THE FISH COMPONENT OF *PYGOSCELIS* PENGUIN DIETS

by

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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 Adelie *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

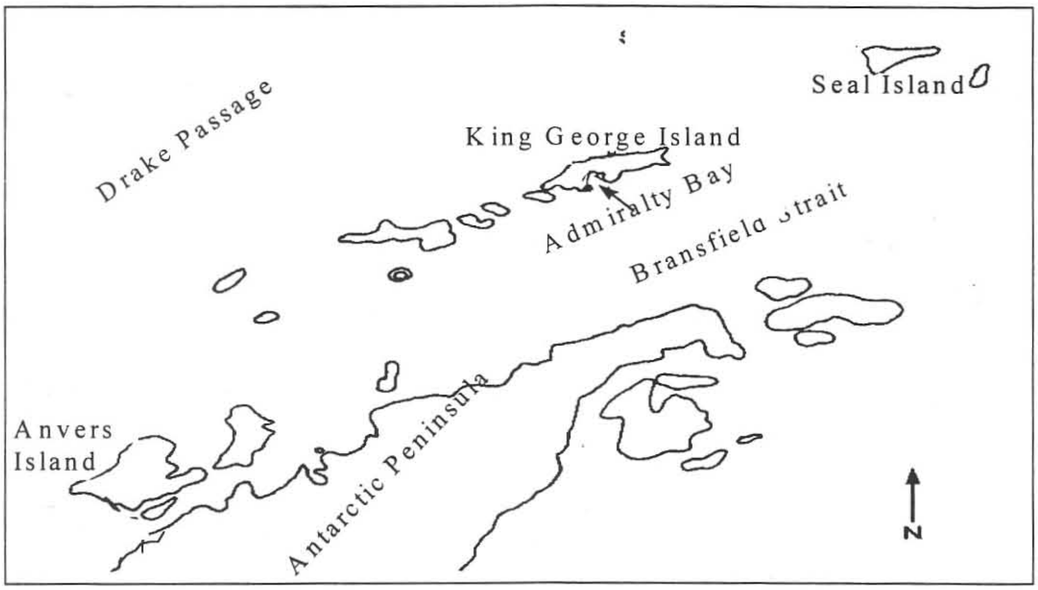

Figure 1. The location of King George Island, South Shetland Islands, Antarctica.

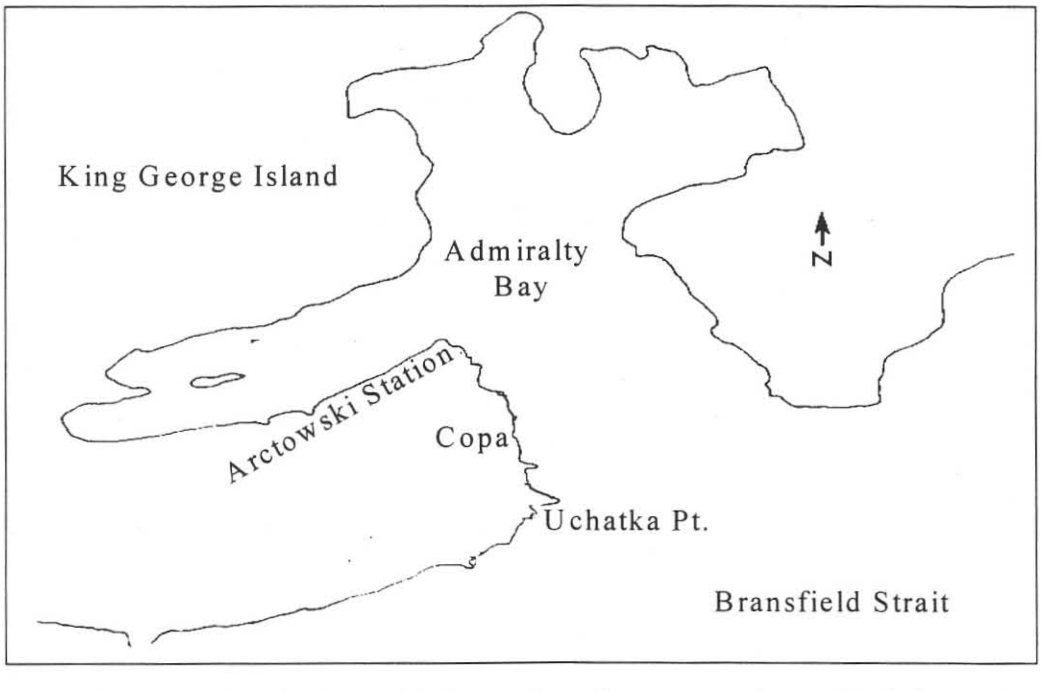

Figure 2. The study site "Copa" is located on the western shore of Admiralty Bay, King George Island.

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 m^3, a decade later the biomass estimates were averaging 23 animals per 1000 m^3 (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 murres *Uria aalgae* 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) then 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 protinaceous 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 degredation of otoliths occured at about 24 hours after the fish were consumed, although as noted above, degredation 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 then 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).

Table 4. Regressions used to calculate original mass and standard lengths of fish.

Species	Length and Mass Regressions	R	n	Ref*
Electrona antarctica	SL = 33.30505 x OW + 2.023806	.988	85	1
	Mass = 9.53 x 10^{-6} SL$^{3.080}$	.988	227	1
Electrona carlsbergi	SL = 24.25848 x OL - 2.49594	.96	20	1
	Mass = 5.314 x 10^{-5} SL $^{2.737}$	.97	20	1
Gymnoscopelus braueri	SL = 50.27563 x OW - 4.40964	.943	41	1
	Mass = 5.639 x 10^{-6} SL$^{3.102}$	.986	41	1
Gymnoscopelus nicholsi	SL = 28.61827 x OL - 20.7910	.889	140	1
	Mass = 5.610 x 10^{-6} SL$^{3.153}$	.981	140	1
Notolepis coatsi	Interpolated from measurements		2	1
Dissostichus eleginoides	SL = 141.9414 x OW - 264.490	.916	160	1
	Mass = 4.59 x 10^{-6} SL$^{3.187}$	.985	159	1
Notothenia coriiceps	SL = 86.59886 x OL - 27.91347	.935	13	1
	Mass = 2.78 x 10^{-5} SL $^{2.943}$	.988	13	1
Notothenia neglecta	SL = 71.41905 x OL - 13.67271	.744	218	1
	Mass = 5.71 x 10^{-6} SL$^{3.259}$	.974	264	1
Notothenia r. rossii	SL = 82.58219 x OL - 43.68991	.884	19	1
	Mass = 3.366 x 10^{-6} SL$^{3.306}$	.994	19	1
Lepidonotothen kempi	SL = 108.6725 x OW - 122.6568	.971	17	1
	Mass = 5.00 x 10^{-6} SL$^{3.217}$	.999	23	1
Lepidonotothen nudifrons	SL = 33.78 x OL $^{0.96}$	.92	11	2
	Mass = 4.01 x 10^{-7} SL $^{3.81}$	.98	11	2
Gobionotothen marionenesis	TL = OL x 76.18		5	2
Notothenia acuta	SL = 37.65546 x OL - 23.2003	.953	40	1
	Mass = 4.08 x 10^{-7} SL$^{3.634}$	.990	40	1
Pagothenia bernacchi	SL = 59.55118 x OW - 5.83741	.786	278	1
	Mass = 7.71 x 10^{-6} SL$^{3.119}$	.978	1283	1
Pleurogramma antarcticum	SL = 69.21882 x OW - 15.81990	.906	759	1
	Mass = 2.71 x 10^{-6} SL$^{3.200}$	.992	1297	1
Notothenia larseni	TL = 42.50 x OL $^{0.89}$		22	2
Trematomus lepidorhinus	SL = 46.34517 x OL + .913925	.88	36	1
	Mass = 9.48 x 10^{-7} SL$^{3.551}$	.976	42	1
Trematomus newnesi	SL = 107.9159 x OW + 37.74691	.719	45	1
	Mass = 8.43 x 10^{-6} SL$^{3.127}$	.967	239	1
Chaenodraco wilsoni	SL = 58.4141 x OW + 85.92148	.842	31	1
	Mass = 1.51 x 10^{-6} SL$^{3.350}$	.995	42	1
Neopagetopsis ionah	Interpolated from measurements		6	1
Pagetopsis maculatus	TL = OL x 83.30		19	2
Pagetopsis macropterus	TL = OL x 150			2

SL = standard length, TL = total length, OW = otolith width, OL = otolith length. *Ref. 1: Williams and McEldowney 1990, ANARE Research Notes 75. *Ref. 2: Hecht, T. 1987, A Guide to the Otoliths of Southern Ocean Fishes.

Data Analysis

I used STATISTICA software (Statistica 1994) for most of the statistical analyses I performed. Throughout these analyses I made the assumption that all fish were independent of each other even if they occurred in the same stomach sample. Independence is probably true for the fish that are solitary bottom dwellers and less true for schooling fish. I used parametric tests for the normally distributed mass and standard length data. I used non-parametric tests for the count data measuring frequency of occurrence. Because fish are relatively scarce in terms of abundance and frequency of occurrence, tests comparing the frequency and abundance of each fish species among years, species, and sexes were done within the group of penguins that had fish in their diets. That is, the sample frame for these tests was the group of fish eating birds.

The statistical tests I chose were to examine differences in: 1) frequency of occurrence of fish, 2) abundances of fish, 3) sizes of fish eaten, and 4) the amount of fresh fish in the stomach samples versus the amount of fish estimated from otolith analyses, among penguin species and between male and female penguins. I calculated frequency of occurrence (presence vs. absence) as percentage of stomach samples containing fish versus those without fish. I measured abundance as the number of individual fish present in each stomach sample. I performed each of the tests on all of the fish data combined together, and on individual species of fish. In order to find the mean mass and standard length of each fish species, I used all the otoliths (both left and right) in the calculations so that the variations within pairs could be incorporated.

Tests Used for Examining Interspecific Dietary Differences

I summarized the total number of otoliths (Appendix C) and number of fish (Table 5) of each fish species consumed by each species of penguins. I used maximum-likelihood (M-L) contingency-table analyses to compare the frequency of different species of fish among penguin species. I report significant results ($p<0.05$) unless otherwise noted. I performed Kruskal-Wallis tests to compare the abundance of different fish among species. For test statistics with $p< 0.1$ or less, I used pairwise comparisons among component terms. I used an Analysis of Variance (ANOVA) to compare the mean weights and standard lengths of all species of fish taken among species. Pairwise comparisons of the means were done with a Tukey honest significant differences test (HSD) for unequal sample sizes. I compared the proportion of birds that returned with fresh fish in their stomachs and the proportion of birds that returned with any fish with a M-L contingency table analyses. I compared the mean mass of fish ingested at sea with the mean mass of fish brought back to the chicks at the nests for each of the three penguin species.

Tests Used for Examining Intraspecific Dietary Differences

I used t-tests to compare stomach sample weights of the male and female penguins of each species. I used contingency table tests to examine sex differences in frequency of occurrence of fish. I used Mann-Whitney tests to compare the abundances of fish between the sexes of each penguin species. I used t-tests to compare the masses and standard lengths of fish between male and female penguins. I used a contingency table analyses to examine sex differences in both the percentage of birds that returned with any evidence of fish, and the percentage of those that had fresh fish in their stomachs. I used a cluster analysis and multi-dimensional scaling to examine the degree of dietary similarity and differentiation among the species and sexes of the penguins.

Caveat about Interannual Dietary Differences

Due to changes in sampling protocols midway through this study, I did not examine changes in the penguin diets over time. However, the results of this study will be used as a baseline for future analyses of interannual variability.

RESULTS

The Occurrence of Fish in Penguin Diet Samples

The average wet weight of the stomach samples across all species and years was 539.7 grams (SD = 209.0, n = 553) with a minimum of 65.03 g and a maximum of 1354.4 g. All but two (99.6%) of the diet samples contained krill. The two samples without krill were made up entirely of fish. I found evidence of fish in 193 out of 553 (35%) diet samples. I found otoliths in 155 of the diet samples (28%), although otoliths of 6 of the 155 samples were lost in the field. I found measurable (i.e. weighing more than .25 grams) fresh fish in 98 of the diet samples (17.7%). In 18 samples, I found measurable fish flesh but did not recover any otoliths. I found traces of fish (scales, eye lenses, bone fragments), but no otoliths nor measurable fish flesh in 21 samples. Of the samples with otoliths, 75 of them had no other evidence of fish consumption. In all, I analyzed 889 otoliths from 149 samples. In 97 samples where fresh fish was found, fish made up an average of 12.6% of the total stomach weight (sd = 25.6; range 0.06% to 100%). Through examination of the otoliths, I identified 26 species of fish from 5 families (Table 5).

Interspecific Comparisons of Penguin Fish Diets

The gentoo diets were the most diverse with 24 fish species representing four families (Table 5). Adelie fish diets were the least diverse with only eight fish species from three families and the chinstrap penguins had ten fish species from four families. All three species of penguins ate fish from Myctophidae, Notothenidae and Channichthyidae. Only gentoo penguins took fish from Harpifager and only chinstrap penguins took fish from the Paralepididae.

Table 5. Number of fish eaten by penguins and percent contribution to diets.

	Adelie		Gentoo		Chinstrap		
Fish Species	#	%	#	%	#	%	Total #
Myctophidae							
Krefftichthys anderssoni			1	0.30	1	0.65	2
*Protomyctophum bolini**	1	2.44	5	1.48			6
*Electrona antarctica**	11	26.8	19	5.61	98	63.64	128
Electrona carlsbergi			1	0.30			1
*Gymnoscopelus braueri**			24	7.08			24
Gymnoscopelus nicholsi	1	2.44	3	0.89	10	6.5	14
Myctophid sp.			1	0.30			1
Paralepididae							
*Notolepis coatsi**					3	1.95	3
Notolepis sp.					3	1.95	3
Paralepididae sp.					2	1.30	2
Harpifager							
Harpifager antarcticus			2	0.59			2
Harpifager sp.			4	1.18			4
Nototheniidae							
Dissostichus eleginoides			1	0.30			1
Notothenia coriiceps					1	0.65	1
*Notothenia neglecta**			6	1.77			6
*Notothenia r. rosii**			5	0.89			5
*Lepidonotothen kempi**	1	2.44	40	11.80			41
Notothenia acuta			1	0.30			1
*Pagothenia bernacchi**			11	3.25			11

Table 5. (continued)

*Gobionotothen marionensis**			54	15.93			54
*Lepidinotothen nudifrons**			46	13.57			46
*Pleurogramma antarcticum**	22	53.7	18	5.31	15	9.74	55
Notothenia larseni			2	0.59			2
Trematomus lepidorhinus			3	0.89			3
*Trematomus newnesi**	1	2.44	32	9.44			33
Notothenia sp.			28	8.26	1	0.65	29
Channichthyidae							
Chaenodraco wilsoni			4	1.18	2	1.30	6
Neopagetosis ionah			1	0.30			1
Pagetopsis macropterus	2	4.88	5	1.48	14	9.09	21
Pagetopsis maculatus	2	4.88	7	2.07	1	0.65	10
Pagetopsis sp.			6	1.77	1	0.65	
Unknown fish			11	3.25	2	1.30	
Totals	41		339		154		534

= number of fish. %=percent of stomach samples fish found in.
* p = <0.05 in M-L Chi-square contingency table tests for differences in occurrence between species.

There were significant differences among the three species of penguins in terms of the presence of any type of fish in their stomach samples ($\chi^2 = 20$, df= 2, $p < 0.001$, Table 6). There were also differences in the number of birds of each species that brought fresh fish back to their chicks ($\chi^2 = 31.9$, df=2, $p < 0.001$, Table 6). In both cases Gentoo penguins differed significantly from Adelie and chinstrap penguins ($p<0.05$).

Table 6. Percentages of stomach samples with any fish and fresh fish only.

Penguin Species	All Fish	Fresh Fish
Adelie	23.8	12.2
Gentoo	45.8	30.2
Chinstrap	34.3	9.4

I calculated the mean mass of fish eaten at sea per penguin and compared this mean to mean mass of fresh fish brought back to the chicks (Table 7). On average, the Adelie and chinstrap penguins fed their chicks approximately 20% of the mass of fish consumed at sea. Gentoo penguins returned with approximately 40% of what was consumed. Overall, chicks received a much reduced amount of the fish consumed by the parent bird.

Table 7. Comparison of average (g) mass of fresh fish versus total mass consumed.

	Adelie			Gentoo			Chinstrap		
	Average	sd	n	Average	sd	n	Average	sd	n
Fresh	6.7	7.0	16	111.6	205	50	8.9	20.5	14
Total	34	28	19	281	431	54	43.0	68	43

Presence vs. absence (frequency of occurrence) of several species of fish differed significantly among the penguins ($p \leq 0.05$). These differences are denoted by an asterix (*) next to the species names in Table 5. There were significant differences in abundances (number of individuals per stomach) of several species of fish when compared among the three species of penguins (Kruskal- Wallis tests, $p < 0.1$, Table 8).

Table 8. Results of Kruskal-Wallis test on abundances of fish among penguin species.

Fish:	Adelie: Gentoo	Adelie: Chinstrap	Chinstrap: Gentoo
E. antarctica		p = 0.000	p = 0.000
G. braueri			p = 0.048
L. nudifrons	p = 0.000	p = 0.000	p = 0.000
G. marionensis	p = 0.009		p = 0.001
N. coatsi		p = 0.092	p = 0.029
L. kempi	p = 0.011		p = 0.000
N. neglecta			p = 0.048
P. antarcticum	p = 0.000	p = 0.000	
P. bernacchi	p = 0.021		p = 0.004
T. newnesi			p = 0.013

Masses of fish varied significantly among species (ANOVA, $p<0.001$). Mass differences of fish in the diet of gentoo penguins differed significantly from that of Adelie

(HSD p<0.01) and chinstrap penguins (HSD p<.001). Gentoo penguins had the highest variance in the masses of fish taken, and took fish, on average, four times heavier than chinstrap penguins and three times heavier than Adelie penguins (Figure 3).

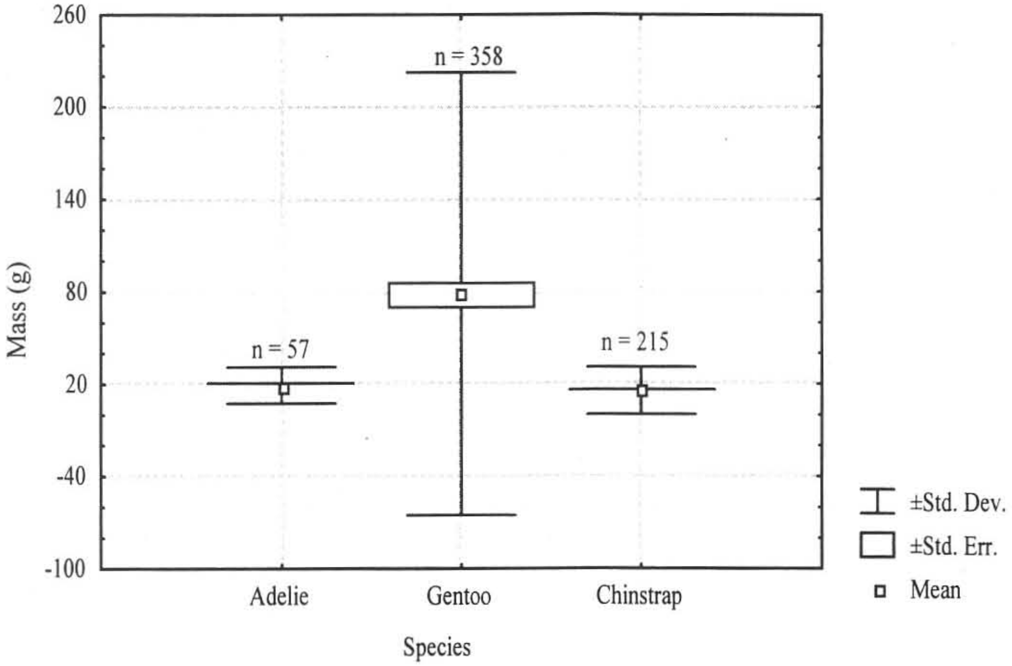

Figure 3. Comparison of masses of fish among penguin species.

Consistent with the results for mass, standard lengths of fish differed significantly among penguin species (ANOVA, p <0.001). On average the chinstrap penguins took the smallest fish and the gentoo penguins took the largest, these species differed significantly (HSD, p<0.001). Gentoo penguins also had the largest variation in fish sizes in their diet (Figure 4).

The size of *P. antarcticum* varied among species (ANOVA, p<0.001, figure 5) with gentoo and chinstrap penguins differing (HSD, p<0.001).

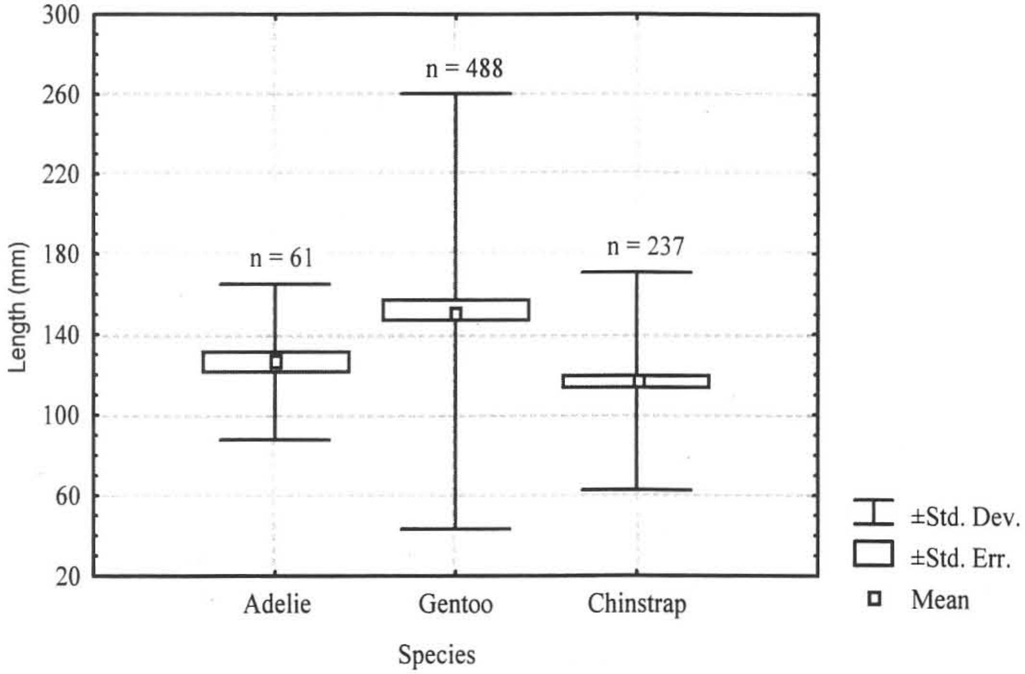

Figure 4. Comparison of fish standard lengths among penguin species.

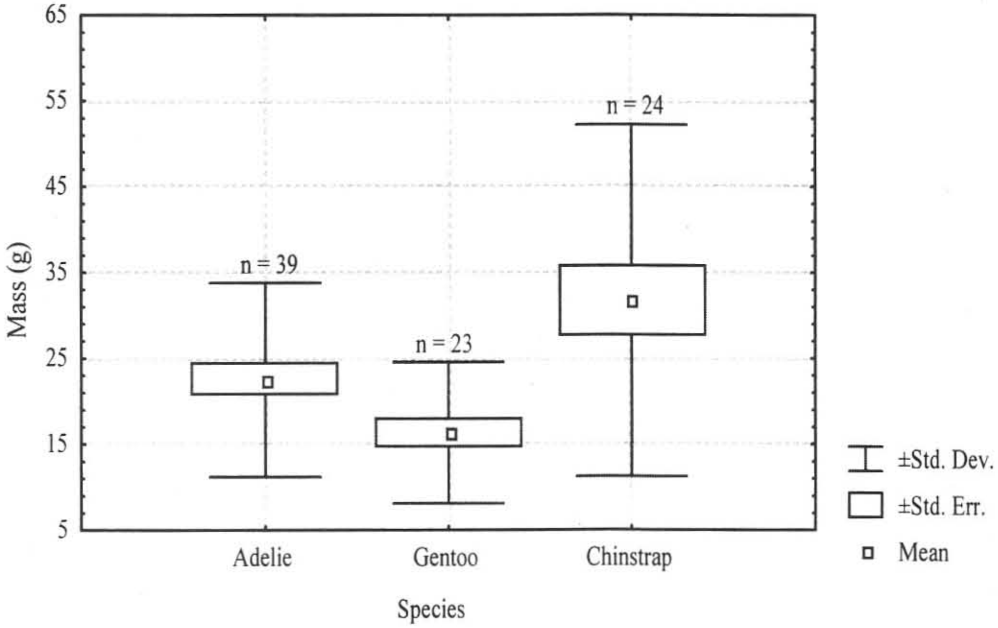

Figure 5. Comparison of masses of *P. antarcticum* among penguin species.

Intraspecific Comparisons of Penguin Fish Diets

Stomach sample weights differed between male and female Adelie and chinstrap penguins (t-test, p =0.04 for both). There were no differences between male and female gentoo penguins (Table 9).

Table 9. Average stomach sample weight of male and female penguins.

	Males			Females		
Species	n	mean wt. (g)	sd	n	mean wt (g)	sd
Adelie*	90	528.8	193.0	90	471.7	169.3
Gentoo	101	538.2	235.5	91	529.2	198.7
Chinstrap*	99	614.2	221.6	77	547.0	198.7

*significant differences between sexes, p = 0.04

Generally, there were no differences between the sexes in terms of abundances of different species in fish although the abundance of *G. marionensis* differed (Kruskal-Wallis test, p= 0.047). There were, however, differences in the presence or absence (contingency table analysis) of fish, fresh fish only and certain species of fish (Table 10).

Table 10. Comparison of fish species found in male and female penguin stomach samples.

Penguin	Fish	% Males	% Females	p-value
Gentoo	All fish	55	35	0.005
	Fresh fish	37	23	0.04
	G. marionensis	21	4	0.03
	T. lepidorhinus	0	7	0.05
	N. rossii	7	0	0.08
	L. nudifrons	33	15	0.08
Chinstrap	*N. coatsi*	0	12	0.03
	C. wilsoni	0	8	0.08

Inter-sexual differences were most pronounced in the sizes of the fish eaten (Table 11).

Table 11. Comparison of four species of fish eaten by male and female penguins. Mass is given as the average for all individuals representing each fish species.

Species	Males			Females			
Adelie	mass (g)	sd	n	mass (g)	sd	n	p-value
E. antarctica	11.8	2.8	6	7.9	3.0	8	p = 0.03
Gentoo							
G. braueri	4.9	1.4	5	6.3	0.8	35	p = 0.002
L. kempi	35.8	66.1	47	7.0	6.2	16	p = 0.080
G. marionensis	314.9	50.1	95	391.2	59.3	4	p = 0.003

In order to assess the degree of dietary similarity of the three penguins of both sexes a cluster analysis and multi-dimensional scaling was done with presence/absence data of the fish species in the penguin diets of both sexes of each species (figure 6). These results summarize some of the univariate tests on the presence/absence of different fish in the diets. Gentoo penguin males differed greatly from females and from both congeners. Male and female chinstrap penguins are closer to each other than to other species, as were male and female Adelie penguins. Adelie penguins and chinstrap penguins are more closely linked to each other than to gentoo penguins.

The distance matrix from the cluster analysis was used in the multi-dimensional scaling analysis (Figure 7). This analysis indicates that chinstrap penguins and Adelie penguins of both sexes differed from gentoo penguins, but are similar to each other. Male and female gentoo penguins have the greatest dietary differentiation among the six species/sex categories.

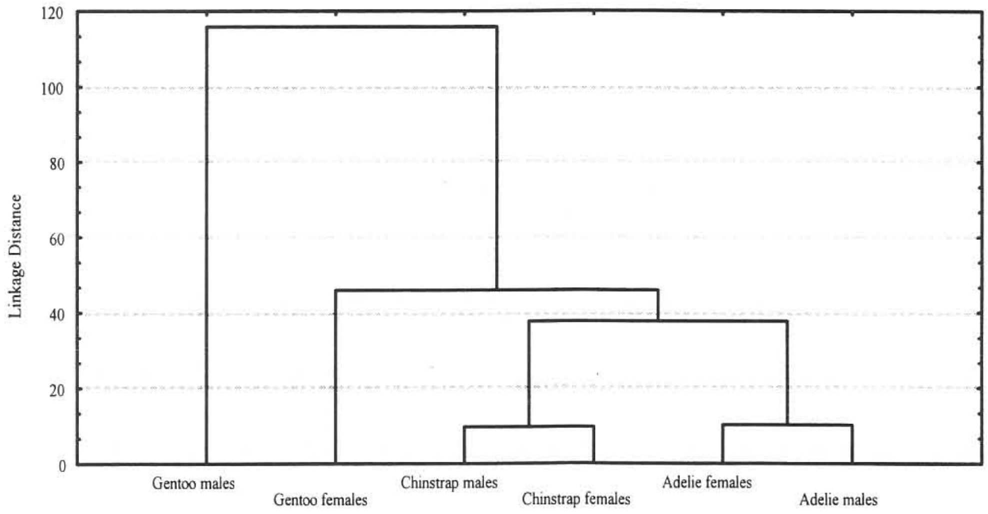

Figure 6. Tree diagram for penguin diets. Configuration was based on single linkage Euclidean distances.

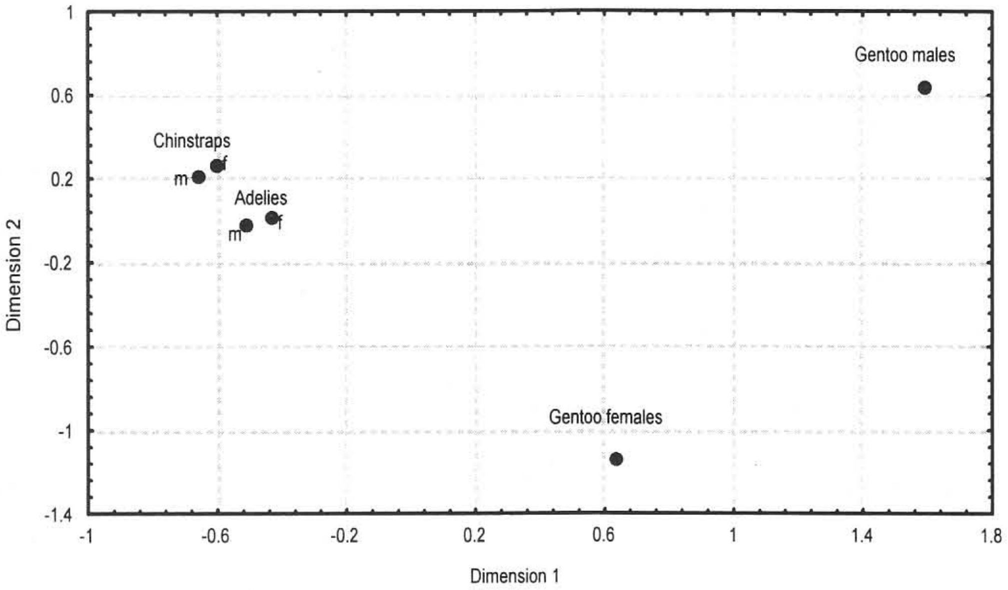

Figure 7. Scatterplot of multidimensional scaling results of penguin diets.

DISCUSSION

Dietary Diversity

The results of this study indicate that *Pygoscelis* penguins ate a much greater diversity and quantity of fish than previously known. Through the inspection of otoliths, I identified 26 species of fish from five families. In contrast, otoliths were not analyzed in earlier studies of these three species of penguins (Volkman et al. 1980, Jablonski 1985, Lishman 1985b, Trivelpiece et al.1990b), and the fish found in the diets of these penguins were highly digested. Except for nine intact fish that were found in gentoo penguin stomachs and identified as *Pleurogramma antarcticum*, these earlier studies were not able to identify fish remains to species (Volkman et al. 1980).

There are several fish identifications that should receive further consideration when additional information on Antarctic fish ranges and otolith morphology are available. In particular, three species from the Family Nototheniidae that were found in gentoo penguin diets are not known to occur in the Antarctic Peninsula region. The fish *Dissostichus eleginoides* occurs in waters north of 55° S latitude (Gon and Heemstra 1990) and *Notothenia acuta* is only known from the Indian sector of the Southern Ocean, around sub-Antarctic islands to depths of 300 m (Gon and Heemstra 1990). There was only one fish of each of these species in the samples, however, by far the most common otolith in gentoo penguin diet samples was *Gobionotothen marionensis* and the closest records for this species are from South Georgia and the South Orkney Islands (Gon and

Heemstra 1990). My records could be a result of misidentifications of the otolith, or actual range extensions for these species. Several otolith experts were consulted on these identifications and opinions on the identity of these otoliths varied (see Appendix B).

This unexpected result could also be due to under-sampling in Admiralty Bay by fish biologists. There are several undescribed species in Admiralty Bay, and the otoliths of several species of fish that are known have not been described. In addition, otoliths from younger life stages of the fish have not been described. The most extensive list of fish found in Admiralty Bay was compiled by Skora and Neyelov (1992). Of the thirty-four species they caught in a variety of traps and trawls, eleven were found in our penguin stomach samples.

Differences in opinion from otolith workers exemplify the difficulty in identifying fish from otolith evidence. Otoliths from Nototheniidae are highly variable morphologically within a species and are similar between species. Three species that are especially difficult to differentiate are *Lepidonotothen kempi*, *Lepidonotothen nudifrons*, and *Notothenia larseni*. Otoliths from juvenile size classes are extremely difficult to identify to species, particularly *Pagothenia bernacchi* and *Trematomis newnesi*. Another identification that might be subject to change for this reason is that of ten small individuals of *Pagetopsis maculatus*, a rare, deep water fish (Gon and Heemstra 1990).

Interspecific Variation

All three penguin species primarily ate krill, but differed with respect to the fish portion of their diets. A major difference was the greater frequency and mass of fish in the diet of gentoo penguins compared to their two congeners. In this study, 23.8% of the Adelie penguins, 45.8% of the gentoo penguins, and 34.3% of the chinstrap penguins had fish in their stomachs. Volkman et al. (1980) found that 13% of the Adelie penguins, 40% of the gentoo penguins and 21% of the chinstrap penguins had fish in their stomachs during an earlier study at Admiralty Bay. The earlier estimates from Volkman et al. (1980) are actually closer to the estimates I found for birds with evidence of fresh fish in their stomachs, where 12.2% of the Adelie penguins, 30.2% of the gentoo penguins, and 9.4% of the chinstrap penguins contained fresh fish. As noted previously, in these earlier studies researchers did not search for otoliths and so the presence or absence of fish was determined mostly from evidence of fresh fish.

However, the earlier estimates are consistent with my data on the relative levels of fish intake for the three species (Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b). Both Volkman et al. (1980) and this study indicate that gentoo penguins, have the highest frequency of fish in their diets and Adelie penguins the least. However, in all studies, the estimates for chinstrap penguins were highly variable from year to year. For example, chinstrap penguins had no fish in their diets in 1992, whereas, in 1993, 63.3% of them had fish in their stomachs. In 1993, the number of chinstrap penguins containing fish was almost twice that of the gentoo penguins. In the previous studies that spanned 1977, 1979-1982, 1984-1986, the percentage of fresh fish by wet weight brought back to the nest was consistently low for Adelie penguins (min 0.0% - max 4.3%) and higher for gentoo penguins (min 15%- max 48.65%, Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b). Chinstrap penguins showed the most variability (min 0% -

65%, Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b). Therefore, chinstrap penguins show a high degree of variability in terms of the number of birds taking fish (frequency) in a given season (this study) and in the percentage of fish in their diet by wet weight (Volkman et al. 1980, Jablonski 1985, Trivelpiece et al. 1990b).

There were several interspecific differences in the abundance, size, and life history characteristics of fish species found in the *Pygosceli*s diets. The relative abundances of several species of fish common in the diets of all three species of penguins varied. These differences may reflect differences in foraging ranges and diving habits among the *Pygoscelids*. Gentoo penguins took larger fish on average than either of its congeners and chinstrap penguins the smallest. These size differences may be a result of differences in the sizes of prey available within the respective feeding zones of the three penguin species, rather than a result of prey selection. For example, the gentoo penguins took smaller *P. antarcticum* than did chinstrap penguins, perhaps reflecting a more pelagic occurrence of the larger fish and of the smaller ones more inshore. Thus, the population of *P. antarcticum* may overlap with gentoo and chinstrap foraging zones at different life stages.

The species of fish taken by the different penguins have different life history traits. Some are largely pelagic and are associated with krill swarms. Others are benthic but rise in the water column to feed. Adelie and chinstrap penguin samples had a higher frequency of pelagic fish found in the upper water column whereas the gentoo penguins took benthic fish more frequently (Table 12).

Table 12. Habitats of the fish species found in penguin diets.

Penguin species/ Fish Species	Adelie	Gentoo	Chinstrap
Myctophidae			
Krefftichthys anderssoni		pelagic	pelagic
Protomyctophum bolini	pelagic	pelagic	
Electrona antarctica	pelagic	pelagic	pelagic
Electrona carlsbergi		pelagic	
Gymnoscopelus braueri		pelagic	
Gymnoscopelus nicholsi	pelagic	pelagic	pelagic
Paralepididae			
Notolepis coatsi			pelagic
Harpifager			
Harpifager antarcticus		benthic (shallow)	
Nototheniidae			
Dissostichus eleginoides		bentho-pelagic	
Notothenia coriiceps			benthic
Notothenia neglecta		benthic	
Notothenia r. rosii		benthic	
Lepidonotothen kempi	benthic	benthic	
Notothenia acuta		benthic	
Pagothenia bernacchi		benthic	
Gobionotothen marionensis ?		benthic	
Lepidonotothen nudifrons		benthic	
Pleurogramma antarcticum	pelagic	pelagic	pelagic
Notothenia larseni		benthic	
Trematomus lepidorhinus		benthic	
Trematomus newnesi	benthic	benthic	
Channichthyidae			
Chaenodraco wilsoni		bentho-pelagic	bentho-pelagic
Neopagetosis ionah ?		bentho-pelagic	
Pagetopsis macropterus	bentho-pelagic	bentho-pelagic	bentho-pelagic
Pagetopsis maculatus ?	benthic	benthic	benthic

Intraspecific Variation

Volkman et al. (1984) reported that male gentoo penguins ate more fish than females. In this study, I also found that male gentoo penguins ate more fish than females, and that males returned to their nests with more fresh fish. In addition, I found significant differences between male and female gentoo penguins in the species of fish eaten. Gentoo males consumed more *N. marionesis*, *N. rossii* and *L. nudifrons,* and only female gentoo penguins ate *T. lepidorhinus,* although the number of these fish was also very small. My study further concurred with Volkman et al. (1984), in not finding any differences in the proportion of male and female Adelie and chinstrap penguins that had eaten fish. However, only chinstrap females had *N. coatsi* and *C. wilsoni* in their diet, although the number of these fish was very low (n=3, *N. coatsi*; n=2, *C. wilsoni*). These differences between the sexes in gentoo and chinstrap penguins could reflect sex related partitioning of foraging habitat, however, it is likely that these results were an artifact of small sample sizes.

The sizes of the fish eaten by males and females did not differ, although there were a few differences in the sizes of some species of fish. For example, Adelie penguin males took larger *E. antarctica* than females, and gentoo penguin males took larger *L. kempi* than females. However, larger males did not consistently take larger fish. Female gentoo penguins took larger *G. braueri* and *G. marionensis*. In summary, gentoo penguins exhibited the most intrasexual dietary differences.

Dietary Segregation in Multi-Species Rookeries

Competition theory predicts that when competition occurs, the niches of closely related sympatric species will diverge (e.g. Taper and Case 1992). Along these lines, White and Conroy (1975) suggested that sympatric *Pygoscelis* penguins breeding on Signy Island select different food items to avoid competition. However, the degree to which sympatrically breeding penguins have different diets varies from location to location. Gentoo penguins on Signy Island ate mostly fish, while the Adelie and chinstrap penguins ate mostly *Euphausia superba* (White and Conroy 1975). In the South Orkney Islands, Lishman (1985b) found that Adelie and chinstrap penguins ate the same size krill for most of the year, but had different size classes in certain times of year. Macaroni and rockhopper penguins breeding on Marion Island had largely overlapping diets (Brown and Klages 1987), but both differed from diets of the highly differentiated king and gentoo penguin diets that breed there as well (Adams and Brown 1989). Macaroni and rockhopper penguins at Heard Island both fed on a mixture of euphausiids and fish but differed in the types and sizes of these prey (Klages et al. 1989). Rockhopper and royal penguins at Macquarie Island had largely overlapping diets (Hindell 1988a, 1988b). King and gentoo penguins at Heard Island ate fish of different types, sizes and amounts (Klages et al. 1990). In a review of the diets of six sympatric populations of crested penguins (*Eudyptes* spp.), Cooper et. al. (1990) concluded that dietary differences varied more with breeding location and breeding chronology than taxonomy.

Dietary differentiation is likely to be, in part, a function of what prey species are available within the feeding areas of a species or population of penguins, and a function of the degree to which the penguins have overlapping breeding seasons. Croxall and Lishman (1987) observed that within most multi-species penguin rookeries, one species of penguin fed in the inshore feeding zone and the other species forage offshore. At Admiralty Bay, the gentoo penguin is the inshore feeder and the chinstrap and Adelie penguins are the offshore feeders (Trivelpiece et al.1987). Adelie and chinstrap penguins are ecologically segregated by their differences in breeding chronology (Lishman 1985a, Trivelpiece et al.1987). Chinstrap penguins initiate breeding up to four weeks later than the Adelie penguins, and therefore, the overlapping period of foraging during the energetically demanding chick rearing period is quite short. The Adelie penguin initiates breeding earlier because it is mainly a continental species which experiences harsh conditions and a short window of time for breeding (Trivelpiece et al. 1987, 1996). It is possible that Adelie and chinstrap penguins feed in different areas when both are foraging for chicks at the same time during January annually. Differences in their foraging time at sea (Trivelpiece et al.1987) and slight differences in their diets (Lishman 1985b, this study), suggest this might be the case.

There is no strong evidence that competition for resources is a primary factor affecting segregation in the ecological niches of the three species. Interspecific differences in foraging range and breeding chronology of the various species of penguins probably evolved in response to conditions experienced at the center of their breeding ranges rather than through competition (Lishman 1985a, Trivelpiece et al. 1987). However, increased divergence may become apparent if competition among the three species, and between the sexes, intensifies if food becomes a limiting resource. For example, Volkman et al. (1984) hypothesized that the intraspecific differences among male and female gentoo penguins may be a result of the sexes competing for limited food resources around the rookeries during winter. The three species are more likely to experience competition during the breeding season when adults are confined to a smaller area.

Parent/chick Dietary Differences

The food that is being brought back to the chicks by all three species is almost entirely made up of *E. superba,* in terms of both number of diet items and contribution by mass. The fish, however, are a diet item being consumed by the adult penguins, the remains of which are carried back to the chicks. In feeding trials of white-chinned petrels *Procellaria aequinoctialis* that were fed a mixture of krill and fish, the fish were digested rapidly, whereas much of the krill mass was recovered (Jackson and Ryan 1986). Jackson and Ryan hypothesized that the slow digestion of krill was due to difficulty in digestion of the chitinous exoskeleton of the crustaceans. Because of their differential digestion rates, krill are a better candidate for long distance foragers to bring back to the chicks. It is difficult for penguins that forage long distances away from the colony to retain fish during their trip back to shore. It is likely that adults that forage far offshore replenish their own reserves by eating fish. Fish being rapidly absorbed would give the bird a quick, high energy meal.

Of the three *Pygoscelids,* only the gentoo penguin, which forages close inshore, frequently fed their chicks fresh fish (30.2 % of the gentoo penguins brought fresh fish back to their chicks). Interestingly, the gentoo penguin probably takes its fish primarily on its return trip back to the colony, as indicated by TDRs deployed on gentoo penguins showing a series of deep dives as the penguins swim towards shore (Trivelpiece, pers comm). Furthermore, these same penguins usually have fresh fish in the top layer of their stomachs (Trivelpiece, pers comm). By taking fish on their return trip rather than on their way out, they supply their chicks with more fish, which have a higher energy content per unit weight than krill.

Chinstrap penguins forage offshore and rarely brought back fresh fish to their chicks (9.4% of the birds) but they had a high number of otoliths in their stomachs. In one year of this study, their level of fish intake exceeded that of gentoo penguins in terms of frequency of birds eating fish. Chinstrap penguins may take fish to sustain themselves on their long foraging trips, while eating krill to feed their chicks. In both Adelie and chinstrap penguin diet samples, the number of fish consumed could have been underestimated because these fish were not in the top layer of their stomachs and were already digested leaving only otoliths.

Because adult Adelie and chinstrap penguins were digesting most of the fish they consumed and feeding their chicks krill, adults and chicks fed at different trophic levels. The difference between parent and chick diets could probably be elucidated in more detail by the use of stable-isotope analysis of adult penguin tissue and chicks tissue. This technique has already been used to evaluate the diets of many other seabirds (Hobson and

Clark 1992, Hobson et al. 1994). These differences in adult and chick diets may also imply that taking stomach samples from penguins during the chick rearing period may not be the best way to understand the full scope of adult penguin diets. In addition, while fish may be a relatively infrequent diet item, it may be essential in supporting the adults feeding far offshore during the energetically taxing chick rearing period.

Prey Switching

Although krill is the major diet item of *Pygoscelis* penguins during the breeding season, they could come to rely more on fish if the krill population continues to decline. Krill populations declined in the recent past, presumably due to a decrease in winter sea-ice on which young individuals depend for survival. In addition, an active krill fishery has developed near the breeding colony. While the results of this six year study did not examine temporal changes in the frequency of fish in the penguins' diets, they do raise some important questions about the potential for prey switching among the three penguin species.

Of the three penguins, the gentoo penguin has the most catholic diet (Volkman et al. 1980, Croxall and Prince 1980b, Croxall et al.1988b, Robinson and Hindell 1996). It has a more localized foraging range, but also has the greatest flexibility in terms of exploiting prey at different depths. In most years it ate the highest amount of fish, and because of its short foraging range, the fish arrived at the colony relatively undigested, resulting in a higher volume of fish in the diets of gentoo chicks compared to chicks of Adelies and chinstrap penguins. Gentoo penguins ate mostly benthic dwelling fish that feed primarily on bottom dwelling amphipods (Gon and Heemstra 1990). While many of these fish do rise in the water column to take advantage of krill swarms, and some spend part of their lives as pelagic larva that eat krill, the notothenid group of fish seems to be less associated with krill (Hureau 1994). Accordingly, they probably constitute a dependable food source if the krill biomass decreased further. Alternatively, the species of fish eaten by chinstrap and Adelie penguins are mostly Myctophidae, which are pelagic and prey on krill swarms. Thus, a decline in the number or size of krill swarms could negatively impact these myctophid fishes. Of course, the recent changes in the ice regime may have negative impacts on the fish community as well. Channichthyids, myctophids, and over 40 species of nototheniids are known to associate with seasonal sea-ice (Hureau 1994).

Directions for Future Research

Because fish are a regular part of the *Pygoscelis* diets, a new sampling regime to explore some of the factors influencing fish intake should be implemented. This study was conducted using protocols developed for another study of the Antarctic krill consumed by the penguins (CCAMLR 1990). As described in the Methods, five birds of the same species of penguin were sampled at the same time on the same day. In a successive day, five more birds of another species were sampled at the same time. In order to explore the influence of time of day on fish intake, the time of day should be varied so that the full range of hours are sampled. While the penguins at our site appear to be predominately diurnal foragers, nocturnal foraging in chinstrap penguins has been described at other sites and these nocturnal foragers have a tendency to return to the colony with more evidence of fish in their stomachs than diurnal foragers (Jansen et al. 1997). In a preliminary study to examine the influence of time of day on fish intake of chinstrap penguins, I found that no birds returned to their nest sites at night. Although sampling over all hours may not be feasible at our site, more attention should be paid to fish intake as related to patterns of foraging trip departures and arrivals.

Another factor that should be addressed are between-day differences in prey species. Adelie penguins may return with a certain species of fish on one day, and then the next day chinstrap penguins may return with a different species of fish. Are those differences because of interspecific dietary differences or because of between-day differences in availability of different fish species? Dietary differences among species have not been separated from temporal changes in the marine environment. Taking samples from all three species simultaneously should help us distinguish interspecific differences from short-term environmental changes. A sampling design that stratifies on the basis of species, date and time is necessary so that a multivariate analysis of all such factors that might influence fish intake could be undertaken. This field site affords a rare opportunity to conduct such a study.

Marine sampling in areas where penguin diets are being studied have revealed that there is a strong concordance of krill found in nets with krill taken by penguins with some differences in krill size, sex, and reproductive condition (Reid et al. 1996, Hill et al. 1996). In this regard, more attention should be focused on the distribution and abundance of fish within penguin foraging ranges. Penguin surveys at sea, and simultaneous sampling of waters with acoustic profiles and nets surrounding penguin colonies, with stomach flushing of penguins on shore, could help answer questions about how penguins respond to variations in the abundance and distribution of different fish.

Most studies have emphasized the feeding habits of older Antarctic fish (Kock 1985, Everson 1977, 1984). The migratory patterns, feeding ecology and otolith morphology of juvenile Antarctic fish need to be studied in more detail. The role of fish in Antarctic marine foodwebs is significant (Hureau 1985, Williams 1985) and warrants more attention.

Our understanding of penguin foraging ecology has been greatly enhanced by attaching instruments to penguins that measure time at-sea, swimming speed, diving depth and dive profiles during foraging trips (Adams and Brown 1983, Croxall et al. 1988, Lishman and Croxall 1983, Trivelpiece et al. 1986, Williams et al. 1992a, 1992b). The gentoo penguin has been the primary subject of these studies because, with its larger size, it can more easily support the instruments. With the development of smaller and more ergonomically designed instruments, more studies can be done with the smaller Adelie and chinstrap penguins. Instruments that measure behavior at-sea coupled with diet sampling could reveal more about the relationship between the marine environment, the penguins foraging habits and their diet.

Predation pressure is another factor that might influence fish consumption in penguins. Leopard seals *Hydrurga leptonyx* prey on penguins and are present in waters surrounding the colonies sporadically during the penguin breeding season. Penguins may alter their feeding strategy to avoid predation when leopard seal activity is high. Length of foraging time at sea and type of prey taken may be influenced by the presence of leopard seals

(Chappell et al. 1993). Alternatively, the presence or absence of leopard seals around the colonies could be a response to temporal changes in the availability of the seals main prey, krill, to which the penguins would respond to as well.

Several species of fish consumed by the penguins breeding on King George Island are also included in the diets of other island inhabitants. Comparison of otolith data collected from penguin stomach samples with otolith data from south polar skua *Catharacta maccormicci* guano (Trivelpiece et al. 1990c) and Antarctic fur seals *Arctocephalus gazella* faeces (Daneri 1996) could reveal more information about the fish prey base of these predators. In particular, more could be learned about the cohort strength of *P. antarcticum, E. antarctica,* and *G. nicholsi,* which are well represented in the diets of the penguins, skuas, and seals.

In summary, to understand more completely the dynamics of fish consumption in penguins future research should include: 1) a diet sampling plan that incorporates time of day and samples multiple species on a given day, 2) marine sampling of prey abundance and distribution coupled with diet sampling, 3) deployment of more instruments to measure foraging behavior with concurrent diet sampling, 4) observations of predator activity coupled with diet sampling, 5) stable isotope analysis of parents and chicks, and 6) comparison of otoliths from other fish eating predators.

CONCLUSION

Previous to this study the extent to which the different penguins in this area relied on fish was largely unknown. Analysis of otoliths has led to the discovery that fish comprise a greater portion of the diet in terms of frequency of and total mass consumed than previously known. While it was known that gentoo penguins were more frequent fish eaters than Adelie or chinstrap penguins, the fact that 34% of the chinstrap penguin samples contained fish was unexpected. Also, through identification of otoliths, the different species of the fish consumed by the three species of penguins was found to differ. The gentoo penguins ate mainly benthic dwelling Notothenid fish while the chinstrap and Adelie penguins ate pelagic Myctophids, Paralepidids, and Channichthyids known to associate with krill swarms. Changes in the age structure, size, and abundance of fish populations may be reflected in the penguin diets, in particular, *Pleurogramma antarcticum*. Differences between the sexes were most pronounced in gentoo penguins, with males taking fish more frequently and generally of larger sizes. The proportion of fish ingested by adult Adelie and chinstrap penguins that is fed to the chicks is minimal. Due to long foraging trips, the fish constitute adult diets more so than chick diets in these species. In contrast, the inshore feeding gentoo penguin is able to feed its young a substantially greater proportion of the fish it captures.

Interspecific dietary differences are most likely the result of feeding adaptations evolved within the centers of their breeding ranges, although competition may be a factor and warrants further attention. Interspecific dietary differentiation may become more intense if food becomes scarce during the breeding season, resulting in increases in competition between the three penguin species.

Presently Antarctic krill remains the dominant component in the diet of these penguins and does not appear to be in limited supply at this site during the breeding season. If krill becomes limiting as a result of climatic change, or in response to expanding commercial fisheries in the area, fish may become more important in the diet of the penguins. Detection of environmental and harvest induced changes in the penguins' prey base will require long-term monitoring. The results of this six year study will serve as baseline information for ongoing dietary research at the site.

During the breeding season, penguins integrate environmental processes over a range of temporal and spatial scales. The signal of annual fluctuations in environmental factors can be traced through observations of dietary changes over time. These penguins also sample prey populations across several spatial scales through their individual diving capabilities and foraging ranges. Furthering our understanding of the amount and type of fish that these penguins consume will make them even more useful indicators of environmental conditions in the Antarctic marine ecosystem.

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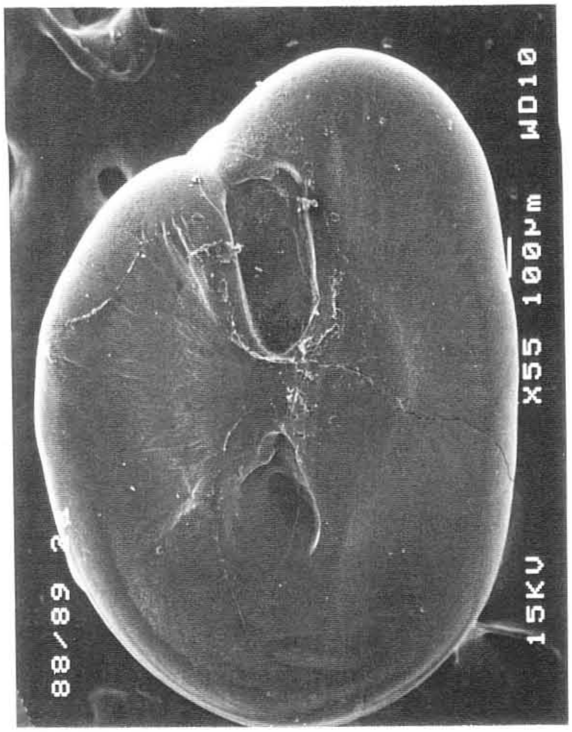
APPENDICES

APPENDIX A

Electron Micrographs of Otoliths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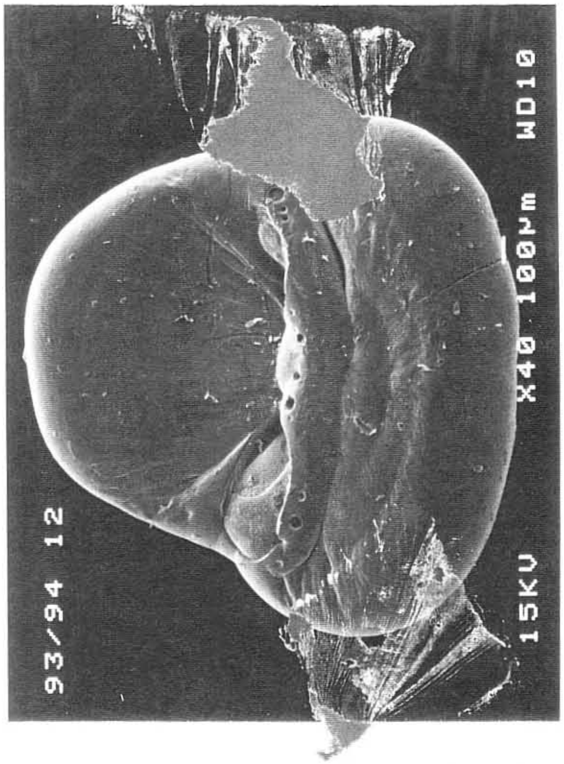
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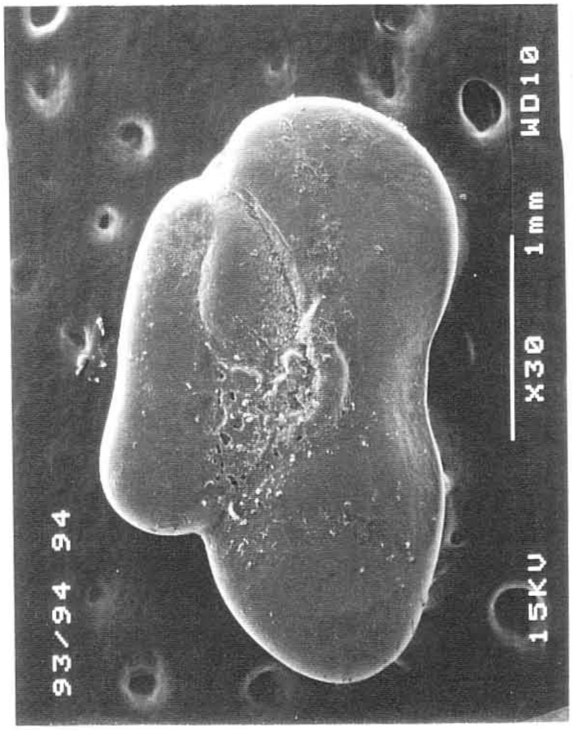
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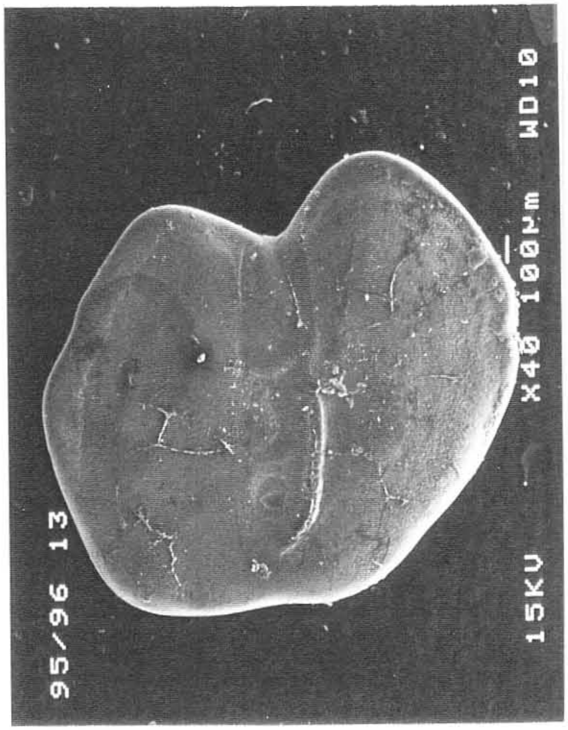
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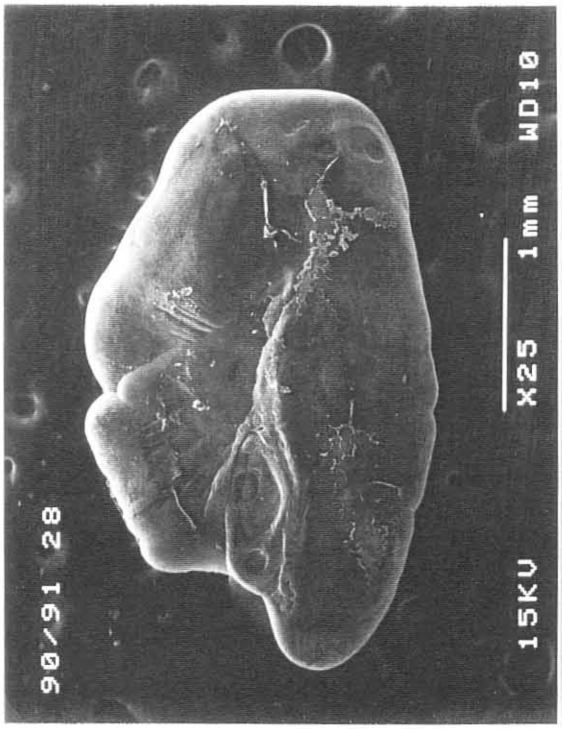
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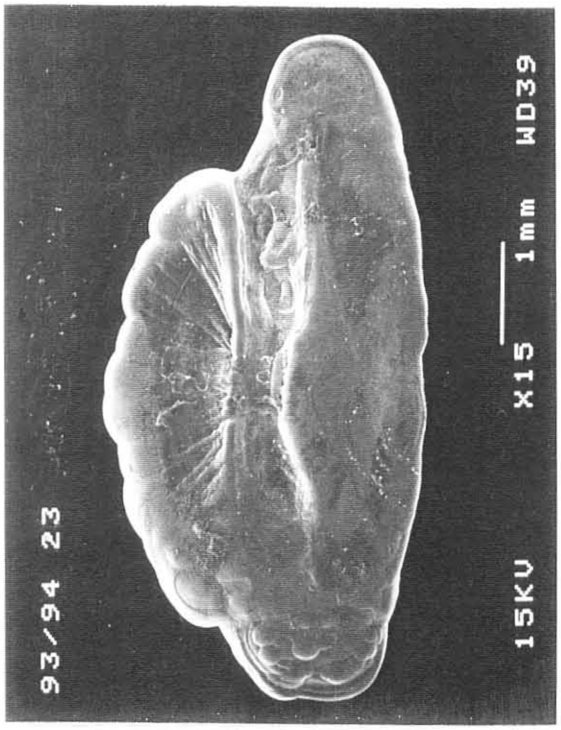
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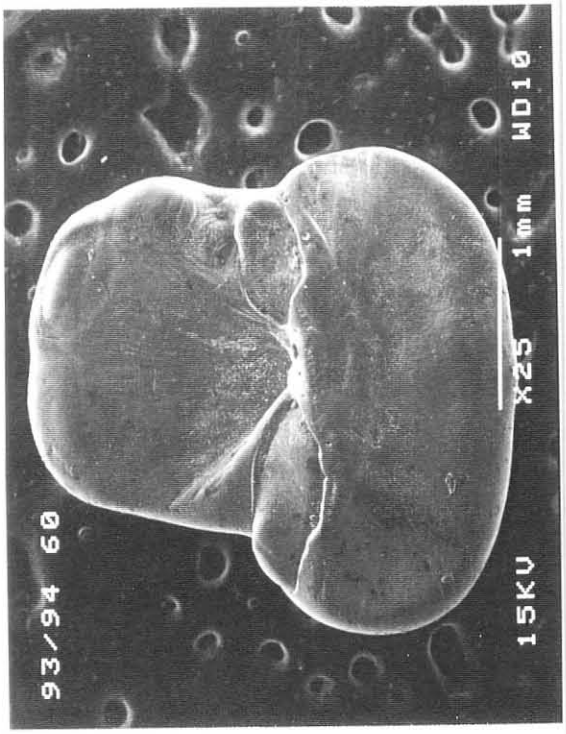
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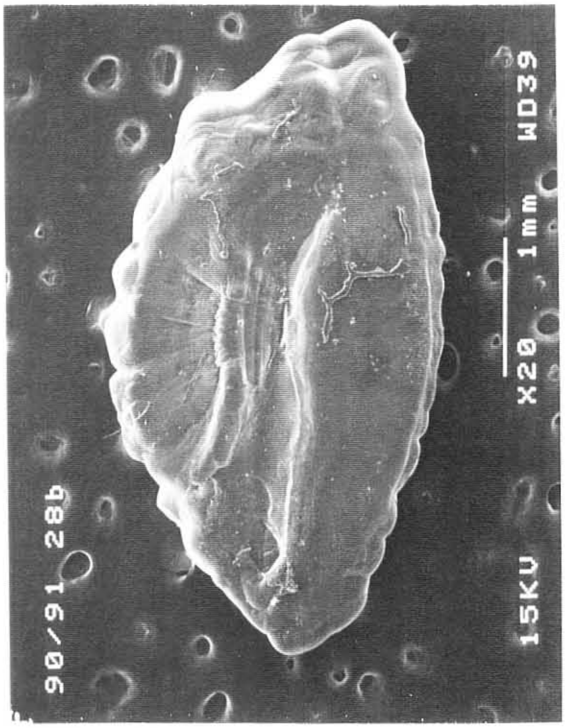
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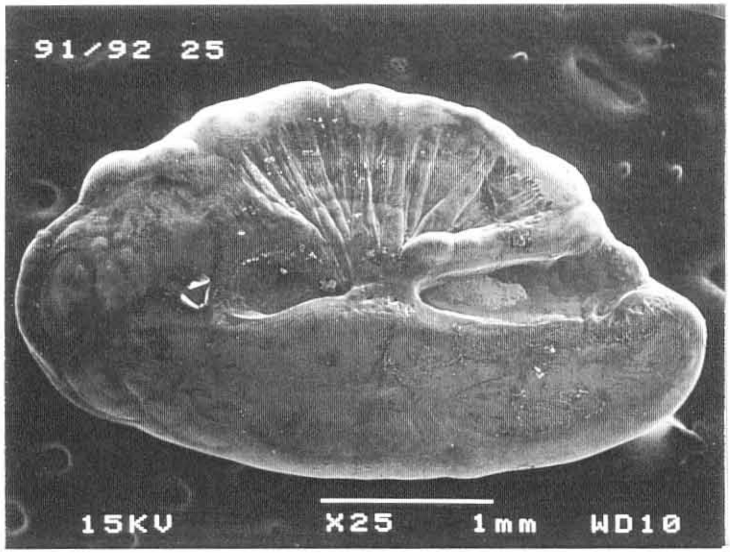
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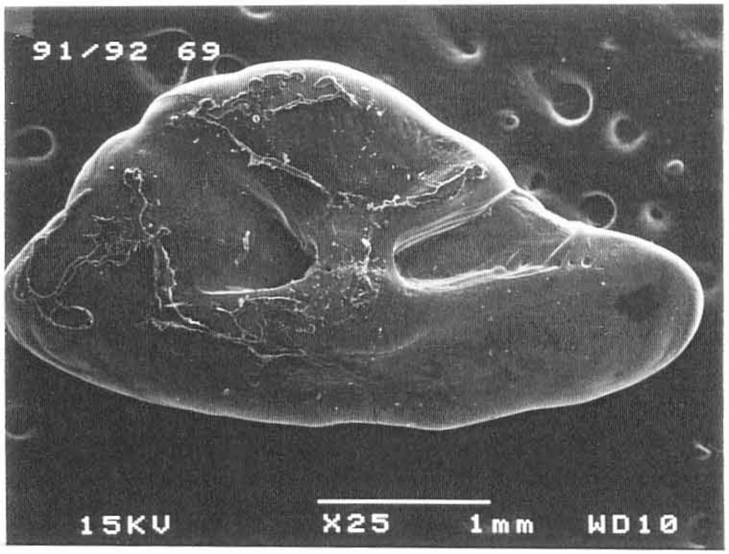
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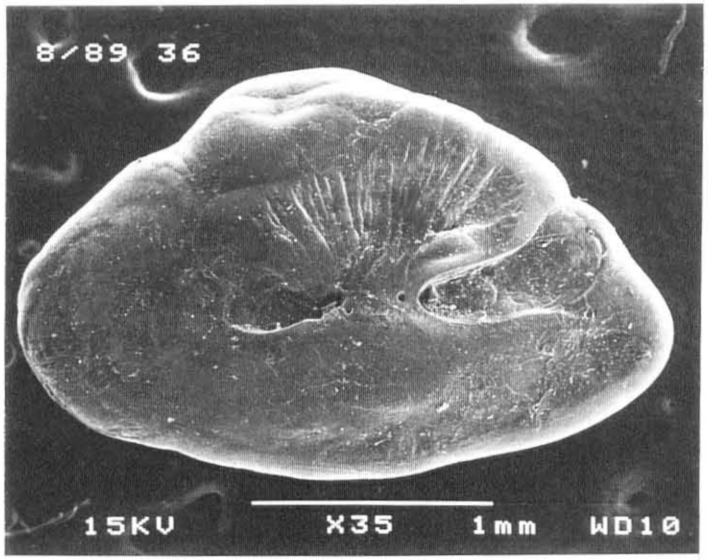
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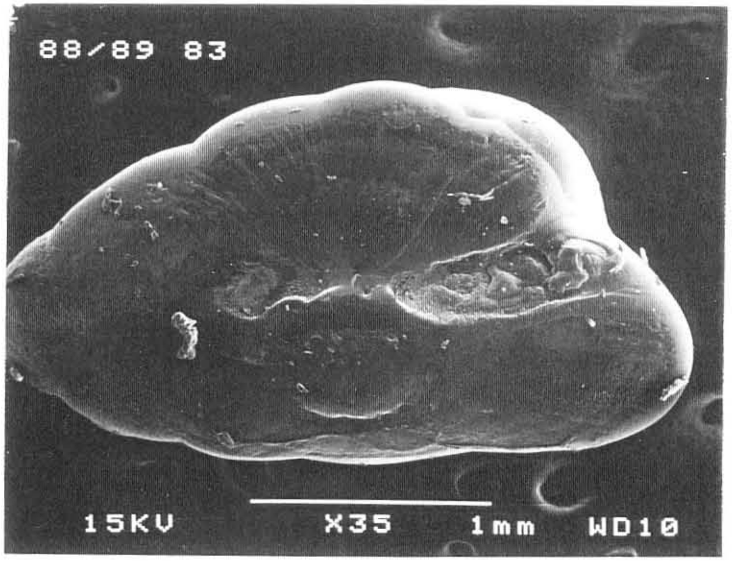
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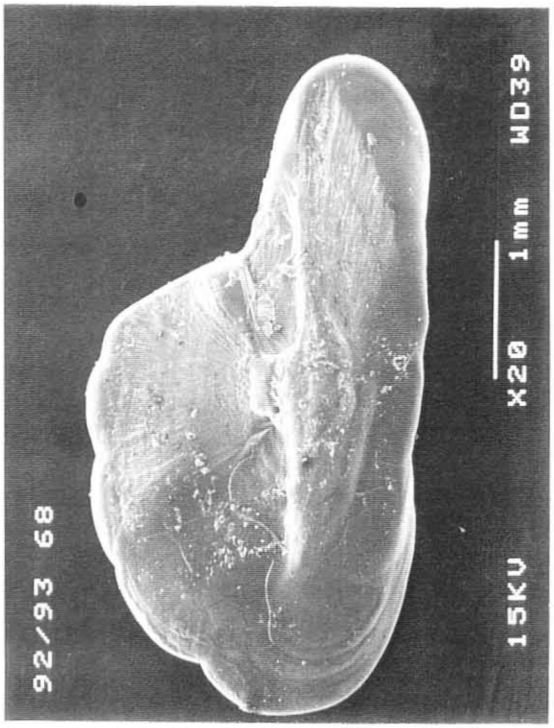
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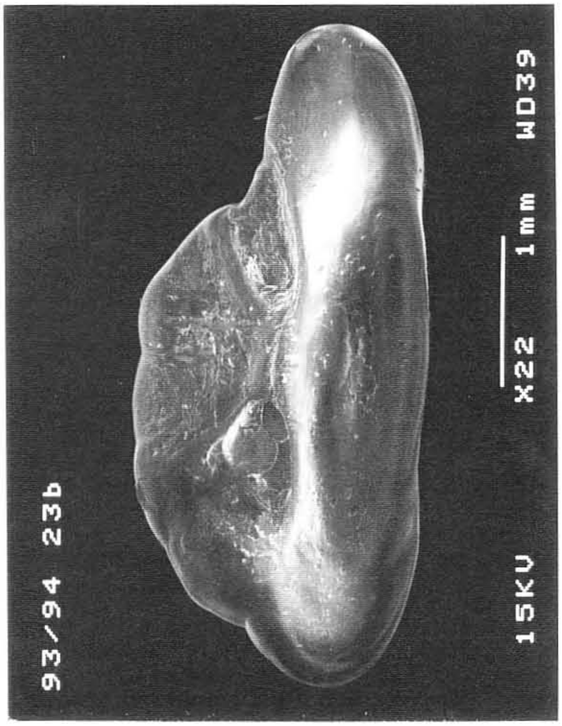
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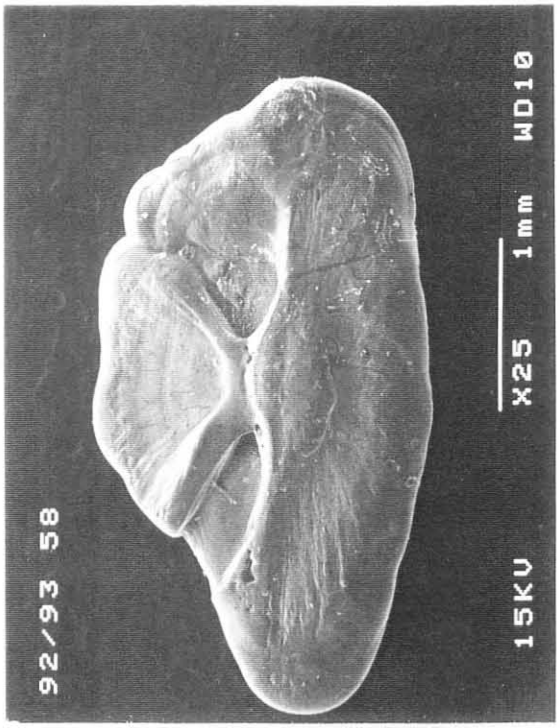
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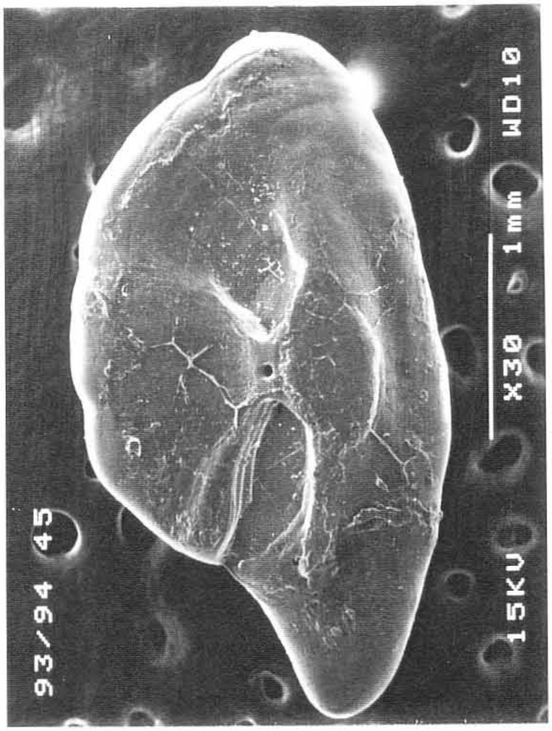
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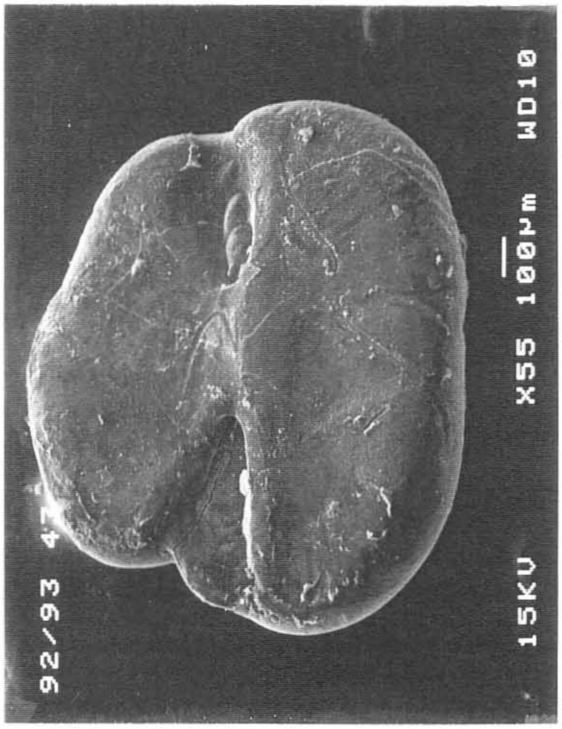
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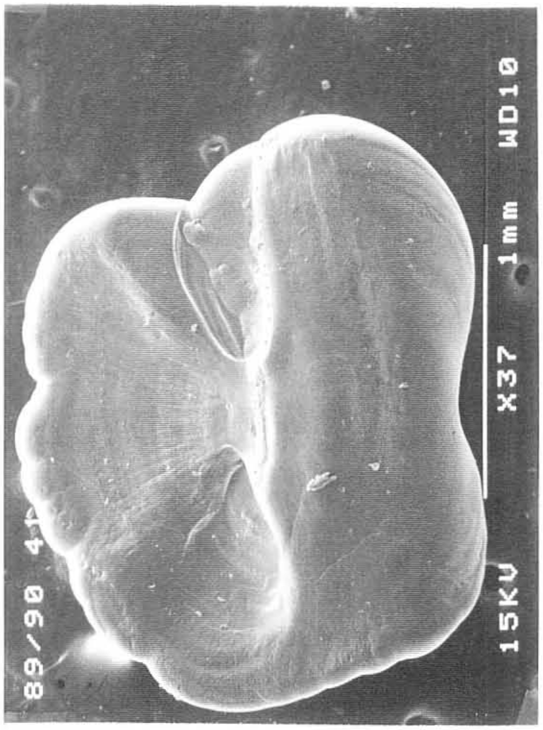
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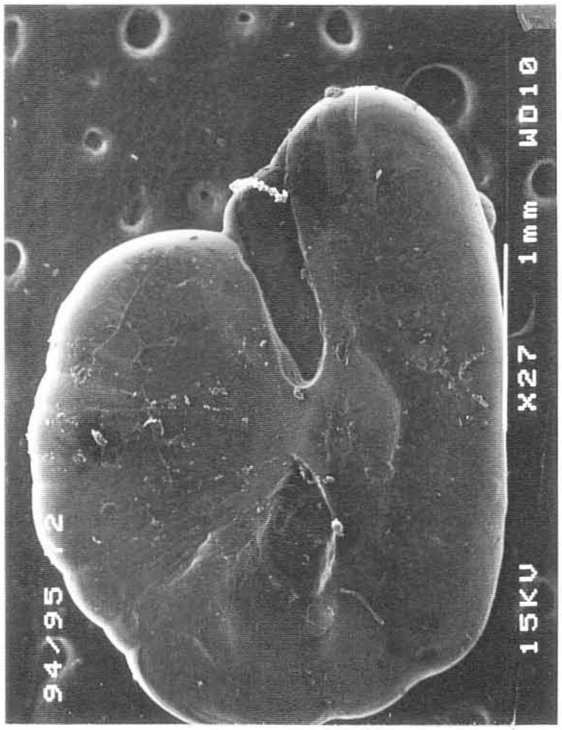
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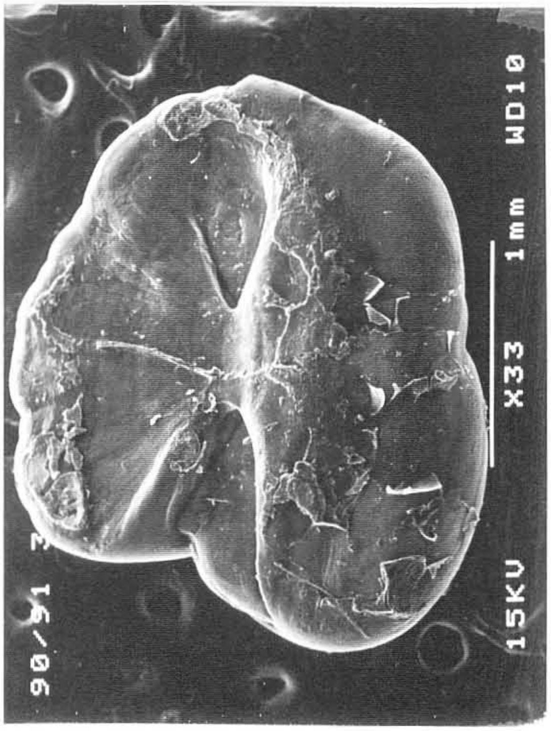
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APPENDIX B

OPINIONS ON OTOLITH IDENTIFICATIONS

Table 13. Identifications of photographs of otoliths by five otolith experts.

Picture	My opinion	Opinion 1	Opinion 2	Opinion 3	Opinion 4	Opinion 5
93/94 94	*Notolepis coatsi*	*N. coatsi* (juvenile)	*N. coatsi*	*N. coatsi*	*N. coatsi*	*N. coatsi*
88/89 2a	unknown	*Notothenia sp.*	*Kriffichthys andersoni*	unkown	Nototheniform	unknown
95/96 13	*Gymonscopelus braueri*	*G. braueri*?	*G. braueri*	*Protomyctophum tenisoni*		*Protomyctophum normani*
93/94 12	*Pagetopsis macropterus*	*a Channichthydid*?	*P. macropterus*	a *Channichthydid*?	*P. macropterus*	a *Channichthydid*?
90/91 28	unknown	*Notothenia r. rossii*	*N. rossii*	*N. kempi*	*Prionodraco evansi*	unknown
93/94 23	*Notothenia acuta*	*N. acuta*	*N. acuta*	*N. kempi*	*Lepidonotothen sp.*	*N. nybelini*
93/94 60	*Chaenodraco wilsoni*	*C. wilsoni*	*Pagetopsis maculatus*	*C. wilsoni*	*C. rastrospinus*	*C. wilsoni*
90/91 28b	*Dissostichus eleginoides*	*D. eleginoides*	*D. eleginoides*	*Paradiplospinus gracilis*	not *D. eleginoides*	not *D. eleginoides*
91/92 69	*Notothenia kempi*	*N. kempi*	*N. kempi*	*N. kempi*	*N. nudifrons*	*N. nudifrons*

Table 13. (continued)

Picture	My Opinion	Opinion 1	Opinion 2	Opinion 3	Opinion 4	Opinion 5
88/89 83	*Harpifager antarcticus*	*H. antarcticus*	*Parachaenicthys charcoti*	*H. antarcticus*	*Artedidraco sp.*	*H. antarcticus*
91/92 25	*N. angustifrons (marionensis)*	*N. angustifrons*	*N. angustifrons*	*Gobionotothen gibberifrons*	*Lepidonotothe n sp.*	*G. gibberifrons*
88/89 36	*Harpifager sp.*	*Harpifager sp.*	*Harpifager sp.*	*Harpifager bispinus*	unknown	unknown
92/93 58	N. kempi	*N. kempi*	*N. kempi*	*Nototheniops larseni*	*Lepidonothen nudifrons*	*L. nudifrons* or *kempi*
92/93 68	*Lepidonothen nudifrons*	*Nototheniops larseni*	*L. nudifrons*	*N. larseni*	*N. kempi*	*N. nudifrons*
93/94 45	*Lepidonothen nudifrons*	*Lepidonothen nudifrons*	*Lepidonothen nudifrons*	*Lepidonothen nudifrons*	*Prionodraco evansi*	probably *N. nudifrons*
93/94 23b	*Notothenia kempi*	*Lepidonothen sp.?*	*Lepidonothen nudifrons*	unknown	*Lepidonothen nudifrons*	*N. nudifrons*
92/93 43	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*
89/90 41	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*

Table 13. (continued)

Picture	My Opinion	Opinion 1	Opinion 2	Opinion 3	Opinion 4	Opinion 5
94/95 72	*Trematomis bernachi*	*Trematomis bernachi*	*Trematomis newnesi* ?	*P. bernacchi* or *T. eulepidotus*	*Trematomis sp.*	Unknown
90/91 3	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis newnesi*	*Trematomis lepidorhinus*	*Trematomis sp.*

APPENDIX C

NUMBER OF OTOLITHS FOUND IN PENGUIN STOMACH SAMPLES

Table 14. Number of otoliths found in each penguin stomach sample and percent of stomach samples otoliths were found in.

	Adelie		Gentoo		Chinstrap		
Fish Species	#	%	#	%	#	%	Total #
Myctophidae							
Krefftichthys anderssoni			2	0.52	2	0.55	4
Protomyctophum bolini	1	0.56	9	2.60			10
Electrona antarctica	14	5.56	31	9.89	162	22.1	207
Electrona carlsbergi			2	0.52			2
Gymnoscopelus braueri			40	2.08			40
Gymnoscopelus nicholsi	1	0.56	6	0.52	18	1.65	25
Myctophid sp.			2	0.52			2
Paralepididae							
Notolepis coatsi					7	2.76	7
Notolepis sp.					3	1.10	3
Paralepididae sp.					2	0.55	2
Harpifager							
Harpifager antarcticus			4	1.04			4
Harpifager sp.			6	0.52			6
Nototheniidae							
Dissostichus eleginoides			2	0.52			2
Notothenia coriiceps					2	0.55	2
Notothenia neglecta			11	2.08			11
Notothenia r. rosii			5	1.56			5
Lepidinotothen kempi	1	0.56	63	7.29			64
Notothenia acuta			2	0.52			2
Pagothenia bernacchi			17	4.17			17
Gobionotothen marionensis			100	5.20			100
Lepidinotothen nudifrons			80	9.38			80
Pleurogramma antarcticum	40	8.89	23	8.33	24	5.52	87
Notothenia larseni			3	1.04			3
Trematomus lepidorhinus			6	1.04			6
Trematomus newnesi	1	0.56	52	3.65			53
Notothenia sp.			56	5.21	1	0.55	57
Channichthyidae							
Chaenodraco wilsoni			8	1.56	2	1.10	10
Neopagetosis ionah			2	0.52			2
Pagetopsis macropterus	2	1.11	9	2.60	20	5.52	31
Pagetopsis maculatus	2	0.56	15	1.04	2	0.55	19
Pagetopsis sp.			11	1.56	1	0.55	12
Unknown fish			14	4.16	2	1.66	15
Totals	63	18.3	590	80.2	252	44.2	905

= number of otoliths. % = percent of stomach samples found in.