

Variation in the feeding of four species of seabird on
Machias Seal Island, New Brunswick

by

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Abstract

Food is theorized to be a primary limiting factor in defining life-history characteristics of breeding birds. Seabirds are useful study species when exploring questions regarding relationships with prey during the breeding season as they tend to breed in dense colonies with restricted foraging ranges and many species carry prey to chicks in their bill, allowing for unobtrusive prey identification and quantification. We used ten years of data from four species of seabird, Arctic Tern (*Sterna paradisaea*), Common Tern (*S. hirundo*), Atlantic Puffin (*Fratercula arctica*), and Razorbill (*Alca torda*) on Machias Seal Island, NB, to examine the relationships seabirds have with prey while providing for chicks.

We investigated the boundaries between dietary niches of the four focal species between and within breeding seasons, and explored the relationships of dietary overlap and diversity with reproductive success. A decline in the proportion of herring fed to seabird chicks was observed from 1995-2004 for all four species, but we saw no consistent trend in the amounts of niche overlap over years nor did we observe any within-season patterns in the proportion herring delivered to chicks or niche overlap between species.

Seabirds rely largely on eyesight when foraging to locate both foraging flocks and individual prey items, but fog is common during the summer breeding season in temperate and polar seas and can limit visibility. We predicted fog would reduce feeding rates of seabirds and result in adults feeding fewer schooling fish while feeding a greater variety of other prey types, but our data did not support our hypotheses.

Our results are restricted by the limiting field conditions in which our data were collected and likely complicated by external and uncontrollable variables. To more rigorously test our questions, we recommend controlled lab experiments to test the dietary niches of seabirds and observations of fog condition on the grounds where seabirds forage.

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CHAPTER 1

Introduction

Seabirds spend almost their entire lives in the marine environment and have life-history characteristics that make them unique in the avian world. Overall, they tend to be long-lived (up to 60 years), have small clutch sizes, and mature slowly (Schreiber & Burger 2002). Nearly all seabirds are colonial (Coulson 2002); they frequently breed in dense colonies and are limited to nesting on islands and other areas free of mammalian predators (Coulson 2002). Seabirds on accessible colonies are useful subjects in biological studies because they are commonly there in large numbers and it is relatively easy to monitor aspects of feeding ecology and reproductive biology.

One of the fundamental concepts in ecology is that of “niche” (Gause 1934; Hutchinson 1959; Schoener 1974; J.M. Diamond 1978; Leibold 1995). Despite being a cornerstone in understanding the living world and having been studied extensively, there are various definitions and perceptions on what a niche is. I follow J.M. Diamond’s (1978) interpretation of the concept that it should “not be defined too rigidly, but, roughly, a niche consists of the resources a species uses, where it finds them, and the strategy by which it harvests them.”

Early in the development of niche theory, the concept of niche was relatively simple as described by Gause’s principle, or the competitive exclusion principle (Gause 1934). Lack’s expansion on Gause’s observations was that two species cannot occupy the same niche in the same place without one species ultimately out-competing the other, driving it to change or go extinct (Gause 1934; Lack 1947a). Not long after the concept

was proposed, it was debated by many as it is all but impossible to “prove”, and was considered to be a tautology by others (Hardin 1960; Slobodkin 1961; Armstrong & McGehee 1980).

There has been fierce debate among ecologists, both criticizing and defending the research involved with the competitive exclusion principle (e.g. Diamond 1978; Connor & Simberloff 1979; Strong et al. 1979; Schoener 1982; Roughgarden 1983). However, subsequent research has largely confirmed that competition plays a large role in the systems of community ecology. A review of 164 experimental studies examining interspecific competition found 90% of all studies cited evidence of competition (Schoener 1983). Exactly how competition plays a role in defining species is still in debate, as are the many theories that expand on the competitive exclusion principle. Many of the results found are conflicting, further clouding attempts to clarify the role of competition in community ecology.

MacArthur and Levins' (1964) theoretical work refined the competitive exclusion principle by showing that the number of species coexisting is limited by the number of resources, allowing the survival of multiple competing species when using multiple resources. Simon Levin's mathematical model (1970) took this concept a step further and found that other limiting factors (such as, but not limited to predators) can increase the number of species coexisting on the same resources. The concept of predation being a limiting factor and thus increasing the number of coexisting competing species has been supported empirically by a number of works (e.g. Paine 1966; Lubechenco 1978; Lawton & Strong 1981) and some ecologists have suggested that predation is a key process defining communities that should not be overshadowed by competition (Connell 1975;

Lawton & Strong 1981; Holt 1984). Many of the studies which found predation to have a greater effect on community structure than competition have examined small organism communities, such as arthropods and marine invertebrates (e.g. Paine 1966; Lawton & Strong 1981; Steffan-Dewenter & Tscharrntke 2000), where the risk of predation may be much greater than for larger vertebrate communities that have been shown to support the competitive exclusion principle (e.g. Abramsky et al. 1979; Munger & Brown 1981; Pacala & Roughgarden 1982; Bosakowski et al. 1992). The discrepancies in predation risk may greatly influence community structure, making it difficult to create generalized theories of competition over all types of organismal communities.

A more complex hypothesis that takes account of the effect of both predation and competition on communities was proposed by Hairston *et al.*, (1960) who suggested competition would be distributed unequally among trophic levels. Specifically, carnivores, producers, and decomposers should be defined by competition, but in herbivores predation should be the factor that limits population size. Empirical studies have supported this hypothesis in terrestrial and freshwater environments (see review: Schoener 1983), suggesting the classic rules of competition do not hold true for herbivores.

The variability in the resources themselves may also influence the number of species relying on a resource. Levins (1979) proposed a theoretical model for this concept, and the theory has seen some experimental support. Naeem (1988) showed that in pitcher plants two species of arthropods were able to coexist as the density of one species varied with the mean resource, while the other species' density was a function of variance of the resource.

Another potential explanation for why not all studies find competition to drive interactions is temporal variation in resources. A hypothesis proposed by Wiens (1977) based on his studies on grassland birds suggests that severe competition only occurs in “crunch” years when resources are highly limited. This theory has been supported by some work, but most studies are not sufficiently long-term to conclusively strengthen the theory (Schoener 1983). Perhaps the most convincing example for Wiens’ hypothesis was recently published based on long-term work in the Galapagos islands. Grant and Grant (2006) found that after the colonization of the large ground finch to an island, the medium and large ground-finch coexisted with little change until a severe drought. The drought caused a food shortage, and the two species diverged in bill size as large-billed medium ground finches were out-competed by the large ground finch. Medium ground finches with smaller bills survived as they could consume seeds the large ground finch could not. After the drought, medium ground finches had significantly smaller bills than prior to the food shortage (Grant & Grant 2006). In addition to being direct evidence of competition causing a morphological change (character displacement), this also helps confirm the importance of “crunch” years in competitive exclusion.

Despite these many varying perspectives on competition and niche theory, the basic concept that competition is a driving force in defining community systems and in evolution is still held by most ecologists. As research continues, we still find more conclusive evidence of the role of competition in evolution in the current literature (e.g. Schuller 2000; Pfennig & Murphy 2002; Grant & Grant 2006).

An interesting aspect of interactions between organisms that is often examined is the amount of niche overlap between species. Organisms that are resource limited should

not show complete overlap in resource use, and overlap has been used as an indicator of competition for decades (e.g. MacArthur & Levins 1967; May 1975). However, overlap has been criticized as a measure for competition (Colwell & Futuyma 1971; Lawlor 1980; Abrams 1983), and one of the greatest concerns is that high overlap may be associated with both food abundance and food shortage (Steenhof & Kochert 1985; Korpimaki 1987; Abrams 1998; Bell & Ford 1990). Research shows that this may be explained by changes in severity of stress: in periods of mild stress overlap decreases, but in times of extreme stress species are forced to rely on the same few resources resulting in a high overlap (Bell & Ford 1990). Thus, by examining changes in niche overlap over periods of time we may better observe the effects of interspecific competition (Korpimaki 1987).

In times of food abundance many species can consume the same prey, and several species can have a restricted dietary niche breadth and high dietary overlap (Wiens 1989; Bell & Ford 1990; Gonzales-Solis et al. 1997). When food is limited during a mild to moderate food shortage, preferred prey items are no longer accessible, and organisms will be less selective in prey items consumed, resulting in broader dietary breadths (Lack 1947a; MacArthur & Pianka 1966; Wiens 1989; Gonzales-Solis et al. 1997; Rodel et al. 2004). Competition between species in times of mild-moderate food stress causes individuals to change foraging behaviour, thus organisms feed on different prey and dietary overlap between species decreases (J.M. Diamond 1978; Schoener 1982; Gonzales-Solis et al. 1997). Consequently, we expect to see high overlap and narrow niche breadth in periods of abundance, and low overlap and broad dietary niche breadth in times of food limitation.

Seabirds have interested biologists since the beginnings of niche theory (Lack 1945) because many of their natural history traits result in apparently high niche overlap, particularly over the breeding season (Diamond 1983). Seabirds tend to have similar nesting requirements: they often are limited to nesting in colonies on islands to limit predation (Coulson 2002). Seabirds are therefore also restricted in foraging range during the breeding season as they must return to the colony to feed their young; this is particularly true for birds that forage inshore (A.W. Diamond 1978). One would expect high competition for food when large colonies of seabirds share a limited foraging range as they feed themselves as well as their offspring. Yet seasonal cycles in marine productivity also cause an abundance of marine organisms during the summer months (Cushing 1975) that results in many seabirds consuming the same prey species (Diamond 1983). Thus, during the breeding season seabirds tend to breed in the same places and feed on similar prey when competition should be high, making it difficult to tease apart the ecological niche held by different species of seabirds. Given the dynamic nature of the prey seabirds consume and limitations in foraging range during breeding seasons, I am particularly interested in addressing the dietary niche of seabirds over time and through periods of differing food availability.

Food limitation is believed to be critical in restricting bird reproduction and populations (Lack 1947b; Martin 1987), and is thought to be a defining limiting characteristic for seabird populations (Ashmole 1963; Ashmole & Ashmole 1967; A.W. Diamond 1978; Safina et al. 1988; Oro et al. 2003). Thus, it is important we understand not only the relationship birds have with each other in regards to food, but also what factors may limit their ability to find food.

When foraging, seabirds rely on visual cues to locate prey (Shealer 2002). With the exception of seabirds in the order Procellariiformes that have been shown to forage at least partially using olfactory senses (Verheyden & Jouventin 1994; Nevitt et al. 2004), seabirds are believed to rely on eyesight to find foraging flocks and individual prey items (Shealer 2002). Seabirds tend to forage in flocks, and finding flocks is believed to be critical in finding where to forage, particularly when searching for schooling fish (Hoffman et al. 1981; Duffy 1983; Shealer 2002). Individuals tend to leave the colony singly and do not search for prey in groups, so it is thought that when seabirds look for food, they look for foraging flocks as a cue for where to find prey (Haney *et al.* 1992).

Social facilitation is when an organism is prompted to behave a certain way after observing that behaviour in another organism, and feeding by social facilitation is common in birds species and other vertebrates (Giraldeau & Beauchamp 1999; Galef & Giraldeau 2001). In the dynamic and vast marine environment, social facilitation may be essential for locating food; information transfer via observation of other foraging individuals is important in schooling fish (Ryer & Olla 1992). Social facilitation may be critical in enabling seabirds to find prey, and if so they require visual contact with foraging flocks. Visibility may be obscured by fog, which occurs where cool water is vaporized by contact with relatively warm air, and thus is common in temperate and polar areas during the summer breeding season. Fog would reduce a bird's ability to locate forage flocks from a distance. If seabirds indeed rely on visual contact with forage flocks to find schooling fish and other prey, we would expect to see fog affecting the feeding of seabird chicks.

Despite the prevalence of fog in many areas during the breeding season of many seabird species and a large body of scientific literature on chick feeding by seabirds, the effect of fog has been rarely addressed in seabird feeding studies. To the best of my knowledge, only two studies examined fog in relation to foraging, both of which were conducted on seabirds in the Bay of Fundy and over one or two summers. One study was during a study of Herring Gulls (*Larus argentatus*) on Kent Island, New Brunswick, that coincided with a severe two-week fog event. Researchers noted high chick mortality and less herring and more euphausiid shrimp delivered on foggy days (Hebert 1987). The other study was by a previous graduate student at University of New Brunswick, Amey (1998), who found fog hindered the feeding rates of Arctic Terns (*Sterna paradisaea*) in one year of a two- year study on Machias Seal Island, New Brunswick.

Thesis Objectives

The primary objective of this thesis is to test hypotheses regarding the relationships that seabirds have with their prey within the ecological context of a community of predators exploiting a limited range of prey. More specifically, I will investigate trends in trophic overlap throughout ten years of seabird feeding data by examining relationships between years and within seasons, and relationships of the dietary characteristics and the breeding successes of the birds. I also investigate the relationship between fog condition and prey deliveries to seabird chicks in terms of feeding rates and prey types.

Study Site

All data for this study were collected on Machias Seal Island, New Brunswick (MSI), a 9.5 hectare island located at the mouth of the Bay of Fundy (44°05'N, 67°01'W).

The island is 19 kilometres southwest of Grand Manan and 15 km east of the Maine coast near Cutler, in productive waters where the cold Bay of Fundy merges with the warmer Gulf of Maine. The island is a granite outcropping, with bedrock and boulder shorelines giving way to a small vegetated interior dominated by herbaceous plants. Approximately 2,800 pairs of Atlantic Puffins (*Fratercula arctica*), 600 pairs of Razorbills (*Alca torda*), and 3,000 pairs of terns (roughly 2,000 Arctic Terns (*Sterna paradisaea*) and 1,000 Common Terns, (*S. hirundo*)) breed from May until August on the island (Diamond & Devlin 2003). These four seabird species, which have been the focus of a long-term study initiated in 1995, differ in their prey-capture tactics. The two tern species are considered surface-feeders: they search for prey on the wing and dip into the water, plucking prey items out of the first few centimetres of the water column. The terns feed a variety of prey items to chicks, but feed mostly schooling fish and euphausiid shrimp (Black et al. 2005). The puffins and razorbills are pursuit-divers when foraging. Pursuit divers swim in the water column, actively chasing their prey under water.

Thesis Overview

Chapters one and four are a general introduction and discussion, respectively, and are not independent from this thesis. Chapters two and three are data-based chapters and stand alone outside this thesis.

Chapter 2 of my thesis examines the amount of overlap between all four of the focal species over ten years and within the breeding seasons. Although previous studies have investigated the amount of niche overlap between organisms, most are short-term (e.g., Lack 1945; Bell & Ford 1990; Baltz & Morejohn 1994; Gonzales-Solis et al. 1997; Kitchen et al. 1999; Day et al. 2003). I will investigate amount of overlap over ten years

as declining amounts of the “preferred” herring prey (Amey 1998) were delivered to seabird chicks (Black et al. 2005). I also investigate changes in overlap throughout the season to test whether as the season progresses birds feed larger, lipid-rich fish to chicks as energy demands increase.

In Chapter 3, I investigate the relationship between fog condition and chick feeding rates and prey types delivered to seabird chicks. I hypothesize that if birds are visual predators as we believe, fog should inhibit their ability to forage and therefore feed seabird chicks. This is the first study I know of that uses long-term data to investigate whether fog reduces the feeding rates of any predatory bird. I examine the relationship between fog and feeding rates, as well as compare fog condition with species richness and types of prey delivered to chicks.

Chapter 4 is a thorough discussion of key results. I synthesize Chapters 2 and 3 as well as make recommendations for future research.

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Table 2.01 Total number of prey items observed delivered to seabird chicks from 1995-2004.

Year	ARTE	COTE	ATPU	RAZO
1995	167	265	596	165
1996	273	305	739	158
1997	268	156	644	286
1998	221	182	995	372
1999	295	424	1700	1172
2000	272	183	1851	660
2001	725	788	2607	837
2002	979	467	1580	317
2003	535	390	1331	471
2004	829	176	1777	1511
Total	4564	3336	13820	5949

Table 2.02 Linear regression of the proportion of herring fed to seabird chicks against year, from 1995-2004. Significant relationships in bold.

Species	Slope	R ²	p
ARTE	-9.23	0.90	<0.001
COTE	-8.31	0.72	0.002
ATPU	-6.21	0.50	0.023
RAZO	-5.59	0.47	0.028

CHAPTER 2

Temporal perspectives on dietary diversity and overlap: four seabird species on Machias Seal Island

Abstract

A fundamental principle in niche theory is that no two organisms can occupy the same niche and use the same resources when resources are limited. The boundaries between ecological niches of different species of seabirds can be difficult to define during the breeding season of many seabirds, as they tend to breed in the same colonies and rely on similar prey resources within foraging range of the colony. We examined feeding data from 1995-2004 from four species of sympatric breeding seabirds to test predictions concerning the dietary niches and the dietary overlap between the species during the breeding season. We looked for trends between years and within years in order to test for a relationship between dietary shifts and reproductive performance. We did not see any consistent trends in dietary niche or overlap over the ten years spanned in this study or within each breeding season. We did not find any relationships between dietary overlap and dietary diversity nor dietary diversity and breeding success. However, for both tern species the amount of dietary overlap and reproductive success were directly related, suggesting that in times of abundance terns feed the same prey and have high reproductive success.

Introduction

In the beginnings of niche theory our concept of niche relations were simple, as Gause's principle states that no two organisms can coexist in the same niche and make use of identical resources (e.g., Gause 1934; Lack 1947). As subsequent research has

revealed, the interactions species have with each other are complicated, and the role of competitive exclusion in structuring communities has been debated. Species may coexist on the same resources if relying on multiple resources (MacArthur & Levins 1964) or when other factors such as predation limit populations (Paine 1966; Levin 1970; Holt 1984). Wiens (1977) hypothesized that competitive exclusion only occurs in rare times of resource shortage, a concept which has seen some support on long-term studies (Schoener 1983; Grant & Grant 2006). Variability of resources themselves can allow multiple species to rely on the same resource (Levins 1979; Naeem 1988).

Some ecologists have doubted the role of competition in ecological communities, and have criticized the studies which have supported competitive exclusion (Connell 1975; Connor & Simberloff 1979; Strong et al. 1979; Holt 1984). However, despite the debate, the bulk of studies investigating interspecific competition have found evidence of competition (e.g. Schoener 1983; Schuler 2000; Grant & Grant 2006) and it is widely accepted among ecologists that competition plays a large role in defining the ecological niche of an organism.

Competition is difficult to quantify, but a common way to infer competitive effects is by measuring the amount of overlap between organisms (MacArthur & Levins 1967; May 1975; Gonzales-Solis et al. 1997; Day et al. 2003). Despite the prevalence of overlap as an indicator of competition in literature, the appropriateness of using overlap as a measure of competition has been questioned (Colwell & Futuyma 1971; Lawlor 1980; Abrams 1983). A central criticism of using overlap as an indicator of competition is that high competition can at times be associated with low overlap (Svardson 1949; Gonzales-Solis et al. 1997; Wiens 1989b), and also with high overlap (Steenhof & Kochert 1985;

Bell & Ford 1990; Wiens 1989b). How overlap varies with competition depends on the severity of competition, as Bell and Ford (1990) found on a long term study of Australian birds. Over four years, dietary overlap between birds decreased initially through drought-induced food shortages, but as the drought continued and food became extremely scarce, overlap between birds increased as they fought for the few remaining food items. Thus, examining overlap over years and in different food conditions may better reveal interspecific competition between organisms (Korpimaki 1987).

Seabirds are long-lived species, top consumers in the marine ecosystem, that are typically abundant and accessible on the colonies where they breed, making them useful for investigating theoretical questions. Boundaries between the ecological niches of coexisting seabirds can become nebulous and difficult to tease apart during the breeding season (Diamond 1983). Seabirds require similar breeding sites and typically a seasonal abundance of marine productivity can result in many predators consuming the same prey species (Cushing 1975; Diamond 1983). Over 96% of all seabird species nest in colonies, and in many cases they are limited to nesting on islands free of mammalian predators (Coulson 2002). Seabirds are restricted in foraging range during the breeding seasons, and as they are central-place foragers they must return to the colony to feed chicks (Orians & Pearson 1979). They therefore must compete with other seabirds in the colony to find sufficient prey for themselves as well as their offspring within a limited area surrounding the colony, which may be depleted of prey by other foraging seabirds (Ashmole 1963; Diamond 1978; Birt et al. 1987). These natural history characteristics result in high overlap and the potential for high competition between seabirds, making them interesting subjects with which to explore niche theory and competition.

Examining the annual composition and size of seabird prey over several years can help us address our questions about changes in feeding niche among and within seasons where we observe changes in the prey types delivered to young. When a food resource is highly abundant and food is not a limiting factor, a variety of species can feed on the same prey, resulting in several species having a narrow niche breadth and high dietary overlap (Bell & Ford 1990; Gonzales-Solis et al. 1997). As food resources diminish competition for limited resources increases and organisms are forced to feed on a greater variety of prey, increasing the niche breadth/diet diversity of each species while reducing overlap (Lack 1947; MacArthur & Pianka 1966; Wiens 1989a; Rodel et al. 2004). However, as mentioned prior, in periods of extended and extreme food shortage dietary overlap between species can increase, particularly if many types of available prey diminish and organisms consume the remaining common resources (Bell & Ford 1990; Wiens 1989b). Thus, in years when less preferred prey is available we expect to see more diverse diets with less niche overlap. As food stress should decrease productivity, we predict an indirect relationship between diet diversity and niche overlap with reproductive success of the breeding birds.

Investigating at a finer scale within each season, we expect niche overlap to change throughout the breeding season as the offspring grow and have greater energy requirements. As offspring demands increase we expect that adults would select larger, more lipid-rich prey to deliver to their young, resulting in different species feeding the same prey types to their offspring and a greater niche overlap. This trend should be particularly strong for organisms that are limited in the amount of prey they deliver to

their young by the amount they carry in the bill (e.g., puffins, razorbills, most terns) rather than regurgitating food (e.g., petrels, gulls).

The four species of seabird we study include two different foraging guilds which should respond differently to changes in the marine environment. The two species of surface-feeding terns, Arctic Terns (*Sterna paradisaea*, ARTE) and Common Terns (*Sterna hirundo*, COTE), can access only the top few centimetres of the water column and therefore depend largely on prey at the surface. The two species of pursuit-divers, Razorbills (*Alca torda*, RAZO) and Atlantic Puffin (*Fratercula arctica*, ATPU), can dive up to 100 metres (Piatt & Nettleship 1985) and 70 metres (Lowther et al. 2002) respectively, and thus have greater access to prey. This increased access to prey generally translates to more schooling fish, such as herring, in the chick diets of alcids than terns (Amey 1998).

We use ten years of data to address our questions regarding prey variation over years and within seasons. Specifically, do we see any changes in the prey types delivered to seabird chicks of Machias Seal Island from 1995 to 2004? If so, as the prey changes do the seabirds respond by feeding the same types of prey to their chicks as each other or do the birds diverge in prey types delivered? Within seasons do we see trends with seabirds delivering more lipid-rich prey such as herring as the dietary requirements of the chicks change?

The long-term study on Machias Seal Island has shown a steady decrease in proportion of herring delivered to seabird chicks over the years (Black et al. 2005). We predict that we will see a decrease in dietary overlap over years as the birds tend to feed

less and less of the preferred prey, herring. We expect to see an increase in diet diversity as preferred prey decreases and dietary overlap decreases.

As the breeding season progresses we expect to chick diets to show increased dietary overlap as they feed a greater proportion of large fatty fish (herring and sandlance). As herring is (or was) the most frequently delivered prey, the increase in fatty fish should be evident through increased herring delivered to seabird chicks later in the season.

Methods

Study Site

The data were all collected on Machias Seal Island (MSI), New Brunswick. For details on the study site refer to Chapter 1.

Feeding Data

All feeding data were collected by observation from semi-permanent blinds that overlooked defined plot areas that are consistent from year to year. When terns were observed, 3-8 nests were watched and all feedings were connected to specific flagged nests. It was impossible to identify individual burrow locations for all feeding alcids, therefore all feedings per plot area were recorded. Researchers observed the plots in three- hour stints, and observation stints were staggered throughout times of the day and over tidal cycles. During these stints observers recorded prey type (identified to the lowest possible taxon), prey size in relation to the bird's culmen, number of prey in each delivery, and provider if identifiable (i.e. which of the two parents), and recipient chick for the terns. Methods for collecting these data have been standard since project

initiation in 1995, and each observer was trained by veteran researchers from previous years to maintain consistency.

Reproductive Data

Approximately 100 puffin burrows and 100 Razorbill nests found throughout the colony were monitored for productivity. The nests were visited several times a season to monitor egg laying, hatching, chick growth (mass, wing, culmen), and chick survival. Razorbill chicks were measured at least three times during their brief (approximately 16 days) time on the island, while puffins were visited at least four times during the 40 days chicks stay in burrows. Approximately 50 Common Tern and 100 Arctic Tern nests were monitored for reproductive parameters. The nests were checked for the same factors as the alcids; they were visited every other day when conditions allowed and chicks measured every five days. In analysis, fledging rate of chicks was used as an indication of reproductive success as it has been shown to be most likely to be correlated with changes in food supply of all breeding parameters (e.g., Cairns 1987; 1992; Gill et al. 2002). We used fledglings per nest as fledgling rates, as well as fledglings per egg for the terns, which often lay more than one egg per season.

Data Analysis

Herring was typically the most common prey item delivered to seabird chicks over the past ten years, but it became less common over the period. To quantify this potential decrease we conducted linear regressions on the proportion of herring fed to all seabird chicks (dependent variable) against year (independent variable).

Morisita's Index was used to measure the amount of dietary overlap between the species (Morisita 1959). We chose this measure because it compares two species without

inflating the value when using a large number of categories (Colwell & Futuyma 1971; Smith & Zaret 1982). Morisita's measure gives a value between zero (no overlap between the two species compared) and one (identical resources used by the two species).

Inter-annual Variation

We calculated Morisita's Index for comparisons between each species for each year, and also calculated the amount of overlap between each two species for every day that the two species were observed feeding. The day-to-day breakdown is needed for within-season comparisons and also to estimate standard error for yearly comparisons. Morisita's Index is the most appropriate measure of overlap for this study, but does not give a standard error. Thus, we calculated overlap measures for each day, allowing us to estimate the inherent variation in overlap. Our calculated standard errors are useful, but are not complete in that not all species are watched each day, and on some days not enough feedings were observed to allow us to calculate Morisita's Index. Thus, for yearly comparisons we focused on the compiled yearly measures and used the values given from each day as an estimate of the variance in diet overlap for each species.

In addition to the six comparisons between each of the four species, we also compared the diet of each species to each of the other three species of seabird. We refer to this as "community overlap". This comparison is useful for identifying how each species differs from the group and to compare the amount of overlap with reproductive success of a species.

We calculated diet diversity using Simpson's Diversity Index to represent niche breadth, as it shows little bias and low coefficient of variation (Mouillot & Lepretre

1999). For each species we then conducted linear regressions for several comparisons to investigate trends with diet and breeding success. We compared diet diversity with the community overlap value, and niche overlap and niche breadth with fledglings per nest.

Intra-annual Variation

To examine how overlap between species changes within seasons we plotted day-to-day overlap against the Julian date. We used linear regression to investigate for trends during the season, and examined the residual plots for curving trends to investigate if other (e.g. quadratic) relationships existed. We also plotted percentage herring delivered to seabird chicks by Julian date and looked for trends using linear regression for each species and for each year. We conducted a Bonferroni correction for each species among yearly analyses. To investigate what temporal scale is appropriate to assess competition, we conducted a linear regression comparing yearly niche overlap values with average daily niche overlap values.

Results

28,869 prey items delivered to seabird chicks were observed over the ten years (Table 2.01). At least half of all prey items delivered were juvenile fish except for 2002-2004 in both tern species and 2002 and 2004 in puffins. 2004 was an unusual year among all ten seasons as fish larvae were often fed to all four species of seabird. These small (typically <6cm) transparent prey were difficult to distinguish from euphausiids during quick prey transfers, resulting in many unidentified prey items.

From 1995 until 2000 herring comprised at least 40% of all the prey delivered to seabird chicks by all four species, except in 1998 when Atlantic Puffins fed mostly hake (Fig. 2.01, Fig. 2.02). In general, over the past 10 years there was a trend of the seabird species feeding less herring to their young. All four species showed a significant decline (Table 2.02) with the weakest relationship in Razorbills ($r^2 = 0.47$).

Inter-annual Variation

The dietary niche overlap between all species declined from 1995 to 1998 in four out of the six interspecific comparisons: ARTE-COTE (Fig. 2.06), RAZO-ATPU (Fig. 2.07), ATPU-ARTE (Fig. 2.08), and ATPU-COTE (Fig. 2.09; Table 2.03). Contrastingly, these four interspecific comparisons show no significant trend when all ten years of data were included (Table 2.04).

The overlap between Razorbills and Common Terns, and Razorbills and Arctic Terns, did not show a decrease in the first four years of the study (Fig. 2.04, Fig. 2.05; Table 2.03). However in both cases there was a general decline over all ten years (Table 2.04).

All ten comparisons of yearly niche overlap showed the same pattern with high overlap in 1995, 1999, 2000, and 2001 (Figs. 2.03 (A-D)- 2.09). The mean overlap values between two species for these years were 0.91, 0.87, 0.84, and 0.93 respectively; the average overlap value overall was 0.75. Examining the community niche overlap values 1995, 1999, 2000, and 2001 had average overlap values of 0.94, 0.91, 0.87, and 0.96, respectively, while the average amount of overlap over all years was 0.79.

We saw no linear trend between the level of diet diversity and community niche overlap for any of the four species (Fig. 2.10, Table 2.05). Diet diversity showed no linear relation to reproductive success when considering fledglings per nest or per egg laid (Fig. 2.11; Tables 2.06, 2.07). Both measures of productivity (fledglings per nest and fledglings per egg) were related to dietary overlap in terns ($p=0.03$) but not in alcids (Fig. 2.12; Tables 2.08, 2.09).

Intra-annual Variation

There was no significant trend in niche overlap throughout the season in any of the interspecific comparisons (Table 2.10). We did not see an overall decline in the proportion of herring delivered to chicks throughout the season for any of the seabird species (Table 2.11). For each species there were a few years with a significant declining proportion of herring delivered to chicks as the season progressed, but there is no pattern among years.

Four out of six of the regressions comparing yearly and average daily overlap had large R^2 values: RAZO-ARTE (0.80), ATPU-COTE (0.61), RAZO-COTE (0.87), and RAZO-ATPU (0.70). The comparisons of yearly and daily Arctic Terns and puffin overlap and Arctic and Common Tern overlap had small R^2 values, 0.18 and 0.00 respectively.

Discussion

This shift away from feeding chicks herring is of interest from a variety of perspectives. The Bay of Fundy supports an Atlantic Herring fishery that has landed an average of 113,000 tonnes of herring a year since 1990, making it a commercially

valuable species (Department of Fisheries and Oceans 2005). Previous research conducted during this long-term study has shown the amount of herring delivered to Arctic Tern chicks on MSI to predict the size of herring weir catches on nearby Grand Manan Island two years later (Amey 1998; Amey et al. 2003).

The prey switch is also biologically interesting. The data collected from the early years of the long term study (1995-1999) show a great deal of overlap in the type of prey the four seabirds feed their young as all species fed primarily herring (Black et al. 2005), which is believed to be the preferred prey item on MSI (Amey 1998). The switch gives us the opportunity to examine how the birds respond to changes in prey availability. Our assumption that availability of herring declines after the year 2000 is based on its dominance of the diet of all four species before then, and the fact that it was not replaced by any other predominant taxon afterwards.

Inter-annual Variation

We did not see the predicted decreasing trend of niche overlap throughout the ten years as the amount of herring delivered decreased. For the first four years of the study we saw a decrease in overlap when a decrease in herring was observed for four comparisons - but not when comparing the two tern species with the Razorbills. These are the only two comparisons that showed a significant decline in overlap over the ten years, although the significance can be explained by the low amount of overlap in the final three years of study relative to the higher overlap values at the beginning of study. The first seven years are high but not decreasing, and the final three years are low but relatively constant; when all years are combined there is a declining trend. It is puzzling

that the four interspecific comparisons that show a decrease in overlap from 1995-1998 do not show a decrease in overlap from 1995-2004. After 2001 the amount of overlap between the four species examined is too variable to show a trend over all ten years.

The consistent pattern in all comparisons of high overlap in 1995, 1999, 2000, and 2001 is explained by the same overall prey delivered with minor variations in proportions. In 1995 all birds fed mostly herring with small proportion of hake. The summers of 1999 and 2000 all birds fed mostly herring with some hake, euphausiids, and sandlance, while in 2001 all birds fed mostly sandlance with some herring, hake, and euphausiids. Although the changes in overlap between the species can be explained upon closer examination, there are no overall trends in dietary niche overlap over the ten years.

The data do not support our prediction that the amount of dietary overlap and the diet diversity are related. We expected that as the overlap decreased due to pressures of food limitation, birds would be forced to respond to changes in prey availability by feeding on what was available and that differences in foraging strategies among the birds would become more apparent through a greater diversity in prey. However, decreasing availability of preferred prey may also lead to a greater niche breadth and more intense competition for fewer prey items, resulting in the birds feeding on the same prey and a greater overlap. In sympatric hawks (*Buteo* spp.) a food shortage resulted in greater overlap between species (Steenhof & Kochert 1985) and in extended studies of food shortage overlap increased in times of extreme stress (Bell & Ford 1990). Our data did not correspond with these studies nor with our prediction based on theoretical frameworks, suggesting the relationship between diversity and overlap is more complicated than expected and a different theory is needed to explain the relationship.

We found no trend in relationship between diet diversity and reproductive success, but for both of the surface-feeding tern species we did see an increase in reproductive success as diet overlap increased. We did not observe the same trend in the two species of alcids, a trend that reflects the different life-history characteristics of the two guilds. Both Razorbills and Atlantic Puffins lay only one egg per breeding season (Lowther et al. 2002; Hipfner & Chapdelaine 2003), and showed consistent reproductive success per egg laid over all ten years of study. Common Terns typically lay 2-3 eggs and Arctic Terns 1-2 on MSI (Black et al. 2005), and the number of chicks fledged per nest is variable, with both species failing in 2004. With a more variable and reactive reproductive success, the terns show a response to changes in prey before the alcids. The fact that the terns had a lower reproductive success in years of low overlap suggests that the birds have high overlap in times of prey abundance, and the ample food supply results in greater reproductive success.

Intra-annual Variation

The amount of overlap between seabirds throughout the season is extremely variable and shows no consistent trend (Table 2.10). Although it seems logical that as chicks increase in size and dietary demands increase the adults would select larger, more fatty fish to feed their chicks, we found no evidence of this from our data nor from previous literature. Our data do not support the prediction that the birds would feed proportionally more herring as the season progressed and dietary demands increased. With the exception of a few years, there was no relationship between Julian date and percent herring delivered to chicks. When the data were analyzed separately by years

there was an increase in herring delivered as the seasons progressed for a few years for each seabird species, but we did not see any consistent trends. We saw no pattern in proportion of herring delivered after averaging all years. Therefore, it appears the birds usually do not select large, more fatty fish such as herring as the season progresses.

Our comparisons of yearly overlap values with average daily values showed that in most cases the daily overlap is very similar to our yearly values. Although this is an intuitive relationship, it is not necessarily always true. If the birds were competing on a daily temporal scale, the birds could feed on the same prey on different days, resulting in high yearly overlap but no daily overlap. Interestingly, the two congeners have no apparent relationship between daily and yearly overlap, suggesting that the two terns tend to not feed on the same prey on the same day but feed on the same prey over the entire summer. It would be interesting to pursue this in a more thorough investigation into the effect of temporal scale on dietary overlap in related seabirds.

Conclusions

The amount of herring delivered to seabird chicks has decreased throughout the ten years of this long-term study. This study did not detect trends in changing dietary niche overlap over years and throughout this transition away from herring, so our data do not fit theoretical models which predict changes in overlap when the availability of preferred prey changes. Our data did not show a relationship between diet diversity and dietary niche overlap nor did they show trends when comparing diet diversity and productivity over years, but showed changes in reproductive success as amount of overlap varied between the two tern species. There appears to be no trend in the amount

of niche overlap throughout the season and rarely a trend showing increase in herring delivered throughout the season, also suggesting daily variations in availability may obscure potential trends. While the decline in the common, favoured resource (herring) might be expected to lead to decreased diet overlap between seabird species, we did not find such a relationship suggesting complex relationships between overlap and preferred prey in seabirds.

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Table 2.03 Linear regressions of Morisita's overlap and year between each pair of species from 1995-1998. Significant relationships and relationships with high R^2 values in bold.

Comparisons	Slope	R^2	p
ATPU-RAZO	-0.19	0.83	0.089
RAZO- ARTE	0.01	0.05	0.78
ARTE-COTE	-0.03	0.82	0.095
ATPU-ARTE	-0.14	0.85	0.078
COTE-RAZO	0.00	0.00	1.00
ATPU-COTE	-0.10	0.91	0.048

Table 2.04 Linear regressions of Morisita's overlap and year between each pair of species from 1995-2004. Significant relationships in bold.

Comparisons	Slope	R^2	p
ATPU-RAZO	-0.004	0.003	0.88
RAZO- ARTE	-0.08	0.54	0.016
ARTE-COTE	-0.01	0.21	0.18
ATPU-ARTE	-0.01	0.04	0.59
COTE-RAZO	-0.07	0.54	0.016
ATPU-COTE	0.001	0.001	0.94

Table 2.05 Linear regressions between diet diversity using Simpson's Diversity Index and community niche overlap using Morisita's Index from 1995-2004.

Species	Slope	R ²	p
ARTE	-0.11	0.02	0.67
COTE	-0.78	0.19	0.21
ATPU	0.33	0.12	0.32
RAZO	-0.30	0.27	0.12

Table 2.06 Linear regressions of productivity (fledglings per nest) against diet diversity using Simpson's Diversity Index from 1995-2004.

Species	Slope	R ²	p
ARTE	-0.236	0.032	0.620
COTE	-0.397	0.052	0.526
ATPU	0.30	0.029	0.64
RAZO	0.09	0.004	0.87

Table 2.07 Linear regressions of productivity (fledglings per egg) against diet diversity using Simpson's Diversity Index from 1995-2004.

Species	Slope	R ²	p
ARTE	-0.359	0.081	0.426
COTE	-0.394	0.092	0.395

Table 2.08 Linear regressions of productivity (fledglings per nest) against community niche overlap using Morisita's Index from 1995-2004. Significant relationships in bold.

Species	Slope	R ²	p
ARTE	0.65	0.47	0.03
COTE	2.17	0.47	0.03
ATPU	-0.004	0.00	0.99
RAZO	0.06	0.026	0.66

Table 2.09 Linear regressions of productivity (fledglings per egg) against community niche overlap using Morisita's Index from 1995-2004. Puffins and Razorbills lay one egg, so fledglings per egg is fledglings per nest. Significant relationships in bold.

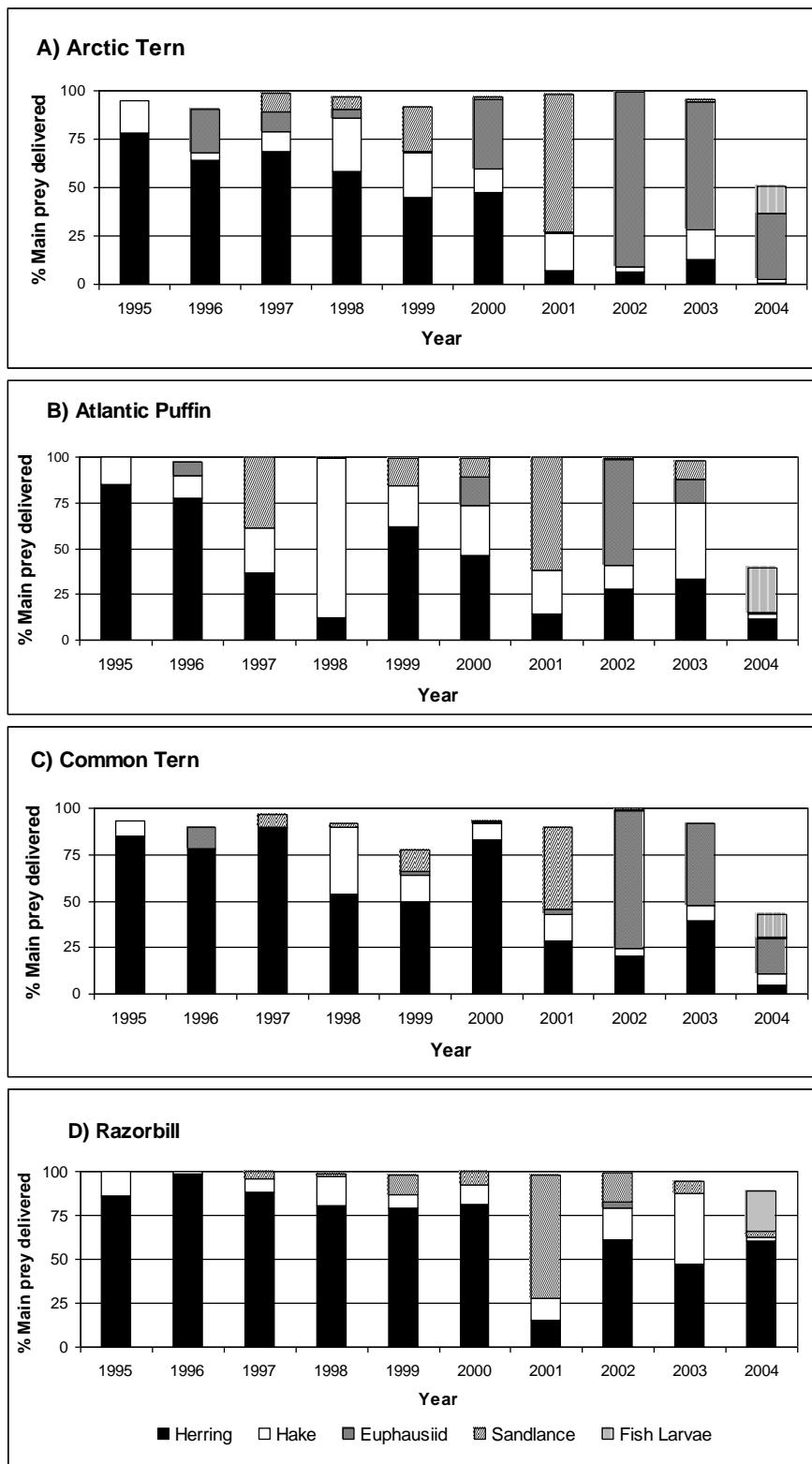
Species	Slope	R ²	p
ARTE	0.371	0.424	0.042
COTE	1.035	0.553	0.014

Table 2.10 Results for linear regressions comparing the amount of dietary overlap using Morisita's Index between each species to species pair by Julian Date

Comparisons	Slope	R ²	p
AATPU-RAZO	-0.003	0.003	0.649
RAZO- ARTE	-0.007	0.010	0.435
ARTE-COTE	-0.005	0.017	0.244
AATPU-ARTE	-0.006	0.035	0.060
COTE-RAZO	-0.006	0.010	0.473
AATPU-COTE	-0.002	0.002	0.652

Table 2.11 Results of linear regressions of the proportion of herring delivered to seabird chicks against Julian date. Significant relationships as determined after Bonferroni corrections are in bold. Relationships noted with asterisks are discussed in text, they have a R^2 of at least 0.5, indicating at least half of the variability observed is explained by Julian date.

Species	Year	Slope	R^2	p
ARTE	1995	-0.001 (0.006)	0.003	0.819
ARTE	1996	0.008 (0.009)	0.037	0.354
***ARTE	1997	0.036 (0.007)	0.687	< 0.001
ARTE	1998	0.023 (0.009)	0.346	0.027
ARTE	1999	0.009 (0.008)	0.07	0.287
ARTE	2000	0.006 (0.008)	0.032	0.411
ARTE	2001	0.011 (0.004)	0.32	0.008
ARTE	2002	0.006 (0.005)	0.063	0.26
ARTE	2003	0.003 (0.002)	0.124	0.181
ARTE	2004	0.004 (0.002)	0.163	0.041
ATPU	1995	0.011 (0.003)	0.322	0.006
ATPU	1996	0.007 (0.007)	0.049	0.36
***ATPU	1997	0.029 (0.005)	0.801	< 0.001
ATPU	1998	-0.004 (0.011)	0.015	0.72
ATPU	1999	0.002 (0.007)	0.01	0.735
ATPU	2000	0.02 (0.005)	0.348	0.002
ATPU	2001	0.009 (0.003)	0.273	0.013
ATPU	2002	0.016 (0.005)	0.362	0.002
***ATPU	2003	0.019 (0.004)	0.579	< 0.001
ATPU	2004	0.004 (0.003)	0.089	0.156
COTE	1995	-0.011 (0.008)	0.104	0.178
COTE	1996	-0.011 (0.007)	0.096	0.115
COTE	1997	0.006 (0.008)	0.045	0.485
COTE	1998	-0.018 (0.011)	0.256	0.135
COTE	1999	0.009 (0.008)	0.089	0.262
COTE	2000	0.012 (0.005)	0.171	0.045
***COTE	2001	0.025 (0.006)	0.6	0.001
COTE	2002	0.021 (0.007)	0.326	0.011
COTE	2003	0.018 (0.009)	0.231	0.06
***COTE	2004	0.008 (0.002)	0.515	0.004
RAZO	1995	0.001 (0.015)	0.001	0.926
***RAZO	1996	0.049 (0.015)	0.553	0.009
RAZO	1997	0.001 (0.003)	0.014	0.714
RAZO	1998	0.003 (0.014)	0.006	0.838
RAZO	1999	0.014 (0.006)	0.306	0.032
RAZO	2000	0.03 (0.01)	0.453	0.012
RAZO	2001	0.014 (0.007)	0.292	0.07
***RAZO	2002	0.047 (0.01)	0.589	0.001
***RAZO	2003	0.044 (0.01)	0.615	0.001
RAZO	2004	-0.003 (0.007)	0.008	0.714
ARTE	Mean	0.006 (0.002)	0.043	0.003
ATPU	Mean	0.011 (0.002)	0.133	< 0.001
COTE	Mean	0.008 (0.003)	0.044	0.006
RAZO	Mean	0.017 (0.003)	0.168	< 0.001



Figures 2.01A-D. The percentages of main prey types delivered to seabird chicks on MSI over all years. Totals less than 100% are due to unidentified prey and rarely delivered prey (i.e. polychaetes, insects, butterfish)

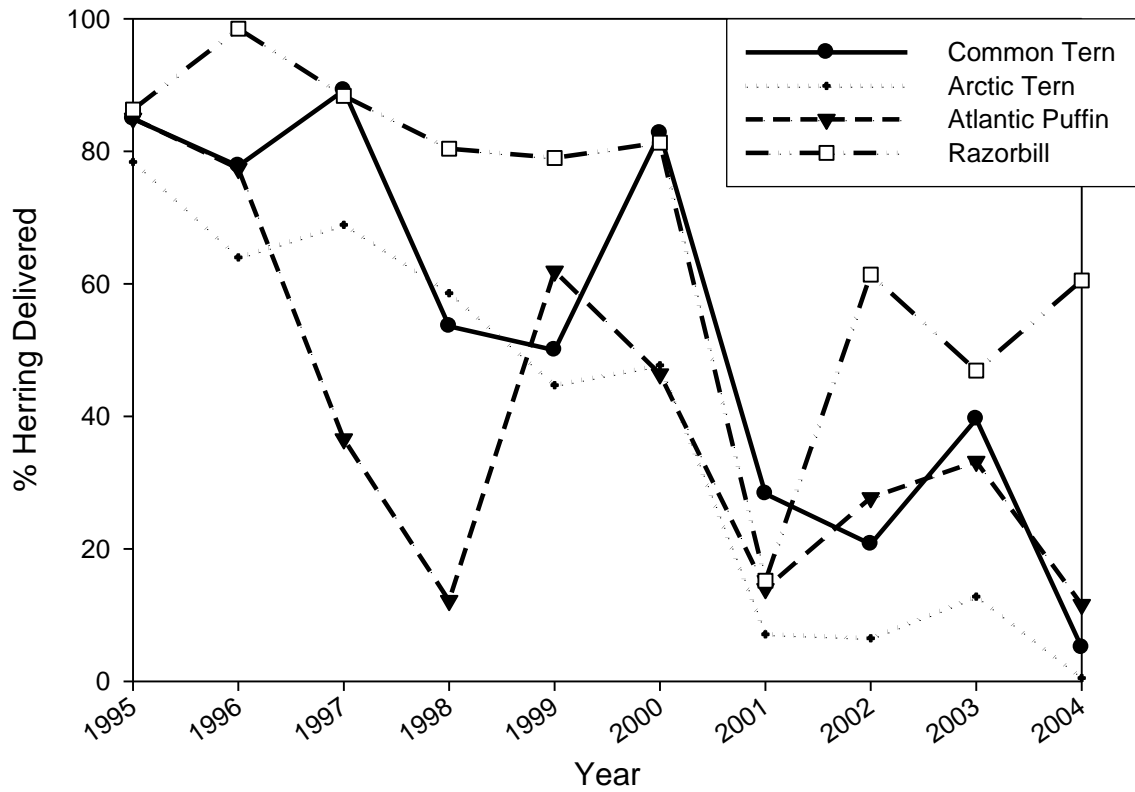
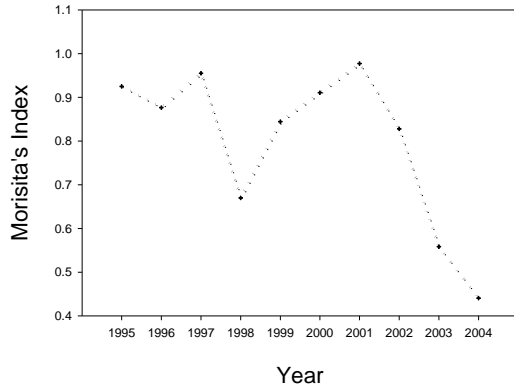
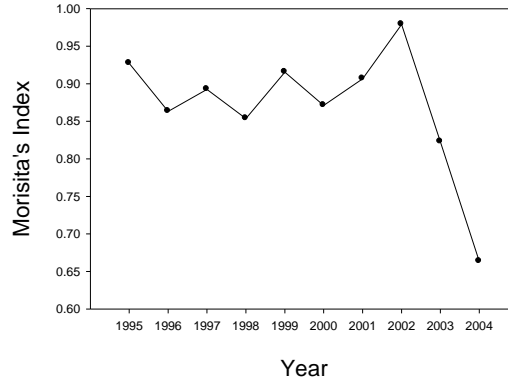


Figure 2.02. The percent herring (by number) delivered to Common and Arctic Tern, Atlantic Puffin, and Razorbill chicks on MSI from 1995-2004.

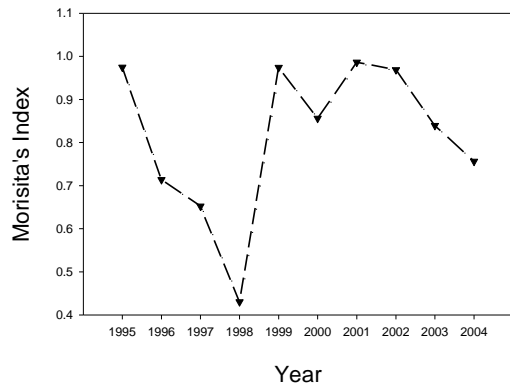
A) ARTE



B) COTE



C) ATPU



D) RAZO

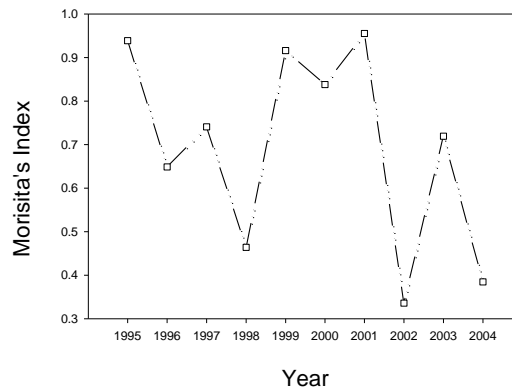


Figure 2.03 (A-D) Dietary overlap for each seabird species compared with the other three seabird species on Machias Seal Island during the breeding season from 1995 to 2004.

ARTE-RAZO Overlap

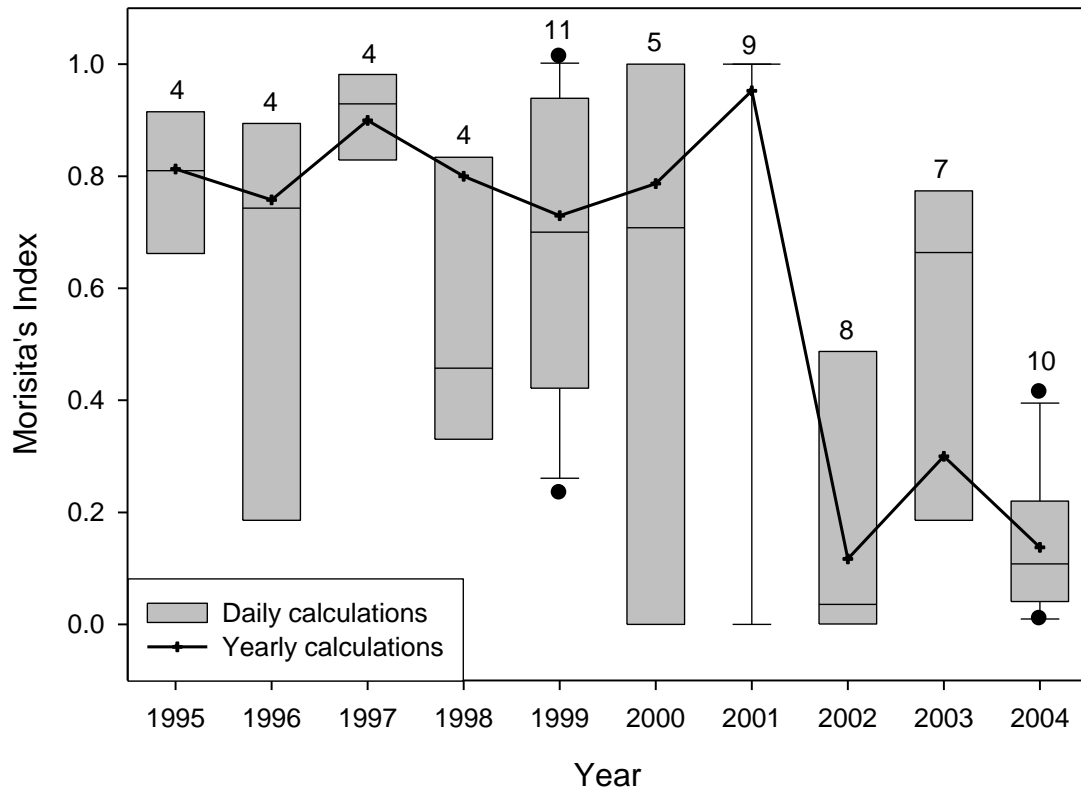


Figure 2.04 Dietary overlap between Arctic Terns and Razorbills from 1995-2004 on MSI. Continuous line shows data pooled over years, box plot represents the daily overlap values. Sample sizes for daily calculations above each box.

RAZO-COTE Overlap

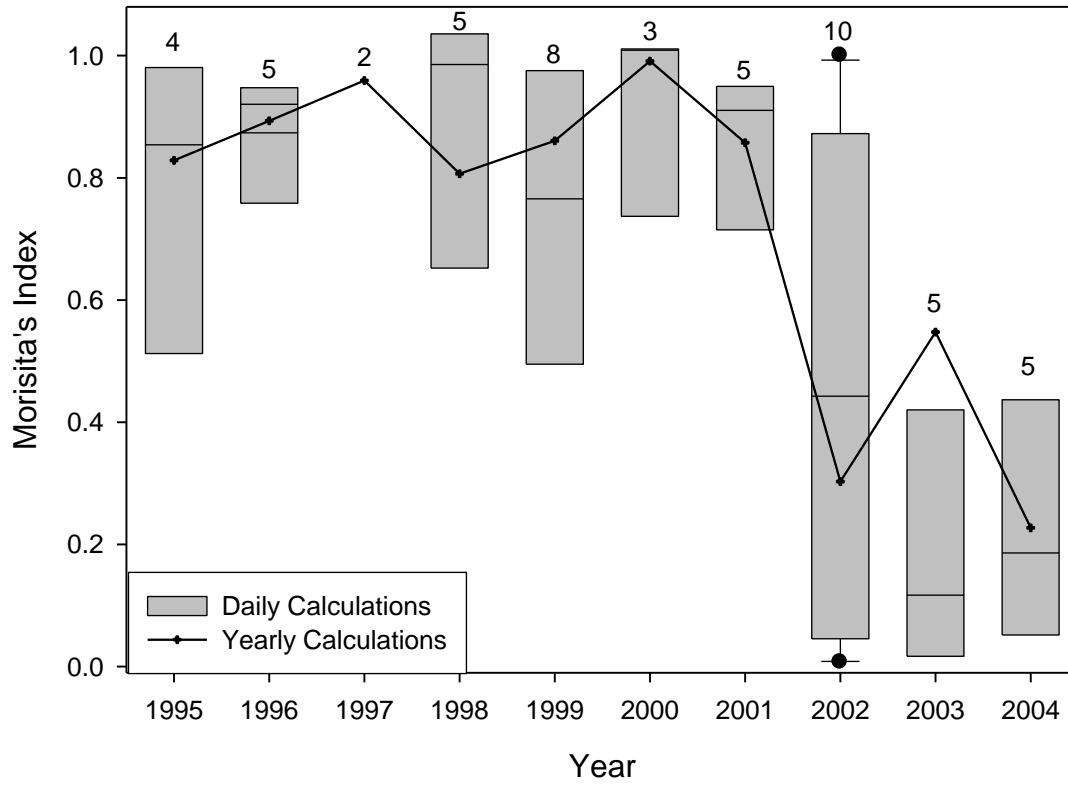


Figure 2.05. Dietary overlap between Razorbills and Common Terns from 1995-2004. Continuous line shows data pooled over years, box plot represents daily overlap values. Sample sizes for daily calculations above each box.

COTE-ARTE Overlap

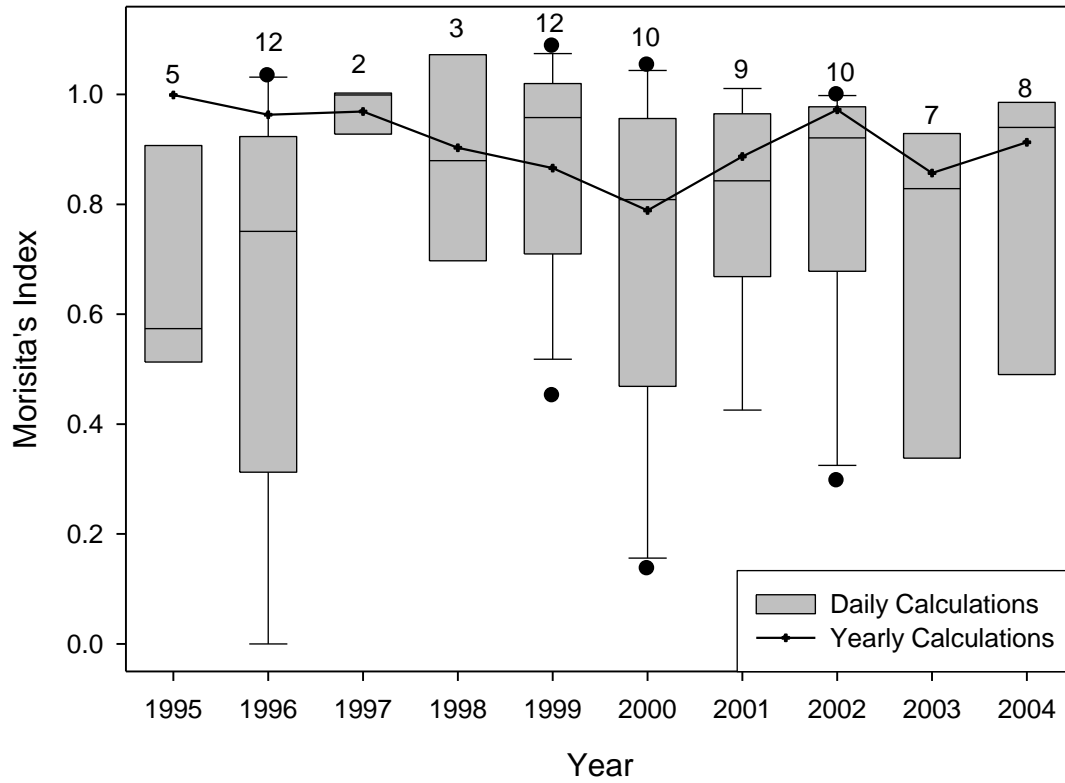


Figure 2.06 Dietary overlap between Common Terns and Arctic Terns from 1995-2004 on MSI. Continuous line shows data pooled over years, box plot represents daily overlap values. Sample sizes for daily calculations above each box.

RAZO-ATPU Overlap

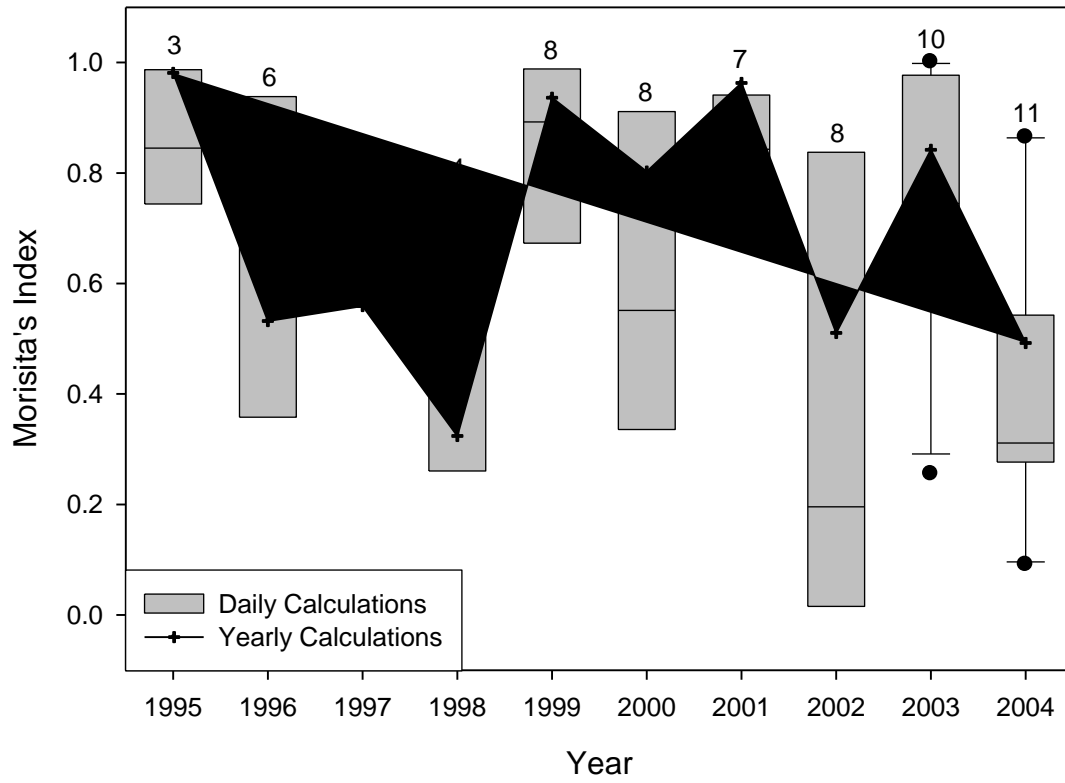


Figure 2.07 Dietary overlap between Razorbills and Atlantic Puffins from 1995-2004 on MSI. Continuous line shows data pooled over years, box plot represents daily overlap values. Sample sizes for daily calculations above each box.

ATPU-ARTE Overlap

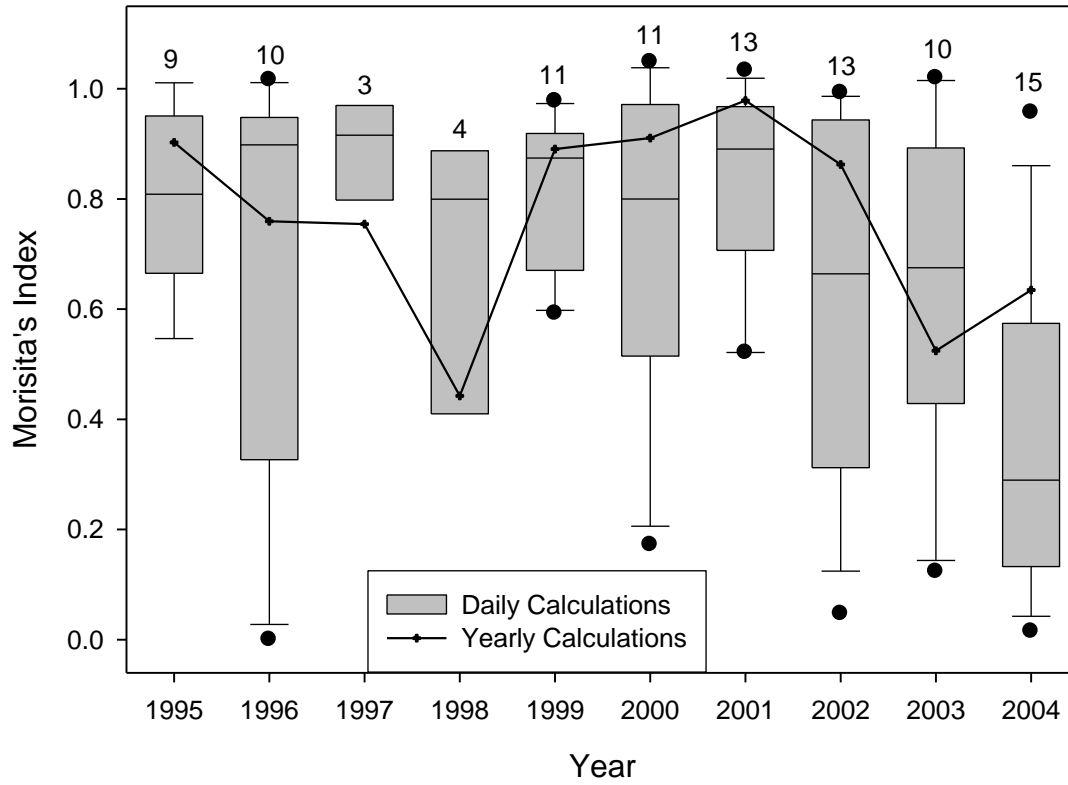


Figure 2.08 Dietary overlap between Atlantic Puffins and Arctic Terns from 1995-2004 on MSI. Continuous line shows data pooled over years, box plot represents daily overlap values. Sample sizes for the daily calculations above each box.

APTU-COTE Overlap

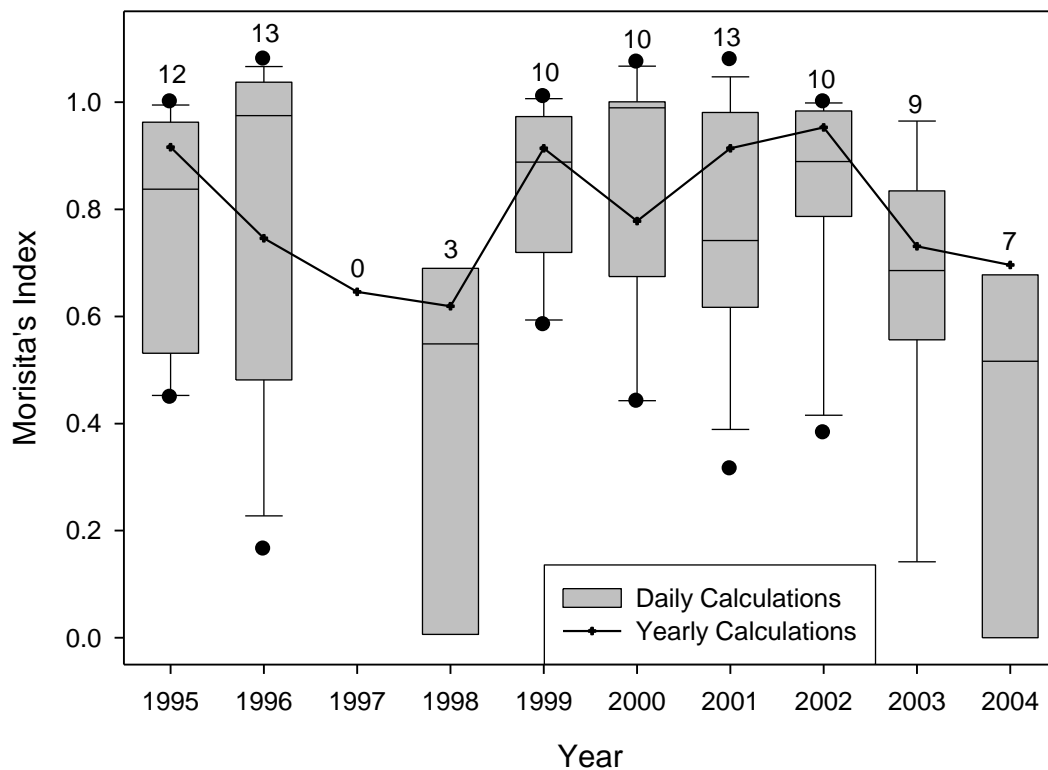


Figure 2.09 Dietary overlap between Atlantic Puffins and Common Terns from 1995-2004 on MSI. Continuous line shows data pooled over years, box plot represents daily overlap values. Sample sizes for the daily calculations above each box.

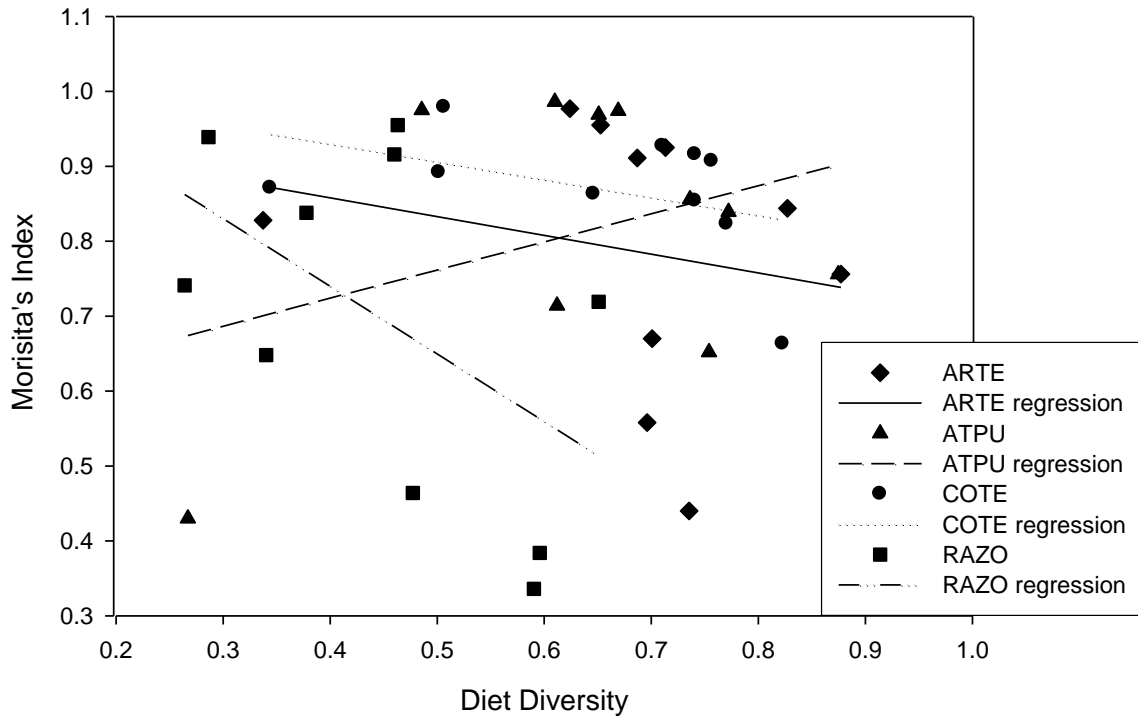


Figure 2.10. Relationship between dietary overlap and diversity for all years (1995-2004) for four seabird species monitored on Machias Seal Island. None of the regressions was significant.

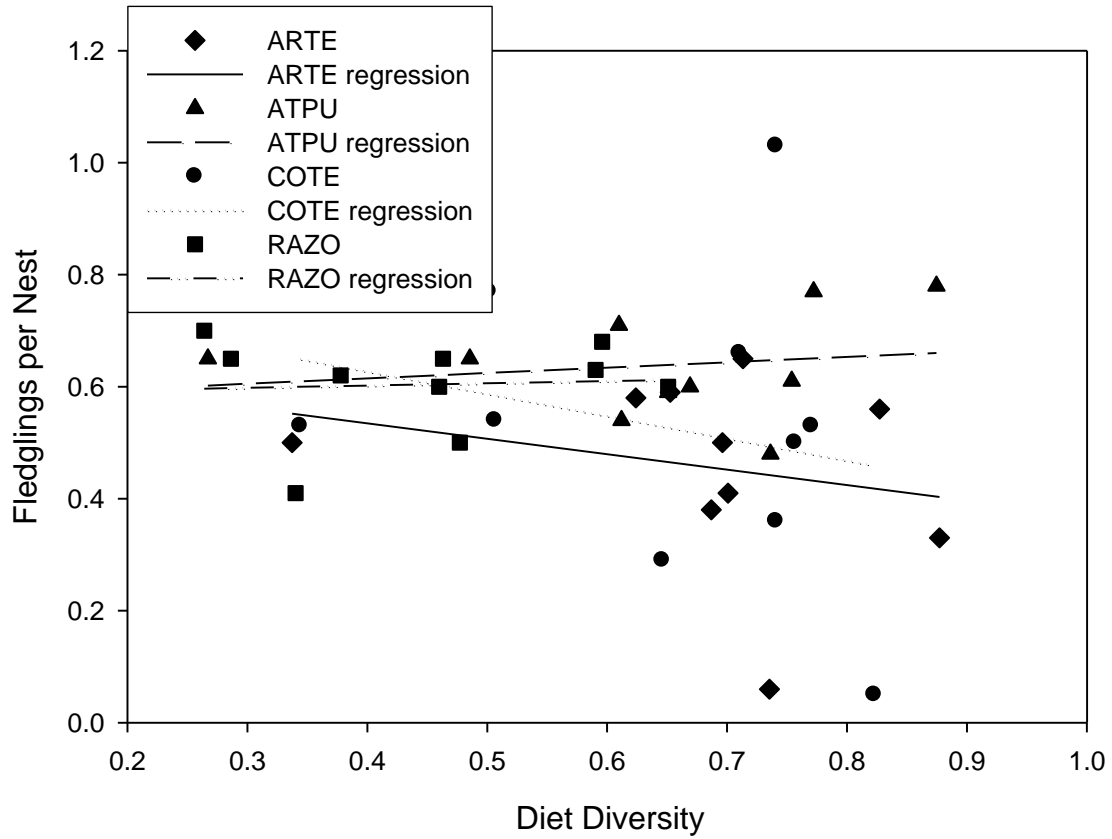


Figure 2.11. Relationship between diet diversity and productivity (fledged chicks per nest) for all four seabird species on MSI from 1995 to 2004. None of the regressions was significant.

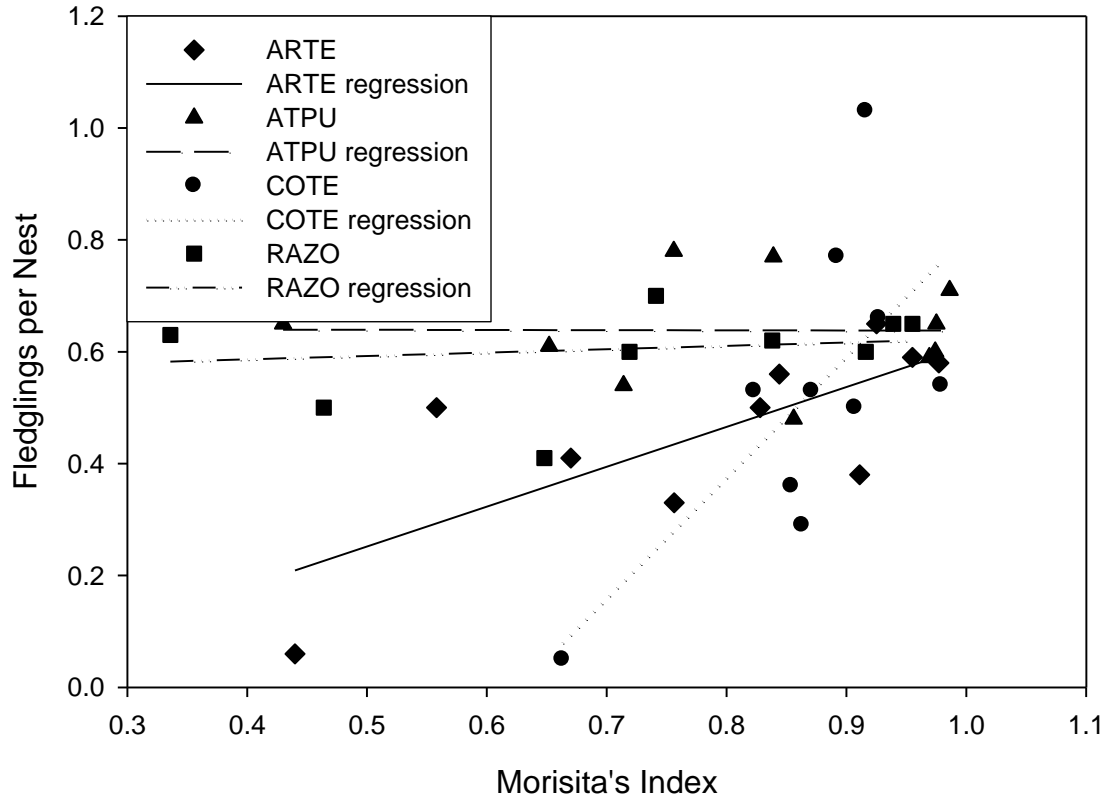


Figure 2.12. Relationship between amount of dietary overlap and the productivity of the species as defined by average number of chicks fledged per year on Machias Seal Island. Regressions for Arctic and Common Tern comparisons were significant ($R^2= 0.47$ and $p=0.03$ for both), puffin and Razorbill comparisons were not ($R^2= 0.00$, $p=0.99$ and $R^2= 0.026$, $p=0.66$ respectively).

CHAPTER 3

A hazy relationship?

The effect of fog on the feeding of four species of Atlantic seabirds

Abstract

Most seabirds rely on observing other birds in foraging flocks to identify locations where to forage. Fog is a common occurrence in the marine environment where seabirds feed, and would hinder a seabird's ability to locate these foraging flocks. We used ten years of weather data and chick feeding data from four species of seabirds on Machias Seal Island, NB, to test whether fog affects the feeding rates of seabirds and the types of prey adults deliver to chicks. We conducted block ANOVAs with year as the blocking variable to test our prediction that fog would reduce feeding rates and increase the species richness of prey delivered to chicks as adults feed whatever prey they encounter. Block MANOVAs were performed to investigate whether birds feed fewer schooling fish on foggy days. We did not find fog to have an effect on feeding rates or on types of prey delivered for three out of four species. We did not have sufficient power to test our hypotheses regarding feeding rates and suggest fog be monitored on foraging grounds to concretely test these questions regarding the effect of fog on foraging.

Introduction

Seabirds are visual predators that depend largely on eyesight to locate both individual prey items and foraging flocks where prey schools are concentrated (Shealer 2002). Although olfactory senses can play a role in prey location by some seabirds, this has been established only for birds in the order Procellariiformes (Verheyden &

Jouventin 1994; Nevitt *et al.* 2004). Thus, seabirds in other orders (Charadriiformes and Pelecaniiformes) must rely entirely on vision to locate forage grounds.

Seabirds forage mainly in flocks (Hoffman *et al.* 1981; Duffy 1983; Shealer 2002); these flocks are thought to be imperative in foraging for many species as they feed on mobile schooling fish such as herring, sandlance, and capelin, often referred to as forage fish (Payne *et al.* 1999). The importance of social facilitation in finding food has been documented across taxa (see reviews Giraldeau & Beauchamp 1999; Galef & Giraldeau 2001) and specifically in the pelagic environment (Ryer & Olla 1992). Since birds do not search in groups for foraging flocks, it is believed that individual birds rely on seeing other birds foraging as a cue on where to locate prey from a distance (Haney *et al.* 1992).

Foggy conditions can greatly limit visibility, therefore reducing the ability of birds to locate other foraging birds from a distance. However, fog is a common occurrence where cold ocean waters coincide with warm, moist air. Therefore, it is often encountered by many seabird species when foraging during the breeding season in temperate and polar areas. If seabirds indeed rely on visual cues to locate feeding flocks, and therefore forage fish, the fog should inhibit foraging success of the birds.

Specifically, we would expect to see a decrease in chick feeding rates in terms of both frequency and mass of prey in foggy conditions. As the seabirds could no longer depend on sighting foraging flocks feeding on schooling fish in foggy conditions, we also expect to see fewer forage fish such as herring and sandlance in chick diets on foggy days.

Despite the fact that fog would be encountered regularly by seabirds and likely affects foraging, the issue is rarely addressed in scientific studies. Fog conditions are often recorded in weather observations, but then not analyzed and compared to diet or

feeding rates. Studies of predatory birds note that fog likely inhibits the ability to locate prey (Herzog 1996) but do not cite data or other studies. It remains unclear if the lack of studies that directly focus on fog and the feeding of birds is due to the fact that fog was found to be insignificant and not mentioned, if fog itself is too variable and ephemeral to measure, or if fog is too difficult to tease apart from other variables such as temperature. Fog is a weather phenomenon with multiple dimensions, thus we see no need to try to separate fog from related variables like temperatures.

The only studies we found that address affects of fog on bird feeding were conducted in the foggy Bay of Fundy region. One is a study of Herring Gull, *Larus argentatus*, that coincidentally was conducted during a severe (two-week) fog event (Hebert 1987). The study documented decreased chick survivorship during this fog event and incidentally documented that fewer forage fish appeared in chick diets on foggy days than on clear days, while more euphausiid shrimp were fed on foggy days (Hebert 1987). In the other study, Amey (1998) found weather affected the feeding frequency of surface-feeding terns more than pursuit-diving alcids. The study focused on four species of seabird and found fog reduced the feeding rates of Arctic Terns, *Sterna paradisaea*. This study considered only two summers, one of which was considerably foggier than the other. We have continued collecting data at the same site as Amey since 1995, and now have ten years of seabird feeding and fog data to address our questions about the effects of fog on feeding seabirds.

The Bay of Fundy is frequently foggy in summer, especially when southerly winds bring warm moist air from the Gulf of Maine over the cold waters of the Bay of Fundy, dropping the air temperature below the dewpoint and creating fog. Machias Seal

Island (MSI) is located in the mouth of the Bay of Fundy and is home to thousands of several species of breeding seabirds, including Atlantic Puffins (*Fratercula arctica*), Razorbills (*Alca torda*), Common Terns (*Sterna hirundo*), and Arctic Terns. Over the past ten years researchers on MSI have monitored the feeding of breeding seabirds on the island and aspects of island weather, including fog. Machias Seal Island and surrounding areas are characterized by frequent bouts of fog, with an average of 45 clear days from mid-May to mid-August (Black *et al.* 2005). On other days, the island and surrounding waters are shrouded in a dense fog at least half the day.

The four focal species of the study are in the order Charadriiformes. Arctic and Common Terns forage while flying above the water's surface and dip into the water, plucking items out of the top few centimetres of the water column. Razorbill and Atlantic Puffins forage by diving into the water and swimming in the water column, actively pursuing their prey; thus, fog does not hinder them when chasing prey. However, all four species would encounter fog while searching for foraging flocks when trying to locate prey.

We are interested in testing the hypothesis that fog condition will affect prey delivery rates to seabird chicks. We predict that the mass of prey delivered per hour and the feeding frequency will decrease on foggy days. We expect that the difference will be more pronounced in the surface-feeding terns than the pursuit-diving alcids.

We also will investigate if the prey types delivered on foggy and clear days differ. We expect to see fewer schooling fish (herring, hake, and sandlance) and more invertebrates (euphausiid shrimp) in chick diets on foggy days. The number of different

kinds of prey types delivered should also increase on foggy days as adults feed on any prey they encounter.

Methods

Study Site

The data were all collected on Machias Seal Island (MSI), New Brunswick, a 9.5 hectare island located at the mouth of the Bay of Fundy (44°05'N, 67°01'W). Refer to Chapter 2 for site details.

Feeding Data

All feeding data were collected by observers in semi-permanent blinds that overlook defined plot areas. To maintain consistency between years, plots are in the same locations, veteran observers train new researchers, and the data collection protocol has been the same since the project started in 1995. Every tern feeding observation is tied to a specific nest, but many alcid burrows frequently have the same entrance, so each alcid feeding is connected with the delineated plot area rather than a nest. As it is not always feasible to differentiate between prey species through observation, the observer identifies the prey to the lowest possible taxon and we refer to the “prey type” delivered (e.g. polychaete). In addition to recording prey types, the observer estimates prey length relative to the bird’s culmen and number of prey items in bill.

Prey Collections

Prey items are collected opportunistically on the island throughout the breeding season for nutrient analysis and to estimate prey mass based on length. Prey samples are collected only if not dried out, and are weighed, measured, and frozen for further analysis.

We conducted regressions of mass of prey on length of prey cubed in order to produce an equation for each prey type that approximates mass of delivered prey based on estimated length (Appendix IV).

Weather Data

All weather data are recorded daily at 0900 and 2100. Overall condition (e.g., foggy, clear) is recorded, as well as distance of visibility. “Fog” is quantified by visibility of landmarks at a known distance; if the observer could not see 2.5 km or more, the conditions were considered foggy. Fog conditions can vary within minutes, but frequently the island is characterized by stretches of entire days with thick fog, followed by days of clear visibility. A difficulty in quantifying fog is its ephemeral nature; within one hour fog can come in, vanish, and reappear. To attempt to simplify this complexity, for all fog analysis we grouped observations by day and included only days where both morning and evening observations were the same (foggy or clear). We feel this is a robust way to measure fog since although it is transient, if the morning and evening conditions are both foggy or clear then that typically indicates the fog condition for the entire day.

Feeding Rates

We examined feeding rates of seabirds to chicks in terms of both frequencies and mass. Feeding frequency (number of feed deliveries per unit time) is an indicator of time spent foraging; however, if birds are feeding on rafts of euphausiids near the island and frequently delivering small amounts of prey to chicks it can appear that the birds are finding sufficient prey, but the mass of prey delivered to chicks can be very small. Thus,

mass of prey delivered to chicks per hour offers another basic estimate of foraging success.

Mass estimates were calculated from regressions based on the collected prey items using prey length estimated by the feeding observer. We calculated for terns the number of feeds and mass per nest per hour, while the alcid rates are based on the number of feeds and mass per plot area per hour.

We know feeding varies by year on MSI (Amey 1998, Chapter 2) and here are interested solely in effects of fog condition. Thus, to compare the means of feeding rates and mass rates with fog condition (clear or foggy) we conducted a randomized block design analysis of variance (ANOVA) with year as our blocking variable. We conducted the following power analyses (Zar 1999) where ϕ is the power of the test for the fog condition factor, k is the number of levels of the fog condition factor ($k = 2$ because the levels are foggy and clear), and δ is minimum detectable difference, which we considered a 20% difference:

$$\phi = \frac{\sqrt{n} \delta^2}{2k s^2}$$

Prey Types

We calculated the percent of the main prey types (herring, hake, euphausiids and sandlance) delivered to seabird chicks on foggy and clear days for each species of seabird. To test for a difference in prey types delivered on clear and foggy days, we conducted a blocked multivariate analysis of variance (MANOVA) for each seabird species with the proportion of four prey types as dependent variables, fog condition (clear or foggy) as the independent variable, and year as the block. To find subsequently which prey types are

affected by fog condition we examine the univariate analysis of variances for each prey type.

We used species richness as an indication on diet diversity as we were interested in absolute number of species delivered, not the evenness of prey types delivered. To investigate how the number of prey types varies in fog condition we compared the species richness of items delivered on foggy and clear days using block ANOVAs with year as the block and conducted post-test power analyses.

Results

Over the past ten years we conducted feeding watches on 150, 126,138, and 105 days that were either fully clear or fully foggy for Arctic Terns, Common Terns, Atlantic Puffins, and Razorbills, respectively. For every seabird species observed we had at least two feeding watches per year on both foggy and clear days, except for Arctic Terns in 1999 where no feeding watches were conducted in fog. Razorbills were observed feeding euphausiids to their young only twice over all ten years; therefore euphausiids were not included in the prey type analysis for Razorbills.

Feeding Rates

The ANOVAs examining feeding rate did not show a significant relationship between fog and frequency of feedings (Tables 3.01A-D; Fig. 3.01 A-B). For all four species there was a significant difference in feeding frequencies over our blocking variable of year (Tables 3.01A-D), as had been expected.

The block ANOVAs did not reveal fog as a significant variable that affects the rate of prey mass delivered to seabird chicks for any of the four species (Tables 3.02A-D;

Fig. 3.02 A-B). Again, the blocking variable, year, was significant in explaining mass rate variability (Tables 3.02A-D).

For all ANOVAs comparing both rates of mass delivered and feeding frequency we had a power under 0.65, but our feeding rate analyses had a collective power at 0.937 and our mass rate analyses had a collective power of 0.76. (Tables 3.01A-D).

Prey Types

The MANOVAS revealed a significant relationship between fog condition and the types of prey delivered to chicks for Razorbills, (Tables 3.03; Figs 3.03, 3.06) but no consistent relationship for Arctic Terns, Common Terns, or for Atlantic Puffins (Tables 3.03; Figs. 3.04, 3.05). Year was a significant factor in the MANOVAs for all four species of seabird ($p < 0.001$) (Tables 3.03). Herring is the only prey type for which there is a significant relationship between fog and prey type for Razorbills, with birds feeding significantly less herring on foggy than clear days (Tables 3.04, Figs 3.03, 3.06). We found a significant interaction between year and fog for both tern species, indicating prey varied with fog in some years but not others.

Common Terns delivered significantly more species of prey on foggy days than clear days (Table 3.05; Fig.3.07). We did not detect a difference in species richness of prey delivered to seabird chicks on foggy and clear days for Arctic Terns, Atlantic Puffins, or Razorbills (Table 3.05; Fig.3.07). For all species taken together, our results show no significant difference in species richness among years and we had sufficient power to test for a relationship between fog and species richness.

Discussion

Feeding Rates

Seabirds are visual predators and fog should inhibit their ability to detect prey patches from a distance. However, our data do not offer empirical support for our predictions on fog affecting the rates at which seabirds feed their chicks. Fog was unrelated to feeding frequencies or rates of mass delivered to seabird chicks for any of the four species, implying that the birds might spend the same amount of time foraging for prey on foggy and clear days and may have similar success rates in foraging on foggy and clear days. This suggests that the seabirds are able to find prey effectively despite the presence of fog, or more likely that we could not detect an effect of fog on feeding.

Contrary to our prediction and previous work, we saw no difference in feeding rates between the two foraging guilds in relation to fog conditions. Amey (1998) found fog hinders feeding frequencies of Arctic Terns. We did not find fog to have a significant effect on the feeding rates of any of our seabird species.

Some seabirds can be site-faithful to foraging areas; individual kittiwakes (*Rissa tridactyla*) were found to often visit the same foraging site on different foraging trips (Irons 1998) and other studies have indicated that seabirds including Common Terns may search for food partially based on memory (Becker *et al.* 1993; Davoren *et al.* 2003). If seabirds rely on memory to locate the general area of reliable foraging sites, perhaps fog would not hinder their ability to locate prey.

Variation in feeding frequencies and mass rates among years was significant for all species, as we expected based on previous work (e.g., Burger & Piatt 1990; Bryant *et al.* 1999; Weimerskirch *et al.* 2001). Feeding rates have been linked to a variety of factors; notably Cairns (1987) theorized that in times of low food supply the percent of

time foraging by seabirds would increase. Previous work on Arctic Terns on MSI (Paquet 2001) and other studies (Bryant *et al.* 1999) did not support this prediction. Other work on seabirds have shown a relationship between time spent foraging and food supply (Burger & Piatt 1990; Zador & Piatt 1999; Weimerskirch *et al.* 2001; Litzow & Piatt 2003); however most of these studies have found that adults use loafing time as a buffer and provisioning rates are constant (Burger & Piatt 1990; Zador & Piatt 1999; Litzow & Piatt 2003). A similar time-budgeting mechanism may be at work while in foggy conditions. Seabirds may be spending more time looking for food but resting less, resulting in the same provisioning rates despite fog condition.

It is possible that we are unable to detect an effect of fog on feeding rates because our measures of fog were inaccurate. Fog is ephemeral, and even within a 3- hour feeding watch the fog conditions can change. Although if fog conditions in the morning and evening are the same it usually represents the fog condition for the entire day; this is not always the case. Our measures of fog may also not represent the fog condition at the foraging grounds where the birds search for prey; fog conditions on MSI may differ from conditions on the ocean. The fog data we collect on the island represent fog conditions for the foraging birds to the best of our ability, and we believe that they are accurate on the whole, however further studies addressing fog conditions at sea and on island would strengthen our results.

We did not have a power of .80 or greater for any of our individual comparisons of feeding frequency or mass rates, so we may have accepted the null hypothesis when the alternative hypothesis is true. However, our F-ratios are very small and the differences observed were so small that it would take an extraordinary amount of

additional data to observe a significant relationship. Rather than simply increasing the sample size, we recommend altering the study design for greater power. This could be accomplished by recording the fog condition during each feeding watch or ideally by knowing the fog condition on the foraging grounds where the birds are foraging.

Prey Types

Previous work on a nearby island has shown a relationship between prey types delivered to seabird chicks and fog conditions (Hebert 1987), while one out of our four study species, the Razorbill, showed a significant difference in prey types delivered on clear and foggy days.

During the early years of this long-term study, Amey (1998) found no difference in proportion of herring delivered on foggy and clear days by any of the four species. The proportion of herring delivered was significantly different for Razorbills, which fed more herring to chicks on clear days. This supports our prediction that the birds have difficulty locating foraging flocks on schooling fish in foggy weather. However, we saw no significant trend in fog effect by foraging guild as the foraging guilds were not consistent among themselves.

Razorbills can dive deeper than Atlantic Puffins (Lowther *et al.* 2002; Hipfner & Chapdelaine 2003) and therefore have a greater access to prey in the water column than the other pursuit-diving species and two surface-feeding species examined in this study. Over the past ten years we have seen a decline in one of the preferred prey items on the island, herring (Amey 1998), delivered to seabird chicks on MSI; but Razorbills are still finding and delivering more herring to their chicks than the other focal species (Black *et al.* 2005). Given the Razorbill's relative success at finding herring while the seabirds on

MSI feed less herring, it is interesting that Razorbills appear to be most susceptible to fog in terms of prey types delivered to chicks (Fig 3.06).

The blocking variable, year, was a significant factor in describing the variability in proportion of main prey types delivered for all four species. Many previous studies have shown variation in seabird diets over years (Safina *et al.* 1988; Hall *et al.* 2000; Rindorf *et al.* 2000; Deguchi *et al.* 2004), and as the ocean environment is dynamic it is not surprising that seabirds would deliver different prey items in different breeding seasons.

The Common Tern was the only of four species that fed significantly different number of prey types on clear and foggy days, and contrary to our predictions they fed a greater variety of prey types on clear days. We expected fog to hinder seabird's ability to locate preferred forage fish on foggy days, and thus to be less selective when delivering prey when foggy. It is puzzling that only one species fed different species richness of prey on foggy and clear days; it is possible that our results was a type I error. Fig. 3.07 shows all years pooled and there appears to be no difference between richness on foggy and clear days, as the trend is only observed when year is a factor. As with the feeding rates, the other comparisons show so little difference in species richness on foggy and clear days that additional data would be of minimal use.

Conclusions

Our results did not support our predictions that we would see a difference in the feeding rates of seabirds on clear and foggy days. Thus, we saw no difference in feeding response to fog in the two foraging guilds we studied.

It remains unclear if we did not find an effect of fog on seabird feeding rates because we simply could not detect the difference or if there is no difference in feeding rates on foggy and clear days. A variety of factors may influence the bird's ability to deliver prey consistently in all fog conditions, as seabirds may not rely as much as we think on visual location of flocks to forage or may have flexible time-budgets. Seabirds may also have a memory bank of reliable foraging sites and know locations despite fog. It also is possible that our fog measurements may not represent fog conditions on foraging grounds. Despite having ten years of data we were not able to have sufficient power to answer our questions regarding feeding rates, which may have led us to fail to reject the null hypothesis when in fact there is a difference in prey delivery rates on foggy and clear days.

Razorbills showed a response to fog by feeding different proportions of the main prey types on foggy and clear days, while our other seabirds demonstrated no response to fog by delivering different prey. Razorbills fed less herring on foggy days, supporting our prediction that birds would feed less schooling fish in the fog. Contrary to our predictions, we saw no trends between foraging guilds in terms of feeding response to fog. The Common Tern was the only species to feed significantly different species richness of prey on clear and foggy days, and opposite to our predictions they fed a greater variety of species to seabird chicks on clear days.

The results of this study leave us with many questions about the nature of seabird foraging and the predator response to poor visibility. Current studies on Machias Seal Island radio-tracking the two tern species and Razorbills should clarify some of our questions. We did not have a high power in many of our analyses, suggesting we have

made a type II error. Given the very small F-ratios we believe that this study design would be improved by different methods rather than increased sample sizes. More intensive sampling of fog conditions during seabird feedings and knowledge of fog conditions at the foraging grounds are needed to test the effect of fog on seabird foraging.

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Tables 3.01 A-D Block ANOVA results for feeding frequencies of prey delivered to seabird chicks on clear and foggy days with year as the blocking variable. Significant relationships in bold.

Feeding Rates

A) ARTE:

N: 141 R²: 0.232

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	0.394	1	0.394	0.124	0.734	0.30
Year	104.161	8	13.020	4.007	0.000	
Year*Fog interaction	25.390	8	3.174	0.977	0.457	

B) COTE:

N: 136 R²: 0.214

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	1.295	1	1.295	2.048	0.168	0.63
Year	18.328	9	2.036	2.340	0.018	
Year*Fog interaction	5.194	9	0.577	0.663	0.741	

C) ATPU:

N: 140 R²: 0.235

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	4.052	1	4.052	0.126	0.731	0.52
Year	598.662	9	66.518	2.011	0.044	
Year*Fog interaction	290.018	9	32.224	0.974	0.465	

D) RAZO:

N: 106 R²: 0.261

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	0.626	1	0.626	0.103	0.755	0.50
Year	115.449	9	12.828	1.968	0.053	
Year*Fog interaction	54.619	9	6.069	0.931	0.503	

Tables 3.02 A-D Block ANOVA results for feeding rates of mass of prey delivered per hour to seabird chicks on clear and foggy days with year as the blocking variable. Significant relationships in bold.

Mass Rates

A) ARTE:

N: 161 R^2 : 0.216

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	0.305		0.305	1.525	0.252	0.30
Year	30.699	8	3.837	4.098	0.000	
Year*Fog interaction	1.601	8	0.200	0.214	0.988	

B) COTE:

N: 151 R^2 : 0.208

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	8.158	1	8.158	1.88	0.204	0.30
Year	48.019	9	5.335	1.310	0.238	
Year*Fog interaction	39.060	9	4.340	1.066	0.392	

C) ATPU:

N: 141 R^2 : 0.465

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	5752.292	1	5752.292	0.850	0.380	0.31
Year	217257.040	9	24139.671	3.380	0.001	
Year*Fog interaction	60872.554	9	6763.617	0.947	0.488	

D) RAZO:

N: 108 R^2 : 0.431

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	46.888	1	46.888	0.016	0.901	0.30
Year	101217.224	9	11246.358	3.598	0.001	
Year*Fog interaction	25707.871	9	2856.430	0.914	0.517	

Tables 3.03 A-D Block MANOVA results of proportion of euphausiids, hake herring, and sandlance delivered to seabird chicks on foggy and clear days with year as the blocking variable. Razorbills rarely feed euphausiids, so only hake, herring and sandlance are included in the analysis for Razorbills. Significant relationships in bold.

A) ARTE:

Effect	Pillai Trace	F-Statistic	df	P
Fog	0.073	2.202	4, 112	0.073
Year	1.735	11.008	32, 460	0.000
Year*Fog interaction	0.380	1.511	32, 460	0.039

B) COTE:

Effect	Pillai Trace	F-Statistic	df	P
Fog	0.025	0.652	4, 103	0.627
Year	1.851	10.142	36, 424	0.000
Year*Fog interaction	0.510	1.720	36, 424	0.007

C) ATPU:

Effect	Pillai Trace	F-Statistic	df	P
Fog	0.012	0.351	4, 115	0.843
Year	1.829	11.049	36, 472	0.000
Fog*Year interaction	0.153	0.522	36, 472	0.991

D) RAZO:

Effect	Pillai Trace	F-Statistic	df	P
Fog	0.109	3.381	3, 83	0.022
Year	1.063	5.183	27, 255	0.000
Year*Fog interaction	0.285	0.993	27, 255	0.479

Tables 3.04 A-D Results from univariate ANOVAs for proportion of main prey types delivered to seabird chicks on foggy and clear days. Significant relationships in bold.

A) ARTE:

Effect	SS	df	MS	F	P
Euphausiids	0.004	1, 115	0.004	0.108	0.743
Hake	0.003	1, 115	0.003	0.090	0.765
Herring	0.168	1, 115	0.168	3.077	0.082
Sandlance	0.023	1, 115	0.023	2.006	0.159

B) COTE:

Effect	SS	df	MS	F	P
Euphausiids	0.008	1, 106	0.008	0.285	0.594
Hake	0.048	1, 106	0.048	0.731	0.394
Herring	0.006	1, 106	0.006	0.323	0.571
Sandlance	0.016	1, 106	0.016	1.853	0.176

C) ATPU:

Effect	SS	df	MS	F	P
Euphausiids	0.000	1, 118	0.000	0.014	0.908
Hake	0.029	1, 118	0.029	0.946	0.333
Herring	0.002	1, 118	0.002	0.032	0.858
Sandlance	0.006	1, 118	0.006	0.379	0.539

D) RAZO:

Effect	SS	df	MS	F	P
Hake	0.058	1, 85	0.058	1.597	0.210
Herring	0.614	1, 85	0.614	8.931	0.004
Sandlance	0.046	1, 85	0.046	2.676	0.106

Tables 3.05 A-D. Results for the block ANOVAs examining species richness on clear and foggy days with year as the blocking variable. Significant relationships in bold.

A) ARTE:

N: 135 R^2 : 0.178

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	0.002	1	0.002	0.001	0.971	0.984
Year	32.759	8	4.095	2.836	0.007	
Year*Fog interaction	11.670	8	1.459	1.010	0.433	

B) COTE:

N: 126 R^2 : 0.480

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	10.637	1	10.637	5.700	0.041	0.975
Year	161.740	9	17.971	9.069	0.000	
Year*Fog interaction	16.792	9	1.866	0.942	0.493	

C) ATPU:

N: 134 R^2 : 0.378

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	1.111	1	1.111	0.306	0.594	0.967
Year	160.709	9	17.857	6.839	0.000	
Year*Fog interaction	32.690	9	3.632	1.391	0.200	

D) RAZO:

N: 88 R^2 : 0.409

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P	Power
Fog	0.015	1	0.015	0.011	0.921	0.86
Year	55.573	9	6.175	3.948	0.000	
Year*Fog interaction	12.829	9	1.425	0.911	0.521	

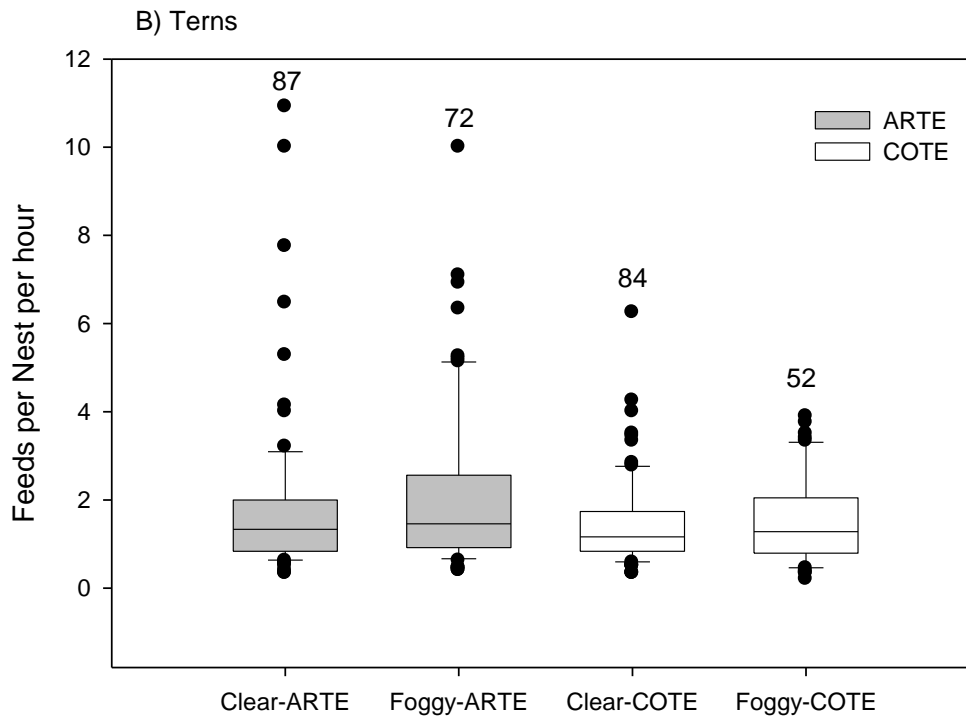
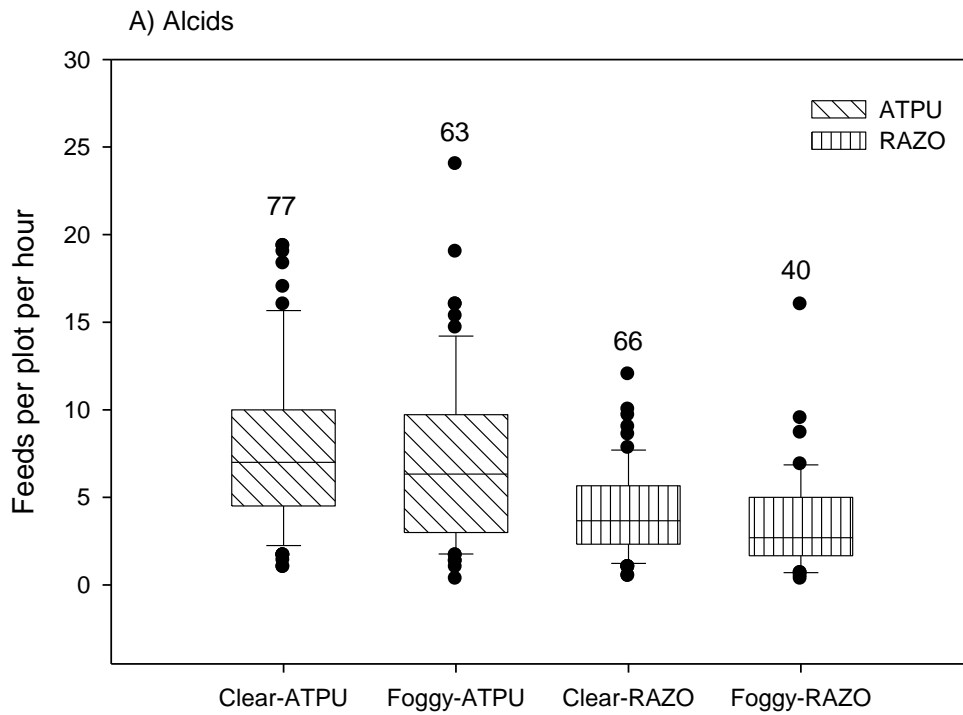


Figure 3.01 A-B Frequency of prey deliveries to seabird chicks on MSI on foggy and clear days from 1995-2004. Sample sizes are noted above each box plot.

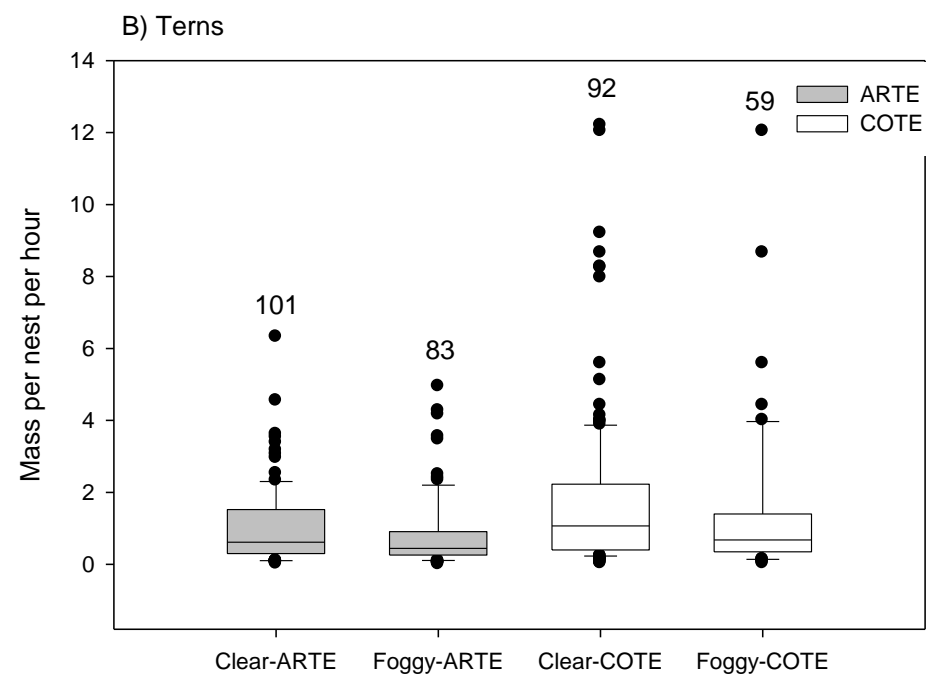
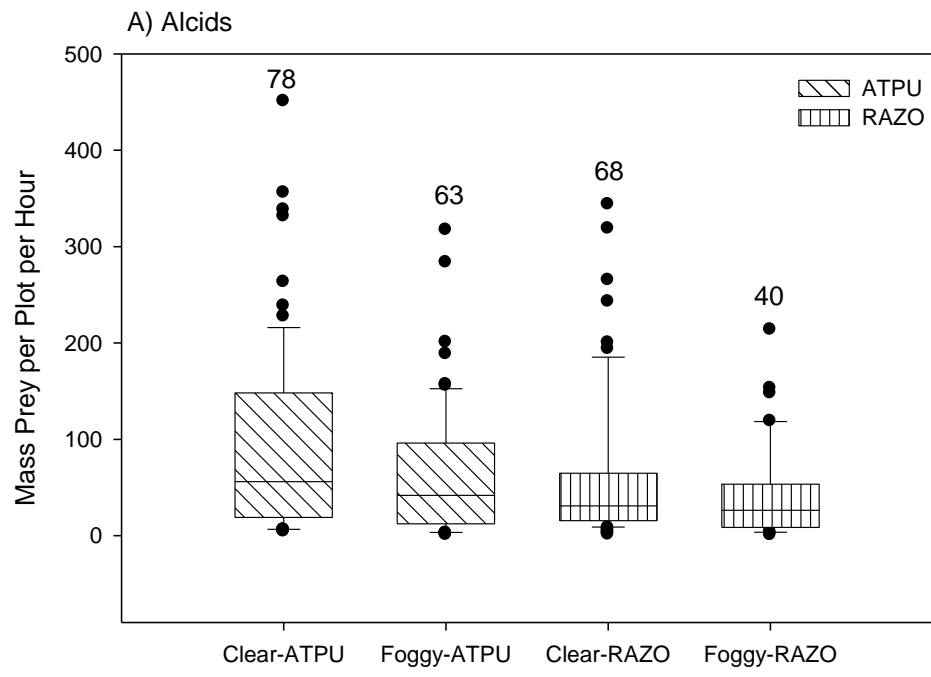


Figure 3. 02 A-B Mass of prey delivered to seabird chicks on MSI on foggy and clear days from 1995-2004. Sample sizes are noted above each box plot

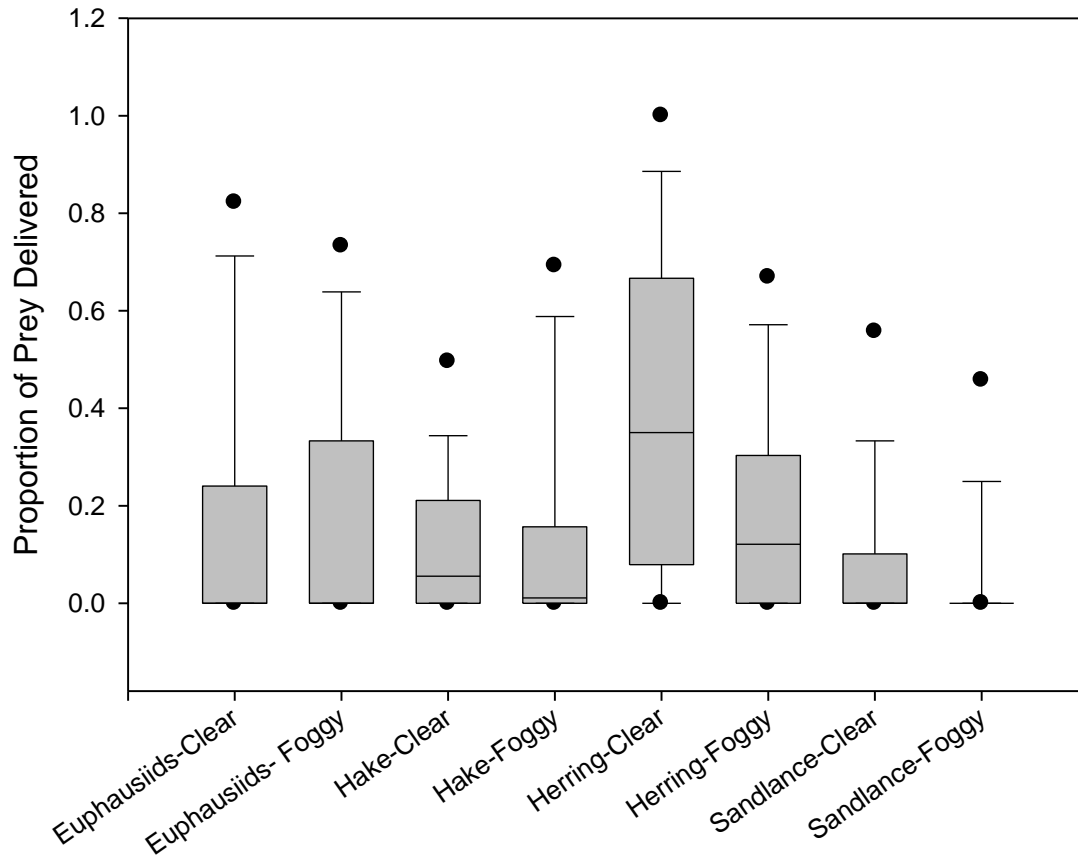


Figure 3.03 Proportion of main prey types delivered to Arctic Tern chicks on foggy and clear days on MSI from 1995-2004.

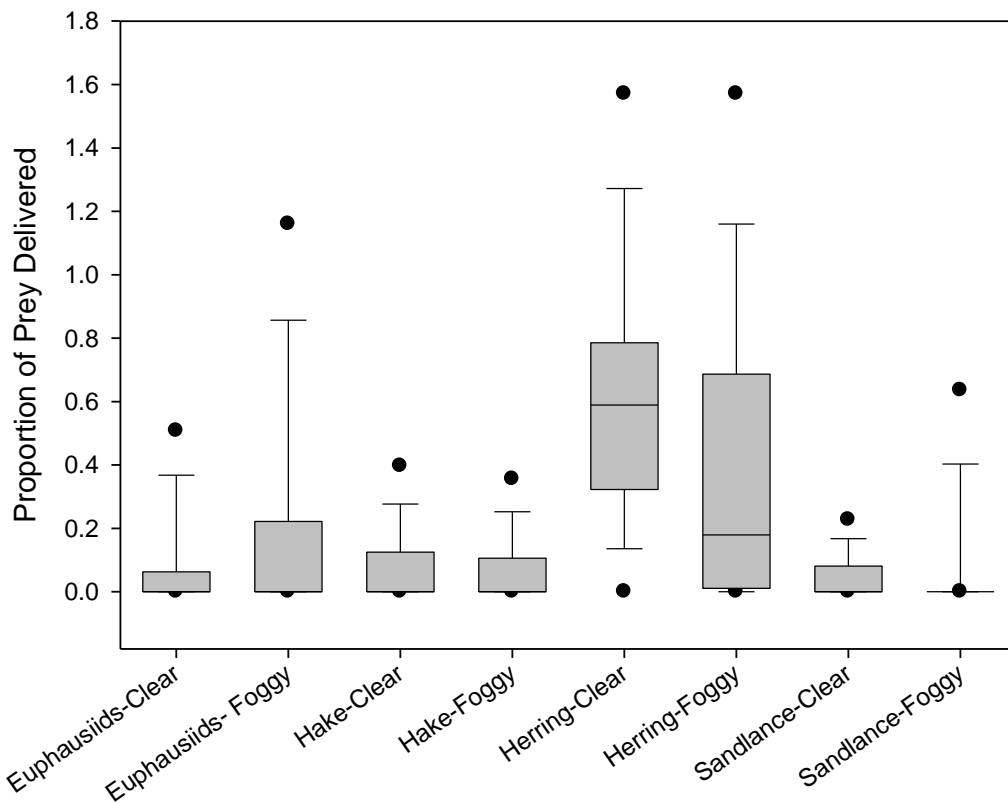


Figure 3.04 Proportion of main prey types delivered to Common Tern chicks on foggy and clear days on MSI from 1995-2004.

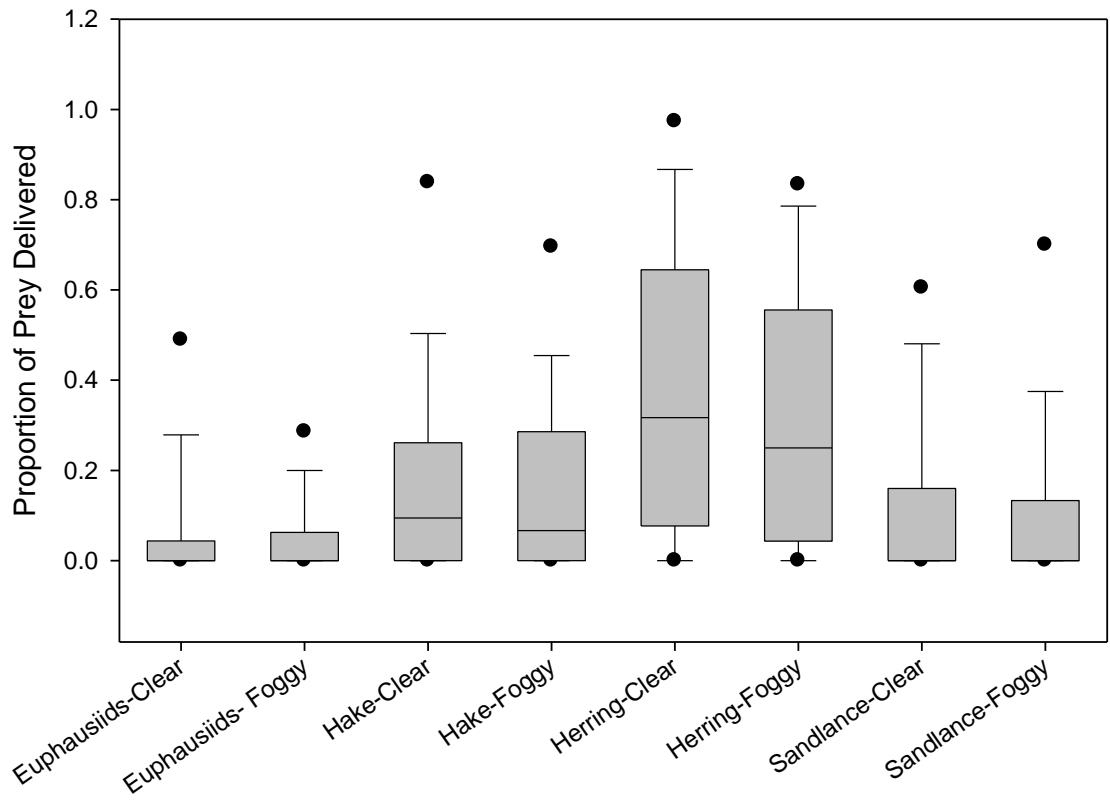


Figure 3.05 Proportion of main prey types delivered to Atlantic Puffin chicks on foggy and clear days on MSI from 1995-2004.

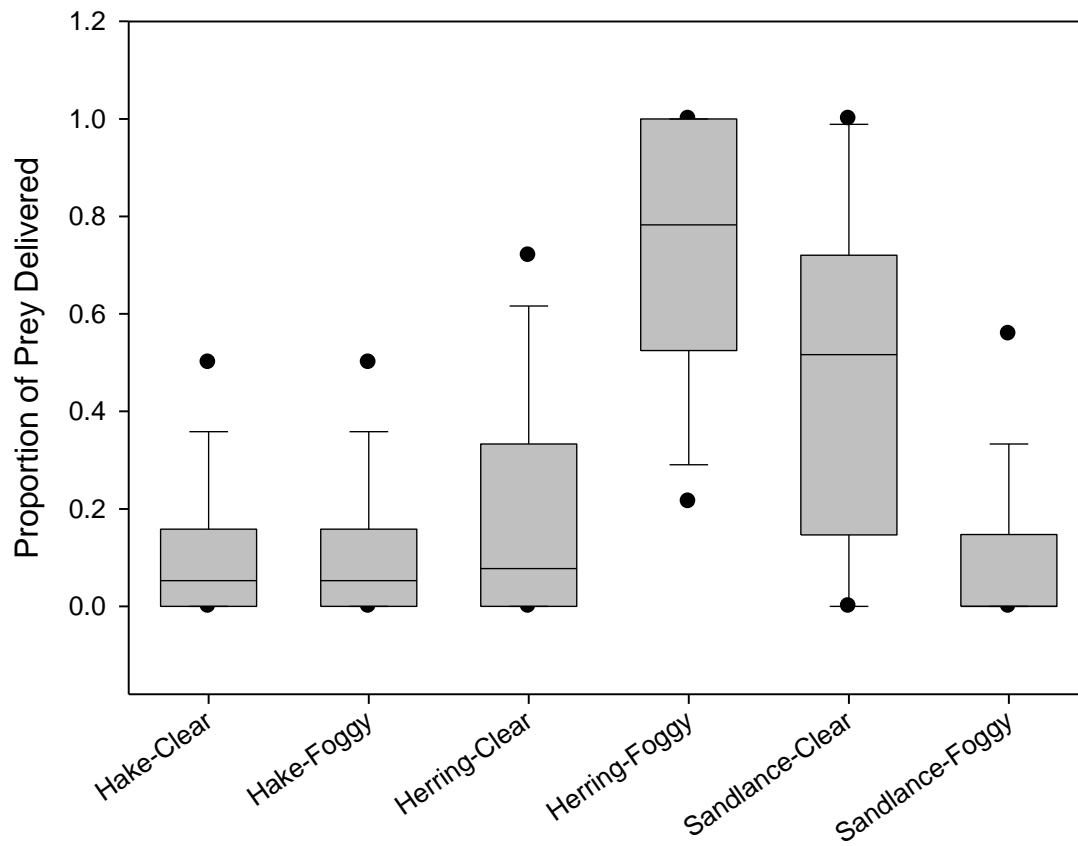


Figure 3.06 Proportion of main prey types delivered to Razorbill chicks on foggy and clear days on MSI from 1995-2004.

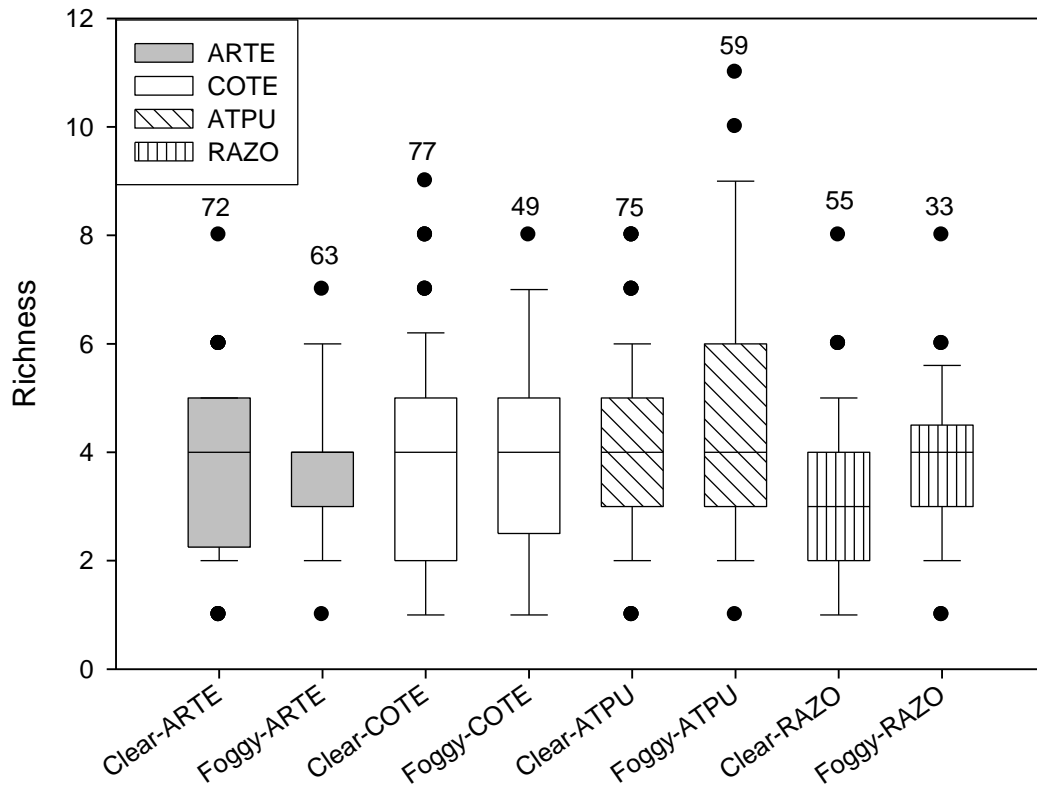


Figure 3.07 Species richness of prey delivered to seabird chicks on MSI on foggy and clear days from 1995-2004. Sample sizes are noted above each box plot.

CHAPTER 4

Synthesis of results and conclusions

Acquiring energy is essential for all life, and limitations on food are believed to restrict the number of offspring birds can produce, thus limiting avian populations (Lack 1947; Martin 1987). Seabirds are theorized to be restricted in numbers by prey, and empirical studies have supported this theory, particularly in the breeding season when birds are constrained to foraging near the nest (Ashmole 1963; Ashmole & Ashmole 1967; A.W. Diamond 1978; Safina et al. 1988; Weimerskirch et al. 2001; Oro et al. 2003).

Given the importance of food to seabird populations, it is critical we have a thorough understanding of the relationship seabirds have with their prey: what they feed on and what affects feeding. We must understand how seabirds interact with other seabirds in terms of prey and in times of food stress, and how environmental conditions affect foraging. I used long-term data collected on MSI to address our questions regarding seabird feeding to learn more about the complex relationships seabirds have with each other and their environment.

There has been a significant decline in the proportion of herring delivered to Arctic Tern, Common Tern, Atlantic Puffin, and Razorbill chicks on Machias Seal Island from 1995 to 2004. From 1995-2001 over half of all prey delivered to chicks consisted of juvenile fish for all four species of seabird. Previous work has shown the importance of herring in the diets of seabirds on MSI (Amey 1998; Diamond & Devlin 2003) and a strong correlation of herring delivered to Arctic Tern chicks with local fishery catches

(Amey 1998; Amey et al. 2003), leading me to interpret the decrease in herring in chick diets as a decrease in herring availability.

Inter-annual Variation of Overlap

In most times of food limitation, as competition between species increases, organisms must respond by varying prey consumed and foraging behaviour (J.M. Diamond 1978; Schoener 1982), typically resulting in a decreased overlap between species (Wiens 1989; Bell & Ford 1990; Gonzales-Solis et al. 1997). I did not see the predicted trend of decreased dietary overlap over the ten years as herring decreased for all the species of seabird studied on MSI. For two of the six interspecific comparisons there was a significant decline in overlap for all ten years, when comparing the Razorbills to the Arctic Terns and Common Terns. For the other four interspecific comparisons I did not see a significant change in dietary overlap from 1995 to 2004. These four comparisons, Atlantic Puffins with Razorbills, Atlantic Puffins with Common Terns, Atlantic Puffins with Arctic Terns, and Common Terns with Arctic Terns, all showed a significant decline in dietary overlap from 1995-1999. Surprisingly, the two overlap comparisons that decreased over all ten years did not show a significant decrease from 1995-1999.

Although overall I did not see the decrease in overlap trends over all years for every species examined, all comparisons showed a significant decreasing trend at some scale. Also, every significant comparison from my regressions was negative; every time my data showed a significant relationship, overlap decreased over years as herring decreased. This does not conclusively confirm my hypothesis that dietary overlap should

decrease as the preferred herring prey decreases, but it does provide some evidence to support my prediction.

I may not be able to detect a strong relationship because the decrease in herring delivered to seabird chicks may represent a minor food limitation for seabirds on MSI. Although previous work found a strong correlation of the herring delivered to Arctic Tern chicks with herring catches on nearby Grand Manan (Amey 1998; Amey et al. 2003), it is difficult to connect seabird prey deliveries to actual prey availability. Based on Amey's (1998) work I perceived herring to be a or the preferred prey item. As less herring has been fed to seabird chicks, we have observed increasing amounts of small prey delivered to chicks, such as euphausiid shrimp (Appendix I). Other work has shown Common Tern chicks have reduced growth rates and survival rates when fed shrimp diets rather than fish diets (Massias and Becker 1990), suggesting that seabird adults should prefer large, fatty fish when feeding chicks. These data support my interpretation that prey availability has been decreasing on Machias Seal Island since 1995, although I cannot know the extent to which the birds are limited by prey availability.

Food limitation has been linked with decrease in dietary overlap between species (Wiens 1989; Diamond 1983; Bell & Ford 1990; Gonzales-Solis et al. 1997), but in times of extreme food stress and in some other situations competition may be intense for the remaining prey items, resulting in a greater dietary overlap between species (Bell & Ford 1990; Steenhof & Kochert 1985). During a drought event in Australia, birds initially demonstrated a decrease in dietary overlap, but as the severe drought continued and food became more limited, overlap between species increased (Bell & Ford 1990). The

relationship between food stress and dietary overlap is clearly complex and would be strengthened by more empirical studies.

Diet diversity showed no discernable relationship with dietary overlap or productivity in the ten years of my study. Reproductive success was positively correlated with dietary overlap in both tern species, but no relation between productivity and overlap was observed in alcids from 1995-2004. Both alcid species consistently lay only one egg and raise at most one chick per year, and both have very consistent reproductive success on MSI year-to-year (Appendix II) . Terns on Machias Seal Island usually lay 1-3 eggs per clutch (Black et al. 2005), and have a much more variable breeding success than alcids. Common Terns have an average fledging success of as many as one chick per nest in some years, while in 2004 both species failed (Appendix II). It is this variability of tern breeding success that allows the tern's productivity to be related to overlap. The positive relationship suggests that in years of prey abundance, terns have a greater reproductive success, but feed on the same prey, thus having a high dietary overlap. The fact that the relationship is observed for the tern species but not the alcids illustrates the importance of using multiple study species when investigating biological questions.

Intra-annual Variation of Overlap

None of the four species showed any trends in dietary overlap as the breeding season progressed, providing no evidence for my prediction that seabirds would select large, lipid-rich fish such as herring as the dietary requirements of chicks increase throughout the season, resulting in a greater overlap. The prediction that as dietary

demands of chicks increase adults feed larger, more lipid-rich fish seems sensible; however there is no evidence in the literature to support my prediction.

Overall, I did not see increasing proportions of herring delivered to seabird chicks as the season progressed. Once data were broken down by year there were a few years that were exceptions for each species, however we did not see any consistent patterns among years, which does not support the hypothesis that the birds select large, fatty fish as the chicks grow.

Daily prey fed to chicks and daily overlap values were highly variable (Appendix IV), and although Morisita's Index shows relatively little bias when using small sample sizes (Smith & Zaret 1982) daily sample sizes may be too small to observe any trends throughout the season. Given the variability of daily prey taken, day-to-day variability may conceal any potential trends on a larger timescale. I found for most interspecific comparisons the relationship between yearly overlap and average daily overlap values were quite similar, but a notable exception was for the two tern species. This indicates the congeners consume the same prey overall, but different prey types on the same days, and may suggest that interspecific competition may work on a daily temporal scale.

Fog and Feeding Rates

Most seabirds, including those in the order Charadriiformes, are believed to rely on eyesight to locate foraging flocks (Shealer 2002). Foraging flocks are thought to be critical to the foraging success of seabirds (Hoffman et al. 1981; Duffy 1983; Shealer 2002), particularly for locating schooling fish such as herring and sandlance. Fog is a common event where cold water meets warm air, and is very common in the Bay of

Fundy region where many seabirds forage. I predicted that fog should hinder the foraging effort of Machias Seal Island seabirds, which would be evidenced by the feeding rates and types of prey delivered to chicks.

The data from Machias Seal Island from 1995-2004 do not support my prediction that fog should hinder the rate at which seabirds feed their chicks. Both feeding frequencies and rates of prey mass delivered to seabird chicks were similar on foggy and clear days.

Although I did not find an effect of fog on seabird feeding rates, that does not necessarily indicate there is no relationship. Fog was measured in the morning and evenings on the island, which may not represent fog conditions at the foraging grounds throughout the day. These results would be stronger had fog conditions been taken during the feeding watches as we would both have more usable data and the fog data would be more credible. Ideally, fog conditions at sea would be known to assess affects of fog on foraging.

Little is understood about how seabirds know where to find prey and how they forage at sea. Based on what we know about seabirds as visual predators, I expected fog to hinder feeding rates, but there are a variety of factors that might allow seabirds to forage successfully in foggy conditions. Some evidence shows seabirds sometimes return to the same foraging locations on subsequent foraging trips (Irons 1998), and other work suggests they have a memory capable of recalling foraging sites and may know reliable places to forage (Becker et al. 1993; Davoren et al. 2003), and may not be entirely dependent on seeing other birds successfully foraging. My results suggest that MSI

seabirds know relatively consistent fishing grounds, and return to these same sites and forage successfully independent of fog condition.

Seabirds also may have flexible time budgets that permit them to spend more time searching for food in times of foraging stress. Cairns (1987) proposed that in times of less prey availability, seabirds would spend less time loafing and more time foraging. Some work has supported this theory (Burger & Piatt 1990; Zador & Piatt 1999; Weimerskirch et al. 2001; Litzow & Piatt 2003), while other work has not (Bryant et al. 1999), including a study on MSI Arctic Terns (Paquet 2001). It is possible that seabirds use loafing time as a behavioural buffer throughout changes in foraging conditions.

I did not have high power in my feeding rate ANOVAs, and thus may have accepted the null hypothesis when the alternative is true and there is a difference in feeding rates on foggy and clear days. It is most probable that a combination of these factors prevents me from detecting an effect of fog on seabird feeding rates.

Fog and Prey Types delivered

I did not see the predicted trend of seabirds delivering different prey types on foggy and clear days for three out of the four study species. It is interesting that Razorbills, the only species that fed significantly different prey on foggy days (fewer herring,) is the species that shows the smallest decline in proportion of herring delivered and also consistently feeds the greatest proportion of herring of all four species (Ch. 2). Razorbills can also dive the deepest of the four species and thus have access to the greatest area with potential prey (Hipfner & Chapdelaine 2003). It may be because of the Razorbills' strong preference for herring that we see the significant trend. The Razorbills

feed more herring than the other seabirds feed on any one prey type, and being a specialist focussing on one species of prey may make them the most sensitive to changes in foraging condition while other birds more easily switch between prey types.

I did not see the expected trend of a greater number of prey types delivered to seabird chicks on foggy days, and I had sufficient power in all ANOVAs. Common Terns actually delivered significantly fewer kinds of prey on foggy days, while the other species showed no relationship. It is puzzling that only one species would show this relationship, and that it was opposite to my prediction. It is possible that individuals record a lesser prey diversity on foggy days because delivered prey items are unclear in the fog and unidentified; however, I think this is unlikely as our plot areas are too small for observers to be affected by fog, especially for the tern species. I believe that the Common Terns delivering less diverse prey on foggy days may be a case where the relationship is statistically significant, but not biologically significant.

Conclusions and Future Research

The aim of this thesis is to explore and clarify questions regarding seabirds and their prey, but my results lead to additional questions and offer few answers. The dietary relationship between similar species and how it changes within and between seasons remains vague and how limiting visibility affects seabird foraging also remains unclear.

I found few clear trends regarding dietary overlap of four species of seabird over ten years as less herring is delivered to seabird chicks, nor did I see trends in prey types or overlap throughout the breeding season. I found overlap and productivity are

directly related for the two tern species, suggesting that in times of abundance terns may feed similar prey types and be able to successfully raise more young.

In order to clarify the dietary relationships between different species in times of food stress, more studies must be conducted in controlled lab experiments through varying degrees of food stress, with different numbers of competing species. Most studies investigating niche and dietary overlap are field-based, with many unknown factors affecting results. Controlled lab experiments are necessary to clarify interactions between prey availability and dietary overlap. Diving seabirds are kept in aquariums for display and could be used in such controlled experiments.

I discovered fog to affect prey types delivered to Razorbill chicks and to affect the diversity of prey types fed to Common Tern chicks; however I found no effect of fog for the other three species and found no effect of fog on feeding rates. It is still possible that fog is an important factor in seabird foraging, but I was unable to detect it in most cases.

For a more accurate test of the effect of fog on seabird foraging we need more intensive studies of the relationship between fog and foraging by recording fog condition during every feed watch. Due to the challenges of following seabirds while foraging and the complexity of factors that play in foraging and prey selection, it is difficult to pinpoint an effect of fog on foraging. If possible, future studies would benefit by small fog monitoring devices that could be attached directly on to breeding seabirds, telling fog conditions at sea as the bird forages and allowing at-sea fog data to be connected with feeding rates and prey types delivered.

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Appendix I.

Mean percent (by number) of main prey types fed to seabird chicks per year on MSI from 1995-2004.

	Common Tern	Herring	Hake	Euphausiid	Butterfish	Sandlance	Fish Larvae	Other
COTE	1995	84.9	8.2	0	0	0	0	6.8
COTE	1996	77.8	0.5	11.8	7.5	0	0	2.4
COTE	1997	89.2	0.8	0	0	6.7	0	3.3
COTE	1998	53.6	36.4	0	3.6	1.8	0	4.5
COTE	1999	50	13.9	2.4	0.8	11.4	0	21.5
COTE	2000	82.7	8.9	1.1	0.6	0.6	0	6.2
COTE	2001	28.3	14.8	2.4	0.6	44	0	9.9
COTE	2002	20.7	3.8	74.1	0	0.7	0	0.7
COTE	2003	39.6	7.9	44.6	5	0	0	2.9
COTE	2004	5.1	5.7	18.8	14.2	1.1	11.9	55.1
ARTE	1995	78.4	16.5	0	2.1	0	0	3.1
ARTE	1996	64	4	22.3	6.9	0	0	2.8
ARTE	1997	68.9	10	10	1	10	0	0
ARTE	1998	58.6	27.2	4.7	0	6.5	0	3
ARTE	1999	44.7	23.1	0.5	4.8	23.1	0	3.8
ARTE	2000	47.7	12	35.7	1.7	1.7	0	1.2
ARTE	2001	7.1	19.2	0.5	1	71.1	0	1.1
ARTE	2002	6.5	2.7	90.2	0.1	0	0	0.4
ARTE	2003	12.8	15.7	65.9	2.1	1.1	0	2.4
ARTE	2004	0.5	2	34.2	3.4	0	14	59.9
ATPU	1995	85	14.8	0.2	0	0	0	0
ATPU	1996	77.4	12.3	7.3	2.3	0	0	0.8
ATPU	1997	36.6	24.9	0	0.2	38.3	0	0
ATPU	1998	12.2	87.3	0	0.4	0.2	0	0
ATPU	1999	61.9	22.4	0	0.4	15.1	0	0.2
ATPU	2000	46.4	27.3	15.4	0.2	9.9	0	0.7
ATPU	2001	14	24.2	0.2	0.1	61.4	0	0.2
ATPU	2002	27.7	13.4	57.8	0.6	0.3	0	0.1
ATPU	2003	33.2	41.3	13.3	1.1	10.4	0	0.7
ATPU	2004	11.6	2.9	11.9	4.6	0.3	24.8	68.7
RAZO	1995	86.3	13.7	0	0	0	0	0
RAZO	1996	98.5	1.5	0	0	0	0	0
RAZO	1997	88.4	7.64	0	0	4	0	0
RAZO	1998	80.4	16.8	0	0	1.4	0	1.4
RAZO	1999	79	8	0	0.6	10.8	0	1.6
RAZO	2000	81.3	10.8	0	0	7.7	0	0.2
RAZO	2001	15.2	12.3	0	0.7	70.1	0	1.6
RAZO	2002	61.4	17.6	3.8	0	16.7	0	0.5
RAZO	2003	46.9	40.4	0	0.7	6.9	0	4.3
RAZO	2004	60.5	2	0	2	3.2	23	32.3

Appendix II.

Breeding success of seabirds nesting on Machias Seal Island between 1995 and 2004.
Alcids lay one egg per nest, so fledglings per nest = fledglings per egg.

Species	Year	N	Fledglings per nest	Fledglings per egg
Common Tern	1995	32	0.66	0.33
Common Tern	1996	56	0.29	0.18
Common Tern	1997	34	0.77	0.38
Common Tern	1998	31	0.36	0.20
Common Tern	1999	31	1.03	0.46
Common Tern	2000	34	0.53	0.30
Common Tern	2001	74	0.50	0.28
Common Tern	2002	72	0.54	0.29
Common Tern	2003	62	0.53	0.31
Common Tern	2004	68	0.05	0.03
Arctic Tern	1995	31	0.65	0.37
Arctic Tern	1996	53	0.33	0.19
Arctic Tern	1997	39	0.59	0.34
Arctic Tern	1998	41	0.41	0.23
Arctic Tern	1999	34	0.56	0.31
Arctic Tern	2000	87	0.38	0.24
Arctic Tern	2001	125	0.58	0.38
Arctic Tern	2002	285	0.50	0.32
Arctic Tern	2003	100	0.50	0.33
Arctic Tern	2004	170	0.06	0.04
Atlantic Puffin	1995	26	0.65	
Atlantic Puffin	1996	60	0.54	
Atlantic Puffin	1997	65	0.61	
Atlantic Puffin	1998	57	0.65	
Atlantic Puffin	1999	83	0.60	
Atlantic Puffin	2000	73	0.48	
Atlantic Puffin	2001	78	0.71	
Atlantic Puffin	2002	76	0.59	
Atlantic Puffin	2003	70	0.77	
Atlantic Puffin	2004	56	0.78	
Razorbill	1995	32	0.65	
Razorbill	1996	73	0.41	
Razorbill	1997	58	0.70	
Razorbill	1998	48	0.50	
Razorbill	1999	60	0.60	
Razorbill	2000	71	0.62	
Razorbill	2001	62	0.65	
Razorbill	2002	57	0.63	
Razorbill	2003	55	0.60	
Razorbill	2004	58	0.68	

Appendix III.

Simpson's Diversity Index of prey delivered to seabird chicks on MSI from 1995-2004.

Year	ARTE	ATPU	COTE	RAZO
1995	0.7132	0.4856	0.7103	0.2864
1996	0.877	0.6119	0.646	0.3402
1997	0.6526	0.7538	0.5016	0.2642
1998	0.7007	0.2672	0.7407	0.4773
1999	0.8271	0.669	0.7408	0.4599
2000	0.6868	0.7361	0.3441	0.3778
2001	0.6239	0.6099	0.7565	0.4631
2002	0.3374	0.6508	0.5064	0.5903
2003	0.6961	0.772	0.7703	0.6507
2004	0.7352	0.8744	0.8226	0.5957

Appendix IV

Linear regression equations calculating mass (y, grams) based on estimated length (x, centimeters).

Prey Type	Formula
Herring	$y=0.203x^3-.171$
Euphausiid/ Marine Invertebrates	$y=0.09x^3+.192$
Hake	$y=0.19x^3-0.083$
Hake or Herring	$y=0.2x^3-.107$
Larvae	$y=0.15x-0.056$
Sandlance	$y=0.14x^3-0.166$
Butterfish	$y-0.24x^3-.126$
Unidentified Fish	$y=0.19x^3-0.04$
Sticklebacks	$y=0.08x^3+.647$
Lumpfish	$y=.26x^3+.284$
Unidentified	$y=0.16x^3+0.148$
Polychaete	$y=.0771x^3$

Appendix V.

Proportion of Euphausiids, Hake, Herring, and Sandlance delivered to seabird chicks per day on MSI from 1995-2004. Unknown and infrequently delivered prey items are not included, so the sums of all daily proportions are often less than 1.

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ARTE	7/2/1995	0.00	0.10	0.60	0.00
ARTE	7/6/1995	0.00	0.00	1.00	0.00
ARTE	7/10/1995	0.00	0.04	0.57	0.00
ARTE	7/12/1995	0.00	0.00	0.40	0.00
ARTE	7/13/1995	0.00	0.33	0.17	0.00
ARTE	7/14/1995	0.00	0.00	0.50	0.00
ARTE	7/16/1995	0.00	0.13	0.50	0.00
ARTE	7/17/1995	0.00	0.00	0.67	0.00
ARTE	7/20/1995	0.00	0.25	0.42	0.00
ARTE	7/21/1995	0.00	0.10	0.40	0.00
ARTE	7/22/1995	0.00	0.23	0.62	0.00
ARTE	7/24/1995	0.00	0.00	0.33	0.00
ARTE	7/26/1995	0.00	0.15	0.46	0.00
ARTE	7/27/1995	0.00	0.14	0.43	0.00
ARTE	7/28/1995	0.00	0.00	0.27	0.00
ARTE	7/29/1995	0.00	0.20	0.20	0.00
ARTE	7/7/1996	0.46	0.12	0.00	0.00
ARTE	7/8/1996	0.50	0.13	0.13	0.00
ARTE	7/9/1996	0.38	0.19	0.00	0.00
ARTE	7/10/1996	0.90	0.00	0.00	0.00
ARTE	7/11/1996	0.17	0.00	0.67	0.00
ARTE	7/12/1996	0.00	0.00	0.60	0.00
ARTE	7/13/1996	0.17	0.00	0.17	0.00
ARTE	7/15/1996	0.00	0.00	0.00	0.00
ARTE	7/16/1996	0.00	0.00	0.50	0.00
ARTE	7/17/1996	0.04	0.00	0.48	0.00
ARTE	7/18/1996	0.00	0.00	1.00	0.00
ARTE	7/19/1996	0.08	0.00	0.69	0.00
ARTE	7/20/1996	0.00	0.00	0.71	0.00
ARTE	7/21/1996	0.00	0.00	0.88	0.00
ARTE	7/22/1996	0.00	0.00	0.56	0.00
ARTE	7/23/1996	0.00	0.00	0.28	0.00
ARTE	7/24/1996	0.00	0.00	0.44	0.00
ARTE	7/25/1996	0.00	0.00	0.00	0.00
ARTE	7/26/1996	0.00	0.00	0.00	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ARTE	7/27/1996	0.00	0.00	0.38	0.00
ARTE	7/28/1996	0.00	0.00	0.89	0.00
ARTE	7/29/1996	0.00	0.00	0.00	0.00
ARTE	7/30/1996	0.00	0.00	0.75	0.00
ARTE	7/31/1996	0.00	0.00	0.27	0.00
ARTE	8/2/1996	0.00	0.00	0.33	0.00
ARTE	6/30/1997	0.33	0.22	0.11	0.22
ARTE	7/1/1997	0.00	0.40	0.20	0.40
ARTE	7/3/1997	0.00	0.41	0.18	0.36
ARTE	7/7/1997	0.00	0.00	0.62	0.08
ARTE	7/8/1997	0.21	0.00	0.71	0.04
ARTE	7/9/1997	0.00	0.00	0.56	0.11
ARTE	7/11/1997	0.21	0.15	0.44	0.03
ARTE	7/12/1997	0.00	0.00	0.40	0.33
ARTE	7/13/1997	0.13	0.11	0.47	0.00
ARTE	7/14/1997	0.03	0.00	0.73	0.00
ARTE	7/15/1997	0.00	0.02	0.74	0.00
ARTE	7/16/1997	0.00	0.00	0.88	0.00
ARTE	7/17/1997	0.00	0.09	0.73	0.00
ARTE	6/26/1998	0.00	0.75	0.00	0.00
ARTE	6/29/1998	0.17	0.06	0.17	0.28
ARTE	6/30/1998	0.33	0.33	0.17	0.17
ARTE	7/1/1998	0.00	0.64	0.07	0.07
ARTE	7/2/1998	0.00	0.50	0.17	0.00
ARTE	7/3/1998	0.00	0.29	0.29	0.00
ARTE	7/5/1998	0.00	0.33	0.33	0.00
ARTE	7/7/1998	0.00	0.13	0.69	0.00
ARTE	7/9/1998	0.05	0.00	0.56	0.00
ARTE	7/10/1998	0.00	0.08	0.75	0.04
ARTE	7/11/1998	0.06	0.00	0.47	0.00
ARTE	7/12/1998	0.00	0.00	0.00	0.25
ARTE	7/15/1998	0.00	0.23	0.42	0.04
ARTE	7/16/1998	0.00	0.38	0.52	0.00
ARTE	6/26/1999	0.00	0.14	0.36	0.00
ARTE	6/27/1999	0.00	0.00	0.64	0.27
ARTE	7/1/1999	0.00	0.08	0.21	0.33
ARTE	7/3/1999	0.00	0.25	0.00	0.00
ARTE	7/4/1999	0.00	0.00	0.63	0.16
ARTE	7/5/1999	0.08	0.08	0.42	0.17
ARTE	7/6/1999	0.00	0.25	0.34	0.03
ARTE	7/8/1999	0.00	0.25	0.42	0.08
ARTE	7/9/1999	0.00	0.39	0.26	0.13
ARTE	7/11/1999	0.00	0.20	0.20	0.10

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ARTE	7/12/1999	0.00	0.12	0.17	0.29
ARTE	7/13/1999	0.00	0.29	0.00	0.43
ARTE	7/15/1999	0.00	0.16	0.16	0.28
ARTE	7/17/1999	0.00	0.10	0.50	0.00
ARTE	7/18/1999	0.00	0.00	1.00	0.00
ARTE	7/19/1999	0.00	0.13	0.63	0.00
ARTE	7/20/1999	0.00	0.00	0.67	0.00
ARTE	7/21/1999	0.00	0.00	0.50	0.17
ARTE	7/2/2000	0.00	0.00	1.00	0.00
ARTE	7/5/2000	0.00	0.00	1.00	0.00
ARTE	7/6/2000	0.25	0.00	0.42	0.00
ARTE	7/7/2000	0.08	0.31	0.54	0.00
ARTE	7/8/2000	0.77	0.00	0.10	0.10
ARTE	7/11/2000	0.44	0.13	0.25	0.00
ARTE	7/12/2000	0.25	0.17	0.50	0.00
ARTE	7/15/2000	0.38	0.00	0.32	0.00
ARTE	7/16/2000	0.00	0.00	0.86	0.00
ARTE	7/17/2000	0.26	0.06	0.65	0.00
ARTE	7/19/2000	0.00	0.00	1.00	0.00
ARTE	7/20/2000	0.20	0.60	0.00	0.00
ARTE	7/21/2000	0.07	0.13	0.67	0.00
ARTE	7/22/2000	0.25	0.25	0.33	0.00
ARTE	7/23/2000	0.63	0.19	0.13	0.00
ARTE	7/24/2000	0.00	0.45	0.55	0.00
ARTE	7/25/2000	0.14	0.14	0.57	0.00
ARTE	7/26/2000	0.00	0.13	0.50	0.00
ARTE	7/27/2000	0.00	0.00	1.00	0.00
ARTE	7/28/2000	0.00	0.25	0.75	0.00
ARTE	7/30/2000	0.00	0.00	1.00	0.00
ARTE	7/31/2000	0.00	0.00	1.00	0.00
ARTE	8/1/2000	0.00	0.00	0.75	0.00
ARTE	6/29/2001	0.00	0.20	0.20	0.40
ARTE	6/30/2001	0.03	0.07	0.13	0.33
ARTE	7/1/2001	0.06	0.00	0.00	0.76
ARTE	7/3/2001	0.00	0.11	0.00	0.89
ARTE	7/4/2001	0.00	0.22	0.06	0.72
ARTE	7/5/2001	0.00	0.04	0.04	0.32
ARTE	7/6/2001	0.00	0.08	0.00	0.87
ARTE	7/7/2001	0.00	0.12	0.00	0.80
ARTE	7/8/2001	0.00	0.05	0.00	0.55
ARTE	7/9/2001	0.00	0.03	0.00	0.92
ARTE	7/12/2001	0.00	0.03	0.00	0.29
ARTE	7/13/2001	0.00	0.31	0.04	0.57

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ARTE	7/14/2001	0.00	0.11	0.00	0.78
ARTE	7/15/2001	0.00	0.74	0.16	0.11
ARTE	7/16/2001	0.00	0.65	0.12	0.09
ARTE	7/19/2001	0.00	0.19	0.00	0.75
ARTE	7/20/2001	0.00	0.19	0.14	0.62
ARTE	7/21/2001	0.00	0.14	0.07	0.34
ARTE	7/22/2001	0.00	0.59	0.24	0.06
ARTE	7/23/2001	0.00	0.16	0.44	0.32
ARTE	7/27/2001	0.00	0.00	0.67	0.33
ARTE	6/28/2002	0.53	0.33	0.00	0.00
ARTE	6/30/2002	0.74	0.07	0.00	0.00
ARTE	7/1/2002	0.91	0.04	0.00	0.00
ARTE	7/2/2002	0.71	0.02	0.00	0.00
ARTE	7/4/2002	0.94	0.03	0.01	0.00
ARTE	7/7/2002	0.95	0.01	0.00	0.00
ARTE	7/8/2002	0.81	0.00	0.00	0.00
ARTE	7/10/2002	0.95	0.00	0.04	0.00
ARTE	7/11/2002	0.56	0.00	0.03	0.00
ARTE	7/13/2002	0.00	0.14	0.86	0.00
ARTE	7/14/2002	0.71	0.00	0.00	0.00
ARTE	7/17/2002	0.25	0.00	0.71	0.00
ARTE	7/19/2002	0.83	0.00	0.11	0.00
ARTE	7/20/2002	0.99	0.00	0.01	0.00
ARTE	7/21/2002	0.82	0.00	0.15	0.00
ARTE	7/22/2002	0.47	0.00	0.27	0.00
ARTE	7/23/2002	0.60	0.00	0.35	0.00
ARTE	7/26/2002	0.87	0.00	0.10	0.00
ARTE	7/27/2002	0.23	0.00	0.31	0.00
ARTE	7/28/2002	0.84	0.00	0.16	0.00
ARTE	7/30/2002	0.64	0.00	0.09	0.00
ARTE	8/2/2002	0.00	0.00	0.00	0.00
ARTE	6/30/2003	0.08	0.62	0.15	0.00
ARTE	7/2/2003	0.06	0.65	0.06	0.12
ARTE	7/4/2003	0.00	0.88	0.00	0.00
ARTE	7/6/2003	0.00	0.59	0.00	0.00
ARTE	7/7/2003	0.06	0.35	0.18	0.00
ARTE	7/8/2003	0.17	0.25	0.17	0.00
ARTE	7/12/2003	0.64	0.00	0.02	0.01
ARTE	7/14/2003	0.10	0.20	0.10	0.10
ARTE	7/16/2003	0.33	0.00	0.11	0.00
ARTE	7/17/2003	0.00	0.10	0.10	0.00
ARTE	7/19/2003	0.25	0.42	0.13	0.00
ARTE	7/22/2003	0.74	0.00	0.00	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ARTE	7/23/2003	0.59	0.03	0.14	0.00
ARTE	7/24/2003	0.73	0.01	0.12	0.00
ARTE	7/25/2003	0.54	0.05	0.19	0.00
ARTE	7/26/2003	0.25	0.00	0.25	0.00
ARTE	6/29/2004	0.00	0.25	0.00	0.00
ARTE	7/1/2004	0.36	0.18	0.00	0.00
ARTE	7/2/2004	0.32	0.00	0.00	0.00
ARTE	7/3/2004	0.00	0.00	0.00	0.00
ARTE	7/4/2004	0.25	0.00	0.00	0.00
ARTE	7/6/2004	0.11	0.11	0.00	0.00
ARTE	7/8/2004	0.13	0.00	0.00	0.00
ARTE	7/9/2004	0.47	0.00	0.00	0.00
ARTE	7/10/2004	0.21	0.00	0.00	0.00
ARTE	7/11/2004	0.48	0.00	0.00	0.00
ARTE	7/12/2004	0.54	0.00	0.00	0.00
ARTE	7/15/2004	0.43	0.05	0.01	0.00
ARTE	7/16/2004	0.13	0.13	0.00	0.00
ARTE	7/18/2004	0.33	0.00	0.00	0.00
ARTE	7/19/2004	0.00	0.00	0.04	0.00
ARTE	7/21/2004	0.31	0.00	0.00	0.00
ARTE	7/22/2004	0.00	0.17	0.00	0.00
ARTE	7/23/2004	0.11	0.00	0.00	0.00
ARTE	7/24/2004	0.00	0.00	0.00	0.00
ARTE	7/25/2004	0.00	0.14	0.00	0.00
ARTE	7/27/2004	0.81	0.00	0.02	0.00
ARTE	7/28/2004	0.04	0.00	0.09	0.00
ARTE	7/29/2004	0.44	0.00	0.00	0.00
ARTE	7/30/2004	0.00	0.00	0.50	0.00
ARTE	7/31/2004	0.48	0.00	0.02	0.00
ARTE	8/1/2004	0.00	0.00	0.14	0.00
ATPU	6/8/1995	0.00	0.00	0.00	0.00
ATPU	6/13/1995	0.00	0.24	0.48	0.16
ATPU	6/29/1995	0.00	0.00	1.00	0.00
ATPU	7/2/1995	0.00	0.00	0.31	0.13
ATPU	7/5/1995	0.00	0.18	0.82	0.00
ATPU	7/7/1995	0.00	0.19	0.62	0.00
ATPU	7/9/1995	0.00	0.03	0.95	0.00
ATPU	7/11/1995	0.00	0.00	1.00	0.00
ATPU	7/13/1995	0.00	0.00	0.47	0.00
ATPU	7/14/1995	0.00	0.25	0.61	0.00
ATPU	7/17/1995	0.00	0.00	0.81	0.00
ATPU	7/19/1995	0.00	0.55	0.39	0.00
ATPU	7/20/1995	0.00	0.45	0.55	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ATPU	7/21/1995	0.00	0.09	0.82	0.00
ATPU	7/22/1995	0.00	0.00	1.00	0.00
ATPU	7/23/1995	0.00	0.02	0.86	0.00
ATPU	7/24/1995	0.00	0.00	0.80	0.00
ATPU	7/26/1995	0.03	0.25	0.65	0.05
ATPU	7/27/1995	0.00	0.00	0.98	0.00
ATPU	7/28/1995	0.00	0.02	0.77	0.00
ATPU	7/29/1995	0.00	0.00	0.83	0.00
ATPU	7/31/1995	0.00	0.00	1.00	0.00
ATPU	7/7/1996	0.39	0.11	0.20	0.02
ATPU	7/8/1996	0.00	0.55	0.03	0.00
ATPU	7/9/1996	0.20	0.00	0.40	0.00
ATPU	7/10/1996	0.00	0.05	0.74	0.00
ATPU	7/11/1996	0.13	0.00	0.66	0.00
ATPU	7/12/1996	0.00	0.00	0.00	0.00
ATPU	7/14/1996	0.00	0.00	0.40	0.00
ATPU	7/15/1996	0.00	0.70	0.10	0.00
ATPU	7/16/1996	0.00	0.12	0.33	0.00
ATPU	7/17/1996	0.00	0.00	0.64	0.00
ATPU	7/18/1996	0.00	0.00	0.83	0.00
ATPU	7/19/1996	0.00	0.00	0.62	0.00
ATPU	7/22/1996	0.00	0.11	0.46	0.00
ATPU	7/23/1996	0.00	0.00	0.57	0.00
ATPU	7/25/1996	0.00	0.00	0.30	0.00
ATPU	7/26/1996	0.02	0.00	0.30	0.00
ATPU	7/28/1996	0.04	0.00	0.59	0.00
ATPU	7/30/1996	0.00	0.00	0.70	0.00
ATPU	8/2/1996	0.00	0.00	0.25	0.00
ATPU	6/28/1997	0.00	0.37	0.24	0.32
ATPU	7/3/1997	0.00	0.46	0.00	0.39
ATPU	7/5/1997	0.00	0.18	0.00	0.78
ATPU	7/10/1997	0.00	0.14	0.60	0.11
ATPU	7/12/1997	0.00	0.22	0.26	0.24
ATPU	7/15/1997	0.00	0.00	0.45	0.19
ATPU	7/20/1997	0.00	0.07	0.88	0.00
ATPU	7/27/1997	0.00	0.00	1.00	0.00
ATPU	8/1/1997	0.00	0.08	0.92	0.00
ATPU	8/2/1997	0.00	0.00	1.00	0.00
ATPU	6/30/1998	0.00	0.63	0.27	0.00
ATPU	7/1/1998	0.00	1.00	0.00	0.00
ATPU	7/7/1998	0.00	0.86	0.11	0.02
ATPU	7/10/1998	0.00	1.00	0.00	0.00
ATPU	7/13/1998	0.00	0.68	0.30	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ATPU	7/14/1998	0.00	0.21	0.62	0.00
ATPU	7/15/1998	0.00	0.12	0.88	0.00
ATPU	7/19/1998	0.00	1.00	0.00	0.00
ATPU	7/21/1998	0.00	0.97	0.03	0.00
ATPU	7/26/1998	0.00	0.97	0.03	0.00
ATPU	7/27/1998	0.00	1.00	0.00	0.00
ATPU	6/25/1999	0.00	0.00	0.40	0.19
ATPU	6/27/1999	0.00	0.06	0.49	0.24
ATPU	7/1/1999	0.00	0.29	0.61	0.10
ATPU	7/5/1999	0.00	0.15	0.72	0.04
ATPU	7/6/1999	0.00	0.05	0.82	0.05
ATPU	7/8/1999	0.00	0.10	0.68	0.16
ATPU	7/9/1999	0.00	0.13	0.40	0.16
ATPU	7/12/1999	0.00	0.40	0.17	0.33
ATPU	7/14/1999	0.00	0.28	0.24	0.30
ATPU	7/17/1999	0.00	0.24	0.29	0.09
ATPU	7/19/1999	0.00	0.44	0.43	0.08
ATPU	7/20/1999	0.00	0.09	0.64	0.06
ATPU	7/21/1999	0.00	0.12	0.82	0.02
ATPU	7/22/1999	0.00	0.00	0.81	0.05
ATPU	6/24/2000	0.00	0.48	0.00	0.52
ATPU	6/25/2000	0.13	0.28	0.14	0.33
ATPU	6/26/2000	0.36	0.54	0.03	0.07
ATPU	6/27/2000	0.02	0.33	0.26	0.25
ATPU	7/2/2000	0.00	0.07	0.49	0.00
ATPU	7/5/2000	0.00	0.00	0.94	0.00
ATPU	7/7/2000	0.04	0.28	0.26	0.02
ATPU	7/8/2000	0.11	0.73	0.14	0.03
ATPU	7/9/2000	0.08	0.20	0.68	0.00
ATPU	7/10/2000	0.61	0.36	0.03	0.00
ATPU	7/14/2000	0.94	0.00	0.05	0.00
ATPU	7/15/2000	0.23	0.53	0.24	0.00
ATPU	7/16/2000	0.04	0.27	0.60	0.08
ATPU	7/17/2000	0.00	0.00	1.00	0.00
ATPU	7/20/2000	0.06	0.00	0.94	0.00
ATPU	7/21/2000	0.09	0.14	0.64	0.05
ATPU	7/22/2000	0.00	0.71	0.06	0.00
ATPU	7/23/2000	0.00	0.45	0.55	0.00
ATPU	7/24/2000	0.00	1.00	0.00	0.00
ATPU	7/25/2000	0.00	0.00	1.00	0.00
ATPU	7/26/2000	0.00	0.00	1.00	0.00
ATPU	7/27/2000	0.02	0.37	0.59	0.00
ATPU	7/28/2000	0.00	0.00	0.92	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ATPU	7/29/2000	0.00	0.00	0.96	0.00
ATPU	7/30/2000	0.00	0.04	0.96	0.00
ATPU	7/31/2000	0.00	0.00	0.97	0.00
ATPU	6/29/2001	0.00	0.13	0.03	0.84
ATPU	6/30/2001	0.00	0.39	0.00	0.58
ATPU	7/1/2001	0.03	0.20	0.00	0.76
ATPU	7/3/2001	0.00	0.12	0.00	0.88
ATPU	7/4/2001	0.00	0.00	0.04	0.37
ATPU	7/5/2001	0.00	0.01	0.00	0.98
ATPU	7/7/2001	0.00	0.00	0.00	0.62
ATPU	7/8/2001	0.00	0.13	0.00	0.87
ATPU	7/9/2001	0.00	0.11	0.00	0.89
ATPU	7/10/2001	0.00	0.03	0.02	0.73
ATPU	7/13/2001	0.00	0.61	0.01	0.38
ATPU	7/19/2001	0.00	0.07	0.35	0.53
ATPU	7/20/2001	0.00	0.09	0.03	0.58
ATPU	7/21/2001	0.00	0.35	0.23	0.39
ATPU	7/22/2001	0.00	0.55	0.27	0.18
ATPU	7/23/2001	0.00	0.11	0.34	0.26
ATPU	7/25/2001	0.00	0.39	0.00	0.57
ATPU	7/26/2001	0.00	0.50	0.48	0.01
ATPU	7/27/2001	0.00	0.00	0.61	0.33
ATPU	7/28/2001	0.00	0.19	0.22	0.58
ATPU	7/29/2001	0.00	0.61	0.00	0.39
ATPU	8/2/2001	0.00	0.47	0.00	0.53
ATPU	6/3/2002	0.58	0.21	0.00	0.01
ATPU	6/25/2002	0.72	0.19	0.08	0.00
ATPU	6/28/2002	0.19	0.38	0.02	0.00
ATPU	6/29/2002	0.45	0.37	0.15	0.00
ATPU	7/1/2002	0.50	0.21	0.00	0.00
ATPU	7/4/2002	0.85	0.11	0.00	0.00
ATPU	7/6/2002	0.91	0.07	0.01	0.00
ATPU	7/8/2002	0.89	0.04	0.01	0.01
ATPU	7/9/2002	0.57	0.17	0.00	0.00
ATPU	7/11/2002	0.00	0.03	0.95	0.00
ATPU	7/12/2002	0.00	0.00	1.00	0.00
ATPU	7/14/2002	0.26	0.00	0.74	0.00
ATPU	7/17/2002	0.13	0.03	0.55	0.00
ATPU	7/18/2002	0.20	0.00	0.59	0.00
ATPU	7/19/2002	0.00	0.00	1.00	0.00
ATPU	7/21/2002	0.19	0.00	0.73	0.00
ATPU	7/22/2002	0.48	0.00	0.48	0.00
ATPU	7/23/2002	0.00	0.00	1.00	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ATPU	7/26/2002	0.10	0.03	0.60	0.00
ATPU	7/27/2002	0.75	0.00	0.25	0.00
ATPU	7/28/2002	0.60	0.00	0.40	0.00
ATPU	7/30/2002	0.00	0.00	0.67	0.00
ATPU	8/2/2002	0.00	0.00	0.67	0.33
ATPU	6/27/2003	0.00	0.88	0.00	0.12
ATPU	6/28/2003	0.17	0.76	0.00	0.06
ATPU	6/30/2003	0.00	0.76	0.00	0.14
ATPU	7/2/2003	0.00	0.68	0.00	0.25
ATPU	7/4/2003	0.00	0.33	0.00	0.21
ATPU	7/5/2003	0.00	0.60	0.00	0.01
ATPU	7/7/2003	0.00	0.26	0.09	0.20
ATPU	7/10/2003	0.14	0.29	0.19	0.16
ATPU	7/12/2003	0.13	0.11	0.41	0.05
ATPU	7/13/2003	0.00	0.02	0.44	0.07
ATPU	7/14/2003	0.08	0.24	0.47	0.00
ATPU	7/15/2003	0.45	0.24	0.16	0.06
ATPU	7/16/2003	0.00	0.03	0.60	0.09
ATPU	7/17/2003	0.00	0.20	0.36	0.00
ATPU	7/18/2003	0.16	0.44	0.17	0.13
ATPU	7/19/2003	0.03	0.00	0.25	0.00
ATPU	7/20/2003	0.00	0.41	0.12	0.00
ATPU	7/22/2003	0.40	0.05	0.35	0.07
ATPU	7/31/2003	0.00	0.00	0.68	0.02
ATPU	7/3/2004	0.00	0.00	0.05	0.00
ATPU	7/4/2004	0.03	0.00	0.33	0.00
ATPU	7/5/2004	0.00	0.00	0.00	0.00
ATPU	7/6/2004	0.00	0.04	0.04	0.00
ATPU	7/7/2004	0.14	0.00	0.28	0.00
ATPU	7/9/2004	0.26	0.00	0.00	0.00
ATPU	7/10/2004	0.33	0.00	0.00	0.00
ATPU	7/11/2004	0.00	0.00	0.42	0.00
ATPU	7/12/2004	0.05	0.00	0.00	0.00
ATPU	7/14/2004	0.00	0.01	0.20	0.00
ATPU	7/17/2004	0.00	0.04	0.16	0.01
ATPU	7/18/2004	0.02	0.00	0.02	0.03
ATPU	7/20/2004	0.04	0.09	0.04	0.00
ATPU	7/21/2004	0.00	0.05	0.00	0.00
ATPU	7/24/2004	0.38	0.02	0.00	0.00
ATPU	7/25/2004	0.43	0.17	0.03	0.00
ATPU	7/26/2004	0.21	0.00	0.20	0.00
ATPU	7/27/2004	0.27	0.13	0.15	0.00
ATPU	7/28/2004	0.36	0.03	0.40	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
ATPU	7/29/2004	0.35	0.00	0.18	0.00
ATPU	7/30/2004	0.03	0.01	0.45	0.00
ATPU	7/31/2004	0.00	0.00	0.33	0.00
ATPU	8/1/2004	0.27	0.01	0.27	0.00
ATPU	8/4/2004	0.22	0.30	0.15	0.00
COTE	7/3/1995	0.00	0.12	0.76	0.00
COTE	7/5/1995	0.00	0.00	0.33	0.11
COTE	7/7/1995	0.00	0.06	0.55	0.00
COTE	7/9/1995	0.00	0.00	0.67	0.00
COTE	7/11/1995	0.00	0.00	0.20	0.00
COTE	7/13/1995	0.00	0.00	0.69	0.00
COTE	7/14/1995	0.00	0.07	0.50	0.00
COTE	7/15/1995	0.00	0.00	0.80	0.00
COTE	7/17/1995	0.00	0.11	0.50	0.00
COTE	7/19/1995	0.00	0.17	0.22	0.00
COTE	7/20/1995	0.00	0.13	0.25	0.00
COTE	7/21/1995	0.00	0.05	0.26	0.00
COTE	7/22/1995	0.00	0.00	0.92	0.00
COTE	7/24/1995	0.00	0.00	0.88	0.00
COTE	7/25/1995	0.05	0.00	0.10	0.00
COTE	7/26/1995	0.00	0.00	0.00	0.00
COTE	7/27/1995	0.00	0.00	0.20	0.00
COTE	7/28/1995	0.00	0.00	0.17	0.00
COTE	7/31/1995	0.00	0.11	0.56	0.00
COTE	7/7/1996	0.00	0.00	0.67	0.00
COTE	7/9/1996	0.17	0.17	0.67	0.00
COTE	7/10/1996	0.00	0.00	0.56	0.00
COTE	7/11/1996	0.00	0.00	0.67	0.00
COTE	7/12/1996	0.00	0.00	0.78	0.00
COTE	7/14/1996	0.00	0.00	0.47	0.00
COTE	7/15/1996	0.00	0.00	1.00	0.00
COTE	7/16/1996	0.00	0.00	0.50	0.00
COTE	7/17/1996	0.00	0.00	0.62	0.00
COTE	7/18/1996	0.00	0.00	0.60	0.00
COTE	7/19/1996	0.00	0.00	0.92	0.00
COTE	7/20/1996	0.00	0.00	0.71	0.00
COTE	7/21/1996	0.00	0.00	0.45	0.00
COTE	7/22/1996	0.00	0.00	0.63	0.00
COTE	7/23/1996	0.00	0.00	0.80	0.00
COTE	7/24/1996	0.00	0.00	0.00	0.00
COTE	7/25/1996	0.00	0.00	0.50	0.00
COTE	7/26/1996	0.00	0.00	0.60	0.00
COTE	7/27/1996	0.00	0.00	0.00	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
COTE	7/28/1996	0.00	0.00	0.62	0.00
COTE	7/29/1996	0.00	0.00	0.65	0.00
COTE	7/30/1996	0.00	0.00	0.90	0.00
COTE	7/31/1996	0.00	0.00	0.00	0.00
COTE	8/2/1996	0.00	0.00	0.82	0.00
COTE	8/3/1996	0.00	0.00	1.00	0.00
COTE	8/4/1996	0.44	0.00	0.00	0.00
COTE	8/5/1996	0.54	0.00	0.09	0.00
COTE	7/7/1997	0.00	0.00	0.25	0.50
COTE	7/8/1997	0.00	0.00	0.83	0.00
COTE	7/9/1997	0.00	0.00	0.50	0.00
COTE	7/11/1997	0.00	0.04	0.48	0.13
COTE	7/14/1997	0.00	0.00	0.77	0.00
COTE	7/18/1997	0.00	0.00	0.72	0.00
COTE	7/19/1997	0.00	0.00	0.93	0.00
COTE	7/23/1997	0.00	0.00	0.55	0.09
COTE	7/25/1997	0.00	0.00	1.00	0.00
COTE	7/27/1997	0.00	0.00	1.00	0.00
COTE	7/29/1997	0.00	0.00	0.53	0.12
COTE	7/31/1997	0.00	0.00	0.33	0.11
COTE	8/3/1997	0.00	0.00	0.75	0.00
COTE	7/2/1998	0.00	0.38	0.38	0.15
COTE	7/3/1998	0.00	0.19	0.69	0.00
COTE	7/4/1998	0.00	0.58	0.33	0.00
COTE	7/9/1998	0.00	0.28	0.48	0.00
COTE	7/13/1998	0.00	0.11	0.78	0.00
COTE	7/14/1998	0.00	0.49	0.21	0.00
COTE	7/15/1998	0.00	0.75	0.00	0.00
COTE	7/16/1998	0.00	0.35	0.47	0.00
COTE	7/21/1998	0.00	0.00	0.07	0.00
COTE	7/23/1998	0.00	0.00	0.18	0.00
COTE	7/1/1999	0.00	0.25	0.25	0.50
COTE	7/4/1999	0.00	0.14	0.64	0.00
COTE	7/5/1999	0.00	0.00	0.67	0.00
COTE	7/6/1999	0.00	0.14	0.64	0.05
COTE	7/8/1999	0.00	0.36	0.50	0.00
COTE	7/9/1999	0.00	0.40	0.15	0.10
COTE	7/11/1999	0.02	0.21	0.17	0.21
COTE	7/12/1999	0.00	0.09	0.38	0.34
COTE	7/13/1999	0.00	0.00	0.38	0.25
COTE	7/15/1999	0.00	0.15	0.33	0.08
COTE	7/17/1999	0.13	0.17	0.27	0.10
COTE	7/18/1999	0.00	0.04	0.52	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
COTE	7/19/1999	0.07	0.02	0.53	0.00
COTE	7/20/1999	0.02	0.00	0.57	0.09
COTE	7/21/1999	0.00	0.00	0.78	0.00
COTE	7/22/1999	0.00	0.00	0.83	0.00
COTE	7/1/2000	0.00	0.00	1.00	0.00
COTE	7/2/2000	0.00	0.13	0.88	0.00
COTE	7/6/2000	0.00	0.06	0.88	0.00
COTE	7/7/2000	0.00	1.00	0.00	0.00
COTE	7/8/2000	0.00	0.20	0.70	0.00
COTE	7/11/2000	0.00	0.00	0.33	0.17
COTE	7/12/2000	0.00	0.27	0.55	0.00
COTE	7/14/2000	0.00	0.33	0.67	0.00
COTE	7/15/2000	0.13	0.00	0.80	0.00
COTE	7/16/2000	0.00	0.10	0.60	0.00
COTE	7/17/2000	0.00	0.00	1.00	0.00
COTE	7/19/2000	0.00	0.00	1.00	0.00
COTE	7/20/2000	0.00	0.10	0.70	0.00
COTE	7/21/2000	0.00	0.00	0.67	0.00
COTE	7/22/2000	0.00	0.00	0.80	0.00
COTE	7/23/2000	0.00	0.29	0.57	0.00
COTE	7/24/2000	0.00	0.00	1.00	0.00
COTE	7/25/2000	0.00	0.00	1.00	0.00
COTE	7/26/2000	0.00	0.13	0.88	0.00
COTE	7/27/2000	0.00	0.00	1.00	0.00
COTE	7/28/2000	0.00	0.00	1.00	0.00
COTE	7/29/2000	0.00	0.00	0.90	0.00
COTE	7/30/2000	0.00	0.00	1.00	0.00
COTE	7/31/2000	0.00	0.00	1.00	0.00
COTE	7/7/2001	0.00	0.07	0.00	0.65
COTE	7/8/2001	0.00	0.07	0.00	0.89
COTE	7/10/2001	0.00	0.18	0.04	0.68
COTE	7/14/2001	0.00	0.10	0.05	0.69
COTE	7/16/2001	0.00	0.34	0.09	0.40
COTE	7/19/2001	0.00	0.17	0.17	0.27
COTE	7/20/2001	0.00	0.05	0.21	0.36
COTE	7/21/2001	0.00	0.42	0.17	0.42
COTE	7/22/2001	0.00	0.14	0.12	0.39
COTE	7/23/2001	0.00	0.09	0.35	0.23
COTE	7/25/2001	0.18	0.27	0.21	0.09
COTE	7/26/2001	0.00	0.04	0.63	0.13
COTE	7/27/2001	0.00	0.15	0.78	0.07
COTE	7/28/2001	0.00	0.13	0.38	0.19
COTE	7/29/2001	0.04	0.04	0.36	0.22

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
COTE	6/24/2002	0.31	0.62	0.08	0.00
COTE	6/29/2002	0.19	0.38	0.00	0.10
COTE	7/1/2002	0.71	0.04	0.08	0.00
COTE	7/2/2002	0.96	0.00	0.03	0.01
COTE	7/3/2002	0.86	0.09	0.05	0.00
COTE	7/6/2002	0.78	0.03	0.00	0.00
COTE	7/7/2002	0.88	0.00	0.05	0.00
COTE	7/9/2002	0.92	0.04	0.03	0.00
COTE	7/10/2002	0.74	0.02	0.21	0.00
COTE	7/12/2002	0.00	0.00	1.00	0.00
COTE	7/13/2002	0.35	0.00	0.65	0.00
COTE	7/17/2002	0.11	0.00	0.89	0.00
COTE	7/18/2002	0.32	0.00	0.32	0.00
COTE	7/19/2002	0.33	0.00	0.67	0.00
COTE	7/21/2002	0.40	0.00	0.60	0.00
COTE	7/23/2002	0.44	0.00	0.25	0.00
COTE	7/26/2002	0.15	0.00	0.85	0.00
COTE	7/28/2002	0.00	0.00	1.00	0.00
COTE	7/30/2002	1.00	0.00	0.00	0.00
COTE	7/5/2003	0.50	0.33	0.00	0.00
COTE	7/8/2003	0.43	0.05	0.00	0.00
COTE	7/10/2003	0.30	0.17	0.17	0.00
COTE	7/13/2003	0.76	0.00	0.02	0.00
COTE	7/15/2003	0.29	0.14	0.00	0.00
COTE	7/16/2003	0.04	0.14	0.18	0.04
COTE	7/18/2003	0.00	0.11	0.44	0.00
COTE	7/19/2003	0.00	0.00	0.55	0.00
COTE	7/20/2003	0.00	0.25	0.25	0.00
COTE	7/22/2003	0.79	0.00	0.00	0.00
COTE	7/23/2003	0.06	0.00	0.72	0.00
COTE	7/24/2003	0.40	0.10	0.23	0.00
COTE	7/25/2003	0.57	0.00	0.00	0.00
COTE	7/26/2003	0.45	0.00	0.18	0.00
COTE	7/27/2003	0.04	0.00	0.80	0.00
COTE	7/28/2003	0.13	0.10	0.31	0.00
COTE	7/5/2004	0.00	0.31	0.00	0.00
COTE	7/7/2004	0.00	0.00	0.00	0.00
COTE	7/9/2004	0.38	0.04	0.04	0.04
COTE	7/11/2004	0.39	0.03	0.00	0.00
COTE	7/13/2004	0.13	0.13	0.00	0.00
COTE	7/14/2004	0.25	0.00	0.00	0.00
COTE	7/15/2004	0.14	0.14	0.00	0.00
COTE	7/16/2004	0.00	0.00	0.07	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
COTE	7/19/2004	0.00	0.11	0.00	0.00
COTE	7/20/2004	0.27	0.00	0.09	0.00
COTE	7/21/2004	0.00	0.00	0.13	0.00
COTE	7/23/2004	0.09	0.00	0.00	0.00
COTE	7/26/2004	0.33	0.00	0.17	0.17
COTE	7/27/2004	0.06	0.00	0.22	0.00
RAZO	7/3/1995	0.00	0.32	0.55	0.00
RAZO	7/6/1995	0.00	0.14	0.72	0.00
RAZO	7/8/1995	0.00	0.13	0.83	0.00
RAZO	7/10/1995	0.00	0.00	1.00	0.00
RAZO	7/12/1995	0.00	0.00	1.00	0.00
RAZO	7/14/1995	0.00	0.00	1.00	0.00
RAZO	7/15/1995	0.00	0.00	1.00	0.00
RAZO	7/16/1995	0.00	0.05	0.95	0.00
RAZO	7/17/1995	0.00	0.00	1.00	0.00
RAZO	7/20/1995	0.00	0.00	1.00	0.00
RAZO	7/21/1995	0.00	1.00	0.00	0.00
RAZO	7/23/1995	0.00	0.00	1.00	0.00
RAZO	7/7/1996	0.00	0.00	0.50	0.00
RAZO	7/9/1996	0.00	0.00	0.00	0.00
RAZO	7/10/1996	0.00	0.10	0.35	0.00
RAZO	7/11/1996	0.00	0.00	0.93	0.00
RAZO	7/12/1996	0.00	0.00	0.65	0.00
RAZO	7/15/1996	0.00	0.00	0.94	0.00
RAZO	7/16/1996	0.00	0.00	1.00	0.00
RAZO	7/17/1996	0.00	0.00	1.00	0.00
RAZO	7/18/1996	0.00	0.00	1.00	0.00
RAZO	7/20/1996	0.00	0.00	1.00	0.00
RAZO	7/24/1996	0.00	0.00	1.00	0.00
RAZO	6/27/1997	0.00	0.00	1.00	0.00
RAZO	7/1/1997	0.00	0.00	0.81	0.14
RAZO	7/8/1997	0.00	0.04	0.96	0.00
RAZO	7/9/1997	0.00	0.02	0.87	0.06
RAZO	7/13/1997	0.00	0.11	0.88	0.01
RAZO	7/17/1997	0.00	0.28	0.62	0.03
RAZO	7/21/1997	0.00	0.00	1.00	0.00
RAZO	7/23/1997	0.00	0.00	1.00	0.00
RAZO	7/25/1997	0.00	0.00	1.00	0.00
RAZO	7/26/1997	0.00	0.00	1.00	0.00
RAZO	7/29/1997	0.00	0.00	1.00	0.00
RAZO	7/31/1997	0.00	0.00	0.80	0.00
RAZO	7/1/1998	0.00	0.13	0.29	0.13
RAZO	7/2/1998	0.00	0.08	0.86	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
RAZO	7/3/1998	0.00	0.04	0.76	0.00
RAZO	7/4/1998	0.00	0.08	0.67	0.00
RAZO	7/7/1998	0.00	0.36	0.56	0.02
RAZO	7/8/1998	0.00	0.09	0.61	0.00
RAZO	7/13/1998	0.00	0.04	0.85	0.00
RAZO	7/14/1998	0.00	0.54	0.31	0.00
RAZO	7/17/1998	0.00	0.04	0.79	0.00
RAZO	6/24/1999	0.00	0.02	0.31	0.22
RAZO	6/26/1999	0.00	0.09	0.68	0.21
RAZO	6/27/1999	0.00	0.03	0.70	0.11
RAZO	6/28/1999	0.00	0.00	0.83	0.17
RAZO	7/1/1999	0.00	0.03	0.72	0.01
RAZO	7/3/1999	0.00	0.17	0.57	0.16
RAZO	7/4/1999	0.00	0.03	0.81	0.00
RAZO	7/5/1999	0.00	0.18	0.67	0.03
RAZO	7/6/1999	0.00	0.07	0.79	0.03
RAZO	7/8/1999	0.02	0.00	0.91	0.08
RAZO	7/9/1999	0.00	0.00	1.00	0.00
RAZO	7/11/1999	0.00	0.06	0.84	0.05
RAZO	7/12/1999	0.00	0.00	0.82	0.10
RAZO	7/14/1999	0.00	0.36	0.56	0.08
RAZO	7/18/1999	0.00	0.00	1.00	0.00
RAZO	6/24/2000	0.00	0.07	0.62	0.32
RAZO	6/26/2000	0.00	0.44	0.11	0.44
RAZO	6/27/2000	0.00	0.31	0.69	0.00
RAZO	6/28/2000	0.00	0.52	0.30	0.17
RAZO	7/1/2000	0.00	0.03	0.92	0.05
RAZO	7/3/2000	0.00	0.03	0.97	0.00
RAZO	7/5/2000	0.00	0.00	0.98	0.00
RAZO	7/6/2000	0.00	0.06	0.91	0.00
RAZO	7/7/2000	0.00	0.04	0.96	0.00
RAZO	7/8/2000	0.00	0.12	0.86	0.02
RAZO	7/9/2000	0.00	0.16	0.84	0.00
RAZO	7/11/2000	0.00	0.20	0.80	0.00
RAZO	7/14/2000	0.00	0.00	1.00	0.00
RAZO	6/26/2001	0.00	0.42	0.05	0.52
RAZO	6/28/2001	0.00	0.09	0.19	0.71
RAZO	7/1/2001	0.00	0.50	0.00	0.45
RAZO	7/3/2001	0.00	0.15	0.32	0.53
RAZO	7/4/2001	0.00	0.00	0.06	0.93
RAZO	7/7/2001	0.00	0.04	0.01	0.91
RAZO	7/8/2001	0.00	0.02	0.15	0.83
RAZO	7/10/2001	0.00	0.00	0.00	1.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
RAZO	7/13/2001	0.00	0.32	0.27	0.39
RAZO	7/14/2001	0.00	0.02	0.41	0.49
RAZO	7/15/2001	0.00	0.17	0.17	0.65
RAZO	7/16/2001	0.00	0.24	0.57	0.19
RAZO	6/24/2002	0.00	0.63	0.19	0.19
RAZO	6/25/2002	0.00	0.76	0.19	0.05
RAZO	6/29/2002	0.00	0.73	0.09	0.18
RAZO	6/30/2002	0.00	0.08	0.56	0.25
RAZO	7/2/2002	0.42	0.05	0.00	0.53
RAZO	7/3/2002	0.00	0.00	0.84	0.16
RAZO	7/4/2002	0.00	0.65	0.00	0.29
RAZO	7/6/2002	0.00	0.14	0.59	0.05
RAZO	7/7/2002	0.00	0.17	0.58	0.03
RAZO	7/8/2002	0.00	0.00	1.00	0.00
RAZO	7/9/2002	0.00	0.00	0.63	0.00
RAZO	7/10/2002	0.00	0.00	0.96	0.02
RAZO	7/11/2002	0.00	0.00	0.67	0.00
RAZO	7/12/2002	0.00	0.00	1.00	0.00
RAZO	7/13/2002	0.00	0.00	1.00	0.00
RAZO	7/14/2002	0.00	0.00	1.00	0.00
RAZO	6/27/2003	0.00	0.97	0.00	0.03
RAZO	6/28/2003	0.00	0.84	0.03	0.13
RAZO	6/30/2003	0.00	0.88	0.03	0.03
RAZO	7/2/2003	0.00	0.42	0.55	0.00
RAZO	7/4/2003	0.00	0.45	0.26	0.18
RAZO	7/5/2003	0.00	0.42	0.45	0.06
RAZO	7/6/2003	0.00	0.16	0.74	0.09
RAZO	7/8/2003	0.00	0.56	0.00	0.11
RAZO	7/10/2003	0.00	0.00	0.77	0.10
RAZO	7/12/2003	0.00	0.00	0.43	0.00
RAZO	7/13/2003	0.00	0.07	0.83	0.00
RAZO	7/14/2003	0.00	0.00	0.91	0.00
RAZO	7/15/2003	0.00	0.00	1.00	0.00
RAZO	7/17/2003	0.00	0.00	0.75	0.00
RAZO	6/30/2004	0.00	0.06	0.76	0.08
RAZO	7/1/2004	0.00	0.00	0.62	0.08
RAZO	7/2/2004	0.00	0.06	0.82	0.00
RAZO	7/3/2004	0.00	0.05	0.50	0.02
RAZO	7/4/2004	0.00	0.01	0.60	0.00
RAZO	7/5/2004	0.00	0.08	0.38	0.03
RAZO	7/6/2004	0.00	0.00	0.55	0.03
RAZO	7/7/2004	0.00	0.01	0.74	0.00
RAZO	7/8/2004	0.00	0.00	0.71	0.00

Species	Date	Euphausiids	Hake	Herring	Sandlance
ARTE	6/29/1995	0.00	0.00	0.00	0.00
ARTE	6/30/1995	0.00	0.00	0.25	0.00
RAZO	7/9/2004	0.00	0.00	0.22	0.00
RAZO	7/10/2004	0.00	0.00	0.71	0.00
RAZO	7/12/2004	0.00	0.00	0.32	0.00
RAZO	7/13/2004	0.00	0.05	0.80	0.00
RAZO	7/17/2004	0.00	0.00	0.67	0.04
RAZO	7/18/2004	0.00	0.00	0.65	0.00
RAZO	7/19/2004	0.00	0.00	0.57	0.00
RAZO	7/20/2004	0.00	0.00	0.66	0.09
RAZO	7/24/2004	0.00	0.00	0.00	0.00
RAZO	7/25/2004	0.00	0.00	1.00	0.00