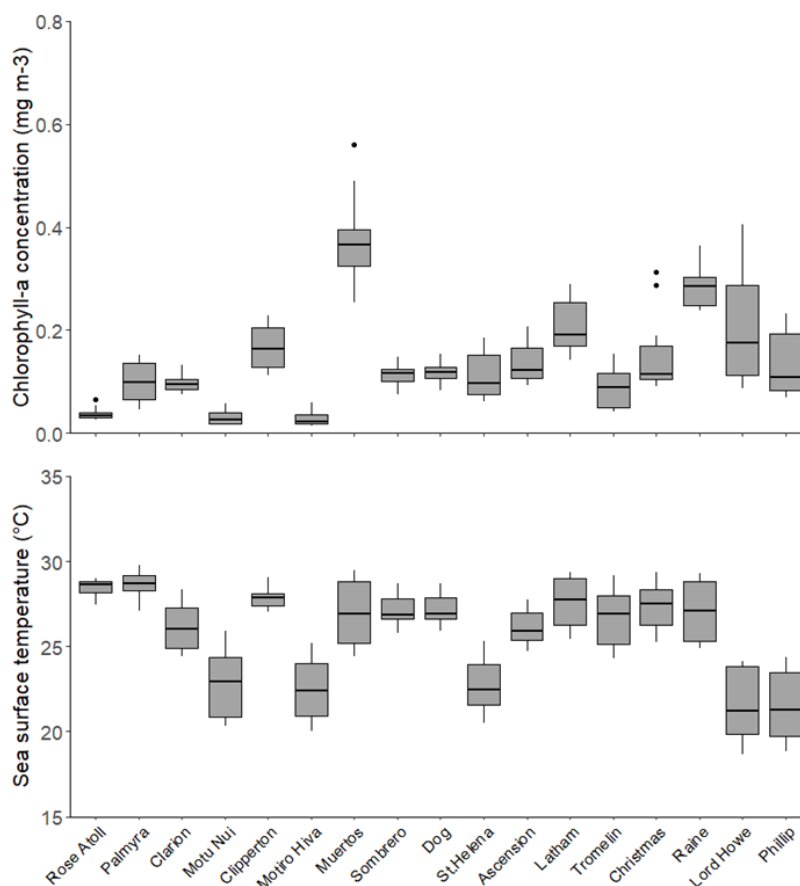
Figure 5.4. Chlorophyll-a concentration and sea surface temperatures at masked booby colonies. Mean and standard deviation are presented, and were calculated using monthly composites from January to December 2018. Islands ordered by latitude from left to right.

Maximum distance from the colony and total distance travelled were not associated with the productivity of the colonies (Table 5.4), but increased significantly with increasing colony size: masked boobies from larger colonies travelled further (Table 5.4 & Figure 5.5). The maximum diving depth and duration were similar to previous reports on masked boobies (dives < 6 m & <10 s) (Table 5.3).

Table 5.4. Analyses of potential variables explaining the foraging ecology of masked boobies. AIC: value of model selection from the Akaike Information Criterion, logColSize: logarithm of colony size, SSTsd: standard deviation of sea surface temperature, logCHLm: logarithm of mean value of chlorophyll-a concentration, SSTm: mean sea surface temperature, CHLsd: standard deviation of chlorophyll-a concentration

	AIC	Variable	Coefficient	F	P
Foraging range (km)	-17.8	logColSize	0.23	14.27	< 0.01
		SSTsd	0.49	3.32	0.09
Trip duration (h)	-4.6	logCHLm	1.14	5.03	0.06
		logColSize	0.26	3.44	0.10
		SSTsd	1.31	2.75	0.13
		CHLsd	-0.31	1.54	0.24
Total distance (km)	-20.5	logColSize	0.34	21.81	< 0.01
Flying fish proportion	56.5	SSTm	4.68	1.86	0.21
		CHLsd	3.38	3.68	0.09
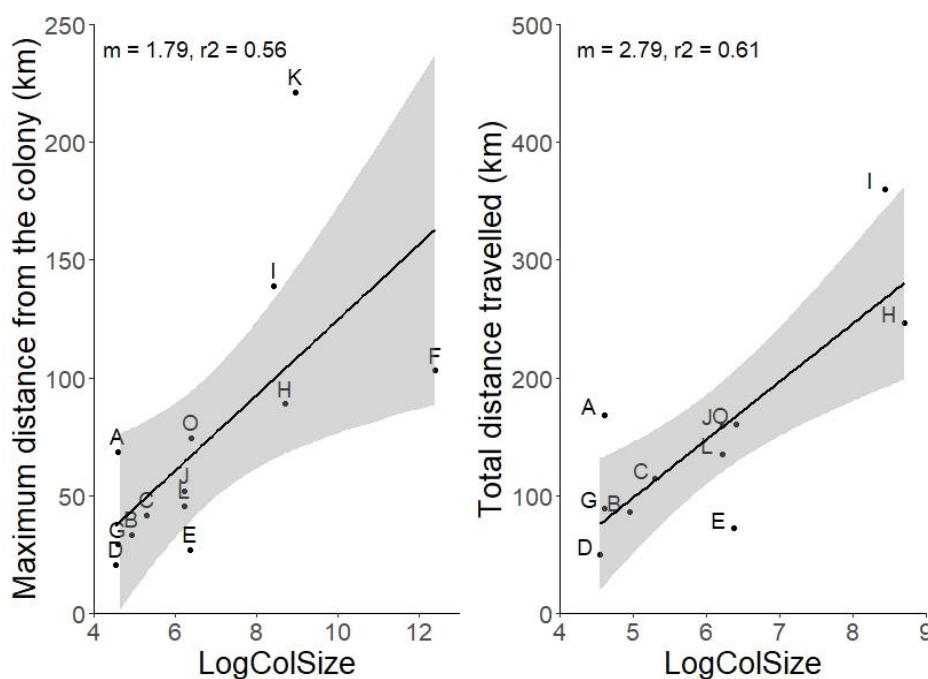
Figure 5.5. Regression showing relationship between colony size and maximum distance from the colony and total distance travelled for masked boobies. A, Clarion Island; B, Motu Nui; C, Motu Motiro Hiva (all this study); D, Dog Island; E, Sombrero Island (both Soanes *et al.* 2016); F, Clipperton Island (Weimerskirch et al. 2009); G, Palmyra Atoll (Young *et al.* 2010); H, Isla Muertos (Poli *et al.* 2017); I, Ascension; J, St. Helena (both Oppel et al. 2015); K, Latham (Asseid *et al.* 2006); L, Tromelin (Kappes *et al.* 2011); O, Phillip Island (Sommerfeld *et al.* 2013).

The diet of masked boobies from all colonies included flying fish, but the proportion of flying fish reported in the literature varied from 47%–96% of all prey (Figure 5.6). The proportion of flying fish in the diet was not significantly related to the productivity gradient of the studied colonies (Table 5.4). Squid were also frequently reported in the diet of masked boobies, while other prey families, besides flying fish and squid, varied from 0 to 6 according to the colony (Figure 5.6).
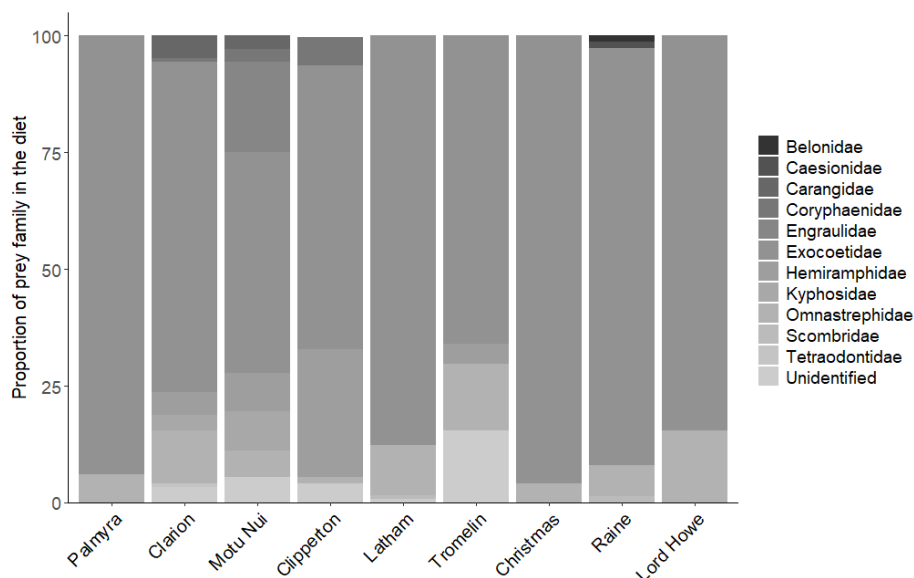
Figure 5.6. Proportions of prey families in diet of masked boobies (*Sula dactylatra*) based on numerical frequency of prey items. Islands ordered by latitude. Information from studies performed on Palmyra (Young *et al.* 2010), Clarion and Motu Nui (this study), Clipperton (Weimerskirch *et al.* 2009), Latham (Asseid *et al.* 2006), Tromelin (Kappes *et al.* 2011), Christmas Island (Schreiber & Hensley 1976), Raine Island (Balber *et al.* 1995), and Lord Howe Island (Priddel *et al.* 2005).

5.5. Discussion

Foraging trip parameters

Contrary to expectations, the maximum distance from the colony and total distance travelled during a foraging trip were both longer in the more productive waters around Clarion Island than in the less productive waters around Motu Nui. The fact that this difference cannot be explained by local environmental conditions suggests that the longer foraging trips at Clarion Island may be caused by differences in inter-specific competition associated with colony size. However, the masked booby colonies on Clarion Island and Motu Nui were similar in size (100 and 77 breeding pairs, respectively), and the effect of this small difference in colony size might be expected to be insignificant.

A possible alternative explanation is the lack of other competing species on Motu Nui (Flores *et al.* 2014), compared with Clarion Island where masked boobies share their foraging grounds with a colony of > 2000 pairs of red-footed boobies (*Sula sula*) (Wanless *et al.* 2009, Almanza-Rodríguez 2019). Although I did not collect data on resource partitioning by species, at-sea surveys suggest that red-footed and masked boobies form mixed flocks and have similar foraging behaviors (Ballance *et al.* 1997, Spear *et al.* 2007), providing support for this hypothesis. Red-footed boobies also consume flying fish (Young *et al.* 2010a) and although masked boobies may have a competitive advantage because of their larger size (Ballance *et al.* 1997), the different foraging parameters of masked boobies from Clarion Island and Motu Nui suggest that intra-specific competition for the same resource may affect masked booby foraging trip parameters.

Considering the distributional range of masked boobies, their foraging parameters did not appear to be related to the productivity of their respective colonies, but differences between colonies were rather explained in terms of the Ashmole hypothesis. Red-footed booby individuals from larger colonies foraged further (Mendez *et al.* 2017), and consistent evidence suggests that this is true for a number of seabird species (Lewis *et al.* 2001, Corman *et al.* 2016, Jovani *et al.* 2016, Bolton *et al.* 2019), including masked boobies (Oppel *et al.* 2015). Although the results are apparently in accord with previous studies of masked boobies, I suggest that they should be treated with caution because of the heterogeneity of the information from the various studies. For example, masked boobies foraged further during incubation than during chick-rearing periods at Ascension, St. Helena (Oppel *et al.* 2015), and Isla Muertos (Poli *et al.* 2017), but several studies only reported information for one breeding stage (Weimerskirch *et al.* 2008, Sommerfeld *et al.* 2015) or reported information based on both breeding stages pooled together (Young *et al.* 2010b). Further data are therefore needed to analyze the intrinsic factors affecting these results in the future.

Diving parameters

The TDR devices failed to record dives more often at Clarion Island than at Motu Nui, and the dives recorded at Clarion Island were deeper and longer than those at Motu Nui. Differences in diving behaviors between these colonies may be associated with the behavior and availability of the prey species. First, the optimal temperature for flying fish to leave the water is 24° C (Davenport 1994), and the warmer waters at Clarion Island (26 ± 1.3° C) may therefore offer better conditions for flying fish to leave the water than at Motu Nui (23 ± 2° C), thus explaining the smaller number of dives recorded at Clarion Island. Second, the diet at Motu Nui was more diverse, and masked boobies at Clarion Island relied almost exclusively on flying fish. Flying fish occur in patchily distributed shoals that are very difficult to predict in space and time (Oxenford *et al.* 1995), and birds may avoid interruptions to their food supply by including supplementary prey species (MacArthur & Pianka 1966, Giraldeau 2008). At Clarion Island, supplementary species such as pufferfish, which are known to occur deeper in the water column (Fischer et al. 1995), may require deeper dives and active pursuit of their prey (Garthe *et al.* 2000), increasing energy costs. Thus, further studies linking nutrition,

physiology, and behavior, as performed in gannets (*Morus serrator*) (Machovsky-Capuska *et al.* 2018) and brown boobies (*Sula leucogaster*) (Miller *et al.* 2018) are needed to elucidate this predator–prey interaction differences among colonies.

Masked boobies are frequently reported to plunge dive (Nelson 1978, Hertel & Ballance 1999, Kappes *et al.* 2011, Sommerfeld *et al.* 2015, Poli *et al.* 2017), using their weight to gain depth (Sommerfeld *et al.* 2015). However, reported diving depths were shallower than 6 m. Thus although it has been suggested that masked boobies are capable of reaching greater depths (up to 35 m; Nelson 1978, Marchant & Higgins 1990), this has not been reported in the recent literature. Red-footed boobies catch flying fish and squid above the surface (Diamond 1978, Hertel & Ballance 1999, Weimerskirch *et al.* 2005), and this behavior may also be important in this booby species under specific conditions. I suggest that masked boobies practice 'aerial chasing' (Ashmole 1971) more often than reported, and future studies including the use of videography (Machovsky Capuska *et al.* 2011) are required to investigate this hypothesis.

Diet

Consistent with previous studies, masked boobies prey primarily on flying fish throughout their distributional range. Flying fish are offshore specialists that prefer low-productivity waters (Churnside *et al.* 2017, Lewallen *et al.* 2018), coinciding with the local oceanographic conditions of most masked booby breeding colonies. The proportions of flying fish and supplementary species in the diet varied among colonies, presumably related to their local availability. The difference in supplementary prey species included in the diet of masked boobies must reflect the fact that geographically separated populations of seabirds are exposed to different environmental and ecological conditions (Garthe *et al.* 2007, Castillo-Guerrero *et al.* 2016). The adaptation of masked boobies to different behavior and abundances of their prey species throughout their range may allow this species to be widely distributed over the tropics.

Local environmental conditions

Although it was not an objective of the study, I noted that local oceanographic conditions included CHL concentrations of < 0.10 mg m^{-3} within the foraging ranges of the masked booby breeding colonies. Compared with coastal waters, which frequently exceed the 0.29 mg m^{-3} average with productive upwellings reaching 1–10 mg m^{-3} (Schalles 2006), masked booby colonies are located in the lower productivity gradient. Productive waters are often associated with abundant food resources, and some seabird species tend to avoid travelling or foraging on oligotrophic areas (Dias *et al.* 2012, Clay *et al.* 2017), raising the question of why masked boobies inhabit less productive waters. It is likely that they inhabit warm and less productive waters because these areas are the preferred habitat of their main prey, flying fish (Churnside *et al.* 2017), and because the lower species richness in these warm and less productive waters

(Ballance *et al.* 1997, Spear *et al.* 2001, Mott & Clarke 2018) reduces competition for the same food resources.

Masked boobies may compete for food resources with frigatebirds (*Fregata* spp.), tropicbirds (*Phaeton* spp), and red-footed boobies, which also prey on flying fish (Ballance 1995, Ballance & Pitman 1999, Young *et al.* 2010a, Soanes *et al.* 2016). However, these other species are smaller than masked boobies and might therefore be outcompeted by them, simply because the larger size of masked boobies increases the risk of injury or collision for other, smaller species (Nelson 1978, Ballance *et al.* 1997). Furthermore, species assemblages segregate in foraging areas, providing additional evidence to suggest that masked boobies outcompete other seabirds (Bocher *et al.* 2000, Cherel *et al.* 2008, Navarro *et al.* 2014, Miller *et al.* 2018); tropicbirds forage in more distant areas and on smaller prey items than masked boobies (Young *et al.* 2010a), while red-footed boobies consume different-sized prey and forage further away from the colonies than masked boobies (Young *et al.* 2010b). Frigatebirds, terns, and tropicbirds travel hundreds to thousands of kilometers to their foraging grounds, while masked boobies have a comparatively small foraging range (Fernández *et al.* 2001, Oppel *et al.* 2018). This suggests that masked boobies in less productive waters may have a competitive advantage that allows them to forage closer to the colony, and thus maintain a shorter foraging range than other tropical seabird species.

5.6. Conclusions

This study provides the first comprehensive evidence for the foraging ecology of masked boobies throughout their range. The results confirmed that masked boobies consistently prey on flying fish in the upper layers of the water column (< 6 m). I also confirmed the importance of colony size as a driver of masked booby foraging parameters, including maximum distance from the colony and total distance travelled. My analyses indicate that the productivity gradient has no significant effect on the foraging ecology of masked boobies; however, further studies are required to analyze the intrinsic information for tracked individuals. Finally, I demonstrated that masked boobies inhabit low-productivity waters, possibly because of the presence of their preferred prey (flying fish), and because of fewer competitive interactions with sympatric species.

6.   General discussion

This study provides the first data on the foraging ecology of a seabird species inhabiting the under-explored areas of Motu Nui and Clarion Island. The study species, masked booby, did not utilize the specific hydrographic features at Motu Nui (Chapter 2) and Clarion Island (Chapter 3). Furthermore, masked boobies did not change their foraging behavior between years, most likely because the environmental conditions at Motu Nui (Chapter 2) and Clarion Island (Chapter 3) remained relatively stable across years. The foraging trip parameters of this species did not differ between the sexes; however, the isotopic signatures of females differed from those of males at Motu Nui, suggesting that, even when the sexes use the same areas, females may be feeding at a different trophic level or have a different physiological state than males (Chapter 4). Foraging ecology was affected by breeding stage: parents at Motu Nui took longer foraging trips during incubation than while rearing chicks (Chapter 4). Masked boobies at Motu Nui foraged closer to their colonies than those at Clarion Island, which was related to colony size rather than to the environmental predictors such as Chlorophyll-a of the colonies (Chapter 5). Masked boobies generally inhabit low-productivity waters, probably because these are the preferred conditions for their main prey, flying fish, but also because they may offer less competition with other seabird species for the same resources (Chapter 5). These results are discussed in their particular context at the end of each chapter. This chapter aims to incorporate the findings, discuss their implications, and highlight information gaps for future studies.

Local conditions

Masked boobies at Motu Nui (Chapter 2) and Clarion Island (Chapter 3) did not utilize specific hydrographic features around their colonies. This is in contrast to the situation at Phillip Island, where masked boobies showed site fidelity to local, but not distant areas (Sommerfeld *et al.* 2015), and at Isla Muertos, where masked boobies associated with sea surface height (Poli *et al.* 2017). The differences among these colonies may be because of the lack of specific hydrographic features guaranteeing prey presence at Clarion and Motu Nui. However, our study was limited to considering environmental predictors such as chlorophyll-a concentration, sea surface temperature, bathymetry, and seamounts, because data for more dynamic oceanographic features such as sea surface height are currently scarce, incomplete, or inaccessible.

The foraging behavior of masked boobies, which made several trips on the same day following different behaviors and travelling to different places, is in accordance with previous studies that showed low foraging-site fidelity in tropical seabirds (Weimerskirch 2007, Kappes *et al.* 2011, Soanes *et al.* 2016, Oppel *et al.* 2017). Flying fish was the main prey item for masked boobies, but shoals of this species are highly unpredictable (Oxenford *et al.* 1995), and travelling to the same area was therefore of limited value to masked boobies. Instead, masked boobies may forage more efficiently by moving in no specific direction, and then travelling directly when they see something of interest, similar to other animals facing unpredictable resources (Venter *et al.* 2017). Notably, fishermen targeting flying fish change

locations both within and between days in the Caribbean (Oxenford *et al.* 1995) and at Rapa Nui (Pau Hito, Rapa Nui fishermen, pers. comm.). These observations suggest that exploring new areas represents a better approach for seabirds, and also fishermen, facing stochastic systems (see O'Farrell *et al.* 2019).

Inter-annual environmental variations

The environmental conditions at Clarion Island (Chapter 2) and Motu Nui (Chapter 3) did not differ significantly between years within the foraging range of the masked boobies. If the environmental conditions did not vary between years, the same should be expected for their food resources and thus for the birds' foraging behavior. This result is interesting, because seabirds typically inhabit areas with varying environmental conditions (Hamer *et al.* 2002) and react by adjusting their foraging areas and diet accordingly (Harding *et al.* 2007, Elliott *et al.* 2008). However, masked boobies inhabit low-productivity waters with similar environmental conditions across years and therefore did not show dramatic adjustments in their foraging ecology.

Although there were no suggestions that environmental variations such as El Niño affected the foraging of masked boobies, current forecasts indicate that tropical areas will continue to get warmer (DiNezio *et al.* 2009), and many parts of the ocean are vulnerable to marine heat waves (Frölicher & Laufkötter 2018, Smale *et al.* 2019). Under scenarios where the sea temperature might exceed the thermal range of flying fish and squid (Lluch-Belda *et al.* 2014, Churnside *et al.* 2017, Doubleday & Connell 2018), or affect the distribution and abundance of subsurface predators (DiLorenzo & Miller 2017), masked boobies may have more problems finding prey, with consequent effects on their populations. These effects might not manifest themselves through changes in foraging, but may reduce breeding success leading to population decline (Tompkins *et al.* 2017). Warming has been slow in the tropics, especially in the marine tropics (Belkin 2009, Burrows *et al.* 2011), and long-term studies, including monitoring of breeding success, may be needed to detect the effects of environmental variability.

Sex-related differences

There were no significant sex-related differences in foraging trip parameters of masked boobies at Clarion Island (Chapter 3) or Motu Nui (Chapter 4). This is consistent with previous reports of masked boobies, which showed scarce sexual differences in foraging throughout their range (Weimerskirch *et al.* 2008, Sommerfeld *et al.* 2013, Oppel *et al.* 2015, Machovsky-Capuska *et al.* 2016). The only observed difference was at Motu Nui, where females and males had different isotopic signatures (δ^{13}C and δ^{15}N) in their blood. However, this difference in isotopic signatures between sexes is in contrast to previous reports that found no differences between male and female masked boobies (Young *et al.* 2010a, Mancini *et al.* 2013).

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Different isotopic signatures can be a consequence of dietary components from different trophic levels (Stauss *et al.* 2012, Cleasby *et al.* 2015), suggesting that, even when both sexes appear to forage similarly, female masked boobies at Motu Nui may have been feeding at a higher trophic level or in a different spatial habitat than males. However, the differences were too small to indicate feeding at a different trophic level, but may suggest that they were feeding on different proportions of similar prey species. Similar results have been found for other members of the Sulidae family, such as Australasian gannets (*Morus serrator*) (Ismar *et al.* 2017) and northern gannets (*Morus bassanus*) (Stauss *et al.* 2012). Alternatively, in addition to the $\delta^{13}C$ and $\delta^{15}N$ values relying on the diet of the consumers (Bearhop *et al.* 2004, Cherel *et al.* 2005, Newsome *et al.* 2007), the isotopic signatures might also be affected by physiological and biochemical factors, which are rarely taken into account or tested. Breeding is one of the most challenging periods for birds (Moreno 1989), with physical and physiological effects on the parents (Drent & Daan 1980). Body condition is reduced during incubation in many seabirds (Gaston & Jones 1989, Monaghan *et al.* 1989, Croll *et al.* 1991, Dearborn 2001, Bauch *et al.* 2010), and among Sulids, females may experience higher costs than males (Velando & Alonso-alvarez 2003, González-Medina *et al.* 2017). The sex-related differences in isotopic signatures may thus reflect differences in body condition associated with breeding, rather than differences in foraging and trophic chains between the sexes. It is therefore important to evaluate the relationship between changes in body condition (preferably using plasma metabolites) and stable isotopes in this tropical species in the future.

Breeding stage

Masked boobies at Motu Nui forage further and for longer periods during the incubation period compared with the chick-rearing period (Chapter 4). However, there is currently no consensus on the prevalence of differences in foraging of Sulids in relation to breeding stage. Current information shows that red-footed boobies made greater foraging efforts during incubation than during chick rearing (Mendez *et al.* 2016), but no differences were found between breeding stages in blue-footed boobies (Zavalaga *et al.* 2008), and no conclusions can be drawn for other species because data for different breeding stages have either been pooled together (Weimerskirch *et al.* 2005, 2009b) or the studies only included one breeding stage (Ludynia *et al.* 2010, Zavalaga *et al.* 2010, 2012, Hennicke & Weimerskirch 2014). Further studies are needed to identify the prevalence of foraging differences between breeding stages in Sulids, and to determine if these differences are also related to local oceanographic conditions at the breeding colonies. Given that breeding stage may affect foraging, future studies should aim to use data for birds at the same breeding stage when comparing foraging parameters between sites or years.

7.   Conclusions

This thesis presents the first information on the foraging ecology of masked boobies at Motu Nui and Clarion Island. Local oceanography, sex, and breeding stage affected different aspects of the foraging ecology of this species. Masked boobies from Motu Nui and Clarion Island preyed mainly on flying fish and squid, did not dive deeper than 6 m, and made foraging trips in no specific direction from their colony. This seabird species did not utilize any specific hydrographic features at Motu Nui and Clarion Island to increase their prey encounter rate. There were no differences in foraging ecology between years at either of the two studied colonies of masked boobies. This was attributed to a lack of major differences in environmental conditions within the areas used by masked boobies across years. Foraging ecology was affected by the interaction between sex and breeding stage: females had different isotopic signatures than males, and birds travelled further and longer during the incubation period compared with during the chick-rearing period at Motu Nui. These factors therefore need to be considered when interpreting the foraging characteristics of this seabird. This study provides baseline information for masked boobies at Motu Nui and Clarion Island, and demonstrates the value of local seabird studies for providing information on under-explored pelagic areas in a cost-effective way. Tracking technology complemented by diet, stable isotopes, and satellite data were useful for detecting inconspicuous differences within and between populations. Furthermore, masked boobies were confirmed as a useful species to cover some gaps in knowledge such as food-web structures and changes affecting these ecosystems. Further studies using these techniques and considering factors affecting foraging in tropical seabirds may improve local-based management decisions and help to fill knowledge gaps for tropical ecosystems.

8.   References

Ainley, D., Sydeman, W.J. & Norton, J. **1995**. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Mar. Ecol. Prog. Ser.* 118: 69–79.

Almanza-Rodríguez, H. **2019**. Aves marinas de la isla Clarión, Archipiélago de Revillagigedo: fenología reproductiva y análisis espacial. Bachelor thesis. Universidad de Guadalajara. Mexico

Alonso, H., Granadeiro, J.P., Dias, M.P., Catry, T. & Catry, P. **2018**. Fine-scale tracking and diet information of a marine predator reveals the origin and contrasting spatial distribution of prey. *Prog. Oceanogr.* 162: 1–12.

Ancona, S., Calixto-Albarrán, I. & Drummond, H. **2012**. Effect of El Niño on the diet of a specialist seabird, Sula nebouxii, in the warm eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 462: 261–271.

Anderson, D.J. **1989**. Differential responses of boobies and other seabirds in the Galapagos to the 1986-87 El Niño- Southern Oscillation event. *Mar. Ecol. Prog. Ser.* 52: 209–216.

Ashmole, N.P. **1963**. The regulation of numbers of tropical oceanic birds. *Ibis.* 103: 458–473.

Ashmole, N.P. **1971**. Seabird ecology and the marine environment. In: *Avian Biology* (D. S. Farner & J. R. King, eds). New York and London.

Assali, C., Bez, N. & Tremblay, Y. **2017**. Seabird distribution patterns observed with fishing vessel's radar reveal previously undescribed sub-meso-scale clusters. *Sci. Rep.* 7: 1–10.

Asseid, B.S., Drapeau, L., Crawford, R.J.M., Dyer, B.M., Hija, A., Mwinyi, A.A., Shinula, P. & Upfold, L. **2006**. The food of three seabirds at Latham Island, Tanzania, with observations on foraging by masked boobies *Sula dactylatra*. *African J. Mar. Sci.* 28: 109–114.

Au, D.W.K. & **Pitman**, R.L. **1986**. Seabird interaction with dolphins and tuna in the Eastern Tropical Pacific. *Condor* 88: 304–317.

Ayal, Y. **2007**. Trophic structure and the role of predation in shaping hot desert communities. *J. Arid Environ.* 68: 171–187.

Balber, S.J.M., Milton, D.A., Smith, G.C. & Farmer, M.J. **1995**. Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.* 127: 1–13.

Ballance, L.T. **1995**. Flight energetics of free-ranging Red-footed boobies (*Sula sula*). *Physiol. Zool.* 68: 887–914.

Ballance, L.T., Pitman, R.L. & Reilly, S.B. **1997**. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology* 78: 1502–1518.

Ballance, L.T. & **Pitman**, R.L. **1999**. Foraging ecology of tropical seabirds. *22nd Int. Ornithol. Congr.* 2057–2071.

Ballance, L.T., Pitman, R.L. & Fiedler, P.C. **2006**. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Prog. Oceanogr.* 69: 360–390.

Barrett, R.T. & Krasnov, Y. V. **1996**. Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. *ICES J. Mar. Sci.* 53: 713–722.

Barrett, R.T., Camphuysen, K.C.J., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hu, O., Leopold, M.F., Montevecchi, W.A., Veit, R.R., Hüppop, O., Leopold, M.F., Montevecchi, W.A. & Veit, R.R. **2007**. Diet studies of seabirds: a review and recommendations. *ICES J. Mar. Sci.* 64: 1675–1691.

Bauch, C., Kreutzer, S. & Becker, P.H. **2010**. Breeding experience affects condition: blood metabolite levels over the course of incubation in a seabird. *J. Comp. Physiol.* 180: 835–845.

Beadell, J.S., Schreiber, E.A., Schreiber, R.W., Schenk, G.A. & Doherty Jr, P.F. **2003**. Survival of Brown boobies (*Sula leucogaster*) at Johnston Atoll: a long-term study. *Auk* 120: 811–817.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. & Macleod, H. **2004**. Determining trophic niche width: A novel approach using stable isotope analysis. *J. Anim. Ecol.* 73: 1007–1012.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M. & Boss, E.S. **2006**. Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752–755.

Belkin, I.M. **2009**. Rapid warming of Large Marine Ecosystems. *Prog. Oceanogr.* 81: 207–213.

Bennison, A., Bearhop, S., Bodey, T.W., Votier, S.C., Grecian, W.J., Wakefield, E.D., Hamer, K.C. & Jessopp, M. **2017**. Search and foraging behaviors from movement data: a comparison of methods. *Ecol. Evol.* 8: 13–24.

Birt, V., Birt, T., Goulet, D., Cairns, D. & Montevecchi, W. **1987**. Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar. Ecol. Prog. Ser.* 40: 205–208.

Bocher, P., Cherel, Y. & Hobson, K.A. **2000**. Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar. Ecol. Prog. Ser.* 208: 249–264.

Bolton, M., Conolly, G., Carroll, M., Wakefield, E.D. & Caldow, R. **2019**. A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. *Ibis.* 161: 241–259.

Bond, A.L. & Jones, I.L. **2009**. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. *Mar. Ornithol.* 37: 183–188.

Booth, D.J., Feary, D.A., Luiz, O.J. & Nakamura, Y. **2017**. Tropical marine fishes and fisheries and climate change. In C*limate change impacts on fisheries and aquaculture.a global analysis* (B. F. Phillips, M. Perez-Ramirez, eds). Wiley Blackweel, UK

Boyd, I.L. & Murray, A.W.A. **2001**. Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.* 70: 747–760.

Brattstrom, B.H. **2015**. Food webs and feeding habits on the Revillagigedo Islands, Mexico. *Pacific Sci.* 69: 181–195.

Bugoni, L., McGill, R.A.R. & Furness, R.W. **2008**. Effects of preservation methods on stable isotope signatures in bird tissues. *Rapid Commun. Mass Spectrom.* 22: 2457–2462.

Burger, A.E. & Piatt, J.F. **1990**. Flexible time budgets in breeding Common murres: buffers against variable prey abundance. *Stud. Avian Biol.* 14: 71–83.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J. & Kappel, C. V. **2011**. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334: 652–656.

Cai, W., Borlace, S., Lengaigne, M., Rensch, P. Van, Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L., England, M., Wang, G., Guilyard, E. & Jin, F.-F. **2014**. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Chang.* 4: 111–116.

Cairns, D.K. **1992**. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. *Condor* 94: 811–824.

Calabrese, J.M., Fleming, C.H. & Gurarie, E. **2016**. Ctmm: an R Package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* 7: 1124–1132.

Calenge, C. **2006**. The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197: 516–519.

Castillo-Guerrero, J.A. & Mellink, E. **2011**. Occasional inter-sex differences in diet and foraging behavior of the Blue-footed booby: maximizing chick rearing in a variable environment ? *J. Orni* 152: 269–277.

Castillo-Guerrero, J.A., Lerma, M., Mellink, E., Suazo-Guillén, E. & Peñaloza-Padilla, E.A. **2016**. Environmentally-mediated flexible foraging strategies in Brown boobies in the Gulf of California. *Ardea* 104: 33–47.

Catry, P., Phillips, R.A. & Croxall, J.P. **2005**. Sexual segregation in birds: patterns, processes and implications for conservation. Cambridge University Press.

Chagnon, C., Thiel, M., Antunes, J., Ferreira, J.L., Sobral, P. & Ory, N.C. **2018**. Plastic ingestion and trophic transfer between Easter Island flying fish (*Cheilopogon rapanouiensis*) and yellowfin tuna (*Thunnus albacares*) from Rapa Nui (Easter Island). *Environ. Pollut.* 243: 127–133.

Champagnon, J., Lebreton, J.-R., Drummond, H. & Anderson, D.J. **2018**. Pacific decadal and El Niño oscillations shape survival of a seabird. *Ecology* 95: 1063–1072.

Charnov, E.L. **1976**. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9: 129–136.

Cherel, Y., Hobson, K.A., Bailleul, F., Groscolas, R., Herel, Y.V.E.S.C., Obson, K.E.A.H. & Re, F. **2005**. Nutrition, physiology , and stable isotopes: new information. *Ecology* 86: 2881–2888.

Cherel, Y. & Hobson, K.A. **2007**. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 329: 281–287.

Cherel, Y., Corre, M. Le, Jaquemet, S., Ménard, F., Richard, P. & Weimerskirch, H. **2008**. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar. Ecol. Prog. Ser.* 366: 281–291.

Churnside, J.H., Wells, R.J.D., Boswell, K.M., Quinlan, J.A., Marchbanks, R.D., Mccarty, B.J. & Sutton, T.T. **2017**. Surveying the distribution and abundance of flying fishes and

other epipelagic in the northern Gulf of Mexico using airborne lidar. *Bull. Mar. Sci.* 93: 591–609.

Cisneros-Mata, M.A., Mangin, T., Bone, J., Rodriguez, L., Smith, S.L. & Gaines, S.D. **2019**. Fisheries governance in the face of climate change: Assessment of policy reform implications for Mexican fisheries. *PLoS One* 14: 1–19.

Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M. & Hall-Spencer, J.M. **2010**. The ecology of seamounts: structure, function, and human impacts. *Ann. Rev. Mar. Sci.* 2: 253–278.

Claustre, H. & **Maritorena**, S. **2003**. The many shades of ocean blue. *Science.* 302: 1514–1515.

Claustre, H., Sciandra, A. & Vaulot, D. **2008**. Introduction to the special section bio-optical and biogeochemical conditions in the South East Pacific in late 2004: the BIOSOPE program. *Biogeosciences* 5: 679–691.

Clay, T.A., Phillips, R.A., Manica, A., Jackson, H.A. & Brooke, M.D.L. **2017**. Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Mar. Ecol. Prog. Ser.* 579: 139–155.

Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier, S.C., Bearhop, S. & Hamer, K.C. **2015**. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar. Ecol. Prog. Ser.* 518: 1–12.

CONANP. **2017**. Programa de Manejo Parque Nacional Revillagigedo. 220 pp.

Cook, W.E. **1997**. Avian desert predators. In: *Adaptations of desert organisms* (J.L. Cloudsley-Thompson, ed) Springer, Berlin.

Corman, A., Mendel, B., Voigt, C.C. & Garthe, S. **2016**. Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecol. Evol.* 6: 974–986.

Courbin, N., Besnard, A., Péron, C., Saraux, C., Fort, J., Perret, S., Tornos, J. & Grémillet, D. **2018**. Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. *Ecol. Lett.* 21: 1043–1054.

Cox, S.L., Miller, P.I., Embling, C.B., Scales, K.L., Bicknell, A.W.J.J., Hosegood, P.J., Morgan, G., Ingram, S.N. & Votier, S.C. **2016**. Seabird diving behaviour reveals the functional significance of shelf-sea fronts as foraging hotspots. *R. Soc. Open Sci.* 3.

Croll, D.A., Gaston, A.J. & Noble, D.G. **1991**. Adaptive loss of mass in Thick-billed murres. *Condor* 93: 496–502.

Croxall, J.P., Reid, K. & Prince, P.A. **1999**. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Prog. Ser.* 177: 115–131.

Croxall, J.P., Butchard, S.H.M., Lascelles, B., Statterfsfield, A.J., Sullivan, B., Symes, A. & Taylor, P. **2012**. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22: 1–34.

Cruz, L.L., McGill, R.A.R., Goodman, S.J. & Hamer, K.C. **2012**. Stable isotope ratios of a tropical marine predator: confounding effects of nutritional status during growth. *Mar.*

Biol. 159: 873–880.

Davenport, J. **1994**. How and why do flying fish fly? *Rev. Fish Biol. Fish.* 4: 184–214.

Dearborn, D. **2001**. Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Beh. Ecol.* 2: 200-206.

Dehnhard, N., Achurch, H., Clarke, J., Michel, L.N., Southwell, C., Sumner, M.D., Eens, M. & Emmerson, L. **2019**. High inter- and intraspecific niche overlap among three sympatrically breeding, closely-related seabird species: generalist foraging as an adaptation to a highly variable environment? *J. Anim. Ecol.* 1–16.

DeNiro, M.J. & **Epstein**, S. **1977**. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science.* 21: 261–263.

DeNiro, M.J. & **Epstein**, S. **1981**. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim.* 45: 341–351.

Diamond, T. **1978**. Feeding strategies and population size in tropical seabirds. *Am. Nat.* 112: 215–223.

Dias, M.P., Granadeiro, J.P. & Catry, P. **2012**. Do seabirds differ from other migrants in their travel arrangements? on route strategies of Cory's shearwater during its trans-equatorial journey. *PLoS One* 7: e49376

DiLorenzo, E. & **Miller**, A. **2017**. Forecasting ENSO Impacts in the California Current System. 10: 41.

DiNezio, P.N., Clement, A.C., Vecchi, G.A., Soden, B.J., Kirtman, B.P. & Lee, S.-K. **2009**. Climate response of the equatorial pacific to global warming. *J. Clim.* 22: 4873–4892.

Dingle, H. & **Drake**, V.A. **2007**. What is migration ? *BioSci.* 57: 113-121

DOF. **2017**. Decreto por el que se declara como área natural protegida, con el carácter de parque nacional, la región conocida como Revillagigedo, localizada en el Pacífico Mexicano. *27/11/2017.*

Dorward, D.F. **1962**. Comparative biology of the White booby and the Brown booby *Sula Spp.* At Ascension. *Ibis.* 103: 174–220.

Doubleday, Z.A. & Connell, S.D. **2018**. Weedy futures: can we benefit from the species that thrive in the marine Anthropocene? *Front. Ecol. Env.* 16: 599-608.

Drent, R.H. & **Daan**, S. **1980**. The prudent parent, energetic adjustment in avian breeding. *Ardea* 68: 225–252.

Durant, J.M., Hjermann, D., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M. & Stenseth, N.C. **2009**. Pros and cons of using seabirds as ecological indicators. *Clim. Res.* 39: 115–129.

Elliott, K. **2009**. Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's halo. *Auk* 126: 613–625.

Elliott, K.H., Woo, K., Gaston, A.J., Benvenuti, S., Dall'Antonia, L. & Davoren, G.K. **2008**. Seabird foraging behaviour indicates prey type. *Mar. Ecol. Prog. Ser.* 354: 289–303.

Fernández, P., Anderson, D.J., R, S.P. & Huyvaert, K.P. **2001**. Foraging destinations of three low-latitude albatross (*Phoebastria*) species. *Zool. Soc. London* 254: 391–404.

Fielder, P.C. **1992.** Seasonal climatologies and variability of Eastern Tropical Pacific surface waters. *NOAA Technical report NMFS* 109: 1–66.

Figueroa, J. **2004**. First record of breeding by the Nazca booby *Sula granti* on Lobos de Afuera island, Peru. *Mar. Ornithol.* 32: 117–118.

Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K.E. & Niem, V.H. **1995**. Guía FAO para la identificación de especies para los fines de la pesca. Pacifico, centro-oriental. FAO. Roma.

Flores, M.A., Schlatter, R.P. & Hucke-Gaete, R. **2014**. Seabirds of Easter Island, Salas y Gomez Island and Desventuradas Islands, southeastern Pacific Ocean. *Lat. Am. J. Aquat. Res.* 42: 752–759.

Fowler, C.W. **1999**. Management of multi-species fisheries: from overfishing to sustainability. *ICES J. Mar. Sci.* 56: 927–932.

Friedlander, A.M., Ballesteros, E., Beets, J., Berkenpas, E., Gaymer, C.F., Gorny, M. & Sala, E. **2013**. Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez, Chile. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 23: 515–531.

Frölicher, T.L. & Laufkötter, C. **2018**. Emerging risks from marine heat waves. *Nat. Commun.* 9: 650.

García-Tarrasón, M., Bécares, J., Bateman, S., Arcos, J.M., Jover, L. & Sanpera, C. **2015**. Sex-specific foraging behavior in response to fishing activities in a threatened seabird. *Ecol. Evol.* 5: 2348–2358.

Garriga, J., Palmer, J.R.B., Oltra, A. & Bartumeus, F. **2016**. Expectation-maximization binary clustering for behavioural annotation. *PLoS One* 11: 1–12.

Garthe, S., Benvenuti, S. & Montevecchi, W.A. **2000**. Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proc. R. Soc. B Biol. Sci.* 267: 1717–1722.

Garthe, S., Montevecchi, W.A., Chapdelaine, G., Rail, J.F. & Hedd, A. **2007**. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Mar. Biol.* 151: 687–694.

Gaston, A.J. & **Jones**, I.L. **1989**. The relative importance of stress and programmed anorexia in determining mass loss by incubating Ancient murrelets. *Auk* 106: 653–658.

Gaston, A.J. & **Powell**, D.W. **1989**. Natural incubation, egg neglect, and hatchability in the Ancient Murrelet. *Auk* 106: 433–438.

Gianuca, D., Votier, S.C., Pardo, D., Wood, A.G., Sherley, R.B., Ireland, L., Choquet, R., Pradel, R., Townley, S., Forcada, J., Tuck, G.N. & Phillips, R.A. **201**9. Sex-specific effects of fisheries and climate on the demography of sexually dimorphic seabirds. *J. Anim. Ecol.* 1366–1378.

Gilardi, J.D. **1992**. Sex-specific foraging distributions of brown boobies in the Eastern Tropical Pacific. *Waterbirds* 15: 148–151.

Gilmour, M.E., Castillo-Guerrero, J.A., Fleishman, A.B., Hernández-Vázquez, S., Young, H.S. & Shaffer, S.A. **2018**. Plasticity of foraging behaviors in response to diverse environmental conditions. *Ecosphere* 9: e02301.

Giraldeau, L.-A. **2008**. Solitary foraging strategies. In: *Behavioral ecology* (E. Danchin, L-A Giraldeau, F Cézilly, eds). Oxford University Press, Oxford.

Gonzáles-Solís, J. & Shaffer, S.A. **2009**. Spatiotemporal dynamics of seabirds in the marine

environment. *Mar. Ecol. Prog. Ser.* 391: 116–306.

González-Medina, E., Castillo-Guerrero, J.A.J.A., Herzka, S.Z., Fernández, G. & Fernandez, G. **2017**. Flexibility in food resource allocation in parents and selectivity for offspring: variations in δ^{15}N and δ^{13}C values during breeding of the Blue-footed booby. *Mar. Biol.* 164: 38.

González-Medina, E., Castillo-Guerrero, J.A., Masero, J.A. & Fernández, G. **2020**. Mate selection based on labile traits affects short-term fitness in a long-lived seabird. *Proceedings. Biol. Sci.* 287: 20192578.

González-Solís, J., Croxall, J.P. & Wood, A.G. **2000**. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, Macronectes halli, during incubation. *Oikos* 90: 390–398.

Granadeiro, J.P., Campioni, L. & Catry, P. **2018**. Albatrosses bathe before departing on a foraging trip: implications for risk assessments and marine spatial planning. *Bird Conserv. Int.* 28: 208–215.

Grecian, W.J., Lane, J. V., Michelot, T., Wade, H.M. & Hamer, K.C. **2018**. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *J. R. Soc. Interface* 15: 20180084.

Grémillet, D. & Boulinier, T. **2009**. Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar. Ecol. Prog. Ser.* 391: 121–137.

Guillemette, M., Grégoire, F., Bouillet, D., Rail, J.F., Bolduc, F., Caron, A. & Pelletier, D. **2018**. Breeding failure of seabirds in relation to fish depletion: is there one universal threshold of food abundance? *Mar. Ecol. Prog. Ser.* 587: 235–245.

Hagihara, R., Jones, R.E., Sheppard, J.K., Hodgson, A.J. & Marsh, H. **2011**. Minimizing errors in the analysis of dive recordings from shallow-diving animals. *J. Exp. Mar. Bio. Ecol.* 399: 173–181.

Hamer, K.C., Schreiber, E.A. & Burger, J. **2002**. Breeding biology, life histories, and life history-environment interactions in seabirds. In: *Biology of marine birds* (Schreiber EA, Burger J eds). CRC Press, NY.

Harding, A., Piatt, J., Schmutz, J., Shultz, M., Van Pelt, T., Kettle, A. & Speckman, S. **2007**. Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology* 88: 2024–2033.

Harrison, C.S., Hida, T.S. & Seki, M.P. **1983**. The diet of Brown booby *Sula leucogaster* and Masked Booby *Sula dactylatra* on Rose Atoll, Samoa. *Ibis.* 588–590.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. **2011**. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* 80: 4–18.

Hennicke, J.C. & **Weimerskirch**, H. **2014**. Coping with variable and oligotrophic tropical waters: foraging behaviour and flexibility of the Abbott's booby *Papasula abbotti*. *Mar. Ecol. Prog. Ser.* 499: 259–273.

Hertel, F. & **Ballance**, L.T. **1999**. Wing ecomorphology of seabirds from Johnston Atoll. *Condor* 101: 549–556.

Hipfner, J.M., Tranquilla, L.A.M., Addison, B. & Hobson, K.A. **2013**. Trophic responses to

the hatching of offspring in a central-place foraging seabird. *J. Ornithol.* 154: 965–970.

Hobson, K. A. & **Clark**, R.G. **1992**. Assessing avian diets using stable isotopes turnover of ^{13}C in tissues. *Condor* 94: 189–197.

Hobson, K.A. **1993**. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* 95: 7–18.

Hobson, K.A. **1999**. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314–326.

Hobson, K.A., Piatt, J.F. & Pitocchelli, J. **1994**. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* 63: 786–798.

Hoegh-Guldberg, O. & **Bruno**, J.F. **2010**. The impact of climate change on the world's marine ecoystems. *Science* 328: 1523–1528.

Hovinen, J.E.H., Tarroux, A., Ramírez, F., Forero, M. & Descamps, S. **2019**. Relationships between isotopic ratios, body condition and breeding success in a high arctic seabird community. *Mar. Ecol. Prog. Ser.* 613: 183–195.

Inger, R. & **Bearhop**, S. **2008**. Applications of stable isotope analyses to avian ecology. *Ibis.* 150: 447–461.

Ishikawa, K. & **Watanuki**, Y. **2002**. Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. *J. Ethol.* 20: 49–54.

Ismar, S.M.H., Raubenheimer, D., Bury, S.J., Millar, C.D. & Hauber, M.E. **2017**. Sex-specific foraging during parental care in a size-monomorphic seabird, the Australasian gannet (*Morus serrator*). *Wilson.* 129: 139–147.

Jahncke, J. & **Goya**, E. **2000**. Responses of three booby species to El Niño 1997-1998. *Waterbirds* 23: 102–108.

Jaquemet, S., Le Corre, M., Marsac, F., Potier, M. & Weimerskirch, H. **2005**. Foraging habitats of the seabird community of Europa Island (Mozambique Channel). *Mar. Biol.* 147: 573–582.

Jaramillo, A., Johnson, M.T.J., Rothfels, C.J. & Johnson, R.A. **2008**. The native and exotic avifauna of Easter Island: then and now. *Bol. Chil. Ornitol.* 14: 8–21.

Jenouvrier, S. **2013**. Impacts of climate change on avian populations. *Glob. Chang. Biol.* 19: 1–68.

Jovani, R., Lascelles, B., Garamszegi, L.Z., Mavor, R., Thaxter, C.B. & Oro, D. **2016**. Colony size and foraging range in seabirds. *Oikos* 125: 968–974.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P.W., Bograd, S.J. & Costa, D.P. **2010**. Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Prog. Oceanogr.* 86: 246–260.

Kappes, M.A., Weimerskirch, H., Pinaud, D. & Le Corre, M. **2011**. Variability of resource partitioning in sympatric tropical boobies. *Mar. Ecol. Prog. Ser.* 441: 281–294.

Kitaysky, A.S., Hunt Jr, G.L., Flint, E.N., Rubega, M.A. & Decker, M.B. **2000**. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.* 206: 283–296.

Kohno, H., Mizutani, A., Yoda, K.. & Yamamoto, T. **2019**. Movements and activity characteristics of the Brown booby *Sula leucogaster* during the non-breeding period.

*Mar. Ornith.*47: 169–174.

Lacerda, L., Goyanna, F., MF, B. & Silva, G. **2017**. Mercury concentrations in Tuna (*Thunnus albacares* and *Thunnus obesus*) from the Brazilian Equatorial Atlantic Ocean. *Bull. Environ. Contam. Toxicol.* 98: 149–155.

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S., Torres, L., Hedd, A., Le Corre, M., Phillips, R.A., Scott, S.A., Weimerskirch, H. & Small, C. **2016**. Applying global criteria to tracking data to define important areas for marine conservation. *Divers. Distrib.* 22: 422–431.

Lescroël, A. & Bost, C. **2005**. Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Mar. Ecol. Prog. Ser.* 302: 245–261.

Lewallen, E.A., Van Wijnen, A.J., Bonin, C.A. & Lovejoy, N.R. **2018**. Flyingfish (Exocoetidae) species diversity and habitats in the eastern tropical Pacific Ocean. *Mar. Biodivers.* 48: 1755–1765.

Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. **2001**. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412: 816–819.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S. & Hamer, K.C. **2002**. Sex-specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. B Biol. Sci.* 269: 1687–1693.

Lewis, S., Harris, M.P., Wanless, S., Sherratt, T.N. & Hamer, K.C. **2003**. Contrasting diet quality of Northern gannets *Morus bassanus* at two colonies. *Ardea* 91: 167–176.

Lewis, S., Schreiber, E. A., Daunt, F., Schenk, G. A., Orr, K., Adams, A., Wanless, S. & Hamer, K.C. **2005**. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis.* 147: 408–414.

Lluch-Belda, D., Lluch-Cota, D.B., Lluch-Cota, S.E., Ramírez-Rodríguez, M. & Salinas-Zavala, C. **2014**. Fisheries of Northwest Mexico. In: *Conservation Science in Mexico`s Northwest Ecosystem Status and Trends in the Gulf of California* (E. V Wehncke, J. R. Lara-Lara, S. Álvarez-Borrego, & E. Ezcurra, eds). UC Mexis, INECC, SEMARNAT. Mexico.

Lluch-Cota, S.E. **2000**. Coastal upwelling in the eastern Gulf of California. *Oceanol. Acta* 23: 731–740.

Longhurst, A.R. & Pauly, D. **1987**. Ecology of tropical oceans. Academic Press, San Diego

Longhurst, A., Sathyendranath, S., Platt, T. & Caverhill, C. **1995**. An estimate of global primary production in the ocean from satellite radiometer data. *J. Plankton Res.* 17: 1245–1271.

Louzao, M., Wiegand, T., Bartumeus, F. & Weimerskirch, H. **2014**. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Mov. Ecol.* 2: 8.

Ludynia, K., Garthe, S. & Luna-Jorquera, G. **2010**. Distribution and foraging behaviour of the Peruvian booby (*Sula variegata*) off northern Chile. *J. Ornithol.* 151: 103–111.

Luna, N., Varela, A.I., Brokordt, K. & Luna-Jorquera, G. **2018**. Assessing potential predation risk by introduced predators on unattended eggs in the Red-tailed tropicbird, *Phaethon rubricauda*, on Rapa Nui (Easter Island) . *Trop. Conserv. Sci.* 11:1–18

MacArthur, R.H. & **Pianka**, E.R. **1966**. On optimal use of a patchy environment. *Am. Nat.* 100: 603–609.

Machovsky Capuska, G.E., Vaughn, R.L., Würsig, B., Katzir, G. & Raubenheimer, D. **2011**. Dive strategies and foraging effort in the Australasian gannet *Morus serrator* revealed by underwater videography. *Mar. Ecol. Prog. Ser.* 442: 255–261.

Machovsky-Capuska, G.E., Miller, M.G.R., Silva, F.R.O., Amiot, C., Stockin, K.A., Senior, A.M., Schuckard, R., Melville, D., Rubenheimer D.,. **2018**. The nutritional nexus: linking niche, habitat variability and prey composition in a generalist marine predator. *J. Anim. Ecol.* 87: 1286–1298.

Machovsky-Capuska, G.E., Senior, A.M., Benn, E.C., Tait, A.H., Schuckard, R., Stockin, K.A., Cook, W., Ogle, M., Barna, K., Melville, D., Wright, B., Purvin, C. & Raubenheimer, D. **2016**. Sex-specific macronutrient foraging strategies in a highly successful marine predator: the Australasian gannet. *Mar. Biol.* 163: 1–14.

Mancini, P.L., Bond, A.L., Hobson, K.A., Duarte, L.S. & Bugoni, L. **2013**. Foraging segregation in tropical and polar seabirds: testing the intersexual competition hypothesis. *J. Exp. Mar. Bio. Ecol.* 449: 186–193.

Mannocci, L., Catalogna, M., Dorémus, G., Laran, S., Lehodey, P., Massart, W., Monestiez, P., Van Canneyt, O., Watremez, P. & Ridoux, V. **2014**. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre. *Prog. Oceanogr.* 120: 383–398.

Marchant, S. & **Higgins**, P. **1990**. Orden Pelecaniformes. In: *Handbook of Australian, New Zealand & Antarctic Birds*. Oxford University Press, Melbourne.

Marin, M. & **Caceres**, P. **2010**. Sobre las aves de isla de Pascua. *Boletín del Mus. Nac. Hist. Nat.* 59: 75–95.

McPhaden, M.J., Zebiak, S.E. & Glantz, M.H. **2006**. ENSO as an integrating concept in earth science. *Science.* 314: 1740–1745.

Mecho, A., Easton, E.E., Sellanes, J., Gorny, M. & Mah, C. **2019**. Unexplored diversity of the mesophotic echinoderm fauna of the Easter Island ecoregion. *Mar. Biol.* 166: 1–17.

Mellink, E. **2003**. Effects of the 1997-1998 El Nño and 1998-1999 La Niña events on breeding waterbirds and sea lions in the Upper Gulf of California, México. *Geofis. Int.* 42: 539–546.

Mendez, L., Cotté, C., Prudor, A. & Weimerskirch, H. **2016**. Variability in foraging behaviour of Red-footed boobies nesting on Europa Island. *Acta Oecologica* 72: 87–97.

Mendez, L., Borsa, P., Cruz, S., De Grissac, S., Hennicke, J., Lallemand, J., Prudor, A. & Weimerskirch, H. **2017**. Geographical variation in the foraging behaviour of the pantropical Red-footed booby. *Mar. Ecol. Prog. Ser.* 568: 217–230.

Miller, M., Silva, F.R.O., Machovsky-Capuska, G.E. & Congdon, B.C. **2018**. Sexual segregation in tropical seabirds: drivers of sex-specific foraging in the Brown booby *Sula leucogaster*. *J. Ornithol.* 159: 425–437.

Monaghan, A.P., Uttley, J.D., Burns, M.D., Thaine, C. & Blackwood, J. **1989**. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea*. *J. Anim. Ecol.* 58: 261–274.

Monahan, W.B. & **Fisichelli**, N.A. **2014**. Climate exposure of US national parks in a new era of change. *PLoS One* 9: e101302.

Montevecchi, W.A., Benvenuti, S., Garthe, S., Davoren, G.K. & Fifield, D. **2009**. Flexible foraging tactics by a large opportunistic seabird preying on forage-and large pelagic fishes. *Mar. Ecol. Prog. Ser.* 385: 295–306.

Moraga, J., Valle-Levinson, A. & Olivares, J. **1999**. Hydrography and geostrophy around Easter Island. *Deep. Res. Part I Oceanogr. Res. Pap.* 46: 715–731.

Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J. & Karl, D. **2010**. Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proc. Natl. Acad. Sci.* 107: 9707–9711.

Morel, A., Claustre, H. & Gentili, B. **2010**. The most oligotrophic subtropical zones of the global ocean: Similarities and differences in terms of chlorophyll and yellow substance. *Biogeosciences* 7: 3139–3151.

Moreno, J. **1989**. Strategies of mass change in breeding birds. *Biol. J. Linn. Soc.* 37: 297–310.

Mott, R. & **Clarke**, R.H. **2018**. Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu* 118: 235–346.

Muramatsu, K., Yamamoto, J., Abe, T., Sekiguchi, K., Hoshi, N. & Sakurai, Y. **2013**. Oceanic squid do fly. *Mar. Biol.* 160: 117–1175.

Nager, R.G., Monaghan, P. & Houston, D.C. **2001**. The cost of egg production: Increased egg production reduces future fitness in gulls. *J. Avian Biol.* 32: 159–166.

Navarro, J., Moreno, R., Braun, L., Sanpera, C. & Hennicke, J.C. **2014**. Resource partitioning between incubating and chick-rearing Brown boobies and Red-tailed tropicbirds on Christmas Island. *Zool. Stud.* 53: 27.

Nelson, J.B. **1978**. *The Sulidae: Gannets and Boobies*. Oxford University Press, Oxford.

Newsome, S.D., Rio, Martinez del, C., Bearhop, S. & Phillips, D.L. **2007**. A niche for isotope ecology. *Front. Ecol. Environ.* 5: 429–436.

Newton, I. **2012**. Obligate and facultative migration in birds: ecological aspects. *J. Ornithol.* 153: 117-180

O'Farrell, S., Sanchirico, J.N., Spiegel, O., Depalle, M., Haynie, A.C., Murawski, S.A., Perruso, L. & Strelcheck, A. **2019**. Disturbance modifies payoffs in the explore-exploit trade-off. *Nature.* 10: 1–9.

Oppel, S., Beard, A., Fox, D., Mackley, E., Leat, E., Henry, L., Clingham, E., Fowler, N., Sim, J., Sommerfeld, J., Weber, N., Weber, S. & Bolton, M. **2015**. Foraging distribution of a tropical seabird supports Ashmole's hypothesis of population regulation. *Behav. Ecol. Sociobiol.* 69: 915–926.

Oppel, S., Weber, S., Weber, N., Fox, D., Leat, E., Sim, J., Sommerfeld, J., Bolton, M., Broderick, A.C. & Godley, B.J. **2017**. Seasonal shifts in foraging distribution due to individual flexibility in a tropical pelagic forager, the Ascension frigatebird. *Mar. Ecol. Prog. Ser.* 585: 199–212.

Oppel, S., Bolton, M., Carneiro, A.P.B., Dias, M.P., Green, J.A., Masello, J.F., Phillips, R.A., Owen, E., Quillfeldt, P., Beard, A., Bertrand, S., Blackburn, J., Boersma, P.D., Borges, A., Broderick, A.C., Catry, P., Cleasby, I., Clingham, E., Creuwels, J., Crofts, S.,

Cuthbert, R.J., Dallmeijer, H., Davies, D., Davies, R., Dilley, B.J., Dinis, H.A., Dossa, J., Dunn, M.J., Efe, M.A., Fayet, A.L., Figueiredo, L., Frederico, A.P., Gjerdrum, C., Godley, B.J., Granadeiro, J.P., Guilford, T., Hamer, K.C., Hazin, C., Hedd, A., Henry, L., Hernández-Montero, M., Hinke, J., Kokubun, N., Leat, E., Tranquilla, L.M.F., Metzger, B., Militão, T., Montrond, G., Mullié, W., Padget, O., Pearmain, E.J., Pollet, I.L., Pütz, K., Quintana, F., Ratcliffe, N., Ronconi, R.A., Ryan, P.G., Saldanha, S., Shoji, A., Sim, J., Small, C., Soanes, L., Takahashi, A., Trathan, P., Trivelpiece, W., Veen, J., Wakefield, E., Weber, N., Weber, S., Zango, L., González-Solís, J. & Croxall, J. **2018**. Spatial scales of marine conservation management for breeding seabirds. *Mar. Policy* 98: 37–46.

Oro, D., Torres, R., Rodríguez, C. & Drummond, H. **2010**. Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology* 91: 1205–1214.

Oro, D. **2014**. Seabirds and climate: knowledge, pitfalls, and opportunities. *Front. Ecol. Evol.* 2: 79.

Oro, D., Álvarez, D. & Velando, A. **2018**. Complex demographic heterogeneity from anthropogenic impacts in a coastal marine predator. *Ecol. Appl.* 28: 612–621.

Owen, E., Daunt, F., Moffat, C., Elston, D.A., Wanless, S. & Thompson, P. **2013**. Analysis of fatty acids and fatty alcohols reveals seasonal and sex-specific changes in the diets of seabirds. *Mar. Biol.* 160: 987–999.

Oxenford, H.A., Mahon, R. & Hunte, W. **1995**. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. *Mar. Ecol. Prog. Ser.* 117: 11–23.

Paiva, V.H., Geraldes, P., Ramírez, I., Meirinho, A., Garthe, S. & Ramos, J.A. **2010**. Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Mar. Ecol. Prog. Ser.* 398: 259–274.

Paiva, V.H., Pereira, J., Ceia, F.R. & Ramos, J.A. **2017**. Environmentally driven sexual segregation in a marine top predator. *Sci. Rep.* 7: 1–11.

Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson, A.L., Grey, J., Kelly, D.J. & Inger, R. **2013**. Bayesian stable isotope mixing models. *Environmetrics* 24: 387–399.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S. & Reid, J.B. **2008**. Seabirds as indicators of the marine environment. *ICES J. Mar. Sci.* 65: 1520–1526.

Patrick, S.C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W.J., Bodey, T.W., Hamer, K.C., Wakefield, E., Le Nuz, M. & Votier, S.C. **2014**. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* 123: 33–40.

Patrick, S.C. & **Weimerskirch**, H. **2014**. Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biol. Lett.* 10: 20140630.

Peck-Richardson, A.G., Lyons, D.E., Roby, D.D., Cushing, D.A. & Lerczak, J.A. **2018**.

Three-dimensional foraging habitat use and niche partitioning in two sympatric seabird species, *Phalacrocorax auritus* and *P . penicillatus*. *Mar. Ecol. Prog. Ser.* 586: 251–264.

Péron, C., Weimerskirch, H. & Bost, C.A. **2012**. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc. R. Soc. B* 279: 2515–2523.

Petersen, A.J. **1955**. The breeding cycle in the bank swallow. *Wilson* 67: 235–286.

Phillips, D.L., Newsome, S.D. & Gregg, J.W. **2005**. Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144: 520–527.

Pichegru, L., Cook, T., Handley, J., Voogt, N., Watermeyer, J., Nupen, L. & McQuaid, C.D. **2013**. Sex-specific foraging behaviour and a field sexing technique for endangered African penguins. *Endanger. Species Res.* 19: 255–264.

Pinet, P., Jaquemet, S., Phillips, R.A. & Le Corre, M. **2012**. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim. Behav.* 83: 979–989.

Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N. & Santos, R.S. **2007**. *Seamounts: Ecology, Fisheries & Conservation*. Blackwell publishing, Oxford

Pitman, R.L. & **Jehl**, J.R. **1998**. Geographic variation and reassessment of species limits in the 'masked' boobies of the Easter Pacific Ocean. *Wilson.* 110: 155–170.

Poli, C.L., Harrison, A.-L., Vallarino, A., Gerard, P.D. & Jodice, P.G.R. **2017**. Dynamic oceanography determines fine scale foraging behavior of Masked boobies in the Gulf of Mexico. *PLoS One* 12: e0178318.

Priddel, D., Olsor, S. & Wheeler, R. **2005**. Breeding biology of Masked boobies (*Sula dactylatra tasmani*) on Lord Howe Island, Australia. *Emu* 105: 105–113.

Pyke, G.H., Pulliam, H.R. & Charnov, E. **1977**. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52: 137–154.

Quillfeldt, P., Schroff, S., van Noordwijk, H.J., Michalik, A., Ludynia, K. & Masello, J.F. **2011**. Flexible foraging behaviour of a sexually dimorphic seabird: large males do not always dive deep. *Mar. Ecol. Prog. Ser.* 428: 271–287.

Quillfeldt, P. & **Masello**, J.F. **2013**. Impacts of climate variation and potential effects of climate change on South American seabirds - a review. *Mar. Biol. Res.* 9: 337–357.

Randall, J.E. & **Cea**, A. **2010**. *Shore fishes of Easter Island*. University of Hawaii Press, Honolulu.

Raya Rey, A., Pütz, K., Scioscia, G., Lüthi, B. & Schiavini, A. **2012**. Sexual differences in the foraging behaviour of Magellanic penguins related to stage of breeding. *Emu* 112: 90–96.

Reboredo-Segovia, A.L., Romano, D. & Armsworth, P.R. **2020**. Who studies where? Boosting tropical conservation research where it is most needed. *Front. Ecol. Environ.* 1–8.

Reid, J.L., Brinton, E., Fleminger, A., Venrick, E.L. & Mcgowan, J.A. **1978**. Ocean circulation and marine life. In: *Advances in Oceanography*. (H. Charnock, G. Deacon, eds). Springer, Boston.

Reintjes, G., Tegetmeyer, H.E., Bürgisser, M., Orlić, S., Tews, I., Zubkov, M., Voß, D.,

Zielinski, O., Quast, C., Glöckner, F.O., Amann, R., Ferdelman, T.G. & Fuchs, B.M. **2019**. On site analysis of bacterial communities of the ultra-oligotrophic South Pacific Gyre. *Appl. Environ. Microbiol.* 85: 14

Reynolds, S.J., Martin, G.R., Dawson, A., Wearn, C.P. & Hughes, B.J. **2014**. The sub-annual breeding cycle of a tropical seabird. *PLoS One* 9: e93582.

Ribic, C.A. & **Ainley**, D.G. **1997**. The relationships of seabird assemblages to physical habitat features in Pacific equatorial waters during spring 1984 – 1991. *ICES J. Mar. Sci.* 54: 593–599.

Riotte-Lambert, L. & Matthiopoulos, J. **2020**. Environmental predictability as a cause and consequence of animal movement. *Trends Ecol. Evol.* 35: 163–174.

Rodrigo, C., Díaz, J. & González-Fernández, A. **2014**. Origin of the Easter Submarine Alignment: morphology and structural lineaments. *Lat. Am. J. Aquat. Res.* 42: 857–870.

Santos, C.D., Campos, L.F.A.S. & Efe, M.A. **2019**. Foraging habitat choice of White-tailed Tropicbirds revealed by fine-scale GPS tracking and remote sensing. *PeerJ* 7: e6261.

Schalles, J. **2006**. Remote sensing of aquatic coastal ecosystem processes. In: *Remote sensing of aquatic coastal ecosystem processes: science and management applications* (L.L. Richardson & E.F. LeDrew, eds), Springer, Netherlands.

Schreiber, R.W. & **Hensley**, D.A. **1976**. The diets of *Sula dactylatra*, *Sula sula*, and *Fregata minor* on Christmas Island, Pacific Ocean. *Pacific Sci.* 241–248.

Schreiber, E.A. & **Schreiber**, R.W. **1989**. Insights into seabird ecology from a global 'natural experiment'. *Natl. Geogr. Res.* 5: 64–81.

Shaffer, S.A., Costa, D.P. & Weimerskirch, H. **2003**. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Funct. Ecol.* 17: 66–74.

Shealer, D.A. **2002**. Foraging behavior and food of seabirds. In: *Biology of marine birds* (E. A. Schreiber & J. Burger, eds), CRC Press. USA

Shoji, A., Aris-Brosou, S., Fayet, A., Padget, O., Perrins, C. & Guilford, T. **2015**. Dual foraging and pair coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. *J. Exp. Biol.* 218: 2116–2123.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L. V, Benthuysen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Gupta, A. Sen, Payne, B.L. & Moore, P.J. **2019**. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Chang.* 9: 306–312.

Soanes, L.M., Bright, J.A., Carter, D., Dias, M.P., Fleming, T., Gumbs, K., Hughes, G., Mukhida, F. & Green, J.A. **2016**. Important foraging areas of seabirds from Anguilla, Caribbean: Implications for marine spatial planning. *Mar. Policy* 70: 85–92.

Sommerfeld, J., Kato, A., Ropert-Coudert, Y., Garthe, S. & Hindell, M.A. **2013**. The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. *J. Avian Biol.* 44: 531–540.

Sommerfeld, J., Kato, A., Ropert-Coudert, Y., Garthe, S., Wilcox, C. & Hindell, M.A. **2015**. Flexible foraging behaviour in a marine predator the Masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions. *J. Exp. Mar. Bio. Ecol.*

463: 79–86.

Spear, L.B., Ballance, L.T. & Ainley, D.G. **2001**. Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the equatorial front. *Mar. Ecol. Prog. Ser.* 219: 275–289.

Spear, L.B., Ainley, D.G. & Walker, W.A. **2007**. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. *Stud. Avian Biol.* 35: 1–99.

Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E., Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J.J. & Votier, S.C. **2012**. Sex-specific foraging behaviour in northern gannets *Morus bassanus*: Incidence and implications. *Mar. Ecol. Prog. Ser.* 457: 151–162.

Steeves, T.E., Anderson, D.J. & Friesen, V.L. **2005**. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the Masked booby (*Sula dactylatra*). *Mol. Ecol.* 14: 3877–3887.

Stoffel, M.A., Nakagawa, S. & Schielzeth, H. **2017**. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* 8: 1639–1644.

Suryan, R.M., Santora, J.A. & Sydeman, W.J. **2012**. New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar. Ecol. Prog. Ser.* 451: 213–225.

Swan, G.J.F., Bearhop, S., Redpath, S.M., Silk, M.J., Goodwin, C.E.D., Inger, R. & McDonald, R.A. **2020**. Evaluating Bayesian stable isotope mixing models of wild animal diet and the effects of trophic discrimination factors and informative priors. *Methods Ecol. Evol.* 11: 139–149.

Tarburton, M.K. **2018**. Evidence for year-round breeding of birds in the Samoan islands, in the context of the Australasian and South Pacific regions. *Notornis* 65: 92–108.

Teo, S.L.H.H., Boustany, A.M. & Block, B.A. **2007**. Oceanographic preferences of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Mar. Biol.* 152: 1105–1119.

Testa, G. **2014**. Variabilidad espacio-temporal de clorofila-a superficial e influencia de los montes submarinos en la Eastern Seamount Chain. Bachelor thesis, Universidad Católica de Valencia, Spain

Tompkins, E.M., Townsend, H.M. & Anderson, D.J. **2017**. Decadal-scale variation in diet forecasts persistently poor breeding under ocean warming in a tropical seabird. *PLoS One* 12: e0182545.

Tremblay, Y. & **Cherel**, Y. **2003**. Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Mar. Ecol. Prog. Ser.* 251: 279–297.

Trenberth, K.E. & **Hoar**, T.J. **1997**. El Niño and climate change. *Geophys. Res. Lett.* 24: 3057–3060.

Valencia-Gasti, J.A., Baumgartner, T. & Durazo, R. **2015**. Effects of ocean climate on life cycles and distribution of small pelagic fishes in the California Current System off Baja California. *Ciencias Mar.* 41: 315–348.

Vandenabeele, S.P., Shepard, E.L., Grogan, A. & Wilson, R.P. **2012**. When three per cent may not be three per cent; device-equipped seabirds experience variable flight

constraints. *Mar. Biol.* 159: 1–14.

Vargas, F.H., Harrison, S., Rea, S. & Macdonald, D.W. **2006**. Biological effects of El Niño on Galapagos penguin. *Biol. Conserv.* 127: 107–114.

Velando, A. & Alonso-alvarez, C. **2003**. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the Blue-footed booby. *J. Anim. Ecol.* 72: 846–856.

Velarde, E., Anderson, D.W. & Ezcurra, E. **2019**. Seabird monitoring provides essential information on the state of marine ecosystems. *Science.* 365: 116–117.

Velarde, E., Ezcurra, E., Cisneros-Mata, M.A. & Lavín, M. **2004**. Seabird ecology, El Niño anomalies, and prediction of sardine fisheries in the Gulf of California. *Ecol. Appl.* 14: 607–615.

Velarde, E., Tordesillas, M.S., Vieyra, L. & Esquivel, R. **1994**. Seabirds as indicators of important fish populations in the Gulf of California. *CalCOFI Rep* 35: 137–143.

Venter, J.A., Prins, H.H.T., Mashanova, A. & Slotow, R. **2017**. Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage. *PeerJ* 5: e3178.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

Wanless, R.M., Aguirre-Muñoz, A., Angel, A., Jacobsen, J.K., Keitt, B.S. & McCann, J. **2009**. Birds of Clarion Island, Revillagigedo Archipelago, Mexico. *Wilson.* 121: 745–751.

Wearmouth, V.J. & Sims, D.W. **2008**. Sexual segregation in marine fish , reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* 54: 2–3.

Weimerskirch, H., Inchausti, P., Guinet, C., Barbraud, C., Weimerskirch, H., Inchiasti, P., Guinet, C. & Barbradu, C. **2003**. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarct. Sci.* 15: 249–256.

Weimerskirch, H., Corre, M. Le, Jaquemet, S. & Marsac, F. **2005**. Foraging strategy of a tropical seabird, the Red- footed booby, in a dynamic marine environment. *Mar. Ecol. Prog. Ser.* 288: 251–261.

Weimerskirch, H., Le, Æ.M., Le Corre, M., Ropert-Coudert, Y., Kato, A. & Marsac, F. **2006**. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the Red-footed booby. *Oecologia* 146: 681–691.

Weimerskirch, H. **2007**. Are seabirds foraging for unpredictable resources? *Deep Sea Res.* 54: 211–223.

Weimerskirch, H., Le Corre, M. & Bost, C.A. **2008**. Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Mar. Ecol. Prog. Ser.* 362: 291–302.

Weimerskirch, H., Le Corre, M., Gadenne, H., Pinaud, D., Kato, A., Ropert-Coudert, Y. & Bost, C.A. **2009a**. Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia* 161:

637–649.

Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. **2009b**. Species- and sex-specific differences in foraging behaviour and foraging zones in Blue-footed and Brown boobies in the Gulf of California. *Mar. Ecol. Prog. Ser.* 391: 267–278.

Weimerskirch, H., Bertrand, S., Silva, J., Bost, C. & Peraltilla, S. **2012**. Foraging in Guanay cormorant and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System. *Mar. Ecol. Prog. Ser.* 458: 231–245.

Williams, C.T., Buck, C.L., Sears, J. & Kitaysky, A.S. **2007**. Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. *Oecologia* 153: 11–18.

Wilson, R.P. & McMahon, C.R. **2006**. Measuring devices on wild animals: what constitutes acceptable practice? *Front. Ecol. Environ.* 4: 147–154.

Wingfield, J.C., Hau, M., Boersma, P.D., Romero, L.M. & Hillgarth, N. **2018**. Effects of El Niño and La Niña Southern Oscillation events on the adrenocortical responses to stress in birds of the Galapagos Islands. *Gen. Comp. Endocrinol.* 259: 20–33.

Winner, K., Noonan, M.J., Fleming, C.H., Olson, K.A., Mueller, T., Sheldon, D. & Calabrese, J.M. **2018**. Statistical inference for home range overlap. *Methods Ecol. Evol.* 9: 1679–1691.

Xavier, J.C. & **Croxall**, J.P. **2005**. Sexual differences in foraging behaviour and diets: a case study of wandering albatrosses. In: *Sexual segregation in vertebrates: ecology of the two sexes* (K. E. Ruckstuhl & P. Neuhaus, eds), Cambridge University Press, UK

Young, H.S., Mccauley, D.J., Dirzo, R., Dunbar, R.B. & Shaffer, S.A. **2010a**. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Mar. Ecol. Prog. Ser.* 416: 285–294.

Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R. & Block, B.A. **2010b**. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Mar. Ecol. Prog. Ser.* 403: 291–301.

Zavalaga, C.B., Benvenuti, S., Dall'Antonia, L. & Emslie, S.D. **2007**. Diving behavior of Blue-footed boobies *Sula nebouxii* in northern Peru in relation to sex, body size and prey type. *Mar. Ecol. Prog. Ser.* 336: 291–303.

Zavalaga, C.B., Benvenuti, S., Antonia, L.D. & Emslie, S.D. **2008**. Foraging areas of breeding Blue-footed boobies *Sula nebouxii* in northern Peru, as determined by direction recorders. *J. Avian Biol.* 39: 405–412.

Zavalaga, C.B., Halls, J.N., Mori, G.P., Taylor, S.A. & Omo, G.D. **2010**. At-sea movement patterns and diving behavior of Peruvian boobies *Sula variegata* in northern Peru. *Mar. Ecol. Prog. Ser.* 404: 259–274.

Zavalaga, C.B., Emslie, S.D., Estela, F.A., Muller, M.S., DellOmo, G. & Anderson, D.J. **2012**. Overnight foraging trips by chick-rearing Nazca boobies *Sula granti* and the risk of attack by predatory fish. *Ibis.* 154: 61–73.

9. Declaration

I hereby declare that:

i. Apart from my supervisor's guidance, the content and design of this thesis is the product of my own work. The co-authors contributions are listed in the dedicated section.

ii. This thesis has not been already submitted either partially or wholly as part of a doctoral degree to another examination body and no other materials are published or submitted for publication than indicated in the thesis.

iii. The preparation of the thesis has been subjected to the Rules of Good Scientific Practices of the German Research Foundation.

iv. Prior to this thesis, I have not attempted and failed to obtain a doctoral degree.

Miriam Janeth del Rocio Lerma Lizarraga

Kiel, 2020