THE DIET OF MASKED, BROWN AND RED-FOOTED BOOBIES (SULIDAE: PELECANIFORMES) IN THE MONA PASSAGE, PUERTO RICO

by

Ricardo López-Ortiz

A thesis submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

MARINE SCIENCES (Biological Oceanography)

UNIVERSITY OF PUERTO RICO MAYAGÜEZ CAMPUS 2009

Approved by:

Nilda E. Aponte, Ph. D. Member, Graduate Committee

Richard S. Appeldoorn, Ph. D. Member, Graduate Committee

Lucy Bunkley Williams, Ph. D. Member, Graduate Committee

Paul M. Yoshioka, Ph. D. President, Graduate Committee

Miguel A. Muñoz, Ph. D. Representative of Graduate Studies

Nilda E. Aponte, Ph. D. Chairperson of the Department

Date
Date
Date
Date
Date

Date

ABSTRACT

From four visits to Monito Islet in the Isla de Mona Natural Reserve, the prev description (diversity, dominance, importance, length, taxonomy and volume), the dietary niche (breadth, contribution and overlap) and the feeding strategy were studied through regurgitation analysis of three pelagic bird species roosting and nesting in sympatry, and constituting the genus *Sula* in the West Indies. This population consumed approximately 28,466 organisms (2.4 metric tons or 17 organisms per bird) per day. Food was abundant and the species differed in diets and feeding strategies. The masked booby (S. dactylatra) regurgitated the largest organisms, with a diet dominated by the clearwing flyingfish (*Cypselerus comatus*). Both the brown (S. leucogaster) and the red-footed booby (S. sula) were generalists and regurgitated organisms similar in size, mostly mackerel scad (Decapterus macarellus) and the sailfin flyingfish (Parexocoetus hillianus), respectively. At the prey family level, the diets were similar in oligotrophic zones of the Pacific Ocean. Prey volume was highest in visits at breeding peaks, especially in the masked booby. Their diets were similar to the diet reported for dolphinfish (Coryphaena hippurus) in contrast to yellowfin tuna (*Thunnus albacares*). The evidence suggests each species feeds from a different resource. The findings have implications in the use of seabirds as indicators of epipelagic fish stock fluctuations.

RESUMEN

De cuatro visitas al Islote Monito en la Reserva Natural de Isla de Mona, la descripción de presa (diversidad, dominancia, importancia, largo, taxonomía y volumen), el nicho dietético (amplitud, contribución y solapamiento) y la estrategia de alimentación fueron estudiados a través del análisis de regurgitaciones de tres especies de aves pelágicas que anidan y pernoctan en simpatría; constituyendo el género Sula en las Indias Occidentales. Esta población consumió aproximadamente 28,466 organismos (2.4 toneladas métricas ó 17 organismos por ave) por día. El alimento fue abundante y las especies contrastaron en dietas y estrategias de alimentación. La boba enmascarada (S. *dactylatra*) regurgitó los organismos más grandes, con una dieta dominada por el pez volador holandés (Cypselerus comatus). Ambas, la boba prieta (S. leucogaster) y la blanca (S. sula) fueron generalistas y regurgitaron organismos similares en tamaños, mayormente macarela caballa (Decapterus macarellus) y el pez volador aletón (Parexocoetus hillianus), respectivamente. A nivel de familia de presa, los organismos regurgitados fueron similares en zonas oligotróficas del Océano Pacifico. El volumen de la presa fue mayor durante los picos reproductivos, especialmente en la boba enmascarada. Sus dietas fueron similares a la reportada para el dorado (Coryphaena hippurus) en contraste con el rabil (Thunnus albacares). La evidencia sugiere que cada especie se alimenta de un recurso distinto. Estos resultados tienen implicaciones en el uso de aves marinas como indicadoras de la reserva de peces epipelágicos.

ACKNOWLEDGMENTS

The Sea Grant Program (project number 5-35648) and the Puerto Rico Department of Natural and Environmental Resources (DNER) supported this work. Particular, thanks go to Att. José L. Chabert, Carlos Diez, Miguel Figuerola, Dr. Miguel A. García, Robert Matos, Aida Rosario, Wilfredo Torres and Dr. Manuel Valdés-Pizzini. The crew of the vessel Orca Too administered by Eng. Francisco García-Huertas (Don Paco, Mona Aquatic Inc.) and steered by Capt. Carlos Vélez-Pabón kindly provided transportation to Mona Island. Carlos Díaz from the US Fish and Wildlife Service shared reports related to epipelagic communities. Dr. Bruce B. Collette provided species identification documents from FAO. Dr. Kent E. Carpenter and Michel Lamboeuf from Old Dominion University and FAO-FIRM, respectively, allowed the use of FAO copyright drawings from Carpenter (2002).

Many friends and colleagues participated in the development and continuity of this work, especially Elvin Binet, Monserrate "Taty" Casiano, Eduardo Cintrón, Yulissa García, Kurt Grove, Hector López, Tony Nieves, Gaspar Pons and Eduardo Ventosa. My coworkers at the DNER Yellow-shouldered Blackbird Project (José Camacho, Arnaldo Falcón and Roseanne Medina), through their own initiative, orchestrated trip logistics. Mona Island DNER Rangers and employees treated us as part of their team. A unique backup was given by my companion, friend and colleague, Katsí Regina Ramos-Álvarez, who also helped in the sample collection and analyses. I owe my interest in the study of fish to my mother, Att. Myrna Ortiz-Lizardi, who saturated me with her patience and perseverance, and provided me with many fish guidebooks and pleased me with numerous beach trips in my childhood. The space and time to finish this work was a loan from my family, specially my mother and kids: Antonio López-Díaz, Sebastián López-Ramos and Regina López-Ramos. Two great friends, Annette Díaz and Julio E. Cardona, awakened in me a curiosity for birds. Dr. Adrianne G. Tossas, Dr. Caldwell Hahn, Julio E. Cardona and Dr. Wayne Arendt revised the earlier draft of this manuscript.

I want to express sincere appreciation to the President of my graduate committee Dr. Paul M. Yoshioka for giving me the opportunity to do research under his guidance. I was privileged to be trained in biostatistics, ecology, ichthyology and ornithology by Dr. Richard S. Appeldoorn, Dr. Carlos Delanoy, Dr. Dannie A. Hensley (R. I. P), Dr. Allen R. Lewis and Dr. Paul M. Yoshioka. Dr. Lucy Bunkley-Williams revised the latest draft of this manuscript and opportunely supports my work with enthusiasm and academic advice. Thanks to Dr. Miguel A. Muñoz for accepting to be representative of Graduate Studies. I would like to express my utmost gratitude to the Director of the Department of Marine Science, Dr. Nilda E. Aponte, for encouraging me overcome difficulties in order to finish the doctoral degree.

Dedico:

Mi vida a mis hijos y este trabajo a mi abuela y gran amiga, Belén Lizardi (D. E. P. 2007) y a un excelente catedrático, Dr. Dannie Hensley (D. E. P. 2008).

I dedicate:

My life to my children and this work to my grandmother and great friend, Belén Lizardi (R. I. P) and to an excellent professor, Dr. Dannie Hensley (R. I. P. 2008).

Table of Contents

RESUMEN
ACKNOWLEDGMENTS
TABLE OF CONTENTS. VII LIST OF TABLES VIII INTRODUCTION. 2 LITERATURE REVIEW. 7 COEXISTENCE 7 THE SULIDS 11 MASKED BOOBY 14
LIST OF TABLES
INTRODUCTION
LITERATURE REVIEW
COEXISTENCE
THE SULIDS
Masked Booby
BROWN BOOBY 16
RED-FOOTED BOOBY
OBJECTIVES
METHODOLOGY
Study Site
SAMPLE COLLECTION
DATA ANALYSIS
RESULTS
PREY SIZE ESTIMATION
MASKED BOOBY
BROWN BOOBY
RED-FOOTED BOOBY
COMPARISONS AMONG SPECIES
DISCUSSION
COLONY THREATS
DIET SIMILARITIES
PREY CATEGORIES AND TEMPORAL DIFFERENCES
FEEDING STRATEGIES
Oceanic Locales
SULID COEXISTENCE
FEEDING ASSOCIATION WITH SUBSURFACE PREDATORS
EPIPELAGIC FISH STOCK
CONCLUSION
REFERENCES
TABLES
APPENDIX A. TAXONOMY AND PREY SIZE ESTIMATION METHOD
APPENDIX B. MORPHOMETRY OF PREY SPECIES 126
APPENDIX C. PREY SIZE REGRESSION VALUES
APPENDIX D. PREY SIZE ESTIMATION SCATTERPLOT: AN EXAMPLE
APPENDIX E. ASPECTS OF FEEDING ECOLOGY; THE COSTELLO METHOD

List of Tables

Tables

Page

List of Figures

Figures

Page

Figure 1. Seabird species targeted in the study in Monito Islet (2003) 115
Figure 2. Study site location (Monito Islet), adapted from Carpenter (2002) 116
Figure 3. Comparison of mean number of prey organisms per regurgitation among visits
(a) and bird species (b) 117
Figure 4. Comparison of mean prey length among visits (a) and bird species (b) 118
Figure 5. Comparison of mean prey volume among visits (a) and bird species (b) 119
Figure 6. Aspect of the masked booby (Sula dactylatra) feeding ecology (biomass by
volume) for each visit (a) and overall (b)
Figure 7. Aspect of the brown booby (Sula leucogaster) feeding ecology (biomass by
volume) for each visit (a) and overall (b) 121
Figure 8. Aspect of the red-footed booby (Sula sula) feeding ecology (biomass by volume)
for each visit (a) and overall (b)
Figure 9. Comparison of diet among <i>Sula</i> spp. and visits, using Shannon's and Simpson's
diversity indexes
Figure 10. Graph showing the results of a canonical discriminant function analysis of the
number of each prey category within each regurgitation sample. Based on Table 14,
each circle, square or triangle represent regurgitations from masked (Sula
dactylatra), brown (S. leucogaster) and red-footed (S. sula) booby, respectively.
Filled square equals group centroid

INTRODUCTION

Unlike most vertebrates, many seabirds and aquatic birds need to perform daily activities related to survival (predation, competition, reproduction, nutrition, etc.) in association with three different environments: air, land and water. Seabirds are fast-moving, wide-ranging, highly efficient top predators of oceanic ecosystems that exploit the upper layers of the water column (Wilson *et al.* 2002). They have some of the largest foraging ranges of any vertebrate (Fisher and Lockley 1954, Harris 1977, Nelson 1979, Dunnet and Ollason 1982). The annual food consumption of all the world's seabirds is similar to the global fisheries landings, ca. 80 million metric tons (Broke 2004). Therefore, their biology is interesting in terms of strategies evolved to effectively utilize the three environments and their interactions with fisheries activities.

As the marine environments mostly used by seabirds to obtain nutrients are also exploited by humans, most studies of seabirds are pelagic and based in their predator prey interactions. Indeed, the aspects of seabird population biology most sensitive to environmental changes are probably diet, adult activity budgets and breeding success (Duffy and Merlen 1986, Furness and Monaghan 1987, Gibbs *et al.* 1987). These three aspects are critical during the peak of egg and chick production. Energy requirements are greatest during the period of chick brooding, but an upper limit to the food size that parents can carry may ultimately limit brood size to one and preclude rapid growth in pelagic species (Ricklefs 1983). Meal size, feeding rate and energy density of the meal influence the rate of energy delivery to the chick. These considerations suggest that data on diet quality, meal size, and feeding frequency may provide a basis for comparing

feeding ecology and corresponding breeding adaptations among species of pelagic seabirds (Ricklefs 1983).

In general, based on diet and behavioral studies, seabirds are considered 1) important predators of small fishes (Montevecchi and Myers 1996, Anderson et al. 1980) and 1982, Sunada et al. 1981); 2) threatened by human fishing activities (Idyll 1973, Crawford and Shelton 1978, Cairns 1987, Montevecchi et al. 1987, Hamer et al. 1991, Tasker et al. 2000); and 3) threatened by exotic animals (Pitman et al.2005). They are also indicators of 1) health of the oceans (e.g., plastics, oil, organochlorines, heavy metals and possibly radionuclides; Ryan 1988, Ryan et al. 1988, Pérez-López et al. 2005), 2) fish stock fluctuations (Kirkham and Morris 1979, Sunada et al. 1981, Cairns 1987, Muck and Pauly 1987, Montevecchi 1993, Montevecchi et al. 1987, Velarde et al. 1994, Regehr and Montevecchi 1997), 3) environmental changes (Boersma 1978, Nelson 1978, Schreiber and Schreiber 1984, Gibbs et al. 1987, Jahncke and Goya 2000, Wilson et al. 2002) and 4) predatory activities of oceanic subsurface predators (Erdman 1967, Au and Pitman 1986, Pitman and Ballance 1992, Ballance and Pitman 1999, Hebshi et al. 2008). Harding et al. (2005) prepared a bibliography of literature on seabirds as indicators of the marine environment.

Stomach contents analyses on seabirds provide important data on feeding ecology, fisheries and trophodynamics (Amundsen *et al.* 1996, Hansson 1998). Prey size combined with other ecological parameters (e.g. frequency of occurrence and abundance) may provide information on the importance of specific prey for a particular predator. This is fundamental in determining possible interactions between human fishery activities and the ecology of marine predators.

The diets of commercially important fish species are well known, but diets of seabird species are generally unknown and studied mostly from the largest seabird species when they interact with industrial fisheries. Ashmole and Ashmole (1967), Montevecchi (1993), Montevecchi and Myers (1996), Arcos-Pros (2001) and Karpouzi (2005) are examples of studies of seabirds preving on small epipelagic fishes that are the main targets of commercial fisheries. The majority of these studies researched seabirdprey interactions in upwelling marine ecosystems such as the Benguela Upwelling System (Berruti and Colclough 1987) off the south coast of Tasmania (Brothers et al. 1993), the Mediterranean Sea (Oro et al. 1997 and González-Solís et al. 1997a), and the Peruvian Upwelling System (Jahnke and Goya 2000). Other scientists studied the detrimental effects of overfishing on seabird populations (Furness and Monaghan 1987, Montevecchi 1993, Bostford et al. 1997, Tasker et al. 2000) and other man-induced changes (Schreiber 2000a, Schreiber and Lee 2000). Fishery scientists have also used seabirds as an indicator of changes in the marine environment (Ashmole and Ashmole 1968, Jahncke and Goya 2000, Ainley et al. 2005), fish stocks (Montevecchi 1993, Furness and Camphuysen 1997) and fishery health (Ryan 1988, Ryan et al. 1988, Pérez-López et al. 2005).

As most diet studies of seabirds were done at temperate convergence zones where the nutrients are abundant due to upwelling, it is logical to assume that in those zones, seabirds are exploiting abundant and available prey resources (Berruti and Colclough 1987, Brothers *et al.* 1993, Oro *et al.* 1997, González-Solís *et al.* 1997a, and Jahnke and Goya 2000). As explained by Ainley and Boekelheide (1983), on a relative scale, cold waters have much larger standing stocks of organisms, such as zooplankton than do warm waters, and thus in cold waters birds should find it easier to locate prey. In the other hand, very few studies have beeg performed in the oligotrophic environment (Schreiber and Hensley 1976, Kepler 1978, Harrison et al. 1983). Compared to colder environments, seabirds foraging in tropical waters should possess morphological adaptations and efficient foraging techniques (Ballance 1995, Ballance and Pitman 1999, Weimerskirch et al. 2005a) in order to survive in such an environment, where food resources are impoverished (Longhurst and Pauly 1987). Food may limit reproduction in seabirds (Clifford and Anderson 2001), therefore, it is reasonable to speculate that competition for prey should increase during food shortages. Then, according to resource partitioning theory (MacArthur 1958, MacArthur and Levins 1967, Schoener 1983a, b) it can be assumed that differences in diets will be more obvious where the food resources are limited; as may be the situation for the pelagic waters of the Western Central Atlantic. Indeed, Berruti and Colclough (1987) suggested that pelagic seabirds may be particularly useful in monitoring changes in the abundance of epipelagic prey species occurring at moderate to low biomasses. Therefore, a study of seabird diet in the Caribbean Sea may suggest whether differences in diets will be more obvious in oligotrophic zones compared to eutrophic environments. Studies of seabird diets in the Caribbean Sea could elucidate 1) whether they are important fish predators in an oligotrophic environment, 2) interspecific differences in diet compared to species in regions of higher productivity, 3) the possibility of using seabird diets as indicators of the Caribbean oceanic health (e.g., plastics, oil) and fish stock fluctuations, and 4) a baseline for future studies in population and dietary changes or trends.

Since oligotrophic environments may increase the potential for competitive interactions with increasing ecological similarity among species, natural selection should favor mechanisms that decrease competition, at least according to resource partitioning theory (Volterra 1926, Lotka 1932, Gause 1934, MacArthur 1958, Hutchinson 1959, MacArthur and Pianka 1966, MacArthur and Levins 1967, Wiens 1977, Schoener 1983). Consequently, if prey resources are limiting for seabirds in oligotrophic oceans, differences in diets should be evident among sympatric congeneric oceanic species.

The most conspicuous Caribbean oceanic seabirds are the magnificent frigatebird (Pelecaniformes: Fregatidae: *Fregata magnificens*) and the sulids (Pelecaniformes: Sulidae). The frigatebird is a scavenger who relies in kleptoparasitism by stealing food from other seabirds (Calixto-Albarran and Osorno 2000). Therefore the frigatebird diet may reflect a mix of diets from different species victims of kleptoparasitism. Other than the frigatebird, there are three species of sulids in the Caribbean, the masked booby (*Sula dactylatra*), the brown booby (*S. leucogaster*), and the red-footed booby (*S. sula*). These species usually feed by plunge diving to depths of a few meters, either passively or actively using their wings and legs under water (Ashmole 1971, Harrison *et al.* 1983, Le Corre 1997, Nelson 2003). They also feed in association with subsurface predators (Au and Pitman 1986, Ballance *et al.* 1997, Ballance and Pitman 1999, Hebshi *et al.* 2008). These species provide an excellent case to study diet differences due to general similarities in feeding strategy and because they co-occur in roosting and nesting grounds.

Few studies have been able to detect differences in diets and feeding strategies among sympatric sulid species. Caribbean sulids feed by repetitive plunge dives for fish and squid (Kepler 1978). In addition, comparing the Caribbean dietary data of sulids with

other studies insights about differences in the feeding ecology of seabirds occurring in regions that differ in oceanic productivity may be detected.

A better understanding of diets and feeding strategies can be obtained by studying intra- and interspecific differences and similarities in food obtained simultaneously and at different times. These comparisons may provide indications of possible fluctuations of food resources. The combination of results should provide a better idea of these seabirds as indicators of fish stock, and allow a comparison of the diet of sulids with the published diet of subsurface predators (e.g. Yellowfin Tuna, *Thunnus albacares*; Dolphinfish, *Coryphaena hippurus*) in order to speculate about possible feeding associations.

LITERATURE REVIEW

Coexistence

The coexistence of similar species is sensitive to external perturbations (e.g. predation, important resource shortage, etc.), therefore, the mechanisms that allow coexistence are intriguing. According to Gause's competitive exclusion principle (Gause 1934, Hardin 1960) two populations (species) cannot long coexist if they compete for the same limiting resource. Consequently, interspecific competition can be seen as a negative interaction through exploitation or interference that has a negative effect on one or both species (Wiens 1977). Nevertheless, similar sympatric species occur practically everywhere in nature (Hutchinson 1959, 1961). So, in order to comprehend natural processes supporting species coexistence, ecologists seek to determine mechanisms that reduce competitive interactions thereby allowing the coexistence of species. Proposed mechanisms include specialization and niche partitioning (Andrewartha and Birch 1954,

MacArthur 1958), exploitation of unlimited resources except during periods of scarcity (Wiens 1977, Schoener 1983b, Grant 1986, Chesson and Case 1986) and disruptive influences (e.g. patchiness, seasonality, predation, storms; Grime 1973, Horn 1975, Connell 1978, Schoener 1983a, b).

Many ecologists analyze coexistence with the presumption that communities are in equilibrium (reviewed by Schoener 1974, 1983a, b, Ross 1986). MacArthur (1958) studied the feeding ecology of congeneric warblers, and found that very similar species may coexist in sympatry by partitioning the same limited food resource by feeding in different parts of evergreen trees. In theory, this process should allow each species to use a subset of the limited resources consequently avoiding competition. MacArthur and Levins (1967) and Walter (1991) among others have proposed models favoring the evolution of resource partitioning. Based on behavior, site characteristics, diet changes and breeding success, several studies suggest that suitable roost and nesting sites and food sources (food being more unpredictable spatially and temporally) are limited resources for seabirds (Lack 1934, Idyll 1973, Crawford and Shelton 1978, Kepler 1978, Kirkham and Morris 1979, Trivelpiece and Volkman 1979, Croxall and Prince 1980, Anderson et al. 1980 and 1982, Whittam and Siegel-Causey 1981, Clark et al. 1983, Squibb and Hunt 1983, Duffy 1984, Cairns 1987, Gibbs et al. 1987, Montevecchi et al. 1987, Hamer et al. 1991, Clifford and Anderson 2001, Chaves-Campos and Torres 2002, Townsend et al. 2002, Huyvaert and Anderson 2004). The same is true for avian scavengers (Wallace and Temple 1987, Lemon 1991, Rodríguez-Estrella 1994, Buckley 1998, Stolen 2000, Margalida and Bertran 2003, Selva et al. 2005). With respect to sympatric seabird species, several studies suggest that resource partitioning occurs by

feeding with different strategies and/or in association with different subsurface predators (Schreiber and Hensley 1976, Harrison *et al.* 1983, Holm and Burger 2002, Hebshi *et al.* 2008). These subsurface predators make prey available to the birds by driving and concentrating prey close to the ocean's surface, thus enhancing the foraging opportunities of surface-feeding and shallow diving birds (Ashmole 1971).

On the other hand, Wiens (1977) suggested that populations might spend much time responding to 'ecological crunches' and little time at resource-defined equilibriums. This non-equilibrium hypothesis states that similar species coexist due to unlimited resources that may become limited (and vital) seasonally resulting in competition only during those lean periods. In this scenario, fishes and squids should usually be abundant and available to seabirds, thereby lessening competition for food among sulids. Competition would occur only during periods of food scarcity possibly due to harsh environmental conditions (i.e. droughts, storms, temperature changes, etc). Perhaps similar to the high mortality and diet changes found in relation to El Niño Southern Oscillation event in seabirds (Duffy and Merlen 1986, Gibbs et al. 1987, Jahncke and Goya 2000) and avian scavenger (Wallace and Temple 1987). Therefore, differences among diets should be minimal and not necessarily related to competition in similar coexisting species. In other words, significant differences in the utilization of resources by ecologically similar sympatric species should be rare, and probably caused by a periodic resource deficiency. Since Wiens (1977) many ecologists examine resource utilization in terms of non-equilibrium conditions (see reviews by Schoener 1983b, Grant 1986, Chesson and Case 1986).

Alternatively, competition for food would not exist among coexisting species exploiting the same food resource if the resource is unlimited and if environmental disturbances, predation and parasitism occur frequently (Grime 1973, Horn 1975, Connell 1978, Strong 1982). High rates of environmental disturbances, predation and parasitism should limit the population growth of potentially competing species reducing the probability of overexploiting resources and subsequent competition. According to Schoener (1983b) competition regulated by interference is more detectable in predators at intermediate trophic levels, which are typically small and compete less on average either because they can be overcome by a greater variety of predators or because they are more sensitive to mortality from harsh climatic conditions or physical disturbance. The idea that predation can enhance coexistence of competing prey has received much support both empirically and theoretically (some reviews in Schoener 1983b).

The use of the same resource by different species does not always have a detrimental effect on the participants. If the food is dispersed (unpredictable spatially and temporally), competitors might take advantage of harvesting together; mutualistic effects. Black vultures (*Coragyps atratus*) search for food visually, sometimes following other vultures (as the turkey vulture; *Cathartes aura*) that locate carrion by olfaction (Stewart 1978, Rabenold 1987a, b, Lemon 1991, Buckley 1996). Similarly, seabirds are expected to use visual and auditory cues from other feeding birds to get to the feeding location (Hoffman *et al.* 1981). Hence, flocks might be more effective in herding and catching food together (Duffy 1983, Götmark *et al.* 1986, With and Morrison 1990, Ballance 1993, Mills 1998), and/or in combination with subsurface predators (Ashmole and Ashmole 1967, Au and Pitman 1986, Pitman and Balance 1992, Montevecchi 1993, Balance and

Pitman 1999, Hebshi *et al.* 2008). However, aggressive interactions between feeding seabirds has being reported (Feare 1981, Hoffman *et al.* 1981, Duffy 1986, Ballance 1993, Ballance *et al.* 1997). This interaction typically occurs when prey is forced to the surface by subsurface predators get densely packed in schools and seabirds descend aggressively to capture prey while simultaneously avoiding mid-air collisions with birds or with subsurface predators that catapult out of the water at high speed (Ballance *et al.* 1997).

The Sulids

Sulids include the boobies and gannets (Nelson 1978 and Van Tets *et al.* 1988). The three gannet species are now placed in the genus *Morus*, Abbott's Booby in *Papasula* (*P. abbotti*), and the remaining boobies in *Sula*. In most aspects, they are so similar that some authorities believe that all sulid species should be considered congeneric, in *Sula* (Nelson 2003).

In comparison with other birds, seabirds are generally long-lived, lay small clutches and delay breeding until at least the second year of life (Furness and Monaghan 1987). They are typically monogamous, colonial breeders, with a strong tendency to return to their natal colony to breed (Greenwood and Harvey 1982, Osorio-Beristain and Drummond 1993, Aebischer 1995, Spendelow *et al.* 1995, Danchin *et al.* 1998, Spear *et al.* 1998, Huyvaert and Anderson 2004). In general, seabirds' reproductive success is tied to food availability (Duffy 1983, Duffy and Merlen 1986, Montevecchi and Barrett 1987, Montevechi 1993, Montevecchi and Myers 1996, Dearborn *et al.* 2001).

Piscivorous birds routinely eat very high fat and high protein diets (Duke 1985, 1997). Seabirds are uniquely able to assimilate wax esters at efficiencies greater than

90% (Jackson and Place 1990). These birds used the high lipid contents available in their prey as an energy store and for buoyancy (Duke 1997). Birds eating high-protein diets generally have less complicated digestive systems than those eating complex carbohydrates (e.g. cellulose; Duke 1997). The muscular stomach of fish-eating birds (McLelland 1979, Duke 1985) is simple; lacking of muscles (known as the thin and thick pairs) used by other birds to push and grind the ingesta.

In seabirds with pelagic foraging strategies, a broad variety of feeding methods exist (Ashmole 1971). Furness and Monaghan (1987) described the feeding methods of pelagic seabirds as underwater pursuit diving using wings (e.g. shearwaters; Procellariidae), plunge diving (e.g. sulids), and feeding from the surface (e.g. fulmars; Procellariidae). Sulids have a number of adaptations for plunge diving including: no external nostrils, which should avoid pressurized water entrance to nasal cavities; air sacs under the skin in the face and chest to absorb the impact with the water; and binocular vision to allow accurate distance sight. Similarly, these birds show a great variety of ecomorphs and flying styles allowing them to forage at low energetic costs (Pennycuick 1982, 1987, Fauchald 1999; Herter and Balance 1999, Weimerskirch *et al.* 2000, Fritz *et al.* 2003).

Hereafter, the term sulid will be used only in reference to the birds in the genus *Sula* in the Caribbean. They are exclusively diurnal offshore foragers, leaving early in the morning, and returning to the colony before or soon after dusk (Nelson 1978, Schreiber *et al.* 1996, Weimerskirch *et al.* 2005a). Their flight is energy efficient (Flint and Nagy 1984; Ballance 1995, Ballance *et al.* 1997). Smaller individuals, usually males, are able to fly further to exploit potentially more productive foraging grounds because of lower

flight costs (Lewis *et al.* 2005). In contrast to other seabirds, sulids tend to return every day to the colonies, indicating that they are able to find scattered food at a limited range about 5 to 400 km from the colonies (Wilson *et al.* 2002).

It is generally believed that sulids consume substantial tonnages of marine organisms (Karpouzi 2005). Diet differences among seabird species might result from differences in fishing zones (Schreiber and Hensley 1976, Elphick and Hunt 1993, Ballance *et al.* 1997, Jahnke and Goya 2000). In the eastern tropical Pacific, sulids flocks in waters of high productivity at shallow thermocline (62.5 m) and high chlorophyll (0.17 mg/m³) areas around breeding islands (Ballance *et al.* 1997).

Seven *Sula* species exist (Nelson 1978), but only the brown, masked, and redfooted boobies are resident in the West Indies (Schreiber 2000b; Figure 1). Masked and red-footed boobies are the most pelagic sulids (Nelson 1978; Schreiber *et al.* 1996). All three species have a pantropical distribution, and there is a mixed population that roosts and nests colonially at Monito Islet (Kepler 1978, Schreiber 2000b). Although breeding stages can be observed at anytime, Kepler (1978) found breeding peaks (egg and chick production) in the masked booby during September, in the brown booby during June, September and October and in the red-footed booby during June. Fledglings (165-225 days post egg laying) can stay in the colony for more than two months (Kepler 1978).

Banding data indicates that sulids are philopatric with little movement between colonies (Woodward 1972, Amerson and Shelton 1976, Schreiber *et al.* 1996). The masked booby nests and roosts on ledges along the cliffs, substantially overlapping with the brown booby who tends to disperse over the ground throughout the islet. Among sulids, only the red-footed booby usually perches and nests in trees or shrubs. Although

sulids nesting habitats are primarily in isolated keys, as other seabirds, they are susceptible to habitat loss, human disturbance and destruction of eggs, and the impact of introduced vertebrate predators (Schreiber and Lee 2000, Pitman *et al.* 2005).

Masked Booby

The masked booby, formerly known as the white or blue-faced booby, is the biggest of the sulids nesting in the Caribbean and weighs from 1.2 to 2.3 kg (Anderson 1993, Figure 1). The subspecies *S. d. dactylatra* is found in the Caribbean and tropical Atlantic (Schreiber 2000b). Six subspecies are recognized, based on morphology and are distributed throughout tropical seas of the Atlantic, Indian and Pacific Oceans. This species inhabits convergence areas with low productivity from 30°N to 30°S (Nelson 1978, Friesen *et al.* 2002), and is not drawn to any major upwelling system (Anderson 1993). However, morphological and ecological differentiation (e.g. differences in diet) of the morph breeding in the Nazca Plate in the eastern Pacific Ocean (Pitman and Jehl 1998) support the recent taxonomic change from subspecies to full species (Nazca booby or *S. granti*; American Ornithologists' Union 2000). Subsequently, genetic research revealed divergence between 400,000-500,000 years ago (Friesen *et al.* 2002).

The Caribbean subspecies (*S. d. dactylatra*) is limited in distribution and abundance (Kepler 1978, Schreiber 2000b). In the West Indies, there are about 550-650 pairs of masked booby nesting in eight known and 3-5 suspected colonies (Schreiber 2000b). It is the rarest among the Caribbean sulids. Kepler (1978) and Schreiber (2000b) reported 50 to 60 pairs as the estimated population of masked booby in Monito Islet.

Recent studies suggest that the Caribbean morph is closer to races from the southern tip of Africa than to the races on both sides of the Isthmus of Panama (Steeves *et al.* 2003, 2005). These findings are additional motivation to study the Caribbean masked booby ecology, in particular its breeding, feeding behavior and diet.

When foraging, this species tends to be strictly pelagic (Anderson and Ricklefs 1987, Anderson 1993) and frequently solitary (Ashmole and Ashmole 1967). This sulid does not follow ships or feed on fishing discards (Tasker *et al.* 2000). Compared to its congeners, "deep plunging" appears to be a better description of the feeding technique of the masked booby (Ashmole and Ashmole 1967, Ballance *et al.* 1997). The Galapagos morph uses two strategies, either diving, while in the center of seabird flocks, presumably near the center of the fish school, or diving simultaneously with a large feeding flock, which facilitates capture of the temporarily stunned and confused fish (Mills 1998). The dives are from a height of up to 30 m into the top 3-4 m of the sea (Oberle 2003).

The masked booby's daily energy needs are approximately 684 kcal (Hunt *et al.* 2000). Muck and Pauly (1987) compared weights and daily consumption of seven *Sula* species. For a masked booby from South Africa that weighs 2.2 kg, Laugksch and Duffy (1984) estimated a daily consumption of 13.1% of the body weight using metabolic equations adjusted for reproduction and other costs.

The mean volume of regurgitation samples taken in May and August 1967 from a Pacific colony at Christmas Island (Kiritimati) was 138 to 192 ml and the individuals regurgitated an average of 3.6 to 5.9 items per sample, respectively (Schreiber and Hensley 1976). Regurgitation samples consisted of two families of fish and unidentified squids. Measurements were taken of moderately digested specimens and average length ranged from 13.1 to 16.3 and 7.7 to 9.6 cm, respectively. All prey fishes were pelagic, with the flyingfish (Exocoetidae) representing 96% of its fish diet, while kawakawa, *Euthynnus affinis* (Scombridae) the remaining 4%.

On Lobos de Tierra Island off the Peruvian coast, this species feeds almost exclusively on oceanic prey (Jahncke and Goya 2000). From May 1996 to June 19998, the mean number of prey items per regurgitation, sampled every other month, ranged from 2.7 to 4.4. Squid represented less than 1% of their diet. The main prey items were chub mackerel *Scomber japonicus* (Scombridae) and flyingfishes (Exocoetidae), although the birds adopted an opportunistic feeding strategy during years of abundant Peruvian anchovies *Engraulis ringens* (Engraulidae).

The diet of this species in Northwestern Hawaiian Islands is similar to that reported from Christmas Island (Schreiber and Hensley, 1976), and Lobos de Tierra Island (Jahncke and Goya 2000). However, scads *Decapterus* sp. (Carangidae) appears to be an important diet component (Harrison *et al.* 1983). The mean number of prey items per regurgitation during 1978-80 was 2.5. The samples averaged 167 ml. Squids represented about 3% of their diet.

Brown Booby

The brown booby is the most common sulid in the West Indies (Raffaele *et al.* 1998). The *Sula leucogaster leucogaster* subspecies ranges through the Caribbean and tropical Atlantic (Schreiber 2000b). Brown boobies nest on much steeper terrain than most boobies and gannets probably to avoid competition with larger species (Chaves-Campos and Torres 2002). Schreiber (2000b) reported an estimated population of

approximately 500 pairs in Monito Islet. As its common name implies, its brown coloration (Figure 1) distinguishes this midsize booby from its Caribbean congeners. However, from a distance it could be mistaken for other brown colored seabirds such as the brown morph of the red-footed booby. Another difference from its congeners is its fearless behavior toward human fishing activities, since it is commonly observed perched on navigation buoys and flying in close proximity to fishing vessels. The brown booby is so unafraid that it can be entangled with floating-bait hooked to a fishing line as it is trolled (pers. obs.). This sulid can follow ships to feed on fishing discards, which can be related to its global population increase (Tasker *et al.* 2000). Nixon and Lee (1998) were able to approach within a meter of feeding individuals by snorkeling slowly to document behavior. As pointed out by Mellink *et al.* (2001), its abundance and proximity to human fishing activity makes the study of its diet an important issue.

Tershy and Breese (1990) also noted its aggressiveness in the Gulf of California. They observed a female of the species employing kleptoparasitism to rob food items from a blue-footed booby (*S. nebouxi*). Despite being easily observed, widespread and common in the West Indies (5,500-7,800 pairs, Schreiber 2000b), little information about the ecology of the brown booby is available.

The weight of the brown booby ranges from one to 1.8 kg; females being 38% heavier than males (Oberle 2003, Lewis *et al.* 2005). Its daily energy needs are approximately 485 kcal (Hunt *et al.* 2000). Among the *Sula* species, the brown booby is near the average in weight and estimated daily consumption (Muck and Pauly 1987). Using metabolic equations adjusted for reproduction and other costs for a booby

weighing 1.3 kg (at the French Frigate Islands, North Western Hawaii), Pettit *et al.* (1984) estimated a daily consumption of 14.2% of the body weight.

The brown booby is generally a near-shore, deep-water feeder that plunge-dives from a height of 1 to 15 m to catch prey (Nelson 1978, Yoda and Kohno 2008). Yoda and Kohno (2008) using acceleration data loggers attached to chick-rearing brown boobies, to document performance of many rapid and shallow V-shaped dives and some W-shaped dives during the daylight period. The average and maximum dive depth and duration were 1.03 m and 3.81 m and 1.83 s and 21 s, respectively. The species used positive buoyancy to ascend to the water surface. Their data suggest that brown boobies mainly depend on shallow-plunging, contrary to pursuit divers. In addition, Nixon and Lee (1998) reported the species feeding from a height of one meter by making angled and rapidly repeated dives in shallow lagoons. This seabird consumes mostly flyingfishes and squids (Dorward 1962, Nelson 1978, Harrison et al. 1983). Yet, it consumes many other food items as well, with considerable variation among localities, and makes important use of certain seasonal resources (Cramp and Simmons 1977, Nelson 1978). For example, in the Northwestern Hawaiian Islands, 244 food items consisted of over 50 different species. Flyingfishes were second to scads or jacks, and their allies (Carangidae) as components of the diet, whereas goatfishes (Mullidae) occupied third place (Harrison et al. 1983). In early spring, 1990, on Isla San Pedro Mártir (Gulf of California), the brown booby fed mostly on Pacific sardines (Sardinops sagax) and northern anchovies (Engraulis mordax). During the summer of the same year, its diet consisted of flyingfish (Cheilopogon papilio), Pacific mackerel (Scomber japonicus), and halfbeaks (Hyporhamphus spp.) (Ángeles-Pérez et al. 1991, Mellink et al. 2001). In the same area in 1991 and 1992, it

consumed mostly northern anchovies. Prey composition was similar in regurgitations from males and females, but regurgitations from females were heavier (Ángeles-Pérez *et al.* 1991). More recently, at Isla San Jorge (Eastern Pacific), this species fed on 30 prey items, including one squid, 14 small pelagic shoaling fishes and 15 benthic fishes with the Pacific anchoveta (*Cetengraulis mysticetus*) as the food of choice (Mellink *et al.* 2001). These researchers also related the availability of benthic fishes to the length of the breeding season and residence. However, the brown booby is considered a generalist, capable of exploiting any prey that becomes available in near-shore deep-water (Harrison *et al.* 1984).

Red-footed Booby

This species is the most common in the Caribbean, and can be found in the seas of north Australia, in the Pacific and Indian Oceans and also in other parts of the tropical Atlantic Ocean (Schreiber 2000b). Within the genus *Sula*, it is the smallest (Schreiber 2000b). In contrast to the other sulids in the Caribbean, this species constructs its nest in a tree or shrub, such as *Capparis flexuosa* intertwined with *Pithecellobium aculeata*, but will nest on the ground if trees are not available (Kepler 1978, Nelson 1978, Schreiber 2000b). Hence, it is almost impossible for this booby to recover its prey if the regurgitation falls off the nest (pers. obs.). Once the regurgitation falls among branches and exposed roots, opportunistic scavengers such as land crabs (*Gecarcinus* sp.) rapidly feed on it (pers. obs.). Based on observation of presence-absence data, Anderson (1991) suggests that the red-footed booby in Galapagos has a nesting distribution most likely limited by Galapagos Hawks (*Buteo galapagoensis*). Introduced predators (such as rhesus

monkeys, *Macaca mulatta*, in Desecheo Island) may decimate their colonies (Oberle 2003). The West Indian subspecies, *Sula sula sula* (Figure 1), is abundant mainly near remote roosting and nesting islands widely scattered throughout the region (Raffaele *et al.* 1998). Kepler (1978) estimated the Monito Islet population at 2,000-3,000 individuals, but later Schreiber (2000b) reported an estimation of 200-400 pairs. The West Indian population is estimated at 8,200-10,000 pairs (Schreiber 2000b). They are frequent victims of kleptoparasitism by magnificent frigatebirds (Oberle 2003). As with the masked booby, this sulid does not follow ships or feed on fishing discards (Tasker *et al.* 2000).

Weimerskirch *et al.* (2005a,b) found that red-footed boobies make extensive use of wind conditions, flying preferentially with crosswinds at median speed of 38 km/h, reaching highest speeds with tail winds, spending 66% of the foraging trip in flight (34% sitting on the water or diving), using a flap-glide flight, and gliding 68% of the flight. They frequently touched water for landing, plunge diving or surface diving (30 landings/h). Most dives were shallow (maximum 2.4 m) but frequent (4.5 dives/h), most being plunge dives. During the foraging and traveling phases red-footed boobies climb regularly to altitudes of 20-50 m to spot prey or congeners, although dives for hunting are from 4-8m (Oberle 2003). During the final phase of the flight, they elevated to high altitudes, up to 500 m. Red-footed boobies are considered long-range foragers compared with other boobies and are able to forage at maximum measured distances of 148 km from the colonies during trips lasting a maximum of 12 h, depending on day length.

The weight of the red-footed booby ranges from 0.9 to 1.1 kg; females being 14% heavier than males (Oberle 2003, Lewis *et al.* 2005), and its daily energy needs was

estimated to be near 416 kcal (Hunt *et al.* 2000). Within the extant *Sula* species, its estimated daily consumption is among the highest relative to body weight (Muck and Pauly 1987). These researchers reported two estimates of daily consumption for a red-footed booby weighing 1.1 kg (in the French Frigate Islands, Northwestern Hawaii). One was from Harrison and Hida (1980), who used stomach contents analysis to estimate a daily consumption of 24.7% of body weight. The other was from Pettit *et al.* (1984) who estimated a daily consumption of 14.2% (same as brown booby) of body weight using metabolic equations adjusted for reproduction and other costs.

The mean volume of regurgitations sampled from May to August of 1967 from the Pacific colony at the Kiritimati or Christmas Island ranged from 69 to 95 ml (Schreiber and Hensley 1976). This species regurgitated an average of 5.6 to 8.3 items per sample. In that study, the regurgitation samples consisted of four families of fishes and unidentified squids. Moderately digested specimens of fish and squid ranged in length average from 7.4 to 9.9 and from 5.8 to 7.1 cm, respectively. All fishes were pelagic, with flyingfish (Exocoetidae) representing 91% of its fish diet and the remainder being organisms associated with *Sargassum*.

The diet of the red-footed booby in the Northwestern Hawaiian Islands (Harrison *et al.* 1983) is similar to that reported from Christmas Island (Schreiber and Hensley 1976). In both sites, it relies on squids as the most common prey. The mean number of prey items per sample collected during 1978-80 was 5.8. The samples averaged 73 ml. Squids represented about 27% of the diet.

Objectives

The following fundamental questions regarding the feeding ecology of sympatric Caribbean sulid species will be addressed: 1) Do diets differ among individuals of a given species? (H₀: no intraspecific difference), 2) Do diets and feeding strategies differ among bird species? (H₀: no interspecific difference), 3) Do sulids feed selectively upon prey categories? (H₀: random feeding), 4) Do these patterns differ among visits? (H₀: no difference through time). The combined answers are outcomes of the evolutionary history of the Caribbean sulids, and may have implications in their usefulness as indicators of subsurface pelagic predators and epipelagic fish stock fluctuations.

Hence, through diet analysis and comparison, the main objectives of this dissertation are 1) to establish a detailed description of the feeding ecology of the Caribbean sulids, and compare it among sulid species in other oligotrophic environments, in upwelling zones and with data of subsurface pelagic predators found in the literature, 2) to determine if these bird species may be useful as indicators of epipelagic fish stock fluctuations, 3) to estimate the tonnage of organisms removed from Caribbean stocks, 4) to determine whether food abundance is a limited resource for Caribbean sulids, and 5) to evaluate the possible mechanisms involved in interspecific competitive interactions.

METHODOLOGY

Study Site

Mona Island, Monito Islet and their surrounding waters up to nine nautical miles (Western Central Atlantic) are administered by the Puerto Rican Department of Natural

and Environmental Resources (DNER), as part of the Mona Island Natural Reserve since 1985 (Wadsworth 2003). This Reserve is located approximately halfway between Puerto Rico and Hispaniola (Figure 2). The Reserve life zone was classified as subtropical dry forest by Ewel and Whitmore (1973). Rainfall is more abundant during September-November and least abundant during February-April (García *et al.* 2002). Historically (1920-1945) was exploited for the extraction of guano (Wadsworth 1973).

Monito Islet is considered to be the most inaccessible island within the Puerto Rican Archipelago (García *et al.* 2002). It is basically a flat plateau (15 ha), surrounded by vertical cliffs (66 m above average sea level). With adjacent waters 15 to 40 m deep with a rubble seafloor extending further out to depths of 35 to 60 m (Van Dam *et al.* 2008). It is located about five kilometers northwest of Mona Island, at Latitude 18° 10' N and Longitude 67° 57' W (Wadsworth 1973). Surrounding oceanic waters and flotsam (*Sargassum* mats) are in contact with the walls of Monito Islet. The *Sargassum* mats originated in the northwest Gulf of Mexico in spring of each year are advected into the Atlantic during July, appearing east of Cape Hatteras as a "*Sargassum* jet," and ending northeast of the Bahamas in February of the following year (Gower and King 2008). The accumulation of *Sargassum* in the Atlantic increases after July and usually drops back to low values by March. In the north of Puerto Rico, the density of *Sargassum* is lower in November than in February (Gower and King 2008).

From 1945 to 1955, Monito Islet was rented to the U.S. Air Force (Operation Salt Air) for target practice (Wadsworth 1973). In 1992, DNER personnel began a program to eradicate invasive black rats (*Rattus rattus*) from Monito Islet (presumably from the

guano industry), and no rats were detected in 1998 (García *et al.* 2002). Visits to Monito Islet are reserved for scientific research purposes only. Its natural isolation, harsh environment and local laws protect Monito Islet from regular human activities. Thus, its geological and biological characteristics remain as described by Rolle *et al.* (1964) and Kepler (1978).

Sample Collection

The collection of regurgitations were use to obtain diet samples because it is considered the least biased method for diet analysis (González-Solis et al. 1997b). Sulid species often regurgitate their gut contents when presented with potential aggressors or in some cases with a gentle massage in the crop (see Montevecchi and Myers 1996). With an assistant and DNER personnel, I visited Monito Islet during four nights in 2003 (June 26, August 30, September 30 and October 28), so that at least one visit was during peak breeding seasons of each bird species (eggs and/or chicks present). Birds incubating eggs or rearing chicks were not sampled. I collected fresh gut contents from the ground when the bird was seen regurgitating or directly from hand-captured birds. About thirteen regurgitation samples per sulid species per visit was aim on each visit, due to logistic limitations (cooler size, transportation and degradation of specimens). The best time for sampling was at dusk, when the maximum number of birds were present in the colony (Kepler 1978). Collection at dusk assures recently captured prev organisms, minimizing the degradation of prey tissues by digestion. An assistant was in charge of packaging and labeling samples while I worked with the birds. The assistant stored each regurgitation individually in a Ziplock ® plastic bag, labeled the samples and placed them in insulated bags with frozen Blue-ice-packs ® until arrival on Mona Island the next morning. Once in Mona Island, the samples were frozen until processed in the Puerto Rico DNER Fishery Research Laboratory.

Sample Processing

Specimens were identified in the Puerto Rico DNER Fishery Research Laboratory at the municipality of Cabo Rojo. Sample items were identified to the lowest possible taxonomic level using the FAO species identification guides (Carpenter 2002). The following length measurements (mm) were taken: head, second dorsal fin base and depth, body depth, peduncle depth, upper and lower caudal lobe, anal fin base and pectoral fin. Volume (ml; by water displacement), and fork-length were directly obtained only from undigested fishes after being rinsed under running water to remove gastric acids and reduce further deterioration of sample.

Data Analysis

Scharf *et al.* (1998) showed that whenever possible, measurement estimation by regression models of the least digested prey items is more accurate than averaging the biomass. Therefore, I used power regression formulas ($Y = aX^b$, where Y = fork length or volume, X = the body part measured, and "a" and "b" are regression coefficients) to predict fork length and volume of partially digested common fishes from the most common body parts recovered. I used a second predictor if the most common body part was not abundant enough to allow estimation of 95% of the sample. The second predictor was not

available. However, measurement of size of partially digested rare prey species or completely damaged organisms was replaced by using the average of the nearest related taxon. I used the average percent prediction error {[(Observed-Predicted)/Predicted] x 100} to assess the strength of individual bivariate relationships (Scharf *et al.* 1998). Because this is part of a standard method, I present a summary of the results in Appendices A to D.

The diet is described in terms of prey-specific abundance and biomass. Using prey length (fork length in fishes and mantle length in squids) and volume as biomass indicators, I ranked the prey categories in an index of relative importance (IRI). Using a modification of the method of Oxenford and Hunte (1999), I assessed dietary importance of prey items in three ways: 1) by numerical abundance (N%) of prey items, calculated as a percentage of the total number of items in all food categories; 2) by frequency of occurrence (F%), calculated as a percentage of all regurgitations examined; and 3) by size contribution (L% or V% for length or volume), which was calculated as a percentage of the combined sizes of all prey items. The index was calculated using the relationship IRI = {N% x (L% or V%) x F%}.

The feeding strategy of the birds is presented graphically using a modification of the Costello (1990) method, with some modifications based on Tokeshi (1991) and Amundsen *et al.* (1996). This method allows prey importance, feeding strategy and the inter- and intra-individual components of niche width to be explored graphically in a two-dimensional representation of prey-specific abundance versus frequency of occurrence of prey types in the diet. Prey-specific abundance (P_i) introduced by Amundsen *et al.* (1996)

is defined as the percentage that a prey taxon comprises of all prey items, using only those predators that take that prey. The formula is $\{P_i = (\Sigma S_i / \Sigma S_t) 100\}$. In this formula P_i is the prey-specific abundance of prey "i", S_i is the regurgitation content (e.g., number of items, volume, length) comprised of prey "i", and S_t is the total regurgitation content in only those predators that regurgitate prey "i". The method plotted P_i against frequency of occurrence (F_i) in proportion for each prey species calculated as follow $\{F_i = (N_i / N_t)\}$. In this formula N_i is the number of predators that regurgitate prey "i" and N_t is the total number of regurgitations.

The Costello (1990) method, modified by Amundsen *et al.* (1996), shows three gradients that constitute three aspects of feeding ecology (Appendix E). 1) A diagonal gradient of prey importance goes from rare prey species (lower left corner) to dominant prey species (upper right corner). Similar to the IRI but graphically, this gradient should provide a visual way to compare the dominance of a particular prey species in terms of being abundant in the regurgitation of most birds in a study(therefore important for most birds) compared to other prey species. By comparing figures, the relative importance of a particular prey species per sulid species or per visit can be visually examined. 2) A second, inverted diagonal gradient represents the niche width contribution. This gradient goes from high between-phenotype contribution (upper left corner) to high within-phenotype contribution (lower right corner). A single tiny individual of a prey species found in each of many regurgitations is not a dominant prey species (low biomass/regurgitation), but it is a component contributing in many regurgitations or a high between phenotype contribution. These prey species should be available to many

bird individuals but not contributing much in terms of biomass/bird individual. The contrary, a huge prey species (or many tiny specimens of the same species) found in a few regurgitations will not be a dominant prey species for the colony but a dominant component in these few birds, giving a high within-phenotype contribution. These prey species should be contributing much in terms of biomass but they are only available to a few birds. 3) A vertical gradient of feeding strategy goes from specialization (top) to generalization (bottom). If the diet is composed of dominant species found in most birds, then the bird species typifies a specialist feeding strategy toward the dominant species. The few dominant prey species of a specialist must by abundant species in the gut content. In the other hand, if the diet is based mostly in many different prey species (none being a true dominant species), found in all or few birds, then the feeding strategy presented for the bird species is toward generalization (relative to the taxon). Comparison of visits can suggest if the strategies are plastic or rigid. For a graphical explanation and a hypothetical example, see Appendix E.

I compared regurgitation contents and description with those reported in the literature. Comparable studies of booby diets in the Caribbean Sea were not available. Alternatively, I used the studies conducted at Christmas Island (Central Pacific Ocean, Schreiber and Hensley, 1976), Lobos de Tierra Island (Eastern South Pacific Ocean, Jahncke and Goya 2000), Northwestern Hawaiian Islands (Northern Pacific Ocean, Harrison *et al.* 1983, 1984) and San Idelfonso, San Jorge and San Pedro Mártir Islands (Central and Northern Gulf of California, Mellink *et al.* 2001). Despite the differences
among study sites (i.e. different oceans), and dates, many conclusions can be reasonably drawn from comparisons with these studies.

I used single ANOVAs and general linear multivariate procedures (two-way) to screen significant inter and intraspecific differences (e.g. visits, breeding vs. nonbreeding seasons, species, prey numbers, diversity, etc.), followed by a Bonferroni multiple comparison post hoc tests to determine which variables differed when the Levene's Test of Equality of Error Variances (tests the null hypothesis that the error variance of the dependent variable is equal across groups) was not significant. Otherwise, I used a Tamhane's multiple comparison tests.

The Tamhane's test is a highly conservative multiple comparison method. It is a set of unequal variances t-test with Sidak adjusted p-values. Sidak adjusted p-values computes adjusted p-values for simple multiple testing procedures from a vector of raw (unadjusted) p-values. The Sidak procedures provide strong control of the family-wise type 1 error rate. In this test, the family-wise type 1 error rate does not exceed alpha. The TMC test is applicable to situations where the variances (or samples) are unequal. It is not an exact test (SPSS 1999).

Another analytic method to describe diet is to measure and compare niche breadth and overlap (Krebs 1989). For this, I used the Levins' measure (1968) of niche breadth which measures how uniformly resources are being utilized by each species. The equation is $\{B = (\Sigma N_j)^2 / \Sigma N_j^2\}$. I standardized the measures by dividing the Levins' measure of niche breadth by the total number of resources states after correcting for a finite number of resources, using the following equation $\{B_a = (B - 1) / (n - 1)\}$ (Krebs 1989). For niche overlap I used the Morisita's (1959) original measure as presented by Smith and Zaret (1982), and Krebs (1989) "C = $\{2\Sigma p_{ij} p_{ik}\}/\{\Sigma^n p_{ij} [(n_{ij} - 1) / (N_j - 1)] + \Sigma^n p_{ik} [(n_{ik} - 1) / (N_k - 1)]\}$ ". Morisita's original measure of overlap gives the most accurate results, especially when using small sample sizes (Smith 1982). In these equations, the subscript "j" and "k" are predator species and "i" is the prey category. The proportion of prey category "i" of the total prey categories regurgitated by predator species "j" is p_{ij}. Similarly, p_{ik} is the proportion prey category "i" is of the total resources used by predator specie "k". The number of individual of predator "j" that use prey category "i" is n_{ij}. Similarly, n_{ik} is the number of individual of predator "k" that use prey category "i". N_j and N_k is the total number of prey individuals of each sampled predator ($\Sigma n_{ij} = N_{ji} \Sigma n_{ik} = N_k$).

Diversity is divided in two components: richness (number of species present) and evenness (a measure of the distribution of population sizes of the respective species) (Levinton 1982). To compare diversity among prey categories, I chose Shannon's and Simpson's indexes (Krebs 1989, Hammer 2001). As there is no perfect diversity index, I used both in an attempt to overcome some of their common biases. Shannon's index {H' $= -\Sigma((N_i / N_t) \ln (N_i / N_t))$ } gives more weight to the rare categories and the Simpson's {D = $1-\Sigma(N_i / N_t)^2$ } index gives more weight to the common categories (Krebs 1989). In this equations N_i is number of individuals of taxon "i" and N_t is the total abundance. Equitability, defined as evenness with which individuals are divided among the taxa present, was measured by dividing the Shannon diversity by the logarithm of number of

taxa. These measures can be related to the diversity of resources available to the species present when competitive interactions are considered (MacArthur 1972).

Assuming independence of prey categories, I developed a predictive model of seabird species diets based on observed number of prey categories per regurgitation, a procedure known as discriminant function analysis (DFA). This procedure generates discriminant functions based on linear combinations of the number of prey organisms per category that provides the best discrimination between the groups (Fowler *et al.* 1998, SPSS 1999). The goal of DFA was to generate a rule based on the observed measurements to separate the sampling units into their true groupings. This pattern produces a scatterplot with associated coordinates that is useful to classify the regurgitations into groups of seabirds. The procedure provides a coordinate by multiplying the abundance of each prey category from a specific regurgitation by the correspondent coefficient in the first discriminant function. The same procedure applied to function two provides its correspondent coordinates.

I used Pearson's correlation (reported as r, df, p) to test association among species and variables. I described gut contents using descriptive statistics: mean ± standard error, sample size, variances, minimum, maximum and percentages, unless otherwise specified. A Monte Carlo Randomization test (MCR) was executed to determine if the description observed differs from the expected by chance (reported as MCp; e.g. to test if the number of organism/prey category regurgitated by a bird species differs from the expected by chance alone). All MCR tests were based on 100000 sampled tables. This test provide an unbiased estimate of the exact significance level, calculated by repeatedly sampling from a reference set of tables with the same dimensions and row and column margins as the observed table (SPSS 1999). The Monte Carlo method allows you to estimate exact significance without relying on the assumptions required for the asymptotic method (Sokal and Rohlf 1995). I provided variance/mean ratio (VMR) to characterize distribution (VMR = 1.0 = random, VMR >1.0 = aggregated, VMR < 1.0 = uniform) followed by a Shapiro-Wilk normality test (reported as SWS, p; df = sample size). I establish the significance of p \leq 0.05 for all the tests and used the Past \circledast (Hammer 2001), Paint \circledast and SPSS \circledast (1999) computer software to generate and edit the figures and statistics.

RESULTS

Prey Size Estimation

I found no inorganic items in 159 regurgitation samples. From the prey remnants, I recognized 984 organisms as food items (all fishes or squids). I identified 34 species in 670 fish specimens (taxonomy, size estimation method and total number of organisms; Appendix A). The percent of identified fish prey per taxonomic level are presented in Table 1. Due to small sample sizes and the deterioration caused by digestion, I did not use regression equations for 22 rare species (n < 15) and three common species, the pelagic juveniles of the spotted goatfish (*Pseudupeneus maculatus*), the yellow jack (*Caranx bartholomaei*) and the black gemfish (*Nesiarchus nasutus*). These three species were usually found too digested to obtain fork length and volume measurements.

However since, the specimens were typically similar in size, I replaced the missing values with the average of the few undigested specimens for each species.

The most common prey remnants were both caudal lobes and the caudal peduncle, with flying gurnards and yellow jacks exceptions to this rule (Appendix B). The least frequently found body parts were those of the fish's anterior body section (e.g., head and its components). The next most common measurements were the second dorsal fin, pectoral fins and body depth.

I developed regression equations to obtain fork length and volume for Atlantic bigeye (*Priacanthus arenatus*), three flyingfish species (Exocoetidae), flying gurnard (*Dactylopterus volitans*), two halfbeak species (Hemiramphidae), little tunny (*Euthynnus alletteratus*), and mackerel scad (*Decapterus macarellus*). The regression related statistics and an example of a scatterplot are shown in Appendices C and D.

Masked Booby

Descriptive statistics and distribution tests for variables related to prey diversity by visit, reproductive season and overall is presented in Table 2. Sample size was too small to rely on distribution tests at the visit or season levels. However, overall, the distribution of the number of organisms per regurgitation was not random (SWS, p < 0.05), VMR values suggest a clumped distribution, but this result could be expected by chance alone (Total MCp > 0.05; Table 2). The distribution of the other variables related to prey diversity, was not random (SWS, p < 0.05), VMR values suggest a uniform distribution and the results differ from the expected by chance (Total MCp < 0.05; Table 2). None of these variables differed among visits (Table 3, Figure 3a) or between 33

breeding and non-breeding seasons (Table 4). Eggs and chicks of masked booby were observed only during the visit in September. Juveniles were observed in all the visits.

Descriptive statistics and distribution tests for variables related to prey size (length and volume) by visit, reproductive season and overall is presented in Table 5. Prey length and volume distribution was not random (SWS, p < 0.05) at visit and season levels, and overall, VMR values suggest an aggregated distribution and practically all the results differ from the expected by chance alone (Total MCp < 0.05; Table 5). Both variables differed among visits (Table 6 and 7, Figure 4a and 5a) and between seasons (Table 8 and 9). Mean prey length and volume were higher in September than in August (Tables 5-7, Figures 4a and 5a) and during the visit at breading peak than in the other visits (Table 8 and 9).

The mean number of prey organisms per regurgitation from masked boobies at Monito Islet was within the values reported for oligotrophic zones in the Pacific Ocean (Table 10). Prey organisms per regurgitation showed a negative correlation with mean prey length (r = -0.536, n = 60, p < 0.001) and volume (r = -0.214, n = 60, p = 0.101), but only the first association was significant.

The family Exocoetidae was the most abundant and most frequent prey category (Table 11). In the Index of relative importance, Exocoetidae and Hemiramphidae ranked as the most important prey families and the clearwing flyingfish (*Cypselerus comatus*) as the most important prey species, particularly during the September visit (Table 11).

In the Costello plots, the clearwing flyingfish was the dominant prey in every visit (Figure 6a). In regurgitations containing clearwing flyingfish, this prey species

represented about 80% of the biomass. Close to 80% of the birds regurgitated the dominant prey. During the September visit, the lowest specific biomass coincided with the highest dominance of the clearwing flyingfish. Overall, except for one large Atlantic leather jack found in August, the other diet components were low to intermediate in specific biomasses (< 70%) and each rare prey species was found in few birds (low percentage of occurrences, < 25%); high between phenotype components of the diet niche width (Figure 6b). The Costello plot (Figure 6b) shows characteristics of a generalist population, with each individual feeding on different rare prey and one dominant species in every visit.

Brown Booby

Descriptive statistics and distribution tests for variables related to prey diversity by visits, reproductive season and overall is presented in Table 12. As with the previous species, due to sample size only the total tests are reliable. The distribution of all the diversity related variables was not random (SWS, p < 0.05). An aggregated pattern was detected in the number of organisms and the number of organism per prey category (VMR > 1; Table 12). The other variables present a uniform pattern (Table 12). However, the distribution of the organisms per prey category, the Shannon H Index and the Simpson 1-D Index can be expected by chance (Total MCp > 0.05; Table 12). None of these variables differed among visits (Table 3, Figure 3a) or between breeding seasons (Table 4). Eggs and chicks of brown booby were observed in all the visits except in August. Juveniles were observed in all the visits. Mean number of prey organisms was within the values reported in the literature for oligotrophic zones in the Pacific Ocean (Table 13).

Descriptive statistics and distribution tests for variables related to prey size by visits, reproductive season and overall is presented in Table 5. Prey length and volume distribution was not random (SWS, p < 0.05) at visit and season levels, and overall VMR suggest an aggregated distribution and practically all the results differs from the expected by chance alone (Total MCp < 0.05; Table 5). Prey organisms per regurgitation show a significant negative correlation with mean prey length (r = -0.411, n = 48, p = 0.004) and volume (r = -0.420, n = 48, p = 0.003). Only August and September, and August and October did not differ in mean prey length. Mean prey length and volume was lowest in June and highest in September (Table 5-7 and Figures 4a and 5a). The mean prey volume of September differs from June and August. Prey length, as opposed to volume, was highest in the non-breeding visit. Only prey length differs significantly between visits at the season level (Table 8 and 9).

The family Carangidae was the most abundant prey family, although it was not detected it in September (Table 14). The families Dactylopteridae and Exocoetidae were also prominently represented taxonomic groups (Table 14). Carangidae and Exocoetidae ranked in the IRI as the most important prey families, whereas the clearwing flyingfish and the mackerel scad constituted the most important prey species (Tables 14). The flying gurnard (*Dactylopterus volitans*) appears profusely only during the June visit and most of these organisms were regurgitated by one of the three birds that regurgitate this prey (Table 14).

In the Costello plots, the clearwing flyingfish (*C. comatus*) was the most dominant prey species during the June and September visits (Figure 7a). The mackerel scad was most dominant in October and August although in less magnitude, due to less specific biomass. Although the combined dominance was not strong, the clearwing flyingfish was the most dominant prey species, represented by ~75% of the biomass regurgitated by ~40% of the sampled birds. The other diet components were found in low to intermediate specific biomasses (<60%) and low percentage of occurrences (< 35%); high between phenotype components of the diet niche width (Figure 7b). The Costello plot shows characteristics of a population with a generalist feeding strategy, with each individual feeding on different organisms and two slightly dominant prey species.

Red-footed Booby

Descriptive statistics and distribution tests for variables related to prey diversity by visits, reproductive season and overall is presented in Table 15. As with the previous species, due to sample size, only the total tests will be considered. The distribution of all the diversity related variables was not random (SWS, p < 0.05). An aggregated pattern was detected in the number of organisms and the number of organism per prey category (VMR > 1; Table 15). The other variables present a uniform pattern (Table 15). Only the distribution of the number of organisms per prey category can be expected by chance (Total MCp > 0.05; Table 15). None of these variables differed among visits (Table 3, Figure 3a) or between breeding seasons (Table 4). Eggs and chicks of red-footed booby were observed only during the visit in June. Juveniles were observed in all the visits. Mean number of prey organisms was within the values reported in the literature for oligotrophic zones in the Pacific Ocean (Table 16). Prey organisms per regurgitation show a significant negative correlation with mean prey fork length (r = -0.563, n = 53, p < 0.001) and volume (r = -0.458, n = 53, p = 0.001).

Descriptive statistics and distribution tests for variables related to prey size by visits, reproductive season and overall is presented in Table 5. Prey length and volume distribution was not random (SWS, p < 0.05) at visit and season levels, and overall, VMR suggest an aggregated distribution and practically all the results differs from the expected by chance alone (Total MCp < 0.05; Table 5). Mean prey length was highest in June and lowest in September and the mean prey volume was highest and lowest in August but none of the variables differed in the visit (Table 6, Figure 4a and 5a) or season level (Table 9).

The family Exocoetidae was the most abundant prey family, although about equal to Gerreidae in September and less abundant than Mullidae in August. The sailfin flyingfish (*Parexocoetus hillianus*) was the most abundant prey species except in August and September, in which the spotted goatfish and the yellowfin mojarra (*Gerres cinereus*) were the most abundant, respectively (Table 17). It was also the most frequently regurgitated except in the August visit. Exocoetidae ranked as the most important prey family (Table 17). The sailfin flyingfish was the most important prey species except in August and September when the spotted goatfish and the clearwing flyingfish were most important, respectively (Table 17).

In the Costello plots, the post larvae of the spotted goatfish and the clearwing flyingfish were the most dominant prey species during August and September, respectively (Figure 8a). The sailfin flyingfish was the most dominant in June and August. Due to less specific abundance and frequency of occurrence, the sailfin flyingfish was less dominant in June than in August. The dominance in June was the less obvious. Although overall, the dominance was almost imperceptible, the sailfin flyingfish was the most common of the prey species, represented by ~40% of the biomass regurgitated by ~45% of the sampled birds. Except for one Atlantic flyingfish, one marginated flyingfish and one spotfin flyingfish (*Cheilopogon* spp.), each one found alone in a different bird, the other diet components were found in low to intermediate specific biomasses (< 75%) and low percentage of occurrences (< 30%); high between phenotype components of the diet niche width (Figure 8b). The Costello plot shows characteristics of a population with a generalist feeding strategy, with each individual feeding on different organisms and three slightly dominant prey species.

Comparisons Among Species

Prey families and species were easier to identify to the family level in the masked booby than in the other two bird species (Table 1). The number of organisms, prey species and organisms per prey species regurgitated by the masked booby were significantly lower than in the other two bird species (Table 2, 4, 12, 15 and 18; Figure 3b). These three variables did not differ between the brown and red-footed boobies. The other diversity related variables did not differ among bird species (Table 4). The masked booby always regurgitated the longest and heaviest prey, but brown and red-footed boobies did not differ in prey size (Table 5, 8 and Figures 4b and 5b). More prey categories overlap among the three sulids than were unique to each one. The masked booby shared 67 and 56% of the categories with the brown and the redfooted boobies, respectively. The brown booby shared 48 and 60% of the categories with the masked and the red-footed boobies, respectively. The red-footed booby shared 45 and 68% of the categories with the masked and the brown boobies, respectively. All three species shared seven (20%) of 35 categories, while three (17%), five (20%) and four (18%) categories were unique to the masked, brown and red-footed booby, respectively.

Descriptive statistics, standardization and distribution tests for Levins' measure of diet niche breadth per bird species, visits and reproductive season are presented in Table 19. Niche breadth total distribution was not random (SWS, p < 0.05), and VMR suggest a uniform distribution for each bird species. Only the distribution found in brown booby was expected by chance (Total MCp > 0.05; Table 19). These measurements did not differ among bird species, visits and reproductive seasons (Table 20).

The mean (n = 4 visits) of Morisita's measure for diet niche overlap was 0.33 ± 0.13 for the masked and brown boobies, 0.36 ± 0.07 for the red-footed and the brown boobies, and 0.45 ± 0.11 for the masked and red-footed boobies. Means did not differ significantly (One Way ANOVA: F = 0.363; df = 2, 9; p = 0.705; Ls = 0.523, p = 0.610). The three species overall mean niche overlap was 0.38 ± 06 . The means of Morisita's measure for the three species did not differ significantly among months (One Way ANOVA: F = 0.714; df = 3, 8; p = 0.570; Ls = 0.523, p = 0.054).

As the goal of the Discriminant Function Analysis is to maximize the separation among bird species in order to be useful in identifying those prey species that discriminate among birds, I performed the test in prey species-size categories. Size categories were set at < 25mm, 25 < 75mm, 75 < 125mm, 125 < 175mm, 175 < 225mm and ≥ 225 mm fork lengths. All prey categories and discriminant functions were used to show a segregation pattern (Figure 10) based on the functions in Table 21. First, the diet of the masked booby and the red-footed booby are virtually separated by the center of function 1, and then most of the diet of the brown booby is separated from the other two by the center of function 2. The functions in Table 21 correctly classified respectively, 94.1%, 71.4% and 81.3% of the masked, brown and red-footed booby regurgitation samples. Overall, 83.0% of the original grouped cases were correctly classified.

DISCUSSION

Colony Threats

Sulids are long-lived seabirds adapted to nest exposed to direct sun rays and to search for food in oceanic waters often relatively far from the nesting/roosting grounds (Furness and Monaghan 1987, Nelson 2003). In Monito Islet, sulids provided heavy regurgitations during the sampling periods. The facts that: 1) all the sampled sulids appeared externally healthy, 2) most provided heavy regurgitations, 3) none regurgitated artificial items, and 4) breeding activities were always present (although in different stages) suggest no obvious immediate threats to the population in Monito Islet. Eggs and chicks were observed during visits of breeding peaks, as reported by Kepler (1978). Few chicks and no fledglings, juveniles/immature or adults were found dead, probably because food appears to be available and due to carcasses removal by scavenging crabs

(*Gecarcinus* sp.; pers. obs.). García *et al.* (2002) reported the presence of black rats and peregrine falcons (*Falco peregrinus*) before and during rat eradication campaigns. During this study, the sulids in Monito Islet appear healthy with no evidence of threats or depredation observed at any developmental stage. Known threats to other seabird colonies include exploitation of seabirds by humans for food, oil, feathers and as fishing bait; habitat destruction; predation by introduced species; chemical pollutants; accidental gill and drift nets captures; and food depletion (reviewed in Furness and Monaghan 1987).

Diet Similarities

Sardines and anchovies are seabird prey species highly abundant in major upwelling system, but rather rare in the epipelagic zones of the Caribbean Sea (Carpenter 2002). If food is limited, compensation for the lack of large prey sizes through an increase in the catching of smaller prey is reasonable under optimal foraging theories (MacArthur and Pianka 1966, McNamara and Houston 1985, Alcock 1993). If food is not limited but dispersed, unpredictable and variable in vulnerability to predation, the catching of vulnerable undersized prey is a feasible alternative if it is profitable in terms of less energy investment, compared to catching challenging large prey (Alcock 1993). Practically all sampled birds provided heavy regurgitations, with a clumped distribution of number of organisms per regurgitation (VMR>1, Tables 2, 12, 15), and not different in means among visits, suggests that food was not limited during the visits. Therefore, the aggregated distribution of number of organisms per regurgitation and the inverse association among prey numbers per regurgitation and prey size suggests that sulids diet is limited by gut or weight lift capacity (Ricklefs 1983) rather than food availability. Consequently, the use of small prey sizes to fill their guts is due to prey vulnerability (see details of differences in prey sizes in next section). These findings are in accordance with similar mean number of prey per regurgitation and the use of different prey sizes reported in comparative studies (Tables 10, 13 and 16; Schreiber and Hensley 1976, Jahncke and Goya 2000, Harrison *et al.* 1983, Mellink *et al.* 2001). Similarly, the diet composition of magnificent frigatebird (at Isla Isabel off the Pacific coast of Mexico) changed during a four month period but the mass of regurgitates did not change (Calixto-Albarran and Osorno 2000).

Other diet characteristics found to be similar among visits in all the bird species were 1) mean number of prey categories per regurgitation with a near uniform distribution, 2) mean prey diversity and 3) equitability indexes with a near uniform distribution (Table 2, 12 and 15). All these statistics suggest that about equal number of prey categories per individual were regurgitated in each visit. Therefore, prey vulnerability must be limited to a very short time window for any individual bird. This could be a product of the dilution effect (Neil and Cullen 1974). If the predator can catch only one prey individual per successful attack and the prey categories appear in small schools, then the chances that any one individual will be eaten during a predation event decreases rapidly with group size. Schools of fishes or squids with a patchy distribution are commonly cited as sulid food (Vlietstra 2005), which are somehow unpredictable in epipelagic tropical waters (Ballance *et al.* 1997, Mills 1998). Flyingfishes in the eastern Caribbean travel in small schools determined by age cohorts (Oxenford *et al.* 1995a, b; Khokiattiwong 1998, Khokiattiwong *et al.* 2000).

Diet niche breadths and diet niche overlaps were also similar among visits in the three bird species (intraspecific). I observed very few prey categories unique to a single sulid species, and those I found in few individuals and mostly in one visit. This makes sense if the predator populations are generalists (as shown by in Figures 6, 7 and 8), meaning that sulids diet near Monito Islet rarely relies on a single prey category. Harrison *et al.* (1983) also found several prey categories in the same species at the Northwestern Hawaiian Islands. In contrast, Jahncke and Goya (2000) report a diet of three species for the masked booby (1996) and one species for the Peruvian booby (*S. variegata*, 1997). However, they argued that both species exploit mostly Peruvian anchovies (*Engraulis ringens*) during cold years of high productivity and results differed in prey categories and numbers during the warmer El Niño years (fewer anchovies, owing to warmer waters).

Prey Categories and Temporal Differences

Trophic interactions occur because predators are in spatial concordance with their prey; therefore, the distribution of predators while foraging is expected to somehow reflect the distribution of their prey (MacArthur and Pianka 1966). As opposed to the other two bird species, the distribution of the number of organisms per prey category per regurgitation of the masked booby differs from that expected by chance (total, Tables 2, 12, 15). VMR numbers and normality tests suggest an aggregated distribution for the number of organisms per categories for the brown and the red-footed boobies, and a uniform distribution for the masked booby. An aggregated distribution for the number of organism per prey category can be obtained if the predator is randomly preying on species with an aggregated distribution. In contrast, a uniform distribution can be

obtained if birds are preferentially selecting a discrete small array of prey species or if birds are fishing at random from prey distributed uniformly. Sulids are known to feed on sardines and anchovies that have a tight patchy distribution (Ángeles-Pérez *et al.* 1991, Jahncke and Goya 2000, Mellink *et al.* 2001). Such prey packed in great abundance characterizes major upwelling systems, but are rare in the epipelagic zones of the Caribbean Sea (Carpenter 2002). An aggregated distribution of organisms per prey category suggested that sulids in Monito Islet feed opportunistically. Opportunistic feeding behavior is common among seabirds (Furness and Monaghan 1987) including these three species (Seki and Harrison 1989, Jahncke and Goya 2000). The case of the masked booby appears different, but is due to its prey size. Being the largest of the sulids, this species feeds on few but large organisms compared to the other two bird species (Figure 3-5; Schreiber and Hensley 1976). Therefore, due to a limited gut capacity, the capturing of a large prey results in fewer individuals and in less prey species per bird.

A direct relationship between prey and bird beak and body sizes is expected in seabirds (Ainley *et al.* 2005, Ashmole and Ashmole 1967, Ashmole 1968, Schreiber and Hensley 1976, Harrison *et al.* 1983). In Monito Islet, dietary niche overlap was relatively small and the masked booby regurgitated larger organisms than the other two bird species. Differences in prey sizes and categories have been used to indicate food resource partitioning, accomplished through differences in feeding methods, feeding zones and feeding times (Ashmole and Ashmole 1967, Schreiber and Hensley 1976, Harrison *et al.* 1983). This is also maintain by the one-third overlap of their dietary niches found in

Monito Islet. MacArthur and Levins (1967) predicted that overlap between adjacent species of less than 54% is necessary for coexistence without competition.

However, variability in prev sizes was also observed. In contrast, to the red-footed booby, the masked and brown booby showed a significant variation in their prey sizes (Tables 5 and Figures 4 and 5) produced by the regurgitation of temporally abundant prey species (e.g. prey categories found only in one visit and in few bird individuals) with sizes relatively large (i.e. juvenile little tunny, in the case of the masked booby) or tiny, (i.e. post larvae of flying gurnard and juvenile black gemfish in the case of the brown booby). In addition, it caused the mean prey size of the brown booby to look slightly smaller than the mean prey size of the red-footed booby (Figure 4b and 5b). This does not mean that the red-footed booby does not take advantage of temporally abundant prey when available. The red-footed booby also regurgitated temporal prey items, but they were within its mean prey size (i.e. post-larvae of spotted goatfish, and yellowfin mojarra, Gerres cinereus; Table 17). Similarly, by analyzing five stomach samples from each species collected weekly between January 1981 and October 1982, Seki and Harrison (1989) suggested that, as with other subtropical seabirds, black noddies (Anous minutus) and red-footed boobies are apex opportunistic predators. So sulids in Monito Islet will feed on juvenile fishes or on post-larva stages when available in surface waters of their feeding path. Seki and Harrison (1989) evidenced the opportunistic character by comparing prey diversity of red-footed boobies in French Frigate Shoals, Hawaii, with diets reported in temperate areas and Peru where anchovies constituted 80-96% of the seabirds' food (Pearson 1968, Jordan 1967). Seki and Harrison (1989) suggested that

incidental prey taken during single seasons, in French Frigate Shoals, is further indicators of an opportunistic predator (also see Diamond 1983). In general, as the frequency of feeds decreases among species, the variability in feed size increases, suggesting that the most pelagically feeding species are faced with the most variable food supplies (Ricklefs 1983).

In Monito Islet some prey species were present in samples in all four visits (e.g. clearwing flyingfish) while others were seen as temporal because they were regurgitated during one or two visit by brown and red-footed boobies. Harrison *et al.* (1983) in the Northwestern Hawaiian Islands and Jahncke and Goya (2000) in Lobos de Tierra Island also reported temporal variations in prey categories. For example, Janhcke and Goya (2000) found that the masked booby was capable of using an opportunistic feeding strategy and periodically exploiting the Peruvian anchovies at the northern edge of the Peruvian Upwelling System. Similarly, sulids in Monito Islet depredate temporally abundant organism. The diet composition of the magnificent frigatebird also changed during a study of four month period, suggesting that availability of some prey species changes over time (Calixto-Albarran and Osorno 2000).

If some prey species are temporally abundant and this abundance is predictable, it would be advantageous to breed during such times. Sulid breeding success is mostly dependent on food provision (Nelson 1978, Ricklefs 1983, Montevecchi and Barret 1987, Hamer *et al.* 1991, Cliford and Anderson 2001, 2002). In Monito Islet, prey volume was larger during the peak breeding season than off peak, particularly in masked booby. Breeding strategies are subject to strong selection pressures, therefore, environmental

conditions, affecting foraging and feeding, will play an important role in shaping breeding strategies. Consequently, breeding peak of sulids, especially the masked booby, could be related to the abundance and availability of large prey (e.g. clearwing flyingfishes in the masked booby peak breeding season).

Most temporal prev around Monito Islet were small size in comparison to the most common regurgitated species. Three possible situations, not mutually exclusive, could explain this finding. First, it is possible that small temporal prey complement the diet when the common prey (frequently found in regurgitations) is unavailable (Ashmole and Ashmole 1967, Harrison et al. 1983 Seki and Harrison 1989). Second, it is possible that small temporal prey provide a higher nutritional value than the common prey (MacArthur and Pianka 1966). Finally, the small temporal prey might be in great quantities and more vulnerable to predation by sulids than prey categories observed in every visit. These possibilities are in accordance with optimal foraging theory, which develops behavioral rules that maximize an animal's short-run rate of intake of energy (MacArthur and Pianka 1966, McNamara and Houston 1985, Alcock 1993). The theory assumes that optimal foraging will be favored by natural selection because increased rate of intake of food energy will result in healthier animals with more resources available for growth and reproduction. Although a combination of the three situations could be operating, my data support only the third possibility. Many of the temporal categories collected at Monito Islet were in the late post-larval or juvenile stages, as Hensley and Hensley (1995) found in the regurgitations of terns and noddies (Laridae) in the Dry Tortugas (Florida, USA). Thorson (1957) estimated that 85 to 95 % of all species in tropical level-bottom communities have a long pelagic life. When adult, the flying gurnards, spotted goatfish, and yellowfin mojarra are benthic dwellers (Carpenter 2002). Goatfish post-larvae appear well adapted to the open sea, with long slender bodies and coloration typical of pelagic species (Caldwell 1963). Many post-larvae and juveniles of other benthic species inhabit the epipelagic zone, usually relying on camouflage (and probably habitat complexity) as they hide under *Sargassum* mats or windrows until migration to benthic habitats occurs (Hardy 1978, Casazza and Ross 2008). Therefore, during that phase of transition, the post-larvae could be temporally and locally abundant, available, and vulnerable to predatory birds. This suggests that sulids in Monito Islet will take advantage of small temporal prey due to vulnerability when present in great quantities, and not necessarily due to population decline of the prey categories regurgitated in all the visits. However, their importance should not be underestimated (Ashmole and Ashmole, 1967).

Sulids usually feed by plunge dives (Ashmole 1971, Harrison *et al.* 1983, Le Corre 1997, Nelson 2003). The regurgitation of many small post-larval fish that were probably associated with *Sargassum* mats or floating debris (Haney 1986) also presents an atypical scene. For example, this situation may present certain difficulties in the logistics of catching 42 small, coin-sized flying gurnards by deep plunge diving (Ashmole 1971, Harrison *et al.* 1983), as observed in one of the regurgitations of a brown booby. Nixon and Lee (1998) reported the brown booby executing an unusual foraging technique to catch small fishes in a shallow lagoon. The birds first targeted the small fishes by floating on the surface and putting their heads repeatedly into the water. The

birds then flew at a height of one meter or less for one to several meters before diving at a very shallow angle. Although the technique described by Nixon and Lee (1998) seems energetically costly for a relatively large bird, sulids near Monito Islet may use foraging techniques other than plunge diving to exploit aggregations of small prey (e.g. juvenile flying gurnards, Atlantic bigeye or deepwater squirrelfish). The use of a variety of feeding techniques may be common at least in this species.

Feeding Strategies

Although all three species use a generalist feeding strategy in the population as a whole, as well as several temporal prey components and with some overlap among diet niche, it is evident that the dominant prey species differ among the species (similar results obtained from different methods: IRI and Costello). At Monito Islet, the clearwing flyingfish was common in all sulids, however, this prey was distinctly dominant in all visits within regurgitations of masked booby, while the same prey species was about as common as mackerel scad in the brown booby and sailfin flyingfish and spotted goatfish post-larvae in red-footed booby (Tables 5, 9 and 12, Figures 6-8). The three prey species are very abundant in the Caribbean Sea (Carpenter 2002). In particular, the clearwing flyingfish is endemic to the Western Central Atlantic and the most common flyingfish in that region (Carpenter 2002). Therefore, sulids in Monito Islet are generally exploiting the most abundant prev species within their foraging zones. It is possible that the prev types that are infrequently encountered tend to be underrepresented in the diet, while those that are more abundant are consumed in excess. Bond (2007) reviewed similar situations in which use of a search image might be involved. He described the evolution

of selective attention in visual search with environmental conditions in which cryptic food items and resemblance of food to the background play a major role. This possibility may occur in sulids, since the coloration of the dominant prey species matches the ocean when seen from the air.

As stated by Amundsen et al. (1996) in their work based on niche theory and the generalist-specialist dichotomy, a population with a broad niche width (generalist) could be composed of individuals specialized in different resources or generalist individuals, or a combination of both. In the three sulid species, most prey categories were regurgitated by few individuals during a given visit, resulting in relatively high between individual differences. The niche width contribution was mostly from high between phenotype components (Figures 6-8), most regurgitated prey categories were obtained from few individuals. Therefore, sulids in Monito Islet appear to depend mostly on solitary or small flock foraging strategies. Predators that feed on patchily distributed prey, variable in time and location, may confront difficulties in keeping current information on all prey patches in an area (McNamara and Houston 1985, Shettleworth et al. 1988). To deal with this situation, predators presumably must sample areas on a regular basis (Shettleworth et al. 1988) or rely on cues from similar consumers (Burger 1997). When prey becomes more difficult to locate in an area, (change distribution or abundance), predators must increase the foraging time or modify their foraging behavior (Davoren 2000).

Predators won't benefit from foraging in a big group when patches of food are small and the prey aggregation isn't sufficiently large to fulfill the requirements of the

whole group members (Davoren 2000). If sulids are foraging solitary or in small flocks, the prey patches attacked by sulids from Monito Islet must be small.

Although the dietary niche width of the three species was wide and relatively similar among species, the feeding strategy differs among them in dominant and rare species (see Amundsen et al. 1996). The masked booby's dominant prey category was the same in every visit, and it was more distant and oriented toward the right upper corner of the feeding strategy chart (Figure 6) than the dominant prey categories of the other two sulids, therefore, this prey was commonly regurgitated by most masked booby individuals. Likewise, the brown booby appears to be the greatest generalist among the three species. I did not record any regurgitation with only one prey category from a brown booby (Figure 7). From the feeding strategy chart, I infer that in the generalistspecialist gradient, the feeding strategy of the red-footed booby resembles the brown booby more than the masked booby (Figure 8). This indicates that, in Monito Islet, within the specialist-generalist gradient, the diet is more generalized in brown and red-footed boobies than in the masked booby. Some seabird species are more capable to subsisting from various prey species (generalist) than others (more specialize). These two contrasting patterns of life history have evolved among seabirds and may explain the vulnerability of certain species to changes in food resources (Tasker et al. 2000). The brown booby global population is increasing. This species is considered an opportunistic species, adaptable to food changes, often able to take advantage of fishing discards (Tasker et al. 2000). On the other hand, specialist species may be tied to a particular set of conditions, may have difficulties in adapting to environmental changes, could be

vulnerable to disturbance, and could show decreases in population size. In a study of the status of sulids in the West Indies, Schreiber (2000b) advised about a possible decreasing population pattern for the three species, with special emphasis on the masked booby. Schreiber (2000b) suggests that the population status of the West Indies masked booby should be classified as endangered of extinction. The causes for the masked booby population decrease are not clear Schreiber (2000b), but, a more specialized diet compared with the other sulids further supports a population status revision for this species. The main causes identified in decreases in populations of seabirds are reproduction, pollutants, mortality due to exotic predators and fishery activities, and food availability (Furness and Monaghan 1987).

As infrequent and exceptional behaviors can provide insight into the ecology and physiology of a particular species, it may be misleading to describe the diet of these three species without considering the rare prey components, especially in cases where the prey was regurgitated abundantly by only a few bird individuals. All prey categories and sizes were used in a Discriminant Function Analysis to maximize the separation among bird species diets (Sokal and Rohlf 1995). Although 17% of the regurgitations are still misclassified, the DFA would be useful in identifying those prey species-sizes which discriminate among bird species (Figure 10). This pattern as a formula (Table 21) produced associated coordinates that group the regurgitations into each of the bird species. DFA showed that knowledge of the sulids diet via gut content greatly increased the ability to predict what species of sulid regurgitate in the field. This also suggests that, even with dietary niche overlap among the three species, at Monito Islet, the arrangement

of prey categories can be used to identify the bird species. Although indirectly, this segregation also supports the contention that they might be feeding from different stocks (see Sulids Coexistence section).

Oceanic Locales

Dominant prey species in the sulids' diet at Monito Islet differ from those reported elsewhere. However, the prey family percentages of masked booby at Monito Islet and Christmas Island (Schreiber and Hensley 1976) were similar except for high squid consumption in the latter location. The masked booby on the Northwestern Hawaiian Islands (Harrison *et al.* 1983) relies on Exocoetidae as in Monito Islet but in the former, it profusely regurgitated food items from the Carangidae family. In Monito Islet, the masked booby rarely regurgitated Carangidae, although it was an important component in the diet of brown booby. Conversely, the masked booby at Lobos de Tierra did not regurgitate Exocoetidae as the main diet component in three sampled years; instead, Engraulidae and Scombridae were the main prey families (Jahncke and Goya 2000). Offshore Brazil (Western South Atlantic) the diet of this sulid was based mainly in Exocoetidae followed by Clupeidae (Serrano and Azevedo-Júnior 2005). Therefore, the masked booby apparently will consume mainly Exocoetidae at low productivity locales.

The Brown booby in Monito Islet regurgitated mainly Carangidae, followed by Exocoetidae. This differs in numbers from the diet found at Northwestern Hawaiian Islands (Harrison *et al.* 1983) where it regurgitated mostly Mullidae and then Carangidae. Nevertheless, by volume the proportions are more similar. By volume, the brown booby

regurgitates mostly Carangidae and then Exocoetidae at Northwestern Hawaiian Islands (Harrison *et al.* 1983). The difference was greater with the regurgitations at San Idelfonso, San Pedro Mártir Islands and San Jorge Island where they regurgitated mostly Engraulidae (Mellink *et al.* 2001), and at Rose Atoll where they regurgitated mostly Decapodiformes and Mullidae (Harrison *et al.* 1984). Based on the regurgitated by the red-footed booby, instead of the brown booby. Offshore Brazil, the diet of this sulid was based mainly in Exocoetidae (Naves *et al.* 2002), and Scianidae, Engraulidae and Batrachoididae (Branco *et al.* 2005). Therefore, the brown booby regurgitates mainly Carangidae, Exocoetidae, Decapodiformes, and Mullidae at low productivity locales changing, as it is available, to Engraulidae and other available prey species at high productivity locales.

The proportion of the prey families regurgitated by the red-footed booby at Monito Islet differs from the diet reported at Christmas Island and Northwestern Hawaiian Islands (Schreiber and Hensley 1976, Harrison *et al.* 1983). On Monito Islet, Exocoetidae was the most abundant component of the regurgitations. Conversely, it was Decapodiformes on Christmas Island and Northwestern Hawaiian Islands (Schreiber and Hensley 1976, Harrison *et al.* 1983). However, this difference dissipated in the comparison of volume proportions. This suggests that the diets of the red-footed booby near Monito Islet and Northwestern Hawaiian Islands (Harrison *et al.* 1983) are similar in regurgitated volume proportions per prey family. Therefore, the red-footed booby regurgitates mainly Exocoetidae and Decapodiformes on different oceanic local.

Sulid Coexistence

Although some aspects of the feeding ecology may be similar among Caribbean sulids (e.g. prey species, niche breadth and overlap, prey diversity), most are different (e.g. dominant prey, prey size, number of prey carried to roosting or nesting grounds, feeding strategies) and niche overlaps are small (see MacArthur and Levins 1967). These findings complemented with studies of the foraging behavior of sulids support the hypothesis of feeding or foraging resource partitioning (MacArthur 1958, MacArthur and Levins 1967, Schoener 1983a) suggested to explain the feeding habits observed among sympatric seabird species by many ornithologists (e.g. Ashmole and Ashmole 1967, Schreiber and Hensley 1976, Harrison *et al.* 1983, Holm and Burger 2002). Therefore, in Monito Islet each sulid species may be feeding from different resources.

Levinton (1982) suggested that niche subdivision among *Hydrobia* species (Gastropoda) with respect to food size was unlikely; available prey will be used regardless of food size. Then it is possible that the size difference found in gut contents is simply a consequence of the structural habitat difference, in other words, the concomitant prey size difference is coincidental. Prey size difference was noticeable between the masked booby and the other two sulids. However, masked and red-footed boobies are both offshore feeders (Anderson and Ricklefs 1987, Weimerskirch *et al.* 2005a). Based on that, there is no reason to believe that for the smallest booby (red-footed booby) small sized prey was not available to masked boobies. A possible explanation is that masked and red-footed boobies in Monito Islet may be feeding differentially by zones (fish patches). Oxenford *et al.* (1995 a, b) and Khokiattiwong *et al.*

(2000) reported a patchy distribution of flyingfishes in the eastern Caribbean with a tendency for discrete geographical distribution both interspecifically and intraspecifically by life history stage (consequently sizes).

Wind conditions and vertical (depth) distribution of prey patches might also play an important role in feeding strategies and diet components. The masked booby fed (on Monito Islet mostly from clearwing flyingfish) by deep plunging (3-4m depth; Ashmole and Ashmole 1967) while the red-footed booby fed (in Monito Islet mostly from sailfin flyingfish) by shallow and surface plunging (0-3m; Weimerskirch et al. 2005b). Khokiattiwong (1988) found difference in the vertical distribution of flyingfishes (e.g. sailfin flyingfish lives closer to the surface than the fourwing flyingfish). Also windy conditions are positively related to catch effort for flyingfishes (Oxenford *et al.* 1995 a, b). Differences in prey size and category between masked and red footed boobies might be related to different feeding depths and methods. Schoener (1983b) reviewed works that established resource partitioning, and found that in those works habitat partitioning was more common than food partitioning, which in turn were more common than temporal (time) partitioning. He also found that large rather than small organisms should have competitively structured resource partitioning because predation more severely affects the latter.

The apparent availability of food, the small dietary niche overlap and the segregation of prey categories found in this study suggest that food resources are partitioned among bird species. However, the ability to adjust foraging behavior (behavioral flexibility) will be important for birds mainly feeding on small, epipelagic,

schooling fish, whose patch size and abundance can be highly variable both temporally and spatially (Davoren 2000). The local feeding niche overlap and the feeding habits observed in different locales (multispecies flocks feeding on sardines in upwelling systems; Montevecchi and Barrett 1987, Jahncke and Goya 2000, Ángeles-Pérez *et al.* 1991), suggest that these three sulid species possess the capacity to overlap diets with subsequent competition during attacks in cases where large vulnerable prey patches are available. Sulids in Monito Islet must have the plasticity to build multispecies flocks and exploit large vulnerable prey patches when available.

Food scarcity due to environmental disturbances (periods of ecological crunches; Wiens 1977) might limit feeding sources and promote competition for the few sources available (Duffy and Merlen 1986, Furness and Monaghan 1987, Gibbs *et al.* 1987, Jahncke and Goya 2000), but during this study that was not observed. Instead, practically all the sulids were able to regurgitate and mortality of adults, juveniles and fledglings was not observed. The evidence does not support that difference in sulids diets in Monito Islet represent an adaptive response to the immediate scarcity of food. In fact, competition is widely believed to occur among seabirds at sea, mostly in the context of feeding flocks (Hoffman *et al.* 1981, Harrison *et al.* 1991, Ballance *et al.* 1997). During active feeding in a flock, direct interference competition for access to prey can be intense (Ballance 2007). This competition can structure the composition of a particular flock and of a particular community (Ballance 2007). Tropical boobies can dive to deeper depths than can tropical terns. Both feed in multispecies flocks, and it has been suggested that interference competition allows masked boobies to numerically dominate feeding flocks

in highly productive waters, whereas Sooty Terns (*Sterna fuscata*) are constrained to feed in greatest numbers in flocks in areas of relatively low productivity (Ballance *et al.* 1997). These relationships are often a function of body size, because size often determines the outcome of interference competition (and energetic requirements, foraging range and prey density requirements; Persson 1985).

Sulids are long-lived, large apex predators in the epipelagic trophodynamics (Furness and Monaghan 1987, Seki and Harrison 1989). At least annually DNER personnel visit the Islet and marked annual declines have not being reported (pers. obs.). Therefore, it is unlikely that individuals in the West Indies became victims of predation or storms in such numbers that competition among sulids for prey could be reduced to an extent of preventing the sulid species to overlap significantly in their diets (but see Grime 1973, Horn 1975, Connell 1978, Leviten and Kohn 1980, Strong 1982)

Schreiber (2000b) advised about a possible decreasing population pattern for the three species in the West Indies. Prey abundance does not appear to be limiting the population growth of sulids at least in Monito Islet. Most threats reported for seabirds (e.g. fishery activities, contamination, fish stock fluctuations, and environmental changes) have not been reported for Monito Islet. An exception is the introduction of rats. It is possible that before rat eradication campaigns (1998; García *et al.* 2002), rats were preying on the population growth of seabirds in Monito Islet. However, within my visits rats where not observed (even during night surveys or preying on food left overnight to attract terrestrial predators; pers. obs.). Another possibility for competition is breeding space (Nelson 1983). In Nelson's (1983) words, "larger colonies (of Pelecaniformes)

presumably provide greater social stimulation and so colony size may help determine the timing of breeding and its synchrony in ways favoring larger colonies. Conversely, large colonies presumably increase interference by conspecifics. Social advantages, however, appear undeniably too slender to account for the presence of very large colonies. But, together with safety and limited availability of breeding locations, they could favor large colonies, the limits on which may then be imposed by site availability and by food. These are often impossible to disentangle."

Feeding association with subsurface predators

Au and Pitman (1986) reported that masked, red-footed and brown boobies were the seabird species most associated with spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins and the yellowfin tuna (*Thunnus albacares*) in eastern tropical Pacific. The feeding association among sulids and dolphins (Delphinidae) was also reported in Puerto Rico by Erdman (1967), in eastern Pacific by Pitman and Ballance (1992) and Ballance and Pitman (1999), and in Hawaii by Hebshi (2008). Au and Pitman (1986) also reported that sooty terns appear to be highly adapted for feeding with skipjack (*Katsuwonus pelamis*) or skipjack-like tuna in the eastern Pacific. On the other hand Harrison *et al.* (1983) determined that, in Hawaii rather than Pelecaniformes, the sooty tern (*Sterna fuscata*), brown noddy (*Anous stolidus*), black noddy (*A. minutes*), white tern (*Gygis alba*) wedge-tailed shearwater (*Puffinus pacificus*) and Christmas shearwater (*P. nativitatis*) were more closely associated with tunas. Similarly, Hebshi *et al.* 2008 did not found a strong association between Pelecaniformes and tunas in Hawaii.

In the literature I did not find comparable dietary data and abundance reported for pelagic dolphins. Alternatively the subsurface oceanic predators most landed in Puerto Rico are the wahoo (Acanthocybium solandri), dolphinfish and yellowfin tuna (Matos-Caraballo 2007). Unfortunately during the preparation of this document, dietary data for these subsurface predators was not available from waters around Monito Islet or western Caribbean. However, dietary data of these predators was published from eastern Caribbean (Oxenford and Hunte 1999), North and tropical Atlantic Ocean (Satoh et al. 2004), and offshore Brazil (Pimenta et al. 2005). On average 18, 17 and 24 % of the organisms reported by those authors as diet components of yellowfin tuna, dolphinfish and wahoo are within the families regurgitated by masked booby, and 46, 88 and 3 % of the organisms found in this booby were within families found in those fishes, respectively. Similarly, 26, 48 and 47 % of the organisms reported by those authors as prey of yellowfin tuna, dolphinfish and wahoo are within the families regurgitated by brown booby, and 48, 60 and 15 % of the organisms found in this booby were within families found in those fishes. Finally, 26, 45 and 47 % of the organisms reported by those authors as prey of yellowfin tuna, dolphinfish and wahoo are within the families regurgitated by red-footed booby, and 32, 58 and 9 % of the organisms found in this booby were within families found in those fishes, respectively. Two scenarios may result in these feeding associations, either the sulid position in the air provide hints about orientation for potential prey to subsurface predators, or sulids simply take advantage of the feeding activity of subsurface predators regardless of the prey. The strongest association should result from the best outcome for both the bird and the subsurface predator. Assuming that

diets reported by Oxenford and Hunte (1999), Satoh *et al.* (2004) and Pimenta *et al.* (2005) are similar for those subsurface predators around Monito Islet, the brown booby and the dolphinfish appear to have the best affinity followed by the red-footed booby and the dolphinfish. Aditional evidence to support the association is: 1) sulid diets are also less similar to the diet of most tuna allies reported by Satoh *et al.* (2004), and Pimenta *et al.* (2005); 2) Harrison *et al.* (1983) and Hebshi *et al.* (2008) determined that sulids were not in the foraging guild most related to tunas in Hawaii; and 3) in Puerto Rico, landings of dolphinfish are at least twice that of any single species of tuna (Matos-Caraballo 2007). However, around Puerto Rico, landings of both yellowfin tuna and dolphinfish occur year-round, but the former is usually present in greater quantities during May-September, while dolphinfish is during January-June (Matos-Caraballo 2007). Therefore, around Monito Islet specific feeding association with dolphinfish and tunas should be temporal.

Epipelagic Fish Stock

I found no estimates of how many prey organisms are removed from the ocean by sulids, and perhaps there is none (Karpouzi 2005). I did some calculations to obtain rough estimates of the prey organisms removed by these three sulids. For this, I used the population estimates provided by Schreiber (2000b) for Monito Islet and the West Indies. To show the mathematics of this rough estimation I will discussed in detail the calculations in the case of the masked booby followed by the estimations of the other two sulids.

Assuming that the average masked booby at Monito Islet weighs about 2.2 kg and its daily food consumption is approximately 13.1% of its body weight (as estimated by

Laugksch and Duffy 1984), by considering a mean prey volume for each individual prey of 45.1ml (0.05 kg), I estimate that the masked booby needs roughly six prey items per day to fulfill its daily consumption food requirement. In population terms, a population of about 110 individuals at Monito Islet will remove nearly 634 organisms per day (0.03 metric tons). About two average regurgitations are enough to fulfill its daily consumption. If the same is true for this species throughout the West Indies, the estimated population (\sim 1,200) removes about 6,917 organisms per day or 0.35 metric tons.

Using the same equation, I found that the other two sulids need about three average regurgitations to fulfill their daily consumption quota. Assuming an average body weight of 1.3 kg, a daily consumption of 14.2% of the body weight (Pettit *et al.* 1984), and a mean prey volume of 12.8ml (0.01 kg), I estimated that the brown booby in Monito Islet needs about 19 organisms per day. Thus at Monito Islet, the population removes nearly 18,460 organisms per day (0.18 metric tons) or about 245,518 organisms per day (2.46 metric tons) in the West Indies.

For the red-footed booby, assuming an average body weight of 1.1 kg, a daily consumption of 14.2% of the body weight (Pettit *et al.* 1984), and a mean prey volume of 13.6ml (0.01 kg), I estimated that this bird needs roughly about 16 organisms per day to fulfill its daily consumption. Its population at Monito needs nearly 9,372 organisms per day (0.09 metric tons) or 284,284 organisms per day (2.84 metric tons) in the West Indies. In the West Indies, to fulfill their consumption quota, the three species could remove from the ocean a rough estimate of 536,719 organisms per day or about 6 metric tons per day.

For reference, the daily consumption of 32,700 sulids in the West Indies is equivalent to the daily consumption of 12,427 average dolphinfishes which represents 100 metric tons of dolphinfish; based on an estimated daily ration of 5.6% of the body weight/day (Olson and Galván-Magaña 2002) and an average dolphinfish of 1000 mm or 8.11 kg for Puerto Rico (Pérez and Sadovi 1992 in Oxenford 1999). FAO statistics for the Western Central Atlantic reported underestimated annual landings of dolphinfish ranging from 3,549 to 4,300 metric tons from 1995 to 1999, indicating that this species is among the top seven pelagic species landed in this region, giving an indication that they are indeed abundant (Carpenter 2002, Oxenford 1999). Similarly, 47 metric tons were reported as commercial landing in Puerto Rico for 2006 (Matos-Caraballo 2007). This suggests that the sulids are not among the highest fish consumers in the West Indies.

With these in mind, a simple model can be worked out indicating the magnitude of the prey removal by sulids from the Caribbean oceanic waters. Assuming a general energy transfer efficiency of 10% from one trophic level to another (Slobodkin 1961), and a daily primary productivity (defined as the sum of all photosynthetic rates or the rate of carbon fixation as a direct result of photosynthesis) of 0.5 g C/m² (Sastre and Armstrong 2000), the following estimates can be made. The respiration takes about 20% and thus the daily net production is 0.4 g C/m^2 . As 1 g C is about 10 kcal, the net daily photosynthetic production equals 4.0 kcal/m². Assuming an energy transfer of 10% and considering that 1 g of wet weight is about 1 kcal, the production of primary consumers will be about 0.4 g/m²/day, secondary consumers 0.04 g/m²/day and tertiary consumers about 0.004 g/m²/day of prey mass. Sulids prey species are mainly either tertiary or
quaternary consumers and then the available prey will depend on the relation between these two groups (Sydeman *et al.* 1997, Hunt *et al.* 2000). Therefore, in the Caribbean Sea (about 2,520,000 km²; Carpenter 2002), the production available to the sulids and other predators at the same trophic level is between 10,080 and 1,008 metric tons/day. The sulids in the Caribbean Sea consume 0.06 to 0.6% of the production of lower trophic levels. Therefore, it is unlikely that the population of sulids in the West Indies, by itself, exert substantial predation pressure on the epipelagic fish stock or to the Caribbean fisheries. By weight, the sulids are not among the seabird species whose total populations consume most prey (Broke 2004). Other predators need to be analyzed to estimate the cumulative effect of predation and fisheries in the fish stock (see Trites *et al.* 1997, Broke 2004). On the other hand, these estimates also suggest that sulids are important contributors to the trophodynamics and nutrient cycle in their nesting and roosting grounds.

Most if not all the studies of seabirds as indicators of fish stock fluctuations have been performed in waters of high productivity (e.g. Kirkham and Morris 1979, Sunada *et al.* 1981, Cairns 1987, Muck and Pauly 1987, Montevecchi 1993, Montevecchi *et al.* 1987, Velarde *et al.* 1994, Regehr and Montevecchi 1997). However, depending on scale, pelagic seabirds appear to be particularly useful in monitoring changes in the abundance of epipelagic prey species occurring at moderate to low biomasses (Berruti and Colclough 1987). As suggested by Cairns (1992), there is no perfect indicator of fish stocks. However, seabird-based indices may be useful supplements to currently available tools. Based in the review of Piat *et al.* (2007), I found reasons to consider sulids as

indicators of oceanic health and fish stock in the Caribbean Sea, including: 1) they are highly visible animals in an environment in which most other organisms are not; 2) they are easily counted in comparison to most highly mobile marine organisms; 3) they are colonial breeders that must congregate at least annually in large numbers at the same location for breeding, a convenient occurrence that allows one to census populations, screen adults, chicks and juveniles, and monitor trends of multiple coexisting species (three sulid species) at various trophic levels simultaneously (34 prey species); finally 4) they are relatively easy to observe and capture at colonies, allowing measurements of a wide variety of demographic, behavioral and physiological parameters. In addition, most sulids in Monito Islet regurgitate heavy loads of prey species and they appear to sample near shore (brown booby), and offshore (three to four meters depth, masked booby; first three meters depth, red-footed booby) providing information of common fish species (e.g. clearwing flyingfish, mackerel, sailfin flyingfish; Carpenter 2002) and different agestages (e.g. adults, juveniles, post-larvae, size classes from 25 to 275 mm, size and category temporal fluctuations as in September for the three Sula spp.). Those common prey species are food found in diet of many pelagic predators of economic importance (Oxenford and Hunte 1999, Satoh et al. 2004, Pimenta et al. 2005). On the other hand, flyingfishes are a common and commercially important component of the eastern Caribbean pelagic fish fauna (Oxenford et al. 1995 a, b, Khokiattiwong et al. 2000).

CONCLUSION

This is the first detailed description of the diet of the genus *Sula* in the Caribbean Sea. The fact that practically all the birds appear healthy and were able to regurgitate

66

Ricardo López-Ortiz, 2007, PhD Dissertation, UPR/RUM

heavy loads of prey, suggests that food is sufficiently available in their foraging grounds to sustain the colony at Monito Islet. Food gathering appears to be limited by gut or weight lift capacity. Other positive indicators found were, lack of evidence of threats and depredation at any developmental stage during my visits.

In general sulid's diet differ most from diets based in sardines and anchovies of eutrophic locales and was most similar to diets reports in oligotrophic locales where diet was based on epipelagic flyingfishes, carangids, mullids, scombrids and squids. Likewise, juveniles and post-larval stages of prey species were regurgitated. Within Monito Islet, interspecific similarities included prey numbers per regurgitation, prey species per regurgitation, prey categories per regurgitation with a near uniform distribution, prey diversity, niche breadth and small niche overlap. The three bird species feed mostly on abundant prey species. These similarities suggest opportunistic feeding behavior mostly by solitary feeding or in small flocks with a prey vulnerability limited to a very short time window. Interspecific differences were prey size, dominant prey species, and feeding strategies suggesting that each bird species could be feeding from a different stock.

The clearwing flyingfish was a common prey in all sulids. However, this prey was distinctly dominant in all visits within regurgitations of masked booby, while the same prey species was about as common as mackerel scad in the brown booby, and sailfin flyingfish and spotted goatfish post-larvae in the red-footed booby. The masked booby feeding strategy was less generalist and regurgitated larger prey than the other two bird species. With this in mind, a discriminant function analysis was performed allowing the bird species determination from regurgitations in 83% of the times.

Although local data of subsurface predators was not available, a comparison with diets reported in the eastern Caribbean, North and tropical Atlantic Ocean and offshore Brazil suggests that the brown booby and the dolphinfish appear to have the best affinity for feeding associations, followed by the red-footed booby and the dolphinfish. However, dolphinfish and yellowfin tuna are seasonal, so the feeding association with these predators is likely to be temporal. Affinity to dolphins (Delphinidae) needs to be tested.

By combining the feeding ecology data found in the literature with the results of this dissertation I inferred that the masked booby is mostly a solitary epipelagic offshore predator that dives from up to 30m and feeds by deep plunging (3-4m depth). Around Monito Islet it may not have the strongest affinity for common fish subsurface predators (dolphinfish and yellowfin), feeding mostly on small patches of clearwing flyingfishes of 150.8 mm (s.e. \pm 2.3) of fork length or 45.1 ml (s.e. \pm 3.6) of volume. The brown booby is a shallow lagoon and near shore epipelagic gregarious predator (i.e. Sargassum mats) that dives from one to 15m and feeds by surface and shallow-plunge dives (0-4m depth). Around Monito Islet it may have strong affinity for common fish subsurface predators, feeding mostly on carangids and flyingfishes of 99.1 mm (s.e. \pm 1.9) of fork length or 12.8ml (s.e. \pm 0.8) of volume. The red-footed booby is an epipelagic offshore predator that dives from two to 32m and feeds by shallow and surface plunging (0-3m). Around Monito Islet it may have strong affinity for common fish subsurface predators, feeding mostly on sailfin flyingfish of 101.3 mm (s.e. \pm 1.8) of fork length or 13.6 ml (s.e. \pm 0.7) of volume.

Ricardo López-Ortiz, 2007, PhD Dissertation, UPR/RUM

These West Indian sulids may remove from the ocean approximately 536,719 organisms per day or about 6 metric tons per day. Prey consumption should be enough to contribute substantially in the trophodynamics of the Islet, but not to exert substantial predation pressure on the epipelagic fish stock or to the Caribbean fisheries.

This work supports the value of monitoring these species, especially the masked booby, which is the rarest among the sulids in the West Indies and has the most specialized diet. Periodic monitoring of diets combined with breeding and numbers of birds should provide information about population trends. Fluctuations in prey species shared among the sulids suggest that a monitoring program for these three species may provide information on epipelagic dynamics, prey sizes and categories, temporal fluctuations, including peak abundance of fish species in their ephemeral stages of postlarvae; these life stages are very difficult and expensive to get otherwise. In the other hand, seabird feeding data combined with new satellite-telemetric techniques and a study of the effect of guano in the ecology of Monito Islet will provide essential data related to their feeding grounds and probably their importance in the nutrient cycle in the Mona Island Natural Reserve.

REFERENCES

- Aebischer, N. J. 1995. Philopatry and colony fidelity of shags *Phalocrocorax aristotelis* on the east coast of Britain. Ibis 137:11-18.
- Ainley, D. G., and R. J. Boeakelheide. 1983. An ecological comparison of oceanic seabirds' communities of the South Pacific Ocean. Stud. Avian Biol. 8: 2-23.
- Ainley, D. G., L. B. Spear, C. T. Tynan, J. A. Barth, S. D. Pierce, R. G. Ford, and T. J. Cowles. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep-Sea Res. II 52:123-143.
- Alcock, J. 1993. Animal Behavior: an evolutionary approach. Fifth Edition. Sinauer Associates Inc. Publishers, Sunderland, Massachusetts, USA, 625 pp.
- American Ornithologists' Union. 2000. Forty-second supplement to the American Ornithologists' Union Check-list of North American Birds. Auk 117:847–858.
- Amerson, A. B., Jr., and P. C. Shelton. 1976. The natural history of Johnston Atoll, Central Pacific Ocean. Atoll Res. Bull. 192:1-479.
- Amundsen, P. A., H. M. Gabler, and F. J. Staldvik. 1996. A new method of graphical analysis of feeding strategy from stomach contents data. J. Fish Biol. 48:607-614.
- Anderson, D. J. 1989. Differential responses of boobies and seabirds in the Galapagos to the 1986-87 Southern Oscillation event. Mar. Ecol. Prog. Ser.52:209-216.
- Anderson, D. J. 1993. Masked booby (*Sula dactylatra*). *In* A. Poole, and F. Gill (eds.). The Birds of North America, No. 73, Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C., 805 pp.
- Anderson, D. J., and R. E. Ricklefs. 1987. Radio-tracking masked and blue-footed boobies (*Sula* spp.) in the Galàpagos Islands. Nat. Geogr. Res. 3:152-163.

- Anderson, D. W., F. Cress, K. F. Mais, and P. R. Kelly. 1980. Brown pelicans as anchovy stock indicators and their relationship to commercial fishing. Calif Coop. Oceanic Fish. Invest. Rep. 21:54-61.
- Anderson, D. W., F. Cress, and K. F. Mais. 1982. Brown pelicans: influence of food supply on reproduction. Oikos 39:3-31.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago, 782 pp.
- Ángeles-Pérez, A., B. R. Tershy, and D. Breese. 1991. Diet of male and female brown boobies on Isla San Pedro Martir, Gulf of California, Mexico. Abstracts of the Pacific Seabird Group Annual Meeting. Monterey, California, 23-27 pp.
- Arcos-Pros, J. M. 2001. Foraging ecology of seabirds at sea: Significance of commercial fisheries in the NW Mediterranean. Thesis Ph. D. Universidad de Barcelona, España, 114 pp.
- Ashmole, M. J., and N. P. Ashmole. 1968. The use of food samples from sea birds in the study of seasonal variation on the surface fauna of tropical oceanic areas. Pac. Sci. 22:1-10.
- Ashmole, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). Syst. Zool. 17:292-308.
- Ashmole, N. P. 1971. Seabird ecology and the marine environment *In* D. S. Farner, and J. R. King (eds.). Avian biology, Vol. I. Academic Press, New York, pp. 223-287.
- Ashmole, N. P., and M. J. Ashmole. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Bull. Peabody Mus. Nat. Hist., Yale University 24:1-131.
- 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. 1993. Community ecology and flight energetics in tropical seabirds of the Eastern Pacific: energetic correlates of guild structure. Ph.D. Diss., Univ. California, Los Angeles, CA. 173 pp.
- Ballance, L. T. 1995. Flight energetics of free-ranging red-footed boobies (*Sula sula*). Physiol. Zool. 68: 887–914.
- Ballance, L.T. 2007. Understanding seabirds at sea: why and how? Mar. Ornithol. 35:127–135.
- Ballance, L. T., and R. L. Pitman. 1999. Foraging ecology of tropical seabirds. *In* N. J. Adams and R. H. Slotow (eds.). Proc. 22nd Int. Ornithol. Congr. Durban, Johannesburg: Birdlife South Africa, pp 2057-2071.
- 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.
- Berruti A., and J. H. Colclough. 1987. A comparison of the quantity of pilchard in Cape gannet diet and commercial catches off the Western Cape, South Africa. S. Afr. J. Mar. Sci. 5:863-869.
- Boersma, P. D. 1978. Breeding of Galapagos penguins as an indicator of oceanographic conditions. Science 200: 1481-1483.
- Bond, A. B. 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. Ann. Rev. Ecol. Evol. Syst. 38: 489-514.
- Bostford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. Science 277:509-514.
- Branco, J. O., H. A. A. Fracasso, I. F. Machado, M. S. Bovendorp, and J. R. Verani. 2005. Dieta de *Sula leucogaster* Boddaert (Sulidae, Aves), nas Ilhas Moleques do Sul, Florianópolis, Santa Catarina, Brasil. Revista Brasileira de Zool. 22:1044-1049.

- Broke, M. de L. 2004. The food consumption of the world's seabirds. Proc. R. Soc. Lond. [B] 271:246–248.
- Brothers, N., R. Gales, and D. Pemberton. 1993. Prey harvest of the Australasian gannet (*Sula serrator*) in Tasmania. Wildl. Res. 20:777-783.
- Buckley, N. J. 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. Auk 113:473-488.
- Buckley, N. J. 1998. Interspecific competition between vultures for preferred roost positions. Wilson Bull. 110:122-125.
- Burger, A. E. 1997. Arrival and departure behavior of common murres at colonies: evidence for an information halo. Colon. Waterbirds 20:55-65.
- Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.
- Cairns, D. K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94:811-824.
- Caldwell, M. C. 1963. Development and distribution of larval and juvenile fishes of the family Mullidae of the Western North Atlantic. Fish. Bull. Fish Wildl. Serv. 62:403-457.
- Calixto-Albarran, I., and J. L. Osorno. 2000. The diet of the magnificent frigatebird during chick rearing. Condor 102:569-576.
- Carpenter, K. E. (ed.). 2002. The living marine resources of the Western Central Atlantic. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. Vols 1-3. Rome, FAO, 2150 pp.

- Casazza, T. L., and S. W. Ross. 2008. Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. Fish. Bull. 106:348-363.
- Chaves-Campos, J., and J. Torres. 2002. Distribution of nests of the brown booby (Sula leucogaster) in relation to the inclination of terrain. Ornitologia Neotropical 13:205-208.
- Chesson, P. L., and T. J. Case. 1986. Overview: nonequilibrium community theories: chance, variability, history, and coexistence. *In* J. Diamond and T. J. Case (eds.). Community Ecology. Harper and Row Publishers, New York, pp 229-239
- Clark, L., R. E. Ricklefs, and R. W. Schreiber. 1983. Nest-site selection by the red-tailed tropicbird. Auk 100: 953-959.
- Clifford, L. D., and D. J. Anderson. 2001. Food limitation explains most clutch size variation in the Nazca booby. J. Anim. Ecol. 70:539-545.
- Clifford, L. D., and D. J. Anderson. 2002. Clutch size variation in the Nazca booby: a test of the egg quality hypothesis. Behav. Ecol. 13: 274–279.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.
- Costello, M. J. 1990. Predator Feeding Strategy and Prey Importance: A New Graphical Analysis. J. Fish Biol. 36:261-263.
- Cramp, S., and K. E. L. Simmons. 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. Vol. 1. Ostriches to ducks. Oxford University Press, Oxford, England, 722 pp.
- Crawford, K. J. M., and P. A. Shelton. 1978. Pelagic fish and seabirds interrelationships off the coast of Southwest and South Africa. Biol. Conserv. 14:85-109.

- Croxall, J. P., and P. A. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol. J. Linn. Soc. 14: 103-131.
- Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415-2428.
- Davoren, G. K. 2000. Variability in foraging in response to changing prey distributions in rhinoceros auklets. Mar. Ecol. Prog. Ser. 198:283-291.
- Dearborn, D. C., A. D. Anders, and E. N. Flint. 2001. Trends in reproductive success of Hawaiian seabirds: is guild membership a good criterion for choosing indicator species? Biol. Conserv. 1001:97-103.
- Diamond, A. W. 1983. Feeding ovelap in some tropical and temperate seabird communities. Stud. Avian Biol. 8:24-46.
- Dorward, D. F. 1962. Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. Ibis 103b:173-220.
- Duffy, D. C. 1983. The foraging ecology of Peruvian seabirds. Auk 100:800-810.
- Duffy, D. C. 1984. Nest site selection by masked and blue-footed boobies on Isla Española, Galapagos. Condor 86:302-304.
- Duffy, D. C. 1986. Foraging at patches: interactions between Common and Roseate Terns. Ornis Scand. 17:47-52.
- Duffy, D. C., and G. Merlen. 1986. Seabird densities and aggregations during the 1983 El Niño in the Galapagos Islands. Wilson Bull. 98:588-591.
- Duke, G. E. 1985. Raptor physiology. *In* M. E. Fowler (ed). Zoo and Wildlife Medicine, 2nd ed. Philadelphia: W. B. Saunders Co., 370-376 pp.

- Duke, G. E. 1997. Gastrointestinal physiology and nutrition in wild birds. Proc. Nutr. Soc. 56: 1049-1056.
- Dunnet, G. M., and J. C. Ollason. 1982. The feeding dispersal of fulmars *Fulmarus* glacialis in the breeding season. Ibis 124:359-361.
- Elphick C. S., and G. L. Hunt. 1993. Variations in the distributions of marine birds with water mass in the northern Bering Sea. Condor 95:33-44.
- Erdman, D. S. 1967. Sea birds in relation to game fish schools off Puerto Rico and the Virgin Islands. Carib. J. Sci. 7:79-85.
- Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Contr. U. S. Natl. Herb. 8:57-269.
- Fauchald, P. 1999. Foraging in a hierarchical patch system. Am. Nat. 153:603-613.
- Feare, C. J. 1981. Breeding schedules and feeding strategies of Seychelles seabirds. Ostrich 52:179–185.
- Fisher, J., and R. M. Lockley. 1954. Seabirds. London, Collins.
- Flint, E. N., and K. A. Nagy. 1984. Flight energetics of free living sooty terns. Auk 101:288-294.
- Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical statistics for field biology. 2nd Ed. John Wiley and Sons, England, 259 pp.
- Friesen, V. L., D. J. Anderson, T. E. Steeves, H. Jones, and E. A. Schreiber. 2002. Molecular support for the species status of the Nazca booby. Auk 119:820-826.
- Fritz, H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long range foraging seabird. Proc. R. Soc. Lond. [B] 270:1143-1148.

- Furness, R. W., and K. C. J. Camphuysen. 1997. Seabirds as monitors of the marine environment. ICES J. Mar. Sci. 54:726-737.
- Furness, R. W., and P. Monaghan. 1987. Seabird ecology. Chapman and Hall, USA, 164 pp.
- García M. A, C. E. Diez, and A. O. Álvarez. 2002. The eradication of *Rattus rattus* from Monito Island, West Indies. *In*: Veitch C. R. and M. N. Clout (eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, International Union for Conservation of Nature, Gland, Switzerland, 116-199 pp.
- Gause, G. F. 1934. The struggle for existence. Hafner, New York, 163 pp.
- Gibbs, H. L., S. C. Latta, and J. P. Gibbs. 1987. Effects of the 1982-83 El Niño event on blue-footed and masked booby populations on Isla Daphne Major, Galápagos. Condor 89:440-442.
- González-Solís, J., D. Oro, L. Jover, X. Ruíz, and V. Pedrocchi. 1997a. Trophic niche width and overlap of two sympatric gulls in the southwestern Mediterranean. Oecol. 112:75-80.
- González-Solís, J., D. Oro, V. Pedrocchi, L. Jover, and X. Ruíz. 1997b. Bias associated with diet samples in Audouin's Gulls. Condor 99:773-779.
- Götmark, F. D., W. Winkler, and M. Anderson. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature 319:589-591.
- Gower, J., and S. King. Satellite Images Show the Movement of Floating *Sargassum* in the Gulf of Mexico and Atlantic Ocean. Available from Nature Precedings http://hdl.handle.net/10101/npre.2008.1894.1 (2008).
- Grant, P. R. 1986. Interspecific competition in fluctuating environments. *In* J. Diamond and T. J. Case (eds.). Community Ecology. New York: Harper and Row, 173-191 pp.

- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1-21.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344-247.
- Hamer, K. C., R. W. Furness, and R. W. G Caldow. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. J. Zool. (London) 223:175-188.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1-9.
- Haney, J. C. 1986. Seabirds patchiness in tropical oceanic waters: the influence of *Sargassum* "reefs". Auk 103:141-151.
- Hansson, S. 1998. Methods of studying fish feeding: a comment. Can. J. Fish. Aquat. Sci. 55:726-738.
- Hardin, G. 1960. The Competitive Exclusion Principle. Science 131:1292-1297.
- Harding, A.M., J.F. Piatt, and W.J. Sydeman. 2005. Bibliography of literature on seabirds as indicators of the marine environment. USGS Alaska Science Center, Anchorage, Alaska, 20 pp.
- Hardy, J. D. Jr. 1978. Development of fishes of the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages. Vol. II. Anguillidae through Syngnathidae. US Fish Wildlife Service, Washington, D. C., 458 pp.
- Harris, M. P. 1977. Comparative ecology of seabirds in the Galapagos Archipelago. *In* B. Stonehous and C. Perrins (eds.). Evolutionary Ecology, London, MacMillan, 65-76 pp.
- Harrison, C. S., and T. S. Hida. 1980. The status of seabird research in the northwestern Hawaiian Islands, p. 17-31. *In* Grigg, R. W., and R. T. Pfund (eds.). Proceedings of

the Symposium on Status of Resource Investigation in the Northwestern Hawaiian Islands. University of Hawaii/Sea Grant Program, 333 pp.

- Harrison, C. S., T. S. Hida, and M. P. Seki. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85:1-71.
- Harrison, C. S., T. S. Hida, and M. P. Seki. 1984. The diet of the brown booby *Sula leucogaster* and masked booby *Sula dactylatra* on Rose Atoll, Samoa. Ibis 126:588-590.
- Harrison, N. M., M. J. Whitehouse, D. Heinemann, P. A. Prince, G. L. Jr. Hunt, and R. R. Veit. 1991. Observations of multispecies seabird flocks around South Georgia. *Auk* 108:801–810.
- Hebshi, A. J., D. C. Duffy, and K. D. Hyrenbach 2008. Associations between seabirds and subsurface predators around Oahu, Hawaii. Aquat Biol 4:89-98.
- Hensley, V. I., and D. A. Hensley. 1995. Fishes eaten by sooty terns and brown noddies in the Dry Tortugas, Florida. B. Mar. Sci. 56:813-821.
- Hertel, F., and L. T. Ballance. 1999. Wing ecomorphology of seabirds from Johnston Atoll. Condor 101:549-556.
- Hoffman, W., D. Heinemann, and J. A. Wiens. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98:437-456.
- Holm, K. J., and A. E. Burger. 2002. Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. Waterbirds 25:312-325.
- Horn, H. S. 1975. Markovian properties of forest succession. *In* M. L. Cody and J. M. Diamond (eds.). Ecology and evolution of communities. Belknap Press. Cambridge, MA, 196-211 pp.

- Hunt, G. L., Jr., H. Kato and S. M. McKinnell (eds.). 2000. Predation by marine birds and mammals in the subarctic North Pacific Ocean. PICES Sci. Rep.14. North Pacific Marine Science Organization. Sidney, B. C. Canada., 168 pp.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. Am. Nat. 93:145-159.

Hutchinson, G.E. 1961. The paradox of plankton. Am. Nat. 95:137-145.

Huyvaert, K. P., and D. J. Anderson. 2004. Limited dispersal by Nazca boobies *Sula granti*. J. Avian Biol. 35: 46–53.

ldyll, C. P. 1973. The anchovy crisis. Sci. Am. 228:22-29.

- Jackson, S., and A. R. Place. 1990. Gastrointestinal transit and lipid assimilation efficiencies in three species of sub-antarctic seabird. J. Exp. Zool. 255:141-154.
- Jahncke, J., and E. Goya. 2000. Responses of three booby species to El Niño 1997-1998. Waterbirds 23:114-120.
- Jordan, R. 1967. The predation of guano birds on the Peruvian anchovy (*Engraulis ringens* Jenyns). Calif. Coop. Ocean. Fish. Invest. Rep. 11:105-109.
- Karpouzi, V. S. 2005. Modeling and mapping trophic overlap between fisheries and the world's seabirds. Thesis M. S. Aristotle University of Thessaloniki, Greece, 159 pp.
- Kepler, C. B. 1978. The breeding ecology of sea birds on Monito Island, Puerto Rico. Condor 80:72-87.
- Khokiattiwong, S. 1988. Seasonal abundance and reproduction of the flyingfish *Hirundichthys affinis* and *Parexocoetus brachypterus* near Barbados. M.S. Thesis, McGill University, Montreal, Canada, 227 pp.

- Khokiattiwonga, S., R. Mahona, and W. Hunte. 2000. Seasonal abundance and reproduction of the fourwing flyingfish, *Hirundichthys affinis*, off Barbados. Environmental Biology of Fishes 59:43–60.
- Kirkham I. R., and R. D. Morris. 1979. Feeding ecology of ring-billed gull (*Larus delawarensis*) chicks. Can. J. Zool. 57:1086-1090.
- Krebs, C. J. 1989. Ecological Methodology. Harper and Row, New York, 654 pp.
- Lack, D. L. 1934. Habitat distribution in certain Icelandic birds. J. Anim. Ecol. 3:81-90.
- Laugksch, R. C., and D. C. Duffy. 1984. Energetics equations and food consumption of seabirds in two marine upwelling areas: Comparisons and the need for standardization. S Afr. J. Mar. Sci. 145-148.
- Le Corre, M. 1997. Diving depths of two tropical pelecaniformes: the red-tailed tropicbird and the red-footed booby. Condor 99:1004-1007.
- Lemon, W. C. 1991. Foraging behavior of a guild of Neotropical Vultures. Wilson Bull. 103:702.
- Leviten, P. J., and A. J. Kohn. 1980. Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecological Monographs 50: 55-75.
- Levinton, J. S. 1982. Marine Ecology. Prentice-Hall. Englewood Cliffs, 526 pp.
- Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton University Press, Princeton, NJ.
- Lewis, S., E. A. Schreiber, F. Daunt, G. A. Schenk, K. Orr, A. Adams, S. Wanless, and K. C. Hamer. 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? Ibis 147:408-414

- Longhurst, A. R., and D. Pauly. 1987. Ecology of Tropical Ocean. San Diego, CA: Academic, 407 pp.
- Lotka, A. H. 1932. The growth of mixed populations: two species competing for a common food supply. J. Wash. Acad. Sci. 22:461-469.
- MacArthur, R. H. 1958. Population ecology of some warblers of North-Eastern coniferous forests. Ecology 39:599-619.
- MacArthur, R. H. 1972. Geographical Ecology. New York: Harper and Row, 269 pp.
- MacArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. Am. Nat. 100:603-609.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. Am. Nat. 101:377-385.
- Margalida, A., and J. Bertran. 2003. Interspecific and intraspecific kleptoparasitic interactions of the Bearded vulture (*Gypaetus barbatus*) at nesting areas. J. Raptor Res. 37:157-160.
- Matos-Caraballo, D. 2007. Puerto Rico/NMFS Interjurisdictional Fisheries Program. Department of Natural and Environmental Resources. Final Report to the National Marine Fisheries Service NOAA, 55 pp.
- McLelland, J. 1979. Digestive system. *In* Form and Function in Birds. A. S. King and J. McLelland (eds), 69-181 pp. London: Academic Press.
- McNamara, J. M., and A. I. Houston. 1985. Optimal foraging and learning. J. Theor. Biol. 117:231-249.
- 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. Mar. Ornithol. 29:23-28.

- Mills, K. L. 1998. Multispecies seabird feeding flocks in the Galapagos Islands. Condor 100:277-285
- Montevecchi, W. A. 1993. Seabirds as indicators of changes in marine fish stocks. *In* Furness, R.W., and J. J. D. Greenwood (eds.). Birds as environmental monitors. Chapman Hall, London, pp 217-266.
- Montevecchi, W. A., and R. A. Myers. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. Sarsia 80:313-322.
- Montevecchi, W. A., and R. T. Barrett. 1987. Prey selection by Gannets at breeding colonies in Norway. Ornis Scand. 18:319-322.
- Montevecchi, W. A., V. L. Birt, and D. K. Cairns. 1987. Dietary changes of seabirds associated with local fisheries failures. Biol. Oceanogr. 5:153-161.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science of Kyushu University Series E Biology 3:65-80.
- Muck, P., and D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982. *In* D. Pauly, and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change, ICLARM Studies and Reviews 15, 219-233 pp. Manila, Philippines.
- Naves, L. C., L. F. Brusque, and C. M. Vooren. 2002. Feeding ecology of Sula leucogaster, Anous stolidus and Anous minutus at Saint Peter and Saint Paul's Rocks Brazil. Ararajuba 10:21-30.
- Neil, S. R. S, and J. M. Cullen. 1974. Experiment on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. J. Zool. Soc. London 172:549-569.

- Nelson, J. B. 1978. The Sulidae: gannets and boobies. Oxford University Press, Oxford, 1024 pp
- Nelson, J. B. 1979. Seabirds: their biology and ecology. New York, A and W. Publ., Inc.
- Nelson, J. B. 1983. Contrasts in breeding strategies between some tropical and temperate marine Pelecaniformes. Stud. Avian Biol.8:95-114.
- Nelson, J. B. 2003. Gannets and Boobies. *In*: Perrins, C. (ed.). The firefly encyclopedia of birds. Firefly Books, Oxford., 82–87 pp.
- Nixon, S., and V. Lee. 1998. A Comparison of foraging techniques of brown pelicans and brown boobies in Sandy Ground Lagoon, Jost Van Dyke, B.V.I. Carib. J. Sci. 34:125-129.
- Olson, R. J., and, F. Galván-Magaña. 2002. Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. Fish. Bull. 100:279-298.
- Oberle, M. W. 2003. Las Aves de Puerto Rico en fotografías. Humanitas, Seattle Washington, 132 pp.
- Oro, D., X. Ruíz, L. Jover, V. Pedrocchi, and J. González-Solís. 1997. Diet and adult time budgets of Audouin's Gull *Larus audouinii* in response to changes in commercial fisheries. Ibis 139:631-637
- Osorio-Beristain, M., and H. Drummond. 1993. Natal dispersal and deferred breeding in the blue-footed booby. Auk 110: 234-239.
- Oxenford, H. A. 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western Central Atlantic. Sci. Mar. 63:227-301.
- Oxenford, H. A., and W. Hunte. 1999. Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the Eastern Caribbean. Sci. Mar. 63:303-315.

- Oxenford, H. A., R. Mahon, and W. Hunte. 1995a. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. Mar. Ecol. Prog. Ser. 117:11-23.
- Oxenford, H. A., R. Mahon, and W. Hunte. 1995b. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. III. Juveniles. Mar. Ecol. Prog. Ser. 117:39-47.
- Pearson. T. H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.
- Pennycuick, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes) observed in South Georgia and its vicinity. Phil. Trans. R. Soc. Lond. B 300:75-106.
- Pennycuick, C. J. 1987. Flight of seabirds. *In* J. P. Croxall (ed.). Seabirds, feeding ecology and role in marine ecosystems. New York Academic Press, 43-62 pp.
- Pérez-López, M., F. Cid-Galán, D. Hernández-Moreno, A. L. Oropesa-Jiménez, A. López Beceiro, L. E. Fidalgo-Álvarez, and F. Soler-Rodríguez. 2005. Contenido de metales pesados en hígado y plumas de aves marinas afectadas por el accidente del "Prestige" en la costa de Galicia. Rev. Toxicol. 22:191-199.
- Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? American Naturalist 126:261-266
- Pettit, T. N., G. C. Whittow, and H. I. Ellis. 1984. Food and energetic requirements of seabirds at French frigate shoals, Hawaii. Proc. Res. Inv. NWHI-Seagrant-MR-84-01:265-282.
- Piatt, J. F., W.J. Sydeman, and F. Wiese. 2007. Introduction: a modern role for seabirds as indicators. Mar. Ecol. Prog. Ser. 352:199–204.

- Pimenta, E. G., G. Lima, C, J. Cordeiro, and A. F. Amorim. 2005. Sustainable system for Istiophoridae and alike off northern Rio de Janeiro State, Brazil. Cal. Vol. Sci. Pap. ICCAT 58:1597-1602.
- Pitman, R. L., and J. R. Jehl. 1998. Geographic variation and reassessment of species limits in the "masked" boobies of the eastern Pacific Ocean. Wilson Bull. 110:155-170.
- Pitman, R. L., and L. T. Ballance. 1992. Parkinson's petrel distribution and foraging ecology in the eastern pacific: aspects of an exclusive feeding relationship with dolphins. Condor 94:825-835.
- Pitman, R. L., L. T. Ballance and C. Bost. 2005. Clipperton island: pig sty, rat hole and booby prize. Mar. Ornithol. 33(2):193-194.
- Rabenold, P. P. 1987a. Recruitment to food in Black Vulture: evidence for following from communal roosts. Anim. Behav. 35:1775-1785.
- Rabenold, P. P. 1987b. Roost attendance and aggression in black vultures. Auk 104: 647-653.
- Raffaele, H. A., J. W. Wiley, O. H. Garrido, A. R. Keith, and J. I. Raffaele. 1989. Guide to the birds of the West Indies. Princeton Univ. Press, Princeton, NJ, 511 pp.
- Regehr, H. M., and W. A. Montevecchi. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. Mar. Ecol. Prog. Ser. 155:249-260.
- Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Stud. Avian Biol.8:84-94.
- Rodríguez-Estrella R. 1994. Group size and flight altitude of Turkey Vultures in two habitats in Mexico. Wilson Bull. 106:749-152.

- Rollé, F. J., H. Heatwhole, R. Levins, and F. Torres. 1964. Faunal notes on Monito Island, Puerto Rico. Carib. J. Sci. 4:321-322.
- Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2: 352-388.
- Ryan, P. G. 1988. Intraspecific variation in plastic ingestion by seabirds and the flux of plastic through seabird populations. Condor 90:446-452.
- Ryan, P. G., A. D. Connell, and B. D. Gardner. 1988. Plastic ingestion and PCBs in seabirds: is there a relationship? Mar. Pollut. Bull. 19:174-176.
- Sastre, M., and R. A. Armstrong. 2000. SeaWiFS Estimates of Ocean Primary Productivity in the Caribbean Sea. NASA University Research Conference. Presentation in Nashville, Tennessee.
- Satoh, K., K. Yokawa, H. Saito, H. Matsunaga, H. Okamoto, and Y. Uozumi. 2004. Preliminary stomach contents analysis of pelagic fish collected by Shoyo-maru 2002 research cruise in the Atlantic Ocean. Cal. Vol. Sci. Pap. ICCAT 56:1096-1114.
- Scharf, F. S., R. M. Yetter, A. P. Summers, and F. Juanes. 1998. Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains. Fish. Bull. 96:575-588.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.
- Schoener, T. W. 1983a. Resource partitioning. *In* D. Anderson and J. Kikkawa (eds.) Community ecology-pattern and process. Blackwell Scientific, Oxford. 91-126 pp.
- Schoener, T. W. 1983b. Field Experiments on Interspecific Competition. Am. Nat. 122:240-285.

- Schreiber, E. A. 2000a. Action plan for conservation of West Indian seabirds. *In* Status and conservation of West Indian seabirds. Society of Caribbean Ornithology Special Publication 1:182-191.
- Schreiber, E. A. 2000b. Status of red-footed, brown and masked boobies in the West Indies. *In* Status and conservation of West Indian seabirds. Society of Caribbean Ornithology Special Publication 1:46-57
- Schreiber, E. A., and D. S. Lee. 2000. West Indians seabirds, a disappearing natural resource. *In* Status and conservation of West Indian seabirds. Society of Caribbean Ornithology Special Publication 1:1-10.
- Schreiber, E. A., R. W. Schreiber, and G. A. Schenk. 1996. Red-footed booby (*Sula sula*). *In* Poole, A., and F. Gill (eds.). The Birds of North American No 241. The Academy of Natural Sciences, Philadelphia, PA. The American Ornithologist' Union, Washington, DC, 23 p.
- Schreiber, R. W., and D. A. Hensley. 1976. The diets of *Sula dactylatra*, *Sula sula*, and *Fregata minor* on Christmas Island, Pacific Ocean. Pac. Sci. 30:241-248.
- Schreiber, R.W., and E. A. Schreiber. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. Science 225:713-716.
- Seki, M. P., and C. S. Harrison. 1989. Feeding ecology of two subtropical seabird species at French Frigate Shoals, Hawaii. B. Mar. Sci. 45:52-67.
- Selva, N., B. Jędrzejewska, W. Jędrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Can. J. Zool. 83:1590–1601.
- Serrano, I. L., and S. M. Azevedo-Júnior. 2005. Dietas das aves marinhas no Parque Nacional dos Abrolhos, Bahia, Brasil. Ornithologia 1:75-92.
- Shettleworth S. J., J. R. Krebs, D. W. Stephens, and J. Gibbon. 1988. Tracking a fluctuating environment: a study of sampling. Anim. Behav. 36:87-105.

- Slobodkin, L. B. 1961. Growth and regulation of animal populations. New York: Holt, Rinehart and Wilson. 184pp.
- Smith, E. P., and T. M. Zaret. 1982. Bias in estimating niche overlap. Ecology 63:1248-1253.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co.: New York, 887 pp.
- Spear, L. B., P. Pyle, and N. Nur. 1998. Natal dispersal in the western gull: proximal factors and fitness consequences. J. Anim. Ecol. 67:165-179.
- Spendelow, J. A., J. D. Nichols, I. C. T. Nisbet, H. Hays, G. D. Cormons, J. Burger, C. Safina, J. E. Hines, and M. Gochfeld. 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. Ecology 76:2415-2428.
- SPSS, Inc. 1999. Statistical Package for the Social Sciences, Users Guide, Base 9.0 SPSS, Inc., Chicago, Illinois.
- Squibb, R., and G. L. Hunt, Jr. 1983. A comparison of nesting-ledges used by seabirds on St. George Island. Ecology 64:727-734.
- Steeves, T. E., D. J. Anderson, H. McNally, M. H Kim, and V. L. Friesen. 2003. Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds. J. Avian Biol. 34:217-223.
- Steeves, T. E., D. J. Anderson, and V. L. Friesen. 2005. The Isthmus of Panamá: a major physical barrier to gene flow in highly mobile pantropical seabirds. J. Evolutionary Biol. 18:1000-1008.
- Stewart, P. A. 1978. Behavioral interactions and Niche separation in black and turkey vultures. Living Bird 17:79-84.

- Stolen, E. D. 2000. Foraging behavior of vultures in central Florida. Florida Field Naturalist 28:173-181.
- Strong, D. R. J. 1982. Harmonious coexistence of hispine beetles on Heliconia in experimental and natural communities. Ecology 63:1039-1049.
- Sunada, J. S., P. R. Kelly, I. S. Yamashita, and F. Gress. 1981. The brown pelican as a sampling instrument of age group structure in the northern anchovy population. Calif. Coop. Oceanic Fish. Invest. Rep. 22:65-68.
- Sydeman, W. J., K. A. Hobson, P. Pyle, and E.B. Mclaren. 1997. Trophic relationships among seabirds in Central California: combined stable isotope and conventional dietary approach. Condor 99:327-336.
- Tasker, M. L., C. J. Camphuysen, J. Cooper, S. Garthe, W. A. Montevecchi, and S. J. M. Blaber. 2000. The impacts of fishing on marine birds. ICES J. Mar. Sci. 57:531-547.
- Tershy, B. R., and D. Breese. 1990. The influence of sexual dimorphism on kleptoparasitism of blue-footed boobies by brown boobies. Can. J. Zool. 68:197-199.
- Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). *In* J. W. Hedgpeth (ed.). Treatise on marine ecology and paleontology, vol. 1, Ecology, p. 461-534. Geological Society of America, Memoir 67, vol 1.
- Tokeshi, M. 1991. Graphical Analysis of Predator Feeding Strategy and Prey Importance. Freshwater Forum 1:179-183.
- Townsend, H. M., K. P. Huyvaert, P. J. Hodum, and D. J. Anderson. 2002. Nesting distributions of Galápagos boobies (Aves: Sulidae): an apparent case of amensalism. Oecologia 132:419–427.
- Trivelpiece, W., and N. J. Volkman. 1979. Nest-site competition between Adelic and Chinstrap penguins: an ecological interpretation. Auk 96:675-681.

- Trites, A. W., V. Christensen, and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J. Northw. Atl. Fish. Sci. 22:173-187.
- Van Tets, G. F., C. W. Meredith, P. J. Fullagar, and P. M. Davidson. 1988. Osteological differences between *Sula* and *Morus*, and a description of an extinct new species of *Sula* from Lord Howe and Norfolk Islands, Tasman Sea. Notornis 35:35-57.
- Van Dam R. P., C. E. Diez, G. H. Balazs, L. A. Colón-Colón, W. O. McMillan, and B. Schroeder. 2008. Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. Endang. Species Res. 4: 85-94.
- Velarde, E., M. S. Tordesillas, L. Vieyra, and R. Esquivel. 1994. Seabirds as indicators of important fish populations in the Gulf of California. CalCOFI Rep. 35:137-143.
- Vlietstra, L. S. 2005. Spatial associations between seabirds and prey: effects of largescale prey abundance on smallscale seabird distribution. Mar. Ecol. Prog. Ser. 291:275-287.
- Volterra, V. 1926. Variatzioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. R. Accad. Linnei Ser. 6, IS.
- Wallace, M. P., and S. A. Temple. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290-295.

Walter, G. H. J. 1991. What is resource partitioning? Theor. Biol. 21:137-43.

- Wadsworth, F. H. 1973. Mona and Monito Islands-An assessment of their natural and historical resources. ELA de P.R., Office of the Governor. Vol. I, pp.1-91.
- Wadsworth, F. H. 2003. Guía para la Isla de la Mona. Una Contribución del Comité de Campamentos del Concilio de Puerto Rico de Niños Escuchas de América, 106 pp.

- Weimerskirch, H., T. Guionnet, J. Martin, S. A. Shaffer, and D. P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc. R. Soc. Lond. [B] Soc. B 267:1869-1874.
- Weimerskirch, H., M. Le Corre, S. Jaquemet, and F. Marsac. 2005a. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Mar. Ecol. Prog. Ser. 288:251-261.
- Weimerskirch, H., M. Le Corre, Y. Ropert-Coudert, A. Kato, and F. Marsac. 2005b. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? Proc. R. Soc. Lond. [B] Soc. B. 272:53-61.
- Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65:590-597.
- Wilson R. P., D. Grémillet, J. Syder, M. A. M. Kierspel, S. Garthe, H. Weimerskirch, C. Schäfer-Neth, J. A. Scolaro, C. A. Bost, J. Plötz, D. Nel. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Prog. Ser. 228:241-261.
- Whittam, T. S., and D. Siegel-Causey. 1981. Species interactions and community structure in Alaskan seabird colonies. Ecology 62:1515-1524.
- With, K. A., and M. L. Morrison. 1990. Flock formation of two parids in relation to cyclical seed production in a pinyon-juniper woodland. Auk 107:522-532.
- Woodward, P. W. 1972. The Natural History of Kure Atoll, Northwestern Hawaiian Islands. Atoll Res. Bull.164:1-318.
- Yoda, K., and H. Kohno. 2008. Plunging Behaviour in Chick-rearing Brown Boobies. Ornithol. Sci. 7:5-13.

TABLES

Table 1. Relative proportion of fish prey identified to the level of family and species per *Sula* spp. and visits to Monito Islet in 2003.

Variable	Visit	June	August	September	October
	Prey (232)	39	53	106	34
Masked booby	Birds (60)	10	12	28	10
(S. dactylatra)	Identified to family level	100%	100%	100%	100%
	Identified to species level	56.4%	69.4%	77.4%	53.1%
	Prey (396)	140	106	39	111
Brown booby	Birds (48)	17	10	8	13
(S. leucogaster)	Identified to family level	97.9%	95.3%	94.9%	86.5%
	Identified to species level	83.6%	80.2%	76.9%	76.6%
	Prey (356)	119	118	40	79
Red-footed	Birds (53)	17	14	10	12
(S. sula)	Identified to family level	91.6%	78.7%	95.0%	93.7%
	Identified to species level	76.5%	60.2%	65.0%	69.6%

Squids not included because they were identified to the order (Decapodiformes).

Visit/Season	Variable	Birds	Mean	s.e.	Var.	Min.	Max.	VMR	SWS	р	МСр
	Number of prey (39)	10	3.9	0.6	3.7	1.0	7.0	0.9	1.0	0.883	0.974
	Number of prey cat.(10)	9	2.1	0.4	1.1	1.0	4.0	0.5	0.9	0.194	0.755
I	Organisms per prey cat.	9	2.1	0.4	1.3	1.0	5.0	0.6	0.7	0.003	0.258
June	Shannon H Index	9	0.6	0.2	0.3	0.0	1.4	0.4	0.9	0.131	0.711
	Simpson 1-D Index	9	0.4	0.1	0.1	0.0	0.8	0.2	0.8	0.023	0.344
	Equitability J Index	9	0.7	0.2	0.3	0.0	1.0	0.4	0.6	< 0.001	0.066
	Number of prey (53)	12	4.4	1.3	20.1	2.0	18.0	4.5	0.6	< 0.001	0.202
	Number of prey cat. (11)	10	1.9	0.5	2.3	1.0	6.0	1.2	0.6	< 0.001	0.094
A	Organisms per prey cat.	10	2.5	0.4	1.9	1.0	6.0	0.8	0.8	0.008	0.448
August	Shannon H Index	10	0.4	0.2	0.2	0.0	1.4	0.6	0.8	0.008	0.265
	Simpson 1-D Index	10	0.3	0.1	0.1	0.0	0.7	0.3	0.7	0.003	0.198
	Equitability J Index	10	0.5	0.2	0.3	0.0	1.0	0.5	0.7	0.001	0.191
	Number of prey (106)	28	3.8	0.3	3.4	1.0	7.0	0.9	0.9	0.032	0.236
	Number of prey cat.(11)	25	2.0	0.2	1.3	1.0	5.0	0.6	0.8	< 0.001	0.011
Contour los	Organisms per prey cat.	25	2.2	0.2	1.1	1.0	5.0	0.5	0.9	0.003	0.075
September	Shannon H Index	25	0.5	0.1	0.2	0.0	1.6	0.5	0.9	0.003	0.164
	Simpson 1-D Index	25	0.3	0.1	0.1	0.0	0.8	0.2	0.9	0.003	0.098
	Equitability J Index	25	0.6	0.1	0.2	0.0	1.0	0.3	0.7	< 0.001	0.043
-	Number of prey (34)	10	3.4	0.5	2.9	2.0	6.0	0.9	0.8	0.008	0.297
	Number of prey cat.(5)	7	1.7	0.4	1.2	1.0	4.0	0.7	0.7	0.006	0.423
0.11	Organisms per prey cat.	7	2.6	0.6	2.7	1.0	6.0	1.1	0.8	0.061	0.670
October	Shannon H Index	7	0.4	0.2	0.3	0.0	1.3	0.7	0.8	0.024	0.341
	Simpson 1-D Index	7	0.2	0.1	0.1	0.0	0.7	0.4	0.8	0.027	0.297
	Equitability J Index	7	0.4	0.2	0.2	0.0	1.0	0.6	0.7	0.005	0.262
Non	Number of prey (126)	32	3.9	0.5	9.2	1.0	18.0	2.3	0.7	< 0.001	0.055
breeding	Number of prey cat.(17)	26	1.9	0.2	1.5	1.0	6.0	0.8	0.7	< 0.001	0.024
(June,	Organisms per prey cat.	26	2.4	0.3	1.8	1.0	6.0	0.8	0.8	< 0.001	0.039
August and	Shannon H Index	26	0.5	0.1	0.3	0.0	1.4	0.5	0.8	< 0.001	0.019
October)	Simpson 1-D Index	26	0.3	0.1	0.1	0.0	0.8	0.3	0.8	< 0.001	0.011
	Equitability J Index	26	0.5	0.1	0.2	0.0	1.0	0.5	0.7	< 0.001	0.008
	Number of prey (106)	28	3.8	0.3	3.4	1.0	7.0	0.9	0.9	0.023	0.235
D 1'	Number of prey cat.(11)	25	2.0	0.2	1.3	1.0	5.0	0.6	0.8	< 0.001	0.010
Breeding	Organisms per prey cat.	25	2.2	0.2	1.1	1.0	5.0	0.5	0.9	0.003	0.076
(September)	Shannon H Index	25	0.5	0.1	0.2	0.0	1.6	0.5	0.9	0.003	0.165
	Simpson 1-D Index	25	0.3	0.1	0.1	0.0	0.8	0.2	0.9	0.003	0.099
	Equitability J Index	25	0.6	0.1	0.2	0.0	1.0	0.3	0.7	< 0.001	0.044
	Number of prey (232)	60	3.9	0.3	6.4	1.0	18.0	1.7	0.7	< 0.001	0.076
	Number of prey cat.(18)	51	2.0	0.2	1.4	1.0	6.0	0.7	0.8	< 0.001	< 0.001
Total	Organisms per prey cat.	51	2.3	0.2	1.5	1.0	6.0	0.6	0.8	< 0.001	0.002
	Shannon H Index	51	0.5	0.1	0.2	0.0	1.6	0.5	0.8	< 0.001	0.002
	Simpson 1-D Index	51	0.3	0.0	0.1	0.0	0.8	0.3	0.8	< 0.001	0.001
	Equitability J Index	51	0.5	0.1	0.2	0.0	1.0	0.4	0.7	< 0.001	< 0.001

Table 2. Descriptive statistics and distribution analysis of prey diversity found masked booby (*Sula dactylatra*) per visit and season in Monito Islet in 2003.

Cat. = categories (fish species and squids order), VMR = variance mean ratio, SWS = Shapiro-Wilk statistic (normality test), MCp = Monte Carlo probability.

Sula spp.	Variable	Test	Sum of	df	Mean Square	F	р
		Among Visits	<u>6 0</u>	3	2 00	0.30	0.824
	Number of prev	Within Visits	370.9	56	6.62	0.50	0.021
		Total	376.9	59			
		Among Visits	0.8	3	0.27	0.18	0.906
	Number of prey	Within Visits	68.2	47	1.45		
	categories	Total	69.0	50			
	o .	Among Visits	1.5	3	0.51	0.34	0.799
	Organisms per prey	Within Visits	71.3	47	1.52		
Masked Booby	category	Total	72.9	50			
(S. dactylatra)		Among Visits	0.4	3	0.12	0.47	0.708
	Shannon H Index	Within Visits	12.0	47	0.25		
		Total	12.3	50			
		Among Visits	0.1	3	0.05	0.55	0.647
	Simpson 1-D Index	Within Visits	3.9	47	0.08		
		Total	4.1	50			
		Among Visits	0.4	3	0.12	0.52	0.670
	Equitability J Index	Within Visits	10.6	47	0.23		
		Total	11.0	50			
		Among Visits	147.4	3	49.15	0.72	0.546
	Number of prey	Within Visits	3009.6	44	68.40		
		Total	3157.0	47			
	Number of prev	Among Visits	8.2	3	2.73	1.44	0.246
	categories	Within Visits	71.9	38	1.89		
	eurogenies	Total	80.1	41			
	Organisms per prev	Among Visits	14.3	3	4.77	0.80	0.501
	category	Within Visits	226.1	38	5.95		
Brown Booby		Total	240.4	41			
(S. leucogaster)	Shannon H Index	Among Visits	1.2	3	0.41	1.74	0.174
		Within Visits	8.9	38	0.23		
		Total	10.1	41	0.12	1.05	0 1 5 5
	<i></i>	Among Visits	0.4	3	0.13	1.85	0.155
	Simpson I-D Index	within visits	2.6	38	0.07		
		I otal	3.0	41	0.27	1.00	0.126
	E-mit-bility I Indee	Among Visits	0.8	3	0.27	1.96	0.136
	Equitability J Index	Within Visits	5.2	38	0.14		
		Among Vigita	0.0	41	20.00	1 70	0.190
	Number of prov	Within Visits	1120.2	- <u>-</u> 3	20.00	1.70	0.180
	Number of prey	Total	120.5	49 52	22.80		
		Among Visits	6.8	32	2.26	1 32	0 279
	Number of prey	Within Visits	75.1	11	1.71	1.52	0.279
	categories	Total	73.1 81.0	44	1./1		
		Among Visits	24.0	3	8.01	1 3/	0 273
	Organisms per prey	Within Visits	24.0	11	5.01	1.54	0.275
Red-footed	category	Total	287.0	47	5.70		
Booby		Among Visits	13	3	0.43	1 66	0 189
(S. sula)	Shannon H Index	Within Visits	11.3	44	0.26	1.00	0.109
		Total	12.6	47	0.20		
		Among Visits	0.4	3	0.13	1 64	0 1 9 4
	Simpson 1-D Index	Within Visits	3.5	44	0.08		
		Total	3.8	47			
		Among Visits	0.8	3	0.28	1.55	0.215
	Equitability J Index	Within Visits	8.0	44	0.18		
		Total	8.9	47			

Table 3. Comparison of prey diversity among visits to Monito Islet in 2003, for each *Sula* spp.

Source	Variable	Type III Sum of Squares	df	Mean Square	F	р			
	Number of organisms	6999.9	6	1166.6	37.3	< 0.001			
	Number of prev cat.	723.7	6	120.6	72.6	< 0.001			
	Organisms per prev cat.	1393.1	6	232.2	52.4	< 0.001			
Model	Shannon H Index	45.7	6	7.6	30.2	< 0.001			
	Simpson 1-D Index	16.0	6	2.7	33.8	< 0.001			
	Equitability J Index	44.6	6	7.4	39.5	< 0.001			
	Number of organisms	674.2	2	337.1	10.8	< 0.001			
	Number of prey cat.	14.2	2	7.1	4.3	0.016			
Sula spp.	Organisms per prey cat.	51.3	2	25.7	5.8	0.004			
	Shannon H Index	1.3	2	0.6	2.6	0.081			
	Simpson 1-D Index	0.3	2	0.2	2.1	0.132			
	Equitability J Index	0.6	2	0.3	1.6	0.198			
	Number of organisms	25.9	1	25.9	0.8	0.365			
	Number of prey cat.	1.3	1	1.3	0.8	0.379			
D	Organisms per prey cat.	0.7	1	0.7	0.2	0.684			
Breeding seasons	Shannon H Index	0.3	1	0.3	1.1	0.303			
	Simpson 1-D Index	0.1	1	0.1	1.2	0.277			
	Equitability J Index	0.1	1	0.1	0.8	0.381			
	Number of organisms	61.9	2	30.9	1.0	0.375			
	Number of prey cat.	6.4	2	3.2	1.9	0.150			
Bird species *	Organisms per prey cat.	1.4	2	0.7	0.2	0.850			
seasons	Shannon H Index	0.8	2	0.4	1.7	0.193			
	Simpson 1-D Index	0.2	2	0.1	1.4	0.260			
	Equitability J Index	0.3	2	0.2	0.9	0.426			
	Number of organisms	4222.1	135	31.3					
	Number of prey cat.	224.3	135	1.7					
Error	Organisms per prey cat.	598.3	135	4.4					
EII0I	Shannon H Index	34.1	135	0.3					
	Simpson 1-D Index	10.7	135	0.1					
	Equitability J Index	25.4	135	0.2					
	Number of organisms	11222.0	141						
	Number of prey cat.	948.0	141						
Total	Organisms per prey cat.	1991.3	141						
Totai	Shannon H Index	79.8	141						
	Simpson 1-D Index	26.7	141						
	Equitability J Index	70.0	141						
Number of organisms R Squared = 0.624 (Adjusted R Squared = 0.607)									
Number of prey cat. R Squared = 0.763 (Adjusted R Squared = 0.753)									
Organisms per prey	Organisms per prey cat. R Squared = 0.700 (Adjusted R Squared = 0.686)								
Shannon H Inde	Shannon H Index R Squared = $0.5/3$ (Adjusted R Squared = 0.554)								
Simpson 1-D Inc	lex R Squared = 0.600 (A	Adjusted R Squared = 0.583)							
Equitability J Inc	tex R Squared = 0.637 (A	Adjusted R Squared = 0.621)	с с I			a 1			

Table 4. Comparisons of prey diversity among *Sula* spp. and between seasons (data collected in Monito Islet 2003).

Seasons = Non-breeding (June, August and October for *S. dactylatra*; August for *S. leucogaster*; August, September and October for *S. sula*) vs. breeding (September for *S. dactylatra*; June, September and October for *S. leucogaster*; June for *S. sula*). Organisms = prey fishes and squids, cat. = categories (fish species and squids order).

Sula spp.	Visit/season	Variable	Ν	Mean	se	Var.	Min.	Max.	VMR	SWS	р	МСр
	June	L	39	149.6	5.7	1286	65	215	8.6	0.88	0.001	0.008
		Vol	39	40.9	3.5	470.1	2	91.4	11.5	0.91	0.004	0.016
	August	L	53	133.8	5.3	1511	63.5	203	11.3	0.92	0.001	0.001
		Vol	53	30.9	3.1	493.2	2	82	16	0.88	< 0.001	0.018
	September	L	106	160.1	2.8	837.6	81.1	271	5.23	0.91	< 0.001	0.002
		Vol	106	55.4	7.4	5815	3	667	105	0.31	< 0.001	< 0.001
Masked booby	October	L	34	149.9	5.4	983.7	63.5	206	6.56	0.93	0.026	0.021
(S. dactylatra)		Vol	34	39.8	3.9	504.8	9.8	86.8	12.7	0.91	0.007	0.123
	Non-	L	126	143	3.3	1342	63.5	215	9.39	0.92	< 0.001	< 0.001
	breeding	Vol	126	36.4	2.0	503.6	2	91.4	13.8	0.91	< 0.001	< 0.001
	Breeding	L	106	160.1	2.8	837.6	81.1	271	5.23	0.91	< 0.001	0.002
		Vol	106	55.4	7.4	5815	3	667	105	0.31	< 0.001	< 0.001
	Total	L	232	150.8	2.3	1180	63.5	271	7.82	0.92	< 0.001	< 0.001
		Vol	232	45.1	3.6	3005	2	667	66.6	0.36	< 0.001	< 0.001
	June	L	140	83.5	3.6	1854	32	201	22.2	0.89	< 0.001	0.002
		Vol	140	10.2	1.3	221.9	0.5	78.8	21.8	0.66	< 0.001	< 0.001
	August	L	106	108.3	3.2	1057	63.5	203	9.76	0.93	< 0.001	0.034
		Vol	106	11.6	1.2	148.9	1.5	68.9	12.8	0.70	< 0.001	< 0.001
	September	L	39	122.6	5.9	1379	25	206	11.2	0.92	0.010	0.349
		Vol	39	22.7	3.5	488	0.5	84.9	21.5	0.79	< 0.001	0.005
Brown booby	October	L	111	101.8	2.9	918.5	56.2	195	9.02	0.89	< 0.001	< 0.001
(S. leucogaster)		Vol	111	13.5	1.4	217.6	1.2	75.7	16.1	0.66	< 0.001	< 0.001
	Non-	L	106	108.3	3.2	1057	63.5	203	9.76	0.93	< 0.001	0.034
	breeding	Vol	106	11.6	1.2	148.9	1.5	68.9	12.8	0.70	< 0.001	< 0.001
	Breeding	L	290	95.7	2.4	1607	25	206	16.8	0.96	< 0.001	0.062
		Vol	290	13.2	1.0	270.3	0.5	84.9	20.5	0.70	< 0.001	< 0.001
	Total	L	396	99.1	1.9	1488	25	206	15	0.97	< 0.001	0.005
		Vol	396	12.8	0.8	237.8	0.5	84.9	18.6	0.70	< 0.001	< 0.001
	June	L	119	103.8	3.5	1453	36.5	214	14	0.97	0.008	0.240
		Vol	119	14.6	1.4	232.9	0.6	94	16	0.71	< 0.001	< 0.001
	August	L	118	100.1	1.8	398.7	52.6	188	3.98	0.89	< 0.001	< 0.001
		Vol	118	11.7	0.7	57.1	1.4	64.8	4.88	0.69	< 0.001	< 0.001
	September	L	40	97.4	7.2	2100	32	195	21.6	0.85	< 0.001	0.065
Red-footed		Vol	40	16.6	2.5	258.5	2.3	73.6	15.6	0.78	< 0.001	0.002
boohy	October	L	79	101.5	3.8	1151	35	200	11.3	0.95	0.003	0.150
(S, sula)		Vol	79	13.3	1.4	145.2	0.6	79.1	10.9	0.64	< 0.001	< 0.001
(0. 5)	Non-	L	237	100.1	2.0	926.8	32	200	9.26	0.95	< 0.001	< 0.001
	breeding	Vol	237	13.1	0.7	122.1	0.6	79.1	9.32	0.70	< 0.001	< 0.001
	Breeding	L	119	103.8	3.5	1453	36.5	214	14	0.97	0.008	0.243
		Vol	119	14.6	1.4	232.9	0.6	94	16	0.71	< 0.001	< 0.001
	Total	L	356	101.3	1.8	1102	32	214	10.9	0.96	< 0.001	< 0.001
		Vol	356	13.6	0.7	159.1	0.6	94	11.7	0.70	< 0.001	< 0.001

Table 5. Descriptive statistics and distribution for prey size per *Sula* spp., visit and season (data collected in Monito Islet in 2003).

L = fish fork length and squid mantle length, Vol = prey volume. Non-breeding = June, August and October for*S. dactylatra*; August for*S. leucogaster*; August, September and October for*S. sula*. Breeding = September for*S. dactylatra*; June, September and October for*S. leucogaster*; June for*S. sula*.

ANOVA							
Sula spp.	Variable	Test	Sum of Squares	df	Mean Square	F	p
	L	Among Visits	24629.4	3	8209.8	7.6	< 0.001
		Within Visits	247865.2	228	1087.1		
Masked booby (S. dactylatra)		Total	272494.5	231			
	Vol	Between Visits	23524.1	3	7841.4	2.7	0.049
		Within Visits	670726.2	228	2941.8		
		Total	694250.3	231			
	L	Among Visits	65626.9	3	21875.6	16.4	< 0.001
		Within Visits	522066.5	392	1331.8		
Brown Booby		Total	587693.4	395			
(S. leucogaster)	Vol	Among Visits	4988.6	3	1662.9	7.3	< 0.001
		Within Visits	88956.3	392	226.9		
		Total	93944.9	395			
	L	Among Visits	1558.3	3	519.4	0.5	0.704
		Within Visits	389791.5	352	1107.4		
Red-footed		Total	391349.7	355			
(S sula)	Vol	Among Visits	915.6	3	305.2	1.9	0.124
(5. 5414)		Within Visits	55570.8	352	157.9		
		Total	56486.4	355			

Table 6. Comparison of prey size among visits to Monito Islet (2003) for each *Sula* spp.

Test of homogeneity of variances									
Sula spp.	Variable	Levene Statistic	df1	df2	р				
Masked booby	L	5.1	3	228	0.002				
(S. dactylatra)	Vol	0.6	3	228	0.606				
Brown booby	L	10.4	3	392	< 0.001				
(S. leucogaster)	Vol	8.0	3	392	< 0.001				
Red-footed booby	L	19.2	3	352	< 0.001				
(S. sula)	Vol	7.2	3	352	< 0.001				

L = fish fork length and squid mantle length. Vol = prey volume. Visits = June, August, September and October 2003.

Sula				Mean			95% Con Inter	fidence val
spp.	Variable	(I) Visit	(J) Visit	Difference (I-J)	s.e	р	Lower Bound	Upper Bound
	L	June	August	15.9	7.8	0.246	-5.2	37.0
			September	-10.5	6.4	0.494	-27.9	7.0
			October	-0.2	7.9	1.000	-21.5	21.1
		August	September	-26.3	6.0	< 0.001	-42.6	-10.1
			October	-16.1	7.6	0.200	-36.6	4.3
Masked		September	October	10.2	6.1	0.462	-6.4	26.8
booby	Vol	June	August	10.0	4.6	0.186	-2.5	22.4
			September	-14.5	8.2	0.387	-36.3	7.3
			October	1.0	5.2	1.000	-13.0	15.1
		August	September	-24.5	8.0	0.016	-45.9	-3.1
			October	-8.9	4.9	0.368	-22.2	4.4
		September	October	15.6	8.3	0.330	-6.7	37.8
	L	June	August	-24.9	4.8	< 0.001	-37.6	-12.1
			September	-39.1	7.0	< 0.001	-58.0	-20.3
			October	-18.4	4.6	0.001	-30.7	-6.1
		August	September	-14.3	6.7	0.208	-32.6	4.0
			October	6.5	4.3	0.564	-4.8	17.9
Brown		September	October	20.8	6.6	0.016	2.8	38.8
booby	Vol	June	August	-1.4	1.7	0.956	-6.0	3.1
			September	-12.5	3.8	0.010	-22.8	-2.2
			October	-3.3	1.9	0.384	-8.3	1.7
		August	September	-11.1	3.7	0.028	-21.3	-0.8
			October	-1.9	1.8	0.884	-6.8	3.0
		September	October	9.2	3.8	0.111	-1.2	19.6

Table 7. Multiple comparison tests for prey size among visits to Monito Islet (2003) in masked booby (Sula dactylatra) and brown booby (S. leucogaster).

Source	Variable	Type III Sum of Squares	df	Mean Square	F	р
Model	L	12853458.9	6	2142243.1	1715.4	< 0.001
	Vol	622278.9	6	103713.2	123.2	< 0.001
Sula spp.	L	413561.1	2	206780.5	165.6	< 0.001
	Vol	181005.1	2	90502.6	107.5	< 0.001
Season	L	1587.1	1	1587.1	1.3	0.260
	Vol	11358.5	1	11358.5	13.5	< 0.001
Sula ann * angan	L	29747.1	2	14873.6	11.9	< 0.001
suid spp. • season	Vol	12805.2	2	6402.6	7.6	< 0.001
Error	L	1221359.8	978	1248.8		
	Vol	823566.4	978	842.1		
Total	L	14074818.7	984			
	Vol	1445845.3	984			

Table 8. Comparisons of prey size among *Sula* spp. and breeding seasons (Monito Islet 2003).

L = fish fork length and squid mantle length. R Squared = 0.430 (Adjusted R Squared = 0.427). Vol = prey volume. R Squared = 0.913 (Adjusted R Squared = 0.913).

Seasons = Non-breeding (June, August and October for *S. dactylatra*; August for *S. leucogaster*; August, September and October for *S. sula*) vs. breeding (September for *S. dactylatra*; June, September and October for *S. leucogaster*; June for *S. sula*).

Levene's Test of Equality of Error Variances	

Variable	F	df1	df2	Sig.
L	11.0	5	978	< 0.001
Vol	7.6	5	978	< 0.001

Variable	(I) <i>Sula</i> spp.	(J) Sula spp.	Mean Difference	s.e.	p	95% Confidence Interval	
			(I-J)		F	Lower Bound	Upper Bound
L	MD	BB	51.7	3.0	< 0.001	44.6	58.8
	IVID	RB	49.5	2.9	< 0.001	42.6	56.3
	BB	RB	-2.2	2.6	0.778	-8.5	4.0
Vol	MD	BB	32.3	3.7	< 0.001	23.5	41.2
	MB	RB	31.5	3.7	< 0.001	22.7	40.3
	BB	RB	-0.8	1.0	0.803	-3.3	1.6

Tamhane Multiple Comparisons

L = fish fork length and squid mantle length. Vol = prey volume. MB = masked booby (S. dactylatra).

BB = brown booby (S. leucogaster). RB = red-footed booby (S. sula).
ANOVA							
Sula spp.	Variable	Test	Sum of Squares	df	Mean Square	F	Р
	L	Between Seasons	16782.7	1	16782.7	15.1	< 0.001
		Within Seasons	255711.9	230	1111.8		
Masked Booby		Total	272494.5	231			
(S. dactylatra)	Vol	Between Seasons	20741.4	1	20741.4	7.1	0.008
		Within Seasons	673508.9	230	2928.3		
		Total	694250.3	231			
	L	Between Seasons	12279.7	1	12279.7	8.4	0.004
		Within Seasons	575413.7	394	1460.4		
Brown Booby		Total	587693.4	395			
(S. leucogaster)	Vol	Between Seasons	180.1	1	180.1	0.8	0.385
		Within Seasons	93764.8	394	238.0		
		Total	93944.9	395			
	L	Between Seasons	1115.5	1	1115.5	1.0	0.315
D . 1 C 1		Within Seasons	390234.3	354	1102.4		
Red-footed		Total	391349.7	355			
Booby (S. sula)	Vol	Between Seasons	193.7	1	193.7	1.2	0.270
(<i>S. suid</i>)		Within Seasons	56292.7	354	159.0		
		Total	56486.4	355			

Table 9. Comparison of prey size among seasons for each Sula spp. (Monito Islet 2003).

L = fish fork length and squid mantle length. Vol = prey volume. Seasons = Non-breeding (June, August and October for*S. dactylatra*; August for*S. leucogaster*; August, September and October for*S. sula*) vs. breeding (September for*S. dactylatra*; June, September and October for*S. leucogaster*; June for*S. sula*).

Table 10. Comparison of mean number of prey per regurgitation from masked boobies (*Sula dactylatra*) among values obtained in Monito Islet and the Pacific Ocean.

	Monito	¹ Christmas	² Northwestern	³ Lobos de Tierra Isl		a Island
	Islet	Island	Hawaiian Islands			
	2003	1967	1978-1980	1996	1997	1998
Total number of	59	39	305	8	11	12
samples						
Prey/regurgitation	3.9	4.8	2.5	4.4	2.7	3.8
1		7 .				

¹Schreiber and Hensley (1976), ²Harrison *et al.* (1983) ³Jahncke and Goya (2000).

T 7	Prev		Frequency of	Su	m	Ι	RI
Visit	categories	N	occurrence	L (mm)	Vol (ml)	L	Vol
June	C. comatus	7	6	1269	470	1	1
(Birds = 9)	E. volitans	3	3	408	101	2	2
	H. affinis	2	2	382	106	3	3
	P. occidentalis	2	2	307	87	4	4
	P. hillianus	2	1	221	24	5	5
	S. bullisi	2	1	130	4	6	9
	E. obtusirostris	1	1	163	46	7	6
	H. balao	1	1	138	16	8	8
	E. alletteratus	1	1	136	17	9	7
	N. gronovii	1	1	66	4	10	10
August	P. hillianus	15	4	1553	132	1	2
(Birds = 10)	C. comatus	7	5	1294	462	2	1
	H. balao	2	2	322	76	3	3
	S. bullisi	3	1	195	6	4	5
	Decapodiformes	3	1	191	39	5	4
	H. brasiliensis	1	1	164	32	6	7
	C. hippurus	1	1	163	30	7	8
	O. saurus	1	1	163	30	7	8
	E. velox	1	1	158	29	9	10
	P. occidentalis	1	1	154	44	10	6
	H. affinis	1	1	124	16	11	11
September	C. comatus	40	16	7799	2484	1	1
(Birds = 25)	H. balao	7	7	1216	266	2	2
	E. alletteratus	5	3	838	1187	3	3
	H. affinis	4	3	830	204	4	4
	P. hillianus	5	3	505	44	5	7
	C. exsiliens	3	3	461	131	6	6
	E. obtusirostris	3	3	452	211	7	5
	P. occidentalis	3	2	613	175	8	8
	E. velox	1	1	158	29	9	9
	O. micropterus	1	1	136	16	10	11
	E. volitans	1	1	132	27	11	10
October	C. comatus	5	4	1138	427	1	1
(Birds = 7)	P. hillianus	8	2	922	103	2	2
	C. cyanopterus	2	2	334	109	3	3
	C. exsiliens	1	1	154	44	4	4
	Decapodiformes	1	1	64	13	5	5

Table 11. Ranked indices of relative importance (IRI) by size for prey regurgitated by masked booby (*Sula dactylatra*) in Monito Islet (2003).

In order of length IRI. Squids were only identified to Order. L = fish fork length and squid mantle length. Vol = prey volume.

Visit/Season	Variable	Birds	Mean	s.e.	Var.	Min.	Max.	VMR	SWS	р	МСр
	Number of prey (140)	17	8.2	2.6	115.3	1.0	45.0	14.0	0.6	< 0.001	0.083
	Number of prey cat.(17)	13	2.7	0.4	1.7	1.0	6.0	0.6	0.8	0.010	0.119
I	Organisms per prey cat.	13	3.5	0.8	8.0	1.0	11.3	2.3	0.8	0.007	0.568
June	Shannon H Index	13	0.7	0.1	0.2	0.0	1.5	0.3	0.9	0.435	0.597
	Simpson 1-D Index	13	0.4	0.1	0.1	0.0	0.8	0.1	0.9	0.573	0.864
	Equitability J Index	13	0.7	0.1	0.1	0.0	1.0	0.1	0.8	0.015	0.302
	Number of prey (106)	10	10.6	2.2	49.6	1.0	27.0	4.7	0.9	0.154	0.640
	Number of prey cat.(12)	9	3.3	0.4	1.5	2.0	5.0	0.5	0.9	0.122	0.821
A	Organisms per prey cat.	9	3.8	0.7	4.7	2.0	8.0	1.2	0.8	0.024	0.339
August	Shannon H Index	9	0.9	0.1	0.2	0.3	1.5	0.2	0.9	0.290	0.497
	Simpson 1-D Index	9	0.5	0.1	0.0	0.1	0.7	0.1	0.8	0.054	0.452
	Equitability J Index	9	0.8	0.1	0.0	0.4	1.0	0.1	0.8	0.007	0.175
	Number of prey (39)	8	4.9	2.0	31.6	1.0	18.0	6.5	0.7	0.001	0.343
	Number of prey cat.(6)	7	2.1	0.6	2.1	1.0	5.0	1.0	0.8	0.059	0.675
0 / 1	Organisms per prey cat.	7	2.2	0.4	1.3	1.0	3.6	0.6	0.9	0.144	0.880
September	Shannon H Index	7	0.5	0.2	0.3	0.0	1.1	0.5	0.8	0.052	0.583
	Simpson 1-D Index	7	0.3	0.1	0.1	0.0	0.7	0.3	0.8	0.025	0.442
	Equitability J Index	7	0.5	0.2	0.3	0.0	1.0	0.5	0.7	0.012	0.554
	Number of prey (111)	13	8.5	1.8	41.4	1.0	22.0	4.9	0.9	0.363	0.785
	Number of prey cat.(11)	13	2.2	0.4	2.2	1.0	6.0	1.0	0.8	0.009	0.315
0	Organisms per prey cat.	13	3.9	0.7	7.1	1.0	11.0	1.8	0.8	0.026	0.714
October	Shannon H Index	13	0.5	0.2	0.3	0.0	1.6	0.6	0.9	0.040	0.572
	Simpson 1-D Index	13	0.3	0.1	0.1	0.0	0.8	0.3	0.9	0.036	0.488
	Equitability J Index	13	0.5	0.1	0.2	0.0	1.0	0.4	0.8	0.011	0.301
	Number of prey (106)	10	10.6	2.2	49.6	1.0	27.0	4.7	0.8	0.019	0.635
Non-	Number of prey cat. (12)	9	3.3	0.4	1.5	2.0	5.0	0.5	0.9	0.122	0.822
breeding	Organisms per prey cat.	9	3.8	0.7	4.7	2.0	8.0	1.2	0.8	0.024	0.337
(August)	Shannon H Index	9	0.9	0.1	0.2	0.3	1.5	0.2	0.9	0.290	0.495
	Simpson 1-D Index	9	0.5	0.1	0.0	0.1	0.7	0.1	0.8	0.054	0.451
	Equitability J Index	9	0.8	0.1	0.0	0.4	1.0	0.1	0.8	0.007	0.174
Breeding	Number of prey (290)	38	7.6	1.4	71.4	1.0	45.0	9.4	0.7	< 0.001	0.048
(June.	Number of prey cat.(21)	33	2.4	0.2	1.9	1.0	6.0	0.8	0.8	< 0.001	0.009
September	Organisms per prey cat.	33	3.4	0.4	6.3	1.0	11.3	1.9	0.8	< 0.001	0.249
and	Shannon H Index	33	0.6	0.1	0.2	0.0	1.6	0.4	0.9	0.010	0.377
October)	Simpson 1-D Index	33	0.3	0.0	0.1	0.0	0.8	0.2	0.9	0.004	0.276
	Equitability J Index	33	0.6	0.1	0.2	0.0	1.0	0.3	0.8	< 0.001	0.133
	Number of prey (396)	48	8.3	1.2	67.2	1.0	45.0	8.1	0.8	< 0.001	0.049
	Number of prey cat.(25)	42	2.6	0.2	2.0	1.0	6.0	0.8	0.9	< 0.001	0.005
Tetal	Organisms per prey cat.	42	3.5	0.4	5.9	1.0	11.3	1.7	0.8	< 0.001	0.238
i otai	Shannon H Index	42	0.7	0.1	0.2	0.0	1.6	0.4	0.9	0.010	0.384
	Simpson 1-D Index	42	0.4	0.0	0.1	0.0	0.8	0.2	0.9	0.001	0.394
	Equitability J Index	42	0.6	0.1	0.1	0.0	1.0	0.2	0.8	< 0.001	0.032

Table 12. Descriptive statistics and distribution analysis of prey diversity in brown booby (*Sula leucogaster*) per visit and season in Monito Islet in 2003.

Cat. = categories (fish species and squids order), VMR = variance mean ratio, SWS = Shapiro-Wilk statistic (normality test), MCp = Monte Carlo probability.

	Monito	¹ Northwestern	² San Idelfonso	² San Jorge
	Islet	Hawaiian	and San Pedro	Island
		Islands	Mártir Islands	
	2003	1978-1980	1999-2000	1998-2000
Total number of samples	48	244	64	200
Prey/regurgitation	7.5	12.0	4.2	5.6

Table 13. Comparison of mean number of prey per regurgitation from brown boobies (*Sula leucogaster*) among values obtained in Monito Islet and the Pacific Ocean.

¹Harrison *et al.* (1983), ²Mellink *et al.* (2001).

Visit	Prey	N	Frequency of	Sı	ım	IF	XI
VISIL	categories	IN	occurrence	L (mm)	Vol (ml)	L	Vol
June	D. volitans	48	3	1968	28	1	2
(Birds = 17)	P. arenatus	18	5	1179	87	2	3
,	C. comatus	6	5	1016	345	3	1
	D. macarellus	13	3	1270	144	4	4
	P. hillianus	8	4	722	51	5	5
	C. bartholomaei	9	2	1224	58	6	6
	Decapodiformes	3	3	191	39	7	7
	C. hippos	3	1	353	19	8	8
	H. speculiger	1	1	155	33	9	9
	N. nasutus	1	1	145	3	10	16
	E. velox	1	1	118	10	11	11
	H. brasiliensis	1	1	114	10	12	10
	H. balao	1	1	112	7	13	12
	E. bipinnulata	1	1	93	6	14	13
	N. ductor	1	1	93	6	14	13
	N. gronovii	1	1	66	4	16	15
	A. combatia	1	1	32	0	17	17
August	D. macarellus	26	5	2140	123	1	1
(Birds = 10)	N. nasutus	17	3	2500	51	2	3
	Decapodiformes	12	3	762	156	3	2
	O. micropterus	6	3	626	47	4	5
	H. affinis	4	3	618	131	5	4
	H. balao	4	3	426	39	6	7
	E. alletteratus	5	2	611	63	7	8
	P. hillianus	5	2	500	43	8	9
	C. comatus	2	2	345	127	9	6
	P. maculatus	2	2	190	16	10	10
	C. equiselis	1	1	161	33	11	11
	E. obtusirostris	1	1	135	32	12	12
September	C. comatus	9	5	1540	505	1	1
(Birds = 8)	H. balao	12	2	1361	114	2	2
	P. hillianus	5	4	523	49	3	3
	G. cinereus	2	2	53	1	4	4
	E. velox	1	1	118	10	5	5
	P. maculatus	1	1	95	8	6	6
October	D. macarellus	47	6	4058	296	1	1
(Birds = 13)	C. comatus	6	5	1084	376	2	2
	C. bartholomaei	8	3	778	45	3	5
	E. alletteratus	5	3	679	96	4	4
	Decapodiformes	5	4	318	65	5	3
	P. hillianus	1	2	646	47	6	6
	N. nasutus	2	2	290	6	1	10
	D. volitans	2	1	112	3	8	10
	C. hippurus	1	1	164	26	9	8
	H. balao	1	1	151	20	10	9
	$\sqrt{\sigma}$			nn	4	11	11

Table 14. Ranked indices of relative importance (IRI) by prey size for prey regurgitated by brown booby (*Sula leucogaster*) in Monito Islet (2003).

In order of length IRI. Squids were only identified to Order. L = fish fork length and squid mantle length. Vol = prey volume.

Visit/Season	Variable	Birds	Mean	s.e.	Var.	Min.	Max.	VMR	SWS	р	МСр
	Number of prey (119)	17	7.0	1.2	22.9	1.0	18.0	3.3	0.9	0.125	0.502
	Number of prey cat.(12)	15	2.3	0.4	2.0	1.0	5.0	0.8	0.8	0.016	0.351
luna	Organisms per prey cat.	15	3.7	0.6	5.6	1.0	10.0	1.5	0.8	0.008	0.262
Julie	Shannon H Index	15	0.5	0.1	0.3	0.0	1.3	0.5	0.8	0.007	0.287
	Simpson 1-D Index	15	0.3	0.1	0.1	0.0	0.7	0.3	0.8	0.004	0.264
	Equitability J Index	15	0.5	0.1	0.2	0.0	0.9	0.4	0.8	0.002	0.190
	Number of prey (118)	14	8.4	1.4	27.2	1.0	18.0	3.2	1.0	0.690	0.988
	Number of prey cat.(12)	12	2.7	0.4	1.7	1.0	5.0	0.6	0.9	0.105	0.256
August	Organisms per prey cat.	12	4.6	1.1	14.1	1.6	15.0	3.0	0.8	0.004	0.590
August	Shannon H Index	12	0.8	0.1	0.3	0.0	1.6	0.3	0.9	0.583	0.899
	Simpson 1-D Index	12	0.4	0.1	0.1	0.0	0.8	0.2	0.9	0.213	0.871
	Equitability J Index	12	0.7	0.1	0.1	0.0	1.0	0.2	0.7	0.001	0.160
	Number of prey (40)	10	4.0	1.1	12.2	1.0	11.0	3.1	0.8	0.014	0.273
	Number of prey cat.(8)	9	1.6	0.2	0.5	1.0	3.0	0.3	0.8	0.008	0.215
Sontombor	Organisms per prey cat.	9	2.6	0.5	2.1	1.0	4.5	0.8	0.8	0.058	0.712
September	Shannon H Index	9	0.3	0.1	0.1	0.0	0.8	0.4	0.7	0.005	0.187
	Simpson 1-D Index	9	0.2	0.1	0.1	0.0	0.5	0.3	0.7	0.003	0.195
	Equitability J Index	9	0.4	0.2	0.2	0.0	1.0	0.6	0.8	0.006	0.185
	Number of prey (79)	12	6.6	1.5	26.4	2.0	19.0	4.0	0.8	0.009	0.201
	Number of prey cat.(12)	12	2.1	0.4	2.3	1.0	5.0	1.1	0.7	0.002	0.281
Ostaban	Organisms per prey cat.	12	3.2	0.3	1.2	2.0	5.0	0.4	0.9	0.161	0.865
October	Shannon H Index	12	0.5	0.2	0.3	0.0	1.4	0.6	0.8	0.010	0.179
	Simpson 1-D Index	12	0.3	0.1	0.1	0.0	0.7	0.3	0.8	0.006	0.136
	Equitability J Index	12	0.4	0.1	0.2	0.0	1.0	0.5	0.7	0.001	0.116
Non-	Number of prey (237)	36.0	6.6	0.8	24.8	1.0	19.0	3.8	0.9	0.006	0.077
breeding	Number of prey cat.(20)	33.0	2.2	0.2	1.7	1.0	5.0	0.8	0.8	< 0.001	0.011
(August,	Organisms per prey cat.	33.0	3.6	0.4	6.5	1.0	15.0	1.8	0.7	< 0.001	0.145
and	Shannon H Index	33.0	0.5	0.1	0.3	0.0	1.6	0.5	0.9	0.001	0.036
October)	Simpson 1-D Index	33.0	0.3	0.0	0.1	0.0	0.8	0.3	0.8	< 0.001	0.019
,	Equitability J Index	33.0	0.5	0.1	0.2	0.0	1.0	0.4	0.7	< 0.001	0.010
	Number of prey (119)	17.0	7.0	1.2	22.9	1.0	18.0	3.3	0.9	0.234	0.504
	Number of prey cat.(12)	15.0	2.3	0.4	2.0	1.0	5.0	0.8	0.8	0.016	0.349
Breeding	Organisms per prey cat.	15.0	3.7	0.6	5.6	1.0	10.0	1.5	0.8	0.008	0.261
(June)	Shannon H Index	15.0	0.5	0.1	0.3	0.0	1.3	0.5	0.8	0.007	0.286
	Simpson 1-D Index	15.0	0.3	0.1	0.1	0.0	0.7	0.3	0.8	0.004	0.263
	Equitability J Index	15.0	0.5	0.1	0.2	0.0	0.9	0.4	0.8	0.002	0.189
	Number of prey (356)	53	6.7	0.7	23.8	1.0	19.0	3.5	0.9	0.001	0.021
	Number of prey cat.(22)	48	2.2	0.2	1.7	1.0	5.0	0.8	0.8	< 0.001	0.004
T . (- 1	Organisms per prey cat.	48	3.6	0.4	6.1	1.0	15.0	1.7	0.8	< 0.001	0.065
i otai	Shannon H Index	48	0.5	0.1	0.3	0.0	1.6	0.5	0.9	< 0.001	0.006
	Simpson 1-D Index	48	0.3	0.0	0.1	0.0	0.8	0.3	0.8	< 0.001	0.003
	Equitability J Index	48	0.5	0.1	0.2	0.0	1.0	0.4	0.8	< 0.001	0.001

Table 15. Descriptive statistics and distribution analysis of prey diversity in red-footed booby (*Sula sula*) per visit and season in Monito Islet in 2003.

Cat. = categories (fish species and squids order), VMR = variance mean ratio, SWS = Shapiro-Wilk statistic (normality test), MCp = Monte Carlo probability.

Table 16. A comparison of mean number of prey per regurgitation from red-footed boobies between values obtained in Monito Islet and the Pacific Ocean.

	Monito Islet 2003	Christmas Island ^a 1967	Northwestern Hawaiian Islands ^b 1978-1980
Total number of samples	53	50	369
Prey/regurgitation	6.7	6.6	5.8

^a Schreiber and Hensley (1976). ^b Harrison *et al.* (1983).

Visit	Prey	Frequency of		S	Sum		RI
V ISIL	categories	IN	occurrence	L (mm)	Vol (ml)	L	Vol
June	P. hillianus	18	6	1845	170	1	1
(Birds = 17)	Decapodiformes	11	4	889	163	2	2
	O. micropterus	11	3	995	72	3	5
	H. balao	8	3	1024	103	4	6
	E. alletteratus	6	3	999	305	5	3
	N. nasutus	4	4	580	12	6	9
	P. maculatus	7	2	665	56	7	8
	C. comatus	3	3	561	205	8	4
	D. macarellus	6	2	595	73	9	7
	D. volitans	13	1	475	8	10	10
	H. affinis	1	1	151	28	11	11
	E. obtusirostris	1	1	118	19	12	12
	E. volitans	1	1	118	19	12	12
	P. occidentalis	1	1	118	19	12	12
August	P. maculatus	29	9	2752	234	1	1
(Birds = 14)	P. hillianus	7	4	676	58	2	3
	H. balao	8	3	924	94	3	2
	S. crumenophthalmus	9	2	805	76	4	4
	O. micropterus	5	2	551	44	5	8
	Decapodiformes	4	3	254	52	6	5
	H. affinis	3	3	350	44	7	6
	C. comatus	2	2	315	90	8	7
	D. macarellus	4	1	299	12	9	9
	E. alletteratus	1	1	114	10	10	11
	C. bartholomaei	1	1	89	8	11	12
	P. arenatus	1	1	84	10	12	10
September	C. comatus	5	3	831	252	1	1
(Birds = 10)	G. cinereus	12	2	420	30	2	2
. ,	P. hillianus	3	3	308	28	3	3
	E. volitans	2	2	237	38	4	4
	C. furcatus	1	1	118	19	5	5
	C. melanurus	1	1	118	19	5	5
	N. nasutus	1	1	110	3	7	7
	E. alletteratus	1	1	93	2	8	8
October	P. hillianus	19	8	2080	220	1	1
(Birds = 12)	Decapodiformes	12	5	762	136	2	2
	E. alletteratus	3	2	470	123	3	3
	N. nasutus	5	1	725	15	4	6
	O. micropterus	3	2	197	6	5	5
	D. volitans	4	1	146	2	6	8
	H. rondeletii	2	1	251	36	7	7
	C. comatus	1	1	200	79	8	4
	H. balao	1	1	158	26	9	9
	C. cyanopterus	1	1	118	19	10	10
	P. arenatus	1	1	48	2	11	12
	G. cinereus	1	1	35	3	12	11

Table 17. Ranked indices of relative importance (IRI) by size for pre	y regurgitated by
red-footed booby (Sula sula) in Monito Islet (2003).	

In order of length IRI. Squids were only identified to Order. L = fish fork length and squid mantle length. Vol = prey volume.

Table 18. Comparisons of prey diversity among Sula spp (Monito Islet, 2003).

Levene's Test of Equality of Error Variances				
Variable	F	df1	df2	Sig.
Number of prey	5.0	5	135	< 0.001
Number of prey cat.	0.8	5	135	0.585
Organisms per prey spp.	2.2	5	135	0.053

Variable	Multiple	(I) Sula spp.		Mean	s.e.		95% Confidence Interval	
v unuble	test		(J) <i>Sula</i> spp.	(I-J)	s.e.	р	Lower Bound	Upper Bound
Number of prey		MD	BB	-5.0	1.3	0.001	-8.3	-1.7
	Tamhane	IVID	RB	-3.1	0.8	0.001	-5.0	-1.2
		BB	RB	1.9	1.5	0.479	-1.7	5.5
		MB	BB	-0.6	0.3	0.071	-1.3	0.0
Number of prev cat	Bonferroni		RB	-0.2	0.3	1.000	-0.9	0.4
proj cui.		BB	RB	0.4	0.3	0.473	-0.3	1.0
		MD	BB	-1.2	0.4	0.018	-2.2	-0.2
Organisms per prey cat.	Tamhane	MB	RB	-1.3	0.4	0.004	-2.3	-0.3
		BB	RB	-0.1	0.5	0.991	-1.4	1.1

Cat. = categories (fish species and squids order). MB = masked booby (*S. dactylatra*). BB = brown booby (*S. leucogaster*). RB = red-footed booby (*S. sula*).

<i>Sula</i> spp.	visit/season	Birds	Mean B	s.e.	Var.	Min.	Max.	VMR	SWS	р	МСр	Mean prey (n)	B _a
	June	9	2.1	0.4	1.1	1.0	4.0	0.5	0.9	0.194	0.758	2.4	77%
	August	10	1.6	0.2	0.5	1.0	3.2	0.3	0.8	0.007	0.275	3.6	24%
	September	25	1.8	0.2	1.0	1.0	4.5	0.6	0.8	< 0.001	0.095	3.2	38%
MB	October	7	1.6	0.4	0.9	1.0	3.6	0.6	0.7	0.006	0.448	2.7	35%
	Non- breeding	26	1.8	0.2	0.8	1.0	4.0	0.5	0.8	< 0.001	0.040	3.0	40%
	Breeding	25	1.8	0.2	1.0	1.0	4.5	0.6	0.8	< 0.001	0.094	3.2	38%
	Total	51	1.8	0.1	0.9	1.0	4.5	0.5	0.8	< 0.001	0.009	3.1	39%
	June	13	2.1	0.3	1.0	1.0	4.0	0.5	0.9	0.041	0.465	9.0	14%
	August	9	2.5	0.3	0.9	1.2	3.9	0.4	0.9	0.666	0.991	9.4	18%
	September	7	1.7	0.3	0.6	1.0	3.0	0.3	0.8	0.117	0.648	4.3	22%
BB	October	13	1.7	0.3	1.1	1.0	4.1	0.6	0.7	0.002	0.179	6.5	13%
	Non- breeding	9	2.5	0.3	0.9	1.2	3.9	0.4	0.9	0.666	0.991	9.4	18%
	Breeding	33	1.9	0.2	0.9	1.0	4.1	0.5	0.8	< 0.001	0.192	7.0	14%
	Total	42	2.0	0.2	1.0	1.0	4.1	0.5	0.9	< 0.001	0.241	7.5	15%
	June	15	1.8	0.2	0.7	1.0	3.3	0.4	0.8	0.006	0.347	6.1	15%
	August	12	2.3	0.3	1.2	1.0	4.5	0.5	0.9	0.334	0.785	6.2	24%
	September	9	1.3	0.2	0.2	1.0	2.0	0.2	0.7	0.003	0.229	2.9	18%
RB	October	12	1.7	0.3	0.8	1.0	3.5	0.5	0.8	0.006	0.251	4.4	21%
	Non- breeding	33	1.8	0.2	0.9	1.0	4.5	0.5	0.8	< 0.001	0.134	4.6	22%
	Breeding	15	1.8	0.2	0.7	1.0	3.3	0.4	0.8	0.006	0.343	6.1	15%
	Total	48	1.8	0.1	0.8	1.0	4.5	0.5	0.8	< 0.001	0.030	5.1	20%

Table 19. Descriptive statistics and distribution of niche breadth per *Sula* spp., visits and season (Monito Islet, 2003).

 \overline{MB} = masked booby (*S. dactylatra*). BB = brown booby (*S. leucogaster*). RB = red-footed booby (*S. sula*).B = Levin's niche breadth. B_a = standardized niche breadth. VMR = variance mean ratio. SWS = Shapiro-Wilk statistic (normality test). MCp = Monte Carlo probability.

ANOVA						
Sula spp.	Test	Sum of Squares	df	Mean Square	F	р
	Among Visits	1.5	3	0.5	0.6	0.649
(S. dactylatra)	Within Visits	43.7	47	0.9		
	Total	45.3	50			
Danara hasha	Among Visits	3.7	3	1.2	1.3	0.296
(S. leucogaster)	Within Visits	36.4	38	1.0		
	Total	40.1	41			
Red-footed	Among Visits	4.6	3	1.5	1.9	0.137
Booby	Within Visits	34.7	44	0.8		
(<i>S. sula</i>)	Total	39.3	47			

Table 20. Comparison of Levin's niche breadth among Sula spp., visit and season.

Tests of Between-Subjects Effects

Đ					
Source	Type III Sum of Squares	df	Mean Square	F	р
Model	495.0	6	82.5	91.4	< 0.001
Sula spp.	3.2	2	1.6	1.7	0.178
Season	1.1	1	1.1	1.2	0.267
Sula spp. * Season	2.3	2	1.1	1.3	0.286
Error	121.8	135	0.9		
Total	616.9	141			

Levins' measure R Squared = 0.802 (Adjusted R Squared = 0.794). Seasons = Non-breeding (June, August and October for *S. dactylatra*; August for *S. leucogaster*; August, September and October for *S. sula*) vs. breeding (September for *S. dactylatra*; June, September and October for *S. leucogaster*; June for *S. sula*).

Prey category (number of prey)	Function				
	1	2			
A. combatia	0.095	0.464			
<i>C. bartholomaei</i> < 75 mm	-0.014	-0.374			
<i>C. bartholomaei</i> 75 to < 125mm	-0.097	0.023			
<i>C. bartholomaei</i> 125 to < 175mm	0.077	0.216			
<i>C. comatus</i> 75 to < 125mm	0.095	0.089			
<i>C. comatus</i> 125 to < 175mm	0.364	-0.136			
<i>C. comatus</i> 175 to < 225mm	0.412	0.109			
<i>C. cyanopterus</i> 75 to < 125mm	-0.182	-0.094			
<i>C. cyanopterus</i> 125 to < 175mm	0.229	-0.097			
<i>C. cyanopterus</i> 175 to < 225mm	0.128	-0.105			
C. equiselis	0.090	0.444			
C. exsiliens	0.069	-0.008			
C. furcatus	-0.182	-0.094			
C. hippos	-0.040	-0.071			
C. hippurus	0.234	0.410			
C. melanurus	-0.182	-0.094			
Decapodiformes < 75 mm	-0.695	-0.235			
Decapodiformes 125 to < 175mm	0.015	-0.071			
<i>D. macarellus</i> < 75 mm	-0.101	-0.030			
<i>D. macarellus</i> 75 to < 125 mm	0.233	0.906			
D. volitans	-0.414	-0.098			
<i>E. alletteratus</i> 75 to < 125 mm	-0.027	0.102			
<i>E. alletteratus</i> 125 to < 175mm	0.024	0.369			
<i>E. alletteratus</i> 175 to < 225mm	-0.219	-0.269			
<i>E. alletteratus</i> \geq 225 mm	0.331	-0.175			
E. bipinnulata	0.029	0.220			
<i>E. obtusirostris</i> 75 to < 125mm	-0.249	0.061			
<i>E. obtusirostris</i> 125 to < 175mm	0.322	-0.170			
<i>E. velox</i> 75 to < 125mm	-0.019	0.416			
<i>E. velox</i> 125 to < 175mm	0.128	-0.050			
<i>E. volitans</i> 75 to < 125 mm	0.088	-0.114			
<i>E. volitans</i> 125 to < 175mm	0.169	-0.208			
G. cinereus	-0.246	-0.157			
<i>H. affinis</i> 75 to < 125mm	-0.185	-0.032			
<i>H. affinis</i> 125 to < 175mm	0.184	-0.127			
<i>H. affinis</i> 175 to < 225mm	0.331	0.097			

Table 21. Standardized canonical discriminant function coefficients from a Discriminant Function Analysis to prey categories

Prey category (number of prey)	Function				
	1	2			
<i>H. balao</i> < 75mm	-0.053	0.339			
<i>H. balao</i> 75 to < 125mm	-0.063	0.370			
<i>H. balao</i> 125 to < 175mm	-0.198	-0.343			
<i>H. balao</i> 175 to < 225mm	0.211	-0.135			
<i>H. brasiliensis</i> 125 to < 175mm	0.121	0.029			
H. rondeletii	-0.182	-0.094			
H. speculiger	0.021	-0.158			
N. ductor	0.486	0.270			
N. gronovii	-0.123	0.101			
<i>N. nasutus</i> 75 to < 125mm	-0.227	-0.036			
<i>N. nasutus</i> 125 to < 175mm	-0.442	-0.411			
<i>N. nasutus</i> 175 to < 225mm	0.955	0.887			
<i>O. micropterus</i> < 75mm	0.048	0.134			
<i>O. micropterus</i> 75 to < 125mm	-0.265	-0.212			
<i>O. micropterus</i> 125 to < 175mm	0.054	0.380			
O. saurus	0.229	-0.097			
<i>P. arenatus</i> <75mm	0.103	0.499			
<i>P. arenatus</i> 75 to < 125mm	-0.080	-0.105			
<i>P. hillianus</i> <75mm	0.122	0.315			
<i>P. hillianus</i> 75 to $<$ 125mm	0.005	-0.088			
<i>P. hillianus</i> 125 to < 175mm	0.060	0.294			
P. maculatus	-0.335	-0.257			
<i>P. occidentalis</i> 75 to < 125mm	-0.182	-0.094			
<i>P. occidentalis</i> 125 to < 175mm	0.308	-0.360			
S. bullisi	0.322	-0.312			
S. crumenophthalmus	-0.180	-0.072			

Continuation of Table 21. Standardized Canonical Discriminant Function Coefficients (Cont.)

Ricardo López-Ortiz, 2007, PhD Dissertation, UPR/RUM

FIGURES



Figure 1. Seabird species targeted in the study in Monito Islet (2003).

(a) A masked booby (*Sula dactylatra*) with a gut content regurgitated in the soil, (b) a brown booby (*S. leucogaster*) rearing its chick, (c) a nesting red-footed booby (*S. sula*).









Circles, squares, triangles and bars represent the masked (*Sula dactylatra*), brown (*S. leucogaster*), red-footed (*S. sula*) booby and 95% confidence intervals, respectively. Samples obtained in 2003 at Monito Islet.



Figure 4. Comparison of mean prey length among visits (a) and bird species (b).

Circles, squares, triangles and bars represent the masked (*Sula dactylatra*), brown (*S. leucogaster*), red-footed (*S. sula*) booby and 95% confidence intervals, respectively. Samples obtained in 2003 at Monito Islet.

Figure 5. Comparison of mean prey volume among visits (a) and bird species (b).

Circles, squares, triangles and bars represent the masked (*Sula dactylatra*), brown (*S. leucogaster*), red-footed (*S. sula*) booby and 95% confidence intervals, respectively. Samples obtained in 2003 at Monito Islet.

Figure 6. Aspect of the masked booby (Sula dactylatra) feeding ecology (biomass by volume) for each visit (a) and overall (b).

Numeric abundance provided for each prey category. Samples obtained at Monito Islet for 9, 10, 25 and 7 birds in June, August, September and October of 2003, respectively.

Figure 7. Aspect of the brown booby (Sula leucogaster) feeding ecology (biomass by volume) for each visit (a) and overall (b).

Numeric abundance provided for each prey category. Samples obtained at Monito Islet for 17, 10, 8 and 13 birds in June, August, September and October of 2003, respectively.

Figure 8. Aspect of the red-footed booby (Sula sula) feeding ecology (biomass by volume) for each visit (a) and overall (b).

Numeric abundance provided for each prey category. Samples obtained at Monito Islet for 17, 14, 10 and 12 birds in June, August, September and October of 2003, respectively.

Figure 9. Comparison of diet among *Sula* spp. and visits, using Shannon's and Simpson's diversity indexes.

Circles, squares, triangles and bars represent the masked (*Sula dactylatra*), brown (*S. leucogaster*), red-footed (*S. sula*) booby and 95% confidence intervals, respectively. Samples obtained in 2003 at Monito Islet.

Figure 10. Graph showing the results of a canonical discriminant function analysis of the number of each prey category within each regurgitation sample. Based on Table 14, each circle, square or triangle represent regurgitations from masked (*Sula dactylatra*), brown (*S. leucogaster*) and red-footed (*S. sula*) booby, respectively. Filled square equals group centroid.

APPENDIX A. TAXONOMY AND PREY SIZE ESTIMATION METHOD

Fish species found in regurgitations of <i>Sula</i> spp. (Sulidae) at Monito Islet (2003)										
Family	Prey common name	Species	Ν	Est. Method						
Exocoetidae	Sailfin flyingfish	Parexocoetus hillianus	103	Reg.						
	Clearwing flyingfish	Cypselerus comatus	100	Reg.						
	Fourwing flyingfish	Hirundichthys affinis	16	Reg.						
	Western bluntnose flyingfish	Prognichthys occidentalis	8	Sp. Avg.						
	Tropical two-wing flyingfish	Exocoetus volitans	7	Sp. Avg.						
	Oceanic two-wing flyingfish	Exocoetus obtusirostris	6	Sp. Avg.						
	Bandwing flyingfish	Cheilopogon exsiliens	4	Sp. Avg.						
	Marginated flyingfish	Cheilopogon cyanopterus	3	Avg.						
	Blackwing flyingfish	Hirundichthys rondeletii	2	Avg.						
	Spotfin flyingfish	Cheilopogon furcatus	1	Avg.						
	Atlantic flyingfish	Cheilopogon melanurus	1	Avg.						
	Mirrowing flyingfish	Hirundichthys speculiger	1	Avg.						
Hemiramphidae	Balao halfbeak	Hemiramphus balao	45	Reg.						
	Atlantic smallwing flyingfish	Oxyporhamphus micropterus	27	Reg.						
	Flying halfbeak	Euleptorhamphus velox	4	Avg.						
	Ballyhoo halfbeak	Hemiramphus brasiliensis	2	Avg.						
Holocentridae	Deepwater squirrelfish	Sargocentron bullisi	5	Sp. Avg.						
Caproidae	Shortspine boarfish	Antigonia combatia	1	Obs.						
Dactylopteridae	Flying gurnard	Dactylopterus volitans	67	Reg.						
Priacanthidae	Atlantic bigeye	Priacanthus arenatus	20	Reg.						
Coryphaenidae	Pompano dolphinfish	Coryphaena equiselis	1	Avg.						
	Common dolphinfish	Coryphaena hippurus	2	Avg.						
Carangidae	Mackerel scad	Decapterus macarellus	97	Reg.						
	Yellow jack	Caranx bartholomaei	18	Sp. Avg.						
	Bigeye scad	Selar crumenophthalmus	9	Sp. Avg.						
	Crevalle jack	Caranx hippos	3	Avg.						
	Rainbow runner	Elagatis bipinnulata	1	Avg.						
	Pilotfish	Naucrates ductor	1	Obs.						
	Atlantic leather jack	Oligoplites saurus	1	Avg.						
Gerreidae	Yellowfin mojarra	Gerres cinereus	15	Sp. Avg.						
Mullidae	Spotted goatfish	Pseudupeneus maculatus	39	Sp. Avg.						
Gempylidae	Black gemfish	Nesiarchus nasutus	30	Sp. Avg.						
Scombridae	Little tunny	Euthynnus alletteratus	27	Reg.						
Nomeidae	Man-of-war fish	Nomeus gronovii	3	Sp. Avg.						
		Total	670							

Method used to estimates fish fork length and volume. Avg. = averaging to its nearest available taxon, Obs. = Observed. Reg. = Power regression used in common species with different sizes. Sp. Avg. = Cases where several specimens of the same species were very similar in size, but some of them were undamaged and allows record of the observed fork length and volume, in those cases an average was calculated for the species.

APPENDIX B. MORPHOMETRY OF PREY SPECIES

Measurable body parts of each fish species regurgitated by *Sula* spp. in Monito Islet (2003).

Family	Species	Head	Second dorsal		Body	Pectoral	Cauc	lal fin
			fin		depth	fin	lo	bes
			Base	Depth			Upper	Lower
Carangidae	D. macarellus	21	23	24	24	15	85	79
Dactylopteridae	D. volitans	7	2	2	3	3	6	5
Exocoetidae	C. comatus	33	85 82		64	72	92	92
	H. affinis	3	15	15	11	14	16	16
	P. hillianus	20	70	77	39	61	90	90
Hemiramphidae	H. balao	14	27	27	19	25	29	30
	O. micropterus	16	16	16	11	23	18	20
Priacanthidae	P. arenatus	8	8	8	12	6	12	12
Scombridae	E. alletteratus	6	8	8	9	3	23	22
	Total	128	254	259	192	222	371	366

Length measurement limits, adapted from K. E. Carpenter (2002).

ADDENDIN C DDEN	SIZE DECDESSION VALUES
APPENDIX C. PREY	SIZE REGRESSION VALUES

Species	Y	X	a		1))	$\frac{\Gamma}{R^2}$	N	Р	%PE
			Mean	Std. err.	Mean	Std. err.				
-	Carangidae									
D. macarellus	FL	LW	21.47	5.61	4.87E-01	8.99E-02	0.677	16	< 0.001	5.55
	VO	LW	6.30E-03	4.81E-03	2.39	2.58E-01	0.886	13	< 0.001	12
				D	actylopteridae	9				
D. volitans	FL	SL	1.54	3.84E-01	9.41E-01	6.71E-02	0.985	5	0.001	1.36
	FL	HL	3.84	5.69E-01	1.02	5.92E-02	0.996	5	0.006	4.30
	VO	SL	7.90E-06	4.11E-06	3.19	1.39E-01	0.996	4	0.002	2.67
	VO	HL	2.30E-05	1.90E-04	4.24	7.40E-01	0.944	5	0.006	14.7
					Exocoetidae					
C. comatus	FL	LO	5.31	1.62	8.80E-01	7.66E-02	0.830	29	< 0.001	4.18
	FL	BD	20.22	9.74	6.19E-01	1.38E-01	0.428	29	< 0.001	8.10
	VO	LO	8.60E-03	1.13E-02	2.21	3.30E-01	0.775	15	< 0.001	13.3
	VO	BD	2.41E-01	4.34E-01	1.57	5.13E-01	0.401	16	0.008	20.3
H. affinis	FL	LO	4.38	1.28	9.30E-01	7.88E-02	0.986	4	0.007	2.16
	VO	LO	2.40E-03	2.91E-03	2.46	3.24E-01	0.966	4	0.017	8.07
P. hillianus	FL	LO	7.86	1.57	7.85E-01	5.98E-02	0.950	11	< 0.001	2.28
	FL	PF	5.41	7.52E-01	7.36E-01	3.43E-02	0.981	11	< 0.001	1.48
	VO	LO	5.00E-04	4.50E-04	2.96	2.61E-01	0.942	10	< 0.001	6.67
	VO	PF	2.30E-03	3.19E-03	2.07	3.46E-01	0.800	11	< 0.001	13.1
				Н	emiramphidae	e				
H. balao	FL	LO	2.41	1.25	1.16	1.49E-01	0.909	8	< 0.001	5.12
	FL	HL	6.59	2.31	8.95E-01	1.04E-01	0.902	10	< 0.001	4.83
	VO	LO	3.50E-06	1.08E-05	4.38	8.84E-01	0.860	6	0.008	17.8
	VO	HL	1.40E-03	1.82E-03	2.72	3.75E-01	0.898	8	< 0.001	13.5

Values related to the power regression ($Y=aX^b$) to predict prey size.

%PE = mean percent prediction error, BD = body depth, FL = fork length, HL = head length, LO = lower caudal fin lobe length, LW = longest caudal fin lobe length, PF = pectoral fin length, SL = standard length, UP = upper caudal fin lobe length and VO = volume.

Species	Y	Х	a		1	0	R^2	Ν	Р	%PE	
			Mean	Std. err.	Mean	Std. err.					
Hemiramphidae											
O. micropterus	FL	LO	4.77	5.65E-01	9.39E-01	3.61E-02	0.990	9	< 0.001	2.07	
	FL	PF	5.89	2.03	8.29E-01	9.91E-02	0.897	10	< 0.001	17.16	
	VO	LO	8.49E-04	7.74E-04	2.76	2.81E-01	0.941	8	< 0.001	6.73	
	VO	PF	2.00E-03	3.29E-03	2.37	4.79E-01	0.778	9	0.002	29.5	
Priacanthidae											
P. arenatus	FL	BD	7.02	9.31E-01	7.39E-01	4.37E-02	0.986	6	< 0.001	1.75	
	FL	LW	5.67	3.82	9.73E-01	2.67E-01	0.769	6	0.022	5.26	
	VO	BD	4.60E-03	5.37E-03	2.28	3.88E-01	0.874	7	0.002	14.1	
	VO	LW	1.70E-03	3.45E-03	3.14	8.19E-01	0.746	7	< 0.012	19.6	
				:	Scombridae						
E. alletteratus	FL	UP	6.99	3.16	9.35E-01	1.43E-01	0.895	7	0.001	6.67	
	FL	SL	1.33	1.75E-01	9.58E-01	2.73E-02	0.996	7	< 0.001	1.39	
	VO	UP	2.36E-06	3.30E-06	4.97	4.24E-01	0.986	4	0.007	9.05	
	VO	SL	8.02E-07	2.12E-06	3.53	5.35E-01	0.956	4	0.022	14.9	

Values related to the power regression ($Y=aX^{b}$) to predict prev	size
Continuation from Appendix C	5120

%PE = mean percent prediction error, BD = body depth, FL = fork length, HL = head length, LO = lower caudal fin lobe length, LW = longest caudal fin lobe length, PF = pectoral fin length, SL = standard length, UP = upper caudal fin lobe length and VO = volume.

APPENDIX D. PREY SIZE ESTIMATION SCATTERPLOT; AN EXAMPLE

Example of a scatterplot to predict fork length of *Decapterus macarellus* from the longest caudal fin lobe length. The triangles and the solid line represent observed and expected values, respectively. Dashed lines represent the lower and upper confidence limits (95%).

APPENDIX E. ASPECTS OF FEEDING ECOLOGY; THE COSTELLO METHOD

100 100 Specialization High BPC Dominant 75 **(d**) 80 80 (1) Prey-specific biomass (%) Prey-specific biomass (%) 50 **60** 60 Prey importance Niche width contribution 25 Feeding strategy **40** · 40 20 20 **a** (a) (\mathbf{c}) ⓒ 5 **(b**) **b**

0

0.2

0.4

Frequence

0.6

a, b, c & d = prey sp.

1.0

0.8

High WPC

1.0

0.8

Rare

0.2

0

0

Generalization

0.6

of ocurrence

0.4

Frequency

The graphical interpretation of the Costello (1990) method, modified by Amundsen *et al.* (1996), shows three gradients that constitute three aspects of feeding ecology.

Prey importance gradient (rare and dominant prey-types)- In a hypothetical example of a diet represented by 10 prey organisms within 4 types or categories, prey-type "a" represent 20% of the regurgitated biomass of 0.1 of the predators. In other words, prevtype "a" account for 20% of the regurgitation biomass in only one predator individual (1/10 individuals). Similarly, prey-type "b" represents 10% of the biomass regurgitated by two predator individuals (2/10 individuals). Note that the prev-specific biomass is based only in the predators that regurgitated such prey-type. The prey-relative abundance can be obtained by multiplying the correspondent values of each axis (i.e. prev-type "a" = $20\% \ge 0.1 = 2\%$ of the total prey population). Both species "a" and "b" (2% of the total population each one) laid under the 5% isopleths of the second graph and toward the rare prey-types in the prey importance gradient, meaning that each of those prey-types represents less than 5% of the regurgitated prey population, in contrast to the dominant prey-type "d". Therefore, the area enclosed by the co-ordinates of the two axes represents the prey-relative abundance. The sum of the areas for all prey-types (i.e. prey-types "c" and "d" equals 16% and 80%, respectively) will equal the total area of the diagram (100%).

<u>Niche width contribution gradient (high between- or within-phenotype components)</u>- In the hypothetical example, the second most important prey-type (c) was regurgitated by 80% of the predators (from the freq. of occurrence axis, 0.8 of 10 predators). However, its average contribution to the regurgitation contents of these predators was low (20% of their regurgitated biomass). In a population with a high within-phenotype component (WPC), most of the individuals should simultaneously regurgitate about the same preytypes. Therefore, the WPC describes the level of variation in resource use by individuals. Contrarily, a population of individuals that differ in their regurgitated prey-types equals a population of predators with a high between-phenotypes component (BPC) to the niche width. Thus, the BPC describes variation among individuals of the species population. Total niche width is given by WPC + BPC.

<u>Feeding strategy gradient (specialization or generalization)</u>- A regurgitation with a high abundance of a single prey-type suggests specialization of the predator individual in contrast to generalization which can be characterized by several prey-types found in low abundance within an individual regurgitation. In the graph, the high BPC area will be populated of prey-types obtained from individuals that specialized in different prey-types In other words, a generalist population of specialized individuals. If the entire predator population specialized in the same prey-types, these prey-types (as prey-type "d") need to be few and will be located in the dominant area of the graph.