UNIVERSITY OF CALIFORNIA
SANTA CRUZ

THE FORAGING ECOLOGY OF SEABIRDS IN RELATION TO CONTAMINANT EXPOSURE AND OCEANOGRAPHIC HABITAT

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

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

Morgan E. Gilmour

June 2018

The Dissertation of Morgan Elizabeth Gilmour
is approved:

_____
Dr. Scott A. Shaffer, Chair

_____
Professor Danial P. Costa

_____
Assistant Professor Carl Lamborg

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

Table of Contents

List of Tables

Chapter 1

List of Figures

Chapter 1

Dissertation Abstract

The foraging ecology of seabirds in relation to contaminant exposure and oceanographic habitat

Morgan E. Gilmour

The vastness of the ocean makes it difficult to study. This is compounded by regional differences in temperature, wind patterns, underwater topography, and primary productivity that extend from the ocean's surface to depths of thousands of meters. Many organisms that inhabit the marine environment navigate many environmental changes as they move between regions in both the horizontal and vertical directions. The ability to navigate through different habitat types indicates that marine animals may be adaptable to multiple environments; however, it also suggests that they may be exposed to multiple hazards, including hazards of anthropogenic origin. Rates of anthropogenic inputs of chemicals and litter to the atmosphere and the ocean are increasing. However, many effects of anthropogenic compounds on marine life are only beginning to be understood. In this dissertation, I assessed foraging ecology, contaminants, and the effects of contaminants, in seabirds, which are unique among marine animals because they hunt for fishes and squid from the air, but breed on land. Land-based breeding enables them to be easily studied, and they are good samplers of the vast ocean because they travel tens to thousands of kilometers from the breeding colony to forage. I first tested the hypothesis that seabirds' foraging behaviors are related to local oceanographic habitats, and that they exhibit behavioral plasticity to exploit the marine environment. GPS-tracking and remotely-sensed environmental data of four species of boobies (*Sula* spp.) demonstrated adaptable behaviors that changed depending on the type of oceanographic habitat in which boobies foraged (e.g. based on depth, sea surface temperature and topography). Second, I measured blood-based

persistent organic pollutants (POP) and mercury contaminant concentrations in boobies and two species of frigatebirds (*Fregata* spp.) from four colonies in the Pacific Ocean and Caribbean Sea. I combined blood-based contaminant measurements with two measures of foraging ecology (blood-based stable isotopes and GPS-tracking). Boobies and frigatebirds were exposed to different contaminants depending on their foraging habitat (e.g. nearshore vs offshore). Though three of the study sites were remote and uninhabited, all birds had contaminants. Lastly, I tested the hypothesis that mercury would negatively affect seabirds' breeding. I measured breeding in Flesh-footed Shearwaters (*Ardenna carneipes*) and Great-winged Petrels (*Pterodroma macroptera*) in the Southern Ocean (Western Australia). Though Great-winged Petrels' blood mercury concentrations were the highest among all seabirds, I did not detect relationships between mercury and breeding in either species. Overall, seabirds are adaptive to their local marine environment. They traverse many habitat types while foraging, which influences the concentrations and types of contaminants that they encounter. However, they may be adapted, or tolerant, to some contaminants like mercury. Seabirds are good samplers of the marine environment, and continue to serve as good indicators of oceanographic processes and contaminants found in the ocean.

Acknowledgements

This dissertation is the product of collaborations, advice, and assistance of many, many people. First, thank you to Scott Shaffer for his support and encouragement over the years, and remembering me from Tern Island in 2006 when I contacted him about grad school several years later. Thank you also for sending me to Tern in 2011 and allowing me to work with frigatebirds. Thank you to Dan Costa for taking me in to his lab, and for his thoughtful comments, ideas, and support with my dissertation. Thank you to Carl Lamborg, for his help with contaminants data, and thank you so much for his collaboration on mercury analyses.

My dissertation research took place in many corners of the globe, and it would not have been possible without several key collaborators. Alfredo Castillo– thank you so much for your continued collaboration with boobies and frigatebirds in Mexico. I hope that Abram and I can get out into the field with you again soon. Hillary Young– thank you for your collaboration on Palmyra, and thank you for your support and suggestions regarding boobies' behavioral analyses. Jenn Lavers– thanks so much for maintaining contact through the years. It's hard to stay in touch with people that you meet in the field, and therefore it has been amazing to be able to collaborate with you in Australia after we met so many years ago on Tern. Thanks for your ideas and support about petrel and shearwater analyses, and willingness to jump into these projects. Olivier Chastel– thank you for running prolactin analyses and for your physiology knowledge. Stephen Kania– thank you for your persistence to figure out the genetic sex determination assays of the petrels and shearwaters. Salvador Hernández-Vázquez– thank you for your assistance in the field; I hope that we can meet in person someday. Sarah Hudson– thank you for generously sharing your frigatebird samples. The data from Barbuda turned out to make a really interesting comparison to birds from the Pacific, which would not have been possible without you. I also hope that we can meet sometime in the future. Jaqueline Garcia Hernandez – thank you for your hospitality in Guaymas, welcoming me into your lab, storing my samples, and your thoughtful discussions

on POP in Mexico. Daniela Aguilera– thank you for your patience while teaching me about POP analyses and for all of your work on the samples. Lucila Armenta– thank you for welcoming me into your home in Guaymas.

Many thanks also go out to Brad Clarke and his RMIT lab for making me feel at home in Melbourne, and teaching me about POP analyses. Special thanks to Phoebe Lewis for her hospitality and for juggling my samples and analyses amidst her own work. Thank you also to Tim Coogan and Tom McGrath for their help in the lab.

Many thanks to everyone who helped in the field: Lisa Hills, Nabilla Zayan, Devyn Orr, Andrea Kristoff, Sarah Youngren, Dan Rapp, H. Almanza, Melinda Conners, D. Gonzalez, A. Piña, and A. Valdez for assistance with fieldwork; Chad Bell, Ty Benally, Paula Hartzell, Stefan Kropidlowski, Cindy Rehkemper, and the US Fish and Wildlife Service for logistical support and access to Laysan and Tern Islands, and the US Fish and Wildlife Service and The Nature Conservancy for logistical support and access to Palmyra Atoll; and Bob Edwards, Peter Collins, Carol and Graham Biddulph, and Western Australia Parks and Wildlife for logistical support and access to Breaksea Island.

On the Santa Cruz homefront, thank you to my Ocean Sciences cohort: Anna Lowe, Jessie Zupcic-Moore, Caitie Kroeger, Diana Baetscher, Michelle Drake, Kim Bitterwolf, Danielle Glynn, and Wilson Sauthoff–Thanks for adopting me! Thank you also to Costa Lab members, past and present. Melinda Conners and Rachael Orben, thanks for your wisdom and advice, and being the other token seabird people in the lab. Caitie Kroeger, thanks for your willingness to do fun things and forgetting about science for awhile. Thanks also to the members of Trailerville: Justine Jackson-Ricketts, Claudio Rojas Leyton, and Sarah Lummis for sharing such a unique office experience with good humor. Thanks to Chandra Goetsch and Sarah Kienle for being awesome officemates in the new building. Thanks to Roxanne Beltran, Caroline Casey, Arina Favilla, Kim Goetz, Rachel Holser, Luis Huckstadt, Theresa Keates, Jessie Kendall-Bar, Liz McHuron, Jen Maresh, Sarah Peterson, Patrick Robinson,

Lisa Schwartz, Ana Valenzuela Toro, and Stella Villegas for taking in yet another seabird person.

Thank you to my family, who are my anchor on the east coast. Rachel Bradford– thanks for being supportive, no matter where in the world, or in what time zone, I happen to be living. Thank you to my parents, Jeremiah and Melissa, and Pam and Joe, for their support through the years as I have traveled non-stop to places none of us had previously heard of in the pursuit of birds. Linda Takahashi– thanks for your support and optimism and friendship, and for visiting Santa Cruz multiple times!

Most of all, I cannot extend a large enough THANK YOU to my partner, Abram Fleishman– Thank you for your assistance in the field and help troubleshooting equipment since the first day that we met. Thanks for returning to Tern Island in 2012 and then moving to Santa Cruz with me. Thank you for your unwavering support throughout this crazy PhD journey, which includes, but is not limited to: coding in R, statistics and all things science, introducing me to Mexico and the wonders of the Gulf of California, endless chats about seabirds, dragging me outside to at least go for a walk, and unlimited supplies of breakfast tacos.

This dissertation also would not have been possible without grants and fellowships: Environmental Protection Agency Science to Achieve Results (STAR) Program under STAR Fellowship Assistance Agreement no. FP91764601; National Science Foundation East Asia and Pacific Summer Institutes (EAPSI) Program; Society for Integrative & Comparative Biology Grants-In-Aid of Research; Dr Earl H. Myers & Ethel M. Myers Oceanographic and Marine Biology Trust; Friends of Long Marine Lab Student Research & Education Award; Sigma Xi Grants-In-Aid of Research. This publication has not been formally reviewed by EPA; the views expressed in this publication are solely those of M.E. Gilmour; and the EPA does not endorse any products or commercial services mentioned in this publication.

This dissertation research was conducted under the approval of the University of California Santa Cruz Institutional Animal Care and Use Committee #COSTD1411. The

Mexican legal requirements for animal welfare and fieldwork was supervised and approved by Dirección General de Vida Silvestre, Secretaría de Gestión para la Protección Ambiental (Permits: SGVA/DGVS/00404/2015, and SGVA/DGVS/02644/15). Research in Australia was conducted University of Tasmania animal ethics board (permit no. A0015319 and A0012279) and W.A. Department of Biodiversity, Conservation and Attractions (permit no. SF010339, SF010159, and CE004240). Research in Papahānaumokuākea Marine National Monument was conducted under the approval of PMNM-2011-016-A1 and PMNM-2012-016-A1.

The text of this dissertation includes a preprint from the following previously published material:

Gilmour, ME, JA Castillo-Guerrero, AB Fleishman, S Hernández-Vázquez, HS Young, SA Shaffer. 2018. Plasticity of foraging behaviors in response to diverse environmental conditions. Ecosphere doi:10.1002/ecs2.2301.

Reproduction of this manuscript as Chapter 1 falls under Wiley-Blackwell's License Agreement for Publishing CC-BY, which is a Creative Commons Attribution License.

The following collaborators acted as co-authors on each dissertation chapter; however, I, Morgan Gilmour, conceived these studies and wrote all parts of each manuscript:

Chapter 1: J. Alfredo Castillo-Guerrero collected field data; Abram B. Fleishman collected field data; Salvador Hernández-Vázquez collected field data; Hillary S. Young collected field data; Scott A. Shaffer collected field data, supervised research, and provided feedback on the manuscript;

Chapter 2: Sarah Trefry Hudson conducted field sampling; Carl Lamborg provided equipment and supplies for mercury analyses and contributed to the interpretation of mercury results; Abram B. Fleishman conducted field sampling; Hillary S. Young contributed to interpretation of results; Scott A. Shaffer supervised research and provided feedback on the manuscript;

Chapter 3: Jennifer L. Lavers helped conceive the study and collect field data; Carl Lamborg provided equipment and supplies for mercury analyses and contributed to the

interpretation of mercury results; Olivier Chastel conducted laboratory analyses; Stephen A. Kania conducted laboratory analyses; Scott A. Shaffer supervised research and provided feedback on the manuscript.

Dissertation Introduction

The vast marine environment is characterized by continuously-changing currents; these movements are essential to the transport of nutrients and organisms. Unfortunately, these same currents, driven by winds, weather patterns, and underwater topography, also facilitate the transport of toxic substances (Iwata et al., 1993; Pacyna et al., 2010). Contaminants like persistent organic pollutants (POP), which include pesticides, industrial compounds, and flame retardants, and heavy metals like mercury, are deposited into the ocean from rivers (Lohmann and Belkin, 2014), and from the atmosphere because many compounds change from solid to gaseous states with changes in temperature (Fitzgerald et al., 2007; Gouin et al., 2004). Thus, atmospheric and oceanic currents can make the identification and control of contaminants and their sources difficult, and can also make the assessment of threats to humans and wildlife challenging. These problems are exacerbated because of spatiotemporal fluctuations in contaminants between habitats (e.g. Finkelstein et al., 2006). Marine organisms are therefore potentially exposed to many types of contaminants in the ocean.

Upper trophic level predators obtain contaminants from their diet, and the diet and foraging behaviors of these marine predators could help elucidate contaminant patterns in the dynamic ocean environment (Roscales et al., 2011; Sebastiano et al., 2017, 2016). The oceanographic processes that govern currents and contaminant distribution also influence marine animals' behaviors. For example, ocean currents collide with seamounts, and upwell deep, nutrient-rich water. Many marine organisms congregate in these places to use nutrients for primary production (Drazen et al., 2011). The resulting increase in primary productivity consequently creates more food resources for upper trophic levels, and creates a potentially rich feeding ground for many types of organisms (Clark et al., 2010). However, POP and mercury are often concentrated in regions of high productivity because of the large concentration of biomass (in which contaminants bioaccumulate in tissues and biomagnify in

food webs; Eisenreich and Jones, 2002; Sunderland et al., 2009). Thus, knowledge of the marine system as a whole and how marine organisms interact with their marine environment is key to understanding their exposure to POP and heavy metals.

In this dissertation, I explored POP and mercury exposure in a unique type of marine predator, the seabird, across the Pacific and Southern Oceans and Caribbean Sea. Seabirds breed on land, but obtain food like fish and squid from the ocean by hunting from the air; some seabird species forage at the ocean's surface and other species dive tens of meters deep to catch prey underwater. Seabirds also travel hundreds of kilometers from the breeding colony to find food. Thus, seabirds integrate diet and, potentially, contaminants over large spatial scales from different parts of the water column (Burger and Gochfeld, 2004; Elliott and Elliott, 2013). Seabirds are found throughout the world ocean, and some species have cosmopolitan distributions. The global distributions of many clades of seabirds make large-scale studies of contaminants and foraging ecology across large expanses of ocean possible. Many seabird species breed in remote regions, and others breed in coastal areas, thereby creating a juxtaposition of contaminant exposures in different environments (e.g. Cunha et al., 2012).

POP like the organochlorine pesticide dichlorodiethyltrichloroethane (DDT), industrial compounds like polychlorinated biphenyls (PCB) and flame retardants (polybrominated diphenyl ethers; PBDE), and heavy metals like mercury are routinely detected in air, water, and biota throughout the world (Baek et al., 2011; Iwata et al., 1993; Lamborg et al., 2014; Shunthirasingham et al., 2010). This is problematic because many contaminants cause adverse changes in humans and wildlife: many compounds are neurotoxins (Ceccatelli et al., 2010), and many can also cause genetic changes like mutations (Bajpayee et al., 2006), behavioral changes that interfere with reproduction (Frederick and Jayasena, 2011), physiological changes that range from eggshell thinning in birds to decreased antioxidant activity (Gress et al., 1971; Sweet et al., 2006), and overall decreased reproductive behaviors and success in wildlife (Burgess and Meyer, 2008). As a result, many POP have been

phased out over the past few decades by international regulations like the Stockholm Convention (United Nations Environmental Program, 2018a). However, POP continue to be used because they are effective at controlling agricultural pests and for synthesizing materials like plasticizers. Some POP also benefit human health: DDT is perhaps the most infamous organochlorine pesticide because it was detected in many birds in the 1960's (Risebrough et al., 1967) and caused eggshell thinning (Bitman et al., 1970). However, though DDT was phased out of global use in 2000, it is an effective control of malaria-bearing mosquitoes, and DDT is still permitted to be manufactured and sprayed in 19 countries around the world to protect human health (United Nations Environmental Program, 2018b). DDT and many other POP compounds, and their degradation products, degrade slowly in the environment; heavy metals like mercury, and many POP are also lipophilic. In the ocean, mercury and many POP that enter surface waters adsorb to floating marine debris (Graca et al., 2014; Rochman et al., 2013), and are also taken up by plankton and through the gills of fish (Randall et al., 1998). These factors enable many POP to persist in the environment and in foodwebs for many years. These processes, combined with the inconsistent regulation and use of many POP (e.g. some POP are banned, others are only banned in some nations, some POP are used illegally or used improperly; Beckford and Campbell, 2013; United Nations Environmental Program, 2018a) creates a complex, and at times, unpredictable, distribution of many anthropogenic compounds in the marine environment.

Mercury in the ocean is also complex: anthropogenic mercury is mainly from coal combustion and artisanal gold mining; mercury is additionally naturally emitted from volcanoes (Lamborg et al., 2014). Inorganic mercury readily volatilizes into the atmosphere, and undergoes a similar volatilization-deposition cycle to many POP (Fitzgerald et al., 2007). Similarly, once deposited into the ocean, mercury adsorbs to particles and sinks, and sulfate-reducing bacteria then methylate inorganic mercury to methyl-mercury (MeHg), which is easily adsorbed by organisms (Blum et al., 2013; Graca et al., 2014; Sunderland et al., 2009). It is this form which is typically detected in biota like seabirds, and is the more harmful form of

mercury. Although anthropogenic input of mercury into the atmosphere has increased over the past century, MeHg appears to be most harmful to humans and wildlife (Driscoll et al., 2013). The inorganic mercury-MeHg process thus complicates the distribution of mercury in marine foodwebs, and mercury is not distributed evenly in the ocean (Mason et al., 2012). However, sulfate-reducing bacteria are typically numerous in benthic sediments and in the mesopelagic region of the ocean (200-1000 m depths), and some predictions can be made about mercury concentrations in organisms that forage in these environments (Peterson et al., 2015; Sackett et al., 2015). Regardless, given the adverse effects of mercury on wildlife, and the increased input of anthropogenic inorganic mercury to the atmosphere, it is imperative that mercury, like other POP, be monitored in marine organisms.

It is clear that POP and mercury are found in the global ocean. In this dissertation, I explored the extent to which contaminants are distributed in seabirds that forage in different oceanographic regions. In Chapter 1, I assessed the foraging ecology of a clade of seabirds, the boobies (*Sula* spp.). Boobies are pan-tropical, and I tested the hypothesis that localized oceanographic conditions (characterized by the ephemeral variables sea surface temperature, chlorophyll-*a* – a proxy for primary productivity, and sea surface height; and the static variables bathymetry, bathymetric topography, and bottom slope) drive boobies' foraging behaviors, regardless of the habitat in which they forage. GPS-tracking data and remotely-sensed environmental data from seven colonies of four species of boobies in Mexico, the Northwestern Hawaiian Islands, and Palmyra Atoll (Line Islands) were used to describe boobies foraging ecology across these diverse marine regions. These data provided information about seabirds' behaviors in the dynamic ocean environment as they searched for food. Because oceanographic processes also affect the distributions of mercury and POP in the ocean, boobies' foraging ecology are important factors to consider in relation to contaminant exposure.

In Chapter 2, I assessed contaminant exposure and its relation to foraging ecology in five seabird species that represented different oceanographic habitats. I measured 89 POP

compounds and mercury concentrations in two clades of seabirds (boobies; and frigatebirds, *Fregata* spp.) from four colonies that spanned the Pacific Ocean (the Northwestern Hawaiian Islands; and Palmyra Atoll, Line Islands) and the Caribbean Sea (Barbuda). These colonies vary in proximity to human habitation and presence of historic POP and heavy metal use and deposition (CARDI, 2018; Maragos et al., 2008; Miao et al., 2000) and oceanographic properties like sea surface temperature and ocean currents (Calil et al., 2008; Hamann et al., 2004; Johns et al., 2002). The variation in habitats enabled me to ask how seabirds' foraging ecology differed between colonies, and how these variations in diet and behaviors influenced contaminant exposure. I used a two-fold approach to describe foraging ecology: in addition to GPS-tracking tags, which provided information on foraging locations and general habitat use, I also used carbon, nitrogen, and sulfur stable isotopes, which provided information on nearshore-offshore foraging and trophic position (Connolly et al., 2004; Hobson, 1993); sulfur can also be used as a proxy for sulfate-reducing bacteria (Elliott and Elliott, 2016). These data are important because they established baseline levels of contaminants for these locations, and shed some light on the processes that contribute to contaminant exposure in coastal and remote marine regions.

In Chapter 3, I tested the hypothesis that mercury negatively affects seabirds' breeding. Mercury is an endocrine-disruptor, thereby disrupting hormone synthesis and subsequent behaviors in many organisms. In seabirds, mercury has had non-linear effects on reproduction and breeding, specifically causing adverse effects that were species-specific and sex-specific (Carravieri et al., 2014; Pollet et al., 2017; Tartu et al., 2015). Prolactin is a hormone important to breeding in seabirds, especially because it enables parents to fast for days to weeks while incubating the egg and guarding the chick while their mate is foraging at-sea (Cherel et al., 1994; Vleck et al., 2000). Mercury may also disrupt egg formation, affecting egg size (Fort et al., 2014), shape (Lundholm, 1995), color (Barr, 1986), and volume (Evers et al., 2003). I tested the correlations between mercury and prolactin and egg volume in two seabird species that breed in Western Australia. Unlike boobies and frigatebirds,

Flesh-footed Shearwaters (*Ardenna carneipes*) and Great-winged Petrels (*Pterodroma macroptera*) forage in the colder Southern Ocean during the breeding season. These species forage on different prey items: Great-winged Petrels are squid specialists (Cooper and Klages, 2009; Ridoux, 1994) and Flesh-footed Shearwaters are shallow divers that hunt mostly fishes and low trophic level prey (Gould et al., 1997), thus providing contrasting foraging environments in which they could obtain mercury. I used carbon and nitrogen stable isotopes and GPS-tracking to further assess the foraging ecology of these species. Both species undergo long incubation shifts of up to two weeks and prolactin could be an important hormone to sustain this fasting behavior. Relatively little research has tested for sublethal effects of mercury on seabirds, making these data important to understanding the impacts of contaminants on breeding seabirds.

Because seabirds occur in all oceans and are wide-ranging, the aim of this research was also to assess foraging ecology and contaminants on large scales. Thus, eight species of seabirds in the Caribbean Sea, Pacific Ocean, and Southern Ocean are studied here. The data resulting from this dissertation provides new information on a large scale, making a unique contribution to science. These data are also important because they were sampled in remote parts of the Pacific, where the environment is typically considered pristine, and less affected by human impacts. Knowledge of contaminants that have affected such remote places from far-away point sources underscores the need to continue baseline monitoring in such remote regions of the ocean.

References

Baek, S.-Y., Choi, S.-D., Chang, Y.-S., 2011. Three-year atmospheric monitoring of organochlorine pesticides and polychlorinated biphenyls in Polar regions and the South Pacific. Environ. Sci. Technol. 45, 4475–4482. https://doi.org/10.1021/es1042996

Bajpayee, M., Pandey, A.K., Zaidi, S., Musarrat, J., Parmar, D., Mathur, N., Seth, P.K., Dhawan, A., 2006. DNA Damage and Mutagenicity Induced by Endosulfan and Its Metabolites 692, 682–692. https://doi.org/10.1002/em

Barr, J., 1986. Population dynamics of the Common Loon (Gavia immer) associated with mercury-contaminanted waters in northwestern Ontario. Can. Wildl. Serv. 56, 1–23.

Beckford, C., Campbell, D., 2013. Domestic food production and food security in the Caribbean: Building capacity and strengthening local food production systems. Palgrave Macmillan, New York, New York, USA.

Bitman, J., Cecil, H.C., Fries, G.F., 1970. DDT-induced inhibition of avian shell gland carbonic anhydrase: a mechanism for thin eggshells. Science. 168, 594–596. https://doi.org/10.1126/science.168.3931.594

Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

Burger, J., Gochfeld, M., 2004. Marine Birds as Sentinels of Environmental Pollution. Ecohealth 1, 263–274. https://doi.org/10.1007/s10393-004-0096-4

Burgess, N.M., Meyer, M.W., 2008. Methylmercury exposure associated with reduced productivity in common loons. Ecotoxicology 17, 83–91. https://doi.org/10.1007/s10646-007-0167-8

Calil, P.H.R., Richards, K.J., Jia, Y., Bidigare, R.R., 2008. Eddy activity in the lee of the Hawaiian Islands. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 1179–1194. https://doi.org/10.1016/j.dsr2.2008.01.008

CARDI, 2018. Caribbean Agricultural Research and Development Institute [WWW Document]. URL www.cardi.org

Carravieri, A., Cherel, Y., Blévin, P., Brault-Favrou, M., Chastel, O., Bustamante, P., 2014. Mercury exposure in a large subantarctic avian community. Environ. Pollut. 190, 51–57. https://doi.org/10.1016/j.envpol.2014.03.017

Ceccatelli, S., Daré, E., Moors, M., 2010. Methylmercury-induced neurotoxicity and apoptosis. Chem. Biol. Interact. 188, 301–308. https://doi.org/10.1016/j.cbi.2010.04.007

Cherel, Y., Mauget, R., Lacroix, A., Gilles, J., 1994. Seasonal and Fasting-related Changes in Circulating Gonadal Steroids and Prolactin in King Penguins, Aptenodytes patagonicus. Physiol. Zool. 67, 1154–1173.

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. https://doi.org/10.1146/annurev-marine-120308-081109

Connolly, R.M., Guest, M.A., Melville, A.J., Oakes, J.M., 2004. Sulfur stable isotopes separate producers in marine food-web analysis. Oecologia 138, 161–167. https://doi.org/10.1007/s00442-003-1415-0

Cooper, J., Klages, N.T.T.W., 2009. The winter diet of the Great-winged Petrel Pterodroma macroptera at sub-Antarctic Marion Island in 1991. Mar. Ornithol. 37, 261–263. https://doi.org/10.2307/3130

Cunha, L.S.T., Torres, J.P.M., Muñoz-Arnanz, J., Jiménez, B.J., 2012. Evaluation of the possible adverse effects of legacy persistent organic pollutants (POPs) on the brown booby (Sula leucogaster) along the Brazilian coast. Chemosphere 87, 1039–44. https://doi.org/10.1016/j.chemosphere.2012.02.009

Drazen, J.C., De Forest, L.G., Domokos, R., 2011. Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. Deep Sea Res. Part I Oceanogr. Res. Pap. 58, 557–566. https://doi.org/10.1016/j.dsr.2011.03.002

Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a global pollutant—sources, pathways, and effects. Environ. Sci. Technol. 47, 4967–4983. https://doi.org/10.1021/es305071v

Eisenreich, S.J., Jones, K.C., 2002. Oceanic biogeochemical controls on global dynamics of persistent organic pollutants. Environ. Sci. Technol. 36, 4229–4237.

Elliott, J.E., Elliott, K.H., 2013. Tracking marine pollution. Science. 340, 556–558. https://doi.org/10.1126/science.1235197

Elliott, K.H., Elliott, J.E., 2016. Origin of Sulfur in Diet Drives Spatial and Temporal Mercury Trends in Seabird Eggs From Pacific Canada 1968–2015. Environ. Sci. Technol. 50, 13380–13386. https://doi.org/10.1021/acs.est.6b05458

Evers, D.C., Taylor, K.M., Major, A., Taylor, R.J., Poppenga, R.H., Scheuhammer, A.M., 2003. Common loon eggs as indicators of methylmercury availability in North America. Ecotoxicology 12, 69–81. https://doi.org/10.1023/A:1022593030009

Finkelstein, M., Keitt, B.S., Croll, D.A., Tershy, B., Jarman, W.M., Rodriguez-Pastor, S., Anderson, D.J., Sievert, P.R., Smith, D.R., 2006. Albatross species demonstrate regional differences in North Pacific marine contamination. Ecol. Appl. 16, 678–686. https://doi.org/10.1890/1051-0761(2006)016[0678:ASDRDI]2.0.CO;2

Fitzgerald, W.F., Lamborg, C.H., Hammerschmidt, C.R., 2007. Marine biogeochemical cycling of mercury. Chem. Rev. 107, 641–662. https://doi.org/10.1021/cr050353m

Fort, J., Robertson, G.J., Grémillet, D., Traisnel, G., Bustamante, P., 2014. Spatial ecotoxicology: Migratory arctic seabirds are exposed to mercury contamination while overwintering in the northwest Atlantic. Environ. Sci. Technol. 48, 11560–11567. https://doi.org/10.1021/es504045g

Frederick, P., Jayasena, N., 2011. Altered pairing behaviour and reproductive success in white ibises exposed to environmentally relevant concentrations of methylmercury. Proc. R. Soc. B Biol. Sci. 278, 1851–1857. https://doi.org/10.1098/rspb.2010.2189

Gouin, T., MacKay, D., Jones, K.C., Harner, T., Meijer, S.N., 2004. Evidence for the "grasshopper" effect and fractionation during long-range atmospheric transport of organic contaminants. Environ. Pollut. 128, 139–148. https://doi.org/10.1016/j.envpol.2003.08.025

Gould, P., Ostrom, P.H., Walker, W., 1997. Food of flesh-tooted shearwaters Puffinus carneipes associated with high seas driftnets in the central north Pacific Ocean. Emu 97, 168–173.

Graca, B., Bełdowska, M., Wrzesień, P., Zgrundo, A., 2014. Styrofoam debris as a potential carrier of mercury within ecosystems. Environ. Sci. Pollut. Res. 21, 2263–2271. https://doi.org/10.1007/s11356-013-2153-4

Gress, F., Risebrough, R.W., Sibley, F.C., 1971. Shell Thinning in Eggs of the Common Murre, Uria aalge, from the Farallon Islands, California. Condor 73, 368–369.

Hamann, I.M., Boehlert, G.W., Wilson, C.D., 2004. Effects of steep topography on the flow and stratification near Palmyra Atoll. Ocean Dyn. 54, 460–473. https://doi.org/10.1007/s10236-004-0091-x

Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar. Ecol. Prog. Ser. 95, 7–18. https://doi.org/10.3354/meps095007

Iwata, H., Tanabe, S., Sakal, N., Tatsukawa, R., 1993. Distribution of Persistent Organochiorines in the Oceanic Air and Surface Seawater and the Role of Ocean on Their Global Transport and Fate. Environ. Sci. Technol. 27, 1080–1098. https://doi.org/10.1021/es00043a007

Johns, W.E., Townsend, T.L., Fratantoni, D.M., Wilson, W.D., 2002. On the Atlantic inflow to the Caribbean Sea. Deep. Res. Part I Oceanogr. Res. Pap. 49, 211–243. https://doi.org/10.1016/S0967-0637(01)00041-3

Lamborg, C.H., Hammerschmidt, C.R., Bowman, K.L., Swarr, G.J., Munson, K.M., Ohnemus, D.C., Lam, P.J., Heimbürger, L.-E., Rijkenberg, M.J.A., Saito, M.A., 2014. A global ocean inventory of anthropogenic mercury based on water column measurements. Nature 512, 65–68. https://doi.org/10.1038/nature13563

Lohmann, R., Belkin, I.M., 2014. Organic pollutants and ocean fronts across the Atlantic Ocean: A review. Prog. Oceanogr. 128, 172–184. https://doi.org/10.1016/j.pocean.2014.08.013

Lundholm, C.E., 1995. Effects of methyl mercury at different dose regimes on eggshell formation and some biochemical characteristics of the eggshell gland mucosa of the domestic fowl. Comp. Biochem. Physiol. Part CPharmacology, Toxicol. Endocrinol. 110, 23–28. https://doi.org/10.1016/0742-8413(94)00081-K

Maragos, J., Miller, J., Gove, J., Demartini, E., 2008. US Coral Reefs in the Line and Phoenix

Islands , Central Pacific Ocean 1 : History, Geology, Oceanography, and Biology. Coral Reefs USA 595–641. https://doi.org/10.1007/978-1-4020-6847-8_15

Mason, R.P., Choi, A.L., Fitzgerald, W.F., Hammerschmidt, C.R., Lamborg, C.H., Soerensen, A.L., Sunderland, E.M., 2012. Mercury biogeochemical cycling in the ocean and policy implications. Environ. Res. 119, 101–117. https://doi.org/10.1016/j.envres.2012.03.013

Miao, X.S., Swenson, C., Woodward, L.A., Li, Q.X., 2000. Distribution of polychlorinated biphenyls in marine species from French Frigate Shoals, North Pacific Ocean. Sci. Total Environ. 257, 17–28. https://doi.org/10.1016/S0048-9697(00)00484-8

Pacyna, E.G., Pacyna, J.M., Sundseth, K., Munthe, J., Kindbom, K., Wilson, S., Steenhuisen, F., Maxson, P., 2010. Global emission of mercury to the atmosphere from anthropogenic sources in 2005 and projections to 2020. Atmos. Environ. 44, 2487–2499. https://doi.org/10.1016/j.atmosenv.2009.06.009

Peterson, S.H., Ackerman, J.T., Costa, D.P., 2015. Marine foraging ecology influences mercury bioaccumulation in deep-diving northern elephant seals. Proc. R. Soc. B Biol. Sci. 282, 20150710. https://doi.org/10.1098/rspb.2015.0710

Pollet, I.L., Leonard, M.L., O'Driscoll, N.J., Burgess, N.M., Shutler, D., O'Driscoll, N.J., Burgess, N.M., Shutler, D., 2017. Relationships between blood mercury levels, reproduction, and return rate in a small seabird. Ecotoxicology 26, 97–103. https://doi.org/10.1007/s10646-016-1745-4

Randall, D.J., Cornell, D.W., Yang, R., Wu, S.S., 1998. Concentrations of persistent lipophilic compounds in fish are determined by exchange across the gills, not through the food chain. Chemosphere 37, 1263–1270. https://doi.org/10.1016/S0045-6535(98)00124-6

Ridoux, V., 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar. Ornithol. 22, 65–128.

Risebrough, R.W., Menzel, D., Martin, D., Olcott, H., 1967. DDT Residues in Pacific Sea Birds: A Persistent Insecticide in Marine Food Chains. Nature 216, 589–590. https://doi.org/10.1038/216589a0

Rochman, C.M., Hoh, E., Hentschel, B.T., Kaye, S., 2013. Long-term field measurement of sorption of organic contaminants to five types of plastic pellets: Implications for plastic marine debris. Environ. Sci. Technol. 47, 1646–1654. https://doi.org/10.1021/es303700s

Roscales, J.L., González-Solís, J., Muñoz-Arnanz, J., Jiménez, B., 2011. Geographic and trophic patterns of OCs in pelagic seabirds from the NE Atlantic and the Mediterranean: a multi-species/multi-locality approach. Chemosphere 85, 432–40. https://doi.org/10.1016/j.chemosphere.2011.07.070

Sackett, D.K., Drazen, J.C., Choy, C.A., Popp, B., Pitz, G.L., 2015. Mercury sources and trophic ecology for Hawaiian bottomfish. Environ. Sci. Technol. 49, 6909–6918. https://doi.org/10.1021/acs.est.5b01009

Sebastiano, M., Bustamante, P., Costantini, D., Eulaers, I., Malarvannan, G., Mendez-Fernandez, P., Churlaud, C., Blevin, P., Hauselmann, A., Dell'Omo, G., Covaci, A., Eens, M., Chastel, O., 2016. High levels of mercury and low levels of persistent organic

pollutants in a tropical seabird in French Guiana, the Magnificent frigatebird, Fregata magnificens. Environ. Pollut. 214, 384–393. https://doi.org/10.1016/j.envpol.2016.03.070

Sebastiano, M., Bustamante, P., Eulaers, I., Malarvannan, G., Mendez-Fernandez, P., Churlaud, C., Blévin, P., Hauselmann, A., Covaci, A., Eens, M., Costantini, D., Chastel, O., 2017. Trophic ecology drives contaminant concentrations within a tropical seabird community. Environ. Pollut. 227, 183–193. https://doi.org/10.1016/j.envpol.2017.04.040

Shunthirasingham, C., Oyiliagu, C.E., Cao, X., Gouin, T., Wania, F., Lee, S.-C., Pozo, K., Harner, T., Muir, D.C.G., 2010. Spatial and temporal pattern of pesticides in the global atmosphere. J. Environ. Monit. 12, 1650–1657. https://doi.org/10.1039/c0em00134a

Sunderland, E.M., Krabbenhoft, D.P., Moreau, J.W., Strode, S.A., Landing, W.M., 2009. Mercury sources, distribution, and bioavailability in the North Pacific Ocean: Insights from data and models. Global Biogeochem. Cycles 23, 1–14. https://doi.org/10.1029/2008GB003425

Sweet, L.I., Passino-Reader, D.R., Meier, P.G., Omann, G.M., 2006. Effects of polychlorinated biphenyls, hexachlorocyclohexanes, and mercury on human neutrophil apoptosis, actin cytoskelton, and oxidative state. Environ. Toxicol. Pharmacol. 22, 179–188. https://doi.org/10.1016/j.etap.2006.03.005

Tartu, S., Bustamante, P., Angelier, F., Lendvai, Á.Z., Moe, B., Blévin, P., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015. Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct. Ecol. 30, 596–604. https://doi.org/10.1111/1365-2435.12534

United Nations Environmental Program, 2018a. Stockholm Convention on POPs [WWW Document]. URL http://chm.pops.int/ (accessed 4.30.18).

United Nations Environmental Program, 2018b. Stockholm Convention; Acceptable purposes: DDT [WWW Document]. URL http://chm.pops.int/Implementation/Exemptionsandacceptablepurposes/RegistersofAcceptablePurposes/AcceptablePurposesDDT/tabid/456/Default.aspx

Vleck, C.M., Ross, L.L., Vleck, D., Bucher, T.L., 2000. Prolactin and parental behavior in Adélie penguins: effects of absence from nest, incubation length, and nest failure. Horm. Behav. 38, 149–58. https://doi.org/10.1006/hbeh.2000.1589

Chapter 1

Plasticity of foraging behaviors in response to diverse environmental conditions

Morgan E. Gilmour

Abstract

Due to rapidly changing global environmental conditions, many animals are now experiencing concurrent changes in both resource availability and the foraging cues associated with finding those resources. By employing flexible, plastic foraging strategies that use different types of environmental foraging cues, animals could adapt to these novel future environments. To evaluate the extent to which such flexibility and plasticity exist, we analyzed a large dataset of a clade (Sulidae; the boobies) of widespread aerial tropical predators that feed in highly variable marine habitats. These surface foragers are typical of many ocean predators that face dynamic and patchy foraging environments and use a combination of static and ephemeral oceanographic features to locate prey. We compared foraging habitats and behaviors of four species at seven colonies in the eastern and central Pacific Ocean that varied greatly in depth, topography, and primary productivity. Foraging behaviors, recorded by GPS-tracking tags, were compared to remotely sensed environmental features, to characterize habitat-behavior interactions. K-means clustering grouped environmental characteristics into five habitat clusters across the seven sites. We found that boobies relied on a combination of static and ephemeral cues, especially depth, chlorophyll-a concentrations, and sea surface height (ocean surface topography). Notably, foraging behaviors were strongly predicted by local oceanographic habitats across species and sites, suggesting a high degree of behavioral plasticity in use of different foraging cues. Flexibility allows these top predators to adapt to, and exploit, static and ephemeral oceanic features. Plasticity may well facilitate these species, and other similarly dynamic foragers, to cope with increasingly changing environmental conditions.

1.1 Introduction

Adaptive foraging behavior specific to an animal's morphology and its environment allow the animal to navigate diverse landscapes while efficiently searching for food (Schoener 1971, Ballance et al. 1997). The degree to which animals can adapt to changes in the foraging cues of their habitats is determined by their foraging strategies. Flexible and specialized foraging strategies are dependent on the stability of available resources (West-Eberhard 1989). Resources that are predictable on temporal and spatial scales enable specialization, and specialist strategies are advantageous because they reduce decision-making (Forister et al. 2012) and physiological costs (Webb 1984). Conversely, more variable ecosystems may produce unpredictable environmental conditions and patchy resources, and a generalist foraging strategy becomes advantageous because there are less constrained diet requirements and less specialized behaviors. Thus, adoption of a more flexible approach to foraging enables animals to efficiently navigate uncertain environments while gaining physiological, survivorship, and fitness benefits (Hadfield and Strathmann 1996). However, given today's rapidly changing environment, animals have been forced to adapt their behaviors rapidly to survive (Kearney et al. 2009, Wong and Candolin 2015).

In the context of current ecosystem changes around the globe, plasticity in foraging behaviors could be advantageous to many species experiencing changes in their environments (Beever et al. 2017). Indeed, flexible strategies enable animals to exploit novel habitats (Manenti et al. 2013). Variations in behaviors and habitat use are two mechanisms through which animals could employ flexible foraging (Jung and Kalko 2010). As habitats change, a flexible foraging strategy could vary the types of cues (static and ephemeral features) used within a habitat. Though traditional studies of behavioral plasticity have aimed to answer broad evolutionary questions that focus on the relationships between plasticity, fitness trade-offs, and genetic variance (Hadfield and Strathmann 1996, Chevin et al. 2010), changes in an animal's behaviors, habitat use, and diet are its immediate response to rapid

environmental change (Van Buskirk 2012). These adaptations are especially important because ecosystem changes are occurring on multiple scales that range from immediate habitat alterations like deforestation (Jenkins et al. 2003) and dredging (Pirotta et al. 2013); episodic events like eutrophication (Phil et al. 1992) and pollution (Michalec et al. 2013); and long-term changes that include annual increases in temperature (Kearney et al. 2009), introductions of invasive species (O'Dowd et al. 2003), and over-fishing (Jackson et al. 2001). It is essential to know how foraging behaviors change, and the degree to which animals rely on static vs ephemeral foraging cues, at these different temporal scales. To assess animals' foraging plasticity in a changing environment, we characterized habitat-behavior interactions within the wide array of environmental conditions found in the variable marine ecosystem.

Marine habitats contain both static and ephemeral features that animals use to navigate and forage. For example, static cues like seamounts provide a permanent structure that upwells nutrients to surface water, and provides a reliable location of nutrients and prey for upper trophic level predators (Ballance et al. 2006, Palacios et al. 2006). Ephemeral processes like currents that shift seasonally (e.g. the Costa Rica Dome; Fiedler 2002) and annually (Philander et al. 1996, Bograd et al. 2004) transport nutrients and plankton larvae. Thus, basic marine features like thermal structure, upwelling, currents, and bathymetric topography shape biological processes like primary productivity (Rutherford et al. 1999, Rykaczewski and Checkley 2008), and subsequently affect the distribution of many organisms like fishes and top predators throughout the year (Kwasniewski et al. 2010, Block et al. 2011, Elliott et al. 2014). The resulting habitat created by the combination of static and ephemeral oceanographic processes with patchy prey distributions may make foraging difficult for predators (Weimerskirch 2007). These challenges are further compounded for seabirds that typically hunt from the air to obtain subsurface prey like fishes and squids.

Seabirds that forage in the marine environment provide an excellent natural experiment with which to assess foraging plasticity in the face of constantly changing environmental conditions. Boobies (Sulidae) are tropical seabirds that inhabit coastal and

pelagic habitats that differ greatly in topography, seasonality, and prey resources. Yet, they forage efficiently in these oceanic environments, employing similar feeding techniques throughout their cosmopolitan range. Boobies are central-place foragers when breeding and thus are constrained spatially and temporally while foraging (boobies forage 0.2-150 km from the nest during breeding; Weimerskirch et al. 2009, Kappes et al. 2011, Young et al. 2015, Poli et al. 2017). Consequently, the constraints of central-place foraging allowed us to evaluate behavioral plasticity in an otherwise vast and ephemeral ocean. We analyzed GPS tracking data from seven colonies in the eastern and central Pacific Ocean (Fig. 1.1) to examine the foraging ecology of four out of the six booby species from the genus Sula: Blue-footed (Sula nebouxii); Brown (S. leucogaster); Masked (S. dactylatra); and Red-footed (S. sula). Three of these species (Brown, Masked, and Red-footed) have a worldwide distribution, allowing the results of our study to extend to populations throughout the globe; though, regional oceanographic differences may also contribute to site-specific behaviors (Suryan et al. 2006). The large environmental variations between our study sites allowed us to fully assess potential differences that boobies encounter between colonies, and the degree to which they rely on static and ephemeral features to forage. Study sites included a semi-enclosed sea and coastal and pelagic regions, and varied greatly in depth, topography, and primary productivity (Table S1.1). Boobies' behaviors such as distance traveled and foraging frequency would likely vary with the features of each of these habitats. For example, patches of chlorophyll on the ocean surface change in size with changes in plankton community composition, nutrient availability, and predation (Haury et al. 1978). A chlorophyll patch that is present at a given time may move or disappear within 24 hours, causing top predators like boobies to increase the size of their search area to compensate for the change in position, or absence, of the chlorophyll patch. Subsequently, the change in chlorophyll would change the distance traveled and the foraging frequency during their foraging trip. Given the rapidly changing environment for many species due to anthropogenic habitat alterations and climate change (Croxall et al. 2012, Wong and Candolin 2015), assessment of boobies' behavioral

plasticity in response to a continuously changing ocean provides insight about inter- and intra-specific adaptability across a widely-distributed clade.

Given the oceanographic differences surrounding our study colonies (Table S1.1) and the potential for some oceanographic conditions like primary productivity to be ephemeral, we tested whether foraging behaviors differed between colonies based on differences in local oceanographic habitats. Using k-means clustering by partitioning, oceanographic characteristics (SST; sea surface height (SSH); chlorophyll-a; depth; slope; and bathymetric position index (BPI)) were characterized into distinct habitat groupings. We hypothesized that differences in oceanographic habitats would drive differences in behaviors between colonies, providing support for adaptive foraging behaviors. We predicted that as opportunistic, flexible foragers, boobies would: 1) have high behavioral plasticity, illustrated by a correlation between behaviors and local habitats; and 2) share similar foraging behaviors with conspecifics and congeners if they shared similar foraging habitat.

1.2 Methods

1.2.1 Location and species

This study took place at seven booby breeding colonies throughout the central and eastern Pacific Ocean (Fig. 1.1) between 2007 – 2016 (Table 1.1). Tracking data were collected from four booby species: Blue-footed, Brown, Masked, and Red-footed during the incubation and chick-brooding stages (Table 1.1). Males and females were distinguished by either vocalizations (Blue-footed & Masked; Nelson 1978), plumage (Brown; Nelson 1978), body mass (Masked & Red-footed), where females are larger than males within the pair (Nelson 1978, Weimerskirch et al. 2006), or through molecular analyses (Young et al. 2010); though sex could not be determined for 10 birds (Table 1.1).

1.2.2 Instrumentation

Foraging movements were recorded with GPS tracking tags (either iGot-u GT-120; Mobile Action Technology, Inc., New Taipei City, Taiwan; or GPS CatTrack1, Catnip Technologies, Anderson, South Carolina, USA). Tags were encapsulated in polyolefin for waterproofing. The total tracking package mass was 22 g, which was 1.1–1.9% of the body mass of the four booby species (mean mass Blue-footed: 1,532 ± 258 g, n=60; Brown: 1,200 ± 189 g, n=70; Masked: 1,998 ± 276 g, n=41; Red-footed: 1,155 ± 167 g, n=36). Birds were captured either by hand or net. Tags were taped underneath the central 2-3 tail feathers with waterproof tape (Tesa #4651, Hamburg, Germany). The duration of tag deployment varied between colonies and species; typically, a tag was programmed to either: (1) start recording at 06:00, due to the diurnal behaviors of many booby species; or (2) programmed to begin recording upon tag attachment to the bird. The sampling interval of the tags also varied between study sites, and ranged 1–120 s. Due to logistical differences between study sites, tags were deployed for 1–9 d, resulting in some individuals having multiple recorded trips.

1.2.3 GPS data processing

GPS tracking tags recorded locations with high precision (10-60 s) and accuracy (ca. 3 m) and thus these data required minimal pre-processing. All track analyses and statistics were conducted in the program R (R Core Team, 2016, version 3.3.2) with custom-built functions, unless otherwise specified. Tracks were manually inspected to remove erroneous locations. Two simple speed filters were then employed to remove additional erroneous locations. First, a speed-filter of 150 km/h was applied to remove erroneous locations, but allow for fast bursts of speed (Zavalaga et al. 2010). Second, because each species has different mean travel speeds, an additional forward-backward speed filter was applied, based on the mean maximum speed per species from these tracking data (mean maximum speeds: Blue-footed: 85 km/h; Brown: 82 km/h; Masked: 93 km/h; Red-footed: 91 km/h), using the function

"vmask" from the R package "argosfilter" (Freitas 2012). Overall, less than 1% of raw GPS points were removed from any foraging track. Finally, all points within a 1-km polygon buffer around study colonies were excluded from analyses, following Kappes et al. (2011) and Young et al. (2015), because boobies do not forage within 1 km of nests (Weimerskirch et al. 2009, Poli et al. 2017).

To compare behaviors among tracked birds with different sample intervals, tracks were interpolated to one position every 60 s using the R package "adehabitatLT" (Calenge 2006). All distances were calculated with great circle distance (distance measured on a sphere) using the "distHaversine" function from the R package "geosphere" (Hijmans 2017a).

1.2.4 Behavior metrics

Trip-length metrics were calculated for each foraging trip. Five parameters described overall foraging behavior: mean travel speed; trip duration; total distance traveled; maximum distance from the colony; and foraging trip pattern (trip type). Three metrics of foraging activity were also identified: total foraging bouts; proportion of time spent on the water; and landings per hour. Landings were identified as locations where the flight speed was <5 km/h (Young et al. 2010). Landing locations often occurred consecutively, so to calculate the number of distinct foraging bouts, consecutive landing points were grouped into one foraging bout. Foraging bouts separated by more than 60 s were considered separate foraging bouts, and the total number of foraging bouts was calculated for each foraging trip. The proportion of time spent on water was calculated as the total time spent foraging divided by the total duration of the foraging trip. Two foraging trip patterns were identified ("focused" and "throughout"; Fig. S1.1) by manually inspecting each foraging track for landing points in relation to the furthest point from the colony. Foraging trips that had landing points only at the furthest points from the colony were labeled "focused" trips (e.g. Visscher and Seeley 1982; Fig. S1.1a); additionally, focused trips included trips where <5 landing points were identified

elsewhere along the trip. Foraging trips that had >5 landing points outside the furthest region were labeled “throughout” trips (Fig S1.1b).

1.2.4.1 Fidelity Index

To assess the degree to which boobies used similar foraging areas among successive foraging trips, a Fidelity Index was estimated using an equation modified from Willis-Norton et al. (2015), Hazen et al. (2016), and Shaffer et al. (2017). The Fidelity Index compares the GPS location that is the furthest distance from the colony between successive foraging trips of one individual. The index is a value between -1 and 1; a value of 1 indicates high similarity of furthest locations between trips, and a value of -1 indicates no similarity. The Fidelity Index was obtained by the equations:

$$\text{delta distance} = \left| \frac{\text{distance}_i - \text{distance}_j}{\text{distance}_i} \right| \quad (1.1)$$

$$\text{delta angle} = \left| \text{angle}_i - \text{angle}_j \right| \quad (1.2)$$

$$\text{delta distance}_{cs} = 1 + \frac{\text{delta distance}}{-1} \quad (1.3)$$

$$\text{delta angle}_{cs} = \frac{\left(\text{delta angle} - 90\right)}{-90} \quad (1.4)$$

$$\text{Fidelity Index} = \frac{\left(\text{delta distance}_{cs} + \text{delta angle}_{cs}\right)}{2} \quad (1.5)$$

where distance_i and distance_j are the great circle distances between the distal point of a foraging trip and the breeding colony; angle_i and angle_j are the bearings to the distal points of foraging trips (Eq. 1.1 and 1.2). Distance and angle calculations were centered to have a mean of 0 and scaled so that they ranged between -1 and 1 (Eq. 1.3 and 1.4). To enable scaling, Eq. 1.3 was multiplied by 1 or -1 if the value was positive or negative, respectively. The Fidelity Index was then calculated as the sum of the distance and angular displacements, and scaled so that it ranged -1 to 1 (Eq. 1.5). The Fidelity Index returns a

bimodal scale that indicates the degree of similarity or difference between two trips' distal points. Values >0 indicate that two distal points are within 90° of each other, with a maximum value of 1 indicating that these two points are also the same distance from the colony. Values <0 indicate that two distal points are >90° apart, with a value of -1 indicating that the distal points are in opposite directions (180° displacement) and are a large distance apart. The Fidelity Index was calculated for all trip combinations, and the values were averaged to obtain one Fidelity Index value per bird.

1.2.5 Habitat variables

1.2.5.1 Oceanographic data

Oceanographic variables like sea surface temperature (SST), chlorophyll-a concentrations, sea surface height (SSH), depth, slope, and bathymetric position index (BPI) were used to describe foraging habitat. In order to interpret boobies' habitat use, habitat variables were categorized as either static (depth, slope, BPI) or ephemeral (SST, chlorophyll-a, SSH). These variables are commonly associated with at-sea feeding aggregations for many marine predators (Ballance et al. 2006, Spear et al. 2007). Gradients of SST aggregate prey, and therefore SST can be used to predict seabird foraging habitat (Mugo et al. 2014). Chlorophyll-a forms the base of the food chain via primary productivity and can attract feeding aggregations; thus, it is also an important predictor of seabird foraging habitat (Palacios et al. 2006, Kappes et al. 2010). SST and chlorophyll-a data were downloaded for each GPS location from the Aqua Spacecraft Moderate Resolution Imaging Spectroradiometer (MODIS; NASA's Goddard Space Flight Center, OceanColor Web 2017), via the "xtracto" function from the R package "xtractomatic" (Mendelssohn 2018). These datasets are 8-day composites of satellite-derived data, with resolutions of 2.7 km, downloaded from an equal angle grid of 0.025° latitude by 0.025° longitude. Chlorophyll-a data were log-transformed after download (hereafter referred to as chlorophyll). SSH is a measure of ocean surface topography, and

SSH is a proxy for upwelling regions and eddies, which bring nutrient-rich water to the surface and enhance primary productivity. SSH data were obtained as hourly means from 0.0833° latitude by 0.0833° longitude grids from a 14-day hindcast model from AVISO satellites via the Copernicus Marine Environment Monitoring Service (E. U. Copernicus Marine Service Information 2017). Depth and slope are commonly used to identify upwelling regions that exhibit high primary productivity in the marine environment. The BPI is a type of terrain index that quantifies the absolute difference between a cell's depth and the mean depth of the surrounding eight cells, and determines whether the location forms part of a bathymetric crest or trough (Wilson et al. 2007). Positive and negative BPI values indicate that the point is higher or lower than its average surrounding points, respectively. Bathymetry data for the variable depth were obtained from the NOAA dataset "ETOPO1" via the R package "marmap" (Pante and Simon-Bouhet 2013). Slope and BPI were calculated from the depth data, using the R package "raster" (Hijmans 2017b).

1.2.5.2 Principal components analysis

Principal components analyses (PCA) and k-means clusters by partitioning were used to characterize the marine habitat for each foraging trip. This method simplified the six habitat variables into linear combinations via PCA, and grouped the environmental patterns via k-means clustering to classify and visualize habitat groupings; this approach has been used on a variety of data types including fisheries and oceanographic data (Plaza et al. 2017), materials engineering (He and Tan 2018) and marine mammal behavioral data (Robinson et al. 2007). PCA is a standard and commonly used tool in oceanographic science (Preisendorfer and Mobley 1988). PCA was conducted on three sets of data: 1) the GPS locations from the entire foraging trip ("full-trip"); 2) transit locations; and 3) landing locations to characterize foraging habitat separately. The PCAs were conducted on the variables SST, chlorophyll, SSH, depth, slope, and BPI with the "prcomp" function from the R package "stats" (R Core Team 2016). Each of the six variables were centered and scaled prior to PCA.

Principal components whose eigenvalues were ≥1.0 were retained. These principal components were saved and used in k-means clustering analysis.

1.2.5.3 K-means clusters by partitioning

The optimal number of centroids for k-means was chosen following Schreer and Testa (1995) and Robinson et al. (2007). First, successive k-means clustering analyses were run on the three retained principal components using 2-20 clusters. Second, the F-statistic from each cluster analysis was plotted against the number of clusters. The resulting scree plots helped to determine that five clusters represented the most variation among the clusters for all three sets of data, and groupings larger than five did not further describe the variance in each analysis. Therefore, the k-means clustering analysis was conducted using five centroids and 25 random starts with the function “kmeans” in the R package “stats” (R Core Team 2016).

The k-means analysis assigned a cluster to each GPS location. Though nearly half of the foraging trips had GPS locations that were assigned to a single full-trip cluster, more than half of the foraging trips had GPS locations in multiple full-trip clusters. To use foraging trips that had multiple full-trip clusters in behavioral analyses, full-trip clusters were combined into a singular categorical variable. For each foraging trip, full-trip clusters were ranked by the proportions of time that a bird spent in each cluster. For example, a bird that traveled within full-trip clusters 1, 3, and 5, and spent 45%, 20%, and 35% of the trip in each cluster, respectively, would be assigned the full-trip cluster category “1.5300”. Thus, the cluster number before the decimal refers to the cluster in which an individual spent the most time, and the cluster numbers after the decimal refer to clusters in which less time was spent, but still visited. This assignment method ultimately resulted in 15 unique full-trip cluster combinations across 444 foraging trips.

1.2.6 Statistical models of behavior

Linear mixed effects models (LME) with restricted maximum likelihood (REML) were used to test whether foraging behaviors and full-trip clusters were related. The significance of the fixed factors of the LME were assessed with ANOVA with Type III sum of squares. Because the trip type variable was binomial, a logistic regression with a logit link was used to test whether trip type was correlated with clusters. Each behavior metric (travel speed; total distance traveled; trip duration; maximum distance from colony; total foraging bouts; proportion of time spent on the water; landing rate) was the response variable in separate LMEs; full-trip cluster, species, sex, and the interaction term species:full-trip cluster were fixed factors; and, to avoid any effects of pseudoreplication, individual bird number was used as a random factor, nested in year (Sommerfeld et al. 2013, Mendez et al. 2015). Sex was included as a fixed factor because behavioral differences have been observed in boobies due to reverse size sexual dimorphism (females are larger than males; Weimerskirch et al. 2006, 2009, Castillo-Guerrero and Mellink 2011; however, Zavalaga et al. 2007, Young et al. 2010, and Kappes et al. 2011 did not observe sex-based differences in flight behaviors). Similarly, species was a fixed factor because the four booby species differ in size (see mean body masses per species in Instrumentation section). Only cluster combinations with >10 trips were included in these analyses. LME were conducted with the function “lmer” from the R package “lme4” (Bates et al. 2015); anovas were conducted with the function “Anova” from the R package “car” (Fox and Weisberg 2011); and logistic regression was conducted with the function “glm” from the R package “stats” (R Core Team 2016).

Response variables for LMEs were visually inspected with histograms and Q-Q plots to test for normality: travel speed was normally distributed; maximum distance from colony and total landings were log-transformed; total distance traveled, trip duration, proportion of time spent on water, and landing rate were square root-transformed. Therefore, the error

structures for these variables approached normal distributions, and a Gaussian family was selected for all models. Significance of models were assessed at $p<0.05$.

We tested the predictions that there would be: 1) different behaviors in different habitats, represented by significant relationships between behaviors and full-trip clusters; and 2) similar foraging behaviors between conspecifics and congeners within habitats, represented by non-significant interaction terms of species:full-trip cluster.

1.3 Results

1.3.1 Environmental characteristics

A total of 444 foraging trips by 183 individual birds were analyzed (Table 1.1). Oceanographic habitat characteristics for foraging trips were described by a combination of PCA and k-means cluster analyses. For the full-trip dataset, the first three principal components explained 40.7%, 20.0%, and 17.3% of the variance, respectively. The first three principal components of the transit points explained 41.0%, 19.3%, and 17.7% of the variance, respectively. Similarly, the first three principal components from the landings dataset explained 40.4%, 21.4%, and 16.7% of the variance, respectively. Both static and ephemeral features had large loading values in the PCA, especially chlorophyll, depth, and SSH (Table 1.2).

Foraging habitat was significantly different from transit habitat (Table S1.2). However, landing and transit locations were grouped similarly by their oceanographic characteristics (Fig. 1.2). To illustrate the oceanographic habitats of foraging trips, the full-trip and landing clusters were overlaid on maps of foraging trips (Fig. 1.3, Fig. 1.4). Cluster 1 was the deepest (median depth ± SE: 3,566 ± 10 m; n=34,507 points) and coldest (median SST ± SE: 22.9 ± 0.01 °C; n=34,507 points; Fig. 1.2), and it occurred only at the pelagic colonies (Isla Clarión, Palmyra, and Tern Island; Fig. 1.3, Fig. 1.4). Cluster 2 was characterized by the highest slope (median slope ± SE: 7.9 ±0.04°; n=9,939 points) and highest BPI (median BPI ± SE: 50.3 ±

0.45; n=9,939 points), indicating that it had complex bottom topography (Fig. 1.2). Cluster 3 was unique to the coastal Mexican colonies of Isla Pajarera and Peña Blanca (Fig. 1.3, Fig. 1.4), and had the warmest SST (median SST ± SE: 30.0 ± 0.01 °C; n=31,715 points) and high chlorophyll (median chlorophyll-a ± SE: 0.44 ± 0.002 mg/m3; n=31,715 points; Fig. 1.3). Cluster 4 had deep (median depth ± SE: -3,166 ± 7.4 m; n=20,670 points), warm (median SST ± SE: 28.4 ± 0.01°C; n=20,670 points) water with high slope (median slope ± SE: 6.32 ± 0.03°; n=20,670 points; Fig. 1.2). Cluster 5 was unique to the Gulf of California (Fig. 1.3, Fig. 1.4), and was the shallowest (median depth ± SE: -16 ± 0.26 m; n=12,461 points) with the highest chlorophyll (median chlorophyll-a ± SE: 2.49 ± 0.01 mg/m3; n=12,461 points) and no slope (median slope ± SE: 0.09 ± 0.01°; n=12,461 points; Fig. 1.2).

1.3.2 Behaviors

Travel speed, total distanced traveled, trip duration, maximum distance traveled from the colony, total foraging bouts, and landing rate were correlated with full-trip clusters and species (Table 1.3). The proportion of time boobies spent on the water (Table 1.3) and trip type (logistic regression: $p=0.316$, $\chi 2=9.32$, $df=8$, $n=423$) were not correlated with the full-trip clusters. The fixed factor species was not correlated with landing rate or the proportion of time spent on the water, and the fixed factor sex was only correlated with total distance traveled (Table 1.3). The interaction term species:full-trip cluster was not a significant factor for any behaviors except for trip duration (Table 1.3). Behaviors ranged widely between clusters (Table 1.4) and between species and colonies (Table S1.3).

The Fidelity Index indicated that boobies from all colonies exhibited a medium to high degree of site fidelity among foraging trips (Fidelity Index: 1.54 ± 0.74; range: 0.15 – 4.24; n=78 birds; Fig. 1.5), suggesting that boobies tended to re-visit foraging locations during successive foraging trips.

1.4 Discussion

Foraging behaviors of seven populations of a clade of aerial marine predators were strongly predicted by local oceanographic habitats, supporting our hypothesis that boobies exhibit adaptive foraging behaviors in a wide range of habitats. The significant relationships between most behaviors and full-trip cluster supported our first prediction that behaviors were different in different habitats. The interaction term of species:full-trip cluster was not a significant factor for any behaviors except trip duration, supporting our prediction that individuals shared behaviors with conspecifics and congeners if they shared similar habitat. Oceanographic habitats were composed of a combination of static and ephemeral features, especially depth, chlorophyll, and SSH, illustrating that boobies exhibit foraging plasticity in response to complex and unpredictable environments. Adaptability to changing environmental conditions is important in the context of rapidly changing environmental conditions, including a potential future of novel environments due to anthropogenic habitat alterations and climate change (Croxall et al. 2012, Beever et al. 2017).

1.4.1 Environmental drivers of foraging behaviors

Foraging plasticity arises in response to differing environmental conditions (West-Eberhard 1989). In this study, environmental conditions varied across seven study colonies, creating the potential for localized differences in behaviors. Four colonies had environmental characteristics unique to their respective regions: Isla Pajarera and Peña Blanca formed a cluster of warm, shallow water and high chlorophyll in southern coastal Mexico (cluster, 3); and Isla San Jorge and Isla El Rancho formed another cluster that was shallow, flat, and had low SSH (cluster 5) in the Gulf of California. Variations in static and ephemeral features can lead to differences in prey distributions and availability (Pierce et al. 2008), and together, habitat and diet cause differences in foraging behaviors in predators (Wong and Candolin 2015). For example, shallow, flat habitat at Islas San Jorge and El Rancho could provide

highly profitable foraging areas for three reasons. First, the northern Gulf of California experiences large diurnal tidal changes (up to 9 m). During low tide, boobies in the northern Gulf of California have access to benthic prey in addition to schooling prey, leading to boobies' diverse diet (Mellink et al. 2001). Second, reliable prey sources in shallow regions could result from seasonal wind-driven upwelling along the coast that drives high productivity (Lavín and Marinone 2003). Third, estuarine and terrestrial input near Isla El Rancho likely provide high productivity and many foraging opportunities (Hidalgo-González and Alvarez-Borrego 2004). Additionally, estuaries in the Gulf of California are nurseries for many fish species, providing another seasonal food source for predators (Zetina-Rejón et al. 2003). Together, the drastically different habitat and diversity of available prey in the Gulf of California likely contributes to behavioral differences compared to boobies in other regions.

Ecological niches shifted in the three pelagic colonies, where environmental characteristics formed three habitat clusters that were shared among colonies that were more than 1000 km apart (clusters 1, 2, and 4). Isla Clarión, Palmyra Atoll, and Tern Island are located in tropical and subtropical pelagic waters, where productivity is typically low, and foraging opportunities for seabirds may be limited (Weimerskirch 2007). However, these pelagic habitats predicted foraging behaviors. The deepest cluster (cluster 1) was not present at the coastal colonies, distinguishing the deep, pelagic water from other types of booby foraging habitat in this study. Deep cluster 1 occurred at the furthest points of foraging trips, where boobies likely rely heavily on subsurface predators like dolphins and tuna to drive prey to the surface in these deep waters (Scott and Cattanach 1998; Bertrand et al. 2002, Spear et al. 2007). Clusters 2 and 4 were shallower than cluster 1 and had higher slopes, which suggest upwelling conditions. For example, Brooks Banks is a shoal to the northwest of Tern Island, and Masked and Red-footed Boobies frequently foraged along its edges (cluster 4; Young et al. 2015). This type of upwelling habitat was also important across several colonies: Brown Boobies at Palmyra Atoll mostly used clusters 2 and 4 – the clusters that are also shared with Brown Booby foraging habitat at the Isla Pajarera and Peña Blanca colonies.

Upwelled water created by shoals aggregates nutrients and prey species, and provides an important, reliable foraging habitat for Brown Boobies. Thus, across all colonies, boobies adapted to their regional foraging habitats to forage most efficiently. This is especially evident for five of the seven colonies that each had three clusters: boobies could forage in three habitat types that contained a mix of static and ephemeral features, but to forage most efficiently, they chose to either search for sub-surface predators in deep water (cluster 1), or focused on upwelling regions that aggregated prey (clusters 2 and 4).

1.4.2 Evidence for behavioral plasticity

Animals modify foraging behaviors to optimize energy expenditure with the amount of energy obtained from food (Schoener 1971, Stephens and Krebs 1986, Sims et al. 2008). To maintain this energy balance, animals use cues to find food. Across the seven study sites, boobies exhibited variations in behaviors, and these behaviors were strongly correlated with local oceanographic habitats. To forage efficiently within these varied habitats, boobies used a combination of static (depth) and ephemeral (chlorophyll, SSH) environmental cues to find food. Boobies also likely used visual cues (e.g. seeing other predators foraging in groups, Au and Pitman 1986; tracking oceanographic features like eddies and fronts, Tew Kai and Marsac 2010) and internal cues (e.g. returning to places that previously had food, Irons 1998; and indicated by high site fidelity indices) while foraging. By using these environmental, visual, and internal cues across study sites, boobies demonstrated behavioral plasticity in relation to local environmental conditions.

Local oceanographic conditions determined whether boobies transited or foraged in a region: foraging and transit habitats were significantly different, and foraging bouts and landing rates were predicted by full-trip clusters. Additionally, landing rates were not predicted by either species or sex. Together, this strongly suggests that foraging activity is determined by local oceanographic conditions, specifically the presence of upwelled water. Foraging

bouts and landing rates were highest in upwelling conditions (clusters 3 and 2, respectively) and lowest in regions that were more influenced by diurnal tidal changes than upwelling (cluster 5 for both behaviors). Upwelling may continually provide prey aggregations, allowing for easy foraging, and thus cause boobies to land frequently. These foraging behaviors are likely driven by localized oceanographic conditions that also drive prey species' distributions (e.g. Pierce et al. 2008). Many foraging bouts and/or high landing rates could represent a large prey patch, where a bird lands frequently in an area full of food, like in the middle of schooling fish at the surface (Sommerfeld et al. 2015). Alternatively, high landing frequencies could imply scarce prey, because individuals repeatedly landed to capture prey and foraging effort was therefore high. The ability to adjust foraging activity to local conditions and high or low prey densities greatly aids predators' adaptability to acute and chronic environmental changes (e.g. Jung and Kalko 2010).

Behaviors related to overall foraging effort (total distance traveled, duration, speed) reflected the amount of time and energy an individual exerted to find food. These behaviors were predicted by full-trip cluster, demonstrating that local oceanographic characteristics are an important factor during optimal foraging. For example, boobies may follow the edges of eddies like other tropical seabirds (Tew Kai and Marsac 2010) in shallow habitats with high chlorophyll, like cluster 3, which is unique to Isla Pajarera and Peña Blanca. Alternatively, a lack of external cues could cause a bird to transit through the habitat quickly: cluster 4 had low chlorophyll and birds that spent the most time in cluster 4 had fast travel speeds and few foraging bouts. This behavior indicates that boobies are more likely to transit through this habitat type to get to a more preferred habitat type, such as cluster 2 (shallow pelagic cluster with complex bottom topography), which had an overall large landing rate (indicative of foraging activity). Similarly, short trip durations took place in association with cluster 3 (high chlorophyll coastal cluster). Short foraging trips close to these colonies may indicate reliable food sources that birds frequently exploit.

The maximum distance metric represented the furthest point at which a foraging booby parent traveled searching for food while maintaining an energy balance (energy expenditure during self-foraging and chick-provisioning, for example) and optimal flight-energy efficiency (Schoener 1971). Therefore, the habitat clusters identified at the furthest points of long trips suggest that these locations were preferable environments that provided predictable foraging opportunities. The largest mean maximum distance traveled was in cluster 1 (cold, deep pelagic cluster), indicating that traveling to this habitat type was worth the energy expenditure to get there. This is further supported by boobies' medium-high site fidelity, where individuals were likely re-visiting profitable foraging habitat. However, our fidelity index varied between colonies, and is also in opposition to other studies that have observed low site fidelity in boobies in the Indian Ocean (Masked and Red-footed boobies; Weimerskirch et al. 2005, Kappes et al. 2011). Site-fidelity in boobies may be related to the predictability of local static and ephemeral cues used at each colony. A high proportion of static (and thus predictable) foraging cues could aid in high site-fidelity at one colony, whereas a high proportion of ephemeral cues could indicate low site fidelity at another colony. Indeed, the Indian Ocean is warmer and less productive than our study areas in the Pacific Ocean, and foraging conditions are less predictable (Weimerskirch 2007, Kappes et al. 2011).

1.4.3 Restrictions on behavioral plasticity

Differences in body size, physiology, and age may have constrained plasticity of some behaviors. Though plasticity allows animals to function within a range of environmental conditions, physiological factors such as morphology or energy reserves limit animals' capacity for behavioral plasticity (Cooke et al. 2013). Body size varied among the four booby species and between sexes. Thus, body size likely affected flight aerodynamics and diving dynamics (Ropert-Coudert et al. 2004, Kappes et al. 2011) and foraging locations (Young et

al. 2010), and may have affected boobies' capacities for behavioral plasticity. For example, a larger body size would enable females to sustain flight for longer distances than males, and in fact, the only behavior predicted by sex was the total distance traveled. The physiological capacity and behavioral plasticity of females to sustain longer flight than males may be advantageous during periods of low food abundance and may ultimately result in better fitness (Hadfield and Strathmann 1996). The opposite trend was observed between species however: Brown and Red-footed Boobies had the smallest body masses, but Blue-footed and Brown Boobies generally had shorter trips than Masked and Red-footed Boobies. This is additionally supported by the significance of the interaction term of species:full-trip cluster for trip duration. The amount of time spent at-sea may be dependent on local oceanographic differences between colonies (Suryan et al. 2006). Overall, some behaviors may be restricted by physiological and morphological capacities, but in this study, inter-specific differences in body size were less important than habitat: this result is consistent with observations that Masked and Red-footed Boobies forage in pelagic regions >50 km from the colony (Young et al. 2010, Mendez et al. 2017).

Age and experience may also affect behavioral plasticity. Long-lived species accumulate a lifetime of responses to chronic environmental changes and may be more adaptable to future changes (Beever et al. 2017). In this study, trip type was not predicted by habitat. Trip type in boobies may be influenced by intrinsic factors like experience and age, where older, more experienced individuals are more likely to make focused trips instead of searching for prey along the entire length of the trip (Rutz et al. 2006). Older, more experienced individuals may also recognize foraging cues more readily and thus know when to alter their behaviors to forage efficiently (Zimmer et al. 2011).

1.4.4 Conclusions

Behaviors were strongly predicted by local oceanographic habitats. These habitats were shared across colonies and species, demonstrating that boobies exhibit great behavioral plasticity. Environmental features that were most prominent in our analyses were both ephemeral (chlorophyll; SSH; SST) and static (depth; slope), reflecting short- and long-term variations in the marine environment. Together, this suggests that as environmental conditions change, boobies could adjust to new conditions. Flexibility of foraging behaviors to seasonal and variable oceanographic conditions is helpful for birds facing changing climates and habitat destruction (Croxall et al. 2012), and changes to nesting habitat availability (Mannocci et al. 2014). For example, low-lying nesting colonies are at risk of disappearing due to rising sea levels (Croxall et al. 2012, Hatfield et al. 2012). If forced to re-locate to new nesting areas, boobies would adapt and be able to forage efficiently in potentially new environments. However, some animals may have less flexible foraging ecologies due to physiological (Webb 1984), reproductive (Boersma and Rebstock 2009), and life history (Abrams 1991) constraints. New environmental regimes could have high foraging effort costs that alter body condition and population dynamics (Wong and Candolin 2015). We suggest that foraging behavioral plasticity in relation to these constrains should be investigated on large scales of populations, species, and clades to assess the degree to which species could adapt to future environmental perturbations.

1.5 References

Abrams, P. A. 1991. Life history and the relationship between food availability and foraging effort. Ecology 72:1242–1252.

Au, D. W. K., and R. L. Pitman. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88:304–317.

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

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

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beever, E. A., L. E. Hall, J. Varner, A. E. Loosen, B. Jason, M. K. Gahl, F. A. Smith, and J. J. Lawler. 2017. Behavioral flexibility as a mechanism for coping with climate change. Frontiers in Ecology and the Environment doi:10.1002/fee.1502.

Bertrand, A., F.-X. Bard, and E. Josse. 2002. Tuna food habits related to the micronekton distribution in French Polynesia. Marine Biology 140:1023–1037.

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

Boersma, P. D., and G. A. Rebstock. 2009. Foraging distance affects reproductive success in Magellanic penguins. Marine Ecology Progress Series 375:263–275.

Bograd, S. J., D. G. Foley, F. B. Schwing, C. Wilson, R. M. Laurs, J. J. Polovina, E. A. Howell, and R. E. Brainard. 2004. On the seasonal and interannual migrations of the transition zone chlorophyll front. Geophysical Research Letters 31:1–5.

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

Castillo-Guerrero, J. A., and E. Mellink. 2011. Occasional inter-sex differences in diet and foraging behavior of the blue-footed booby: Maximizing chick rearing in a variable environment? Journal of Ornithology 152:269–277.

Chevin, L., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biology 8:e1000357 doi:10.1371/journal.pbio.1000357

Cooke, S. J., L. Sack, C. E. Franklin, A. P. Farrell, J. Beardall, M. Wikelski, and S. L. Chown. 2013. What is conservation physiology? Perspectives on an increasingly integrated

and essential science. Conservation Physiology 1: https://doi.org/10.1093/conphys/cot001

Croxall, J. P., S. H. M. Butchart, B. Lascelles, A. J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22:1–34.

Elliott, K., L. S. Chivers, L. Bessey, A. J. Gaston, S. A. Hatch, A. Kato, O. Osborne, Y. Ropert-Coudert, J. R. Speakman, and J. F. Hare. 2014. Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. Movement Ecology 2:17.

E. U. Copernicus Marine Environment Monitoring Service. 2017. Global sea physical analysis and forecasting product. http://www.marine.copernicus.eu

Fiedler, P. C. 2002. The annual cycle and biological effects of the Costa Rica Dome. Deep-Sea Research Part I: Oceanographic Research Papers 49:321–338.

Forister, M. L., L. A. Dyer, M. S. Singer, J. Stireman III, and J. T. Lill. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. Ecology 93:981–991.

Fox, J., and S. Weisberg. 2011. An {R} companion to applied regression, Second edition. Thousand Oaks, CA: Sage. URL:http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Freitas, C. 2012. argosfilter: Argos locations filter. R package version 0.63. https://CRAN.R-project.org/package=argosfilter.

Hadfield, M., and M. Strathmann. 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. Oceanologica Acta 19:323–334.

Hatfield, J. S., M. H. Reynolds, N. E. Seavy, and C. M. Krause. 2012. Population dynamics of Hawaiian seabird colonies vulnerable to sea-level rise. Conservation Biology 26:667–678.

Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277-327 *in* J. H. Steele, editor. Spatial pattern in plankton communities. Springer US.

Hazen, E. L., D. M. Palacios, K. A. Forney, E. A. Howell, E. Becker, A. L. Hoover, L. Irvine, M. DeAngelis, S. J. Bograd, B. R. Mate, and H. Bailey. 2016. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology 54:1415-1428.

He, H., and Y. Tan. 2018. Pattern clustering of hysteresis time series with multivalued mapping using tensor decomposition. IEEE Transactions on Systems, Man, and Cybernetics: Systems: DOI: 10.1109/TSMC.2017.2737578

Hidalgo-González, R. M., and S. Alvarez-Borrego. 2004. Total and new production in the Gulf of California estimated from ocean color data from the satellite sensor SeaWIFS. Deep-Sea Research Part II: Topical Studies in Oceanography 51:739–752.

Hijmans, R. J. 2017a. geosphere: Spherical trigonometry. R package version 1.5-7. https://CRAN.R-project.org/package=geosphere.

Hijmans, R. J. 2017b. raster: Geographic data analysis and modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647–655.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jenkins, R. K. B., L. D. Brady, M. Bisoa, J. Rabearivony, and R. A. Griffiths. 2003. Forest disturbance and river proximity influence chameleon abundance in Madagascar. Biological Conservation 109:407–415.

Jung, K., and E. K. V. Kalko. 2010. Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. Journal of Mammalogy 91:144–153.

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

Kappes, M. A., H. Weimerskirch, D. Pinaud, and M. Le Corre. 2011. Variability of resource partitioning in sympatric tropical boobies. Marine Ecology Progress Series 441:281–294.

Kearney, M., R. Shine, and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. Proceedings of the National Academy of Sciences of the United States of America 106:3835–3840.

Kwasniewski, S., M. Gluchowska, D. Jakubas, K. Wojczulanis-Jakubas, W. Walkusz, N. Karnovsky, K. Blachowiak-Samolyk, M. Cisek, and L. Stempniewicz. 2010. The impact of different hydrographic conditions and zooplankton communities on provisioning little auks along the west coast of Spitsbergen. Progress in Oceanography 87:72–82.

Lavín, M., and S. Marinone. 2003. An overview of the physical oceanography of the Gulf of California. Pages 173–204 *in* O. U. Velasco Fuentes, editor. Nonlinear Processes in Geophysical Fluid Dynamics. Kluwer Academic Publishers. Netherlands.

Manenti, R., M. Denoël, and G. F. Ficetola. 2013. Foraging plasticity favours adaptation to new habitats in fire salamanders. Animal Behaviour 86:375–382.

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

Mellink, E., J. Domínguez, and J. Luévano. 2001. Diet of eastern Pacific brown boobies *Sula leucogaster brewsteri* on Isla San Jorge, north-eastern Gulf of California, and an April comparison with diets in the middle Gulf of California. Marine Ornithology 29:23–28.

Mendelssohn, R. 2018. xtractomatic: Accessing environmental data from ERD's ERDDAP server. R package version 3.4.2. https://CRAN.R-project.org/package=xtractomatic.

Mendez, L., C. Cotté, A. Prudor, and H. Weimerskirch. 2015. Variability in foraging behaviour of red-footed boobies nesting on Europa Island. Acta Oecologica:1–11.

Mendez, L., P. Borsa, S. Cruz, S. De Grissac, J. Hennicke, J. Lallemand, A. Prudor, and H. Weimerskirch. 2017. Geographical variation in the foraging behaviour of the pantropical red-footed booby. Marine Ecology Progress Series 568:217–230.

Michalec, F., M. Holzner, D. Menu, J. Hwang, and S. Souissi. 2013. Behavioral responses of the estuarine calanoid copepod *Eurytemora affinis* to sub-lethal concentrations of waterborne pollutants. Aquatic Toxicology 138-139:129–138.

Mugo, R. M., S. I. Saitoh, F. Takahashi, A. Nihira, and T. Kuroyama. 2014. Evaluating the role of fronts in habitat overlaps between cold and warm water species in the western North Pacific: A proof of concept. Deep-Sea Research Part II: Topical Studies in Oceanography 107:29–39.

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, and NOAA CoastWatch Program. 2017. Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Ocean Color Data, NASA OB.DAAC. http://doi.org/10.5067/ORBVIEW-2/SEAWIFS_OC.2014.0. Accessed on 2017/04/04.

Nelson, B. 1978. The Sulidae: Gannets and Boobies. Oxford University Press, United Kingdom.

O'Dowd, D. J., P. T. Green, and P. S. Lake. 2003. Invasional 'meltdown' on an oceanic island. Ecology Letters 6:812–817.

Palacios, D. M., S. J. Bograd, D. G. Foley, and F. B. Schwing. 2006. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. Deep Sea Research Part II: Topical Studies in Oceanography 53:250–269.

Pante, E., and B. Simon-Bouhet. 2013. marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS ONE 8(9): e73051. https://doi.org/10.1371/journal.pone.0073051.

Phil, L., S. P. Baden, R. J. Diaz, and L. C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Marine Biology 112:349–361.

Philander, S. G. H., D. Gu, D. Halpern, G. Lambert, N. C. Lau, T. Li, and R. C. Pacanowski. 1996. Why the ITCZ is mostly north of the equator. Journal of Climate 9:2958–2972.

Pierce, G. J., V. D. Valavanis, A. Guerra, P. Jereb, L. Orsi-Relini, J. M. Bellido, I. Katara, U. Piatkowski, J. Pereira, E. Balguerias, I. Sobrino, E. Lefkaditou, J. Wang, M.

Santurtun, P. R. Boyle, L. C. Hastie, C. D. MacLeod, J. M. Smith, M. Viana, A. F. González, and A. F. Zuur. 2008. A review of cephalopod–environment interactions in European Seas. Hydrobiologia 612:49–70.

Pirotta, E., B. E. Laesser, A. Hardaker, N. Riddoch, M. Marcoux, and D. Lusseau. 2013. Dredging displaces bottlenose dolphins from an urbanized foraging patch. Marine Pollution Bulletin 74:396–402.

Plaza, F., R. Salas, and E. Yañez. 2017. Identifying ecosystem patterns from time series of anchovy (Engraulis ringens) and sardine (Sardinops sagax) landings in northern Chile. Journal of Statistical Computation and Simulation: DOI:10.1080/00949655.2017.1410150

Poli, C. L., A. Harrison, A. Vallarino, P. D. Gerard, and P. G. R. Jodice. 2017. Dynamic oceanography determines fine scale foraging behavior of masked boobies in the Gulf of Mexico. PLoS ONE 12(6): e0178318. https://doi.org/10.1371/journal.pone.0178318

Preisendorfer, R. W., and C. D. Mobley. 1988. Principal component analysis in meterology and oceanography. Vol. 425. Amsterdam: Elsevier Science Publishers. 425 pp.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://r-project.org

Robinson, P. W., Y. Tremblay, D. E. Crocker, M. A. Kappes, C. E. Kuhn, S. A. Shaffer, S. E. Simmons, and D. P. Costa. 2007. A comparison of indirect measures of feeding behaviour based on ARGOS tracking data. Deep Sea Research Part II: Topical Studies in Oceanography 54:356–368.

Ropert-Coudert, Y., D. Grémillet, P. Ryan, A. Kato, Y. Naito, and Y. Le Maho. 2004. Between air and water: the plunge dive of the cape gannet *Morus capensis*. Ibis 146:281–290.

Rutherford, S., S. D'Hondt, and W. Prell. 1999. Environmental controls on the geographic distribution of zooplankton diversity. Nature 400:749–753.

Rutz, C., M. J. Whittingham, and I. Newton. 2006. Age-dependent diet choice in an avian top predator. Proceedings of the Royal Society B: Biological Sciences 273:579–86.

Rykaczewski, R. R., and D. M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the United States of America 105:1965–1970.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Schreer, J. F., and J. W. Testa. 1995. Statistical classification of diving behavior. Marine Mammal Science 11:85–93.

Scott, M. D., and L. Cattanach. 1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. Marine Mammal Science 14:401–428.

Shaffer, S. A., S. Cockerham, P. Warzybok, R. W. Bradley, J. Jahncke, C. A. Clatterbuck, M. Lucia, J. A. Jelincic, A. L. Cassell, E. C. Kelsey, and J. Adams. 2017. Population-level plasticity in foraging behavior of Western Gulls (*Larus occidentalis*). Movement Ecology 5:27. DOI 10.1186/s40462-017-0118-9.

Sims, D.W., E.J. Southall, N.E. Humphries, G.C. Hays, C.J. Bradshaw, J.W. Pitchford, A. James, M.Z. Ahmed, A.S. Brierley, M.A. Hindell, and D. Morritt. 2008. Scaling laws of marine predator search behaviour. Nature, 451:1098–1102. DOI:10.1038/nature06518.

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

Sommerfeld, J., A. Kato, Y. Ropert-Coudert, S. Garthe, C. Wilcox, and M. A. Hindell. 2015. Flexible foraging behaviour in a marine predator, the masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions. Journal of Experimental Marine Biology and Ecology 463:79–86.

Spear, L. B., D. G. Ainley, and W. Walker. 2007. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. Studies in Avian Biology 35:1–109.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, USA.

Suryan, R. M., D. B. Irons, E. D. Brown, P. G. R. Jodice, and D. D. Roby. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Progress in Oceanography 68:303–328.

Tew Kai, E., and F. Marsac. 2010. Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. Progress in Oceanography 86:214–223.

Van Buskirk, J. 2012. Behavioral plasticity and environmental change. Pages 145–158 *in* Candolin, U., and B. B. M. Wong, editors. Behavioral responses to a changing world: mechanisms and consequences. Oxford University Press, United Kingdom.

Visscher, P. K., and T. D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63:1790–1801.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist 24:107–120.

Weimerskirch, H., M. Le Corre, Y. Ropert-Coudert, A. Kato, and F. Marsac. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? Proceedings of the Royal Society B: Biological Sciences 272:53–61.

Weimerskirch, H., M. Le Corre, Y. Ropert-Coudert, A. Kato, and F. Marsac. 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 Research Part II: Topical Studies in Oceanography 54:211–223.

Weimerskirch, H., S. A. Shaffer, Y. Tremblay, D. P. Costa, H. Gadenne, A. Kato, Y. Ropert-Coudert, K. Sato, and D. Aurioles. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267–278.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20:249–278.

Willis-Norton, E., E. L. Hazen, S. Fossette, G. Shillinger, R. R. Rykaczewski, D. G. Foley, J. P. Dunne, and S. J. Bograd. 2015. Climate change impacts on leatherback turtle pelagic habitat in the southeast Pacific. Deep-Sea Research Part II: Topical Studies in Oceanography 113:260–267.

Wilson, M. F. J., B. O'Connell, C. Brown, J. C. Guinan, and A. J. Grehan. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy 30:3–35.

Wong, B. B. M., and U. Candolin. 2015. Behavioral responses to changing environments. Behavioral Ecology 26:665–673.

Young, H. S., S. A. Shaffer, D. J. McCauley, D. G. Foley, R. Dirzo, and B. A. Block. 2010. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Marine Ecology Progress Series 403:291–301.

Young, H. S., S. M. Maxwell, M. G. Conners, and S. A. Shaffer. 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. Biological Conservation 181:226–235.

Zavalaga, C. B., S. Benvenuti, L. Dall'Antonia, and S. D. Emslie. 2007. Diving behavior of blue-footed boobies *Sula nebouxii* in northern Peru in relation to sex, body size and prey type. Marine Ecology Progress Series 336:291–303.

Zavalaga, C. B., J. Halls, and G. Dell'Omo. 2010. Marine habitat use of Peruvian boobies: A geographic and oceanographic comparison between inshore and offshore islands. ICES Journal of Marine Science 67:940–951.

Zetina-Rejón, M. J., F. Arreguín-Sánchez, and E. A. Chávez. 2003. Trophic structure and flows of energy in the Huizache-Caimanero lagoon complex on the Pacific coast of Mexico. Estuarine, Coastal and Shelf Science 57:803–815.

Zimmer, I., Y. Ropert-Coudert, A. Kato, A. Ancel, and A. Chiaradia. 2011. Does foraging performance change with age in female little penguins (*Eudyptula minor*)? PLoS ONE 6(1): e16098. doi:10.1371/journal.pone.0016098

Table 1.1 Summary of tracking data of boobies' foraging trips

Summary of tracking data of booby foraging trips. Species abbreviations: BFBO=Blue-footed Booby; BRBO=Brown Booby; MABO=Masked Booby; RFBO=Red-footed Booby. Breeding stage indicates whether tracked bird was incubating eggs (I), brooding chicks (B), or if breeding stage was unknown (unk).

Colony	Species	Tracking Period (MM/YYYY)	Sex			Breeding Stage			No. foraging trips (No. GPS pts)
			F	M	unk	I	B	unk	
Peña Blanca	BRBO	10/2015	1	2	0	0	3	0	11 (2,785)
		11/2015	1	1	0	1	1	0	6 (2,811)
		05–06/2016	6	7	0	0	13	0	107 (21,085)
Pajarera	BRBO	06-07/2016	6	5	0	1	10	0	87 (13,994)
Isla El Rancho	BFBO	02–05/2015	5	13	0	9	9	0	31 (5,677)
		03/2016	6	5	0	0	11	0	15 (2,643)
Isla San Jorge	BRBO	02/2015	4	8	0	6	6	0	15 (5,155)
Isla Clarión	MABO	01/2016	1	2	0	3	0	0	5 (1,218)
	RFBO	01/2016	0	0	4	3	1	0	6 (3,993)
Tern Island	MABO	03/2009	8	3	0	11	0	0	14 (4,769)
		02–03/2010	7	9	0	16	0	0	16 (8,700)
		03/2012	8	7	0	15	0	0	16 (6,057)
	RFBO	03/2009	0	3	0	3	0	0	3 (2,569)
		03/2010	3	2	0	5	0	0	5 (3,781)
		03/2012	4	4	0	8	0	0	8 (5,381)
Palmyra Atoll	BRBO	08–09/2010	3	4	0	4	3	0	20 (4,636)
		07–09/2014	1	3	2	2	4	0	19 (3,675)
	MABO	11/2008	7	5	1	3	9	1	29 (4,856)
		09/2010	4	2	0	3	3	0	16 (4,286)
	RFBO	06/2007	0	1	0	0	0	1	1 (13)
		09/2007	0	1	0	1	0	0	1 (798)
		10/2008	6	1	1	7	0	1	8 (4,164)
		09/2010	2	2	2	4	0	2	7 (2,969)

Table 1.2 Loadings of principal components of environmental variables from boobies' foraging trips

Loadings of components for each environmental variable on the first three principal components from the full dataset (all GPS points; n=109,292). Variables that have the greatest magnitude of regression coefficients in each principal component are highlighted in bold. SSH= sea surface height, SST= sea surface temperature, and BPI= bathymetric position index. PC1 is most strongly correlated with chlorophyll, SSH, and depth. PC2 is most strongly correlated with SST and slope. PC3 is most strongly correlated with BPI.

	Component loadings		
Environmental variable	PC 1	PC 2	PC 3
Depth	**0.46**	-0.16	0.29
Chlorophyll	**0.60**	0.09	-0.10
SSH	**-0.57**	0.15	0.12
SST	0.10	**-0.78**	0.06
Slope	-0.31	**-0.56**	0.14
BPI	0.04	0.17	**0.93**

Table 1.3 Summary statistics of fixed effects from models of boobies' behaviors predicted by cluster, species, and sex

Assessment of significance of fixed effects (obtained via type 3 Anova tests) from linear mixed effect models, where booby behaviors were response variables, and habitat cluster, species, sex, and the interaction of species:full-trip cluster were predictor variables. Bird number was nested in sample year as random factors. All response variables (except travel speed) were transformed prior to analyses to meet assumptions of normality: maximum distance and total foraging bouts were log-transformed; and total distance traveled, trip duration, landing rate, and proportion of time spent on water were square root-transformed.

Behavior	n	Cluster			Species			Sex			Species:Cluster		
		χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
Travel speed	430	18.4	8	0.019	1.9	8	0.983	11.3	3	0.010	1.9	8	0.983
Total distance traveled	430	80.4	8	<0.001	14.4	8	0.073	21.5	3	<0.001	14.4	8	0.073
Trip duration	430	56.5	8	<0.001	19.4	8	0.013	33.7	3	<0.001	19.4	8	0.013
Max. distance	430	55.7	8	<0.001	5.8	8	0.671	11.3	3	0.010	5.8	8	0.671
Total foraging bouts	422	17.5	8	0.025	14.6	8	0.067	28.2	3	<0.001	14.6	8	0.067
Landing rate	422	16.6	8	0.035	2.9	8	0.940	3.6	3	0.315	2.9	8	0.940
Proportion time on water	422	11.0	8	0.200	5.5	8	0.708	1.3	3	0.737	5.5	8	0.708

Table 1.4 Boobies' behaviors per cluster category

Summarized booby behaviors (mean ± SD) from foraging trips per cluster category, where each category represents the proportion of time a bird spent in each of five full-trip cluster habitats.

Cluster category	No. trips	Travel speed (km hr^{-1})	Total distance traveled (km)	Trip duration (hr)	Maximum distance (km)	No. foraging bouts	Landing rate (landings hr^{-1})	% time spent on water
1	59	25 ± 8	212 ± 121	8.7 ± 5.5	82 ± 44	47.0 ± 39.2	6.2 ± 5.0	26.7 ± 15.1
1.2	11	24 ± 7	170 ± 110	7.1 ± 4.5	70 ± 47	34.7 ± 31.8	4.7 ± 2.4	27.5 ± 15.4
1.4	6	20 ± 5	155 ± 62	7.9 ± 3.0	59 ± 26	48.0 ± 20.2	6.2 ± 1.8	38.8 ± 15.0
2	3	9 ± 7	8 ± 12	0.5 ± 0.7	7 ± 5	6.3 ± 7.5	22.7 ± 15.3	48.5 ± 27.3
2.1	1	19	235	12.5	77	103.0	8.3	30.5
2.4	13	20 ± 6	85 ± 51	5.5 ± 5.9	29 ± 17	29.5 ± 25.5	5.9 ± 1.8	31.9 ± 20.3
3	192	20 ± 8	56 ± 43	2.8 ± 1.9	22 ± 16	20.8 ± 14.5	8.3 ± 4.4	34.6 ± 21.3
3.4	13	27 ± 6	164 ± 66	6.0 ± 2.1	64 ± 21	35.5 ± 25.7	5.45 ± 3.13	18.4 ± 11.1
3.5	1	16	56	3.5	27	32.0	9.1	47.9
4	47	24 ± 8	67 ± 45	2.9 ± 2.2	30 ± 16	20.3 ± 21.0	6.4 ± 3.5	27.8 ± 21.8
4.1	11	25 ± 6	147 ± 101	6.4 ± 4.1	59 ± 33	33.3 ± 28.7	5.2 ± 2.3	24.0 ± 14.8
4.2	23	25 ± 7	104 ± 71	4.7 ± 3.4	40 ± 25	27.0 ± 21.7	5.6 ± 2.6	23.0 ± 18.4
4.3	2	22 ± 3	232 ± 25	10.9 ± 2.6	85 ± 5	87.0 ± 36.8	7.8 ± 1.5	35.3 ± 0.2
4.32	1	29	142	4.9	57	16.0	3.3	9.2
5	61	23 ± 9	75 ± 69	3.6 ± 3.4	31 ± 26	19.6 ± 27.5	5.0 ± 2.7	31.1 ± 19.8

Table S1 1.1 Summary statistics of environmental habitat variables per booby colony and tracking period

Summary statistics (mean ± SD, range in parentheses) of oceanographic habitat variables for each colony associated with GPS locations from Booby foraging trips. For colonies with multiple tracking periods, variables are also summarized separately for each tracking period. SST= sea surface temperature; SSH=sea surface height; BPI=bathymetric position index.

Colony	Tracking period (MM/YYYY)	No. points	Chlorophyll *a* (mg m^{-3})	SST (°C)	SSH (m)	Depth (m)	Slope (°)	BPI
Pajarera	06–07/ 2016	12,520	0.40 ± 0.31 (0.13 – 1.96)	30.9 ± 0.4 (30.0 – 31.9)	0.26 ± 0.02 (0.24 – 0.31)	-559 ± 1079 (-4974 – 0)	1.9 ± 2.2 (0.2 – 19.3)	2.6 ± 19.5 (-220.8 – 345.4)
Peña Blanca	10/ 2015	2,698	0.50 ± 0.60 (0.13 – 3.44)	31.2 ± 0.4 (30.1 – 31.7)	0.47 ± 0.04 (0.41 – 0.56)	-594 ± 411 (-2059 – -4)	3.6 ± 1.8 (0.9 ± 8.9)	-2.0 ± 32.7 (-148.3 – 112.8)
	12 /2015	2,783	0.17 ± 0.03 (0.13 – 0.28)	30.6 ± 0.5 (29.5 – 32.3)	0.40 ± 0.05 (0.34 – 0.46)	-1041 ± 902 (-2527 – 0)	3.7 ± 2.0 (0.5 – 9.4)	7.0 ± 43.0 (-138.5 – 169.0)
Isla El Rancho	02–05 /2015	4,826	2.55 ± 1.44 (0.41 – 7.83)	24.8 ± 1.4 (22.6 – 28.1)	0.10 ± 0.02 (0.05 –0.12)	-9 ± 12 (-205 – 0)	0.1 ± 0.2 (0 – 3.6)	0.5 ± 3.7 (-23.8 – 39.3)
	03/ 2016	2,546	1.43 ± 0.60 (0.43 – 3.50)	24.4 ± 0.7 (23.4 – 25.6)	0.11 ± 0.01 (0.10 – 0.13)	-11 ± 16 (-167 – 0)	0.1 ± 0.2 (0 – 1.9)	0.1 ± 3.6 (-16.4 – 18.6)
Isla San Jorge	02/ 2015	5,052	2.92 ± 0.66 (1.68 – 5.83)	19.7 ± 0.5 (18.2 – 21.0)	0.05 ± 0.003 (0.04 – 0.06)	-48 ± 30 (-185 – -1)	0.2 ± 0.2 (0.0 – 0.8)	-0.1 ± 5.1 (-20.3 – 23.4)
Isla Clarión	01/ 2016	5,211	0.10 ± 0.01 (0.09 – 0.13)	25.0 ± 0.3 (24.3 – 25.8)	0.41 ± 0.033 (0.36 – 0.48)	-3361 ± 782 (-3914 – -119)	2.9 ± 4.1 (0.0 – 20.4)	0.8 ± 30.4 (-213.1 – 178.8)
Tern Island	03/ 2009	7,161	0.50 ± 0.60 (0.13 – 3.44)	31.2 ± 0.4 (30.1 – 31.7)	0.47 ± 0.04 (0.41 – 0.56)	-594 ± 411 (-2059 – -4)	3.6 ± 1.8 (0.9 – 8.9)	-2.0 ± 32.7 (-148.3 – 112.8)
	02–03/ 2010	12,315	0.17 ± 0.03 (0.13 – 0.28)	30.6 ± 0.5 (29.5 – 32.3)	0.40 ± 0.05 (0.34 – 0.46)	-1041 ± 902 (-2757 – 0)	3.7 ± 2.0 (0.5 – 9.4)	7.0 ± 43.0 (-138.5 –

								169.0)
	03/ 2012	11,358	0.54 ± 0.28 (0.13 – 2.72)	28.4 ± 1.0 (26.0 – 30.3)	0.26 ± 0.05 (0.18 – 0.39)	-646 ± 1087 (-5074 – 0)	2.9 ± 1.9 (0.2 – 15.6)	2.2 ± 32.2 (-183.3 – 169.0)
Palmyra Atoll	06/ 2007	12	0.19 ± 0.00 (0.19 – 0.20)	27.8 ± 0 (27.8 – 27.8)	0.34 ± 0.00 (0.34 – 0.34)	-389 ± 183 (-639 – -212)	9.9 ± 1.3 (8.7 – 11.2)	65.1 ± 10.8 (53.9 – 74.8)
	09/ 2007	769	0.11 ± 0.02 (0.08 – 0.15)	28.3 ± 0.2 (27.9 – 28.7)	0.35 ± 0.00 (0.34 – 0.35)	-2876 ± 970 (-4317 – -1)	7.9 ± 5.2 (0.4 – 41.7)	9.7 ± 95.2 (-979.5– 1471.8)
	10–11/ 2008	8,850	0.09 ± 0.02 (0.05 – 0.16)	28.6 ± 0.3 (27.6 – 29.2)	0.41 ± 0.04 (0.33 – 0.48)	-3117 ± 967 (-4646 – -38)	6.0 ± 4.5 (0.1 – 24.6)	-2.6 ± 43.7 (-372.5 – 381.8)
	08–09/2010	11,776	0.13 ± 0.01 (0.08 – 0.16)	27.7 ± 0.3 (26.5 – 28.5)	0.50 ± 0.04 (0.41 – 0.55)	-3122 ± 960 (-4490 – -115)	6.1 ± 4.7 (0.0 – 24.6)	-5.6 ± 41.0 (-372.5 – 381.8)
	07–09/2014	2,836	0.05 ± 0.01 (0.05 – 0.11)	29.4 ± 0.5 (28.3 – 30.6)	0.53 ± 0.02 (0.50 – 0.60)	-1838 ± 1032 (-4150 – -3)	10.4 ± 4.8 (0.4 – 24.6)	0.1 ± 92.7 (-372.5 – 611.8)
	05–06/2016	18,579	0.54 ± 0.28 (0.13 – 2.72)	28.43 ± 1.02 (25.97 – 30.25)	0.26 ± 0.05 (0.18 – 0.39)	-646 ± 1087 (-5074 – 0)	2.9 ± 1.9 (0.2 – 15.6)	2.2 ± 32.2 (-183.3 – 169.0)

Table S1.2 Summary statistics of oceanographic variables between transit and foraging locations of boobies' foraging trips

Summary of comparisons between oceanographic characteristics of the transit (n=79670 points) and foraging (n=36817 points) portions of booby foraging trips, using Welch's two sample t-test. Results were assessed at an adjusted significance level of α=0.001 (Bonferroni correction) to compensate for the multiple t-tests comparisons. Foraging locations were determined as locations where travel speed was <5 km hr-1. Species abbreviations: BFBO=Blue-footed Booby; BRBO=Brown Booby; MABO=Masked Booby; RFBO=Red-footed Booby.

Oceanographic variable	Colony	Species	t	Degrees of freedom	p-value
Sea surface temperature	Peña Blanca	BRBO	0.35	16,218	0.725
	Pajarera	BRBO	-2.62	7,886	0.009
	Isla El Rancho	BFBO	-0.64	7,182	0.523
	Isla San Jorge	BRBO	-22.4	3,177	<0.001
	Isla Clarión	MABO	-1.84	726	0.066
		RFBO	-1.44	2,325	0.150
	Tern Island	MABO	-2.38	7,903	0.017
		RFBO	6.96	7,164	<0.001
	Palmyra	BRBO	8.79	4,609	<0.001
		MABO	-17.69	5,626	<0.001
		RFBO	-10.31	3,970	<0.001
log(chlorophyll-*a*)	Peña Blanca	BRBO	-7.98	15,562	<0.001
	Pajarera	BRBO	5.78	8,551	<0.001
	Isla El Rancho	BFBO	10.06	6,596	<0.001
	Isla San Jorge	BRBO	5.07	3,886	<0.001
	Isla Clarión	MABO	-3.35	875	0.001
		RFBO	-0.28	2,042	0.778
	Tern Island	MABO	11.66	8,588	<0.001
		RFBO	-2.29	9,044	0.022
	Palmyra	BRBO	-11.88	4,552	<0.001
		MABO	2.63	5,015	0.009
		RFBO	5.26	4,339	<0.001
Sea surface height	Peña Blanca	BRBO	10.96	17,757	<0.001
	Pajarera	BRBO	-7.36	10,431	<0.001
	Isla El Rancho	BFBO	5.83	6,669	<0.001
	Isla San Jorge	BRBO	12.06	4,854	<0.001
	Isla Clarión	MABO	4.28	775	<0.001
		RFBO	-1.08	2,232	0.279
	Tern Island	MABO	13.24	7,708	<0.001
		RFBO	-10.08	6,036	<0.001
	Palmyra	BRBO	19.86	6,813	<0.001
		MABO	6.82	5,142	<0.001
		RFBO	7.70	4,466	<0.001

Depth	Peña Blanca	BRBO	-17.89	15,004	<0.001
	Pajarera	BRBO	10.11	9,502	<0.001
	Isla El Rancho	BFBO	4.98	7,582	<0.001
	Isla San Jorge	BRBO	-1.49	4,078	0.137
	Isla Clarión	MABO	0.63	710	0.527
		RFBO	-5.81	3,797	<0.001
	Tern Island	MABO	8.84	7,988	<0.001
		RFBO	-9.71	6,745	<0.001
	Palmyra	BRBO	0.92	4,727	0.358
		MABO	-24.43	6,036	<0.001
		RFBO	4.81	5,529	<0.001
Slope	Peña Blanca	BRBO	13.46	15,592	<0.001
	Pajarera	BRBO	-15.94	11,511	<0.001
	Isla El Rancho	BFBO	-11.17	7,970	<0.001
	Isla San Jorge	BRBO	-3.85	3,231	<0.001
	Isla Clarión	MABO	-1.29	840	0.197
		RFBO	-8.17	3,492	<0.001
	Tern Island	MABO	-21.86	10,205	<0.001
		RFBO	-18.72	8,638	<0.001
	Palmyra	BRBO	3.59	4,410	<0.001
		MABO	-27.27	6,286	<0.001
		RFBO	5.27	4,678	<0.001
Bathymetric position index	Peña Blanca	BRBO	4.90	14,483	<0.001
	Pajarera	BRBO	0.53	10,947	0.597
	Isla El Rancho	BFBO	0.53	8,095	0.598
	Isla San Jorge	BRBO	-1.68	3,375	0.093
	Isla Clarión	MABO	-3.37	562	0.001
		RFBO	4.00	3,706	<0.001
	Tern Island	MABO	9.91	10,227	<0.001
		RFBO	1.64	9,844	0.101
	Palmyra	BRBO	-6.91	3,949	<0.001
		MABO	7.33	5,965	<0.001
		RFBO	-3.79	6,382	<0.001

Table S1.3 Foraging trip behaviors per booby species and colony

Summary statistics (mean ± SD) of foraging trip behaviors by species and colony. Species abbreviations: BFBO=Blue-footed Booby; BRBO=Brown Booby; MABO=Masked Booby; RFBO=Red-footed Booby.

Behavior		Travel speed (km hr^{-1})	Total distance traveled (km)	Trip duration (hr)	Max. distance (km)	No. foraging bouts	Landing rate (landings hr^{-1})	Time spent on water (%)
Colony	**Species**							
Peña Blanca	BRBO	20.7 ± 6.7	71.9 ± 53.2	3.5 ± 2.9	28.7 ± 20.3	23.8 ± 18.5	7.3 ± 3.7	30.5 ± 18.3
Pajarera	BRBO	19.0 ± 10.0	55.4 ± 55.4	2.7 ± 2.1	21.8 ± 19.9	21.1 ± 15.9	9.2 ± 5.0	38.3 ± 24.1
Isla El Rancho	BFBO	21.3 ± 9.5	57.3 ± 49.5	2.9 ± 2.3	25.0 ± 20.6	12.2 ± 10.4	4.7 ± 2.5	33.1 ± 20.8
Isla San Jorge	BRBO	27.2 ± 7.7	129.9 ± 90.8	5.7 ± 5.2	50.6 ± 30.5	43.0 ± 46.8	6.1 ± 3.2	25.3 ± 15.6
Isla Clarión	MABO	17.0 ± 8.8	84.1 ± 74.1	4.0 ± 3.4	27.7 ± 20.2	22.0 ± 22.8	12.0 ± 15.7	43.5 ± 21.4
	RFBO	19.3 ± 3.1	211.7 ± 60.9	11.0 ± 2.5	78.7 ± 24.7	96.5 ± 35.4	8.7 ± 2.5	29.2 ± 7.3
Tern Island	MABO	26.6 ± 8.3	193.0 ± 114.5	7.0 ± 3.9	78.5 ± 47.1	29.9 ± 22.3	5.8 ± 5.5	25.5 ± 16.2
	RFBO	21.8 ± 4.0	250.3 ± 145.4	12.1 ± 7.8	89.6 ± 43.5	72.2 ± 48.0	5.7 ± 2.0	27.4 ± 13.0
Palmyra Atoll	BRBO	22.8 ± 9.0	78.8 ± 56.8	3.6 ± 2.7	31.6 ± 20.6	23.5 ± 21.7	6.8 ± 3.8	28.8 ± 23.6
	MABO	25.0 ± 6.0	75.1 ± 40.0	3.3 ± 2.3	33.9 ± 14.7	19.6 ± 16.8	5.5 ± 2.3	25.1 ± 15.7
	RFBO	19.5 ± 5.8	154.8 ± 106.9	7.7 ± 4.1	54.9 ± 39.2	48.4 ± 29.8	7.0 ± 3.4	29.6 ± 18.7

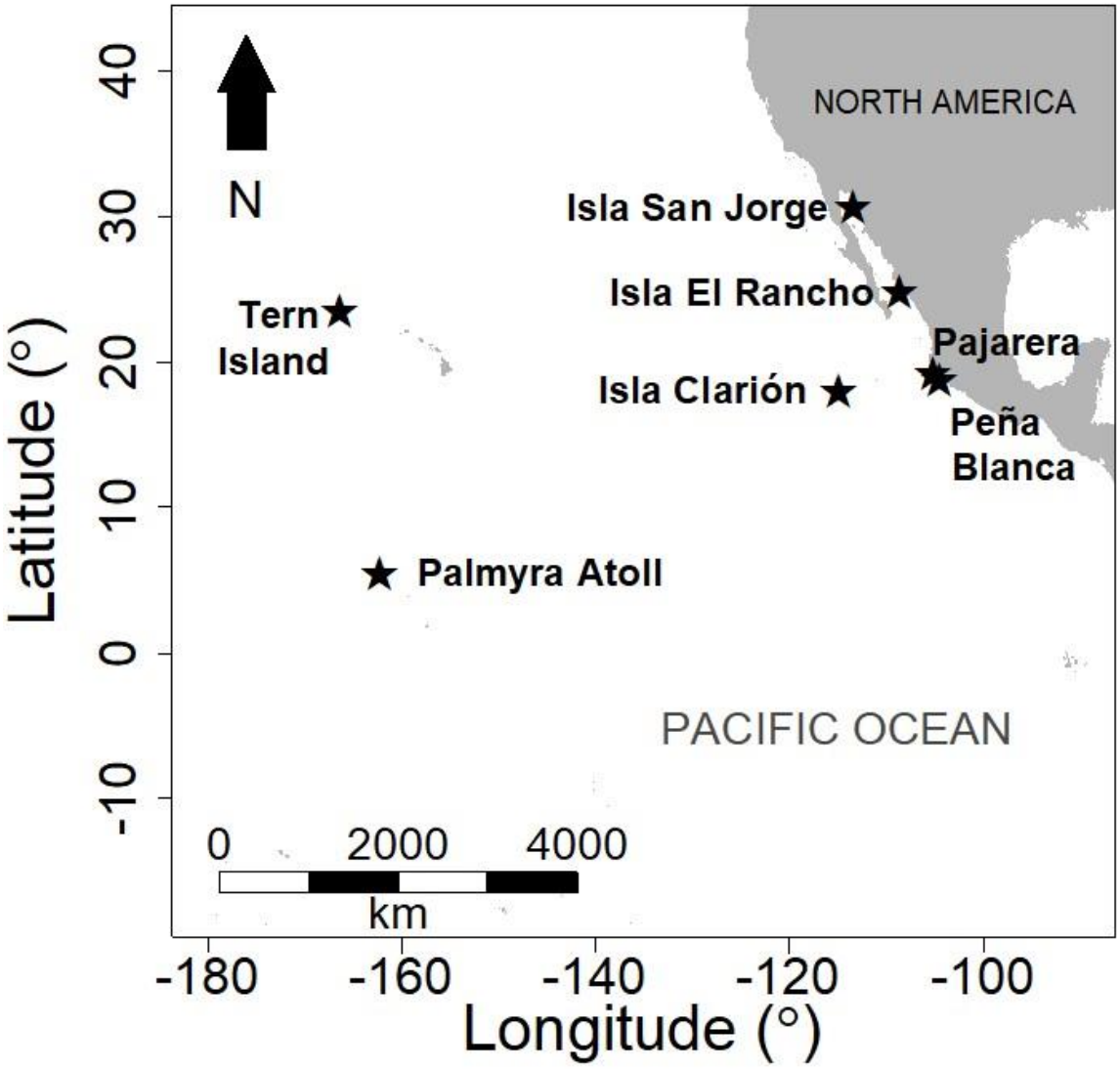

Figure 1.1 Map of study sites of boobies' foraging ecology

Map of study sites (black stars) of foraging habitats and behaviors of booby species, 2007-2016.

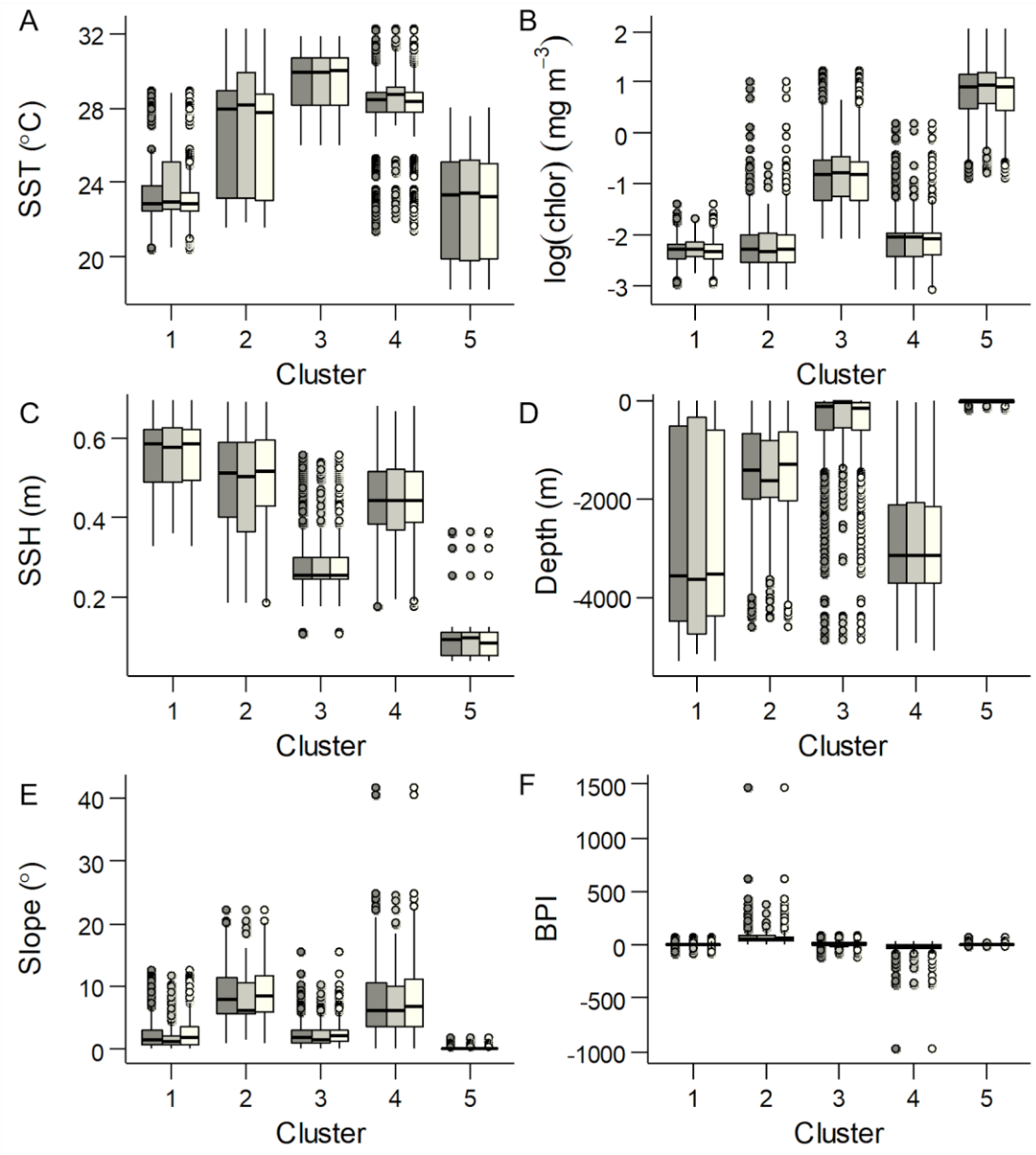

Figure 1.2 Boxplots of environmental variables per habitat cluster

Boxplots representing summary statistics of oceanographic habitat clusters from overall foraging trips (dark gray boxes), and from foraging habitat (light gray boxes) and transit habitat (white boxes). Clusters were identified by k-means clusters by partitioning of the first three Principal Components retained from PCA on (A) sea surface temperature (SST), (B) chlorophyll, (C) sea surface height (SSH), (D) depth, (E) slope, and (F) bathymetric position index (BPI; the difference between the peak/trough of one point and the surrounding eight points) of all locations (n=109,292 points), landing locations (n=34,032 points), and transit locations (n=75,260 points) from booby foraging trips. Horizontal bars represent the median and vertical bars represent ± SE.

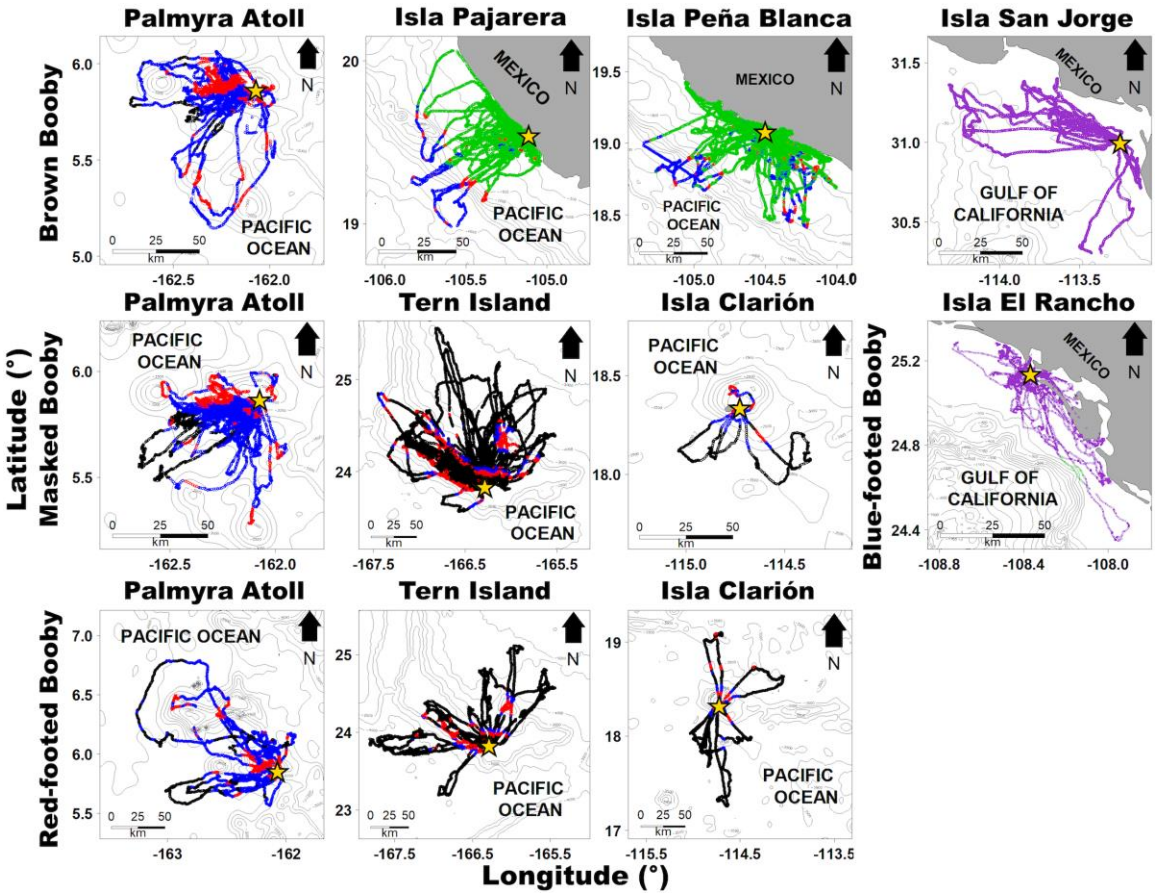

Figure 1.3 Maps of boobies' foraging trips, colored by full-trip cluster

Maps of boobies' foraging trips, colored by full-trip cluster (colored circles). Study species are listed by row, and study colonies are listed by column. Colonies are represented by yellow stars. Solid gray corresponds to land. Gray lines correspond to bathymetry (m); contour intervals vary between colonies: the contour interval for Isla San Jorge is 50 m; for Isla El Rancho is 100 m; for Isla Clarión, Isla Pajarera, Palmyra Atoll, and Peña Blanca is 500 m; and for Tern Island is 1000 m. Full-trip cluster colors: black circles=cluster 1 (cold, deep pelagic cluster); red circles=cluster 2 (shallow pelagic cluster with complex bottom topography); green circles=cluster 3 (high chlorophyll coastal cluster); blue circles=cluster 4 (warm, deep pelagic cluster); purple circles=cluster 5 (benthic Gulf cluster).

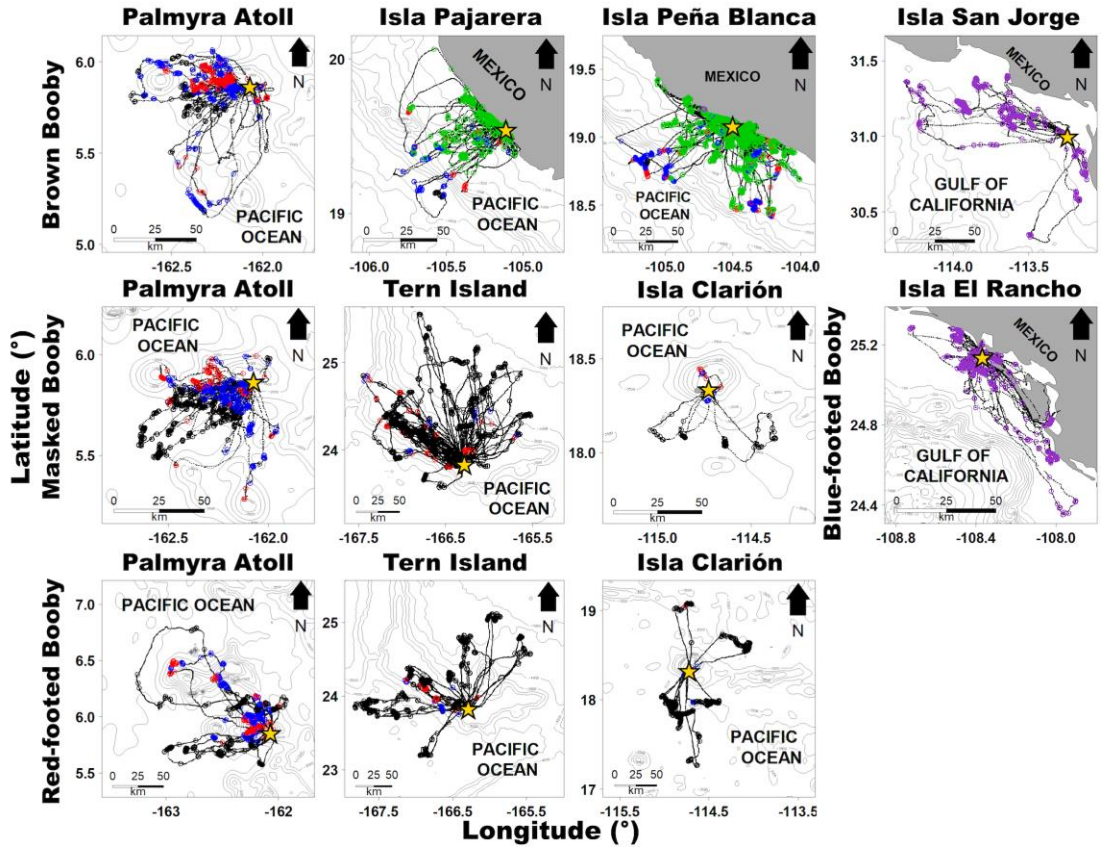

Figure 1.4 Maps of boobies' foraging trips, colored by landing cluster

Maps of boobies' foraging trips (black dots) and foraging events (open circles) colored by landing cluster. Study species are listed by row, and study colonies are listed by column. Colonies are represented by yellow stars. Solid gray corresponds to land. Gray lines correspond to bathymetry (m); contour intervals vary between colonies: the contour interval for Isla San Jorge is 50 m; for Isla El Rancho is 100 m; for Isla Clarión, Isla Pajarera, Palmyra Atoll, and Peña Blanca is 500 m; and for Tern Island is 1000 m. Landing cluster colors: black circles=cluster 1 (cold, deep pelagic cluster); red circles=cluster 2 (shallow pelagic cluster); green circles=cluster 3 (high chlorophyll coastal cluster); blue circles=cluster 4 (warm, deep pelagic cluster); purple circles=cluster 5 (benthic Gulf cluster).

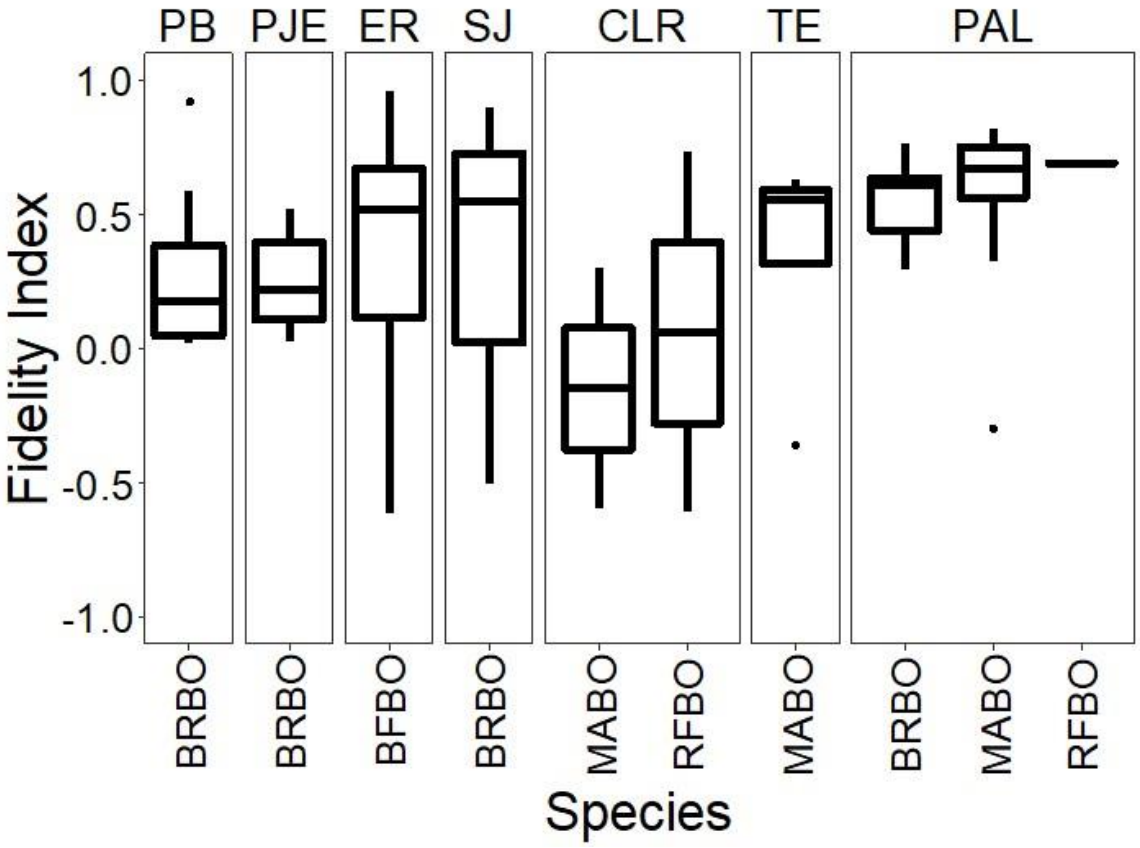

Figure 1.5 Boxplots of Fidelity Index per booby species and colony

Boxplots of fidelity index of boobies that had at least two foraging trips (n=78 birds). Fidelity index ranges from no fidelity (-1) to high fidelity (1). Species abbreviations: BFBO=Blue-footed Booby; BRBO=Brown Booby; MABO=Masked Booby; RFBO=Red-footed Booby. Colony abbreviations: CLR=Isla Clarión; ER=Isla El Rancho; PAL=Palmyra Atoll; PB=Peña Blanca; PJE=Pajarera; SJ=Isla San Jorge; TE=Tern Island. Bars represent median ± SE.

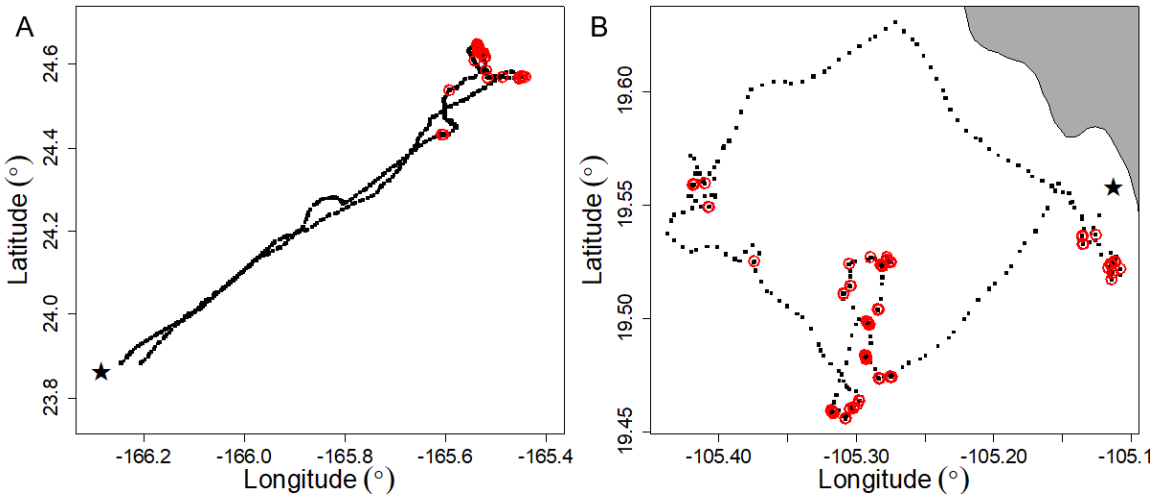

Figure S 1.1 Representative diagrams of booby foraging trip pattern types

Representative diagram depicting two types of foraging trips of boobies. Circles represent landings, where travel speed was less than 5 km hr-1. (A) A Red-footed Booby at Tern Island (star) exhibited a “focused” trip, where landings only occurred at the furthest points from the colony. (B) A Brown Booby at Pajarera (star) exhibited along-trip foraging, where landings occurred throughout the foraging trip, called “throughout” trips. Solid gray corresponds to land.

Chapter 2

Foraging ecology and oceanographic processes determine contaminant exposure in tropical seabirds

Morgan E. Gilmour

Abstract

Tropical marine predators are exposed to many persistent organic pollutant (POP) and mercury (Hg) contaminants because volatile compounds travel large distances via air currents, and less volatile compounds tend to remain at low latitudes. However, contaminants in remote tropical oceanic regions are understudied. Marine animals like seabirds are highly mobile, and often forage in multiple regions for fishes and squid, making them excellent samplers of contaminants in the marine environment. I assessed seabirds' foraging ecology and Hg and POP concentrations from four colonies in the central Pacific Ocean (Laysan and Tern Islands, Hawaii; Palmyra Atoll) and the eastern Caribbean Sea (Barbuda) to determine how contaminants were distributed in seabird predators that foraged in different environments. Total mercury (THg) and 89 POP compounds were measured in two families of seabirds: surface-foraging frigatebirds (*Fregata* spp.), and plunge-diving boobies (*Sula* spp.). To assess routes of contaminant exposure, I employed a two-fold approach to determine overall foraging patterns: stable isotope sampling of carbon, nitrogen, and sulfur, and GPS-tracking tags. DDT, PCBs and THg were the most frequently detected compounds among all birds sampled. Foraging habitat and trophic position helped to explain contaminant exposure: $\delta^{13}C$ and $\delta^{34}S$ (indicative of nearshore/offshore habitat) were negatively correlated with DDT at Palmyra Atoll and positively correlated with THg at Tern Island, respectively. $\delta^{15}N$ (representative of trophic position) was positively correlated with THg at Laysan Island. ΣPOP was highest in Magnificent Frigatebirds from Barbuda, but THg and POP were not associated with foraging ecology, indicating that regardless of foraging strategies, seabirds in this region are exposed to large concentrations of contaminants. At Laysan, Palmyra, and Tern, species generally foraged in either nearshore or offshore habitats, which also reflected the distributions of POP in samples: DDT was high in pelagically foraging Great Frigatebirds, but very low in nearshore foraging Brown and Masked Boobies. Likewise, nearshore foraging boobies had endosulfan and brominated diphenyl ether (PBDE) that were either not detected,

or had very low concentrations, in pelagic birds. Ocean currents differed between some nearshore/offshore areas; additionally, the island mass effect may help retain POP nearshore, indicating that local oceanography contributed to seabirds' contaminant exposure. Overall, foraging ecology and local oceanography described contaminant exposure in remote Pacific locations, but proximity to industrial and agricultural centers in more populated regions drove contaminant exposure at Barbuda. Seabirds were good samplers of these marine environments, and demonstrate that POP and Hg pollution continues to be a global issue.

2.1 Introduction

Anthropogenic contaminants are ubiquitous in today's environment. In addition to detecting persistent organic pollutants (POP) and heavy metals near point sources (e.g. pesticides near agricultural regions; industrial compounds like polychlorinated biphenyls (PCB) and heavy metals near developed, industrial areas), anthropogenic contaminants are also detected in remote locations around the world (Bacon et al., 1992; Baek et al., 2011; Iwata et al., 1993; Shunthirasingham et al., 2010). The ability of these compounds to travel thousands of kilometers on atmospheric and oceanic currents heightens the risk to humans and wildlife, regardless of location. This is problematic because mercury (Hg) and POP cause adverse changes in humans and wildlife that include neurotoxic, genetic, behavioral, and reproductive effects (Burgess and Meyer, 2008; Ceccatelli et al., 2010; Sweet et al., 2006).

The ocean serves as a sink for many POP, which increases exposure risks to marine organisms. For example, primary productivity is low in open, tropical oceans, and because there is less biomass to absorb and adsorb Hg and POP, there is a net accumulation of some POP compounds (Morales et al., 2015). Warm air and water temperatures at low latitudes also influence POP distributions. For example, some POP (e.g. di-, tri-, and tetra-PCB congeners) are volatile at warm (25°C) temperatures and are deposited into the ocean as air temperatures cool, and these compounds may then revolatilize with subsequent warming temperatures; this cycle can occur repeatedly, creating an uneven POP distribution (Gouin et al., 2004). Other POP (e.g. hexa- and nona-PCBs) that arrive to tropical oceans via surface currents are less likely to volatilize, and tend to remain at low latitudes (Wania and Mackay, 1993). However, localized point sources deposit many types of POP into local waters, and both volatile and less volatile compounds adsorb to particulates in the water, which may either sink or be absorbed by biota, and enter the foodweb (Heskett et al., 2012). This process is especially prevalent in areas of high productivity (Eisenreich and Jones, 2002). Conversely, Hg undergoes a more versatile process: it is subject to advection and

atmospheric transport, but once deposited into the ocean, it often adsorbs to particulates and sulfate-reducing bacteria then synthesize it into methylmercury (MeHg), a form that is easily assimilated by biota (Fitzgerald et al., 2007). Hg methylation occurs most frequently at depths of 200-1000 m (Blum et al., 2013). Plankton often uptake POP and MeHg, and fish also absorb POP through gills (Randall et al., 1998), thus linking elevated POP and Hg concentrations with increased trophic positions (Cai et al., 2007; Kawano et al., 1988). It is evident that tropical marine predators are potentially exposed to many types of POP because of the presence of heavy and lightweight POP compounds and sulfate-reducing bacteria in the ocean. Many marine organisms inhabit the low latitude, open ocean; many people also rely on fisheries resources for food from these areas, compounding Hg and POP exposure (Domingo et al., 2007).

Monitoring Hg and POP in remote regions of the open ocean is difficult, and is even more so when considering the dynamic marine environment, where continuously shifting currents dramatically alter habitats hourly, seasonally, and annually (Bograd et al., 2004; Fiedler, 2002; Lavín and Marinone, 2003). Logistical challenges generally limit Hg and POP sampling in these regions to oceanographic cruise routes and research stations (Baek et al., 2011; Hammerschmidt and Bowman, 2012; Iwata et al., 1993). While valuable, these data are restricted to shipping lanes or common ocean transects, and large swaths of ocean are under-sampled. However, some marine organisms travel large distances when foraging, thus covering wide ranges of locations and habitat types, and are thus good samplers of the dynamic marine environment (Elliott and Elliott, 2013; Piatt et al., 2007). Here, I aim to fill a gap in Hg and POP knowledge of the tropical open ocean by measuring Hg, organochlorine, organophosphate, and polybrominated diphenyl-ethers (PBDEs) in two clades of seabirds from four tropical locations. Boobies (*Sula* spp.) and frigatebirds (*Fregata* spp.) exhibit different foraging strategies (plunge-diving and surface-feeding, respectively) to catch a variety of fish and squid species, and thus obtain their diets from different parts of the water column. Because contaminants in seabirds are derived from diet, I also assessed the at-sea

foraging ecology of these seabirds with a combination of carbon, nitrogen, and sulfur stable isotopes and GPS-tracking tags. Carbon and sulfur stable isotopes are used to assess the relative contributions of base sources to primary producers, and thus yield information about nearshore and offshore marine habitats (Connolly et al., 2004; Hobson, 1993). Sulfur stable isotopes are also used as a proxy for concentrations of sulfate-reducing bacteria, which are the main synthesizers of MeHg (Elliott and Elliott, 2016). Nitrogen stable isotopes fractionate in a predictable way that represents trophic position within a system (Hobson, 1993). GPS-tracking tags provide locations of foraging regions (Block et al., 2011).

I studied four booby species and two frigatebird species in the central Pacific Ocean (Laysan and Tern Island, Northwestern Hawaiian Islands; Palmyra Atoll, Line Islands) and the eastern Caribbean Sea (Barbuda). These colonies exhibit different oceanographic properties and histories, and thus provide an intriguing comparison of seabirds' Hg and POP exposure across colonies. The Northwestern Hawaiian Islands sit in the middle of the North Pacific subtropical gyre and the North Pacific garbage patch (Van Sebille et al., 2012). Continuous northeasterly trade winds and the Equatorial Current, North Hawaiian Ridge Current, and Hawaiian Lee Current influence water movement and nutrient exchange (Calil et al. 2008, Yoshida et al. 2010; Fig. 2.1B). Tern Island is a former U. S. Coast Guard base that underwent significant habitat alteration in the 1940s, and buildings and debris remain on the island and in the water (Miao et al., 2001, 2000), but is now a U. S. Wildlife Refuge. Laysan Island is also an uninhabited Wildlife Refuge, but was never modified by the military. Further to the south, Palmyra Atoll is near the equator, and has consistently warm (25°C) sea surface temperatures. Palmyra is in the middle of two major ocean currents: the Equatorial Current and the Equatorial Counter-current (Hamann et al. 2004; Fig. 2.1C). Palmyra also sits in the Intertropical Convergence Zone, a region where northern and southern trade winds converge, which deepens the thermocline and decreases primary productivity (Ramage et al., 1981). Like Tern Island, Palmyra was also modified and occupied by the U. S. military in the 1940s, and buildings and debris also remain on land and in the water (Maragos et al., 2008), but is

now also a Wildlife Refuge. Conversely, Barbuda sits between the Atlantic Ocean and the shallower Caribbean Sea, where the combination of northeasterly winds and the westward-flowing Equatorial Current, northward-flowing Antilles Current, and the northward-flowing Caribbean Current contribute to productivity (Müller-Karger 1989, Johns et al. 2002, Rueda-Roa and Muller-Karger 2013; Fig. 2.1D). The Caribbean has a dense human population in which there are likely many POP and anthropogenic Hg point sources that get distributed throughout the Caribbean in similar ways to the distribution of local marine debris (Corbin and Singh, 1993; Ivar do Sul and Costa, 2007; Leite et al., 2014). Due to the oceanographic differences between colonies, I tested the hypothesis that Hg and POP concentrations would be different between seabirds from different colonies. I predicted that: 1) due to its proximity to human populations, Barbuda seabirds would have higher concentrations of POP than seabirds in more remote parts of the Pacific Ocean; and 2) because localized foodwebs are greatly influenced by oceanographic conditions (e.g. productivity), foraging ecology would be correlated with Hg and POP concentrations.

2.2 Materials and methods

2.2.1 Location and species

Blood samples were collected from three booby species (Masked, *Sula dactylatra*; Brown, *S. leucogaster*; Red-footed, *S. sula*) and two frigatebird species (Great Frigatebird, *Fregata minor*; Magnificent Frigatebird, *F. magnificens*) at four breeding colonies in three oceanographic regions (Fig. 2.1A). Samples from Barbuda, Palmyra Atoll, and Tern Island were collected either during the incubation or chick-brooding stages. Samples from Laysan Island were from birds of unknown breeding status. Males and female boobies were distinguished by either vocalizations (Masked Boobies; Nelson 1978), plumage (Brown Boobies; Nelson 1978), body mass (Masked and Red-footed Boobies), where females are larger than males within the pair (Nelson, 1978; Weimerskirch et al., 2006), or through

molecular analyses (Young et al., 2010a); though sex could not be determined for 10 boobies. Male and female frigatebirds were distinguished by plumage (Nelson, 1975).

2.2.2 Blood sampling

Birds were captured by hand or with a net. Approximately 1mL of blood was sampled from the brachial vein or tarsal vein by a heparinized 25G needle and plastic syringe. Due to restrictions of field logistics between study sites, blood samples were processed and stored differently. Blood samples from Barbuda, Palmyra, and Tern Island were transferred into polypropylene Eppendorf tubes (Eppendorf North America, Hauppauge, New York, USA); Laysan samples were transferred into amber glass vials with a Teflon lid (Sigma-Aldrich, St. Louis, Missouri, USA). Samples were kept cold for 1-4 hours. Whole blood from Barbuda was collected in February 2009, freeze-dried (LABCONCO FreeZone1 bench-top dryer, Missouri, USA) for 24 hr, and stored at room temperature in polypropylene Eppendorf tubes. Whole blood from Laysan Island (collected in September 2014) and Tern Island (collected in March and December 2012) was frozen at -20°C. Blood from Palmyra Atoll was collected in August-September 2014, and was centrifuged for 1 minute at 2200X g and then separated into plasma and red blood cells by pipette. Plasma was stored in amber vials with a Teflon lid. Red blood cells were stored in polypropylene Eppendorf tubes, and these samples were frozen at -20°C until processing.

2.2.3 Organochlorine, organophosphate and PBDE analyses

To determine blood concentrations of POP, plasma (Palmyra Atoll, n=11) and whole blood (Barbuda, n=15; Laysan Island, n=29) were analyzed at the Geochemical and Environmental Research Group at Texas A & M University, College Station, Texas, USA. Samples underwent liquid-liquid extraction with methylene chloride; sample purification via fused silica column chromatography for sample clean-up; and quantification of organochlorine

compounds via a gas chromatograph mass spectrometer with electron capture detection (GCMA-ECD). A total of 89 individual compounds were searched for in analyses, using an in-house standard of 100 compounds. Compounds were grouped into 11 chemical families for statistical analyses: $\Sigma chlordanes_7$ (α-chlordane, γ-chlordane, heptachlor, heptachlor epoxide, cis-nonachlor, oxychlordane, trans-nonachlor); $\Sigma chlorobenzenes_4$ (CBZ; tetrachlorobenzene 1,2,4,5; tetrachlorobenzene 1,2,3,4; pentachlorobenzene; hexachlorobenzene); a chlorophenol, pentachloroanisole; cyclodienes (aldrin, dieldrin, endrin, endrin-aldehyde); endosulfan II; dichlorodiethyltrichloroethane (DDT; 2,4'DDE, 4,4' DDE, 2,4'DDD, 4,4'DDD, 2,4'DDT, 4,4'DDT); $\Sigma hexachlorocyclohexanes_4$ (HCH; α-, β-, γ-, δ-); a cyclopentadiene, mirex; ΣPCB_{22} (congeners: 8/5, 18/17, 28, 29, 44, 52, 66, 101/90, 87/115, 105, 110/77, 118, 128, 153/132, 138/160, 187, 201/157/173, 180, 170/190, 195/208, 206, 209); and polybrominated diphenyl ethers (PBDE; congeners: 1, 2, 3, 7, 8/11, 10, 12, 13, 15, 17, 25, 28, 30, 32, 33, 35, 37, 47, 49, 66, 71, 75, 77, 85, 99, 100, 116, 118, 119, 126, 138, 153, 154, 155, 166, 181, 183, 190, 209). The average surrogate compound recoveries were: DBOFB (94.2%, n=55), PCB103 (94.7%, n=55), and PCB198 (87.7%, n=55). The average method detection limits for organochlorines was 1.51 ng mL^{-1} (SD=1.54, n=27 compounds); for PCB congeners was 0.03 ng mL^{-1} (SD=0.02, n=22 congeners); and for PBDE was 6.86 ng mL^{-1} (SD=37.41, n=39 congeners). In all analyses, 0.3-1.0 g of sample material were used. Method blanks were included every 20 samples during extraction. Procedural blanks contained either no, or insignificant traces of organic compounds. POP concentrations are expressed in ng mL^{-1} wet weight (ww).

2.2.4 Hg Analyses

Red blood cells (Palmyra, n=17) and whole blood (Barbuda, n=12; Laysan Island, n=12; Tern Island, n=29) were analyzed for total mercury (THg) at the University of California, Santa Cruz. Blood was analyzed for THg because avian blood Hg concentrations contain nearly all

MeHg (Rimmer et al., 2005). Frozen blood samples were thawed at room temperature. Liquid blood was pipetted into quartz sample boats and dried blood was transferred to sample boats with a stainless-steel spatula. Samples were weighed to achieve a mass that ranged between 0.01600-0.03000 g for all samples with a Sartorius microbalance (Brinkman Instruments, Inc., Westbury, New York, USA). Samples were analyzed for THg content by thermal decomposition, catalytic conversion, amalgamation, and atomic absorption spectrophotometry (DMA-80; Milestone, Shelton, Connecticut, USA; (U. S. Environmental Protection Agency, 2007). Quality assurance/quality control procedures included analysis of a method blank every ten samples; analysis of two standard reference materials (SRM 320R-Channel sediment, and SRM 414-plankton, European Commission Community Bureau of Reference, Belgium); and a duplicate sample. Minimum detection limits were defined as three times the concentration of blank samples; the minimum detection limit was 7.60 X 10^{-6} μg g^{-1} ww. Because dried blood is dehydrated, a 79% moisture content was applied to THg values for samples from Barbuda and one dehydrated frozen sample from Tern Island (Eagles-Smith et al., 2008). THg concentrations are expressed in μg g^{-1} wet weight (ww).

2.2.5 Stable Isotope Analyses

Approximately 1.0 g of red blood cells (Palmyra samples) and whole blood (Barbuda, Laysan, and Tern Islands) were dried in an oven at 50°C to constant mass for 48 hours. Samples were weighed into tin capsules to achieve a mass between 0.55-0.77 mg ($\delta^{13}C$ and $\delta^{15}N$ analyses) or 3.0-5.0 mg ($\delta^{34}S$ analyses) to the nearest 10^{-6} g with a Sartorius microbalance (Brinkman Instruments, Inc., Westbury, New York, USA). Carbon and nitrogen isotope analyses were conducted using a Carlo Erba Elemental Analyzer interfaced with a ThermoFinnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California, Santa Cruz). Isotope analysis of $\delta^{34}S$ were conducted using an Elementar vario ISOTOPE cube interfaced to a SerCon 20-22 IR Mass Spectrometer at the Stable Isotope

Facility at the University of California, Davis. Stable isotope ratios are expressed in delta notation (δ) as parts per thousand (‰) relative to international standards V-PDB (Vienna PeeDee Belemnite) for carbon, air for nitrogen, and Vienna-Canyon Diablo Troilite for sulfur using the equation: $\partial X = \frac{R_{sample}}{R_{standard}} - 1$, where X is ^{13}C, ^{15}N, or ^{34}S, and R is the corresponding ratio of $^{13}C/^{12}C$, $^{15}N/^{14}N$, or $^{34}S/^{32}S$. Acetanilide was used as secondary isotope reference materials in carbon and nitrogen analyses: the average standard deviations within runs were: $\delta^{13}C$: ±0.02 ‰; $\delta^{15}N$: ±0.04 ‰. Mahi-mahi (*Coryphaena hippurus*) fish muscle and human hair were used as secondary isotope reference materials in sulfur analyses: the average standard deviations within runs were ± 0.66 ‰ and ± 0.39 ‰, respectively.

2.2.6 GPS-tracking

Seabirds' at-sea habitat use was determined with GPS-tracking tags (either iGot-u GT-120; Mobile Action Technology, Inc., New Taipei City, Taiwan; or GPS CatTrack1, Catnip Technologies, Anderson, South Carolina, USA) and kernel density estimations at Palmyra Atoll and Tern Island. Tags were encapsulated in polyolefin for waterproofing. The total tracking package mass was 22 g, which was on average 1.1–1.9% of the body mass of the three booby species (mean mass Brown: 1,200 ± 189 g, n=70; Masked: 1,998 ± 276 g, n=41; Red-footed: 1,155 ± 167 g, n=36) and 2.0% of the body mass of Great Frigatebirds (mean mass: 1104 ± 191 g, n=6). Tags were taped underneath the central 2-3 tail feathers with waterproof tape (Tesa #4651, Hamburg, Germany). The duration of tag deployment varied among colonies and species; typically, a tag was programmed to either: 1) start recording at 0600, due to the diurnal behaviors of many booby species; or 2) programmed to begin recording upon tag attachment. Due to logistical differences between study sites, tags were deployed for 1-8 days, resulting in multiple trips for some individuals.

GPS tracking tags recorded locations with high precision (1-120 seconds) and accuracy (ca. 3 m). All track analyses and statistics were conducted in the program R

(version 3.4.3; R Core Team, 2017). Tracks were manually inspected to remove erroneous locations. To compare behaviors among tracked birds with different sample intervals, tracks were interpolated to one position every 60 sec using the R-package “adehabitatLT” (Calenge, 2006). Coordinates were re-projected into equal-area Universal Transverse Mercator UTM3N. To determine the overall patterns of at-sea habitat use, kernel density distributions were estimated using the “kernelUD” function from the R-package “adehabitatHR” (Calenge, 2006). Kernel density distributions describe the probability density of an individual’s presence in an area (Worton, 1989). Kernel density distributions are smoothed to include an area of influence surrounding each kernel; the smoothing parameter, *h*, was the smallest scale (in km) at which a movement pattern was identified via the “scaleARS” function (Lascelles et al., 2016). Kernel density distributions were then overlaid onto grids of bathymetric data (resolution= 4 arc-minutes) for each study region; bathymetric data were obtained from the NOAA dataset “ETOPO1” via the R-package “marmap” (Pante and Simon-Bouhet, 2013). To describe at-sea habitat use, two kernel estimates were used: a “general” use, and a “core” use area, which were comprised of the 95% isopleth and the 50% isopleth of kernel estimates, respectively (Soanes et al., 2013). To measure distances between GPS-locations and the breeding colony, the Great Circle Distance was calculated with the “distHaversine” function on the R-package “geosphere” (Hijmans, 2017).

2.2.7 Statistical analyses

To test hypotheses, contaminants were grouped into POP families (Section 2.2.3) and THg. The DDT metabolite, 4,4’ DDE (hereafter, DDE), was treated separately from the other five DDT compounds (ΣDDT_5) in statistical analyses due to its well-known persistence in the environment (Ricca et al., 2008). However, 4,4’ DDE was included in ΣDDT_6 for percent composition calculations.

A subset of PCB congeners (PCB IUPAC # 28, 52, 101, 118, 153, 138, and 180) were also assessed together because these compounds are recommended by the International Council for the Exploration of the Sea (ICES) for comparison across studies (Duinker et al., 1988), and because they represent PCB compounds of varying chlorination levels (tri-, tetra-, penta-, hexa-, and hepta-PCBs).

Both whole blood and plasma were analyzed for POP compounds, and both red blood cells and whole blood were analyzed for THg and stable isotopes. Blood tissue turnover rates (regeneration of new tissues) are shorter in plasma (3 d to 1 week) than red blood cells (2-4 weeks; Hobson and Clark 1993, Hahn et al. 2012), and represent diet and contaminants integrated over these time periods (Ramos and González-Solís, 2012). Because diet-derived contaminants are continuously integrated into the body in seabirds, whole blood and plasma, and whole blood and red blood cells, were considered together for POP analyses to assess POP concentrations across colonies; similarly, whole blood and red blood cells were considered together for THg analyses.

For statistical analyses of organochlorines, only samples that were greater than or equal to the minimum detection level (MDL) were included in analyses, including percent composition and family groupings, so that rare compounds would not be overestimated (Ricca et al., 2008). For POP analyses, the MDL is based on sample mass, and thus differs between samples and between compounds. There were 92 occurrences of compounds below the MDL in 41 birds; samples below the MDL were most common for four PBDE compounds (PBDE-47, n=18 samples; PBDE-85, n=1; PBDE-99, n=24; PBDE-100, n=19). Additionally, compounds that had a low (<50%) detection frequency among all samples were omitted from statistical analyses that compared inter-colony POP (all compounds from the families cyclodienes, endosulfan, and HCH). The sum of all POP (ΣPOP_{53}) was calculated for each colony-species group to compare general POP patterns between species and colonies.

Non-parametric tests (Mann-Whitney) were used to test for differences in stable isotopes and distances traveled from the colony between species. Because tracked birds at

Palmyra Atoll had multiple foraging trips, a linear mixed effects model with restricted maximum likelihood was used to test for distances traveled between species at Palmyra Atoll, with BirdID as a random effect; this was conducted with the function “lme” from the R-package “nlme” (Pinheiro et al., 2017). The significance of fixed factors from this model was assessed with analysis of variance (ANOVA) with Type III sum of squares, conducted with the function “Anova” from the R-package “car” (Fox and Weisberg, 2011). Non-parametric Spearman Rank correlations were used to assess relationships between $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ stable isotopes, and between stable isotopes and POP and THg. To assess species-related POP concentrations within a colony, one-way ANOVAs were conducted for Laysan Island (small sample sizes of individual POP per species did not allow for the same comparisons to be made at Palmyra Atoll). One-way ANOVAs were used to test for inter-colony differences in POP and THg, with the contaminant concentration as the response variable and island and sex as fixed factors. Sex was included because female birds deposit contaminants into their eggs (Ackerman et al., 2016; Verreault et al., 2006), which can result in smaller contaminant concentrations in females than males (Lerma et al. 2016, Costantini et al. 2017; but see Tavares et al. 2013). Contaminant exposure between sexes can also differ due to differences in foraging ecology (Mott et al., 2017a). To further explore POP exposure between male and female birds, differences in POP concentrations between males and females within a species were assessed when sample sizes permitted with Mann-Whitney tests; this comparison was thus made for Magnificent Frigatebirds at Barbuda and for Great Frigatebirds at Laysan Island for a subset of POP. For ANOVAs, THg and POP concentrations were log-transformed, except for cyclodienes, which were square-root-transformed, and endosulfan was not transformed, to fit a Gaussian distribution. Significance of models was assessed at $p<0.05$.

2.3 Results

2.3.1 Foraging ecology

Overall, there were large inter-specific and inter-colonial variations in foraging ecology. Masked and Red-footed Boobies at Tern Island had significantly different $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$: Mann-Whitney U test, W=66, p=0.0002; $\delta^{15}N$: Mann-Whitney U test, W=66, p=0.001; Table 2.1). Red-footed Boobies foraged on average up to 96 km from the island (Table 2.1), however the core foraging habitats of Masked and Red-footed Boobies overlapped along Brooks Banks, to the northwest of the atoll, and neither species used the regions directly to the east and south (Fig. 2.3A). Masked Boobies at Tern Island had the largest range of $\delta^{34}S$ values (SD= ± 4.28 ‰; Fig. 2.2). Among boobies and frigatebirds at Tern Island, $\delta^{34}S$ and $\delta^{13}C$ were slightly negatively correlated (Spearman's Rank Correlation, p=0.05, r_s=-0.48, Fig. 2.2C), and $\delta^{13}C$ and $\delta^{15}N$ were positively correlated (Spearman's Rank Correlation, p=0.03, r_s=0.47, Fig. 2.2D). At Palmyra Atoll, Brown Boobies concentrated foraging within a ~500 km^2 core area that was 50 km west of the atoll, and Great Frigatebirds' core habitat regions were in pelagic regions >100 km from the atoll (Fig. 2.3B), where they traveled significantly further from the colony than Brown Boobies (type III Anova, p<0.0001, χ^2_1=25.7) and covered more than two times the area traveled by Brown Boobies (Table 2.1). Additionally, Great Frigatebirds' $\delta^{13}C$ values were significantly depleted compared to Brown Boobies (Mann-Whitney U test, W=63, p=0.001, Table 2.1). Conversely, species' $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values overlapped at Laysan Island (Fig. 2.2). Magnificent Frigatebirds at Barbuda exhibited some inter-individual variation in $\delta^{34}S$ and $\delta^{13}C$, but $\delta^{15}N$ values were more similar (small standard deviations; Table 2.1).

2.3.2 Detection of contaminants

2.3.2.1 THg

THg was detected in all samples, exhibited considerable variation between species and colonies (Fig. 2.2, Table 2.2), and was significantly different between colonies (Table 2.3). Magnificent Frigatebirds at Barbuda had the highest median THg concentration, which was 3.7 times larger than Laysan birds, which had the lowest median THg overall (Table 2.2). Red-footed Boobies at Laysan had the lowest THg concentrations, which were four times smaller than Great Frigatebirds and Masked Boobies at Laysan (Table 2.2). Similarly, Great Frigatebirds at Tern Island had twice the THg concentrations of the booby species (Table 2.2). THg was positively correlated with two measures of foraging ecology: $\delta^{34}S$ at Tern Island (Spearman's Rank Correlation, r_s=0.70, S=247.9, p=0.002, Fig. 2.2A), and $\delta^{15}N$ at Laysan Island (Spearman's Rank Correlation, r_s=0.95, S=6, p=0.0004, Fig. 2.2B). THg was not significantly different between sexes for any species (Table 2.4).

2.3.2.2 POP

POP were detected in all samples from Barbuda, Laysan Island, and Palmyra Atoll (Fig. 2.4). ΣPCB_{22}, ΣDDT_5, and ΣCBZ_4 were the most frequently detected organochlorines, with DDE, $\Sigma chlordane_7$, pentachloroanisole, and mirex also detected in >50% of samples (Table 2.2). Fifty-three of 89 compounds were detected among all samples; the compounds that were not detected were 35/39 PBDE (only PBDE-47, PBDE-85, PBDE-99, and PBDE-100 were detected) and the cyclodiene endrin-aldehyde. Generally, Magnificent Frigatebirds from Barbuda had high detection frequencies of most compounds, and exhibited twice the median concentrations of most POP compared with birds at Laysan Island and Palmyra Atoll (Fig. 2.4), with even larger concentrations for some POP, including ΣCBZ_4 (3.5-11x > other species), $\Sigma chlordane_7$ (4-6x > other species), ΣHCH_4 (1.4-9x > other species), and

pentachloroanisole (2-3x > other species; Table 2.2). Additionally, the cyclodiene aldrin, 4,4'-DDD, oxychlordane, and the α-HCH and β-HCH isomers were only detected in Barbuda samples (Fig. 2.5). Interestingly, only one Magnificent Frigatebird at Barbuda had any PBDE, whereas PBDE was detected in 71-100% of all other species (Table 2.2). Generally, frigatebirds from all colonies had the highest DDE and ΣDDT_5 concentrations, and were highest in Magnificent Frigatebirds from Barbuda and Great Frigatebirds from Palmyra Atoll (Table 2.2).

Other POP had different distribution patterns: median mirex concentrations were highest at Laysan Island, and concentrations were significantly different between species (one-way Anova, $p<0.0001$, $F_{2,19}=3.76$). Chlorpyrifos was only detected in samples from Barbuda and Laysan Island, and within Laysan, chlorpyrifos was only detected in Great Frigatebirds and Red-footed Boobies (Table 2.2). ΣPCB_{22} concentrations were significantly different between species at Laysan Island (one-way Anova, $p=0.027$, $F_{2,26}=4.17$) and both ΣPCB_{22} and ΣPOP_{53} were significantly different between male and female Great Frigatebirds (Table 2.5). Endosulfan concentrations were twice as high in Brown Boobies from Palmyra Atoll than all other samples, and $\Sigma PBDE_4$ was also highest in Brown Boobies (Table 2.2). One Brown Booby also had the only detection of the PBDE-85 congener.

Within POP families, there were uneven detection rates of individual compounds. Endrin, the degradation product of aldrin, made up more than 50% of $\Sigma cyclodiene_4$, and trans-nonachlor was the most frequently detected chlordane (Fig. 2.5). β-, δ-, and γ-HCH were more frequently detected than α-HCH, and DDE was the most common ΣDDT_6 compound (Fig. 2.5). The relative contribution of PCB isomers to the total ΣPCB_{22} varied between study sites, such that there were generally equal contributions of each chlorination group to ΣPCB_{22} in Magnificent Frigatebirds from Barbuda, but boobies and frigatebirds from Laysan Island and Palmyra Atoll had higher proportions of hexa- and hepta-PCBs than other congeners (Table 2.4, Fig. 2.6). All $\Sigma PCB_{ICES\ 7}$ compounds were detected in nearly all samples; concentrations of $\Sigma PCB_{ICES\ 7}$ ranged 0.71–39.86 ng mL^{-1} (n=53; Table 2.2).

Magnificent Frigatebirds from Barbuda had all $\Sigma PCB_{ICES\ 7}$ compounds. The most frequently detected $\Sigma PCB_{ICES\ 7}$ among colonies were PCB-138 and PCB-153.

Due to the fast degradation rates of some compounds, ratios of some POP congeners are used to assess the relative age of compounds. The ratio of trans: cis-chlordane indicates whether newly synthesized technical chlordane is present (Ding et al., 2015; Ricca et al., 2008). Only six samples had trans-chlordane, and of those, three birds had "fresh" trans-chlordane because they did not have any cis-chlordane: one Brown Booby from Palmyra Atoll (trans:cis ratio= 0.24:0) and two Magnificent Frigatebirds from Barbuda (trans:cis ratios= 0.12:0 and 0.06:0; Table 2.6). Similarly, DDT degrades to DDE, and 19 birds had ΣDDT_5: DDE ratios >1, including four birds that did not have any DDE (all were Brown Boobies from Palmyra Atoll). Additionally, ΣDDT_5: DDE ratios were highest in Magnificent Frigatebirds from Barbuda (Table 2.6). γ-HCH has a shorter residence time in the atmosphere than α-HCH (Simonich and Hites, 1995; Su et al., 2006); only frigatebirds from Barbuda and Laysan Island had detections of α-HCH and γ-HCH, and only three birds (all Magnificent Frigatebirds from Barbuda) had α-HCH (Table 2.6). The ratio of ΣDDT_6:ΣPCB_{22} is used to determine the relative contribution of agricultural and agricultural sources to contaminant concentrations. Most birds had small ratios (Table 2.6), and three birds had ratios >1: a Magnificent Frigatebird from Barbuda (ΣPCB_{22}:ΣDDT_6 ratio: 2.36); a Red-footed Booby from Laysan Island (ΣPCB_{22}:ΣDDT_6 ratio: 1.64), and a Great Frigatebird from Palmyra Atoll (ΣPCB_{22}:ΣDDT_6 ratio: 1.55).

Only one compound was correlated with stable isotopes: ΣDDT_5 was negatively correlated with $\delta^{13}C$ values at Palmyra, such that birds with less enriched $\delta^{13}C$ values had larger ΣDDT_5 concentrations (Spearman's Rank Correlation, r_s=1.0, S=0, p<0.0001).

2.4 Discussion

Tropical seabirds exhibited distinct foraging ecologies that generally partitioned into nearshore and pelagic regions; these trends were most evident in $\delta^{13}C$ and $\delta^{34}S$ values between species, and spatial patterns from GPS-tracking data. THg and ΣDDT_5 were significantly correlated with stable isotopes, suggesting that exposure risk to some POP can be predicted based on seabirds' foraging ecologies. POP also partitioned into distinct groupings between colonies, indicating that an additional predictor of seabirds' exposure to contaminants is the proximity to point sources of pollution, with links to regional oceanographic processes through which POP are distributed.

2.4.1 Foraging ecology drives contaminant exposure

Nearshore foragers might be expected to be exposed to more POP and Hg if these areas are proximal to agricultural and industrial regions. Three of the four colonies sampled in this study were remote (>1000 km from the nearest human settlement), and thus only Barbuda samples represented an inhabited area that likely contained POP and Hg point sources. The large, densely populated Caribbean region likely contributed to the high frequencies and concentrations of THg and POP detected in Magnificent Frigatebirds. $\delta^{13}C$ and $\delta^{34}S$ values indicated that individuals foraged in a mix of nearshore and pelagic habitats, and birds from this colony foraged east of Barbuda, and nearshore to Antigua and Guadeloupe, to the south (Trefry and Diamond, 2017). The detection "fresh" DDT, trans-chlordane, and aldrin – compounds with relatively short half-lives that had not yet decomposed into degradation products – are indicative of exposure to recent uses (Beyer et al., 2000; Cortes and Hites, 2000). Local oceanographic processes likely contribute to the high POP and THg observed in these birds: ocean currents that originate from the northwestward flowing Caribbean Current and the westward flowing Equatorial and Antilles Currents could introduce POP into the foodweb. Though pesticides like DDT do not originate from Antigua and Barbuda due to the

islands' arid environment and lack of agriculture, Barbuda is within 500 km of the Virgin Islands, Puerto Rico, Dominica, and other agricultural nations that have documented historic and current use of pesticides (CARDI, 2018). Additionally, Venezuela and Senegal use DDT to control mosquito-borne malaria (United Nations Environmental Program, 2018), and could be transported via northeastward eddies (Andrade and Barton, 2000) and the Caribbean and Equatorial Currents. The combination of compounds like PCBs in consumer products and the common practice of burning trash also contribute to substantial POP concentrations in this region (Forde et al., 2014).

Foraging strategies were better predictors of POP exposure in the three remote Pacific colonies, where there was a clear POP and THg distribution pattern between nearshore and pelagic regions, though POP and THg distributions varied between colonies. Great Frigatebirds and Red-footed Boobies are pelagic foragers, and Brown and Masked Boobies forage closer to the colony (Gilmour et al., 2012, 2018; Young et al., 2015). These inter-specific differences in foraging ecology likely contributed to variations in the types and amounts of POP detected. For example, the negative correlation between $\delta^{13}C$ and ΣDDT_5 at Palmyra Atoll indicated higher ΣDDT_5 (representing both fresh and old DDT compounds) in more pelagic regions. Conversely, nearshore-foraging Brown Boobies at Palmyra had "fresh" DDT and trans-chlordane, endosulfan, and BDE-85; POP that were not detected in Great Frigatebirds. Brown Boobies also had mean $\Sigma PBDE_4$ concentrations were three times higher than Great Frigatebirds. Differences in these species' foraging ecologies appear to directly contribute to inter-specific differences in contaminant loads; similar relationships have also been observed in other seabird communities (Colabuono et al., 2014; Harwani et al., 2011; Roscales et al., 2011; Sebastiano et al., 2017).

Birds that foraged in more pelagic regions (high $\delta^{34}S$ values) at Tern Island had high THg concentrations. MeHg is found in higher concentrations in the mesopelagic zone (Hammerschmidt and Bowman 2012, Blum et al. 2013), and many organisms like squid that vertically migrate at night to the surface (Roper and Young, 1975) may transport MeHg from

depth to the surface. Great Frigatebirds sometimes forage at night (unpublished data; Spear et al. 2007, Gilmour et al. 2012), which may account for elevated THg compared to Red-footed Boobies that also foraged in pelagic areas. Masked Boobies at Tern Island had some of the lowest $\delta^{34}S$ values in this study, which suggests some foraging occurred in areas with a less enriched marine signature, like the shallow (<40 m) lagoon within the atoll. Though mercury was high in benthic fishes in the Northwestern Hawaiian Islands (Sackett et al., 2015), it appears that there may be less sulfate-reducing bacteria that synthesize MeHg in the nearshore shallow water at Tern Island.

Inter-specific diet differences also likely contributed to POP and THg distributions. THg was positively correlated with trophic level ($\delta^{15}N$) at Laysan Island. Great Frigatebirds and Masked Boobies had three times more THg than Red-footed Boobies, suggesting that diet might be a more useful indicator of THg exposure than spatial foraging ecology at Laysan. At Laysan, Great Frigatebirds and Masked Boobies exhibited diverse and flexible diets that encompassed many of the same species (Harrison et al., 1983), and could explain the similarity in THg concentrations. Masked Boobies consumed a much larger proportion of fish than squid that were on average larger in size compared to Great Frigatebirds and Red-footed Boobies (Harrison et al., 1983; Spear et al., 2007), which could elevate their trophic position. Larger, older fish may grow slowly, which could increase the time of overall mercury bioaccumulation (Lavoie et al., 2013). Masked Boobies foraged more inshore, where they also could have consumed benthic fish that had elevated mercury concentrations in the Northwestern Hawaiian Islands (Sackett et al., 2015). ΣPCB_{22} were much higher in Laysan Masked Boobies, which could also indicate that diet influences PCB exposure: PCB are lipophilic and PCB concentrations are positively related to trophic position in fishes (Matsuo et al., 2009; Takeuchi et al., 2009; Walters et al., 2011). Masked Boobies also had HCH, which were not detected in Red-footed Boobies, and cyclodienes and lower chlorinated PCBs (di-, tri-, and tetra-congeners), which were generally not detected in either Great Frigatebirds or Red-footed Boobies. Taken together, this suggests that fishes in Laysan's nearshore

foodweb may be exposed to POP and Hg. Sex-based diet differences may also be important: female Great Frigatebirds at Laysan Island had significantly higher ΣPCB_{22} and ΣPOP_{53} concentrations than males. Great Frigatebirds exhibit reverse-size sexual dimorphism (females are larger), which may contribute to spatial foraging differences (Mott et al., 2017b), which in turn could influence POP exposure (Mott et al., 2017a).

2.4.2 Routes of contaminant exposure

The routes of POP deposition to the nearshore and offshore foodwebs at each colony are likely complex, and vary among POP due to intrinsic physiochemical properties and extrinsic environmental factors. For example, molecular mass and vapor pressure reflect a POP's potential for atmospheric transport, which in turn can provide information about the length of time it remains in the environment (Mackay et al., 1982). PCB congeners are a good illustration of these patterns: the proportions of heavy congeners (hexa- to deca-PCB) per sample were higher than the lighter congeners (di- to tetra-PCB) at Laysan and Palmyra, which is expected for remote, low latitude locations (Iwata et al., 1993). Conversely, the even distribution of PCB congeners at Barbuda reflected the local input of light congeners and the persistence of heavy congeners in this ecosystem.

In addition to temporal information provided by POP physiochemical properties, oceanographic processes that influence water movement around each colony can help describe POP deposition into each colony's foodweb. Oceanic currents transport POP, distributing them from coastal regions to the vast ocean (Howell et al., 2012). For example, at Palmyra Atoll, the North Equatorial Countercurrent flows eastward, carrying water directly from Asia past Palmyra, and the Equatorial Current, originating from Central America, flows westward just north of the atoll (7-8° N; Hamann et al. 2004). This latter region occurs 100 km from Palmyra, where only Great Frigatebirds foraged and thus possibly contributed to differences in POP detections and concentrations compared with Brown Boobies. On a more

local scale, the Hawaiian Lee Current and the North Hawaiian Ridge Current flow from the main Hawaiian Islands directly past both Tern and Laysan Islands in the Northwestern Hawaiian Islands (Calil et al., 2008). Lighter PCB congeners were highest near the main Hawaiian Islands in a cross-ocean transect, indicating a mix of PCB sources and deposition in Hawaii (Morales et al., 2015). Currents likely transport these PCBs and other POP to the Northwestern Hawaiian Islands: Hawaiian Monk Seals (*Monachus schauinslandi*) sampled in the Northwestern Hawaiian Islands exhibited POP concentrations that were greater than or equal to seals from the main Hawaiian Islands (Lopez et al., 2012), suggesting that POP may persist for a long time after their use in the main Hawaiian Islands.

Localized currents around oceanic islands and atolls may also play a role in the distribution and retention of POP. The island mass effect describes enhanced productivity and biomass around oceanic islands (Doty and Oguri, 1956) due to the wake formed in the lee of the island that has disrupted the flow of an ocean current and the subsequent formation of eddies that trap nutrients, particles, and organisms (e.g. fish larvae), and increase productivity (Boehlert and Mundy, 1993; Hamann et al., 2004; Signorini et al., 1999). This process could affect POP distribution around islands in two ways. First, POP that are transported long distances on surface currents, or deposited from the atmosphere, could get trapped near the island (Gelado-Caballero et al., 1996). This could help explain POP distributions at Laysan Island, where Masked Boobies had higher concentrations of ΣPCB_{22}, ΣDDT_5, ΣHCH_4, and had the only detections of $\Sigma cyclodiene_3$ compared with Great Frigatebirds and Red-footed Boobies. There is no documented historic use of POP at Laysan Island except for habitat management by the U.S. Fish and Wildlife Service with a pyridine herbicide, triclopyr (ABF, pers obs), and it is unlikely that POP detected in this study are from local point sources. However, the pesticide carbofuran mysteriously appeared on the island in 1988, and appeared to degrade slowly (Campbell et al., 2004), demonstrating the persistence of POP in remote, tropical regions.

Second, some POP may originate from structures on the islands (e.g. abandoned military buildings and equipment; Miao et al. 2000, 2001), and the island mass effect could help retain localized POP that are leached from islands in the same way that nutrients from islands are retained nearby (Blain et al., 2001; Boden, 1988). Two of the remote Pacific locations sampled in this study are unique because they have documented historical uses that included significant habitat modification and use by the U. S. military, which left behind debris on land and in the surrounding water that included batteries, transformers, fuel tanks, and buildings (Maragos et al., 2008; Miao et al., 2001, 2000). Consequently, PCB and heavy metals have been detected in biota in nearshore waters at Palmyra Atoll and Tern Island (McFadden et al., 2014; Miao et al., 2001, 2000). At Palmyra Atoll, annual rainfall is high (4.5 m yr^{-1}; Young et al. 2010b), which may contribute to wet deposition of POP (Jurado et al., 2005) and also increase terrestrial runoff into the ocean, potentially increasing leachates into the local water surrounding the atoll (e.g. Miao et al. 2000).

Pathways of MeHg exposure are somewhat different than POP because MeHg is thought to be mainly synthesized by anaerobes. The resulting in-situ methylation of Hg is therefore dependent on sources of inorganic Hg (Hg_0) and the bacteria that synthesize it (Blum et al., 2013; Hammerschmidt and Fitzgerald, 2004). More than half of the input of Hg_0 to the ocean is from anthropogenic sources, and Hg_0 is transported via atmospheric and ocean currents (Lamborg et al., 2014). THg was significantly different between colonies, suggesting that regional oceanographic factors like productivity contribute to in-situ MeHg synthesis and differences in MeHg exposure between colonies (Mason et al., 2012). For example, MeHg concentrations were high in the oligotrophic ocean near Palmyra Atoll, where there is high nutrient-low chlorophyll water; Hg recycling is frequent because there is less biomass, and MeHg is more concentrated in plankton and zooplankton (Gosnell and Mason, 2015), which likely have substantial effects on Hg concentrations in the foodweb.

A small percentage of Hg_0 is released from volcanoes, and it is possible that the combination of 19 active volcanoes in the Caribbean that are within 500 km of Barbuda could

contribute to the high amounts of THg observed in Magnificent Frigatebirds (Pyle and Mather, 2003). Because sulfur is also emitted from volcanoes, $\delta^{34}S$ stable isotopes could be a proxy for dietary sources of Hg: more lithogenic $\delta^{34}S$ values could indicate a volcanic source of sulfur, indicated by a negative correlation between $\delta^{34}S$ and THg. However, $\delta^{34}S$ values at Barbuda were high, indicative of a marine signature. But, THg and $\delta^{34}S$ were not correlated, suggesting that $\delta^{34}S$ is not representative of THg sources. The lack of a relationship between $\delta^{34}S$ and THg also indicates that $\delta^{34}S$ cannot be used as a proxy for sulfate-reducing bacteria (Elliott and Elliott, 2016) at this colony, unlike Tern Island. At Barbuda, Magnificent Frigatebirds mainly foraged on flying fishes that had less enriched $\delta^{13}C$, indicating more pelagic sources (Trefry and Diamond, 2017), which may result in elevated THg concentrations. Because the Caribbean region contains >160 million people, there are likely many local sources of POP and anthropogenic Hg; these inputs into the marine foodweb may be difficult to disentangle between natural and anthropogenic sources of Hg, and methods that incorporate Hg stable isotopes might be more helpful for understanding the source of these pollutants (Blum et al., 2013).

2.4.3 Conclusions

THg and PCB were detected in all seabird blood samples, regardless of whether samples were from remote oceanic islands or the densely-populated Caribbean Sea. Many other POP were also detected, demonstrating the persistence of many pollutants in the environment and biota. These data also illustrate that localized uses of THg and POP easily become globally distributed, reflected by POP measured in remote biota in this and other studies (Carravieri et al., 2014; Stemmler and Lammel, 2013). These data are especially important because they represent low latitude, tropical regions, where less POP are generally expected due to short half-lives and high rates of volatility (Iwata et al., 1993). Because seabirds obtain THg and POP from the diet, monitoring seabirds' foraging ecology can help to determine spatial and

temporal exposure patterns in the marine environment. The relationships between stable isotopes and THg and DDT in this study, and the nearshore-offshore THg and POP patterns observed, demonstrate that foraging ecology is an important factor that illuminates patterns of contaminant exposure. Largescale monitoring studies such as this one establish baseline levels of contaminants, and help elucidate trends across and within populations and species. Due to myriad emerging pollutant compounds, establishment of baseline values of both new compounds and those that have been phased out are important to continually monitor the persistence of POP in the foodweb (Gavrilescu et al., 2015). In the face of a changing climate, these data are especially important, because it is predicted that warming air and sea surface temperatures could enhance the re-volitization of some POP and decrease POP storage capacity in the Arctic (via melted ice and warming water) and the tropics (via vegetation; Ma et al. 2011, Kallenborn et al. 2012), and could also change trophic interactions (Richardson and Schoeman, 2004). The combination of monitoring foraging ecology and oceanographic processes in relation to contaminant concentrations in marine organisms can help place Hg and POP distributions in the context of local and global uses.

2.5 References

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., 2016. Maternal transfer of contaminants in birds: Mercury and selenium concentrations in parents and their eggs. Environ. Pollut. 210, 145–154. https://doi.org/10.1016/j.envpol.2015.12.016

Andrade, C.A., Barton, E.D., 2000. Eddy development and motion in the Caribbean Sea. J. Geophys. Res. Ocean. 105, 26191–26201. https://doi.org/10.1029/2000JC000300

Bacon, C.E., Jarman, W.M., Costa, D.P., 1992. Organochlorine and polychlorinated biphenyl levels in Pinniped milk from the Arctic, the Antarctic, California and Australia. Chemosph. 24, 779-791.

Baek, S.-Y., Choi, S.-D., Chang, Y.-S., 2011. Three-year atmospheric monitoring of organochlorine pesticides and polychlorinated biphenyls in Polar regions and the South Pacific. Environ. Sci. Technol. 45, 4475–4482. https://doi.org/10.1021/es1042996

Beyer, A., Mackay, D., Matthies, M., Wania, F., Webster, E., 2000. Assessing Long-Range Transport Potential of Persistent Organic Pollutants. Environ. Sci. Technol. 34, 699–703.

Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Jezequel, V.M., Fevre, J. Le, Mayzaud, P., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep. Res. Part I Oceanogr. Res. Pap. 48, 163–187.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90. https://doi.org/10.1038/nature10082

Blum, J.D., Popp, B.N., Drazen, J.C., Choy, C.A., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

Boden, B.P., 1988. Observations of the island mass effect in the Prince Edward archipelago. Polar Biol. 9, 61–68. https://doi.org/10.1007/BF00441765

Boehlert, G.W., Mundy, B.C., 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. Bull. Mar. Sci. 53, 336–361.

Bograd, S.J., Foley, D.G., Schwing, F.B., Wilson, C., Laurs, R.M., Polovina, J.J., Howell, E.A., Brainard, R.E., 2004. On the seasonal and interannual migrations of the transition zone chlorophyll front. Geophys. Res. Lett. 31, 1–5. https://doi.org/10.1029/2004GL020637

Burgess, N.M., Meyer, M.W., 2008. Methylmercury exposure associated with reduced productivity in common loons. Ecotoxicology 17, 83–91. https://doi.org/10.1007/s10646-007-0167-8

Cai, Y., Rooker, J.R., Gill, G.A., Turner, J.P., 2007. Bioaccumulation of mercury in pelagic fishes from the northern Gulf of Mexico. Can. J. Fish. Aquat. Sci. 64, 458–469. https://doi.org/10.1139/f07-017

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.

Calil, P.H.R., Richards, K.J., Jia, Y., Bidigare, R.R., 2008. Eddy activity in the lee of the Hawaiian Islands. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 1179–1194. https://doi.org/10.1016/j.dsr2.2008.01.008

Campbell, S., David, M.D., Woodward, L.A., Li, Q.X., 2004. Persistence of carbofuran in marine sand and water. Chemosphere 54, 1155–1161. https://doi.org/10.1016/j.chemosphere.2003.09.018

CARDI, 2018. Caribbean Agricultural Research and Development Institute. URL www.cardi.org

Carravieri, A., Bustamante, P., Tartu, S., Meillere, A., Labadie, P., Budzinski, H., Peluhet, L., Barbraud, C., Weimerskirch, H., Chastel, O., Cherel, Y., 2014. Wandering albatrosses document latitudinal variations in the transfer of persistent organic pollutants and mercury to Southern Ocean predators. Environ. Sci. Technol. 48, 14746–14755. https://doi.org/10.1021/es504601m

Ceccatelli, S., Daré, E., Moors, M., 2010. Methylmercury-induced neurotoxicity and apoptosis. Chem. Biol. Interact. 188, 301–308. https://doi.org/10.1016/j.cbi.2010.04.007

Colabuono, F.I., Barquete, V., Taniguchi, S., Ryan, P.G., Montone, R.C., 2014. Stable isotopes of carbon and nitrogen in the study of organochlorine contaminants in albatrosses and petrels. Mar. Pollut. Bull. 83, 241–7. https://doi.org/10.1016/j.marpolbul.2014.03.046

Connolly, R.M., Guest, M.A., Melville, A.J., Oakes, J.M., 2004. Sulfur stable isotopes separate producers in marine food-web analysis. Oecologia 138, 161–167. https://doi.org/10.1007/s00442-003-1415-0

Corbin, C.J., Singh, J.G., 1993. Marine debris contamination of beaches in St-Lucia and Dominica. Mar. Pollut. Bull. 26, 325–328. https://doi.org/10.1016/0025-326X(93)90575-5

Cortes, D.R., Hites, R.A., 2000. Detection of statistically significant trends in atmospheric concentrations of semivolatile compounds. Environ. Sci. Technol. 34, 2826–2829. https://doi.org/10.1021/es990466l

Costantini, D., Sebastiano, M., Müller, M.S., Eulaers, I., Ambus, P., Malarvannan, G., Covaci, A., Massa, B., Dell'Omo, G., 2017. Individual variation of persistent organic pollutants in relation to stable isotope ratios, sex, reproductive phase and oxidative status in Scopoli's shearwaters (Calonectris diomedea) from the Southern Mediterranean. Sci. Total Environ. 598, 179–187. https://doi.org/10.1016/j.scitotenv.2017.04.014

Ding, S., Dong, F., Wang, B., Chen, S., Zhang, L., Chen, M., Gao, M., He, P., 2015. Polychlorinated biphenyls and organochlorine pesticides in atmospheric particulate matter of Northern China: distribution, sources, and risk assessment. Environ. Sci.

Pollut. Res. 22, 17171–17181. https://doi.org/10.1007/s11356-015-4949-x

Domingo, J.L., Bocio, A., Falcó, G., Llobet, J.M., 2007. Benefits and risks of fish consumption. Part I. A quantitative analysis of the intake of omega-3 fatty acids and chemical contaminants. Toxicology 230, 219–226. https://doi.org/10.1016/j.tox.2006.11.054

Doty, M.S., Oguri, M., 1956. The Island Mass Effect. ICES J. Mar. Sci. 22, 33–37.

Duinker, J.C., Schultz, D.E., Petrick, G., 1988. Selection of chlorinated biphenyl congeners for analysis in environmental samples. Mar. Pollut. Bull. 19, 19–25. https://doi.org/10.1016/0025-326X(88)90748-5

Eagles-Smith, C.A., Ackerman, J.T., Adelsbach, T.L., Takekawa, J.Y., Miles, A.K., Keister, R.A., 2008. Mercury correlations among six tissues for four waterbird species breeding in San Francisco Bay, California, USA. Environ. Toxicol. Chem. 27, 2136–2153. https://doi.org/10.1897/08-038.1

Eisenreich, S.J., Jones, K.C., 2002. Oceanic biogeochemical controls on global dynamics of persistent organic pollutants. Environ. Sci. Technol. 36, 4229–4237.

Elliott, J.E., Elliott, K.H., 2013. Tracking marine pollution. Science. 340, 556–558. https://doi.org/10.1126/science.1235197

Elliott, K.H., Elliott, J.E., 2016. Origin of Sulfur in Diet Drives Spatial and Temporal Mercury Trends in Seabird Eggs From Pacific Canada 1968–2015. Environ. Sci. Technol. 50, 13380–13386. https://doi.org/10.1021/acs.est.6b05458

Fiedler, P.C., 2002. The annual cycle and biological effects of the Costa Rica Dome. Deep. Res. Part I Oceanogr. Res. Pap. 49, 321–338. https://doi.org/10.1016/S0967-0637(01)00057-7

Fitzgerald, W.F., Lamborg, C.H., Hammerschmidt, C.R., 2007. Marine biogeochemical cycling of mercury. Chem. Rev. 107, 641–662. https://doi.org/10.1021/cr050353m

Forde, M.S., Dewailly, E., Robertson, L., Laouan Sidi, E.A., Cote, S., Dumas, P., Ayotte, P., 2014. Prenatal exposure to persistent organic pollutants and polybrominated diphenyl ethers in 10 Caribbean countries. Env. Res 133, 211–219. https://doi.org/10.1016/j.envres.2014.05.021

Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, Second Edition. Sage, Thousand Oaks, California.

Gavrilescu, M., Demnerová, K., Aamand, J., Agathos, S., Fava, F., 2015. Emerging pollutants in the environment: Present and future challenges in biomonitoring, ecological risks and bioremediation. N. Biotechnol. 32, 147–156. https://doi.org/10.1016/j.nbt.2014.01.001

Gelado-Caballero, M.D., Torres-Padrón, M.E., Hernández-Brito, J.J., Herrera-Melián, J.A., Pérez-Peña, J., Herrera-Melian, J.A., Pérez-Peña, J., 1996. Aluminium distributions in Central East Atlantic waters (Canary Islands). Mar. Chem. 51, 359–372. https://doi.org/10.1016/0304-4203(95)00069-0

Gilmour, M., Schreiber, E., Dearborn, D., 2012. Satellite telemetry of great frigatebirds Fregata minor rearing chicks on Tern Island, North Central Pacific Ocean. Mar. Ornithol. 23, 17–23.

Gilmour, M.E., Castillo-Guerrero, J.A., Fleishman, A.B., Hernandez-Vazquez, S., Young, H.S., Shaffer, S.A., 2018. Plasticity of foraging behaviors in response to diverse environmental conditions. Ecosphere doi:10.1002/ecs2.2301.

Gosnell, K.J., Mason, R.P., 2015. Mercury and methylmercury incidence and bioaccumulation in plankton from the central Pacific Ocean. Mar. Chem. 177, 772–780. https://doi.org/10.1016/j.marchem.2015.07.005

Gouin, T., MacKay, D., Jones, K.C., Harner, T., Meijer, S.N., 2004. Evidence for the "grasshopper" effect and fractionation during long-range atmospheric transport of organic contaminants. Environ. Pollut. 128, 139–148. https://doi.org/10.1016/j.envpol.2003.08.025

Hahn, S., Hoye, B.J., Korthals, H., Klaassen, M., 2012. From food to offspring down: Tissue-specific discrimination and turn-over of stable isotopes in herbivorous waterbirds and other avian foraging guilds. PLoS One 7, e30242. https://doi.org/10.1371/journal.pone.0030242

Hamann, I.M., Boehlert, G.W., Wilson, C.D., 2004. Effects of steep topography on the flow and stratification near Palmyra Atoll. Ocean Dyn. 54, 460–473. https://doi.org/10.1007/s10236-004-0091-x

Hammerschmidt, C.R., Bowman, K.L., 2012. Vertical methylmercury distribution in the subtropical North Pacific Ocean. Mar. Chem. 132–133, 77–82. https://doi.org/10.1016/j.marchem.2012.02.005

Hammerschmidt, C.R., Fitzgerald, W.F., 2004. Geochemical Controls on the Production and Distribution of Methylmercury in Near-Shore Marine Sediments. Environ. Sci. Technol. 38, 1487–1495. https://doi.org/10.1021/es034528q

Harrison, C.S., Hida, T.S., Seki, M.P., 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85, 3–71.

Harwani, S., Henry, R.W., Rhee, A., Kappes, M.A., Croll, D.A., Petreas, M., Park, J.-S., 2011. Legacy and contemporary persistent organic pollutants in North Pacific albatross. Environ. Toxicol. Chem. 30, 2562–9. https://doi.org/10.1002/etc.664

Heskett, M., Takada, H., Yamashita, R., Yuyama, M., Ito, M., Geok, Y.B., Ogata, Y., Kwan, C., Heckhausen, A., Taylor, H., Powell, T., Morishige, C., Young, D., Patterson, H., Robertson, B., Bailey, E., Mermoz, J., 2012. Measurement of persistent organic pollutants (POPs) in plastic resin pellets from remote islands: toward establishment of background concentrations for International Pellet Watch. Mar. Pollut. Bull. 64, 445–8. https://doi.org/10.1016/j.marpolbul.2011.11.004

Hijmans, R.J., 2017. geosphere: Spherical Trigonometry. R package version 1.5-7. https://CRAN.R-project.org.

Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds: insights from tissue-

dependent stable-isotope models. Mar. Ecol. Prog. Ser. 95, 7–18. https://doi.org/10.3354/meps095007

Hobson, K.A., Clark, R.G., 1993. Turnover of 13C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110, 638–641.

Howell, E.A., Bograd, S.J., Morishige, C., Seki, M.P., Polovina, J.J., 2012. On North Pacific circulation and associated marine debris concentration. Mar. Pollut. Bull. 65, 16–22. https://doi.org/10.1016/j.marpolbul.2011.04.034

Ivar do Sul, J.A., Costa, M.F., 2007. Marine debris review for Latin America and the Wider Caribbean Region: From the 1970s until now, and where do we go from here? Mar. Pollut. Bull. 54, 1087–1104. https://doi.org/10.1016/j.marpolbul.2007.05.004

Iwata, H., Tanabe, S., Sakai, N., Tatsukawa, R., 1993. Distribution of persistent organochlorines in the oceanic air and surface seawater and the role of ocean on their global transport and fate. Environ. Sci. Technol. 27, 1080–1098. https://doi.org/10.1021/es00043a007

Johns, W.E., Townsend, T.L., Fratantoni, D.M., Wilson, W.D., 2002. On the Atlantic inflow to the Caribbean Sea. Deep. Res. Part I Oceanogr. Res. Pap. 49, 211–243. https://doi.org/10.1016/S0967-0637(01)00041-3

Jurado, E., Jaward, F.M., Lohmann, R., Jones, K.C., Simo, R., Dachs, J., 2005. Wet deposition of persistent organic pollutants to the global oceans. Environ. Sci. Technol. 39, 2426–2435.

Kallenborn, R., Halsall, C., Dellong, M., Carlsson, P., 2012. The influence of climate change on the global distribution and fate processes of anthropogenic persistent organic pollutants. J. Environ. Monit. 14, 2854–69. https://doi.org/10.1039/c2em30519d

Kawano, M., Inoue, T., Wada, T., Hidaka, H., Tatsukawa, R., 1988. Bioconcentratlon and Residue Patterns of chlordane compounds in marine animals: invertebrates, fish, mammals, and seabirds. Environ. Sci. Technol. 22, 792–797.

Lamborg, C.H., Hammerschmidt, C.R., Bowman, K.L., Swarr, G.J., Munson, K.M., Ohnemus, D.C., Lam, P.J., Heimbürger, L.-E., Rijkenberg, M.J.A., Saito, M.A., 2014. A global ocean inventory of anthropogenic mercury based on water column measurements. Nature 512, 65–68. https://doi.org/10.1038/nature13563

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., Shaffer, 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. https://doi.org/10.1111/ddi.12411

Lavín, M., Marinone, S., 2003. An Overview of the Physical Oceanography of the Gulf of California, in: Velasco Fuentes, O.U. et al. (Ed.), Nonlinear Processes in Geophysical Fluid Dynamics. pp. 173–204.

Lavoie, R.A., Jardine, T.D., Chumchal, M.M., Kidd, K.A., Campbell, L.M., 2013. Biomagnification of mercury in aquatic food webs: A worldwide meta-analysis. Environ. Sci. Technol. 47, 13385–13394. https://doi.org/10.1021/es403103t

Leite, A.S., Santos, L.L., Costa, Y., Hatje, V., 2014. Influence of proximity to an urban center in the pattern of contamination by marine debris. Mar. Pollut. Bull. 81, 242–247. https://doi.org/10.1016/j.marpolbul.2014.01.032

Lerma, M., Castillo-Guerrero, J.A., Ruelas-Inzunza, J., Fernández, G., 2016. Lead, cadmium and mercury in the blood of the blue-footed booby (Sula nebouxii) from the coast of Sinaloa, Gulf of California, Mexico. Mar. Pollut. Bull. 110, 293–298. https://doi.org/10.1016/j.marpolbul.2016.06.049

Lopez, J., Boyd, D., Ylitalo, G.M., Littnan, C., Pearce, R., 2012. Persistent organic pollutants in the endangered Hawaiian monk seal (Monachus schauinslandi) from the main Hawaiian Islands. Mar. Pollut. Bull. 64, 2588–2598. https://doi.org/10.1016/j.marpolbul.2012.07.012

Ma, J., Hung, H., Tian, C., Kallenborn, R., 2011. Revolatilization of persistent organic pollutants in the Arctic induced by climate change. Nat. Clim. Chang. 1, 255–260. https://doi.org/10.1038/nclimate1167

Mackay, D., Bobra, A., Chan, D.W., Shiu, W.Y., 1982. Vapor pressure correlations for low-volatility environmental chemicals. Environ. Sci. Technol. 16, 645–649.

Maragos, J., Miller, J., Gove, J., Demartini, E., 2008. US Coral Reefs in the Line and Phoenix Islands , Central Pacific Ocean 1 : History, Geology, Oceanography, and Biology. Coral Reefs USA 595–641. https://doi.org/10.1007/978-1-4020-6847-8_15

Mason, R.P., Choi, A.L., Fitzgerald, W.F., Hammerschmidt, C.R., Lamborg, C.H., Soerensen, A.L., Sunderland, E.M., 2012. Mercury biogeochemical cycling in the ocean and policy implications. Environ. Res. 119, 101–117. https://doi.org/10.1016/j.envres.2012.03.013

Matsuo, H., Kawano, M., Omori, K., Nakajima, K., Takeuchi, I., 2009. Stable isotope-guided analysis of congener-specific PCB concentrations in a Japanese coastal food web. Mar. Pollut. Bull. 58, 1615–1623. https://doi.org/10.1016/j.marpolbul.2009.07.007

McFadden, K.W., Gómez, A., Sterling, E.J., Naro-Maciel, E., 2014. Potential impacts of historical disturbance on green turtle health in the unique & protected marine ecosystem of Palmyra Atoll (Central Pacific). Mar. Pollut. Bull. 89, 160–167. https://doi.org/10.1016/j.marpolbul.2014.10.012

Miao, X.-S., Woodward, L.A., Swenson, C., Li, Q.X., 2001. Comparative Concentrations of Metals in Marine Species from French Frigate Shoals , North Pacific Ocean. Mar. Pollut. Bull. 42, 1049–1054.

Miao, X.S., Swenson, C., Woodward, L.A., Li, Q.X., 2000. Distribution of polychlorinated biphenyls in marine species from French Frigate Shoals, North Pacific Ocean. Sci. Total Environ. 257, 17–28. https://doi.org/10.1016/S0048-9697(00)00484-8

Morales, L., Dachs, J., Fernández-Pinos, M.-C., Berrojalbiz, N., Mompean, C., González-Gaya, B., Jiménez, B., Bode, A., Ábalos, M., Abad, E., 2015. Oceanic Sink and Biogeochemical Controls on the Accumulation of Polychlorinated Dibenzo- *p* -dioxins, Dibenzofurans, and Biphenyls in Plankton. Environ. Sci. Technol. 150710105722000. https://doi.org/10.1021/acs.est.5b01360

Mott, R., Herrod, A., Clarke, R.H., 2017a. Post-breeding dispersal of frigatebirds increases their exposure to mercury. Mar. Pollut. Bull. 119, 204–210. https://doi.org/10.1016/j.marpolbul.2017.03.050

Mott, R., Herrod, A., Clarke, R.H., 2017b. Resource partitioning between species and sexes in Great Frigatebirds and Lesser Frigatebirds. Auk 134, 153–167. https://doi.org/10.1642/AUK-16-184.1

Müller-Karger, F.., 1989. Pigment distribution in the Caribbean Sea.Observation from space 23, 23–64.

Nelson, J.B., 1978. The Sulidae: gannets and boobies. Oxford University Press, Oxford, U. K.

Nelson, J.B., 1975. The breeding biology of frigatebirds - a comparative review. Living Bird 14, 113–155.

Pante, E., Simon-Bouhet, B., 2013. marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R. PLoS One 8, e73051. https://doi.org/doi:10.1371/journal.pone.0073051

Piatt, J.F., Sydeman, W.J., Weise, F., 2007. Seabirds as indicators of marine ecosystems. Mar. Ecol. Prog. Ser. 352, 199–204. https://doi.org/10.3354/meps07070

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131. https://cran.r-project.org/package=nlme.

Pyle, D.M., Mather, T.A., 2003. The importance of volcanic emissions for the global atmospheric mercury cycle. Atmos. Environ. 37, 5115–5124. https://doi.org/10.1016/j.atmosenv.2003.07.011

Ramage, C.S., KHALSA, S.J.S., Meisner, B.N., 1981. The Central Pacific Near-Equatorial Convergence Zone. J. Geophys. Res. Atmos. 86, 6580–6598. https://doi.org/10.1029/JC086iC07p06580

Ramos, R., González-Solís, J., 2012. Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. Front. Ecol. Environ. 10, 258–266. https://doi.org/10.1890/110140

Randall, D.J., Cornell, D.W., Yang, R., Wu, S.S., 1998. Concentrations of persistent lipophilic compounds in fish are determined by exchange across the gills, not through the food chain. Chemosphere 37, 1263–1270. https://doi.org/10.1016/S0045-6535(98)00124-6

Ricca, M.A., Keith Miles, A., Anthony, R.G., 2008. Sources of organochlorine contaminants and mercury in seabirds from the Aleutian archipelago of Alaska: Inferences from spatial and trophic variation. Sci. Total Environ. 406, 308–323. https://doi.org/10.1016/j.scitotenv.2008.06.030

Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305, 1609–12. https://doi.org/10.1126/science.1100958

Rimmer, C.C., Mcfarland, K.P., Evers, D.C., Miller, E.K., Aubry, Y., Busby, D., Taylor, R.J.,

2005. Mercury concentrations in Bicknell's thrush and other insectivorous passerines in montane forests of northeastern North America. Ecotoxicology 14, 223–240. https://doi.org/10.1007/s10646-004-6270-1

Roper, C.F.E., Young, R.E., 1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. to Zool. 1–51. https://doi.org/10.5479/si.00810282.209

Roscales, J.L., González-Solís, J., Muñoz-Arnanz, J., Jiménez, B., 2011. Geographic and trophic patterns of OCs in pelagic seabirds from the NE Atlantic and the Mediterranean: a multi-species/multi-locality approach. Chemosphere 85, 432–40. https://doi.org/10.1016/j.chemosphere.2011.07.070

Rueda-Roa, D.T., Muller-Karger, F.E., 2013. The southern Caribbean upwelling system: Sea surface temperature, wind forcing and chlorophyll concentration patterns. Deep. Res. Part I Oceanogr. Res. Pap. 78, 102–114. https://doi.org/10.1016/j.dsr.2013.04.008

Sackett, D.K., Drazen, C., Choy, C.A., Popp, B., Pitz, G.L., 2015. Mercury Sources and Trophic Ecology for Hawaiian Bottom fi sh. https://doi.org/10.1021/acs.est.5b01009

Sebastiano, M., Bustamante, P., Eulaers, I., Malarvannan, G., Mendez-Fernandez, P., Churlaud, C., Blévin, P., Hauselmann, A., Covaci, A., Eens, M., Costantini, D., Chastel, O., 2017. Trophic ecology drives contaminant concentrations within a tropical seabird community. Environ. Pollut. 227, 183–193. https://doi.org/10.1016/j.envpol.2017.04.040

Shunthirasingham, C., Oyiliagu, C.E., Cao, X., Gouin, T., Wania, F., Lee, S.-C., Pozo, K., Harner, T., Muir, D.C.G., 2010. Spatial and temporal pattern of pesticides in the global atmosphere. J. Environ. Monit. 12, 1650–1657. https://doi.org/10.1039/c0em00134a

Signorini, S.R., McClain, C.R., Dandonneau, Y., 1999. Mixing and phytoplankton bloom in the wake of the Marquesas Islands. Geophys. Res. Lett. 26, 3121–3124. https://doi.org/10.1029/1999GL010470

Simonich, S.L.M., Hites, R.A., 1995. Global Distribution of Persistent Organochlorine Compounds. Science. 269, 1851–1854.

Soanes, L.M., Arnould, J.P.Y., Dodd, S.G., Sumner, M.D., Green, J.A., 2013. How many seabirds do we need to track to define home-range area? J. Appl. Ecol. 50, 671–679. https://doi.org/10.1111/1365-2664.12069

Spear, L.B., Ainley, D.G., Walker, W., 2007. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. Stud. Avian Biol. 35, 1–109.

Stemmler, I., Lammel, G., 2013. Evidence of the return of past pollution in the ocean: A model study. Geophys. Res. Lett. 40, 1373–1378. https://doi.org/10.1002/grl.50248

Su, Y., Hung, H., Blanchard, P., Patton, G.W., Kallenborn, R., Konoplev, A., Fellin, P., Li, H., Geen, C., Stern, G., Rosenberg, B., Barrie, L.A., 2006. Spatial and seasonal variations of hexachlorocyclohexanes (HCHs) and hexachlorobenzene (HCB) in the Arctic atmosphere. Environ. Sci. Technol. 40, 6601–6607. https://doi.org/10.1021/es061065q

Sweet, L.I., Passino-Reader, D.R., Meier, P.G., Omann, G.M., 2006. Effects of polychlorinated biphenyls, hexachlorocyclohexanes, and mercury on human neutrophil

apoptosis, actin cytoskelton, and oxidative state. Environ. Toxicol. Pharmacol. 22, 179–188. https://doi.org/10.1016/j.etap.2006.03.005

Takeuchi, I., Miyoshi, N., Mizukawa, K., Takada, H., Ikemoto, T., Omori, K., Tsuchiya, K., 2009. Biomagnification profiles of polycyclic aromatic hydrocarbons, alkylphenols and polychlorinated biphenyls in Tokyo Bay elucidated by δ13C and δ15N isotope ratios as guides to trophic web structure. Mar. Pollut. Bull. 58, 663–671. https://doi.org/10.1016/j.marpolbul.2008.12.022

Tavares, S., Xavier, J.C., Phillips, R.A., Pereira, M.E., Pardal, M.A., 2013. Influence of age, sex and breeding status on mercury accumulation patterns in the wandering albatross Diomedea exulans. Environ. Pollut. 181, 315–320. https://doi.org/10.1016/j.envpol.2013.06.032

Trefry, S.A., Diamond, A.W., 2017. Exploring hypotheses for sexual size dimorphism in frigatebirds. Evol. Ecol. Res. 18, 225–252.

U. S. Environmental Protection Agency, 2007. Method 7473, Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry, Test Methods for Evaluating Solid Waste, Physical/Chemical Methods; SW 846. Washington, D. C., USA.

United Nations Environmental Program, 2018. Stockholm Convention; Acceptable purposes: DDT. URL http://chm.pops.int/Implementation/Exemptionsandacceptablepurposes/RegistersofAcceptablePurposes/AcceptablePurposesDDT/tabid/456/Default.aspx

Van Sebille, E., England, M.H., Froyland, G., 2012. Origin, dynamics and evolution of ocean garbage patches from observed surface drifters. Environ. Res. Lett. 7. https://doi.org/10.1088/1748-9326/7/4/044040

Verreault, J., Villa, R. a., Gabrielsen, G.W., Skaare, J.U., Letcher, R.J., 2006. Maternal transfer of organohalogen contaminants and metabolites to eggs of Arctic-breeding glaucous gulls. Environ. Pollut. 144, 1053–1060. https://doi.org/10.1016/j.envpol.2005.10.055

Walters, D.M., Mills, M.A., Cade, B.S., Burkard, L.P., 2011. Trophic magnification of PCBs and its relationship to the octanol-water partition coefficient. Environ. Sci. Technol. 45, 3917–3924. https://doi.org/10.1021/es103158s

Wania, F., Mackay, D., 1993. Global Fractionation and Cold Condensation of Low Volatility Organochlorine Compounds in Polar-Regions. Ambio 22, 10–18.

Weimerskirch, H., Corre, M. Le, 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.

Worton, B.J., 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70, 164–168.

Yoshida, S., Qiu, B., Hacker, P., 2010. Wind-generated eddy characteristics in the lee of the island of Hawaii. J. Geophys. Res. 115, 1–15. https://doi.org/10.1029/2009JC005417

Young, H.S., Maxwell, S.M., Conners, M.G., Shaffer, S.A., 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. Biol. Conserv. 181, 226–235. https://doi.org/10.1016/j.biocon.2014.10.027

Young, H.S., McCauley, D.J., Dunbar, R.B., Dirzo, R., 2010b. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. Proc. Natl. Acad. Sci. 107, 2072–2077. https://doi.org/10.1073/pnas.0914169107

Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R., Block, B.A., 2010a. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Mar. Ecol. Prog. Ser. 403, 291–301. https://doi.org/10.3354/meps08478

Table 2.1 Blood-based stable isotopes and GPS-based foraging metrics of boobies and frigatebirds
Summary statistics (mean ± SD, sample size, and minimum and maximum values) of carbon, nitrogen, and sulfur stable isotope values from booby and frigatebird blood samples, and foraging trip metrics recorded by GPS tracking tags, from four breeding colonies, sampled in 2009-2014. Dash indicates that GPS tracking data were not obtained.

Colony	Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)	Max. distance from colony (km)	Size of general (95% kernel density) habitat area (km^2)	Size of core (50% kernel density) habitat area (km^2)
Barbuda	Magnificent Frigatebird	-16.28 ± 0.34 (-16.83 – -15.64) 9	8.02 ± 0.23 (7.84 – 8.55) 9	19.99 ± 0.90 (18.00 – 20.70) 8	–	–	–
Laysan Island	Great Frigatebird	-17.75 ± 0.19 (-17.96 – -17.57) 5	8.58 ± 0.55 (8.15 – 9.52) 5	20.20 ± 0.18 (19.90 – 20.40) 6	–	–	–
	Masked Booby	-17.50 ± 0.45 (-17.82 – -17.18) 2	9.07 ± 0.33 (8.84 – 9.30) 2	19.90 ± 0.42 (19.60 – 20.20) 2	–	–	–
	Red-footed Booby	-17.95 ± 0.04 (-17.98 – -17.93) 2	8.10 ± 0.06 (8.06 – 8.14) 2	19.60 ± 0.00 (19.6 – 19.6) 2	–	–	–
Palmyra Atoll	Brown Booby	-17.10 ± 0.70 (-17.21 – -17.03) 9	15.70 ± 0.56 (15.05 – 16.75) 9	20.99 ± 0.49 (20.20 – 21.6) 8	20.7 ± 14.9 (2.9 – 52.2) 20 trips, 7 birds	3,320.1	497.1
	Great Frigatebird	-17.51 ± 0.19 (-17.96 – -17.57) 5	16.05 ± 1.08 (14.28 – 17.12) 5	20.26 ± 0.38 (19.60 – 20.60) 7	129.3 ± 69.5 (44.5 – 242.4) 9 trips, 6	7,409.2	1,978.4

					birds		
Tern Island	Masked Booby	-17.20 ± 0.17 (-17.48 – -16.89) 11	8.63 ± 0.29 (8.22 – 9.17) 11	16.16 ± 4.28 (7.00 – 20.60) 11	77.9 ± 55.6 (1.4 – 209.7) 17	14,861.3	2,760.0
	Red-footed Booby	-17.92 ± 0.09 (-18.02 – -17.80) 6	7.87 ± 0.17 (7.64 – 8.16) 6	20.40 ± 0.14 (20.30 – 20.60) 4	95.6 ± 37.4 (16.6 – 143.7) 13	20,479.7	3,500.8
	Great Frigatebird	-17.74 ± 0.09 (-17.80 – -17.64) 3	9.07 ± 0.07 (9.02 – 9.15) 3	20.65 ± 0.71 (20.60 – 20.7) 2	–	–	–

Table 2.2 Blood-based POP and mercury concentrations in boobies and frigatebirds

Median (bolded) ± SE concentrations, minimum and maximum values, number of samples, and detection frequency (%) of persistent organic pollutants (POP; ng mL^{-1} ww) and total mercury (THg; µg g^{-1} ww) in booby and frigatebird blood samples (plasma for POP and red blood cells for THg from Palmyra Atoll; whole blood from Barbuda, Laysan, and Tern Islands) sampled 2009-2014. POP are grouped into compound families, and then listed by their primary intended use (pesticide or industrial); the number of detections per compound family out of the total number of samples analyzed for that compound is also listed. ΣPOP_{53} represents the sum of all POP detected per colony-species group. ND indicates that POP concentration was not detected. Dash represents POP compound that was not analyzed. POP compound abbreviations: CBZ=chlorobenzene; DDE=dichlorodiphenyldichloroethylene; DDT=dichlorodiphenyltrichloroethane; HCH=hexachlorocyclohexane; PCB=polychlorinated biphenyl; PBDE=polybrominated diphenyl ether.

Colony	Barbuda	Laysan Island			Palmyra Atoll		Tern Island		
Compound Species	Magnificent Frigatebird	Great Frigatebird	Masked Booby	Red-footed Booby	Brown Booby	Great Frigatebird	Great Frigatebird	Masked Booby	Red-footed Booby
Pesticides									
$\Sigma chlordane_7$	**0.70** ± 0.44 (0.09–5.59) 15 100%	**0.15** ± 0.06 (0.09–0.47) 6 33%	**0.23** ± 0.07 (0.11–0.36) 4 57%	**0.22** ± 0.12 (0.10–0.35) 2 50%	**0.32** ± 0.16 (0.15–0.48) 2 25%	**0.37** – 1 33%	–	–	–
30/55									
chlorpyrifos	**0.26** ± 0.20 (0.11–1.85) 9 60%	**0.85** ± 0.13 (0.27–2.39) 17 94%	ND	**0.22** ± 0.03 (0.16–0.28) 3 75%	ND	ND	–	–	–
29/55									
$\Sigma cyclodiene_3$	**1.45** ± 0.52 (0.15–5.30) 12 80%	ND	**0.22** ± 0.05 (0.12–0.35) 4 57%	ND	**0.32** ± 0.03 (0.29–0.35) 2 25%	**0.36** – 1 33%	–	–	–
19/55									

DDE 47/55	**0.56** ± 0.82 (0.17 – 10.80) 15 100%	**1.10** ± 0.20 (0.52 – 3.43) 18 100%	**0.78** ± 0.29 (0.36 – 2.43) 7 100%	**0.97** ± 0.21 (0.38–1.03) 3 75%	**0.34** – 1 13%	**3.53** ± 0.51 (2.17 – 3.83) 3 100%	–	–	–
ΣDDT_5 41/55	**1.03** ± 0.58 (0.08 – 7.62) 15 100%	**0.60** ± 0.08 (0.25 – 0.79) 8 44%	**0.96** ± 0.27 (0.11 – 2.06) 7 100%	**0.76** ± 0.39 (0.28–1.61) 3 75%	**0.49** ± 0.17 (0.36 – 1.21) 5 63%	**4.11** ± 1.10 (1.22 – 4.8) 3 100%	–	–	–
endosulfan 13/40	–	**0.20** ± 0.03 (0.15–0.24) 3 17%	**0.16** ± 0.03 (0.05–0.23) 6 86%	**0.14** ± 0.01 (0.13–0.15) 2 50%	**0.40** ± 0.03 (0.37–0.43) 2 25%	ND	–	–	–
ΣHCH_4 21/55	**1.76** ± 0.93 (0.32–12.45) 14 93%	**0.19** ± 0.03 (0.12–0.22) 3 17%	**0.76** ± 0.34 (0.30–1.47) 3 43%	ND	ND	**1.22** – 1 33%	–	–	–
mirex 36/55	**0.06** ± 0.08 (0.02–0.94) 12 80%	**0.20** ± 0.04 (0.11–0.55) 15 83%	**0.12** ± 0.04 (0.02–0.20) 4 57%	**0.16** ± 0.04 (0.15–0.28) 3 75%	**0.11** – 1 13%	**0.08** – 1 33%	–	–	–
pentachloroanisole 30/55	**0.29** ± 0.18 (0.05–2.72) 15 100%	**0.12** ± 0.02 (0.05–0.15) 6 33%	**0.09** ± 0.02 (0.02–0.10) 5 71%	**0.08** – 1 25%	**0.18** – 1 13%	**0.15** ± 0.02 (0.13–0.17) 2 67%	–	–	–

Industrial compounds	**2.02** ± 0.72 (0.62–11.65) 15 100%	**0.57** ± 0.08 (0.10–1.27) 16 89%	**0.18** ± 0.12 (0.04–0.94) 7 100%	**0.30** ± 0.01 (0.17–0.50) 3 75%	**0.27** ± 0.11 (0.20–0.79) 5 63%	**0.47** ± 0.13 (0.26–0.72) 3 100%	–	–	–
ΣCBZ$_4$									
49/55									
ΣPCB$_{22}$	**8.02** ± 3.39 (1.99–49.63) 15 100%	**2.68** ± 0.34 (1.35–6.19) 18 100%	**4.21** ± 1.05 (1.92–9.31) 7 100%	**1.60** ± 0.40 (1.38–3.11) 4 100%	**2.84** ± 1.07 (1.02–10.20) 8 100%	**5.73** ± 1.44 (4.06–8.95) 3 100%	–	–	–
55/55									
ΣPCB$_{ICES}$	**3.22** ± 2.65 (0.84–39.9) 15 100%	**1.87** ± 0.28 (0.71–4.98) 18 100%	**4.08** ± 0.77 (1.32–6.98) 7 100%	**1.20** ± 0.31 (1.03–2.37) 4 100%	**2.46** ± 0.52 (1.02–5.25) 8 100%	**3.22** ± 1.43 (2.73–7.23) 3 100%			
ΣPBDE$_4$	**1.16** – 1 7%	**3.88** ± 0.49 (0.86–7.76) 17 94%	**3.34** ± 0.43 (1.43–3.50) 5 71%	**2.86** ± 1.36 (0.93–6.70) 4 100%	**6.14** ± 0.93 (2.08–9.36) 8 100%	**1.84** ± 1.36 (1.28–5.60) 3 100%	–	–	–
38/55									
ΣPOP$_{53}$	**18.80** ± 5.36 (3.58–72.2) 15	**9.46** ± 0.84 (3.08–16.9) 18	**10.00** ± 2.22 (3.03–18.4) 7	**5.76** ± 1.99 (4.40–13.20) 4	**10.60** ± 1.62 (5.43–20.0) 8	**14.30** ± 3.10 (13.4–23.1) 3	–	–	–
THg	**0.97** ± 0.04 (0.69–1.12) 12 100%	**0.32** ± 0.09 (0.17–0.72) 5 100%	**0.34** ± 0.11 (0.27–0.62) 3 100%	**0.11** ± 0.01 (0.09–0.14) 4 100%	**0.56** ± 0.07 (0.16–0.92) 10 100%	**0.63** ± 0.10 (0.48–1.11) 7 100%	**0.77** ± 0.11 (0.51–2.76) 7 100%	**0.42** ± 0.02 (0.13–1.17) 14 100%	**0.46** ± 0.03 (0.35–0.58) 8 100%
70/70									

Table 2.3 Summary statistics of one-way ANOVA models of blood-based POP and mercury concentrations between colonies of boobies and frigatebirds

Summary statistics of one-way ANOVA models (type 3), where blood-based concentrations of each persistent organic pollutant family and mercury (THg) were response variables, and colony and sex were predictor variables. Due to multicollinearity between some colony-species combinations, species was not included as a factor in models. Only compound families that had >50% detection frequencies were included in models. All response variables were log-transformed prior to analyses to meet assumptions of normality. Compound abbreviations: chlorobenzene (CBZ); dichlorodiphenyldichloroethylene (DDE); dichlorodiphenyltrichloroethane (DDT); polychlorobiphenyl (PCB); polybrominated diphenyl ether (PBDE). A Bonferroni correction was used to assess significance; p-values were considered significant when p=0.05/10=0.005 (in bold).

Compound	n	Colony			Sex		
		F	df	P	F	df	P
$\Sigma chlordane_7$	30	6.51	2	**0.005**	0.41	2	0.668
chlorpyrifos	29	2.69	1	0.114	2.64	2	0.092
DDE	47	1.70	2	0.195	0.30	2	0.744
ΣDDT_5	41	1.05	2	0.361	0.38	2	0.687
mirex	36	3.17	2	0.056	0.17	2	0.841
pentachloroanisole	30	3.86	2	0.035	0.36	2	0.704
ΣCBZ_4	49	21.15	2	**<0.0001**	0.32	2	0.729
ΣPCB_{22}	55	13.12	2	**<0.0001**	0.04	2	0.962
$\Sigma PBDE_4$	38	3.29	2	0.050	2.97	2	0.065
THg	70	9.96	3	**<0.0001**	2.98	2	0.058

Table 2.4 Blood-based PCB congener concentrations in boobies and frigatebirds

Median ± SE concentrations, minimum and maximum values, and number of samples of polychlorinated biphenyl (PCB) congeners (ng mL^{-1}) from booby and frigatebird blood samples (plasma from Palmyra Atoll; whole blood from Barbuda and Laysan Island) sampled 2009-2014. ND indicates that PCB congener was not detected.

Congener Group	Colony Species / Compound	Barbuda Magnificent Frigatebird	Laysan Island Great Frigatebird	Masked Booby	Red-footed Booby	Palmyra Atoll Brown Booby	Great Frigatebird
Di	8/5	0.97 ± 0.08 (0.80 – 1.06) 3	ND	0.12 ± 0.03 (0.02 – 0.26) 6	ND	ND	0.20 ± 0.04 (0.16 – 0.24) 2
Tri	18/17	0.44 ± 0.68 (0.18 – 10.70) 15	ND	0.28 ± 0.13 (0.14 – 0.41) 2	ND	1.33 – 1	ND
	28	0.53 ± 0.27 (0.14 – 4.08) 14	ND	1.20 ± 0.20 (0.29 – 1.63) 7	ND	1.83 ± 0.34 (1.37 – 2.55) 3	3.15 ± 1.73 (1.41 – 4.88) 2
	29	0.15 ± 0.21 (0.03 – 2.82) 13	ND	ND	ND	ND	ND
Tetra	44	0.19 ± 0.09 (0.05 – 1.11) 15	ND	ND	ND	ND	ND
	52	0.34 ± 0.14 (0.12 – 1.35) 9	ND	ND	ND	ND	ND
	66	0.14 ± 0.04 (0.03 – 0.41) 10	ND	0.50 ± 0.13 (0.20 – 0.73) 4	ND	ND	1.22 – 1
	87/115	0.37 ± 0.12 (0.10 – 0.94) 6	ND	0.19 – 1	ND	ND	ND
	101/90	0.22 ± 0.12 (0.03 – 1.14) 9	ND	0.74 ± 0.11 (0.26 – 1.04) 7	0.19 ± 0.06 (0.13 – 0.25) 2	ND	ND

	105	0.36 ± 0.09 (0.05 – 1.01) 13	0.36 – 1	0.42 ± 0.06 (0.35 – 0.48) 2	ND	ND	0.69 ± 0.16 (0.41 – 0.97) 3
Penta	110/77	0.45 ± 0.38 (0.07 – 0.84) 2	ND	0.49 – 1	ND	ND	ND
	118	0.28 ± 0.12 (0.04 – 1.12) 12	0.29 ± 0.01 (0.24 – 0.32) 5	0.60 – 1	ND	ND	ND
Hexa	128	0.51 ± 0.13 (0.17 – 2.11) 15	0.12 ± 0.03 (0.09 – 0.14) 2	0.17 ± 0.05 (0.06 – 0.23) 3	ND	ND	ND
	138/160	0.62 ± 0.51 (0.10 – 6.86) 14	0.63 ± 0.06 (0.35 – 1.47) 18	0.89 ± 0.19 (0.24 – 1.66) 7	0.43 ± 0.02 (0.37 – 0.44) 3	0.66 ± 0.12 (0.46 – 1.15) 5	0.72 ± 0.18 (0.65 – 1.21) 3
	153/132	1.00 ± 1.32 (0.13 – 19.79) 15	0.85 ± 0.15 (0.28 – 1.79) 11	0.43 ± 0.21 (0.17 – 1.72) 7	0.22 ± 0.08 (0.18 – 0.43) 3	0.63 ± 0.11 (0.37 – 1.11) 7	1.03 ± 0.22 (0.55 – 1.32) 3
Hepta	170/190	0.26 ± 0.34 (0.05 – 4.46) 13	0.47 ± 0.06 (0.27 – 1.23) 18	0.06 – 1	0.27 ± 0.01 (0.25 – 0.27) 3	ND	ND
	180	0.45 ± 0.82 (0.08 – 11.78) 15	0.72 ± 0.13 (0.36 – 2.19) 18	0.27 ± 0.11 (0.13 – 0.93) 7	0.31 ± 0.02 (0.31 – 0.36) 3	0.41 ± 0.06 (0.26 – 0.65) 6	0.49 ± 0.05 (0.38 – 0.54) 3
	187	0.50 ± 0.19 (0.08 – 2.38) 14	0.22 ± 0.03 (0.11 – 0.48) 12	0.15 ± 0.06 (0.06 – 0.34) 5	0.11 ± 0.03 (0.08 – 0.14) 2	0.27 ± 0.13 (0.17 – 0.60) 3	0.20 ± 0.08 (0.12 – 0.29) 2
Octa	195/208	0.13 ± 0.04 (0.04 – 0.42) 10	0.15 ± 0.02 (0.09 – 0.23) 6	0.11 ± 0.01 (0.11 – 0.15) 3	0.15 – 1	ND	0.18 ± 0.02 (0.15 – 0.20) 2
	201/157/173	0.26 ± 0.06 (0.11 – 0.68) 12	0.42 ± 0.09 (0.17 – 0.61) 4	0.14 ± 0.04 (0.03 – 0.24) 5	ND	ND	0.36 – 1
Nona	206	0.25 ± 0.06 (0.10 – 0.98) 15	0.09 ± 0 (0.08 – 0.09) 2	0.10 ± 0.02 (0.02 – 0.14) 7	ND	0.22 ± 0.02 (0.17 – 0.31) 6	0.22 ± 0.10 (0.09 – 0.44) 3

Deca	209	0.07 ± 0.02 (0.03 – 0.36) 15	ND	ND	ND	0.10 – 1	ND

Table 2.5 Summary statistics of Mann-Whitney tests of blood-based POP concentrations between female and male frigatebirds

Summary of statistics from Mann-Whitney tests of persistent organic pollutant (POP) concentrations from whole blood between male and female Magnificent and Great Frigatebirds from Barbuda and Laysan Island, respectively. Dash indicates insufficient sample sizes for comparison. A Bonferroni correction was used to assess significance; p-values were considered significant when p=0.05/17=0.003 (in bold). POP compound abbreviations: CBZ=chlorobenzene; DDE=dichlorodiphenyldichloroethylene; DDT=dichlorodiphenyltrichloroethane; HCH=hexachlorocyclohexane; PBDE=polybrominated diphenyl ether; PCB=polychlorinated biphenyl.

POP	Magnificent Frigatebird				Great Frigatebird			
	W	P	Female	Male	W	P	Female	Male
Σchlordane$_7$	27.0	0.999	0.65 ± 0.84 (6)	0.72 ± 0.52 (9)	–	–	–	–
chlorpyrifos	–	–	–	–	57.0	0.048	1.03 ± 0.20 (8)	0.54 ± 0.13 (9)
ΣCBZ$_4$	23.0	0.690	1.63 ± 0.79 (6)	2.32 ± 1.12 (9)	37.5	0.599	0.68 ± 0.15 (8)	0.53 ± 0.09 (8)
Σcyclodiene$_3$	16.5	0.935	0.46 ± 0.98 (5)	1.72 ± 0.62 (7)	–	–	–	–
DDE	21.0	0.529	0.53 ± 0.20 (6)	1.03 ± 1.3 (9)	64.0	0.040	1.56 ± 0.30 (9)	0.86 ± 0.20 (9)
ΣDDT$_5$	21.0	0.529	0.47 ± 1.22 (6)	1.12 ± 0.61 (9)	–	–	–	–
ΣHCH$_4$	18.0	0.477	1.54 ± 1.25 (6)	1.80 ± 1.40 (8)	–	–	–	–
mirex	15.0	0.686	0.05 ± 0.05 (6)	0.07 ± 0.15 (6)	50.5	0.011	0.31 ± 0.06 (8)	0.14 ± 0.02 (7)
pentachloroanisole	28.0	0.955	0.30 ± 0.16 (6)	0.29 ± 0.28 (9)	–	–	–	–
ΣPBDE$_4$	–	–	–	–	51.0	0.167	4.62 ± 0.77 (9)	3.32 ± 0.56 (8)
ΣPCB$_{22}$	16.0	0.224	6.10 ± 3.14 (6)	8.46 ± 5.13 (9)	68.0	**0.014**	4.7 ± 0.50 (9)	2.45 ± 0.19 (9)
ΣPOP$_{53}$	18.0	0.328	16.50 ± 6.95 (6)	19.06 ± 7.61 (9)	76.0	**0.0008**	11.09 ± 0.98 (9)	8.04 ± 0.75 (9)

Table 2.6 Ratios of blood-based POP compounds in boobies and frigatebirds

Mean ± SD, minimum and maximum values, and sample sizes of persistent organic pollutant (POP) ratios for compounds whose ratios are used to determine relative exposure. If an individual did not have a POP detected, a value of half the minimum detection limit was substituted for the POP concentration to calculate the ratio for that individual. NA indicates that neither POP was detected. POP compound abbreviations: DDE=dichlorodiphenyldichloroethylene; DDT=dichlorodiphenyltrichloroethane; HCH=hexachlorocyclohexane; PCB=polychlorinated biphenyl.

Colony	Barbuda	Laysan Island			Palmyra Atoll	
Species	Magnificent Frigatebird	Great Frigatebird	Masked Booby	Red-footed Booby	Brown Booby	Great Frigatebird
Compound ratio						
trans:cis-chlordane	1.3 ± 1.8	1.1 ± 0.5	NA	0.6 ± 0.6	2.1 ± 2.9	0.8 ± 0.6
	(0.01–7.0)	(0.04–1.5)		(0.07–1.33)	(1.0–9.2)	(0.1–1.2)
	15	18		4	8	3
ΣDDT_5:DDE	10.3 ± 18.8	0.3 ± 0.4	1.9 ± 1.12	1.8 ± 2.2	5.6 ± 6.9	3.5 ± 2.6
	(0.01–67.9)	(0–1.56)	(0.4–3.54)	(0–5.0)	(0–19.0)	(0.6–5.7)
	15	18	7	4	8	3
α-HCH:γ-HCH	1.9 ± 4.8	1.3 ± 0.6	NA	NA	NA	NA
	(0.01–19.0)	(0.02–2.0)				
	15	18				
ΣDDT_6:ΣPCB_{53}	6.1 ± 11.5	2.0 ± 1.13	3.3 ± 1.1	5.0 ± 4.0	3.0 ± 1.5	7.3 ± 3.9
	(0.3–44.8)	(0.5–4.1)	(2.1–4.8)	(2.1–11.0)	(0.9–5.5)	(3.6–11.4)
	15	18	7	4	8	3

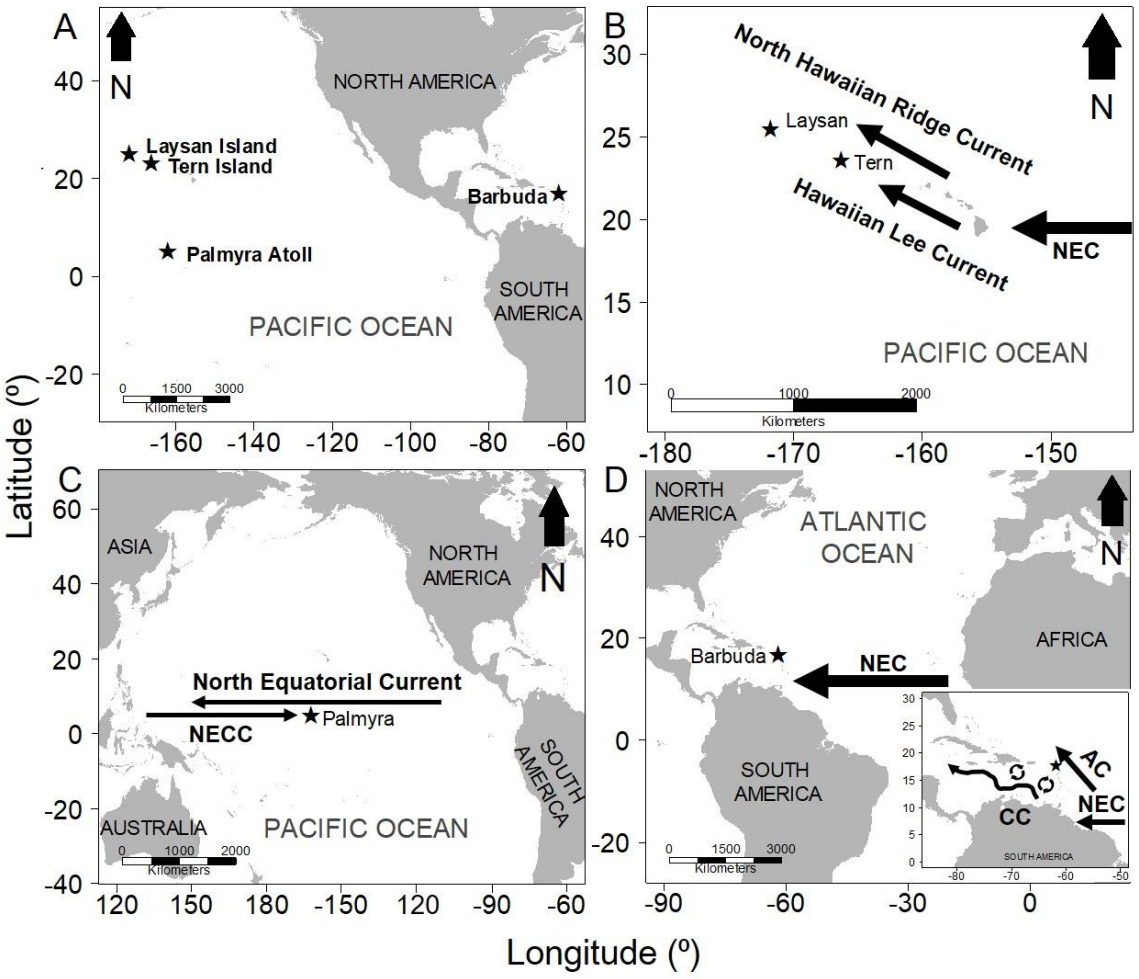

Figure 2.1 Maps of study sites of foraging ecology and contaminant measurements of boobies and frigatebirds, with major ocean currents

(A) Study sites where boobies and frigatebirds were sampled for mercury and persistent organic pollutant (POP) contaminants in 2009-2014. (B-D) Study colonies (indicated by stars) within the context of regional ocean currents (arrows). Inset in D shows Caribbean Sea currents and seasonal eddy activity (circles). Current abbreviations: NEC=north equatorial current; AC=Antilles current; CC=Caribbean current; NECC=north equatorial counter current.

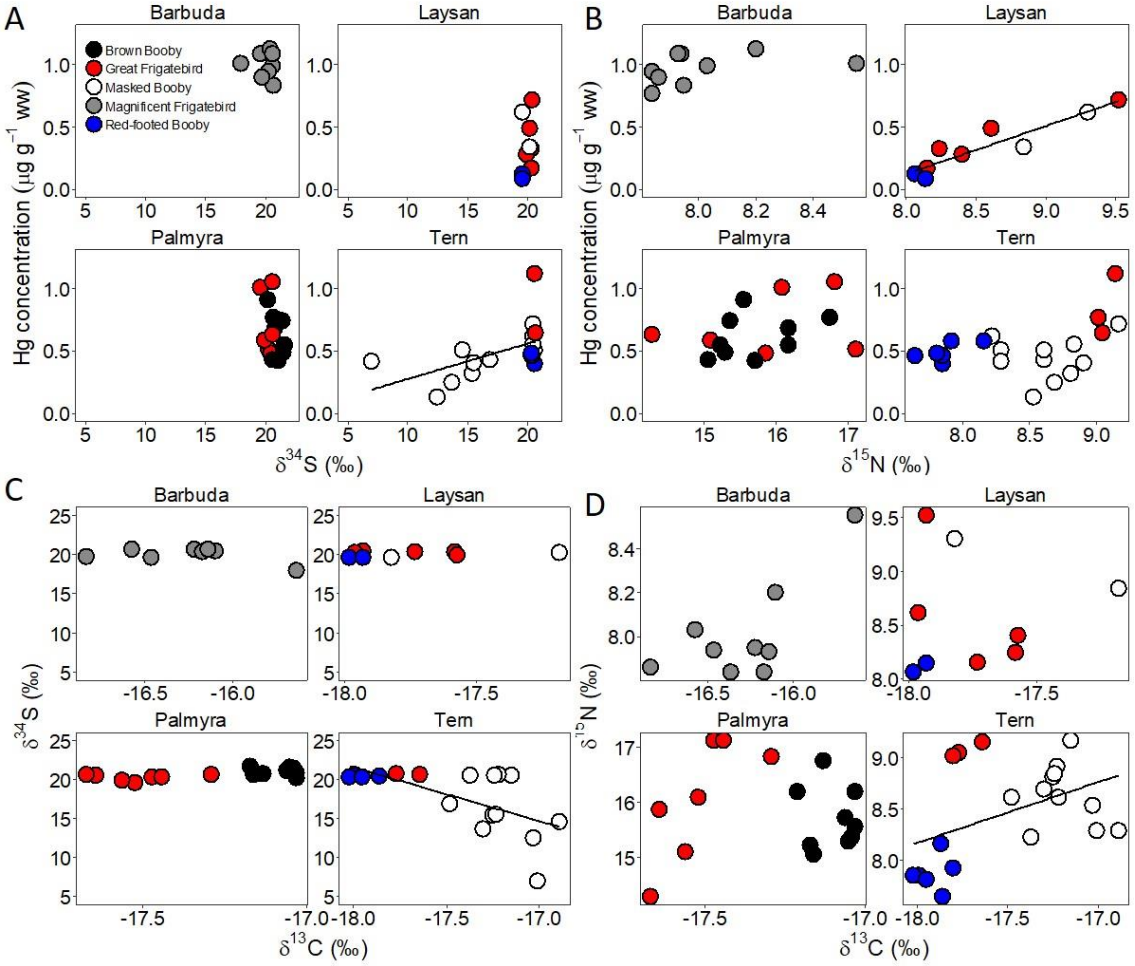

Figure 2.2 Scatterplots of blood-based mercury and carbon, sulfur, and nitrogen stable isotopes in boobies and frigatebirds

Scatterplots of total mercury concentrations (µg g^{-1}) and (A) $\delta^{34}S$ (‰) and (B) $\delta^{15}N$ (‰), and $\delta^{13}C$ (‰) and (C) $\delta^{34}S$ (‰), and (D) $\delta^{15}N$ (‰) in red blood cells (Palmyra) and whole blood (remaining colonies) from boobies and frigatebirds sampled 2009-2014. Trendlines indicate statistically significant relationship detected with Spearman Rank correlations (see Sections 2.3.1 and 2.3.2.1 for statistics).

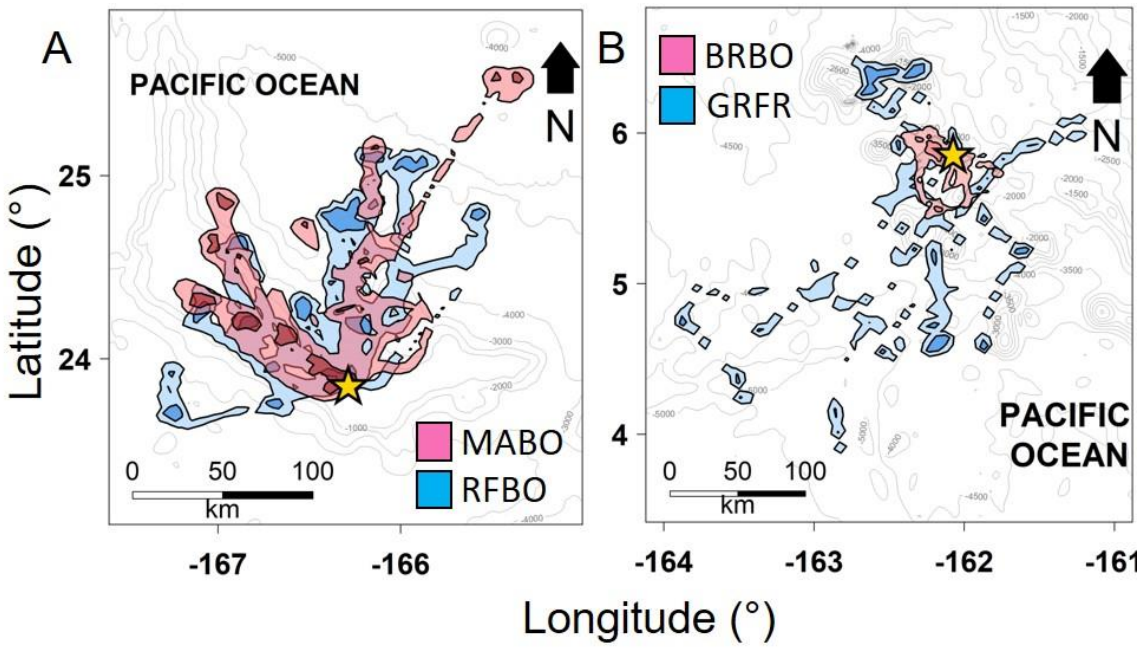

Figure 2.3 Kernel density estimates of at-sea habitat for boobies and frigatebirds

Kernel density estimates of boobies and frigatebirds during the breeding season at (A) Tern Island in 2012 (Masked Booby (MABO): 17 birds; Red-footed Booby (RFBO): 13 birds), and (B) Palmyra Atoll in 2014 (Brown Booby (BRBO): 20 trips, 7 birds; Great Frigatebird (GRFR): 9 trips, 6 birds); colonies are indicated by yellow stars. Light and dark colors correspond to 95% and 50% isopleth of kernel estimates that are considered “general use” and “core use” areas, respectively. Light gray lines delineate bathymetry.

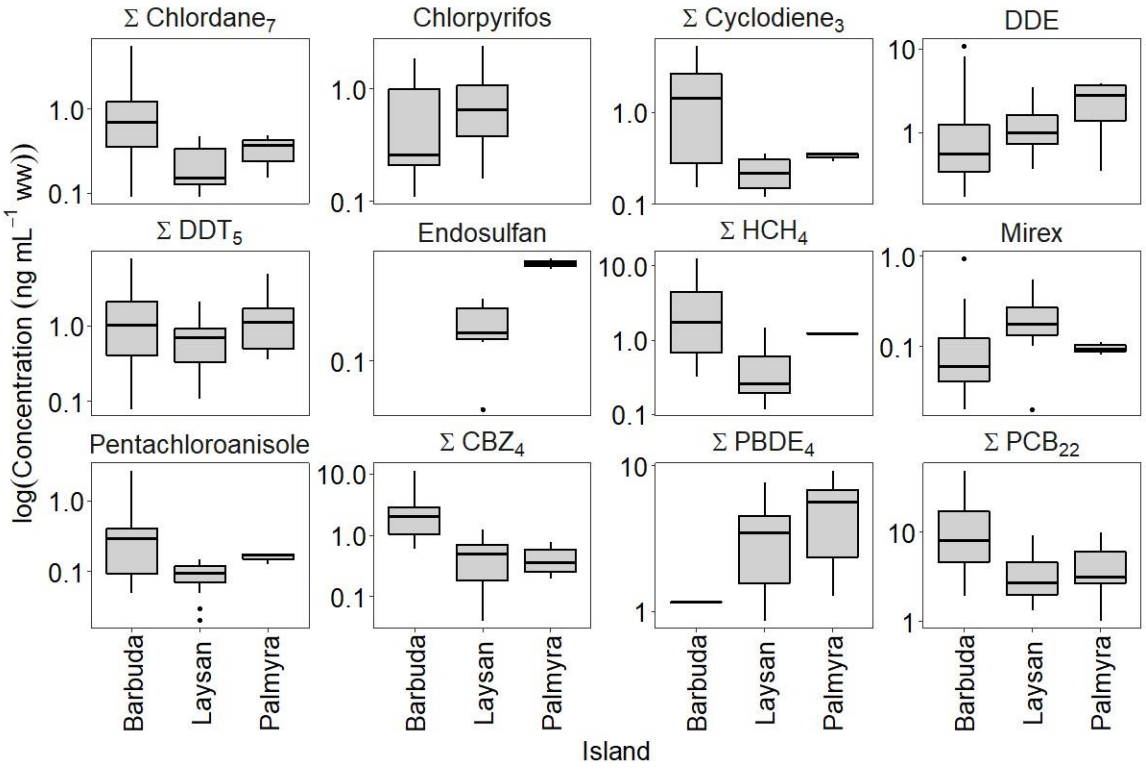

Figure 2.4 Boxplots of blood-based POP concentrations of each POP family measured in boobies and frigatebirds

Boxplots of persistent organic pollutant (log(POP); ng mL^{-1} ww) concentrations in booby and frigatebird blood samples (plasma from Palmyra Atoll; whole blood from Barbuda, Laysan, and Tern Islands) sampled 2009-2014. POP compound abbreviations: CBZ=chlorobenzene; DDE=dichlorodiphenyldichloroethylene; DDT=dichlorodiphenyltrichloroethane; HCH=hexachlorocyclohexane; PCB=polychlorinated biphenyl; PBDE=polybrominated diphenyl ether.

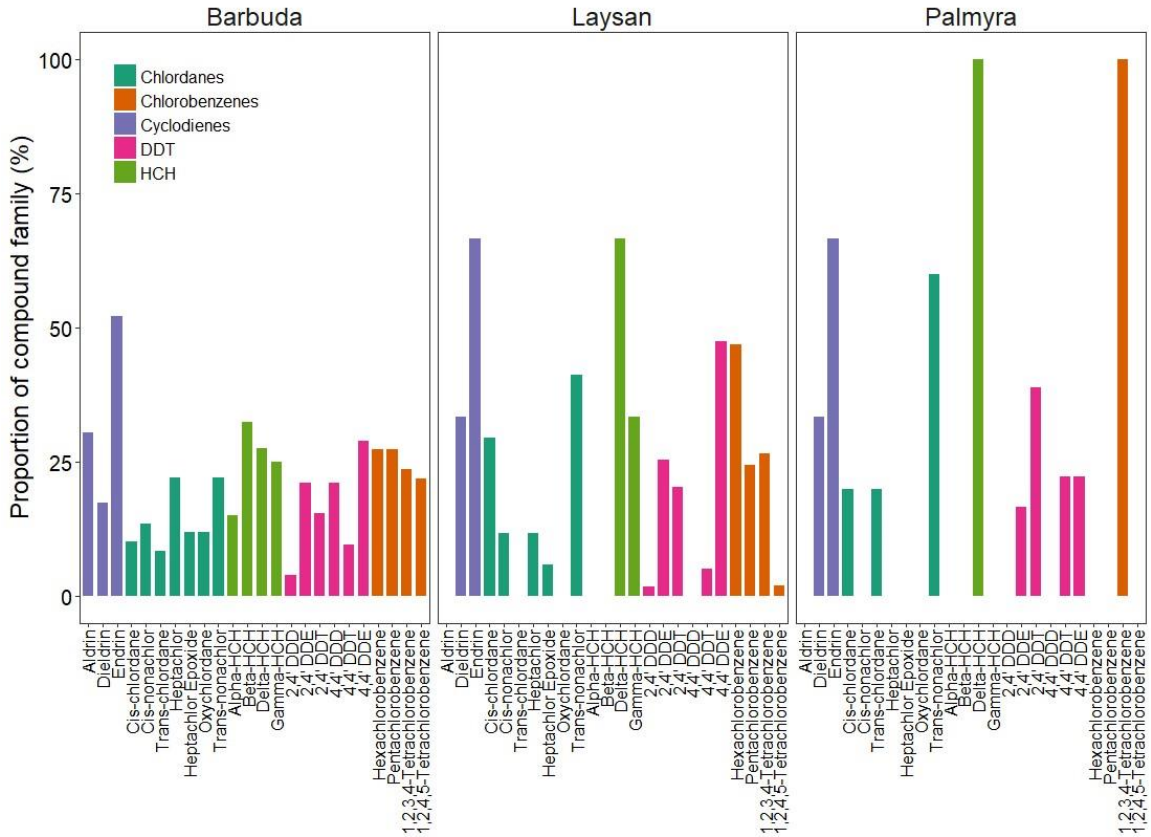

Figure 2.5 Proportional contributions of POP compounds to POP families per colony in blood-based POP concentrations measured in boobies and frigatebirds

The proportion of persistent organic pollutant (POP; ng mL^{-1} ww) compounds detected per compound family in booby and frigatebird blood samples (plasma from Palmyra Atoll; whole blood from Barbuda and Laysan Island) sampled 2009-2014. Family abbreviations: DDT= dichlorodiphenyltrichloroethane, HCH= hexachlorocyclohexane. Compound abbreviations: DDD= dichlorodiphenyldichloroethane, DDE= dichlorodiphenyldichloroethylene.

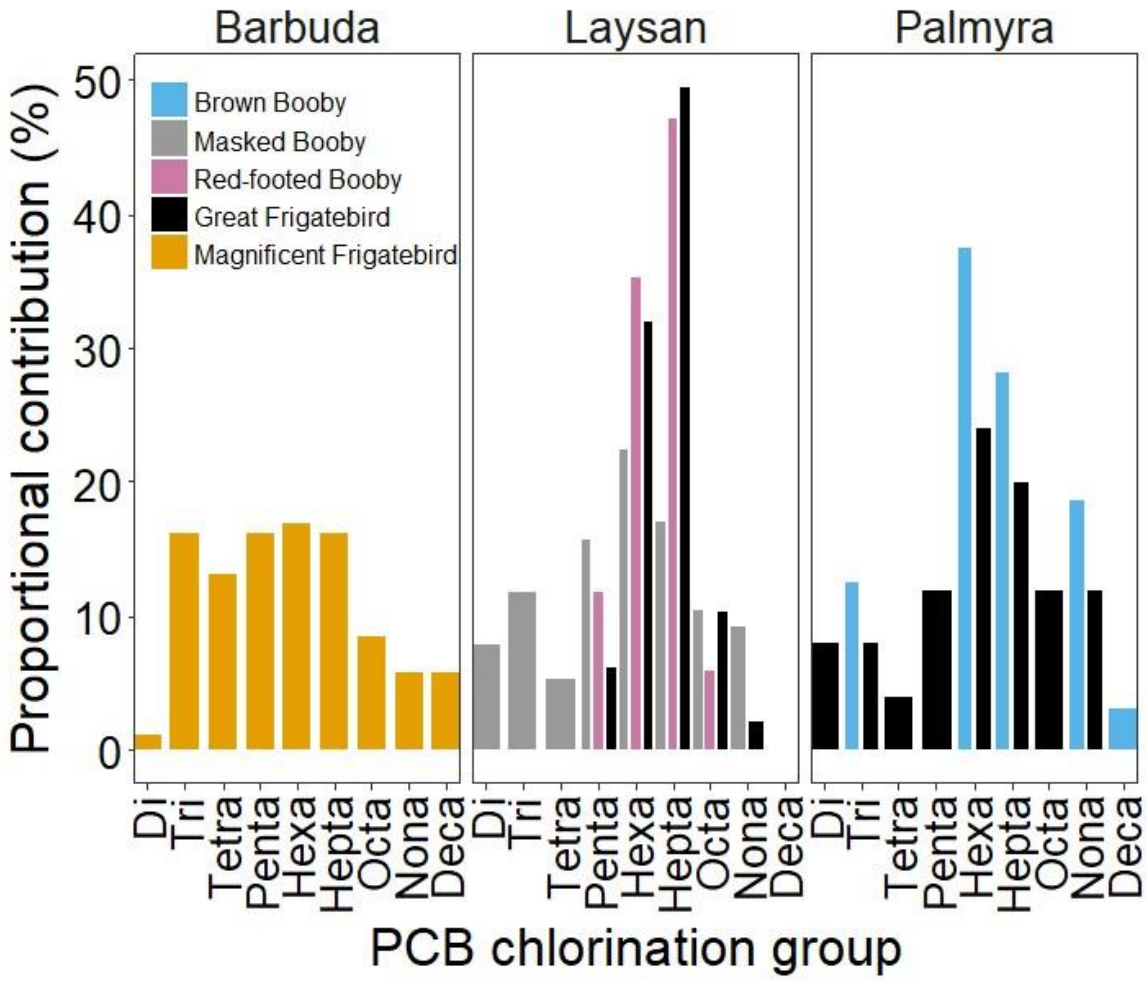

Figure 2.6 Proportional contributions of PCB congeners to ΣPCB_{22} per colony and species in blood-based POP concentrations measured in boobies and frigatebirds

The proportional contributions of each of nine polychlorinated biphenyl (PCB) congeners in booby and frigatebird blood samples (plasma from Palmyra Atoll; whole blood from Barbuda and Laysan Island) sampled 2009-2014.

Chapter 3

Does mercury impact seabirds' breeding physiology? A case study of two sympatric species

Morgan E. Gilmour

Abstract

Anthropogenic contaminants are ubiquitous, and the ocean is a sink for many compounds. Marine predators are frequently exposed to contaminants through their diet, and so consideration of foraging ecology is important to assess exposure to contaminants like mercury, which biomagnifes in foodwebs. Mercury's neurotoxic and endocrine-disrupting effects can have far-ranging consequences for both individuals and populations. However, mercury concentration thresholds and the effects of mercury vary between species. Mercury concentrations in top marine predators like seabirds are often elevated because many species forage on vertically-migrating fishes and squid, which have high mercury concentrations; yet, the links between seabirds' foraging ecology, mercury exposure, and adverse effects are under-studied. Here, I investigated foraging ecology via carbon and nitrogen stable isotopes and GPS-tracking, mercury exposure, and breeding physiology via the hormone prolactin and egg volume, in two seabird species that exhibit different foraging strategies: Flesh-footed Shearwaters (*Ardenna carneipes*) are coastal foragers that associate with fishing vessels, and are a species listed as Vulnerable in Western Australia; Great-winged Petrels (*Pterodroma macroptera*) are pelagic squid-specialists whose populations are under-studied. Great-winged Petrels foraged in inshore and offshore habitats on prey that was more enriched in $\delta^{15}N$ than coastal feeding Flesh-footed Shearwaters. Mercury was five times higher in Great-winged Petrels' blood (median ± SE: 3.670 ± 0.180 μg g^{-1} ww, n=15) than Flesh-footed Shearwaters (0.625 ± 0.109 μg g^{-1} ww, n=12), supporting the view that foraging ecology plays a central role in mercury exposure. Furthermore, Great-winged Petrels' mercury concentrations are among the highest reported in seabirds. However, no relationships between mercury and either reproductive parameter were detected. Mercury may affect other aspects of reproduction that I did not measure. Overall, these results provide a snapshot of mercury exposure in marine predators in the temperate and coastal waters

south of Western Australia, and stress the importance of considering foraging ecology in marine predators when sampling species for contaminants.

3.1 Introduction

Exposure to contaminants like mercury varies between environments and species due to differences in habitat types, diets, and physiology. This is problematic because mercury is ubiquitous, and has well-documented adverse effects on both humans and wildlife. Because mercury can cause adverse effects, the extent of mercury exposure may dictate the severity of effects experienced between organisms. These adverse effects include neurotoxicity, altered gene expression, and inhibited or reduced reproduction (Burgess and Meyer, 2008; Ceccatelli et al., 2010; Frederick and Jayasena, 2011; Grandjean et al., 1997; Sweet et al., 2006). Therefore, consideration of organisms' habitats and diets are imperative to understanding mercury exposure, which could then facilitate a better understanding of the extent of the potential for mercury's adverse effects in individuals (e.g. neurotoxicity and gene expression) and populations (e.g. reproduction).

Many organisms are exposed to mercury through their diet. Inorganic mercury originates from industrial emissions from coal combustion and from natural sources (e.g. volcanoes; Driscoll et al., 2013; Pacyna et al., 2010,). Inorganic mercury then deposits into the ocean where microbes transform it in biochemical reactions (Blum et al., 2013; Hammerschmidt and Fitzgerald, 2004), and where it can also adsorb to plastic marine debris (Graca et al., 2014; Turner, 2018). Mercury enters foodwebs via the methylated form, methyl-mercury (MeHg), which is synthesized in sediments, and throughout the water column (Blum et al., 2013; Hollweg et al., 2010; Sunderland et al., 2009). Once absorbed, MeHg is difficult for organisms to depurate, and it therefore accumulates in tissues, and biomagnifies with increasing age, size, and trophic position (Bank et al., 2007; Cai et al., 2007; Kojadinovic et al., 2007). MeHg concentrations are especially high in the mesopelagic layer (~400 – 1000 m deep; Blum et al., 2013), and predators that forage on organisms from these depths exhibit elevated MeHg concentrations (Monteiro et al., 1996; Peterson et al., 2015). Long-lived predators that forage at high trophic levels are thus potentially exposed to large MeHg

concentrations over their lifetimes. Due to the high incidence of plastic ingestion by marine organisms (Bravo Rebolledo et al., 2013; Lusher et al., 2018; Rapp et al., 2017; Rummel et al., 2016; Schuyler et al., 2014), exposure to contaminants like mercury adsorbed to plastic litter could further compound individuals' body burdens (e.g. Tanaka et al., 2013; Lavers et al., 2014). Because MeHg synthesis varies between habitats due to differential input of inorganic mercury sources (Mason et al., 2012), and because MeHg concentrations vary with trophic position (Campbell et al., 2005), knowledge of animals' foraging ecology is helpful to assess MeHg exposure, which can then help to assess the extent of adverse effects of MeHg.

Dietary exposure to mercury is of global concern in part because mercury is an endocrine-disruptor. MeHg has a high affinity for adrenal and reproductive organs and hormones, and these associations disrupt the hypothalamus-pituitary-adrenal and hypothalamus-pituitary-gonadal pathways, thereby altering or inhibiting hormone synthesis and changing behaviors (Tan et al., 2009). Consequently, complex relationships between MeHg and hormone concentrations have been observed (Oliveira et al., 2006; Tartu et al., 2013). For example, male, but not female, birds had negative relationships between hormones and MeHg concentrations (Tartu et al., 2013; Tartu et al., 2015a; Tartu et al., 2015b). Differences between sexes were also observed in an Arctic seabird, the Black-legged Kittiwake (*Rissa tridactyla*), where mercury concentrations were higher in males that successfully raised two chicks than males that successfully raised only one chick (Tartu et al., 2015b). Variable and non-linear interactions between MeHg and reproductive hormones and behaviors among species and between sexes suggest that the relationships between mercury, foraging ecology, and breeding physiology require more attention. Because the ocean is a sink for mercury (Driscoll et al., 2013), and biomagnification pathways increase MeHg exposure at high trophic positions, investigation of these relationships in a marine top predator would illuminate MeHg processes in the marine foodweb, and the relationships between MeHg and physiological processes within species.

Seabirds are top predators that can act as sentinels of the ocean environment because they integrate resources (e.g. diet) across spatial scales ranging from tens to thousands of kilometers (Piatt et al., 2007; Young et al., 2010), and seabirds are long-lived and exposed to potentially high concentrations of MeHg over their lifetimes (Burger and Gochfeld, 2004; Elliott and Elliott, 2013). Therefore, a study of seabird foraging ecology, MeHg concentrations, and physiology should provide insight into the interactions of these processes. Due to the endocrine-disrupting nature of MeHg, which has well-known and documented adverse relationships on many hormones, especially reproductive hormones (Tan et al., 2009), it is critical to consider the interactions of MeHg and reproductive physiology in these seabird sentinels. To better understand these relationships, mercury concentrations were measured in conjunction with two aspects of seabirds' reproductive physiology: concentrations of the pituitary hormone prolactin; and egg volume. Prolactin is a hormone that is involved in the expression and maintenance of parental behaviors in birds (Buntin et al., 1991; Smiley and Adkins-Regan, 2018; Vleck et al., 2000). Prolactin is especially important for seabird species that undergo long incubation shifts because one parent fasts on the nest while their mate forages at-sea for up to several weeks at a time, and prolactin induces the fasting parent to remain on the nest (e.g. Cherel et al., 1994). Prolactin concentrations are thus expected to be the highest during the incubation period (Angelier et al., 2016). Mercury concentrations have been negatively correlated with prolactin concentrations (Tartu et al., 2015a; Tartu et al., 2015b). Similarly, mercury concentrations have also been negatively correlated with egg size (Fort et al., 2014; Olivero-Verbelet al., 2013), egg shape (Lundholm, 1995), egg volume (Evers et al., 2003) and egg color (Barr, 1986), suggesting that Hg may disrupt egg formation. Egg volume has been correlated with chicks' body mass, suggesting that egg volume is an important factor for developing offspring (Karell et al., 2008). Due to these previously established relationships, and mercury's role as an endocrine disruptor, I predicted that there would be a negative relationship between mercury and prolactin concentrations and between mercury and egg volumes in seabirds.

To assess relationships between mercury exposure and breeding physiology in seabirds, I measured mercury concentrations, assessed foraging ecology via stable isotopes and GPS-tracking, and measured prolactin concentrations and egg volumes in two seabird species that have different foraging ecologies and thus potentially different mercury exposures. Flesh-footed Shearwaters (*Ardenna carneipes*) and Great-winged Petrels (*Pterodroma macroptera*) breed in south Western Australia during the summer and winter, respectively. Stable isotopes provide information about marine foraging habitat ($\delta^{13}C$, inshore vs offshore; Graham et al., 2010) and trophic position ($\delta^{15}N$; Hobson, 1993). Great-winged Petrels mainly forage on squid (Cooper and Klages, 2009; Falla, 1934; Marchant and Higgins, 1990; Ridoux, 1994; Schramm, 1986), and have long incubation shifts (up to 17 days; Imber, 1976), indicating that they forage in pelagic regions far from the breeding colony. Conversely, Flesh-footed Shearwaters forage nearshore on sardines (Powell, 2009) and follow fishing boats, leading to high incidences of fisheries by-catch (Dunlop, 2008; Lavers, 2015; Thalman et al., 2009). GPS-tracking devices are an additional tool to determine foraging ranges and locations in many marine predators, including seabirds (e.g. Young et al., 2015). Recent population surveys have observed that the Western Australia population of Flesh-footed Shearwaters is declining (Lavers, 2015). These factors have led to Flesh-footed Shearwaters listed as a “vulnerable” species by the Western Australia government (Western Australia Government, 2015). Because Flesh-footed Shearwaters and Great-winged Petrels exhibit varying foraging ecologies and declining and unknown population trends, respectively, the measurement of mercury and its relation to breeding physiology could provide information about potential factors that affect productivity and population trends in these species. Contaminants like mercury are ubiquitous in the environment (Pacyna et al., 2010), and assessment of mercury in two sentinel seabird species that exhibit inshore and offshore foraging strategies provided an opportunity to sample the dynamic ocean surrounding south Western Australia. Therefore, the objectives of this study were to: 1) measure blood mercury concentrations to establish baseline levels; 2) compare mercury concentrations between

species to establish exposure risk; 3) assess the foraging ecology of each species because contaminants in seabirds are derived from diet; and 4) assess the extent to which mercury exposure may affect reproduction with concurrent measurements of the breeding hormone prolactin, and egg volume.

3.2. Methods

3.2.1 Sampling locations and study species

Blood samples were collected from Great-winged Petrels and Flesh-footed Shearwaters during the late-incubation breeding phase at Breaksea Island and Shelter Island in July and December 2015, respectively. Breaksea Island (35.0642°S, 118.0577°E; 100 ha) is located in eastern King George Sound, 12 km offshore of Albany, Western Australia and has a breeding population of <100 pairs of Great-winged Petrels (Marchant and Higgins 1990; MEG, pers obs). Shelter (Muttonbird) Island (35.0515°S, 117.6935°E; 2.7 ha) is located 130 m offshore of Torbay, Western Australia and has a breeding population of approximately 200 pairs of Flesh-footed Shearwaters (Lavers, 2015).

Birds were captured by hand from their nesting burrows. Approximately 1 mL of blood was sampled from the brachial vein by a 25G needle and plastic syringe, transferred into polypropylene Eppendorf tubes (Eppendorf North America, Hauppauge, New York, USA), and kept cold for 6–8 hr. Blood was centrifuged for 1 min at 2200X g and then separated into plasma and red blood cell factions by pipette. Plasma for prolactin analysis and red blood cells for mercury, stable isotope analyses, and molecular sex determination were stored in polypropylene Eppendorf tubes; all samples were stored at -20°C until analyses. The lengths and breadths of eggs were measured to the nearest 0.1 mm with calipers, and egg volume was determined following Hoyt (1979).

Foraging movements were recorded with GPS tracking tags (GPS CatTrack1, Catnip Technologies, Anderson, South Carolina, USA). Tags were encapsulated in polyolefin for

waterproofing. The total tracking package mass was 22 g, which was 3.8 and 4.3% of the body mass of Flesh-footed Shearwaters (633.8 ± 64.0 g, n=16) and Great-winged Petrels (mean mass: 512.8 ± 49.6 g, n=20), respectively. Tags were taped to the central 3-4 tail feathers at the base of the upper tail with waterproof tape (Tesa #4651, Hamburg, Germany). Tags were programmed to record latitude and longitude at five-minute intervals with data stored to internal memory and downloaded when the unit was recovered. Six tags were deployed on Flesh-footed Shearwaters, and nine tags were deployed on Great-winged Petrels.

3.2.2 Molecular sex determination

Molecular sex determination was used to identify female and male petrels and shearwaters at the University of Tennessee School of Veterinary Medicine. Briefly, red blood cells were digested with lysis buffer and proteinase K; DNA was isolated via ethanol precipitation; and sex-specific markers were amplified and visualized with modified PCR protocols (Boutette et al., 2002). The sexes of 12 out of 14 Great-winged Petrels and all 12 Flesh-footed Shearwaters were determined molecularly; the sexes of two Great-winged Petrels could not be determined.

3.2.3 Mercury analysis

Red blood cells were analyzed for total mercury (THg) concentrations at the University of California Santa Cruz. Blood was analyzed for THg because avian blood mercury concentrations are composed of nearly all methylmercury (Rimmer et al., 2005). Frozen blood samples were thawed at room temperature. Liquid blood was pipetted into quartz sample boats, and samples were weighed to achieve a mass that ranged 0.02–0.03 g to the nearest 10^{-5} g with a Sartorius microbalance (Brinkman Instruments, Inc., Westbury, NY, USA). Samples were analyzed for THg content by thermal decomposition, catalytic

conversion, amalgamation, and atomic absorption spectrophotometry (DMA-80, Milestone, Shelton, CT, USA), according to U.S. E.P.A. Method 7473 (2007). Quality assurance/quality control procedures included analysis of a method blank every ten samples; analysis of two standard reference materials (SRM 320R-Channel sediment, and SRM 414-plankton, European Commission Community Bureau of Reference, Belgium); and a duplicate sample. Minimum detection limits were defined as three times the concentration of blank samples; the minimum detection limit was 1.86 X 10^{-3} µg g^{-1} ww.

3.2.4 Prolactin analysis

Plasma samples were analyzed for prolactin concentration following (Chastel et al., 2005; Tartu et al., 2015b) at Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, France. Briefly, plasma prolactin concentrations were determined by heterologous radioimmunoassay. Pooled samples of petrels and of shearwaters each produced a separate species-specific dose response curve that paralleled chicken prolactin standard curves (AFP 4444B, Dr. Parlow, N.H.P.P. Harbor-UCLA Medical Center, Torrance, CA, USA). The parallelism observed between the petrel and shearwater curves and the chicken curve indicated that the concentration-dependent binding dynamics of the petrel and shearwater prolactin with the antibody were similar to the binding dynamics of the chicken prolactin, and thus that radioimmunoassay could be used to assess relative levels of plasma prolactin in Great-winged Petrels and Flesh-footed Shearwaters. The intra-assay coefficient of variation was 10.9% and 7.07% for Great-winged Petrels and Flesh-footed Shearwaters, respectively (n=4 duplicates for each species).

3.2.5 Stable isotope analyses

Red blood cells were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Light Stable Isotope Lab at the University of California Santa Cruz. Red blood cells represent diet integrated into blood over

the previous one month prior to sampling (Hahn et al., 2012; Hobson and Clark, 1993). The ratio of C:N in the sample can also be used as a proxy for dietary lipids (Post et al., 2007). Briefly, red blood cells were dried for 48 h and weighed into tin capsules to achieve a mass of 0.7-0.9 mg, to the nearest 10^{-6} g with a Sartorius microbalance (Brinkman Instruments, Inc., Westbury, NY, USA). Samples were then analyzed with an EA 1108 Carlo Erba Elemental Analyzer coupled with a ThermoFinnigan Delta Plus XP mass spectrometer (Thermo Fisher Scientific). Stable isotope ratios are expressed in standard delta (δ) notation in parts per thousand (‰) as relative to international standards Vienna Pee Dee Belemnite for carbon and air for nitrogen as: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Acetanilide was used as a standard, and the SD for $\delta^{13}C$ was 0.15‰ and the SD for $\delta^{15}N$ was 0.17‰. An in-house standard (Pugel) was used to calculate the average experimental precision for isotope samples with the mean of the SD among all isotope runs: $\delta^{13}C$ = 0.29‰; $\delta^{15}N$ = 0.36‰.

3.2.6 Statistical analyses

Non-parametric Mann-Whitney tests were used to examine differences in stable isotope values, prolactin, and THg concentrations between species and sexes; due to the uneven sample sizes of sex in Flesh-footed Shearwaters (11 females and one male), sex-based differences were only tested in Great-winged Petrels. All analyses were conducted in the program R (R Core Team, 2016, version 3.3.2). All data are presented as median ± SE unless otherwise noted.

3.3. Results

3.3.1 Total mercury (THg)

THg was significantly higher in Great-winged Petrels (median ± SE: 3.670 ± 0.180 μg g^{-1} ww, n=15) than Flesh-footed Shearwaters (0.625 ± 0.109 μg g^{-1} ww, n=12; Mann-Whitney U test:

W=0, p<0.001; Fig. 3.1). THg was not different between male and female Great-winged Petrels. Flesh-footed Shearwater THg concentrations were within the range of THg concentrations of other seabird species, but Great-winged Petrel THg concentrations were much higher (Fig. 3.2).

3.3.2 Foraging ecology

3.3.2.1 Stable isotopes

Great-winged Petrels had significantly more enriched $\delta^{15}N$ values (14.31 ± 0.12 ‰, n=14) than Flesh-footed Shearwaters (12.00 ± 0.16 ‰, n=11; Mann-Whitney U test: W=0, p<0.0001). There was more variation in $\delta^{13}C$ values in Great-winged Petrels (SD=0.27), whereas the distribution of $\delta^{13}C$ in Flesh-footed Shearwaters was tighter (SD=0.14; Fig. 3.3). $\delta^{13}C$ and $\delta^{15}N$ values were not different between male and female Great-winged Petrels. Great-winged Petrels (3.10 ± 0.05 ‰, n=14) had significantly higher ratios of carbon to nitrogen than Flesh-footed Shearwaters (3.00 ± 0.04 ‰, n=11; Mann-Whitney U test: U=30, p=0.007). There were no relationships between $\delta^{13}C$, $\delta^{15}N$, or C:N and mercury or prolactin concentrations.

3.3.2.2 GPS-tracking

All six GPS tags were recovered from Flesh-footed Shearwaters; four of nine tags were recovered from Great-winged Petrels. Data from five of the Flesh-footed Shearwater tags indicated that the birds remained in their burrows, incubating their egg for seven consecutive days. Data from the sixth tag (a male) contained one foraging trip: the bird spent 19.5 hours at-sea (Fig. 3.4) before returning to its burrow at dusk where it remained for the next five days. Data from three of the Great-winged Petrel tags indicated that the birds remained in their burrows, incubating their egg for eight consecutive days. Data from the fourth tag (a male) contained two foraging trips (Fig. 3.4): one long (5 d) trip that traveled up to 400 km

from Breaksea Island, and a shorter (2 d) trip that went 100 km from Breaksea Island. Of the five Great-winged Petrel tags that were not recovered: four nests contained the mate of the tagged bird, indicating that the tagged bird was out at sea; and the last nest was empty, indicating that that nest had failed during the previous eight days from an unknown cause.

3.3.3 Breeding ecology

Prolactin concentrations varied widely in Flesh-footed Shearwaters (SD=19.0) but were more tightly distributed in Great-winged Petrels (SD=13.6; Fig. 3.5A). Prolactin concentrations were significantly larger in female Great-winged Petrels (41.8 ± 4.5 ng mL^{-1}, n=7) than males (23.7 ± 3.0 ng mL^{-1}, n=5; Mann-Whitney U test: W=90, p=0.005). There was no relationship between THg and prolactin concentrations in either species. The mean (± SD) of egg volume for Flesh-footed Shearwaters was 113.0 ± 14.8 cm^3 (n=6) and for Great-winged Petrels was 107.9 ± 6.3 cm^3 (n=4). There were no relationships detected between egg volume and either THg or prolactin concentrations in either species (Fig. 3.5). THg concentrations for Flesh-footed Shearwaters and Great-winged Petrels were within the range of THg values measured in other studies that observed negative correlations between THg and reproductive parameters (Table 3.1).

3.4. Discussion

Interspecific differences in foraging ecology likely drove differences in mercury exposure between Flesh-footed Shearwaters and Great-winged Petrels breeding in southwestern Australia. THg concentrations were five times greater in Great-winged Petrels than Flesh-footed Shearwaters. Differences in foraging ecology were distinct: Great-winged Petrels foraged on prey that were more enriched in $\delta^{15}N$ than Flesh-footed Shearwaters, and variation in $\delta^{13}C$ isotope values indicated that within species, Flesh-footed Shearwaters foraged in similar habitats to each other, but Great-winged Petrels foraged in habitats that

were more variable (Graham et al., 2010). The agreement between the Great-winged Petrel stable isotope values and the tracking data illustrate that the petrels foraged in diverse environments. Furthermore, the tracking data from this individual represents the only published movement data for this species and demonstrates the high value of data obtained from one individual (Sequeira et al. in review). Taken together, these data highlight that diet and foraging regions are important factors of THg exposure in marine species. No relationship was detected between prolactin concentrations or egg volume and THg concentrations in either species, but small sample sizes may have masked any relationships. Additionally, it is possible that other breeding behaviors and hormones not measured in this study may be impacted by THg in these seabirds. Given the established negative relationships between mercury and health, including neurotoxicity, developmental and reproductive impairment, and mortality, the baselines that I established for these species highlight the need to consider foraging ecology in relation to contaminant exposure, and that contaminant exposure in many organisms, especially top predators, is likely complex, and the effects may not be apparent during a short sampling period.

3.4.1 THg exposure via foraging ecology

Great-winged Petrels had significantly higher THg than Flesh-footed Shearwaters; a difference that was likely driven by inter-specific differences in foraging ecology. Flesh-footed Shearwaters are shallow divers that hunt their prey underwater, and rely heavily on Australian pilchards (*Sardinops sagax*), a shallow-dwelling schooling fish, and other low trophic level prey (Gould et al., 1997). Flesh-footed Shearwaters also frequently associate with fishing vessels in Western Australia (Lavers, 2015) and throughout the Pacific Ocean (Thalman et al., 2009). Conversely, Great-winged Petrels are surface-feeders that mainly eat squid (Cooper and Klages, 2009; Falla, 1934; Marchant and Higgins, 1990; Ridoux, 1994; Schramm, 1986). Great-winged Petrels had significantly more enriched $\delta^{15}N$ than Flesh-

footed Shearwaters, suggesting that these petrels fed on higher trophic level prey like squid (Navarro et al., 2013). Great-winged Petrels also had significantly higher C:N ratios than Flesh-footed Shearwaters, indicating a larger proportion of lipids in their diet (Post et al., 2007). The range of Flesh-footed Shearwater $\delta^{13}C$ values was very small, suggesting that individuals foraged in a similar region to each other, supporting observations that this species forages exclusively nearshore (Lavers et al., 2018; Powell, 2009). Slightly more variable $\delta^{13}C$ values and tracking data of Great-winged Petrels suggested that this species foraged both on the continental shelf and offshore, similar to foraging observations of this species in other regions (Camphuysen, 2007; Imber, 1973).

Mercury is patchily distributed in the marine environment (Mason et al., 2012) and the habitats in which Flesh-footed Shearwaters and Great-winged Petrels foraged in southern Australia likely contained both point sources of mercury, and bacteria that methylate mercury throughout the water column. In Western Australia, there are only historical point sources of inorganic Hg in industrial municipalities, including a fertilizer plant in Albany (the closest city to the study colonies; (Jackson et al., 1986) and agricultural, mining, shipping, and dredging activities (Western Australia Environmental Protection Authority, 2007; Australian Government, 2012). Therefore, terrestrial point sources of inorganic Hg from coastal Australia are likely limited in this region. In-situ methylation of mercury is a more likely source to the marine foodwebs in which seabirds in southern Australia forage. Biological and oceanographic factors contribute to these MeHg distributions. For example, because MeHg is thought to be mainly synthesized by bacteria, the distribution of MeHg is dependent on population sizes of sulfate-reducing bacteria (which change seasonally; Hammerschmidt and Fitzgerald, 2004), the availability of inorganic Hg (Hammerschmidt et al., 2004; Hammerschmidt and Bowman, 2012), and the availability of organic matter, because Hg methylation requires a substrate such as sediment (Hammerschmidt and Fitzgerald, 2004; Hollweg et al., 2010) or particles and dissolved organic matter throughout the water column (Hammerschmidt and Bowman, 2012). Additionally, inorganic Hg is remineralized from

sinking organic matter, and this remineralization process also produces MeHg (Sunderland et al., 2009). Therefore, each of these processes could potentially influence MeHg exposure to predators that forage at different spatial and temporal scales.

Due to inter-specific differences in diet, and seasonal variations in the amount of organic matter, bacteria population sizes, and ocean currents in southern Australia, it is possible that diet items of summer-foraging Flesh-footed Shearwaters and winter-foraging Great-winged Petrels are exposed to differing amounts of MeHg. The prey of Great-winged Petrels include nocturnal vertically migrating mesopelagic fishes and high trophic level squid (Imber, 1973; Navarro et al., 2013) that may have high MeHg concentrations (Anderson et al., 2009; Monteiro et al., 1996). High rates of mercury remineralization occur at depth in the mesopelagic layer (Sunderland et al., 2009) where remineralization in general is greatest (Fitzgerald et al., 2007), giving rise to higher MeHg concentrations and therefore higher MeHg availability to predators via plankton grazing and subsequent biomagnification at these depths (Monteiro et al., 1996). The lower trophic level pilchards along the continental shelf on which Flesh-footed Shearwaters forage extensively may subsequently contain much smaller MeHg concentrations (e.g. Finger et al. 2017). Seasonal oceanographic differences may also affect productivity, which may then affect MeHg availability. For example, seasonal changes in oceanic and atmospheric currents can induce upwelling, which bring nutrients to surface waters that enhance primary productivity and organic matter production. Primary productivity enhances food availability (Mannocci et al., 2014; Polovina et al., 2001) and increases the amount of organic matter available as a substrate for inorganic Hg methylation (Sunderland et al., 2009). During the summer, Flesh-footed Shearwaters foraged in nearshore waters (Powell 2009, Lavers et al. 2018) that are influenced by a weak Leeuwin Current and continuous southerly winds that enable localized upwelling on the continental shelf, so primary productivity is generally high (Hanson et al., 2005; Middleton and Cirano, 2002). Conversely, in the winter, Great-winged Petrels foraged both inshore and offshore, where the Leeuwin Current is strong and there is high regional eddy activity, but primary production is

generally low due to reduced light attenuation (Hanson et al., 2005). Therefore, seasonal changes in primary productivity may not be a good predictor of MeHg exposure in the ocean near south Western Australia, and inter-specific differences in diets may be more informative (e.g. Anderson et al., 2009).

3.4.2 THg & breeding ecology

No relationships were detected between THg and prolactin concentrations or females' egg volumes in either Flesh-footed Shearwaters or Great-winged Petrels. Given that the Great-winged Petrels' THg levels were high, this result was surprising. Several factors may explain these results. First, it is possible that Hg affected breeding physiology parameters that were not measured in this study. For example, egg volume and prolactin concentrations have been associated with chick growth and survival (Bolton, 1991; Christians 2002), and overall breeding success (Angelier et al., 2016), respectively. Because Hg affected chick growth and survival and breeding success in other studies (Burgess and Meyer, 2008; Goutte et al., 2014a; Goutte et al., 2014b; Tartu et al., 2013; Tartu et al., 2014), long-term measurements of these parameters over the course of the breeding season could provide information on temporal trends of Hg in relation to reproductive effort and success. Given changes in seabirds' diet and thus THg exposure throughout the breeding season (Lavoie et al., 2014; Lerma et al., 2016), studying additional reproductive parameters (e.g. hatch success; chick growth; fledging success) would be helpful to assess the potential for negative THg impacts over a longer time period. Second, THg may have interacted with other hormones and compounds, thereby masking any direct relationship with prolactin and egg volume. Mercury has an affinity for sulfhydryl groups, which can disrupt antioxidant activity of enzymes like glutathione (Rooney, 2007). The hormones testosterone and estradiol modulate metabolism of glutathione in the liver and kidneys, which regulates retention and excretion of mercury in these tissues (Hirayama et al., 1987; Malagutti et al., 2009). Mercury also binds to lutenizing

hormone, which may have disrupted the hypothalamus within the hypothalamus-pituitary-gonadal axis in another seabird, Black-legged Kittiwakes (Tartu et al., 2013). Prolactin secretion is also affected by other hormones: the antagonist actions of dopamine also regulate prolactin secretion, and thus prolactin may be under control of multiple factors that may be difficult to disentangle (Freeman et al., 2000). Because of the non-linear interactions between many hormones and compounds, it is likely that a direct correlation between mercury and hormones like prolactin may be difficult to observe. Third, the threshold of contaminant concentration required to provoke a relationship with prolactin could be much higher than the THg concentrations observed in the current study; however, studies that observed relationships between THg and prolactin had much lower THg concentrations (Tartu et al., 2013; Tartu et al., 2015b). Similarly, comparable or higher THg concentrations were observed in other studies that had nonsignificant results between THg and breeding behaviors (Carravieri et al., 2014; Pollet et al., 2017; Tartu et al., 2013). Because mercury methylation is high in the mesopelagic zone (Sunderland et al., 2009), organisms that forage on mesopelagic prey may have evolved to tolerate high concentrations of MeHg (Thompson, 1996). For example, some species use selenium to detoxify MeHg in the liver, which may enable a greater tolerance of elevated THg concentrations (Campbell et al., 2005; Ikemoto et al., 2004). However, with a global increase in anthropogenic Hg into the atmosphere and ocean (Lamborg et al., 2014), organisms not adapted to elevated concentrations may be more at risk to mercury toxicity because they do not have well-developed MeHg detoxification mechanisms (e.g. Thompson, 1996). Taken together, these results suggest that interactions between THg and reproductive hormones and behaviors are not linear, and may be dose-dependent. Inter-specific differences in THg exposure and detoxification mechanisms may also be important factors for investigating the endocrine-disrupting potential of THg and other contaminant compounds.

Prolactin concentrations were significantly higher in female Great-winged Petrels than males. Sex-related differences in parental care are associated with variation in prolactin

concentrations, where the sex that invests more parental effort also has higher prolactin concentrations (Van Roo et al., 2003), inducing behaviors like longer incubation shifts and longer foraging trips than their mates (Lormée et al., 2000). The significantly higher prolactin concentrations in female Great-winged Petrels could indicate that females invest more effort into incubation than males. Female Masked Boobies (*Sula dactylatra*), Red-footed Boobies (*S. sula*), Red-tailed Tropicbirds (*Phaeton rubricauda*; Lormée et al., 2000) and Snow Petrels (*Pagodroma nivea*; Tartu et al., 2015a) also had higher prolactin concentrations than males during incubation. These observations may suggest that high prolactin concentrations are necessary to maintain breeding effort throughout the breeding season because females already invested internal resources into the egg. Despite the high prolactin concentrations in female Great-winged Petrels, however, no relationship was detected with THg. Although male Great-winged Petrels also did not exhibit a relationship between prolactin and THg, negative relationships between THg and prolactin were observed in males, but not females, of two other seabird species (Black-legged Kittiwakes, *Rissa tridactyla*; Tartu et al. 2015b; Snow Petrels; Tartu et al. 2015a). During the breeding season, female birds dispose of Hg in their eggs (Ackerman et al., 2016a; Monteiro and Furness, 2001), which may explain some THg differences between sexes observed in other studies. If female Great-winged Petrels had high THg during late-incubation, it suggests that exposure to MeHg via their diet remained high, even after disposing of Hg in their eggs. Thus, THg may be consistently elevated in Flesh-footed Shearwaters and Great-winged Petrels, but they have developed a high tolerance and can cope with elevated THg during the breeding season.

3.4.3 THg toxicity

The THg concentrations observed in Flesh-footed Shearwaters and Great-winged Petrels reflect a range of THg that has been associated with observed adverse toxicity effects in other bird species (Ackerman et al., 2016b). For example, THg can impair individuals' health

and physiology when concentrations are as low as 0.2 μg g^{-1} ww (Custer et al., 2000). Though all sampled Flesh-footed Shearwaters had THg concentrations greater than 0.2 μg g^{-1} ww, birds did not exhibit visible health problems during sampling. Because THg concentrations as small as 0.2 μg g^{-1} ww have altered gene expression in Double-crested Cormorants (*Phalacrocorax auritus*; Gibson et al., 2014), increased egg neglect in Black-legged Kittiwakes (Tartu et al., 2013), and decreased current and future reproduction in Common Loons (*Gavia immer*; Burgess and Meyer, 2008) and South Polar Skuas (*Stercorarius maccormicki*; Goutte et al. 2014b), it is possible that Flesh-footed Shearwaters may experience genetic or behavioral effects that were not measured in this study.

Mean THg concentrations observed in Great-winged Petrels corresponded to severe reproductive impairment in several waterbird species, including decreased reproduction and reproductive failure in Common Loons (Barr, 1986; Burgess and Meyer, 2008; Evers et al., 2008), and embryonic deformities in Forster's Terns (*Sterna forsteri*; Herring et al., 2010). The highest observed THg in Great-winged Petrels from Breaksea Island was 4.6 μg g^{-1} ww, which corresponded to reduced reproduction in Common Loons (Burgess and Meyer, 2008) and reduced antioxidant activity in Surf Scoters (*Melanitta perspicillata*) that increased oxidative stress (Hoffman et al., 1998), which in turn may affect reproduction (Catoni et al., 2008). While these concentrations were not lethal, it is possible that these high THg concentrations may cause cellular or metabolic changes in Great-winged Petrels that I did not measure or observe, and that may be harmful over the long-term in these long-lived species.

Though this study focused on blood-based THg concentrations during the breeding season, it is interesting to note that feathers sampled from Flesh-footed Shearwaters and Great-winged Petrels at other colonies (Flesh-footed Shearwater: Lord Howe Island, Australia, and New Zealand, Bond and Lavers, 2011; Great-winged Petrel: Kerguelen Island, Atlantic Ocean, Carravieri et al., 2014; Marion Island, Indian Ocean, Becker et al., 2016), plus a closely-related species, the Grey-faced Petrel (Lyver et al., 2017) had moderate to very high feather Hg concentrations (mean concentrations ranged 6-36 μg g^{-1} dw) that were

molted during both the breeding and non-breeding season. Additionally, Great-winged Petrels from this study had high heavy metal (Pb, Se, Zn) feather concentrations (Philpott et al. *in review*), indicating that these birds are also exposed to other toxic metals. These data suggest that both species may maintain similar foraging ecologies and diets throughout the year that continuously expose them to elevated Hg.

3.4.4 Conclusions

Great-winged Petrels in Western Australia had five times more THg than sympatric Flesh-footed Shearwaters. The large inter-specific difference in THg is likely due to differences in diet and foraging location, where Great-winged Petrels foraged in pelagic regions on mesopelagic prey. However, I did not detect relationships between THg concentrations and the breeding hormone prolactin or egg volume. Adverse effects may occur with other aspects of reproduction, and may also occur on a molecular scale that was not tested in this study (e.g. Gibson et al. 2014; Goutte et al. 2014a; Hoffman et al. 1998). Given that many seabirds are long-lived, it is also possible that subtle adverse effects are more harmful over the long-term than the parameters that I measured during the incubation period of one breeding season. For example, adverse effects of contaminants on seabirds may be more exacerbated during years of low prey availability (Golet et al., 2002). Little data exist on long-term effects of contaminant compounds on individuals and populations of many long-lived species. Though some species appear to tolerate elevated mercury concentrations, species that have not evolved mercury detoxification mechanisms may be more susceptible to increased mercury exposure through both increased anthropogenic mercury into the atmosphere and oceans, and through changes in diets and foodwebs (Thompson, 1996). Foraging ecology can inform exposure to anthropogenic contaminants in marine predators, and land-based seabirds provide a unique opportunity to sample many parts of the ocean for contaminants

(Elliott and Elliott, 2013). Linking foraging ecology to reproductive parameters is the next step to providing a better monitoring system of both individuals and populations.

3.5 References

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., 2016a. Maternal transfer of contaminants in birds: Mercury and selenium concentrations in parents and their eggs. Environ. Pollut. 210, 145–154. https://doi.org/10.1016/j.envpol.2015.12.016

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., Peterson, S.H., Evers, D.C., Jackson, A.K., Elliott, J.E., Pol, S.S. Vander, Bryan, C.E., 2016b. Avian mercury exposure and risk across western North America: a synthesis. Sci. Total Environ. 568, 749–769. https://doi.org/10.1016/j.scitotenv.2016.03.071

Anderson, O.R.J., Phillips, R.A., McDonald, R.A., Shore, R.F., McGill, R.A.R., Bearhop, S., 2009. Influence of trophic position and foraging range on mercury levels within a seabird community. Mar. Ecol. Prog. Ser. 375, 277–288. https://doi.org/10.3354/meps07784

Angelier, F., Wingfield, J.C., Tartu, S., Chastel, O., 2016. Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review. Horm. Behav. 77, 18–29. https://doi.org/10.1016/j.yhbeh.2015.07.014

Australian Government, 2012. Species group report card - Seabirds. Supporting the marine bioregional plan for the South-west Marine Region. Department of Sustainability, Environment, Water, Population, and Communities, Canberra, ACT.

Bank, M.S., Chesney, E., Shine, J.P., Maage, A., Senn, D.B., 2007. Mercury bioaccumulation and trophic transfer in sympatric snapper species from the Gulf of Mexico. Ecol. Appl. 17, 2100–2110. https://doi.org/10.1890/06-1422.1

Barr, J., 1986. Population dynamics of the Common Loon (Gavia immer) associated with mercury-contaminanted waters in northwestern Ontario. Can. Wildl. Serv. 56, 1–23.

Becker, P.H., Goutner, V., Ryan, P.G., González-Solís, J., 2016. Feather mercury concentrations in Southern Ocean seabirds: Variation by species, site and time. Environ. Pollut. 216, 253–263. https://doi.org/10.1016/j.envpol.2016.05.061

Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

Bocher, P., Caurant, F., Miramand, P., Cherel, Y., Bustamante, P., 2003. Influence of the diet on the bioaccumulation of heavy metals in zooplankton-eating petrels at Kerguelen archipelago, Southern Indian Ocean. Polar Biol. 26, 759–767. https://doi.org/10.1007/s00300-003-0552-6

Bolton, M., 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. J. Anim. Ecol. 60, 949-960.

Bond, A.L., Diamond, A.W., 2009. Mercury concentrations in seabird tissues from Machias Seal Island, New Brunswick, Canada. Sci. Total Environ. 407, 4340–4347. https://doi.org/10.1016/j.scitotenv.2009.04.018

Bond, A.L., Lavers, J.L., 2011. Trace element concentrations in feathers of Flesh-footed Shearwaters (Puffinus carneipes) from across their breeding range. Arch. Environ.

Contam. Toxicol. 61, 318–326. https://doi.org/10.1007/s00244-010-9605-3

Boutette, J.B., Ramsay, E.C., Potgieter, L.N.D., Kania, S.A., 2002. An improved polymerase chain reaction-restriction fragment length polymorphism assay for gender identification in birds. J. Avian Med. Surg. 16, 198–202.

Bravo Rebolledo, E.L., Van Franeker, J.A., Jansen, O.E., Brasseur, S.M.J.M., 2013. Plastic ingestion by harbour seals (Phoca vitulina) in The Netherlands. Mar. Pollut. Bull. 67, 200–202. https://doi.org/10.1016/j.marpolbul.2012.11.035

Buntin, J.D., Becker, G.M., Ruzycki, E., 1991. Facilitation of parental behavior in ring doves by systemic or intracranial injections of prolactin. Horm. Behav. 25, 424–444. https://doi.org/10.1016/0018-506X(91)90012-7

Burger, J., Gochfeld, M., 2004. Marine Birds as Sentinels of Environmental Pollution. Ecohealth 1, 263–274. https://doi.org/10.1007/s10393-004-0096-4

Burgess, N.M., Meyer, M.W., 2008. Methylmercury exposure associated with reduced productivity in common loons. Ecotoxicology 17, 83–91. https://doi.org/10.1007/s10646-007-0167-8

Burnham, J.H., Burnham, K.K., Chumchal, M.M., Welker, J.M., Johnson, J.A., 2018. Correspondence between mercury and stable isotopes in high Arctic marine and terrestrial avian species from northwest Greenland. Polar Biol. https://doi.org/10.1007/s00300-018-2302-9

Cai, Y., Rooker, J.R., Gill, G.A., Turner, J.P., 2007. Bioaccumulation of mercury in pelagic fishes from the northern Gulf of Mexico. Can. J. Fish. Aquat. Sci. 64, 458–469. https://doi.org/10.1139/f07-017

Campbell, L.M., Norstrom, R.J., Hobson, K.A., Muir, D.C.G., Backus, S., Fisk, A.T., 2005. Mercury and other trace elements in a pelagic Arctic marine food web (Northwater Polynya, Baffin Bay). Sci. Total Environ. 351–352, 247–263. https://doi.org/10.1016/j.scitotenv.2005.02.043

Camphuysen, K.C.J., 2007. Where two oceans meet: distribution and offshore interactions of great-winged petrels Pterodroma macroptera and Leach's storm petrels Oceanodroma leucorhoa off southern Africa. J. Ornithol. 148, 333–346. https://doi.org/10.1007/s10336-007-0135-3

Carravieri, A., Bustamante, P., Tartu, S., Meillere, A., Labadie, P., Budzinski, H., Peluhet, L., Barbraud, C., Weimerskirch, H., Chastel, O., Cherel, Y., 2014. Wandering albatrosses document latitudinal variations in the transfer of persistent organic pollutants and mercury to southern ocean predators. Environ. Sci. Technol. 48, 14746–14755. https://doi.org/10.1021/es504601m

Carvalho, P.C., Bugoni, L., Mcgill, R.A.R., Bianchini, A., 2013. Metal and selenium concentrations in blood and feathers of petrels of the genus procellaria. Environ. Toxicol. Chem. 32, 1641–1648. https://doi.org/10.1002/etc.2204

Catoni, C., Peters, A., Martin Schaefer, H., 2008. Life history trade-offs are influenced by the diversity, availability and interactions of dietary antioxidants. Anim. Behav. 76, 1107–

1119. https://doi.org/10.1016/j.anbehav.2008.05.027

Catry, T., Ramos, J.A., Corre, M., Kojadinovic, J., Bustamante, P., 2008. The role of stable isotopes and mercury concentrations to describe seabird foraging ecology in tropical environments. Mar. Biol. 155, 637–647. https://doi.org/10.1007/s00227-008-1060-6

Ceccatelli, S., Daré, E., Moors, M., 2010. Methylmercury-induced neurotoxicity and apoptosis. Chem. Biol. Interact. 188, 301–308. https://doi.org/10.1016/j.cbi.2010.04.007

Chastel, O., Lacroix, A., Weimerskirch, H., Gabrielsen, G.W., 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. Horm. Behav. 47, 459–466. https://doi.org/10.1016/j.yhbeh.2004.10.009

Cherel, Y., Mauget, R., Lacroix, A., Gilles, J., 1994. Seasonal and Fasting-related Changes in Circulating Gonadal Steroids and Prolactin in King Penguins, Aptenodytes patagonicus. Physiol. Zool. 67, 1154–1173.

Christians, J.K., 2002. Avian egg size: variation within species and inflexibility within individuals. Biol. Rev. 77, 1-26.

Conners, M. G., C. Goetsch, S. M. Budge, W. A. Walker, Y. Mitani, D. P. Costa, and S. A. Shaffer. 2018. Fisheries exploitation by albatross quantified with lipid analysis. Frontiers in Marine Science doi: 10.3389/fmars.2018.00113.

Cooper, J., Klages, N.T.W., 2009. The winter diet of the Great-winged Petrel Pterodroma macroptera at sub-Antarctic Marion Island in 1991. Mar. Ornithol. 37, 261–263. https://doi.org/10.2307/3130

Croxall, J.P., Prince, P.A., 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol. J. Linn. Soc. 14, 103–131.

Custer, T.W., Custer, C.M., Hines, R.K., Sparks, D.W., Melancon, M.J., Hoffman, D.J., Bickham, J.W., Wickliffe, J.K., 2000. Mixed-function oxygenases, oxidative stress, and chromosomal damage measured in lesser scaup wintering on the Indiana Harbor Canal. Arch. Environ. Contam. Toxicol. 38, 522–529. https://doi.org/10.1007/s002449910068

Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a global pollutant—sources, pathways, and effects. Environ. Sci. Technol. 47, 4967–4983. https://doi.org/10.1021/es305071v

Dunlop, J.N. 2008. Protected species by-catch in Zone-1 of the South Coast Purse Seine Managed Fishery 2007/08 [unpublished report to the SCPSMF work group]. 10 pp.

Eagles-Smith, C.A., Ackerman, J.T., Adelsbach, T.L., Takekawa, J.Y., Miles, A.K., Keister, R.A., 2008. Mercury correlations among six tissues for four waterbird species breeding in San Francisco Bay, California, USA. Environ. Toxicol. Chem. 27, 2136–2153. https://doi.org/10.1897/08-038.1

Elliott, J.E., Elliott, K.H., 2013. Environmental science. Tracking marine pollution. Science. 340, 556–558. https://doi.org/10.1126/science.1235197

Environmental Protection Authority. 2007. State of the Environment Report. EPA, Western

Australia. http://www.epa.wa.gov.au/state-environment-report-2007

Evans, A.F., Roby, D.D., Collis, K., Cramer, B.M., Sheggeby, J.A., Adrean, L.J., Battaglia, D.S., Lyons, D.E., 2011. Recovery of coded wire tags at a caspian tern colony in san francisco bay: A technique to evaluate impacts of avian predation on juvenile salmonids. North Am. J. Fish. Manag. 31, 79–87. https://doi.org/10.1080/02755947.2011.562429

Evers, D.C., Savoy, L.J., Desorbo, C.R., Yates, D.E., Hanson, W., Taylor, K.M., Siegel, L.S., Cooley, J.H., Bank, M.S., Major, A., Munney, K., Mower, B.F., Vogel, H.S., Schoch, N., Pokras, M., Goodale, M.W., Fair, J., 2008. Adverse effects from environmental mercury loads on breeding common loons. Ecotoxicology 17, 69–81. https://doi.org/10.1007/s10646-007-0168-7

Evers, D.C., Taylor, K.M., Major, A., Taylor, R.J., Poppenga, R.H., Scheuhammer, A.M., 2003. Common loon eggs as indicators of methylmercury availability in North America. Ecotoxicology 12, 69–81. https://doi.org/10.1023/A:1022593030009

Falla, R.A., 1934. The distribution and breeding habits of petrels in northern New Zealand. Rec. Auckl. Inst. Museum 1, 245–260.

Finger, A., Lavers, J.L., Dann, P., Kowalczyk, N.D., Scarpaci, C., Nugegoda, D., Orbell, J.D., 2017. Metals and metalloids in Little Penguin (Eudyptula minor) prey, blood and faeces. Environ. Pollut. 223, 567–574. https://doi.org/10.1016/j.envpol.2017.01.059

Finger, A., Lavers, J.L., Orbell, J.D., Dann, P., Nugegoda, D., Scarpaci, C., 2016. Seasonal variation and annual trends of metals and metalloids in the blood of the Little Penguin (Eudyptula minor). Mar. Pollut. Bull. 110, 261–273. https://doi.org/10.1016/j.marpolbul.2016.06.055

Finkelstein, M., Keitt, B.S., Croll, D.A., Tershy, B., Jarman, W.M., Rodriguez-Pastor, S., Anderson, D.J., Sievert, P.R., Smith, D.R., 2006. Albatross species demonstrate regional differences in North Pacific marine contamination. Ecol. Appl. 16, 678–686. https://doi.org/10.1890/1051-0761(2006)016[0678:ASDRDI]2.0.CO;2

Finkelstein, M.E., Grasman, K.A., Croll, D.A., Tershy, B.R., Keitt, B.S., Jarman, W.M., Smith, D.R., 2007. Contaminant-associated alteration of immune function in black-footed albatross (Phoebastria nigripes), a North Pacific predator. Environ. Toxicol. Chem. 26, 1896–1903. https://doi.org/10.1897/06-505R.1

Fitzgerald, W.F., Lamborg, C.H., Hammerschmidt, C.R., 2007. Marine biogeochemical cycling of mercury. Chem. Rev. 107, 641–662. https://doi.org/10.1021/cr050353m

Fletcher, W.J., Tregonning, R.J., 1992. Distribution and timing of spawning by the Australian pilchard (Sardinops sagax neopilchardus) off Albany, Western Australia. Marine and Freshwater Research 43:1437–1449.

Fort, J., Lacoue-labarthe, T., Linh, H., Boué, A., Spitz, J., Bustamante, P., 2015. Mercury in wintering seabirds , an aggravating factor to winter wrecks? Sci. Total Environ. 527–528, 448–454. https://doi.org/10.1016/j.scitotenv.2015.05.018

Fort, J., Robertson, G.J., Grémillet, D., Traisnel, G., Bustamante, P., 2014. Spatial ecotoxicology: Migratory arctic seabirds are exposed to mercury contamination while

overwintering in the northwest Atlantic. Environ. Sci. Technol. 48, 11560–11567. https://doi.org/10.1021/es504045g

Frederick, P., Jayasena, N., 2011. Altered pairing behaviour and reproductive success in white ibises exposed to environmentally relevant concentrations of methylmercury. Proc. R. Soc. B Biol. Sci. 278, 1851–1857. https://doi.org/10.1098/rspb.2010.2189

Freeman, M., Kanyicska, B., Lerant, A., Nagy, G., 2000. Prolactin : Structure, Function, and Regulation of Secretion. Physiol. Rev. 80, 1523–1631.

Fromant, A., Carravieri, A., Bustamante, P., Labadie, P., Budzinski, H., Peluhet, L., Churlaud, C., Chastel, O., Cherel, Y., 2016. Wide range of metallic and organic contaminants in various tissues of the Antarctic prion, a planktonophagous seabird from the Southern Ocean. Sci. Total Environ. 544, 754–764. https://doi.org/10.1016/j.scitotenv.2015.11.114

Gibson, L.A., Lavoie, R.A., Bissegger, S., Campbell, L.M., Langlois, V.S., 2014. A positive correlation between mercury and oxidative stress-related gene expression (GPX3 and GSTM3) is measured in female Double-crested Cormorant blood. Ecotoxicology 23, 1004–1014. https://doi.org/10.1007/s10646-014-1243-5

Golet, G.H., Seiser, P.E., McGuire, A.D., Roby, D.D., Fischer, J.B., Kuletz, K.J., Irons, D.B., Dean, T.A., Jewett, S.C., Newman, S.H., 2002. Long-term direct and indirect effects of the “Exxon Valdez” oil spill on pigeon guillemots in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 241, 287-304.

González-Solís, J., Sanpera, C., Ruiz, X., 2002. Metals and selenium as bioindicators of geographic and trophic segregation in giant petrels Macronectes spp. Mar. Ecol. Prog. Ser. 244, 257–264. https://doi.org/10.3354/meps244257

Goodale, M.W., Evers, D.C., Mierzykowski, S.E., Bond, A.L., Burgess, N.M., Otorowski, C.I., Welch, L.J., Hall, C.S., Ellis, J.C., Allen, R.B., Diamond, A.W., Kress, S.W., Taylor, R.J., 2008. Marine foraging birds as bioindicators of mercury in the Gulf of Maine. Ecohealth 5, 409–425. https://doi.org/10.1007/s10393-009-0211-7

Gould, P., Ostrom, P.H., Walker, W., 1997. Food of flesh-tooted shearwaters Puffinus carneipes associated with high seas driftnets in the central north Pacific Ocean. Emu 97, 168–173.

Goutte, A., Barbraud, C., Herzke, D., Bustamante, P., Angelier, F., Tartu, S., Clément-Chastel, C., Moe, B., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015. Survival rate and breeding outputs in a high Arctic seabird exposed to legacy persistent organic pollutants and mercury. Environ. Pollut. 200, 1–9. https://doi.org/10.1016/j.envpol.2015.01.033

Goutte, A., Barbraud, C., Meillère, A., Carravieri, A., Bustamante, P., Labadie, P., Budzinski, H., Delord, K., Cherel, Y., Weimerskirch, H., Chastel, O., 2014a. Demographic consequences of heavy metals and persistent organic pollutants in a vulnerable long-lived bird, the wandering albatross. Proc. R. Soc. London. Ser. B Biol. Sci. 281, 1–8. https://doi.org/10.1098/rspb.2013.3313

Goutte, A., Bustamante, P., Barbraud, C., Delord, K., Weimerskirch, H., Chastel, O., 2014b.

Demographic responses to mercury exposure in two closely related antarctic top predators. Ecology 95, 1075–1086. https://doi.org/10.1890/13-1229.1

Graca, B., Bełdowska, M., Wrzesień, P., Zgrundo, A., 2014. Styrofoam debris as a potential carrier of mercury within ecosystems. Environ. Sci. Pollut. Res. 21, 2263–2271. https://doi.org/10.1007/s11356-013-2153-4

Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems, in: Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping. pp. 299–318. https://doi.org/10.1007/978-90-481-3354-3_14

Grandjean, P., Weihe, P., White, R.F., Debes, F., Araki, S., Yokoyama, K., Murata, K., Sørensen, N., Dahl, R., Jørgensen, P.J., 1997. Cognitive Deficit in 7-Year-Old Children with Prenatal Exposure to Methylmercury. Neurotoxicol. Teratol. 19, 417–428. https://doi.org/10.1016/S0892-0362(97)00097-4

Hahn, S., Hoye, B.J., Korthals, H., Klaassen, M., 2012. From food to offspring down: Tissue-specific discrimination and turn-over of stable isotopes in herbivorous waterbirds and other avian foraging guilds. PLoS One 7, e30242. https://doi.org/10.1371/journal.pone.0030242

Hammerschmidt, C.R., Bowman, K.L., 2012. Vertical methylmercury distribution in the subtropical North Pacific Ocean. Mar. Chem. 132–133, 77–82. https://doi.org/10.1016/j.marchem.2012.02.005

Hammerschmidt, C.R., Fitzgerald, W.F., 2004. Geochemical Controls on the Production and Distribution of Methylmercury in Near-Shore Marine Sediments. Environ. Sci. Technol. 38, 1487–1495. https://doi.org/10.1021/es034528q

Hammerschmidt, C.R., Fitzgerald, W.F., Lamborg, C.H., Balcom, P.H., Visscher, P.T., 2004. Biogeochemistry of methylmercury in sediments of Long Island Sound. Mar. Chem. 90, 31–52. https://doi.org/10.1016/j.marchem.2004.02.024

Hanson, C.E., Pattiaratchi, C.B., Waite, A.M., 2005. Seasonal production regimes off south-western Australia: Influence of the Capes and Leeuwin Currents on phytoplankton dynamics. Mar. Freshw. Res. 56, 1011–1026. https://doi.org/10.1071/MF04288

Herring, G., Ackerman, J.T., Eagles-Smith, C.A., 2010. Embryo malposition as a potential mechanism for mercury-induced hatching failure in bird eggs. Environ. Toxicol. Chem. 29, 1788–1794. https://doi.org/10.1002/etc.208

Hipfner, J.M., Hobson, K. a., Elliott, J.E., 2011. Ecological factors differentially affect mercury levels in two species of sympatric marine birds of the North Pacific. Sci. Total Environ. 409, 1328–1335. https://doi.org/10.1016/j.scitotenv.2010.12.022

Hirayama, K., Yasutake, A., Inoue, M., 1987. Effect of Sex Hormones on the Fate of Methylmercury and on Glutathione Metabolism in Mice. Biochem. Pharmacol. 36, 1919–1924.

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

https://doi.org/10.3354/meps095007

Hobson, K.A., Clark, R.G., 1993. Turnover of 13C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110, 638–641.

Hoffman, D.J., Ohlendorf, H.M., Marn, C.M., Pendleton, G.W., 1998. Association of mercury and selenium with altered glutathione metabolism and oxidative stress in diving ducks from the San Francisco Bay region, USA. Environ. Toxicol. Chem. 17, 167–172. https://doi.org/10.1002/etc.5620170205

Hollweg, T., Gilmour, C., Mason, R., 2010. Mercury and methylmercury cycling in sediments of the mid-Atlantic continental shelf and slope. Limnol. Oceanogr. 55, 2703–2722. https://doi.org/10.4319/lo.2010.55.6.2703

Ikemoto, T., Kunito, T., Tanaka, H., Baba, N., Miyazaki, N., Tanabe, S., 2004. Detoxification mechanism of heavy metals in marine mammals and seabirds: Interaction of selenium with mercury, silver, copper, zinc, and cadmium in liver. Arch. Environ. Contam. Toxicol. 47, 402–413. https://doi.org/10.1007/s00244-004-3188-9

Imber, M.J., 1976. Breeding biology of the Grey-faced Petrel Pterodroma macroptera gouldi. Ibis (Lond. 1859). 118, 51–64.

Imber, M.J., 1973. The food of grey-faced petrels (Pterodroma macroptera gouldi (Hutton)), with special reference to diurnal vertical migration of their prey. J. Anim. Ecol. 42, 645–662. https://doi.org/10.2307/3130

Jackson, M., Hancock, D., Schulz, R., Talbot, V., Williams, D., 1986. Rock phosphate: The source of mercury pollution in a marine ecosystem at Albany, Western Australia. Mar. Environ. Res. 18, 185–202. https://doi.org/10.1016/0141-1136(86)90032-2

Karell, P., Kontiainen, P., Pietiäinen, H., Siitari, H., Brommer, J.E., 2008. Maternal effects on offspring Igs and egg size in relation to natural and experimentally improved food supply. Funct. Ecol. 22, 682–690. https://doi.org/10.1111/j.1365-2435.2008.01425.x

Kojadinovic, J., Potier, M., Le Corre, M., Cosson, R.P., Bustamante, P., 2007. Bioaccumulation of trace elements in pelagic fish from the Western Indian Ocean. Environ. Pollut. 146, 548–566. https://doi.org/10.1016/j.envpol.2006.07.015

Lamborg, C.H., Hammerschmidt, C.R., Bowman, K.L., Swarr, G.J., Munson, K.M., Ohnemus, D.C., Lam, P.J., Heimbürger, L.-E., Rijkenberg, M.J.A., Saito, M.A., 2014. A global ocean inventory of anthropogenic mercury based on water column measurements. Nature 512, 65–68. https://doi.org/10.1038/nature13563

Lavers, J. L., S. Lisovski, and A. L. Bond. 2018. Survival and movement of adult Flesh-footed Shearwaters (Ardenna carneipes carneipes) in Western Australia. Bird Conservation International.

Lavers, J.L., 2015. Population status and threats to Flesh-footed Shearwaters (Puffinus carneipes) in South and Western Australia. ICES J. Mar. Sci. 72, 316–327.

Lavers, J.L., Bond, A.L., Hutton, I., 2014. Plastic ingestion by flesh-footed shearwaters (Puffinus carneipes): Implications for fledgling body condition and the accumulation of

plastic-derived chemicals. Environ. Pollut. 187, 124–129. https://doi.org/10.1016/j.envpol.2013.12.020

Lavoie, R.A., Baird, C.J., King, L.E., Kyser, T.K., Friesen, V.L., Campbell, L.M., 2014. Contamination of mercury during the wintering period influences concentrations at breeding sites in two migratory piscivorous birds. Environ. Sci. Technol. 48, 13694–13702. https://doi.org/10.1021/es502746z

Lavoie, R.A., Hebert, C.E., Rail, J.F., Braune, B.M., Yumvihoze, E., Hill, L.G., Lean, D.R.S., 2010. Trophic structure and mercury distribution in a Gulf of St. Lawrence (Canada) food web using stable isotope analysis. Sci. Total Environ. 408, 5529–5539. https://doi.org/10.1016/j.scitotenv.2010.07.053

Lerma, M., Castillo-Guerrero, J.A., Ruelas-Inzunza, J., Fernández, G., 2016. Lead, cadmium and mercury in the blood of the blue-footed booby (Sula nebouxii) from the coast of Sinaloa, Gulf of California, Mexico. Mar. Pollut. Bull. 110, 293–298. https://doi.org/10.1016/j.marpolbul.2016.06.049

Lormée, H., Jouventin, P., Lacroix, A., Lallemand, J., Chastel, O., 2000. Reproductive endocrinology of tropical seabirds: sex-specific patterns in LH, steroids, and prolactin secretion in relation to parental care. Gen. Comp. Endocrinol. 117, 413–26. https://doi.org/10.1006/gcen.1999.7434

Lundholm, C.E., 1995. Effects of methyl mercury at different dose regimes on eggshell formation and some biochemical characteristics of the eggshell gland mucosa of the domestic fowl. Comp. Biochem. Physiol. Part CPharmacology, Toxicol. Endocrinol. 110, 23–28. https://doi.org/10.1016/0742-8413(94)00081-K

Lusher, A.L., Hernandez-Milian, G., Berrow, S., Rogan, E., O'Connor, I., 2018. Incidence of marine debris in cetaceans stranded and bycaught in Ireland: Recent findings and a review of historical knowledge. Environ. Pollut. 232, 467–476. https://doi.org/10.1016/j.envpol.2017.09.070

Lyver, P.O.B., Aldridge, S.P., Gormley, A.M., Gaw, S., Webb, S., Buxton, R.T., Jones, C.J., 2017. Elevated mercury concentrations in the feathers of grey-faced petrels (Pterodroma gouldi) in New Zealand. Mar. Pollut. Bull. 119, 195–203. https://doi.org/10.1016/j.marpolbul.2017.03.055

Malagutti, K.S., da Silva, A.P., Braga, H.C., Mitozo, P.A., Soares dos Santos, A.R., Dafre, A.L., de Bem, A.F., Farina, M., 2009. 17B-Estradiol Decreases Methylmercury-Induced Neurotoxicity in Male Mice. Environ. Toxicol. Pharmacol. 27, 293–297. https://doi.org/10.1016/j.etap.2008.11.005

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. https://doi.org/10.1016/j.pocean.2013.11.005

Marchant, S., Higgins, P., 1990. Order Procellariiformes, in: Handbook of Australian, New Zealand & Antarctic Birds. pp. 410–420.

Mason, R.P., Choi, A.L., Fitzgerald, W.F., Hammerschmidt, C.R., Lamborg, C.H., Soerensen,

A.L., Sunderland, E.M., 2012. Mercury biogeochemical cycling in the ocean and policy implications. Environ. Res. 119, 101–117. https://doi.org/10.1016/j.envres.2012.03.013

Middleton, J.F., Cirano, M., 2002. A northern boundary current along Australia's southern shelves: The Flinders Current. J. Geophys. Res. 107, 3129. https://doi.org/10.1029/2000JC000701

Monteiro, L.R., Costa, V., Furness, R.W., Santos, R.S., 1996. Mercury concentrations in prey fish indicate enhanced bioaccumulation in mesopelagic environments. Mar. Ecol. Prog. Ser. 141, 21–25. https://doi.org/10.3354/meps141021

Monteiro, L.R., Furness, R.W., 2001. Kinetics, dose-response, and excretion of methylmercury in free-living adult Cory's shearwaters. Environ. Sci. Technol. 35, 739–746. https://doi.org/10.1021/es000114a

Navarro, J., Coll, M., Somes, C.J., Olson, R.J., 2013. Trophic niche of squids: Insights from isotopic data in marine systems worldwide. Deep. Res. Part II Top. Stud. Oceanogr. 95, 93–102. https://doi.org/10.1016/j.dsr2.2013.01.031

Oliveira, F.R.T., Ferreira, J.R., Dos Santos, C.M.C., Macedo, L.E.M., De Oliveira, R.B., Rodrigues, J.A., Do Nascimento, J.L.M., Faro, L.R.F., Diniz, D.L.W.P., 2006. Estradiol reduces cumulative mercury and associated disturbances in the hypothalamus-pituitary axis of ovariectomized rats. Ecotoxicol. Environ. Saf. 63, 488–493. https://doi.org/10.1016/j.ecoenv.2004.12.024

Olivero-Verbel, J., D. Agudelo-Frias, and K. Caballero-Gallardo. 2013. Morphometric parameters and total mercury in eggs of snowy egret (Egretta thula) from Cartagena Bay and Totumo Marsh, north of Colombia. Mar. Poll. Bull. 69, 105-109.

Pacyna, E.G., Pacyna, J.M., Sundseth, K., Munthe, J., Kindbom, K., Wilson, S., Steenhuisen, F., Maxson, P., 2010. Global emission of mercury to the atmosphere from anthropogenic sources in 2005 and projections to 2020. Atmos. Environ. 44, 2487–2499. https://doi.org/10.1016/j.atmosenv.2009.06.009

Peterson, S.H., Ackerman, J.T., Costa, D.P., 2015. Marine foraging ecology influences mercury bioaccumulation in deep-diving northern elephant seals. Proc. R. Soc. B Biol. Sci. 282, 20150710. https://doi.org/10.1098/rspb.2015.0710

Piatt, J.F., Sydeman, W.J., Weise, F., 2007. Seabirds as indicators of marine ecosystems. Mar. Ecol. Prog. Ser. 352, 199–204. https://doi.org/10.3354/meps07070

Philpot, S. M., J. L. Lavers, D. Nugegoda, M. E. Gilmour, I. Hutton, and A. L. Bond. In review. Trace element concentrations in feathers of seven petrels (Pterodroma spp.). Env. Sci. Poll. Res., in review.

Pollet, I.L., Leonard, M.L., O'Driscoll, N.J., Burgess, N.M., Shutler, D., O'Driscoll, N.J., Burgess, N.M., Shutler, D., 2017. Relationships between blood mercury levels, reproduction, and return rate in a small seabird. Ecotoxicology 26, 97–103. https://doi.org/10.1007/s10646-016-1745-4

Polovina, J.J., Howell, E.A., Kobayashi, D.R., Seki, M.P., 2001. The Transition Zone Chlorophyll Front, a dynamic global feature defining migration and forage habitat for

marine resources. Prog. Oceanogr. 49, 469–483. https://doi.org/10.1016/S0079-6611(01)00036-2

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189. https://doi.org/10.1007/s00442-006-0630-x

Powell, C.D.L., 2009. Foraging movements and the migration trajectory of Flesh-footed Shearwaters Puffinus carneipes from the south coast of Western Australia. Mar. Ornithol. 37, 115–120.

Rapp, D.C., Youngren, S.M., Hartzell, P., David Hyrenbach, K., 2017. Community-wide patterns of plastic ingestion in seabirds breeding at French Frigate Shoals, Northwestern Hawaiian Islands. Mar. Pollut. Bull. 123, 269–278. https://doi.org/10.1016/j.marpolbul.2017.08.047

Ridoux, V. 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Marine Ornithology 22:65-128.

Rimmer, C.C., Mcfarland, K.P., Evers, D.C., Miller, E.K., Aubry, Y., Busby, D., Taylor, R.J., 2005. Mercury concentrations in Bicknell's thrush and other insectivorous passerines in montane forests of northeastern North America. Ecotoxicology 14, 223–240. https://doi.org/10.1007/s10646-004-6270-1

Rooney, J.P.K., 2007. The role of thiols, dithiols, nutritional factors and interacting ligands in the toxicology of mercury. Toxicology 234, 145–156. https://doi.org/10.1016/j.tox.2007.02.016

Rummel, C.D., Löder, M.G.J., Fricke, N.F., Lang, T., Griebeler, E.M., Janke, M., Gerdts, G., 2016. Plastic ingestion by pelagic and demersal fish from the North Sea and Baltic Sea. Mar. Pollut. Bull. 102, 134–141. https://doi.org/10.1016/j.marpolbul.2015.11.043

Schramm, M., 1986. The Diet of Chicks of Greatwinged, Kerguelen and Softplumaged Petrels At the Prince Edward Islands. Ostrich 57, 9–15. https://doi.org/10.1080/00306525.1986.9633632

Schuyler, Q.A., Wilcox, C., Townsend, K., Hardesty, B.D., Marshall, N.J., 2014. Mistaken identity? Visual similarities of marine debris to natural prey items of sea turtles. BMC Ecol. 14, 1–7. https://doi.org/10.1186/1472-6785-14-14

Sebastiano, M., Bustamante, P., Costantini, D., Eulaers, I., Malarvannan, G., Mendez-Fernandez, P., Churlaud, C., Blevin, P., Hauselmann, A., Dell'Omo, G., Covaci, A., Eens, M., Chastel, O., 2016. High levels of mercury and low levels of persistent organic pollutants in a tropical seabird in French Guiana, the Magnificent frigatebird, Fregata magnificens. Environ. Pollut. 214, 384–393. https://doi.org/10.1016/j.envpol.2016.03.070

Sebastiano, M., Bustamante, P., Eulaers, I., Malarvannan, G., Mendez-Fernandez, P., Churlaud, C., Blévin, P., Hauselmann, A., Covaci, A., Eens, M., Costantini, D., Chastel, O., 2017. Trophic ecology drives contaminant concentrations within a tropical seabird community. Environ. Pollut. 227, 183–193. https://doi.org/10.1016/j.envpol.2017.04.040

Sequeira, A. M. M., M. R. Heupel, M. Lea, V. M. Eguíluz, C. M. Duarte, M. G. Meekan, M. Thums, R. H. Carmichael, D. P. Costa, L. C. Ferreira, J. Fernandéz-Gracia, R. Harcourt, I. Jonsen, C. McMahon, D. W. Sims, R. Wilson, and G. C. Hays. In review. The importance of sample size in animal tracking studies. Ecological Applications, in review.

Smiley, K.O., Adkins-Regan, E., 2018. Lowering prolactin reduces post-hatch parental care in male and female zebra finches (Taeniopygia guttata). Horm. Behav. 98, 103–114. https://doi.org/10.1016/j.yhbeh.2017.12.011

Sunderland, E.M., Krabbenhoft, D.P., Moreau, J.W., Strode, S.A., Landing, W.M., 2009. Mercury sources, distribution, and bioavailability in the North Pacific Ocean: Insights from data and models. Global Biogeochem. Cycles 23, 1–14. https://doi.org/10.1029/2008GB003425

Sweet, L.I., Passino-Reader, D.R., Meier, P.G., Omann, G.M., 2006. Effects of polychlorinated biphenyls, hexachlorocyclohexanes, and mercury on human neutrophil apoptosis, actin cytoskelton, and oxidative state. Environ. Toxicol. Pharmacol. 22, 179–188. https://doi.org/10.1016/j.etap.2006.03.005

Tan, S.W., Meiller, J.C., Mahaffey, K.R., 2009. The endocrine effects of mercury in humans and wildlife. Crit. Rev. Toxicol. 39, 228–269. https://doi.org/10.1080/10408440802233259

Tanaka, K., Takada, H., Yamashita, R., Mizukawa, K., Fukuwaka, M. aki, Watanuki, Y., 2013. Accumulation of plastic-derived chemicals in tissues of seabirds ingesting marine plastics. Mar. Pollut. Bull. 69, 219–222. https://doi.org/10.1016/j.marpolbul.2012.12.010

Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015a. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. Sci. Total Environ. 505, 180–188. https://doi.org/10.1016/j.scitotenv.2014.10.008

Tartu, S., Bustamante, P., Angelier, F., Lendvai, Á.Z., Moe, B., Blévin, P., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015b. Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct. Ecol. 30, 596–604. https://doi.org/10.1111/1365-2435.12534

Tartu, S., Bustamante, P., Goutte, A., Cherel, Y., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2014. Age-related mercury contamination and relationship with luteinizing hormone in a long-lived antarctic bird. PLoS One 9, e103642. https://doi.org/10.1371/journal.pone.0103642

Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. Biol. Lett. 9, 20130317. https://doi.org/10.1098/rsbl.2013.0317

Tavares, S., Xavier, J.C., Phillips, R.A., Pereira, M.E., Pardal, M.A., 2013. Influence of age, sex and breeding status on mercury accumulation patterns in the wandering albatross Diomedea exulans. Environ. Pollut. 181, 315–320. https://doi.org/10.1016/j.envpol.2013.06.032

Thalman, S.J., Baker, G.B., Hindell, M., Tuck, G.N., 2009. Longline Fisheries and Foraging Distribution of Flesh-Footed Shearwaters in Eastern Australia. J. Wildl. Manage. 73, 399–406. https://doi.org/10.2193/2007-461

Thompson, D.R. 1996. Mercury in birds and terrestrial mammals. Environmental Contaminants in Wildlife: Interpreting Tissues Concentrations. Lewis Publishers, Boca Raton, Florida, pp.341-356.

Turner, A., 2018. Mobilisation kinetics of hazardous elements in marine plastics subject to an avian physiologically-based extraction test. Environ. Pollut. 236, 1020–1026. https://doi.org/10.1016/j.envpol.2018.01.023

U.S. EPA [United States Environmental Protection Agency]. 2007. Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry. EPA Method 7473 Report. U.S. Environmental Protection Agency, Washington, D.C., USA.

Van Roo, B.L., Ketterson, E.D., Sharp, P.J., 2003. Testosterone and prolactin in two songbirds that differ in paternal care: The blue-headed vireo and the red-eyed vireo. Horm. Behav. 44, 435–441. https://doi.org/10.1016/j.yhbeh.2003.07.001

Vleck, C.M., Ross, L.L., Vleck, D., Bucher, T.L., 2000. Prolactin and parental behavior in Adélie penguins: effects of absence from nest, incubation length, and nest failure. Horm. Behav. 38, 149–58. https://doi.org/10.1006/hbeh.2000.1589

Western Australia Government. 2015. Wildlife Conservation (Rare Flora) Notice 2015. Accessed online https://www.slp.wa.gov.au/gazette/gazette.nsf/ 14 November 2015.

Young, H., McCauley, D., Dirzo, R., Dunbar, R., Shaffer, S., 2010. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. Mar. Ecol. Prog. Ser. 416, 285–294. https://doi.org/10.3354/meps08756

Young, H.S., Maxwell, S.M., Conners, M.G., Shaffer, S.A., 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. Biol. Conserv. 181, 226–235. https://doi.org/10.1016/j.biocon.2014.10.027

Table 3.1 Relationships between blood mercury concentrations and reproduction in seabirds from other studies

Summary of correlational field studies in which effects of blood THg were tested on reproductive parameters in free-living adult seabirds. Studies are listed in order of increasing THg concentration (μg g^{-1} ww). Either mean or median of sample population is presented, and THg concentrations are grouped into categories tested, if this distinction was provided in the literature. n= sample size; in some cases, only sample size for whole study was given.

Species	Summary statistic type Group	THg concentration (μg g^{-1} ww) (n)	Tissue type	Reproductive parameter	Correlation with Hg	Reference
Cassin's Auklet (*Ptychoramphus aleuticus*)	Mean ± SE, chick-feeders:	0.13 ± 0.02[a] (24)	Whole blood	Breeding stage (pre-lay, incubation, or chick-feeding)	No	Hipfner et al., 2011
Black-legged Kittiwake (*Rissa tridactyla*)	Median, males that raised one chick: females that raised one chick: males that raised two chicks: females that raised two chicks:	0.25[a] 0.17[a] 0.2[a] 0.17[a] (173)	Red blood cells	Prolactin concentration Breeding success (number of eggs hatched; number of chicks successfully raised)	Yes, but only males Yes, but only males	Tartu et al., 2015b
Blue-footed Booby (*Sula nebouxii*)	Mean, males: females:	0.29[a] 0.20[a] (243)	Whole blood	Breeding status (laying or not laying an egg) Number of eggs Number of chicks	No No No	Lerma et al., 2016
Black-legged Kittiwake (*Rissa tridactyla*)	Median, breeding females: non-breeding females: breeding males: non-breeding males:	0.34[a] (40) 0.40[a] (26) 0.40[a] (48) 0.42[a] (42)	Red blood cells	Breeding probability Lutenizing hormone concentration (in birds that skipped breeding) Egg lay-date Clutch size Breeding success	Yes negative in males, positive in females No No No	Tartu et al., 2013

Rhinoceros Auklet (*Cerorhinca monocerata*)	Mean ± SE, chick-feeders:	0.4 ± 0.02[a] (25)	Whole blood	Breeding stage (pre-lay, incubation, or chick-feeding)	Yes	Hipfner et al., 2011
Snow Petrel (*Pagodroma nivea*)	Mean ± SD, both sexes:	0.4 ± 0.2[a] (49)	Red blood cells	Stress-induced prolactin concentration Egg neglect	Yes, but only males Yes, but only males	Tartu et al., 2015a
Black-legged Kittiwake (*Rissa tridactyla*)	Mean ± SD, pre-lay females, 2008: pre-lay females, 2009: pre-lay males, 2008: pre-lay males, 2009:	0.42 ± 0.09[a] 0.42 ± 0.09[a] 0.43 ± 0.09[a] 0.49 ± 0.12[a] (105)	Red blood cells	Breeding probability, current year Probability of successfully raising one or two chicks in following year	Yes No	Goutte et al., 2015
South Polar Skua (*Catharacta maccormicki*)	Mean ± SE:	0.5 ± 0.04[a] (76)	Red blood cells	Breeding probability Breeding success in following year Probability of successfully raising two chicks in following year	No Yes No	Goutte et al., 2014b
Flesh-footed Shearwater (*Ardenna carneipes*)	Median ± SE:	0.625 ± 0.109	Red blood cells	Prolactin concentration Egg volume	No No	This study
Snow Petrel (*Pagodroma nivea*)	Mean ± SD, females: males:	0.76 ± 0.21[a] (29) 0.47 ± 0.19[a] (16)	Red blood cells	Lutenizing hormone concentration GnRH-induced Lutenizing hormone concentration	Yes, but only in birds <23 y/o No	Tartu et al., 2014
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	Mean ± SD:	0.9 ± 0.4 (90)[b]	Whole blood	Egg lay-date Egg volume Hatch rate Chick growth Fledging rate	No No No No No	Pollet et al., 2017
Wandering Albatross	Mean ± SD:	1.6 ± 0.8[a] (169)	Red blood cells	Breeding status (breeding vs non-breeding)	No	Carravieri et al., 2014

Brown Skua (*Catharacta lonnbergi*)	Mean ± SE:	1.7 ± 0.05[a] (68)	Red blood cells	Breeding probability Breeding success in following year Probability of successfully raising two chicks in following year	No Yes Yes	Goutte et al., 2014b
Wandering Albatross (*Diomedea exulans*)	Mean ± SD, females: males:	2.3 ± 0.1[a] (57) 1.3 ± 0.6[a] (90)	Red blood cells	Breeding probability in following four years Hatching probability in following four years Fledging probability in following four years	Yes Yes Yes	Goutte et al., 2014a
Great-winged Petrel (*Pterodroma macroptera*)	Median ± SE:	3.670 ± 0.180 (15)	Red blood cells	Prolactin concentration Egg volume	No No	This study

[a] Dry weight values reported in literature were converted to wet weight values by multiplying THg concentrations by 0.21, which assumed a 79% moisture content in blood (Eagles-Smith et al., 2008).
[b] Mean taken from five years of Hg concentrations.

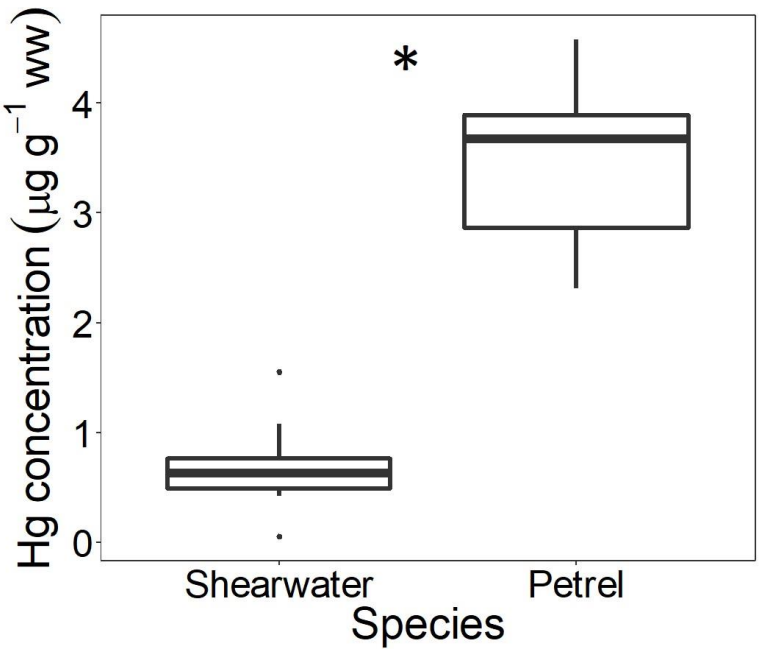

Figure 3.1 Boxplots of blood mercury concentrations in Flesh-footed Shearwaters and Great-winged Petrels

Total red blood cell mercury (μg g^{-1}) concentrations of Flesh-footed Shearwaters and Great-winged Petrels sampled during the incubation period in Western Australia in 2015. *indicates $p<0.05$.

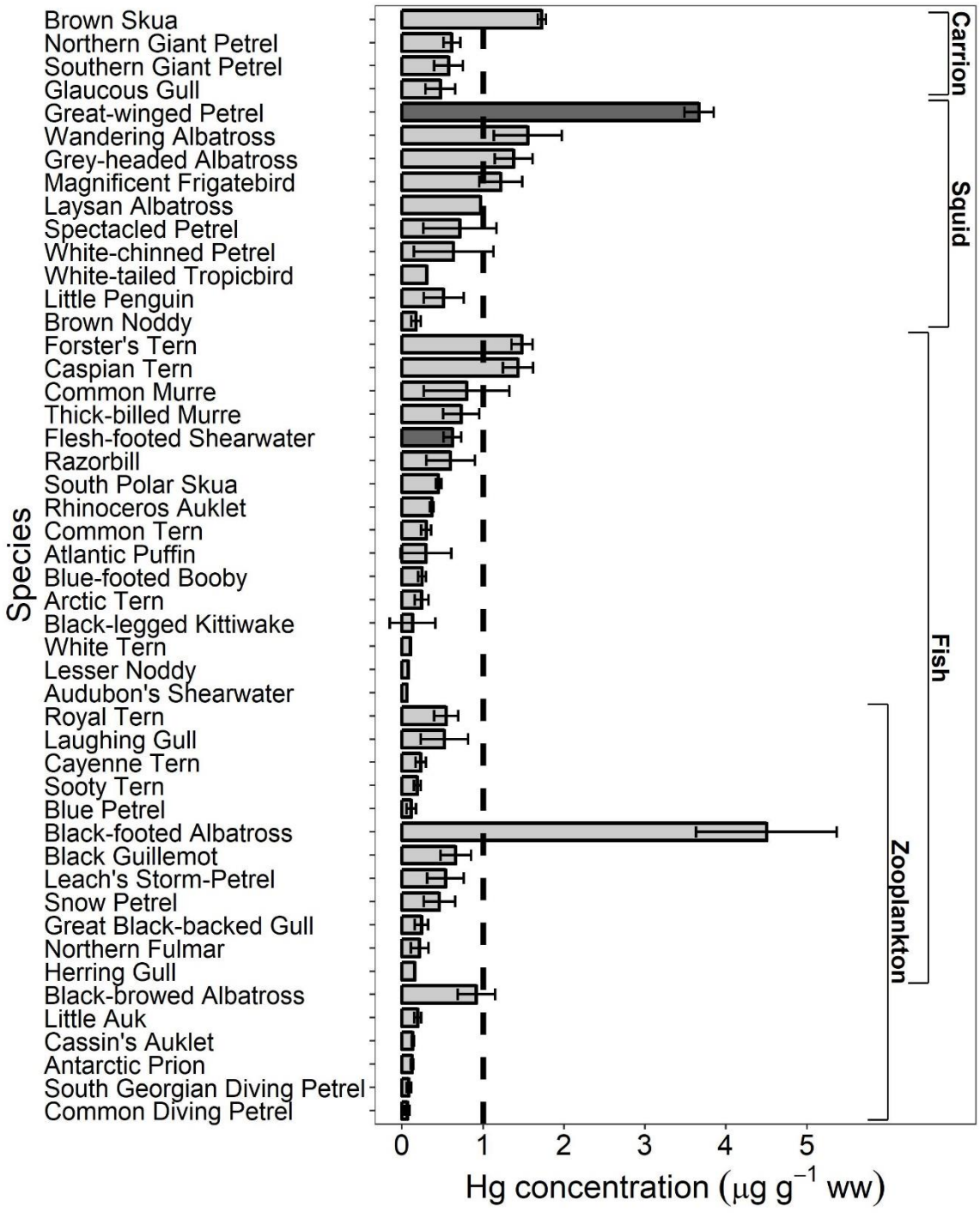

Figure 3.2 Blood mercury concentrations of adult seabirds measured in other studies

Total blood Hg concentrations (μg g^{-1} ww) of adult seabirds from other studies, grouped by general diet category. Values are reported as mean ± SD or median ± SE (SD or SE

represented as error bars, when available). Dark grey bars correspond to Flesh-footed Shearwaters and Great-winged Petrels from the current study. Dashed line corresponds to the toxicity benchmark of 1.0 μg g^{-1}, above which, general health, physiology, behavior, and reproduction tend to be affected by mercury (Ackerman et al., 2016b). Some species' values are medians of values from multiple studies (see Sources, below). Dry weight values reported in literature were converted to wet weight values by multiplying THg concentrations by 0.21, which assumed a 79% moisture content in blood (Eagles-Smith et al., 2008). Diet categories are based on information provided in the source study; if no diet information was available, additional studies were used to assign species to general diet categories (see Sources, below). This list is not exhaustive, and the aim is to present the THg concentrations of Great-winged Petrels and Flesh-footed Shearwaters within a context of global seabird THg concentrations.

Sources (listed in alphabetical order by Species):
Antarctic Prion (*Pachyptila desolata*): Anderson et al., 2009; Fromant et al., 2016; **Arctic Tern** (*Sterna paradisaea*): Bond and Diamond, 2009; Burnham et al., 2018; **Atlantic Puffin** (*Fratercula arctica*): Bond and Diamond, 2009; Burnham et al., 2018; Fort et al., 2015; Goodale et al., 2008; **Audubon's Shearwater** (*Puffinus lherminieri*): Catry et al., 2008; **Black-browed Albatross** (*Thalassarche melanophrys*): Anderson et al., 2009, and diet source: Croxall and Prince, 1980; **Black-footed Albatross** (*Phoebastria nigripes*): Finkelstein et al., 2007, and diet source: Conners et al., 2018; **Black-legged Kittiwake** (*Rissa tridactyla*): Burnham et al., 2018; Fort et al., 2015; Goutte et al., 2015; Lavoie et al., 2010; Tartu et al., 2013; Tartu et al., 2015a; **Black Guillemot** (*Cepphus grylle*): Burnham et al., 2018, and diet source: Hobson, 1993; **Blue-footed Booby** (*Sula nebouxii*): Lerma et al., 2016; **Blue Petrel** (*Halobaena caerulea*): Anderson et al., 2009, and diet source: Bocher et al., 2003; **Brown Noddy** (*Anous stolidus*): Catry et al., 2008; Sebastiano et al., 2017; **Brown Skua** (*Catharacta lonnbergi*): Goutte et al., 2014b; **Caspian Tern** (*Hydroprogne caspia*): Eagles-Smith et al., 2008, and diet source: Evans et al., 2011; **Cassin's Auklet** (*Ptychoramphus aleuticus*): Hipfner et al., 2011; **Cayenne Tern** (*Thalasseus sandvicensis*): Sebastiano et al., 2017; **Common Diving Petrel** (*Pelecanoides urinatrix*): Anderson et al., 2009, and diet source: Bocher et al., 2003; **Common Murre** (*Uria aalge*): Bond and Diamond, 2009; Fort et al., 2015; **Common Tern** (*Sterna hirundo*): Bond and Diamond, 2009; Goodale et al., 2008; **Flesh-footed Shearwater**: this study; **Forster's Tern** (*Sterna forsteri*): Eagles-Smith et al., 2008, and diet source: Ackerman et al., 2016a; **Glaucous Gull** (*Larus hyperboreus*): Burnham et al., 2018; **Great-winged Petrel**: this study; **Great Black-backed Gull** (*Larus marinus*): Goodale et al., 2008; Lavoie et al., 2010; **Grey-headed Albatross** (*Thalassarche chrysostoma*): Anderson et al., 2009; **Herring Gull** (*Larus argentatus*): Goodale et al., 2008; Lavoie et al., 2010; **Laughing Gull** (*Leucophaeus atricilla*): Sebastiano et al., 2017; **Laysan Albatross** (*Phoebastria immutabilis*): Finkelstein et al., 2006, and diet source: Conners et al., 2018; **Leach's Storm-petrel** (*Oceanodroma leucorhoa*): Bond and Diamond, 2009; Goodale et al., 2008; Pollet et al., 2017; **Lesser Noddy** (*Anous tenuirostris*): Catry et al., 2008; **Little Auk** (*Alle alle*): Burnham et al., 2018; Fort et al., 2014; **Little Penguin** (*Eudyptula minor*): Finger et al., 2016; **Magnificent Frigatebird** (*Fregata magnificens*): Sebastiano et al., 2016; **Northern Fulmar** (*Fulmarus glacialis*): Burnham et al., 2018, and diet source: Hobson, 1993; **Northern Giant Petrel** (*Macronectes halli*): Anderson et al., 2009; González-Solís et al., 2002, and diet source: Croxall and Prince, 1980; **Razorbill** (*Alca torda*): Bond and Diamond, 2009; Fort et al., 2015; Goodale et al., 2008; Lavoie et al., 2010; **Rhinoceros Auklet** (*Cerorhinca monocerata*): Hipfner et al., 2011; **Royal Tern** (*Thalassues maximus*): Sebastiano et al., 2017; **Snow Petrel** (*Pagodroma nivea*): Tartu et

al., 2014; Tartu et al., 2015a; **Sooty Tern** (*Onychoprion fuscatus*): Sebastiano et al., 2017; **Southern Giant Petrel** (*Macronectes giganteus*): Anderson et al., 2009; González-Solís et al., 2002, and diet source: Bocher et al., 2003; **South Georgian Diving Petrel** (*Pelecanoides georgicus*): Anderson et al., 2009; **South Polar Skua** (*Catharacta maccormicki*): Goutte et al., 2014b; **Spectacled Petrel** (*Procellaria conspicillata*): Carvalho et al., 2013; **Thick-billed Murre** (*Uria lomvia*): Burnham et al., 2018; **Wandering Albatross** (*Diomedea exulans*): Anderson et al., 2009; Carravieri et al., 2014; Tavares et al., 2013; **White-chinned Petrel** (*Procellaria aequinoctialis*): Anderson et al., 2009; Carvalho et al., 2013; **White-tailed Tropicbird** (*Phaethon lepturus*): Catry et al., 2008; **White Tern** (*Gygis alba*): Catry et al., 2008.

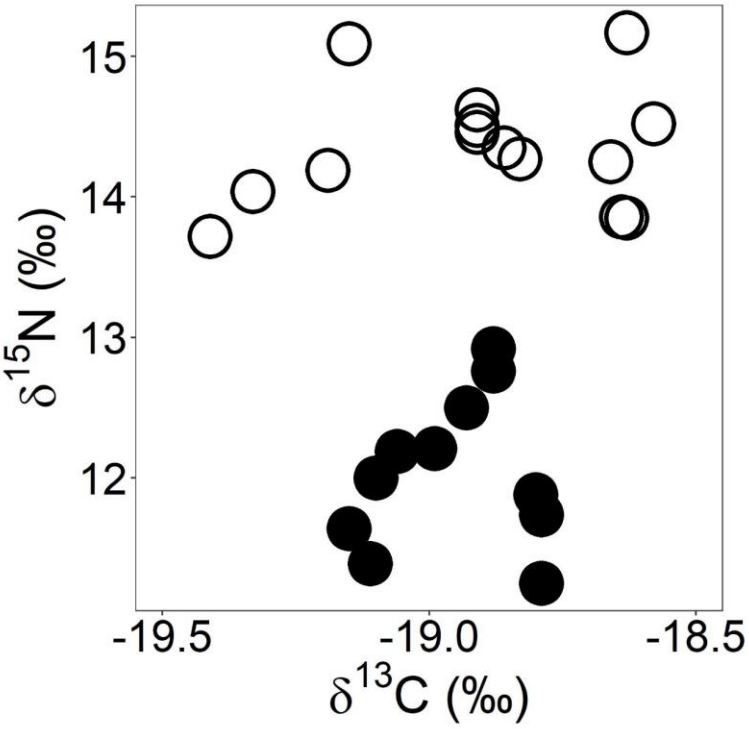

Figure 3.3 Scatterplot of carbon and nitrogen stable isotopes in Flesh-footed Shearwaters and Great-winged Petrels

Scatterplot of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of incubating Flesh-footed Shearwater (filled circles) and Great-winged Petrel (open circles) red blood cells, sampled in Western Australia in 2015. Two Great-winged Petrels had very similar stable isotope values at (-18.63, 13.85) and (-18.64, 13.86) and two more at (-18.91, 14.46) and (-18.91, 14.51), and consequently, these pairs of circles overlap.

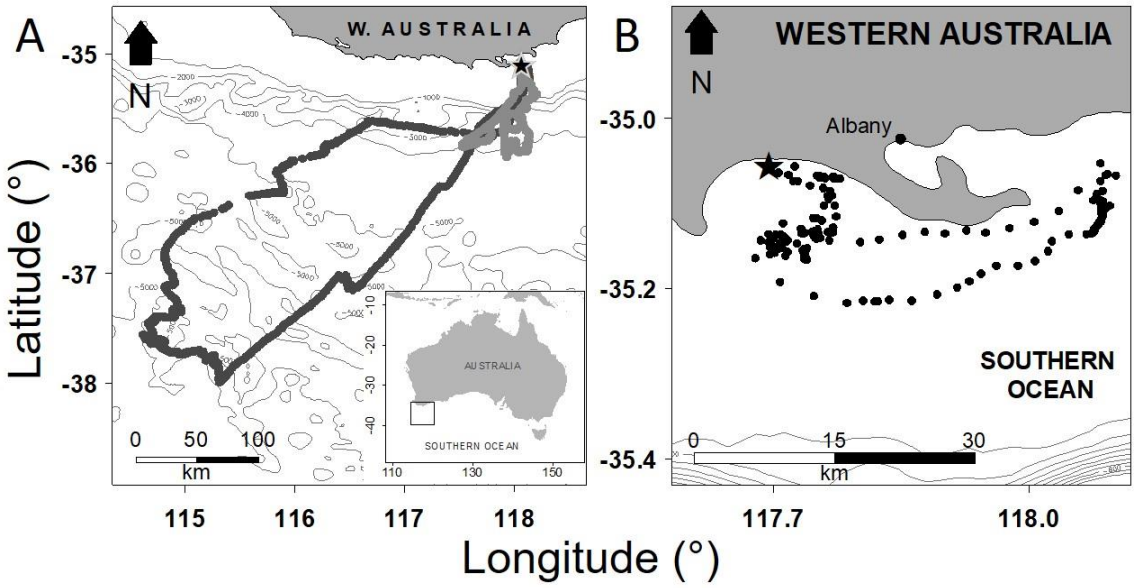

Figure 3.4 GPS locations of Flesh-footed Shearwaters and Great-winged Petrels in Western Australia

GPS-recorded foraging trips from incubating Great-winged Petrel (A) at Breaksea Island (indicated by star), and Flesh-footed Shearwater (B) at Shelter Island (indicated by star). For the Great-winged Petrel, two different foraging trips are represented by dark grey points (trip 1) and light grey points (trip 2). Thin light grey lines correspond to bathymetry. Rectangle in map inset indicates sampling location within the context of Australia.

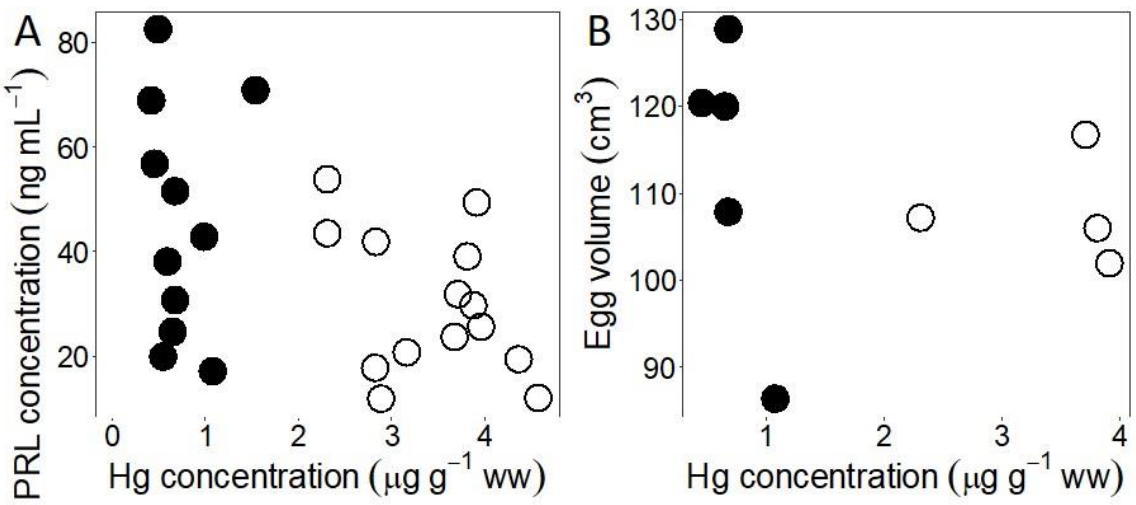

Figure 3.5 Scatterplots of mercury, prolactin, and egg volume in Flesh-footed Shearwaters and Great-winged Petrels

Scatterplots of total red blood cell mercury concentration (μg g^{-1}) vs (A) plasma prolactin concentration (ng mL^{-1}) and (B) egg volume (cm^3) in Flesh-footed Shearwaters (filled circles) and Great-winged Petrels (open circles) sampled during the incubation period in Western Australia in 2015.

Dissertation Conclusions

Seabirds are often considered sentinels of the marine environment because they are predators that forage at upper trophic levels and they are wide-ranging, and thus can sample the ocean on scales of tens to thousands of kilometers (Parsons et al., 2008; Piatt et al., 2007). In this dissertation, I measured the foraging ecology of eight species of seabirds from eleven colonies in the Pacific and Southern Oceans, the Caribbean Sea, and the Gulf of California to elucidate information on seabirds' behaviors, the oceanographic habitats in which they forage, and potential contaminant exposure. I took a three-fold, multi-species approach to obtain a large sample size that best represented seabirds' behaviors, habitat use, and contaminant exposure within the vast and dynamic marine environment. I then assessed the potential for sublethal effects of a contaminant, mercury, on seabirds' breeding. To accomplish this, I tested the hypotheses that: 1) local oceanographic conditions would drive foraging behaviors; 2) local oceanographic processes would contribute to seabirds' contaminant concentrations; and 3) mercury would negatively affect seabirds' breeding.

First, I characterized the oceanographic habitat in which four booby species (*Sula dactylatra*, *S. leucogaster*, *S. nebouxii*, and *S. sula*) foraged in relation to their foraging behaviors across seven colonies in the Pacific Ocean and the Gulf of California. Seabirds forage in proximity to some known oceanographic habitats like seamounts and zones of converging atmospheric and oceanic surface currents (Palacios et al., 2006). My objective, however, was to identify more finescale oceanographic features and behaviors and to assess similarities between colonies. Boobies exhibited behavioral plasticity by changing their behaviors in relation to local oceanographic conditions. Furthermore, behaviors were similar across colonies that shared oceanographic conditions (e.g. similarities in local sea surface temperature, chlorophyll-*a* –a proxy for primary productivity, and bathymetric topography). These data suggest that boobies can forage efficiently in a variety of habitats, where foraging may be patchy (Weimerskirch, 2007). Behavioral plasticity enables animals to be more

adaptive to changes in environmental conditions (Beever et al., 2017; Hadfield and Strathmann, 1996). In light of the changing climate, where many low-lying islands and atolls are predicted to become submerged underwater (including several islands in this study), seabirds that breed on these islands will be forced to nest at other colonies with potentially different oceanographic habitats (Baker et al., 2006; Hatfield et al., 2012). Evidence of behavioral plasticity suggests that boobies and other seabirds that are flexible foragers will be successful with this change. These data were also important because they represent the first published GPS-tracking data of boobies in several of these colonies (Isla Clarión, Revillagigedo Archipelago; Isla San Jorge, Gulf of California; Isla Pajarera, Jalisco; and Isla Peña Blanca, Colima, México).

In Chapter 2, I applied the concept of using seabirds as sentinels to sample the ocean in a variety of locations for contaminants (Burger and Gochfeld, 2004; Elliott and Elliott, 2013). My objective was to sample seabirds' blood to establish baseline contaminant concentrations in tropical and sub-tropical colonies and relate these contaminants to local foraging ecology. I measured persistent organic pollutants (POP) and mercury contaminants in seven species of boobies (*S. dactylatra*, *S. leucogaster*, and *S. sula*) and frigatebirds (*Fregata magnificens* and *F. minor*) from four colonies in the Pacific Ocean and the Caribbean Sea. Mercury and polychlorinated biphenyls (PCB) were detected in all birds, and many other organochlorine pesticides and industrial compounds were also detected. Seabirds' foraging ecology was helpful in explaining some contaminant distributions: habitat (represented by carbon and sulfur stable isotopes) was correlated with DDT at Palmyra Atoll and mercury at Laysan Island, and trophic position (represented by nitrogen stable isotopes) was correlated with mercury at Tern Island. Additionally, there were distinct distribution patterns of POP between habitats, such that some POP like DDT and the organophosphate pesticide chlorpyrifos were detected in birds that mostly foraged in pelagic regions far from the breeding colony, but higher concentrations of other organochlorine pesticides like endosulfan and flame retardant compounds (polybrominated diphenyl ethers; PBDE) were

highest in birds that foraged closer to the colony. Thus, both spatial ecology and diet contributed to contaminant exposure in tropical seabirds, though the importance of these factors varied between colonies. While limited point sources in some of these regions likely contributed to the detections of some compounds (e.g. the presence of equipment, materials, and buildings leftover from use by the U. S. military; Maragos et al., 2008; Miao et al., 2001, 2000), most of these contaminants had likely been transported via atmospheric and oceanic currents to the coastal and pelagic foodwebs in which boobies and frigatebirds foraged. The nearshore-offshore patterns observed suggested that the island mass effect may help to retain some compounds nearshore (Gelado-Caballero et al., 1996), while compounds detected offshore might be due to specific ocean current movements that only occur offshore (e.g. the Equatorial Current emanates from Central America and flows westward to the north of Palmyra Atoll, but the Equatorial Countercurrent originates in Asia, and flows eastward around Palmyra; Hamann et al., 2004). Furthermore, mercury, which is thought to be mainly synthesized by anaerobes, tends to be elevated in pelagic regions due to high rates of methylation in the mesopelagic zone (200 – 1000 m; Blum et al., 2013). Mesopelagic predators typically exhibit higher mercury concentrations than predators that forage in other regions of the ocean (Anderson et al., 2009; Monteiro et al., 1996; Peterson et al., 2015), which may also contribute to diet-related differences in mercury concentrations in seabirds. Overall, these results demonstrate that POP and mercury are globally distributed, which is especially well-illustrated by the detection of these compounds in upper trophic level predators in remote regions of the tropical ocean.

In Chapter 3, I assessed the relationship between mercury and its potential adverse effects on seabirds. Seabirds have been at the forefront of contaminants affecting wildlife; for example, DDT's association with eggshell thinning (Bitman et al., 1970) is the most well-known, but contaminants like mercury cause other adverse effects that decrease reproductive success, alter behaviors, and cause antioxidant and genetic damage (Burgess and Meyer, 2008; Ceccatelli et al., 2010; Frederick and Jayasena, 2011; Grandjean et al.,

1997). However, many relationships between contaminants, specifically mercury, and adverse effects are surprisingly non-linear, and exhibit species-specific and sex-specific responses (Carravieri et al., 2014; Pollet et al., 2017; Tartu et al., 2015). My objective was to establish baseline mercury concentrations and relate them to breeding in two seabirds in the Southern Ocean: Flesh-footed Shearwaters (*Ardenna carneipes*) and Great-winged Petrels (*Pterodroma macroptera*). I measured mercury concentrations, foraging ecology, and two aspects of breeding: concentrations of the breeding hormone prolactin, and egg volume. Mercury in Great-winged Petrels was among the highest of seabird blood reported (Eagles-Smith et al., 2008; Finkelstein et al., 2006; Goutte et al., 2014); yet I did not detect a correlation between mercury and prolactin or egg volume. Shearwaters' mercury concentrations were much smaller than petrels, but I also did not detect a relationship between mercury and breeding for this species. Diet likely played a role in mercury exposure between species: Great-winged Petrels are mesopelagic squid specialists (Imber, 1973; Ridoux, 1994), and Flesh-footed Shearwaters forage in shallow, nearshore waters on low trophic level prey (Gould et al., 1997; Powell, 2009). It is possible that mesopelagic predators like Great-winged Petrels have evolved to tolerate high mercury concentrations in their diet, and thus they may not exhibit adverse effects from high mercury concentrations. However, anthropogenic mercury emissions are increasing (Lamborg et al., 2014), and species that have not evolved to tolerate high mercury concentrations may be more at-risk to mercury exposure and the adverse effects associated with it (Thompson, 1996). These data are especially important because I established baseline mercury concentrations for Flesh-footed Shearwaters, whose populations are declining (Lavers 2015) and Great-winged Petrels are an under-studied species whose population trends are unknown.

Foraging locations and diet, elucidated with stable isotopes and GPS-tracking tags, helped to describe seabirds' use of marine habitats. These data, in turn, helped to describe seabirds' exposure to POP and mercury contaminants. Overall, seabirds are an excellent sentinel to assess contaminants in remote regions of the world ocean. Though mercury

concentrations were among the highest observed in seabird blood, Great-winged Petrels did not appear to exhibit any adverse effects on breeding related to these mercury concentrations. The behavioral plasticity exhibited by boobies also indicates that seabirds are adaptable to changes in their environment. Due to behavioral plasticity and the tolerance of elevated mercury concentrations, some seabird species appear to be robust inhabitants of the dynamic marine environment because they navigate the ocean, land, and air to find food and breed. Many threats still face seabirds in each of these environments, including becoming fisheries' by-catch at sea, and experiencing decreased reproductive success, and even mortality, due to invasive predators on land (Croxall et al., 2012). Though I established baseline blood-based contaminant concentrations for seabirds in all colonies that I sampled, much more research is needed to determine sublethal effects of contaminants, and to establish baseline contaminant concentrations at further locations. Research is also needed to assess emerging compounds that have POP-like properties (Gavrilescu et al., 2015). However, seabirds' ability to adapt and evolve in the face of these threat may be helpful over the long term, as anthropogenic threats like emerging compounds of concern and climate change increase the pressures on these birds (Beever et al., 2017; Hatfield et al., 2012; Hazen et al., 2012; Ma et al., 2011).

References

Anderson, O.R.J., Phillips, R.A., McDonald, R.A., Shore, R.F., McGill, R.A.R., Bearhop, S., 2009. Influence of trophic position and foraging range on mercury levels within a seabird community. Mar. Ecol. Prog. Ser. 375, 277–288. https://doi.org/10.3354/meps07784

Baker, J., Littnan, C., Johnston, D., 2006. Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the Northwestern Hawaiian Islands. Endanger. Species Res. 2, 21–30. https://doi.org/10.3354/esr002021

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Jason, B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. doi:10.1002/fee.1502. https://doi.org/10.1002/fee.1502

Bitman, J., Cecil, H.C., Fries, G.F., 1970. DDT-induced inhibition of avian shell gland carbonic anhydrase: a mechanism for thin eggshells. Science (80-.). 168, 594–596. https://doi.org/10.1126/science.168.3931.594

Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

Burger, J., Gochfeld, M., 2004. Marine Birds as Sentinels of Environmental Pollution. Ecohealth 1, 263–274. https://doi.org/10.1007/s10393-004-0096-4

Burgess, N.M., Meyer, M.W., 2008. Methylmercury exposure associated with reduced productivity in common loons. Ecotoxicology 17, 83–91. https://doi.org/10.1007/s10646-007-0167-8

Carravieri, A., Cherel, Y., Blévin, P., Brault-Favrou, M., Chastel, O., Bustamante, P., 2014. Mercury exposure in a large subantarctic avian community. Environ. Pollut. 190, 51–57. https://doi.org/10.1016/j.envpol.2014.03.017

Ceccatelli, S., Daré, E., Moors, M., 2010. Methylmercury-induced neurotoxicity and apoptosis. Chem. Biol. Interact. 188, 301–308. https://doi.org/10.1016/j.cbi.2010.04.007

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, 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. https://doi.org/10.1017/S0959270912000020

Eagles-Smith, C.A., Ackerman, J.T., Adelsbach, T.L., Takekawa, J.Y., Miles, A.K., Keister, R.A., 2008. Mercury correlations among six tissues for four waterbird species breeding in San Francisco Bay, California, USA. Environ. Toxicol. Chem. 27, 2136–2153. https://doi.org/10.1897/08-038.1

Elliott, J.E., Elliott, K.H., 2013. Tracking marine pollution. Science (80-.). 340, 556–558. https://doi.org/10.1126/science.1235197

Finkelstein, M., Keitt, B.S., Croll, D.A., Tershy, B., Jarman, W.M., Rodriguez-Pastor, S., Anderson, D.J., Sievert, P.R., Smith, D.R., 2006. Albatross species demonstrate regional differences in North Pacific marine contamination. Ecol. Appl. 16, 678–686.

https://doi.org/10.1890/1051-0761(2006)016[0678:ASDRDI]2.0.CO;2

Frederick, P., Jayasena, N., 2011. Altered pairing behaviour and reproductive success in white ibises exposed to environmentally relevant concentrations of methylmercury. Proc. R. Soc. B Biol. Sci. 278, 1851–1857. https://doi.org/10.1098/rspb.2010.2189

Gavrilescu, M., Demnerová, K., Aamand, J., Agathos, S., Fava, F., 2015. Emerging pollutants in the environment: Present and future challenges in biomonitoring, ecological risks and bioremediation. N. Biotechnol. 32, 147–156. https://doi.org/10.1016/j.nbt.2014.01.001

Gelado-Caballero, M.D., Torres-Padrón, M.E., Hernández-Brito, J.J., Herrera-Melián, J.A., Pérez-Peña, J., 1996. Aluminium distributions in Central East Atlantic waters (Canary Islands). Mar. Chem. 51, 359–372. https://doi.org/10.1016/0304-4203(95)00069-0

Gould, P., Ostrom, P.H., Walker, W., 1997. Food of flesh-tooted shearwaters Puffinus carneipes associated with high seas driftnets in the central north Pacific Ocean. Emu 97, 168–173.

Goutte, A., Bustamante, P., Barbraud, C., Delord, K., Weimerskirch, H., Chastel, O., 2014. Demographic responses to mercury exposure in two closely related antarctic top predators. Ecology 95, 1075–1086. https://doi.org/10.1890/13-1229.1

Grandjean, P., Weihe, P., White, R.F., Debes, F., Araki, S., Yokoyama, K., Murata, K., Sørensen, N., Dahl, R., Jørgensen, P.J., 1997. Cognitive Deficit in 7-Year-Old Children with Prenatal Exposure to Methylmercury. Neurotoxicol. Teratol. 19, 417–428. https://doi.org/10.1016/S0892-0362(97)00097-4

Hadfield, M., Strathmann, M., 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. Oceanol. Acta 19, 323–334.

Hamann, I.M., Boehlert, G.W., Wilson, C.D., 2004. Effects of steep topography on the flow and stratification near Palmyra Atoll. Ocean Dyn. 54, 460–473. https://doi.org/10.1007/s10236-004-0091-x

Hatfield, J.S., Reynolds, M.H., Seavy, N.E., Krause, C.M., 2012. Population Dynamics of Hawaiian Seabird Colonies Vulnerable to Sea-Level Rise. Conserv. Biol. 26, 667–678. https://doi.org/10.1111/j.1523-1739.2012.01853.x

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P., Crowder, L.B., Block, B.A., 2012. Predicted habitat shifts of Pacific top predators in a changing climate. Nat. Clim. Chang. 2, 1–5. https://doi.org/10.1038/nclimate1686

Imber, M.J., 1973. The food of grey-faced petrels (Pterodroma macroptera gouldi (Hutton)), with special reference to diurnal vertical migration of their prey. J. Anim. Ecol. 42, 645–662. https://doi.org/10.2307/3130

Lamborg, C.H., Hammerschmidt, C.R., Bowman, K.L., Swarr, G.J., Munson, K.M., Ohnemus, D.C., Lam, P.J., Heimbürger, L.-E., Rijkenberg, M.J.A., Saito, M.A., 2014. A global ocean inventory of anthropogenic mercury based on water column measurements. Nature 512, 65–68. https://doi.org/10.1038/nature13563

Lavers, J.L., 2015. Population status and threats to Flesh-footed Shearwaters (Puffinus carneipes) in South and Western Australia. ICES J. Mar. Sci. 72, 316–327.

Ma, J., Hung, H., Tian, C., Kallenborn, R., 2011. Revolatilization of persistent organic pollutants in the Arctic induced by climate change. Nat. Clim. Chang. 1, 255–260. https://doi.org/10.1038/nclimate1167

Maragos, J., Miller, J., Gove, J., Demartini, E., 2008. US Coral Reefs in the Line and Phoenix Islands , Central Pacific Ocean 1 : History, Geology, Oceanography, and Biology. Coral Reefs USA 595–641. https://doi.org/10.1007/978-1-4020-6847-8_15

Miao, X.-S., Woodward, L.A., Swenson, C., Li, Q.X., 2001. Comparative Concentrations of Metals in Marine Species from French Frigate Shoals , North Pacific Ocean. Mar. Pollut. Bull. 42, 1049–1054.

Miao, X.S., Swenson, C., Woodward, L.A., Li, Q.X., 2000. Distribution of polychlorinated biphenyls in marine species from French Frigate Shoals, North Pacific Ocean. Sci. Total Environ. 257, 17–28. https://doi.org/10.1016/S0048-9697(00)00484-8

Monteiro, L.R., Costa, V., Furness, R.W., Santos, R.S., 1996. Mercury concentrations in prey fish indicate enhanced bioaccumulation in mesopelagic environments. Mar. Ecol. Prog. Ser. 141, 21–25. https://doi.org/10.3354/meps141021

Palacios, D.M., Bograd, S.J., Foley, D.G., Schwing, F.B., 2006. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. Deep Sea Res. Part II Top. Stud. Oceanogr. 53, 250–269. https://doi.org/10.1016/j.dsr2.2006.03.004

Parsons, M., Mitchell, I.P., 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. https://doi.org/10.1093/icesjms/fsn155

Peterson, S.H., Ackerman, J.T., Costa, D.P., 2015. Marine foraging ecology influences mercury bioaccumulation in deep-diving northern elephant seals. Proc. R. Soc. B Biol. Sci. 282, 20150710. https://doi.org/10.1098/rspb.2015.0710

Piatt, J.F., Sydeman, W.J., Weise, F., 2007. Seabirds as indicators of marine ecosystems. Mar. Ecol. Prog. Ser. 352, 199–204. https://doi.org/10.3354/meps07070

Pollet, I.L., Leonard, M.L., O'Driscoll, N.J., Burgess, N.M., Shutler, D., O'Driscoll, N.J., Burgess, N.M., Shutler, D., 2017. Relationships between blood mercury levels, reproduction, and return rate in a small seabird. Ecotoxicology 26, 97–103. https://doi.org/10.1007/s10646-016-1745-4

Powell, C.D.L., 2009. Foraging movements and the migration trajectory of Flesh-footed Shearwaters Puffinus carneipes from the south coast of Western Australia. Mar. Ornithol. 37, 115–120.

Ridoux, V., 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar. Ornithol. 22, 65–128.

Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H.,

Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. Sci. Total Environ. 505, 180–188. https://doi.org/10.1016/j.scitotenv.2014.10.008

Thompson, D., 1996. Mercury in birds and terrestrial mammals, in: Environmental Contaminants in Wildlife: Interpreting Tissues Concentrations. Lewis Publishers, Boca Raton, Florida, USA, pp. 341–356.

Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? Deep. Res. Part II Top. Stud. Oceanogr. 54, 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013