FEEDING ECOLOGY OF SOME FISHES OF THE ANTARCTIC PENINSULA[1]

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ABSTRACT

Feeding ecology of 19 species of Antarctic fishes is examined. All species are carnivorous; the most important prey are amphipods, polychaetes, and isopods. Seven of the species examined (*Notothenia neglecta, N. gibberifrons, N. nudifrons, N. larseni, N. kempi, Trematomus scotti,* and *T. bernacchii*) are feeding generalists with diets varying with size of fish, season, and locality of capture. Seven other species (*Trematomus newnesi, Pleuragramma antarcticum, Cryothenia peninsulae, Artedidraco skottsbergi, Harpagifer bispinis, Prionodraco evansii,* and *Parachaenichthys charcoti*) are specialists, feeding predominantly upon prey either from a single taxon or from very few taxa. Five species (*Notothenia rossii, Trematomus eulepidotus, Cryodraco antarcticus, Pagetopsis macropterus,* and *Chaenocephalus aceratus*) were not well represented in the samples, but a qualitative description of their diet is included. The fishes studied consume a wide variety of food types and use several feeding behaviors. Based on field and laboratory observations, most species are ambush predators. However some species use an indiscriminant slurp method, grazing, or a search and capture form of feeding. Some species switch feeding behaviors seasonally or with locality. Diet similarity is high only in morphologically similar species. Where a high degree of diet similarity occurs, overlap in distribution tends to be low. Although most species are high-level carnivores and at least some occur sympatrically, direct competition for food among the species does not appear to exist. This partitioning of food resources adds to the complexity of the structure of Antarctic communities. The position of these fishes in the Antarctic trophic structure should be further examined and considered before extensive exploitation is begun.

Feeding ecology in Antarctic fishes has, until recently, attracted little attention. Richardson (1975) described the diets of four species of fish found along the Antarctic Peninsula and discussed diet overlap. In a thorough study, Targett (1981) examined the trophic structure of five demersal fish communities off Antarctic and sub-Antarctic islands. Permitin and Tarverdiyeva (1972, 1978) examined degree of diet similarity among 10 fishes from the sub-Antarctic island, South Georgia, and in nototheniids and channichthyids collected from the South Orkney Islands, an archipelago north of the Antarctic Peninsula. Moreno and Osorio (1977) examined diet changes with depth in one species, and Wyanski and Targett (1981) reported on diets of nine harpagiferids. Others (Arnaud and Hureau 1966; Holloway 1969; Arnaud 1970; Hureau 1970; Everson 1970; Permitin 1970; Meier 1971; Yukov 1971; DeWitt and Hopkins 1977; Moreno and Zamorano 1980; Duarte and Moreno 1981) described one component of the diet of various fishes, the diet of one species or qualitative descriptions of stomach contents. This study examines several aspects of feeding ecology of Antarctic fishes, including seasonal, spatial, and size-related changes. With increasing interest in the exploitation of Antarctic resources (Lyubimova et al. 1973), the need to understand the feeding ecology of these fishes and their position in Antarctic communities has become important.

STUDY AREA

The Antarctic Peninsula reaches north from the continent to lat. 63°18′S, long. 55°02′W. Its west coast is flanked by numerous islands which create many bays, inlets, straits, and small coves. Weather conditions and longevity and distribution of fast and brash ice vary along the peninsula seasonally, yearly, and with area. Water temperatures at Palmer Station (lat. 64°46′S, long. 64°04′W) fluctuate approximately 2°C from 0°C; salinities range from 32.2‰ to 33.5‰ except immediate to shore and in surface waters during the spring thaw; dissolved oxygen remains near saturation at 6-10 cc/l; pH ranges from 7.9 to 8.5 (Krebs 1974; Showers et al. 1977). Primary productivity varies greatly along the peninsula (Krebs 1974) and in the Antarctic in

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general (El-Sayed 1968) through the year. The composition of the sea bed varies among mud, rubble, and bedrock. Mud bottoms, consisting of glacial flour and diatomaceous oozes, are most common and are found in most straits, bays, and large inlets. Rubble bottoms, composed of heterogeneous mixtures of gravel, cobbles, and boulders, are generally found in small, protected, nearshore coves. Rock cliffs are common along coastal areas and on many submerged mounts. Each bottom type supports a distinctive fauna (Lowry 1969; DeLaca 1976; Kauffman 1977; Daniels and Lipps 1982). Approximately 40 species of fish are found off the Antarctic Peninsula (DeWitt 1971). Table 1 provides a brief description of the species included in this study.

METHODS

Fish used in this study were collected at 11 sites from Terra Firma Islands, Margurite Bay (lat. 68°42′S, long. 67°32′W) to Low Island (lat. 63°25′S, long. 62°10′W) using otter and Isaacs-Kidd trawls, long lines, barrel nets, mud grabs, and hand nets used by scuba divers between 27 January and 28 December 1975 (Fig. 1). Samples were taken at most sites in February or March; a second collection was taken in December at four sites. In areas adjacent to Palmer Station, fish were collected at monthly intervals from January to December.

Fish were preserved immediately in 4% buffered formaldehyde solution; preservative was injected into the stomach cavities of larger specimens. Most species did not regurgitate stomach contents when placed in preservative. However, most channichthyids everted their stomachs when caught; therefore, these species are not included in the analysis and only a qualitative description of their diets is presented. A total of 1,609 stomachs of 19 species were examined. Each of the major Antarctic families is represented: 12 nototheniids, 2 harpagiferids, 2 bathydraconids, and 3 channichthyids. Specimens were later measured (standard length

TABLE 1.—Distribution and morphometric data of fishes collected off the Antarctic Peninsula, 1975. Information on ranges from Norman (1940) and DeWitt (1971).

Species	Distribution	Probable habitat	Relative abundance in samples	Basic body shape	Adult size range (SL mm)	Position of mouth
Nototheniidae						
Notothenia neglecta	circumpolar	rubble-algae	common	bullheadlike	200-300	terminal
Notothenia gibberifrons	Antarctic Pen. South Georgia Scotia Ridge	mud	abundant	bullheadlike	200-300	subterminal
Notothenia nudifrons	Antarctic Pen. South Georgia Scotia Ridge	rocky cliff, mud	abundant	fusiform	100-150	terminal
Notothenia larseni	Antarctic Pen. South Georgia Scotia Ridge	column, bentho-pelagic	abundant	fusiform	100-150	terminal
Notothenia rossii	circumpolar	rubble-algae	rare	bullheadlike	200-300	terminal
Notothenia kempi	Antarctic Pen.	pelagic, bentho-pelagic	rare	fusiform	150-300	slightly supraterminal
Trematomus scotti	circumpolar	pelagic, bentho-pelagic	abundant	fusiform	100-150	terminal
Trematomus newnesi	circumpolar	pelagic, bentho-pelagic	common	fusiform	150-200	supraterminal
Trematomus bernacchii	circumpolar	rubble-algae	common	bullheadlike	150-250	terminal
Trematomus eulepidotus	circumpolar	rubble-mud	rare	fusiform	150-250	supraterminal
Pleuragramma antarcticum	circumpolar	pelagic	common	fusiform	100-150	supraterminal
Cryothenia peninsulae	Antarctic Pen.	pelagic	rare	fusiform	100-150	slightly supraterminal
Harpagiferidae						
Artedidraco skottsbergi	circumpolar	mud	rare	bullheadlike	75-100	terminal
Harpagifer bispinis	Antarctic Pen. South Georgia Falkland Is.	rubble-algae	common	bullheadlike	75-100	terminal
Bathydraconidae						
Prionodraco evansii	circumpolar	mud	rare	wedgelike	100-125	terminal
Parachaenichthys charcoti	Antarctic Pen. Scotia Ridge	rubble-algae	rare	wedgelike	200-250	terminal
Channichthyidae						
Cryodraco antarcticus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Pagetopsis macropterus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Chaenocephalus aceratus	Antarctic Pen. South Georgia Scotia Ridge	mud	rare	wedgelike	200-300	terminal

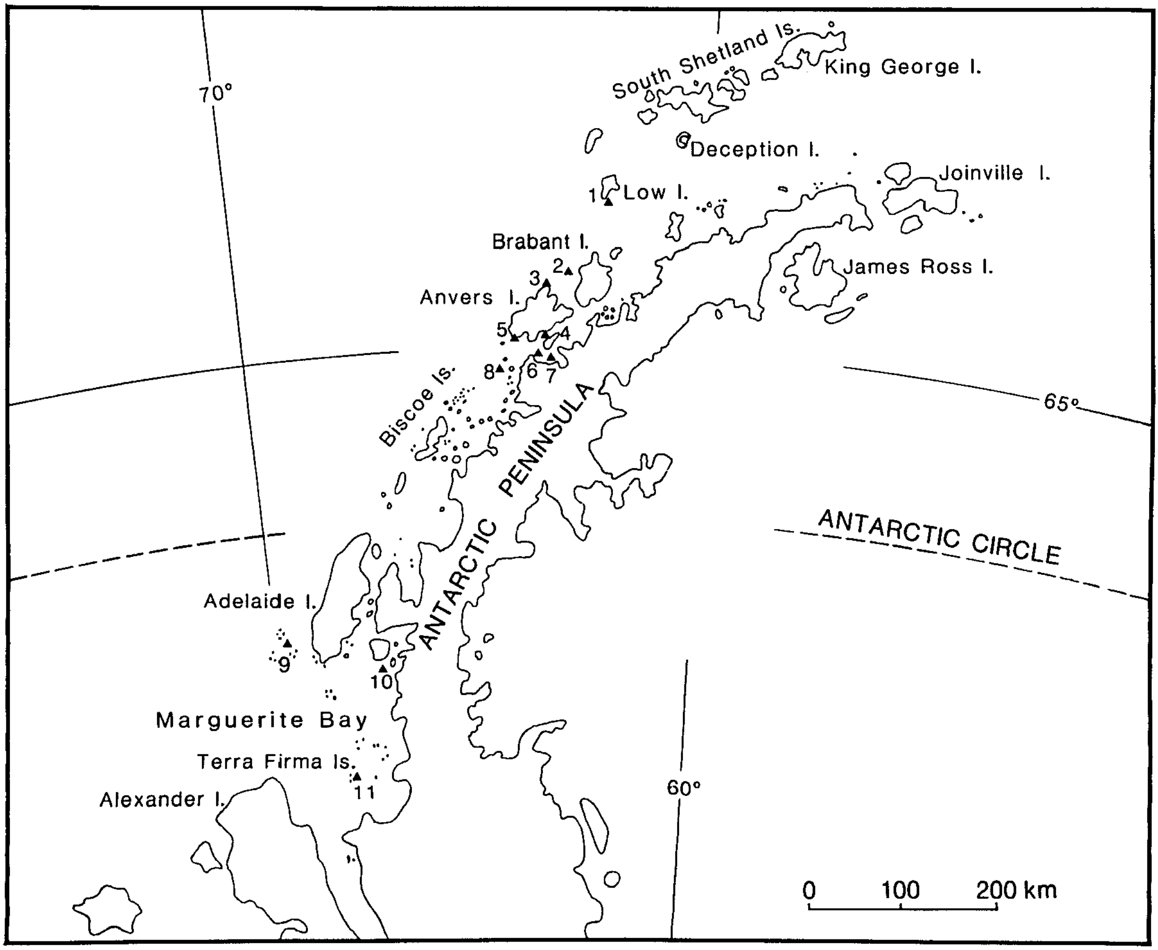

FIGURE 1.—Antarctic Peninsula showing sites where major collections of fish were made, 1975: Low Island (1), Dallmann Bay (2), The Sound, Melchior Islands (3), Port Lockroy (4), Arthur Harbor, site of Palmer Station (5), Peltier Channel (6), Paradise Harbor (7), Argentine Islands (8), Adelaide Island (9), Square Bay (10), and Terra Firma Islands (11).

(SL)), weighed, and dissected. Stomachs were removed, opened, and all contents flushed onto petri dishes. Prey items were sorted, counted, and assigned a point volume (Hynes 1950). One point is approximately equivalent to an isopod *Munna* sp. with an approximate volume of 0.25 ml and approximate dimensions of 15 × 5 × 3 mm; one point was also approximately equivalent to 2 mg dry weight. To test the accuracy of the estimated volumes, the contents of 60 stomachs of *Harpagifer bispinis* were assigned a point volume, volume was measured by displacement, and the contents were dried and weighed. There was little difference between the three measurements (Friedman's Test, $0.2<P<0.3$) (Langley 1970). Individual pieces of algae were not counted and were excluded from all calculations involving number of prey items consumed.

The feeding and foraging behavior of eight species were observed in tanks at Palmer Station and on 140 scuba dives. Twenty-two dives were specifically planned to observe feeding and foraging behavior. In the laboratory, observations were made on recently collected fishes which were introduced into a small cage in a tank where several species of invertebrates were established. The tanks had a gravel substrate, larger rocks, and algae. Invertebrates included in the tanks were scaleworms (*Harmothoe spinosa*), amphipods (*Bovallia gigantea*, *Eurymera monticulosa*), isopods (*Serolis polita*, *Munna* sp., *Cymodocea antarctica*), molluscs (*Patinigera polaris*, *Margarella antarctica*, *Trophon* sp., *Neobuccinum eatoni*), and echinoderms (*Stere-*

chinus neumayeri, Odontaster validus). After a suitable acclimation period (24-48 h), the fish or fishes were released and allowed to feed. Observations were made from above and provided information on feeding method. Foraging strategy is inferred from the feeding method, morphology, and diet of the fish and microhabitat in which it was captured or observed.

Percentage frequency of occurrence of each prey taxon and percentage composition of diet by number and point volume were calculated for each species. Hoffman (1978) suggested a method for determining an adequate sample size in feeding studies. Using this method, three samples containing 35 individuals of each of four species were examined. No additional information was obtained in sample sizes >9-23 individuals ($\bar{x} = 17$). Where possible, at least 20 individuals were examined. When a sufficient number of specimens was collected, the sample was segregated by size of fish, season, or area of capture. These subsamples were then compared using a χ^2 test for association (Remington and Schork 1970). Fullness indices, measures of feeding intensity (Windell 1971), were calculated for each subsample, and significance was determined by Wilcoxon sum of ranks test (paired samples) or Kruskal-Wallis χ^2 test (3 or more samples) (Langley 1970). Mean prey size was calculated by dividing total volume per taxon by total number of prey items consumed. Percentage diet similarity by number and volume was determined using:

$$S = 100\,(1 - \tfrac{1}{2} \sum_i |p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the proportions of the diets of species x and y respectively of prey item i (Linton et al. 1981; Abrams 1980; Schoener 1970). Diet diversity was examined by the number of taxa found in the diet of each species (P) and diversity index $H = -\Sigma p_i \ln(p_i)$, where p_i = the proportion of the ith species in the sample (Shannon and Weaver 1949).

RESULTS

Feeding Behaviors

Fishes were observed using variations of four basic behaviors: ambush feeding, bottom slurping, water column feeding, and grazing. Ambush feeding was observed most frequently in the field. *Harpagifer bispinis, Notothenia neglecta, Trematomus bernacchii* usually, and *N. gibberifrons*, on occasion, perched among rocks or partially buried themselves in soft mud and waited for a prey organism to approach. As the prey neared, the fish lunged and then engulfed the item. Treatment of the prey after capture depended upon its relative size and morphology. If possible, the item was swallowed whole. Exceptions to this were scaleworms. In the laboratory, I observed *H. bispinis* capture a scaleworm on 16 occasions, pull it into its mouth, spit it out, immediately pull it into its mouth again, and repeat the process several more times ($\bar{x} = 6$, range = 2-16). This procedure successfully removed all scales from the worm before the fish actually consumed it. This process apparently occurred in the wild since scales are rarely found in *H. bispinis* stomachs although scaleworms are an important part of its diet (below). If the prey item was too large to engulf whole, it was eaten in parts. I observed *N. neglecta* capturing fish one-third to one-half as long as itself on five occasions in laboratory tanks. The predatory *N. neglecta* pulled the prey fish *T. bernacchii* or *N. nudifrons* into its mouth, usually head first, retreated to a protected area, and began to digest that part of the fish in its mouth and stomach. This process took up to 12 h during which time the predator was quiescent. Large prey items taken from the stomachs of *N. neglecta* commonly showed signs of differential digestion, which indicates that this method of feeding occurs in the wild. Fish using ambush feeding tended to be largely carnivorous and preyed upon relatively large, motile organisms. Fishes were observed to take only moving organisms. On many occasions in the laboratory, *H. bispinis* ignored stationary amphipods close to its mouth and readily visible. When the amphipod moved, it was consumed. Often movement consisted only of a twitching antenna.

The slurp feeding method was observed most frequently in *N. gibberifrons* which swam over mud bottoms, sucked up and sifted through large quantities of mud, and consumed the organisms encountered (Daniels and Lipps 1978). Mud and small rocks were also swallowed and passed through the gut. Fish using this method usually fed upon sedentary or slow-moving invertebrates and rarely consumed plant matter. Bacteria adherent to mud may also have been an important part of their diet.

Water column feeding was characteristic of the pelagic *P. antarcticum*, juvenile *T. newnesi*, and, on occasion, demersal forms like *N. neglecta*.

Pleuragramma antarcticum was observed under fast ice in schools of several thousand individuals on three occasions. Individuals darted about and frequently approached the ice-water interface where they appeared to bite at and consume small amphipods (*Nototropis* sp.). Individual juvenile *T. newnesi* also entered the water column under an ice cover or during other periods of low light intensity. These fish generally were found in shallow-water brown algae, *Desmeristia anceps*, beds except when ice was present and light conditions were favorable. They then left the beds individually and occupied the water column where they fed on the undersurface of the ice, or the substrate or in the column. On one occasion, one large *N. neglecta* (400 mm SL) entered the water column and ate several *P. antarcticum* from a school before returning to a rock outcropping. Fishes using this feeding method usually fed upon motile invertebrates, such as eupausiids, pteropods, and amphipods, or other fishes often associated with the pelagic or cryopelagic communities.

Grazing, although never observed, appeared to be an important feeding method in some species, most notably *N. neglecta*, during spring and summer. Individuals were collected with large sheets of macroalgae (e.g., *Phyllogigas grandifolius*, *Iridaea obovata*, or *Desmeristia* spp.), solitary, epiphytic diatoms (*Trigonium acticum*, *Cocconeis imperatrix*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., and *Achnanthes* sp.), and epibenthic diatoms (*Biddulphia anthropomorpha*, *Melosira sol*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., *Achnanthes* sp., and *Isthmia* sp.) in their stomachs.

It was inferred from stomach contents that fishes commonly switched from one feeding method and/or foraging area to another with season. *Notothenia neglecta* ambushed prey from rock outcroppings and algae beds through much of the year. During the spring and summer plankton blooms, however, some individuals began to search for food on homogeneous mud bottoms away from any protective rock crannies, as evidenced by large numbers of mud-bottom isopod *Serolis polita* in some stomachs in December. During spring and summer, individual *N. neglecta* cropped macroalgae and harvested diatom mats from mud and gravel bottoms. *Notothenia gibberifrons* used the slurp feeding method to forage in more northern areas but ambushed its prey in southern areas (Daniels and Lipps 1978).

Diets

Diets varied among the 14 species examined so that fishes could be ranked from specialized feeders to feeding generalists (Tables 2, 3, 4). Seven species were generalists (high P and H) and seven species were specialists (low P and H). Generalists consumed a variety of organisms which were phylogeneticly and morphologically distinct. Specialists preyed upon organisms with similar morphologies or in the same prey taxon. There appeared to be two types of specialists: in one group, *Cryothenia peninsulae*, *Harpagifer bispinis*, *Artedidraco skottsbergi*, and *Parachaenichthys charcoti*, the diet consisted largely of organisms from one prey taxon; while in the second, *Trematomus newnesi*, *Pleuragramma antarcticum*, and *Prionodraco evansii*, relatively few prey taxa were consumed in approximately equal numbers. Although quantitative data on food availability were not collected, generalists also appeared to be feeding opportunists that ate the most abundant available prey. Individuals in the generalist species also tended to be generalists. Individual *N. neglecta* commonly consumed prey from 5 to 10 taxa (87% of sample) and most of the available prey in the algae beds of Arthur Harbor (Lowry 1969) were found in stomachs of *N. neglecta*. Specialists tended to be more selective. In the rubble bottom community where *H. bispinis* was collected, gastropods, small echinoderms, and errant polychaetes were abundant, yet, except for the scaleworms, which became seasonally important, were rarely found in *H. bispinis* stomachs. Individuals in the specialist species also tended to be specialists; 91% of the *H. bispinis* examined had consumed prey from one or two taxa.

Amphipods were the prey item most fequently taken by fish (Tables 2, 3, 4). However, they were the most important component by volume in only *H. bispinis* and *A. skottsbergi*. Polychaetes were also frequently consumed and were an important part of the diet of *N. nudifrons*, *N. larseni*, *T. scotti*, and *A. skottsbergi* by both number and volume. Isopods, gastropods, and pelecypods also occurred consistently, but were relatively minor components in most diets. Other taxa were important dietary items for only particular species or at particular times of year. Euphausiids, *Euphausia superba* and *E. chrystallorophias*, dominated the diets of *N. larseni*, *T. scotti*, *T. newnesi*, *T. bernacchii*, *Pleuragramma antarcticum*, and *C. peninsulae* by number and volume.

TABLE 2.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of fishes of the genus *Notothenia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	N. neglecta			*N. gibberifrons*			*N. nudifrons*			*N. larseni*			*N. kempi*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		173			339			164			278			18	
Foraminifera	<1	<1	<1	28	4	<1	<1	<1	<1	4	2	<1	6	2	1
Porifera	<1	<1	<1	4	<1	<1									
Coelenterata	<1	<1	<1	<1	<1	<1				<1	<1	<1			
Ctenophora	2	<1	<1							<1	<1	<1			
Nemertea	10	<1	6	4	<1	1	<1	<1	<1	<1	<1	1			
Nematoda				7	1	<1	3	1	<1						
Bryozoa	1	<1	<1	<1	<1	<1									
Brachiopoda				<1	<1	<1									
Oligochaeta				<1	<1	<1									
Polychaeta, sedentary				65	21	27									
errant	21	<1	2	21	2	9	43	22	45	18	10	12	44	19	31
Mollusca															
Gastropoda	75	10	4	15	2	1	12	4	3	1	<1	<1	11	7	4
Pelecypoda	6	<1	<1	38	8	6	1	<1	<1	<1	<1	<1			
Scaphopoda				3	<1	<1									
Cephalopoda	1	<1	<1	<1	<1	<1				<1	<1	<1			
Arthropoda															
Crustacea															
Amphipoda	94	84	21	54	51	19	66	56	31	39	36	12	22	25	17
Isopoda	15	1	7	7	1	3	23	8	7	5	3	1	28	25	20
Cumacea				9	2	1	1	<1	<1	3	3	<1	17	7	8
Euphausiacea	6	<1	4	6	<1	5	2	<1	1	30	27	54	11	4	9
Ostracoda	3	<1	<1	7	<1	<1	7	2	<1	<1	<1	<1			
Copepoda	15	1	<1	3	<1	<1	1	<1	<1				17	9	4
Pycnogonida	1	<1	<1	2	<1	5	7	2	4	<1	<1	<1			
Echinodermata															
Asteroidea										<1	<1	<1			
Echinoidea	<1	<1	<1	<1	<1	<1	<1	<1	<1						
Holothurioidea	3	<1	<1	1	<1	1									
Crinoidea				1	<1	<1	4	1	5	<1	<1	<1			
Ophiuroidea				9	2	8	<1	<1	<1	1	<1	<1			
Chordata															
Tunicata	<1	<1	<1	2	<1	1	1	<1	<1	3	<1	<1	6	2	1
Pisces	13	<1	28	<1	<1	3				1	2	2			
Egg mass	3	1	1							2	3	7			
Macroalgae	80		21	12		2	3		<1	3		1			
Diatoms	12		3												
Miscellaneous			<1			3			<1			2			5
Taxa (*P*)		24			28			18			22			9	
Diversity (*H*)		1.99			2.31			1.53			1.61			1.88	

Fish are a major part of the diet of *N. neglecta* and *Parachaenichthys charcoti* by volume but were unimportant by number.

Changes with Locality

In *N. gibberifrons*, *N. larseni*, *T. scotti*, and *H. bispinis*, the diets of individuals of a similar size group caught at the same time of year but in different localities showed significant differences in the prey taken (Fig. 2) and in the amount of food consumed (Table 5). In each species, approximately the same number of prey taxa were consumed, but only in *H. bispinis* were the taxa identical. The other species consumed not only different amounts from each taxa, but also different types of prey. This change in diet is most dramatic in *N. gibberifrons* (Fig. 2). Individuals from the more northerly Peltier Channel tended to consume sedentary invertebrates such as sedentary annelids, clams, and cumaceans which are often found buried up to several centimeters in the mud. Individuals from the samples of the southern Terra Firma Islands tended to consume motile, rubble-bottom organisms, such as errant polychaetes, amphipods, and fish.

Ontogenetic Changes

Sample sizes were large enough in six species to compare differences in diet with fish size. Within each species, individuals collected from the same locality at the same time but of different size tended to consume prey from the same taxa, but the relative importance of each taxon by volume varied significantly (χ^2, $P<0.02$) (Figs. 3, 4). In all species mean prey size, mean number of prey items consumed, and number of different prey types consumed increased with fish size. Diet diversity showed no size-related change in any species except in *T. bernacchii* (Table 6).

TABLE 3.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of fishes of the genera *Trematomus*, *Pleuragramma*, and *Cryothernia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	T. scotti			*T. newnesi*			*T. bernacchii*			*P. antarcticum*			*C. peninsulae*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		146			37			76			17			18	
Foraminifera										3	13	2			
Coelenterata	<1	<1	<1												
Nemertea	5	2	2				12	<1	23						
Nematoda	2	<1	<1												
Brachiopoda	<1	<1	1												
Polychaeta, sedentary	23	29	16				4	<1	4				17	6	4
errant	36	14	18	11	6	6	22	2	10	3	2	2	6	1	<1
Mollusca															
Gastropoda	4	2	1	6	3	1	12	1	4						
Pelecypoda	8	3	<1				3	<1	<1						
Arthropoda															
Crustacea															
Amphipoda	29	19	6	47	33	23	72	89	26	7	5	2	6	1	<1
Isopoda	4	3	<1	6	3	1	18	3	12						
Cumacea	7	5	<1							33	53	10			
Euphausiacea	35	13	48	35	53	68	8	4	2	40	24	69	100	92	95
Ostracoda	<1	<1	<1				1	<1	<1						
Copepoda							1	<1	<1						
Pycnogonida	3	1	1				1	<1	<1						
Echinodermata															
Holothurioidea	<1	<1	<1												
Crinoidea	<1	<1	<1												
Ophiuroidea	4	2	1												
Chordata															
Tunicata	1	<1	<1				1	<1	3						
Pisces							1	<1	<1	7	3	3			
Egg mass	<1	1	<1												
Macroalgae	2		1				16		3						
Miscellaneous			2						12						
Taxa (*P*)		20			5			14			6			4	
Diversity (*H*)		1.60			0.84			1.97			0.79			0.33	

TABLE 4.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of harpagiferids and bathydraconids collected off the Antarctic Peninsula, 1975. See text for explanation of terms.

	Artedidraco scottsbergi			*Harpagifer bispinis*			*Prionodraco evansii*			*Parachaenichthys charcoti*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		17			237			21			12	
Foraminifera	6	3	<1									
Polychaeta, errant	47	25	47	27	4	16	28	7	19			
Mollusca												
Gastropoda				4	<1	<1						
Pelecypoda				1	<1	<1						
Arthropoda												
Crustacea												
Amphipoda	59	61	46	88	88	79	24	19	29	38	72	8
Isopoda	12	10	5	24	5	4						
Cumacea							38	65	31			
Euphausiacea							19	8	21	50	22	15
Ostracoda				2	<1	<1						
Pisces										25	6	76
Egg mass				6	1	<1						
Macroalgae				8		<1				13		1
Taxa (*P*)		4			8			4			4	
Diversity (*H*)		0.88			0.68			1.53			0.72	

Seasonal Changes

Changes in diet in *N. neglecta* and *H. bispinis* were monitored at monthly intervals in Arthur Harbor through the year. *Notothenia neglecta* showed a significant seasonal diet change ($\chi^2 = 727$, df $= 104$, $P<0.01$); these fishes switched from being omnivores in the austral spring and summer to a carnivorous diet through autumn and winter. *Notothenia neglecta* also consumed a large variety of organisms, including individuals from several different microhabitats such as isopod *Serolis polita* and nemertean worm *Lineas corrugatus* from mud bottom areas,

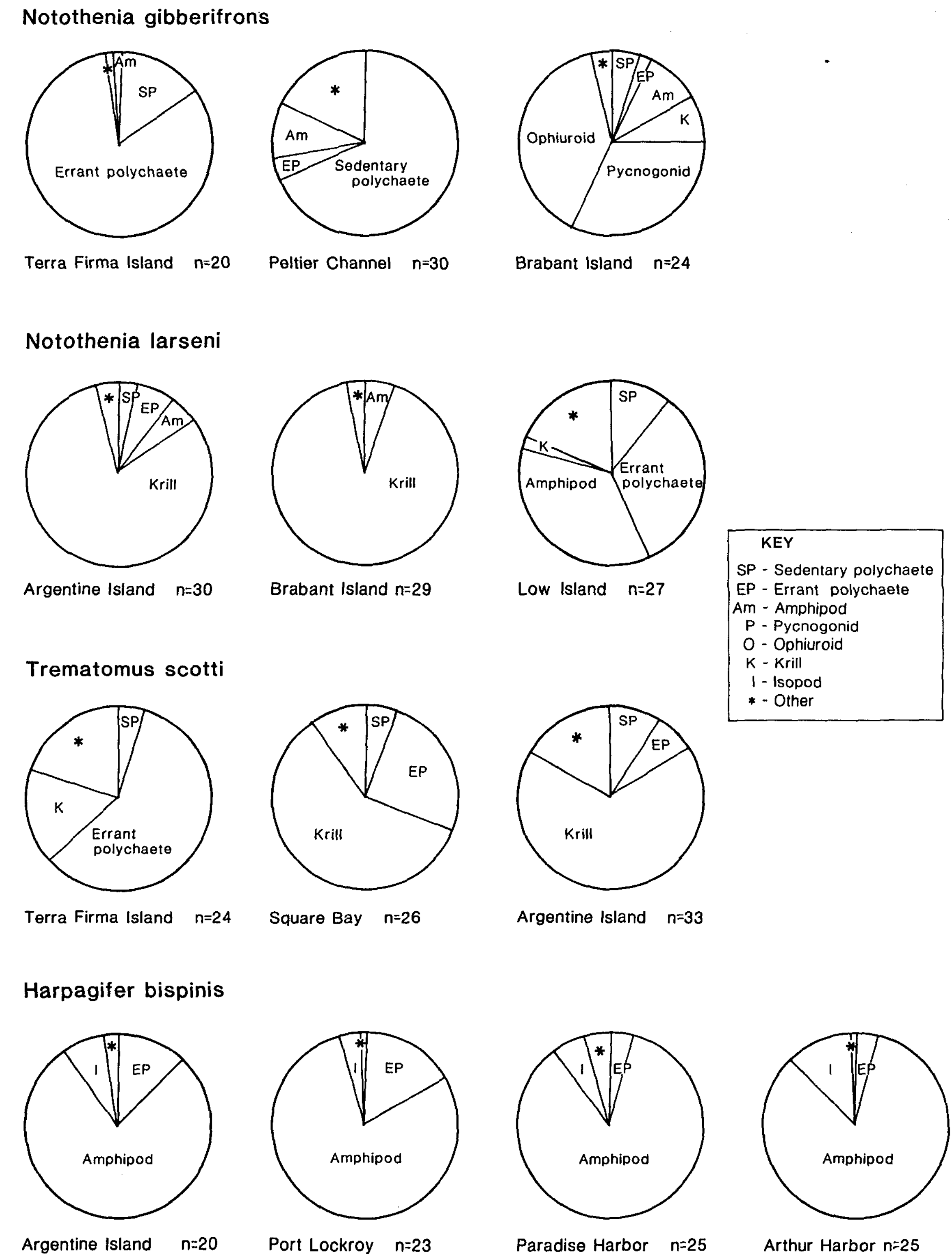

FIGURE 2.—Changes in feeding associated with locality of capture in four notothenioid fishes. Fishes used in comparisons are similar in size and were taken during the same season.

TABLE 5.—Changes in diet by locality of capture in fishes of similar size and taken during the same season off the Antarctic Peninsula, 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed; a Kruskal-Willas χ^2 test was used to examine changes in feeding intensity (fullness index).

Species	Area	*n*	SL (mm)	Range (mm)	No. taxa consumed	Volume χ^2	Volume *P*	Fullness index $\bar{X}$	Fullness index χ^2	Fullness index *P*
Notothenia	Peltier Chan.	30	146	106-217	13			6.8		
gibberifrons	Terra Firma Is.	20	123	100-146	13			8.2		
	Brabant I.	24	134	87-260	12	393.1	<0.01	7.5	8.5	<0.05
N. larseni	Brabant I.	29	120	70-150	4			8.1		
	Low I.	27	114	84-152	8			6.6		
	Argentine Is.	30	113	72-162	10	224.6	<0.01	2.4	20.2	<0.01
Trematomus	Terra Firma Is.	24	69	45-90	7			7.0		
scotti	Square Bay	26	98	61-137	9			4.9		
	Argentine Is.	33	99	63-126	15	104.9	<0.01	6.9	15.8	<0.01
Harpagifer	Argentine Is.	20	71	58-80	6			4.4		
bispinis	Port Lockroy	23	67	43-82	5			8.4		
	Paradise Harbor	25	68	57-88	5			5.5		
	Arthur Harbor	25	70	51-85	5	42.1	<0.01	8.2	14.1	<0.01

TABLE 6.—Size-related changes in diet in Antarctic fishes, Antarctic Peninsula, 1975. Fish in each species were collected at the same time from the same locality.

Species	Capture	Size group	*n*	SL $\bar{X}$ (mm)	SL range (mm)	Mean no. items/stomach	Mean prey size (vol./item)	No. taxa consumed	Mean *H*
Notothenia	Arthur Harbor	I	10	80	71-90	13.8	0.9	7	0.5
neglecta	December	II	8	199	165-231	82.0	4.5	8	0.8
		III	9	292	258-313	37.0	12.8	12	0.6
Notothenia	Peltier Chan.	I	14	80	49-99	5.8	0.6	10	0.8
gibberifrons	February	II	20	129	116-148	8.0	1.2	13	0.8
		III	20	193	163-217	10.9	1.8	15	0.9
Notothenia	Dalmann Bay	I	28	50	32-65	4.7	0.2	10	0.7
nudifrons	December	II	16	116	93-153	4.3	0.7	11	0.7
Notothenia	Low I.	I	16	94	82-105	2.7	1.8	4	0.3
larseni	March	II	19	139	113-157	2.4	3.7	7	0.5
Trematomus	Argentine Is.	I	18	84	63-99	3.0	1.6	11	0.5
scotti	March	II	17	121	108-144	2.7	3.3	13	0.8
Trematomus	Arthur Harbor	I	13	69	60-78	15.0	0.5	4	0.1
bernacchii	June	II	14	138	107-160	31.4	2.7	8	0.3
		III	14	200	180-233	10.1	8.1	10	0.7

krill and *Pleuragramma antarcticum* from the pelagic and cryopelagic communities, limpet *Patinigera polaris* from rocky cliffs, and a large number of organisms from rubble-bottom areas, the habitat from which this species was most frequently collected. *Harpagifer bispinis* consumed prey from the same taxa through the sampling period, but the importance of each taxon differed ($\chi^2 = 149$, df = 21, $P<0.01$). The significance results from a midwinter peak in abundance of scaleworms. This species consumed organisms from the rubble-bottom community which consisted largely of the amphipods *Bovallia gigantea*, *Eurymera monticulosa*, the scaleworm *Harmothoe spinosa*, and the isopods, *Munna* sp. and *Cymodocea antarctica*.

Differences in diet of similar-sized individuals of *Notothenia gibberifrons*, *N. nudifrons*, *N. larseni*, and *T. scotti* collected at the same locality at different times of year were significant in the relative importance of each prey taxon, but tended to show no significance in the amount of food consumed (Table 7). In all four species individuals tended to consume prey from the same number of taxa. Spring samples tended to contain individuals of a smaller size than late summer samples.

Dietary Similarity

Diets were >60% similar in 17 species pairs by number and in 11 species pairs by volume (Table 8). Similarity in diet by number of prey items consumed is greater due to the large number of amphipods taken by most fishes. A high percentage similarity by volume, a value more indicative of the importance of each food type, was obtained for morphologically similar species such as the two harpagiferids, *A. scottsbergi* and *Harpagifer bispinis*, and the pelagic-benthopelagic complex of *N. larseni*, *T. scotti*, *T. newnesi*, *Pleuragramma antarcticum*, and *Cryothenia peninsulae*. Species that were generalists showed 30-60% similarity in diet with other

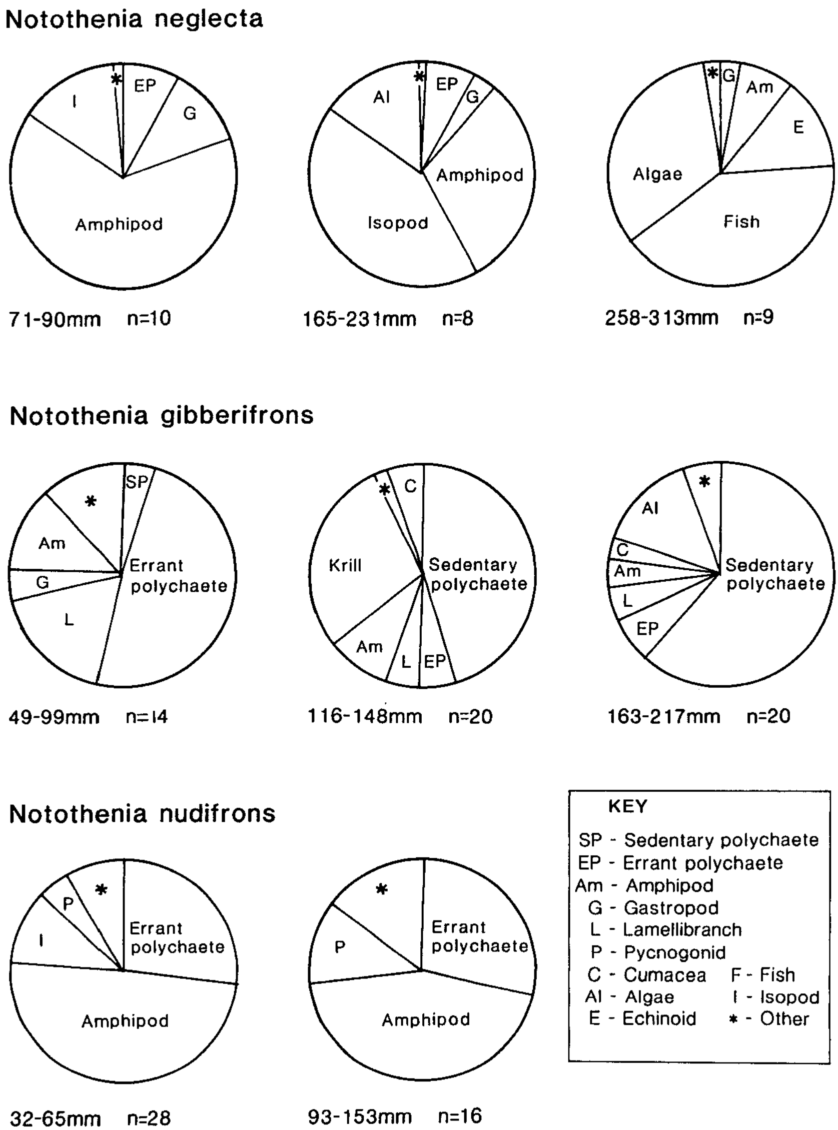

FIGURE 3.—Size-associated changes in feeding in three *Notothenia* spp. collected at the same locality on the same day.

generalists and <30% similarity with the more specialized feeders. Generalists were often collected at sites with other generalists and specialists. The tendency among specialized feeders was one of low percentage similarity in both diet and distribution.

Other Species

Four *N. rossii*, morphologically similar to *N. neglecta*, consumed prey from six taxa. Amphipods were most important by number (81%); krill (31%) and demersal fish (51%) were important by volume. Krill was the most important component by number and volume in the diets of five *T. eulepidotus*, seven *Pagetopsis macropterus*, and eight *Cryodraco antarcticus*. These species consumed prey from relatively few taxa and were exclusively carnivorous. *Trematomus eulepidotus*, morphologically similar to *T. scotti*, in addition to the pelagic krill, also consumed cumaceans which are typically associated with mud bottoms. The channichthyids, *P. macropterus* and *C. antarcticus* also consumed fish, such as

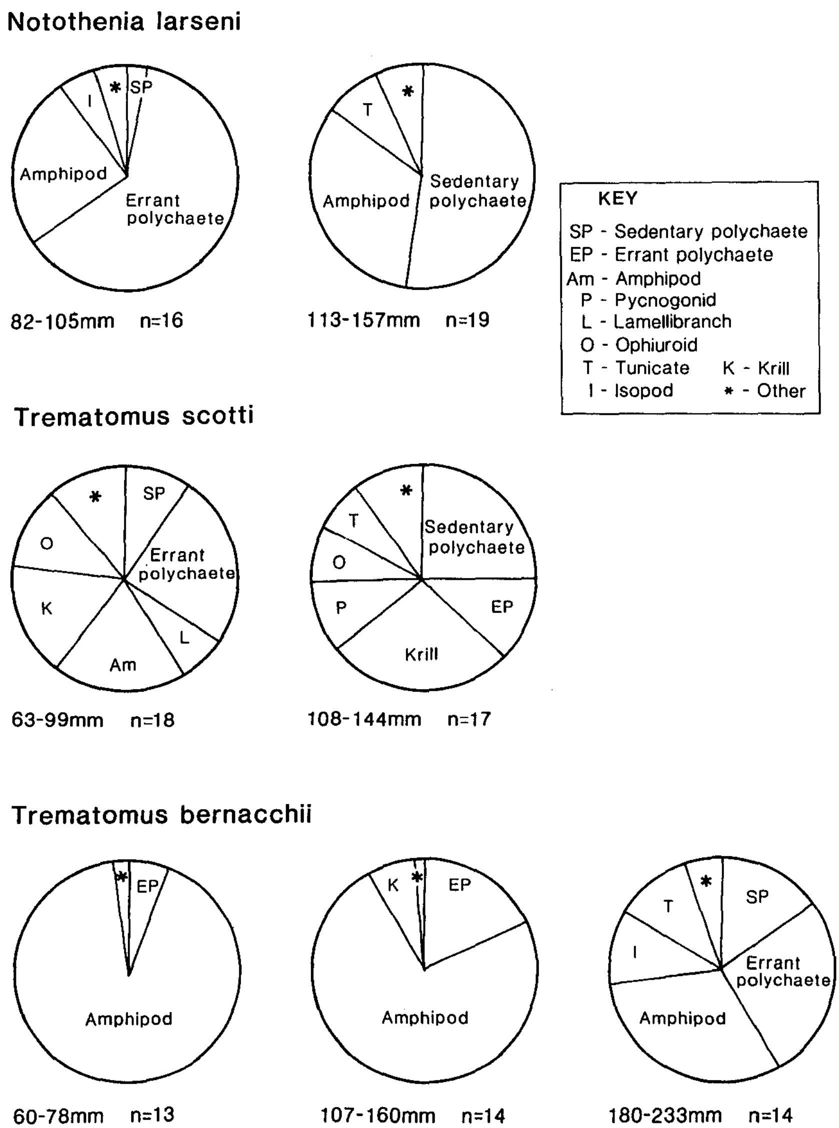

FIGURE 4.—Size-associated changes in feeding in three nototheniids collected at the same locality on the same day.

the pelagic *Pleuragramma antarcticum* and the demersal *N. nudifrons*. In one *Pagetopsis macropterus* collected in Margurite Bay, both species of krill found in the area were present. The stomachs of 42 *Chaenocephalus aceratus* were examined and found to be empty.

DISCUSSION

Antarctic fishes show great variety in the type of prey consumed and the behavior used to capture prey. Yet all occupy a similar position in the community, that of a high-level carnivore. Of the 19 species included in this study, all consumed actively moving prey frequently and, with the exception of *N. gibberifrons*, active prey dominated diets. Although the diets of the prey are poorly known, at least some, like *Bovallia gigantea*, *Harmothoe spinosa*, and *Sterechinus neumayeri*, are themselves high-level carnivores (Bone 1972; Brand 1976).

In this study the nototheniids show the greatest diversity in both diets and feeding behaviors although a high degree of similarity in diet

TABLE 7.—Seasonal dietary changes in fishes of similar size collected at the same locale off the Antarctic Peninsula. 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed. A Wilcoxon sum of ranks test was used to examine changes in feeding intensity.

Species	Area	Date	*n*	$\overline{SL}$ (mm)	Range (mm)	No. taxa consumed	Volume χ^2	Volume *P*	Fullness index $\overline{X}$	Fullness index *R*	Fullness index *P*
Notothenia gibberifrons	Peltier Chan.	Summer	30	146	106-217	13			6.8		
		Spring	49	138	100-229	13	31.3	<0.01	6.0	1,301	<0.30
	Brabant I.	Summer	25	134	87-260	12			7.5		
		Spring	22	123	106-167	9	114.6	<0.01	2.1	294	<0.01
Notothenia nudifrons	Low I.	Summer	20	107	72-140	8			5.6		
		Spring	34	95	47-127	5	80.9	<0.01	5.8	500	<0.74
Notothenia larseni	Low I.	Summer	27	114	84-152	8			6.6		
		Spring	25	99	90-142	9	66.7	<0.01	9.5	544	<0.08
	Brabant I.	Summer	29	120	70-150	4			8.1		
		Spring	30	86	60-126	5	27.9	<0.01	2.2	735	<0.04
Trematomus scotti	The Sound	Summer	8	112	88-134	5			6.4		
		Spring	7	101	85-114	5	109.4	<0.01	3.4	47	<0.20

TABLE 8.—Percentage diet similarity by number of prey items consumed (upper triangle) and point volume (lower triangle) in fishes taken off the Antarctic Peninsula, 1975.

	Notothenia neglecta	*Notothenia gibberifrons*	*Notothenia nudifrons*	*Notothenia larseni*	*Notothenia kempi*	*Trematomus scotti*	*Trematomus newnesi*	*Trematomus bernacchii*	*Pleuragramma antarcticum*	*Cryothenia peninsulae*	*Artedidraco skottsbergi*	*Harpagifer bispinis*	*Prionodraco evensii*	*Parachaenichthys charcoti*
N. neglecta	—	58	63	46	33	26	37	89	5	8	61	86	18	71
N. gibberifrons	39	—	61	52	34	51	39	56	13	14	57	55	24	51
N. nudifrons	36	42	—	58	58	44	46	64	10	3	87	66	27	54
N. larseni	28	40	31	—	52	49	67	43	38	29	41	44	37	60
N. kempi	34	40	61	39	—	48	41	32	20	6	56	35	37	29
T. scotti	19	42	30	70	38	—	45	32	27	23	36	27	20	32
T. newnesi	28	31	32	72	34	62	—	43	32	56	42	41	33	55
T. bernacchii	52	37	50	27	42	34	39	—	10	5	66	93	25	77
P. antarcticum	16	11	6	61	22	61	79	18	—	26	10	7	67	30
C. peninsulae	3	11	3	55	10	53	70	12	76	—	2	2	10	23
A. skottsbergi	28	31	67	25	53	25	30	41	5	2	—	70	27	61
H. bispinis	27	33	52	26	38	23	30	41	4	2	66	—	24	72
P. evensii	25	34	49	46	53	46	50	38	35	23	49	44	—	28
P. charcoti	39	16	9	25	17	21	23	12	20	16	9	8	23	—

among similar species is often present. Results from other studies, using fewer species, are similar (Permitin and Tarverdiyeva 1972, 1978; DeWitt and Hopkins 1977; Richardson 1975; Moreno and Osorio 1977; Moreno and Zamorano 1980). This high diversity is attributable to diet changes with size of fish, capture locality, and season.

The harpagiferids, bathydraconids, and channichthyids tend to be more specialized than the nototheniids in both their choice of prey and in the method used to obtain it. Results for *Harpagifer bispinis* can be compared to those of Meier (1971), Richardson (1975), and Wyanski and Targett (1981). In all cases, *H. bispinis* was shown to consume amphipods overwhelmingly. *Artedidraco skottsbergi* consumed polychaetes and amphipods; similar results were reported by Wyanski and Targett (1981). No comparable data are available for the bathydraconids or the channichthyids examined in this study. However, the diets of the five channichthyids examined by Permitin and Tarverdiyeva (1972, 1978) show them to be specialized feeders and, with the exception of *C. aceratus*, planktivorous; my remarks regarding the diets of *P. macropterus* and *Cryodraco antarcticus* corroborate these findings.

The high degree of dietary similarity that I observed among certain fishes and the similarity of diets reported by Permitin and Tarverdiyeva (1972, 1978), and Richardson (1975) do not necessarily imply interspecific competition over food, but do suggest a complex trophic structure not normally associated with communities of high latitudes (Cushing 1975). The benthic fishes studied use a wide variety of mechanisms to assure a constant food supply. For the generalists, these include switching prey types and feeding strategies; the specialists consume prey types which are themselves capable of maintaining stable populations either by switching food by becoming inactive (Dearborn 1967) or by possessing a reproductive biology which includes high fecundity and long mean generations (Cushing 1975). These stabilization mechanisms provide a constant source of food despite disbalanced primary production. With this constant and relatively abundant food source, competition, which requires a limiting resource (Larkin 1963), does not appear to be common among Antarctic fishes. The fact that high diet similarity is observed argues against competition over a limited food resource as a major factor structuring Antarctic fish associations (Zaret and Rand 1971; Tyler 1972). Where competition may be important, e.g., in the pelagic-benthopelagic fish association, the major prey item is krill, which is abundant. However, this abundance may be temporary and of recent origin. This would obscure the importance of competition in structuring Antarctic associations and points to the need for further study.

The position of fishes in the trophic structure of Antarctic communities is also not well understood. All are carnivorous and many are second or third level carnivores. Whether or not these fishes are themselves consumed in large numbers by the abundant birds and mammals of the Antarctic is poorly known. Some birds consume small species or juveniles of large species (Watson 1975) and several species of seals are reported to consume fish (Dearborn 1965; Stonehouse 1972). However, the species consumed and the relative importance of fish in the diets of these predators remain unknown. It does appear that such predators do not have much of an impact on the large benthic fish populations, since the fishes are extremely slow growing and long lived (Emerson 1970). Thus the impact of heavy and unaccustomed predation (fishing) on this system could be very disruptive. Before extensive exploitation begins, the life history of the organisms to be harvested should be understood.

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