



The fish component of *Pygoscelis* penguin diets
by Nina J Karnovsky

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Sciences
Montana State University
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Abstract:

Long-term research on the breeding biology and foraging ecology of Antarctic seabirds has shown that these birds are excellent indicators of the environmental conditions of the Southern Ocean marine ecosystem. Since 1976 three species of penguins, the gentoo, Adelie and chinstrap, have been studied on King George Island, Antarctica. The coexistence of the three species during their breeding season could be a result of species-specific differences in prey, foraging habitat and/or feeding behavior. Previous studies have shown that krill is the major component of the diet of all three species. The importance of fish in their diet has been underestimated and not well understood. The objective of this study was to analyze which kinds of fish species, and to what extent, the different penguins rely on fish. I examined interspecific, intraspecific differences in the piscivorous portion of diet of the three penguin species. These data will be used for examinations of interannual variation in the penguin diets in the future.

Changes in the percentage of, or a shift in species assemblages of fish eaten (preyswitching) could reflect variations in environmental conditions. Such a change might be expected because krill populations have declined in the past decade due to a decrease in winter sea ice. Krill depend on sea-ice for protection from predators and for feeding on the ice-algae populations. To examine the possibility of prey-switching, diet samples were obtained by lavaging five breeding adults of each species every week of the chick rearing period for six consecutive austral summers. Identification of the fish and calculation of the mass and length of the fish was accomplished through the inspection of otoliths. These data indicate major differences in diets among penguin species. Intraspecific differences were most pronounced between male and female gentoo penguins. Differences were found between the sexes and among the three penguin species in types, sizes, frequency of occurrence and abundances of fish species constituting their respective diets. The results of this study emphasize the necessity of paying more attention to diet items heretofore considered incidental and recommendations for future research are given herein.

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MONTANA STATE UNIVERSITY-BOZEMAN
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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Aena J. Karnovsky

Date

July 14, 1997

This thesis is dedicated to my friend, mentor, and inspiration,
Larry Spear,
who taught me that otoliths are worth their weight in gold.

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ABSTRACT

Long-term research on the breeding biology and foraging ecology of Antarctic seabirds has shown that these birds are excellent indicators of the environmental conditions of the Southern Ocean marine ecosystem. Since 1976 three species of penguins, the gentoo, Adelie and chinstrap, have been studied on King George Island, Antarctica. The coexistence of the three species during their breeding season could be a result of species-specific differences in prey, foraging habitat and/or feeding behavior. Previous studies have shown that krill is the major component of the diet of all three species. The importance of fish in their diet has been underestimated and not well understood. The objective of this study was to analyze which kinds of fish species, and to what extent, the different penguins rely on fish. I examined interspecific, intraspecific differences in the piscivorous portion of diet of the three penguin species. These data will be used for examinations of interannual variation in the penguin diets in the future.

Changes in the percentage of, or a shift in species assemblages of fish eaten (prey-switching) could reflect variations in environmental conditions. Such a change might be expected because krill populations have declined in the past decade due to a decrease in winter sea ice. Krill depend on sea-ice for protection from predators and for feeding on the ice-algae populations. To examine the possibility of prey-switching, diet samples were obtained by lavaging five breeding adults of each species every week of the chick rearing period for six consecutive austral summers. Identification of the fish and calculation of the mass and length of the fish was accomplished through the inspection of otoliths. These data indicate major differences in diets among penguin species. Intraspecific differences were most pronounced between male and female gentoo penguins. Differences were found between the sexes and among the three penguin species in types, sizes, frequency of occurrence and abundances of fish species constituting their respective diets. The results of this study emphasize the necessity of paying more attention to diet items heretofore considered incidental and recommendations for future research are given herein.

INTRODUCTION

In the Antarctic marine environment, biological processes are driven by a variety of physical factors. In particular, trophic dynamics are largely affected by interannual variability in the extent and distribution of winter sea ice, upwelling of nutrient rich water at shelf breaks, and shifts in current boundaries (Ashmole 1971, Croxall 1987). The reproductive success, distribution, and diet of Antarctic seabirds are sensitive to the variability of their environment (Croxall et al. 1988a, Trivelpiece et al. 1990b). Long-term studies of penguins have shown that they are excellent indicators of changes in the ecosystem (Boersma 1978, Croxall et al. 1988a, Trivelpiece et al. 1990b, Bost et al. 1994). Several factors make them attractive as indicator species including their longevity, accessibility at breeding colonies, philopatry, and the fact that they forage solely in their surrounding marine environment (CCAMLR 1985). Although *Pygoscelis* penguins rely on Antarctic krill *Euphausia superba* as their main food source, they also take appreciable amounts of fish and an occasional amphipod or squid (Volkman et al. 1983, Jazdzewski 1978, Jablonski 1985, pers. obs.). It is within the context of understanding the ecosystem as a whole that this study of the fish component of the diets of the Adelle *Pygoscelis adeliae*, gentoo *P. papua*, and chinstrap penguin *P. antarctica*, has been undertaken.

Purpose

The purpose of this study was to quantify the frequency, abundance and type of fish consumed by the *Pygoscelis* penguins breeding at Admiralty Bay, King George Island, Antarctica. The objectives were: 1) to quantify the percentage of fish taken by the three *Pygoscelis* species breeding on King George Island, 2) to classify the different species of fish selected by the different penguins, and 3) to determine if there are intersexual differences within the penguins in the fish component of the diet. In this study, I quantified the original mass and length of the fish consumed, and identified the species of fish, through otolith analysis. By identifying the species of fish and quantifying the percentage of fish in their diets, I determined the extent to which there are interspecific and intraspecific dietary differences among the penguins. Knowing the extent to which the penguins partition resources is essential in assessing shifts in their prey base over time. Changes in either the percentage of fish that make up penguin diets, or a shift in the types of fish eaten, could reflect variations in environmental conditions and/or impacts caused by human commercial activities. Finally, I reassessed sampling protocols and proposed changes in analyses in order to assure that future studies of penguin diets will be more sensitive to the highly variable and dynamic marine ecosystem.

Study Area

King George Island at 80 kilometers (km) long and 25 wide, is the largest of the South Shetland Islands and is located approximately 100 km northwest of the tip of the

Antarctic Peninsula (Fig. 1). Five percent of the island becomes ice free in the austral summer and this exposed area supports 12 species of nesting seabirds. The study site, "Copa," is on the western side of Admiralty Bay which is on the southeast shore of the island at 62°10'S, 58°27'W (Fig. 2). Admiralty Bay is made up of three deep fjords. The mouth of the bay is five kilometers wide and opens out to the Bransfield Strait (Fig. 2). The shelf break (> 1000 m depth) is approximately 20 km off King George Island adjacent to the bay.

Oceanographic Characteristics of the Study Area

The water of Admiralty Bay is derived from Bransfield Strait waters and an annual influx of glacial melt fresh water. Organic and inorganic matter in these nutrient rich waters is derived from benthic macrophytes, phytoplankton, run-off containing nitrogenous wastes from penguin rookeries and glacial water which is rich in minerals and detritus (Myrcha et al. 1983, Dawson et al. 1983).

Admiralty Bay opens into the Bransfield Strait (Fig. 2) which is characterized by three distinct layers of water. The surface layer is a mixed layer, the middle layer (between 50 and 100 m) is a water mass referred to as 'Winter water' because it is very cold (-1.5 to -1.8°C). The bottom layer known as the Circumpolar Deep Water (CDW) is warm (+2°C) and salty (Capella et al. 1992, Hofmann et al. 1996). The currents that sweep past both sides of King George Island move in a northeasterly direction (Capella 1992) and prevailing winds in the region are westerly. As the winter pack ice breaks up, these winds push ice up against the Northwestern shores of the islands and clear the waters on the

southeastern side of the island (Trivelpiece et al. 1987, 1990b, Trivelpiece and Fraser 1996).

Human Activities in the Study Area

Presently, there is a developing krill fishery in the area (Everson and Goss 1991). Fishing activities overlap with penguin foraging activities both spatially and temporally (Agnew 1992). Although it was not the purpose of this study to determine the impact of fishing on krill dependent predators of the area, the results can possibly be used to evaluate how the penguins might respond to human induced changes in their prey base by describing the full range of diet items for each species. This information could be used to make recommendations to fishery managers.

Environmental Variability in the Study Area: Implications for Krill and Penguins

Knowledge of environmental trends in the region has been recently expanded through the analysis of temperature data and satellite imagery. In recent decades the Antarctic Peninsula region has experienced an overall rise in mean annual temperature. Temperature records from long-term weather stations show a 3-5 °C increase in mean mid-winter temperature since the 1940s (Smith et al. 1996, Murphy et al. 1995). In addition, recent analysis of passive microwave satellite imagery data from 1978 to 1991, shows extreme interannual variability in the extent of ice coverage, the timing of the annual advance and retreat of sea-ice, and the duration of sea-ice coverage in this region (Stammerjohn and Smith 1996). A thermodynamic model coupling temperature and

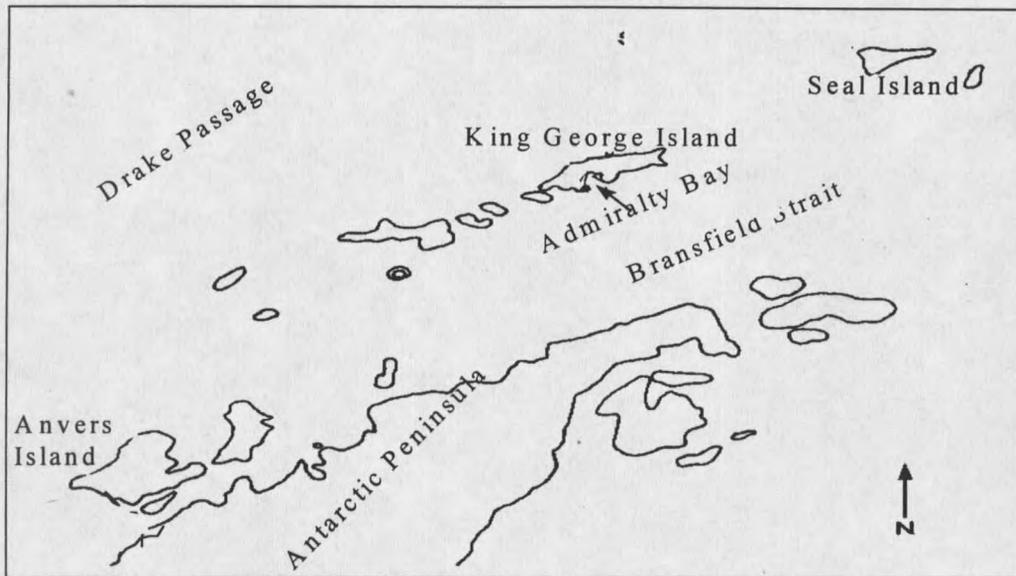


Figure 1. The location of King George Island, South Shetland Islands, Antarctica.

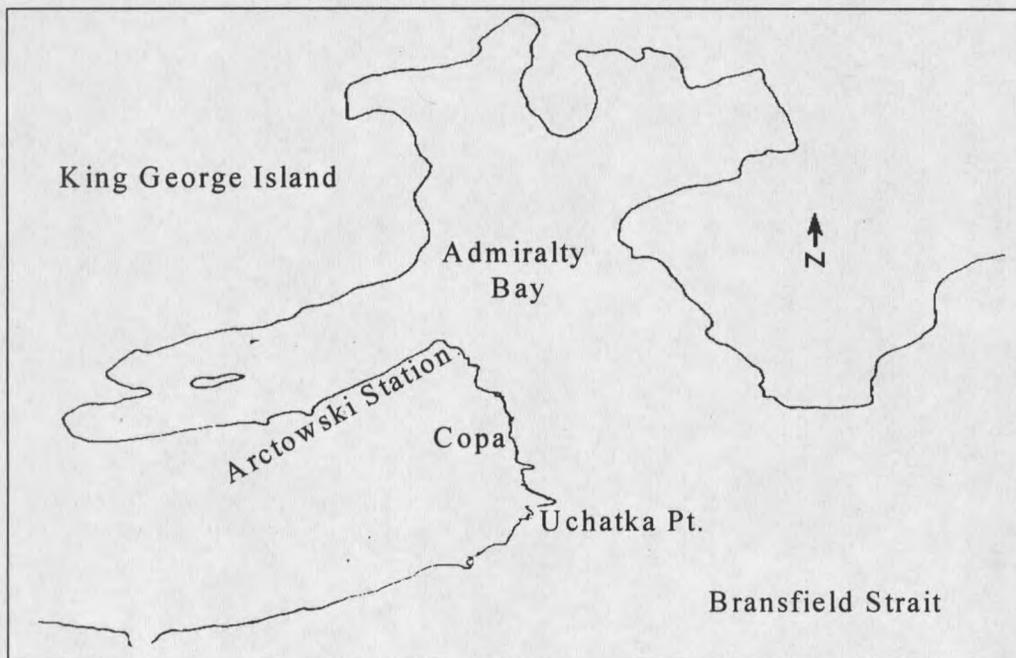


Figure 2. The study site "Copa" is located on the western shore of Admiralty Bay, King George Island.

satellite imagery data revealed a decline in the frequency of years with extensive sea-ice forming in the winter (Fraser et al. 1992). This warming trend and change in winter sea-ice extent has now been reported in the South Orkney Island area (Murphy et al. 1995). Vaughan and Doakes (1996) report that this warming has caused extensive retreat of permanent ice shelves in the Antarctic peninsula region. The current ice regime appears to be two heavy ice years occurring every six to eight years (Trivelpiece and Trivelpiece, in press).

Krill productivity is closely linked to the extent and duration of winter sea-ice coverage (Marschall 1988, Daly 1990, Smetacek 1991, Quetin and Ross 1991). The ice provides an abundant feeding habitat for krill and protection from predators. Juvenile krill are dependent on the abundant ice algae that grow under the ice for survival (Quetin and Ross 1991) and female krill need the ice algae to prepare for reproduction. When winter sea-ice extends into spawning areas off the South Shetland and South Orkney Islands, female krill are in good reproductive condition the following summer and have a high reproductive output. If the following winter has extensive ice then the offspring from those females have a high survival rate (Siegel and Loeb 1995, Loeb et al., in press). Therefore, if heavy ice conditions occur two winters in a row, a strong cohort of krill is added to the population, while in intervening light ice years or when a heavy ice year is followed by a light ice year, there is very little juvenile recruitment into the population (Siegel and Loeb 1995, Trivelpiece and Trivelpiece, in press). Essentially, one cohort carries the population through the years of low ice cover (Trivelpiece and Trivelpiece, in press).

Recently, the decrease in the frequency of heavy ice years has had two dramatic effects on krill populations: 1) the age structure has shifted, and 2) there has been an overall decrease in krill biomass in our Antarctic Peninsula region. Siegel and Loeb (1995) have documented an order of magnitude decrease in the krill population from the 1970s to the present in the Antarctic Peninsula region. Krill biomass estimates prior to the 1970s were averaging 200 animals per 1000 m³, a decade later the biomass estimates were averaging 23 animals per 1000 m³ (Siegel and Loeb 1995).

Concurrent with the decline in krill biomass, the Adelie penguin population at the Copa study site experienced a significant decline. Trivelpiece and Trivelpiece (in press) have documented a 30% decline in the breeding population and a 50% decrease in the survival of fledglings. The reduction in the Adelie population at Copa may be explained by changes in food availability of krill, which in turn is linked to a decrease in the frequency and intensity of heavy ice years (Trivelpiece and Trivelpiece, in press). The chinstrap penguin population has also declined, but the decrease preceded the decline in krill biomass and may have had additional factors influencing it. However, a recent decline in the numbers of chinstrap penguins breeding in the South Orkney islands has been observed and researchers there have proposed that this trend may be linked to the same warming conditions and changes in the frequency of ice cycles (Tratham et al. 1996).

Prey-switching

A decline in the biomass of these penguins' main prey, krill, might be expected to lead to a greater dependence on other food sources such as fish. The extent to which a secondary food source can be used is determined by both prey availability and the foraging habits of the predators. The manner in which the different species and sexes of penguins respond to changes in the abundance and distribution of their prey base will only be understood through long term examinations of their diets, their foraging capabilities and feeding zones. Inshore generalists like the gentoo penguin will respond differently than the more pelagic specialist feeders like chinstrap and Adelie penguins. Croxall and Prince (1979, 1980a) found that in years where local krill swarms were sparse around South Georgia, inshore feeding, krill dependent seabirds experienced reproductive failures, whereas squid eaters and offshore krill eaters reproduced normally. Prey switching in penguins has recently been documented in the African jackass penguin *Spheniscus demersus*. When the availability of their main prey, the Cape anchovy *Engraulis capensis* was low, jackass penguins fed on the South African sardine *Sardinops sagax* (Crawford and Dyer 1995). Likewise, during El Nino events off the California coast, the various breeding alcids responded according to their foraging capabilities. For example, Cassin's auklets *Ptychoramphus aleuticus* which are dependent on euphausiids close to the breeding colonies, failed; whereas common murre *Uria aalga*e took advantage of alternate prey by flying further distances for energy rich anchovies, and experienced no decrease in reproductive success (Ainley and Boekelheide 1990).

The Penguins and Their Foraging Habits

There are a total of 12 species of seabirds that breed on King George Island including three species of penguins: the Adelie, gentoo, and chinstrap. The gentoo penguin population represents the smaller sub-species of gentoo *P. p. ellsworthii* found south of the Antarctic convergence (Murphy 1947, Stonehouse 1968). The Copa study site is at the northern edge of the range of the Adelie penguin, the southern extent of the range of the gentoo penguin and is in the middle of the chinstrap penguin's range (Watson 1975, Trivelpiece and Trivelpiece 1990a). Two decades of studies of these penguins at this site have elucidated many of the ecological differences among the species that allow them to breed sympatrically with overlapping breeding seasons (Trivelpiece et al. 1987, Trivelpiece and Trivelpiece 1990b). These factors include differences in breeding chronology, mate fidelity, site tenacity, migration, wintering localities, diving ability, and foraging range. This study examines the extent to which there are differences among the three penguins in terms of the types and amount of fish they eat.

The Adelie Penguin

Adelie penguins are the most numerous penguin in our study area with a mean of 5,673 breeding pairs (Trivelpiece and Trivelpiece, in press). Individuals have a mean weight of 5.4 kilograms (kg). They spend their winters on the edge of the winter pack ice (Trivelpiece et al. 1990b, Fraser et al 1992), and they are the first to initiate breeding (Trivelpiece et al. 1987). Of the three penguins, Adelie penguins have the largest

foraging range (mean maximum 50 km) based on time at sea (Trivelpiece et al. 1987) and dive to depths of 100 m (Trivelpiece, unpubl. data). Until Adelie chicks creche at approximately three weeks of age, they are fed by a parent approximately once a day (Trivelpiece et al. 1987). At several study sites throughout the Antarctic region, fish apparently make up a small percentage of Adelie diets (summarized in Marchant and Higgins 1990).

The Chinstrap Penguin

The chinstrap penguin is the smallest of the *Pygoscelis* penguins, with a mean weight of 4.8 kg. During the non-breeding season, they spend their winters in the open ocean (Trivelpiece et al. 1990b, Fraser et al. 1992). Chinstrap penguins are the last to arrive at the breeding colonies, the last to initiate breeding, and breed up to a month later than the Adelie penguins (Trivelpiece et al. 1987, 1990a). Chinstrap penguins forage an average of 27 km from the breeding colonies (Jablonski 1985, Trivelpiece et al. 1986, 1987). Lishman and Croxall (1983) found that 90% of the chinstrap penguin dives were shallower than 45 m and 40% of the dives were less than 10 m with none greater than 70 m. Prior to creching, chinstrap chicks are fed approximately 1.44 times per day (Trivelpiece et al. 1987). Trivelpiece et al. (1986) found that at the Copa study site, they forage primarily during the day, however, this varies from region to region. For example, Chinstrap penguins at Signy island feed at night (Lishman 1985b) and at Elephant island feed during the day and night (Jansen et al. 1997). There are approximately 2,000 chinstrap penguin breeding pairs in the Uchatka Point colonies where the diets data for

this study were obtained (Fig. 2). Previous to this study, fish have rarely been documented in chinstrap penguin diets (Volkman et al. 1980, Cooper et al. 1984, Jablonski 1985, Lishman 1985b).

The Gentoo Penguin

The gentoo penguin is the largest of the three *Pygoscelis* penguins (mean weight 6.0 kg) and is non-migratory, with birds remaining at the colonies throughout the winter as ice conditions allow (Trivelpiece et al. 1987, Trivelpiece and Trivelpiece 1990b). During the breeding season they forage inshore not more than 24 km and on average 17 km away from their breeding colony (Trivelpiece et al. 1986, 1987). Gentoo penguins are deep divers, as indicated by time depth recordings (TDRs) at our site in which gentoo penguins foraged to depths of 165 m (Trivelpiece unpubl. data). In addition mean dive depth of gentoo penguins breeding at Macquarie Is. was 89 m and at South Georgia, 81 m (Robinson and Hindell 1996). Gentoo penguins return to their chicks an average of every 6.1 hours and are diurnal foragers who spend the night on shore at their nest sites (Trivelpiece et al. 1986). Prior to the time when both of the parents leave to forage simultaneously, chicks are fed at the nest approximately twice a day. The gentoo penguins spend most of their foraging time diving, whereas the chinstrap penguins spend most of their foraging time traveling (Trivelpiece et al. 1986). Trivelpiece et al. (1986) hypothesized that this may be because of the nocturnal vertical migration of krill. During the day, krill swarms in Admiralty Bay descend to depths of 100-120 m (Kalinowski and Witek 1980). Gentoo penguins have access to this deep water krill, whereas the chinstrap

penguins may have to travel farther to find available krill within their shallower diving range (Trivelpiece et al. 1986). There are approximately 2000 breeding pairs of gentoo penguins in the colony where this study took place. Varying amounts of fish have regularly been reported in the diets of gentoo penguins at several sites (summarized in Marchant and Higgins 1990).

Understanding the fish component in the diet of the penguins is especially imperative for the gentoo penguin. This bird has recently been selected as an indicator species for the CCAMLR Ecosystem Monitoring and Management (EMM) Program (Croxall and Williams 1990). Most published studies on gentoo penguin foraging habits and prey have been conducted on the nominate Northern race *P. p. papua* and not on the smaller Southern race *P. p. ellsworthi* breeding on King George Island and the Antarctic Peninsula. While the gentoo penguin has the most limited foraging range it has the most plasticity in its foraging options, being the deepest diver (Trivelpiece et al. 1986, Croxall et al. 1987, 1988b, Williams et al. 1992a). Williams et al. (1992a) hypothesized that the gentoo foraging patterns are a reflection of prey availability rather than physiological constraints. Therefore, if the abundance and distribution patterns of krill and fish changes, these changes may be prominently reflected in the diet of breeding gentoo penguins.

Early Diet Studies at Admiralty Bay

Three diet studies have been conducted on the Admiralty bay penguins spanning the years from 1977 - 1982 (Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b).

1990b). Early assessment of penguin diets on King George Island revealed that there were some interspecific differences in the percentage of fish found in their diets. During those six years, 95.4% of Adelie penguin and 83.6% chinstrap penguin diets by wet weight were made up of krill (Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b). The average intake of fish by wet weight was 1.6% for Adelie penguins and 11.1% for chinstrap penguins. The gentoo penguin diet was 75.9% krill and 23.8% fish (Volkman et al 1980, Jablonski 1985, Trivelpiece et al. 1990b).

In addition to these interspecific differences, previous evaluations of penguin diets indicated that male and female penguins may have specific dietary adaptations (Volkman et al. 1984). *Pygoscelis* penguins are sexually dimorphic with males being larger than females (Ainley and Emison 1972). This dimorphism is most pronounced in the gentoo penguin (Volkman et al. 1984). Additionally, gentoo penguins are the most fish dependent of the *Pygoscelis* species (Volkman et al. 1980, White and Conroy 1975, Croxall and Prince 1980b, Croxall et al. 1988b, William et al. 1992a, 1992b). Male gentoo penguins were found to select a significantly higher proportion of fish (by wet weight) than female gentoo penguins (Volkman et al. 1984). Volkman suggested that this intersexual difference was a mechanism whereby food niches could be further partitioned.

Despite these suggestions of dietary partitioning, all the early studies were done with methods that grossly underestimated the role of fish in *Pygoscelis* diets. Most studies classified penguin diets in terms of percentages of weights of different prey types found in stomach samples and did not determine the assemblage of fish species eaten by these penguins. Fish flesh rapidly dissolves in penguin stomachs. In feeding trials of Jackass

penguins, 50 g of anchovy were completely digested after ten hours (Wilson et al. 1985). Hence, the fresh fish brought back to chicks is a very small portion of what was actually consumed and in most studies the fish were so far digested, most could not be identified. Therefore, information on fish in penguin diets, even at higher taxonomic levels, is lacking. Now with improved methods of diet analyses using fish otoliths, it is possible to obtain this information. Reevaluating the role of fish in the diets of the three *Pygoscelis* penguins has facilitated a more accurate assessment of dietary niche segregation among and within species.

The Use of Otoliths

The difference between this study and the previous studies conducted on the King George Island penguins, is mainly in my use of fish otoliths. Otoliths are the equivalent of inner ear bones in fish. There are three pairs of otoliths in each fish, the saccular (sagitta), the utricular (lapillus) and the lagenar (astericus). Only the sagittal otoliths are used because they are morphologically distinct in each species and their size is correlated with the size of the fish they came from. Hence, sagittal otoliths have been essential in diet studies of many seabird, seal and cetacean populations (Ainley 1984, Prime and Hammond 1990, Pierce et al. 1991). Otoliths are denser than the other bones in the bodies of fishes, so they don't deteriorate easily. They are made from an aragonite form of calcium carbonate and otoline, a proteinaceous material (Gon and Heemstra 1990). Because they are so dense, they are often all that remains of the fish consumed. The

otoliths size expands as the fish grows with regular layers of material being laid down on the otolith, much like the annual growth rings of a tree.

Very few otoliths were recorded in the early diet samples collected from penguins at our site, as otoliths were only searched for if there was visual or olfactory evidence of fish in the sample. In 1993, I changed the sampling protocols so that all samples were systematically examined for otoliths.

While otoliths have allowed us to identify fish prey to species and to assess more accurately the sizes of the fish consumed, these estimates can be grossly underestimated. Even though otoliths are the most resistant structure of a teleost fish to digestion, they are digested while in the penguins stomachs (Gales 1988). During feeding trials on Little Penguins *Eudyptula minor*, Gales (1988) found that otoliths length and weight decreased as the time after ingestion increased. Van Heezik and Seddon (1989) found that smaller otoliths were digested faster in yellow-eyed penguins which implies that smaller otoliths could be underestimated.

These studies also showed that severe degradation of otoliths occurred at about 24 hours after the fish were consumed, although as noted above, degradation time varied with the size of the otolith (Gales 1988, Van Heezik and Seddon 1989). Therefore, both the number of fish and the masses of fish could be underestimated. Because I did not include otoliths showing considerable erosion in the length/ weight back-calculations, my analyses pertain to fish eaten within less than 24 hours from the time I obtained them from penguin stomachs.

METHODS

The Stomach Flushing Technique

The scope of seabird dietary studies have expanded with the development of a non-lethal, and effective, technique to obtain stomach samples. I obtained diet samples by using what is known as the stomach-flushing, water-offloading, or stomach-lavage technique (Wilson 1984, Duffy and Jackson 1986). This technique does not appear to alter the reproductive success of the birds sampled (Robertson 1993, Clarke and Kerry 1994). Prior to the development of the stomach-flushing technique, birds were killed to obtain the stomach samples (Volkman et al. 1980, Croxall and Furse 1980, Croxall and Prince 1980b, Lishman 1985b) or given emetics to regurgitate (Jablonski 1985).

Penguins are particularly good candidates for dietary studies because they lack crops and gizzards which are known to retain otoliths and squid beaks in other seabirds (Furness et al. 1984). Retention of otoliths and squid beaks from multiple feeding bouts could result in overestimation of their importance (Jobling and Breiby 1986).

Two requirements of the stomach-flushing technique are that it is possible to obtain the full stomach sample, and that the sample represents the most recent meal. Gales (1987) stomach flushed five Little penguins and then killed them and found no food remained in the stomachs, indicating that entire stomach samples can be obtained from the proper use of this technique. In addition, Gales force fed Little penguins varying

numbers of fish and waited from one to sixteen hours before stomach-flushing them. Gales found that penguins fed small numbers of fish digested all the remains including the otoliths after waiting the longer time intervals (Gales 1987, 1988). These feeding trials show that only evidence of the most recent meals can be recovered.

Collecting Diet Samples

I used a modification of the stomach pump described by Wilson (1984). I filled a hot water bottle with luke warm water and attached an enema tube to the bottle. I inserted the nozzle of the enema tube into the throat of the bird approximately three inches. The water was a mixture of fresh and sea water in approximately 1:3 proportions, respectively. I gravity fed water into the penguin by holding the bottle above the immobilized penguin. When the bird gurgled or water overflowed out of the mouth, I removed the enema tube and turned the bird upside down. One person held the beak open and massaged the throat and while another held the bird's legs in one hand and applied pressure to the abdomen with another. This procedure was repeated on average two or three times until only clear water was expelled by the bird. Whenever possible I kept the fresh upper layer of the diet sample separate from the more digested layer by switching buckets under the inverted penguin at the first sign of the darker and pastier digested food layer.

Sample Size and Time Period

I collected 553 stomach samples from Adelie, gentoo, and chinstrap penguins from 1990 to 1995 (Table 1). The sampling periods spanned January first of each year; therefore the name of each sampling season is the year prior to January first. For example, the 1990/1991 season is called 1990.

Table 1. Number of stomach samples collected each year.

Year	Adelie	Gentoo	Chinstrap	Total
1990	31	31	25	87
1991	30	30	25	85
1992	30	30	30	90
1993	30	34	30	94
1994	30	35	30	95
1995	29	32	41	102
Totals	180	192	181	553

Sampling Chronology

I collected samples throughout the chick rearing period of each penguin species. The beginning of the chick rearing period varied from year to year due to variations in the initiation of egg laying for each species each year. The span of each sampling period for each penguin species is listed in Table 2.

Table 2. Inclusive dates of the diets sampling period each year.

Year	Species	First sample	Last sample
1990	Adelie	December 29-	January 25
	Gentoo	December 29-	February 6
	Chinstrap	January 11-	February 20
1991	Adelie	December 10-	January 13
	Gentoo	December 30-	February 7

Table 2. (continued)

	Chinstrap	January 7-	February 14
1992	Adelie	December 15-	January 18
	Gentoo	December 29-	February 1
	Chinstrap	January 6-	February 2
1993	Adelie	December 6-	January 12
	Gentoo	December 16-	December 23
	Chinstrap	January 5-	February 7
1994	Adelie	December 19-	January 23
	Gentoo	January 6-	February 27
	Chinstrap	January 12-	February 8
1995	Adelie	December 12-	January 22
	Gentoo	December 22-	January 22
	Chinstrap	December 29-	February 6

I began diet sampling when approximately 90% of the chicks of the species had hatched. During this time, adult penguins go to sea daily to forage for themselves and return to their nest sites with stomach loads of food which they regurgitate to their chicks. At least one parent returns daily in order to meet the high energy requirements of their chicks. I sampled five birds of each species each week from the time of chick hatching to fledging according to the Convention for the Conservation of Antarctic Marine Living Resources sampling protocols (CCAMLR 1990). I sampled approximately 30 birds of each species each austral summer with approximately equal numbers of males and females.

I chose penguins that appeared to have full stomachs, were clean (indicating that they had just returned from the sea), and were walking directionally to their nests. Once they reached their nests, I noted the number of chicks in the nest. All the birds sampled were part of active nests, that is, they had one or two chicks. I approximated the ages of the chicks with reference to the size of known-aged chicks being followed in the colonies.

During the first two and a half to three weeks of age, the chicks are incubated or guarded by one parent while the other forages at sea. Therefore, both parents are present when the foraging bird returns to the nest at this time. This is important because it reduces the risk of predation of the small chicks while I sample the returning parent. There is a much greater risk of predation by brown skuas when the chicks are young (Trivelpiece et al. 1980, Emslie et al. 1995). In addition, having the second parent at the nest facilitates being able to determine the sex of the bird in hand.

Determining Sex of Adults

Pygoscelis penguins are sexually dimorphic with the males being larger than the females (Ainley and Emison 1972). Although there is considerable size overlap in bill length measurements between the sexes in randomly selected samples, Volkman et al. (1984) reported zero percent overlap within pairs of *Pygoscelis* penguins. Therefore, I visually compared the size of the bill of the returning bird to its mate to determine the sex of the penguin to be sampled. When the chicks are approximately three weeks in age, both parents forage at sea leaving the chicks in a creche. During this time, birds returned to their chicks alone and I estimated the sex of the bird on the basis of its overall size.

Of the 553 birds sampled, the sex was recorded for all but five chinstrap penguins, the remaining 548 birds were included in the analysis of sexual differences (Table 3).

Table 3. Sample sizes of the sexes of the different penguins.

Species	Male	Female	Total
Adelie	90	90	180
Gentoo	101	91	192
Chinstrap	99	77	176

Sorting Stomach Samples

I drained the samples over buckets in 1/8th inch mesh sieves. In 1992 and 1993, I placed each sample in plastic bags and weighed them on a balance to the nearest tenth of a gram. In 1994 and 1995, samples were placed on clean plates and weighed on a zeroed electronic balance. In all years of the study, I used a portion (generally 50 individuals) of the fresh sample for a krill demography and monitoring study. In all years, the fresh portion of the samples were examined for fresh fish parts and other prey items (e.g. squid, amphipods). All intact fish and fish parts were measured and weighed. I placed the stomach samples in large trays and floated them in water. They were sifted through and all fish flesh, scales, eye lenses and vertebrae were picked out and weighed separately. I found the otoliths by placing portions of the sample in pie pans and swirling them in a circular, 'panning for gold' motion. Otoliths are dense and therefore they sink and drag along the bottom of the pan where they can be easily picked out.

Until the 1993/1994 season, researchers followed the protocol that only samples with an indication of fish in the sample (e.g. fish smell, color or parts) should be examined further for otoliths. In 1993/1994, I changed the protocols so that the fresh and digested portions of all the samples were 'panned' regardless if there was any evidence of fish. In addition, before 1993/1994 a white pan was used; afterwards, I substituted a black pan.

This may have increased the number of otoliths spotted as the ivory colored otoliths were more noticeable against the black background. All otoliths were stored dry in "paleocavity" slide containers or in plastic mass spectrophotometry vials.

Identifying Fish Remains

I examined all otoliths with a light microscope. I referred to Hecht (1987) and Williams and McEldowney (1990) to identify the otoliths. Bill Walker of the National Marine Fisheries Service (NMFS) identified several samples against reference collections of otoliths housed at the NMFS lab, Seattle, Washington and the John Fitch collection at L.A. County Museum, Los Angeles, California. During the winter of 1993, the Polish Antarctic Expedition at Arctowski station (Fig. 2) on Admiralty Bay collected fish in traps and with nets. They donated one hundred and thirty of these fish to this project. These fish were identified by Bill Walker who created an otolith reference collection which I used in this study. Further identifications were made by several people from photos of electron micrographs of unknown otoliths that I scanned onto a homepage of the internet (Appendix A). I consulted otolith experts from South Africa, Britain, Scotland, Argentina, and Australia through this medium (Appendix B). When possible, I identified the fish to species. If the otoliths were worn or undescribed in the literature and not identifiable to the species level, I identified them to genus or family.

Estimating Sizes of Fish

Because otoliths occur in pairs, each otolith could not be counted as an individual fish. In addition, the size of the left and right otoliths can vary slightly within a pair, so pairs can't always be identified on the basis of size. In very rare cases two otoliths were known to be from the same fish because they were still paired in the skull encasement. In order not to overcount the number of fish in a diet sample, many otolith workers use only the left or right otoliths in a sample. I felt that this would reduce the power of analysis in a sample of already rare diet items; therefore, I chose to use the most numerous otoliths in each sample. If there were more lefts than rights of a certain species of fish in a stomach sample then all lefts were used and visa versa. In this way the maximum number of fish was found without overcounting. From the 905 otoliths, 534 fish were counted.

I estimated the size of the fish from otoliths that did not appear to be worn by digestion and that were identifiable to species. I measured each of these otoliths' maximum width (dorsal-ventral) and length (anterior-posterior) to the 0.05 mm level using a micrometer eyepiece mounted on a light microscope, following the procedure done by other otolith workers (Gales 1988). I calculated the corresponding fish mass and length using regressions published in the guides (Hecht 1987, Williams and McEldowney 1990). I used the equations that were derived from the largest sample sizes and with the highest R value (Table 4).

