The specialized diet of Harpagifer bispinis:

Its effect on the diversity of Antarctic intertidal amphipods

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Abstract

The diet of *Harpagifer bispinis* (Pisces:Nototheniidae) from two localities of the South Shetland Archipelago was studied. Simultaneous to the capture of *H. bispinis* and at the same sites the availability of food was considered, and amphipod diversity was compared with the density of *Harpagifer.* It was found that three quarters of the fish fed only on amphipods (mainly *Gondogeneia antarctica*) and for the rest amphipods were also the main component, even when other prey species were available. The high selectivity of *G. antarctica* is due to its high mobility and to the fact that *Harpagifer* is an ambush feeder. At different predator densities the amphipod fraction of the community appears to be highly modified by the predator both numerically and in species evenness. We postulate that *Harpagifer* can be a key species in structuring the mobile epibenthic community, even when this environment is subject to strong physical stress.

Introduction

The most common fish in the rubble bottom community and in tidal pools in the northern region of the Antarctic Peninsula and South Shetland Archipelago is *Harpagifer bispinis* (Pisces: Nototheniidae). Moreno (1971) found that their food consisted only of amphipods. This observation was confirmed by Richardson (1975) who found that the diversity of food types in the diet of *Harpagifer* was small, *Pontogeniella brevicornis* being the major food source. Later, Daniels (1980) studied the food habit of *H. bispinis* in Arthur Harbour, and suggested that this species is an ambush feeder with specialized diet and that it does not switch its food seasonally. However, Arnaud (1977), who reviewed the diet of several antarctic and subantarctic fishes, concluded that the apparently specialized diet of *H. bispinis* reflects only the rarity or absence of any other prey in the habitat.

All previous studies have been made examining only the gut contents, except for the studies of Daniels (1978, 1980) who emphasized feeding behaviour. We believe that in order to establish the trophic specialization of this fish without ambiguity, an analysis of the availability of prey species must be considered at the same time as that of stomach content. This is not a trivial matter since predation has been postulated as an important factor in structuring the community (Paine, 1966; Zaret & Paine, 1973; Dodson, 1970). It is probable that a specialized predator could perform an important role in the determination of hierarchies of abundance and diversity of its prey.

This paper presents a simultaneous analysis of the stomach content of *H. bispinis* and availability of food in two localities of the South Shetland Archipelago, West Antarctica. It also seeks to demonstrate the role of this predator fish in determining the abundance and diversity of the amphipod fraction of the intertidal community.

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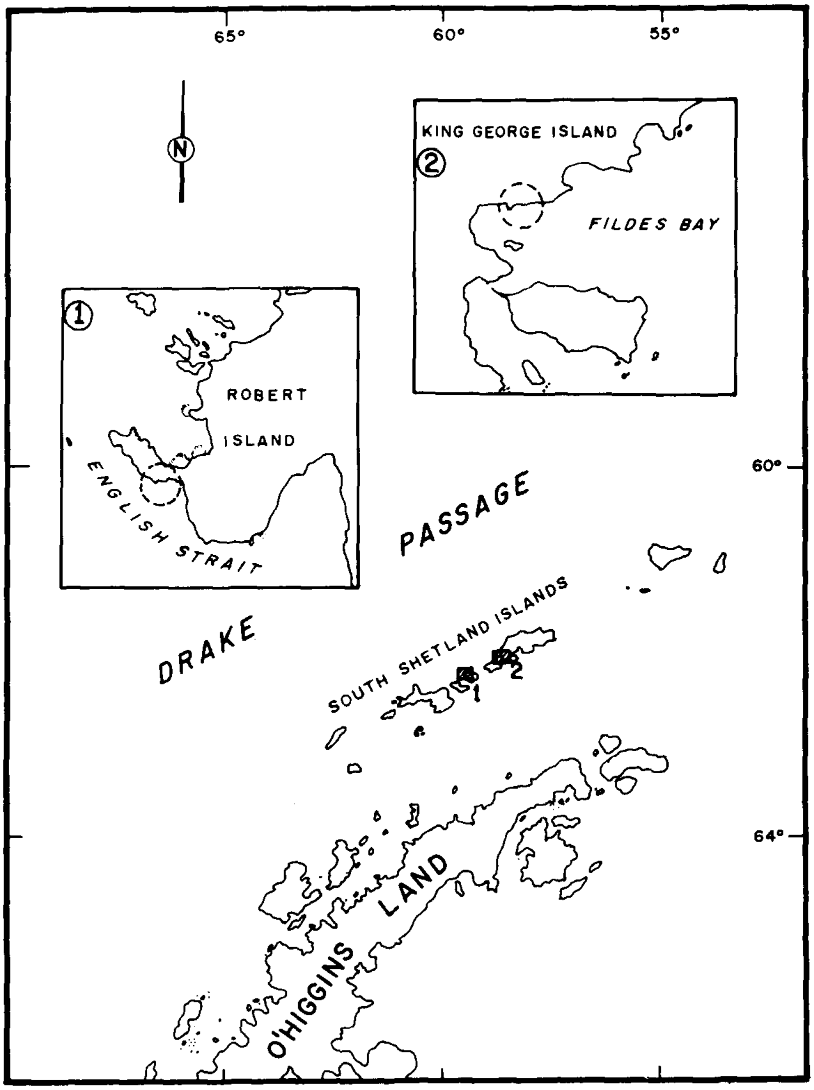

Fig. 1. Geographic location of the research sites. Circles in squares 1 and 2 show Coppermine Cove and Ardley Cove respectively.

Materials and methods

The work was carried out in Ardley Cove, King George Island (62° 12′ S; 58° 54′ W) and Coppermine Cove, Robert Island (62° 23′ S; 59° 42′ W) both in the South Shetland Archipelago in the West Antarctic region (fig. 1).

H. bispinis was collected by hand, under stones in tidal pools during low tide periods in January 1979. The number of specimens collected in each pool was related to the total area of each pool under consideration, for the purpose of obtaining a density measure. Ten pools were examined in Ardley Cove and forteen in Coppermine Cove.

At the same time and in the same pools, from both places, seven quantitative rubble bottom community samples (0.10 m^2 each) were taken removing all organisms by hand.

The stomach contents of 80 specimens of *H. bispinis* from Ardley Cove and 42 from Coppermine Cove were analyzed. Windell's (1971) numerical and gravimetrical method was used. Size is given as the total length in millimetres. In order to relate the rubble bottom community samples to

Table 1. Stomach contents of *Harpagifer Bispinis* from two localities of the South Shetland Archipelago, West Antarctica.

PREY SPECIES	ARDLEY COVE (N = 74)					COPPERMINE COVE (N = 36)				
	Number of Individuals	Occurrence N°	Occurrence %	Weight* (g)	Weight* %	Number of Individuals	Occurrence N°	Occurrence %	Weight* (g)	Weight* %
MOLLUSCA										
GASTROPODA				0.115	1.34				0.018	0.17
Laevilitorina cf. umbilicata	69	32	43.2			1	1	2.7		
Laevilacunaria bransfieldensis	-	-	-			2	2	5.5		
Patinigera polaris	1	1	1.3			-	-	-		
BIVALVIA				0.005	0.06				-	-
Gaimardia sp.	2	2	2.7			-	-	-		
CRUSTACEA										
ISOPODA				0.004	0.05				0.011	0.10
Munna sp.	6	4	5.4			4	3	8.3		
Cymodocella tubicauda	-	-	-			5	1	2.7		
AMPHIPODA				8.285	97.01				10.491	99.61
Gondogeneia antarctica	262	61	82.4			279	36	100.0		
Eurymera monticulosa	10	8	10.8			5	4	11.1		
Pontogeneia sp.	55	30	40.5			13	11	30.5		
Orchomene sp.	49	22	29.7			1	1	2.7		
Pariphimedia sp.	-	-	-			3	2	5.5		
Bovallia gigantea	-	-	-			1	1	2.7		
POLYCHAETA				0.132	1.54				-	-
Phyllodocidae	3	2	2.7			-	-	-		
NEMERTINA	-	-	-			2	2	5.5	0.012	0.12
GRAND TOTAL OF ALL ITEMS	457			8.541	100	316			10.532	100

* Weight considering the total weight (g) of each taxonomic group from a subsample of 20 stomachs for each locality.

stomach contents the Ivlev (1961) electivity index was used:

$$E = (r_i - p_i)/(r_i + p_i)$$

where r_i is the relative content of any ingredient in the diet (expressed as a percentage) and p_i is the relative value of the same food items in the food complex of the environment.

The diversity value for the amphipod fraction in each rubble bottom sample was obtained with the Shannon-Weaver (H′) function, modified by Lloyd *et al.* (1968) and H'_{max} was calculated after Pielou (1975).

Results

Of the 80 specimens from Ardley Cove 92.5% contained food: of the 42 from Coppermine Cove 85.7% contained food. Prey types were identified to species level when possible. At both localities amphipods were the major food item. Other prey consisted of isopods *(Munna sp., Cymodocella tubicauda)*, nemertineans, polychaets (Phyllodocidae), bivalve molluscs *(Gaimardia sp.)* and gastropods *(Laevilitorina cf. umbilicata, Laevilacunaria bransfieldensis, Patinigera polaris)* which represent a very small fraction of the diet (Table 1).

The *Harpagifer*-amphipod predator-prey relationship appears to be very strong, and the results can be compared with those of Moreno (1971)*, Richardson (1975), Showers *et al.* (1977) and Daniels (1980). Five species of amphipods were identified in stomach contents of which *Gondogeneia antarctica* was the principal species predated. It appears that *H. bispinis* does have a set of preferred prey, since the amphipod fraction repre-

*Wrongly cited as Meier (1971) by the English-speaking scientists.

Table 2. Intertidal rubble bottom community from two islands of the south shetland archipelago, West Antarctica*

SPECIES	ARDLEY COVE (N = 7) Number of individuals	Mean of individuals/ sample ± S.D.	Total weight (g)	Occurrence N°	%	COPPERMINE COVE (N = 7) Number of individuals	Mean of individuals/ sample ± S.D.	Total weight (g)	Occurrence N°	%
MOLLUSCA										
GASTROPODA										
Laevilitorina cf. umbilicata	123	17.5 ± 13.8	0.32	6	85.7	4	0.6 ± 0.9	<0.01	2	28.5
Laevilacunaria bransfieldensis	-	-	-	-	-	71	10.1 ± 10.5	1.49	6	85.7
Patinigera polaris	74	10.6 ± 8.6	88.17	7	100	28	4.0 ± 1.8	32.32	7	100
Indet.	60	8.6 ± 14.8	0.01	2	28.5	87	12.4 ± 14.9	0.31	6	85.7
BIVALVIA										
Gaimardia sp.	132	18.8 ± 26.3	0.50	6	85.7	9	1.3 ± 3.4	0.01	1	14.3
Ennucula grayi	-	-	-	-	-	39	5.5 ± 7.4	0.27	4	57.1
CRUSTACEA										
ISOPODA										
Munna sp.	2	0.3 ± 0.7	<0.01	1	14.3	17	2.4 ± 2.7	0.04	4	57.1
Cymodocella tubicauda	-	-	-	-	-	11	1.6 ± 2.4	0.19	3	42.8
AMPHIPODA										
Gondogeneia antarctica	6	0.8 ± 0.7	0.21	5	71.4	1309	187.0 ± 144.1	12.22	7	100
Eurymera monticulosa	187	26.7 ± 50.0	24.71	7	100	28	4.0 ± 4.5	6.90	5	71.4
Pontogeneia sp.	130	18.5 ± 41.4	0.94	6	85.7	85	12.1 ± 12.9	1.01	7	100
Orchomene sp.	60	8.6 ± 12.7	2.06	5	71.4	12	1.7 ± 2.3	0.13	3	42.8
Pariphimedia sp.	2	0.3 ± 0.7	0.08	1	14.3	-	-	-	-	-
Bovallia gigantea	5	0.7 ± 1.1	3.10	3	42.8	18	2.6 ± 3.1	15.07	5	71.4
Proboloides sp.	5	0.7 ± 1.8	0.05	1	14.3	-	-	-	-	-
Paraceradocus miersii	1	0.1 ± 0.3	0.05	1	14.3	1	0.1 ± 0.3	0.44	1	14.3
POLYCHAETA										
Phyllodocidae	1	0.1 ± 0.3	0.01	1	14.3	12	1.7 ± 1.2	0.09	6	85.7
Terebellidae	7	1.0 ± 1.0	0.39	4	57.1	8	1.1 ± 2.6	0.40	2	28.5
Arabellidae	-	-	-	-	-	10	1.4 ± 3.7	0.04	1	14.3
Cirratulidae	-	-	-	-	-	12	1.7 ± 4.5	0.02	1	14.3
Ident.	2	0.3 ± 0.5	0.10	2	28.5	22	3.1 ± 5.8	0.48	4	57.1
NEMERTINA	8	1.1 ± 0.7	0.92	6	85.7	20	2.8 ± 3.3	1.99	4	57.1
CNIDARIA	2	0.3 ± 0.5	0.05	2	28.5	-	-	-	-	-
TURBELLARIA	18	2.6 ± 5.6	0.34	2	28.5	13	1.8 ± 2.2	0.35	5	71.4
PRIAPULIDAE										
Priapulus sp.	1	0.1 ± 0.3	3.23	1	14.3	-	-	-	-	-

* According to the analysis of 7 quantitative benthic samples (0.10 m^2) from each site.

sents 95.5% by number and 99.6% by weight at Coppermine Cove and 82.1% by number and 97.0% by weight at Ardley Cove. Thus, *G. antarctica* is the principal food item in both sites.

In Coppermine Cove the size of *G. antarctica* consumed by *H. bispinis* ranged from 4.5 mm to 19.5 mm with an average of 12.9 mm (S.D. = 3.5) being the most conspicuous prey with 123 individuals; *Pontogeneia sp* ranged from 5.5 mm to 15.1 mm with an average of 10.8 mm (S.D. = 3.7) represented only by 10 individuals. Only two individuals of *Eurymera monticulosa,* one of 4.0 mm and one of 18.5 mm were found; as were two individuals of *Pariphimedia sp* (13.5 mm and 14.0 mm); two nemertineans (2.7 mm and 7.0 mm); one individual of *Laevilitorina cf. umbilicata,* (5.2 mm) and three small isopods *Munna sp.* between 3.4 mm and 4.3 mm in length.

Amphipods represent the entire prey weight in 75% of the stomachs under analysis, in the other 25% they fluctuate between the 81.4% and 99.6% of it.

At Ardley Cove *Gondogeneia antarctica* is also the most important prey and its size ranges from 4.8 mm to 21.1 mm with an average of 11.6 mm (S.D. = 3.8) and exhibits the largest value with 103 specimens; *Pontogeneia sp.* fluctuated between 5.0 mm and 18.0 mm with an average of 8.1 mm (S.D. = 3.3) with 13 individuals; *Orchomene sp.* ranged from 6.5 mm to 12.6 mm averaging 10.7 mm (S.D. = 2.0) with 26 individuals. Two specimens of the isopod *Munna sp.* (1.9 mm and 3.4 mm) were present in one stomach. Likewise *Laevilitorina cf. umbilicata* with 22 individuals (1.2 mm to 5.0 mm with an average of 2.1 mm) (S.D. = 1.1), *Patinigera polaris* (7.4 mm) and the bivalve *Gaimardia sp.* (2.4 mm) were present only in one stomach each. Only one stomach had polychaets (Phyllodocidae)

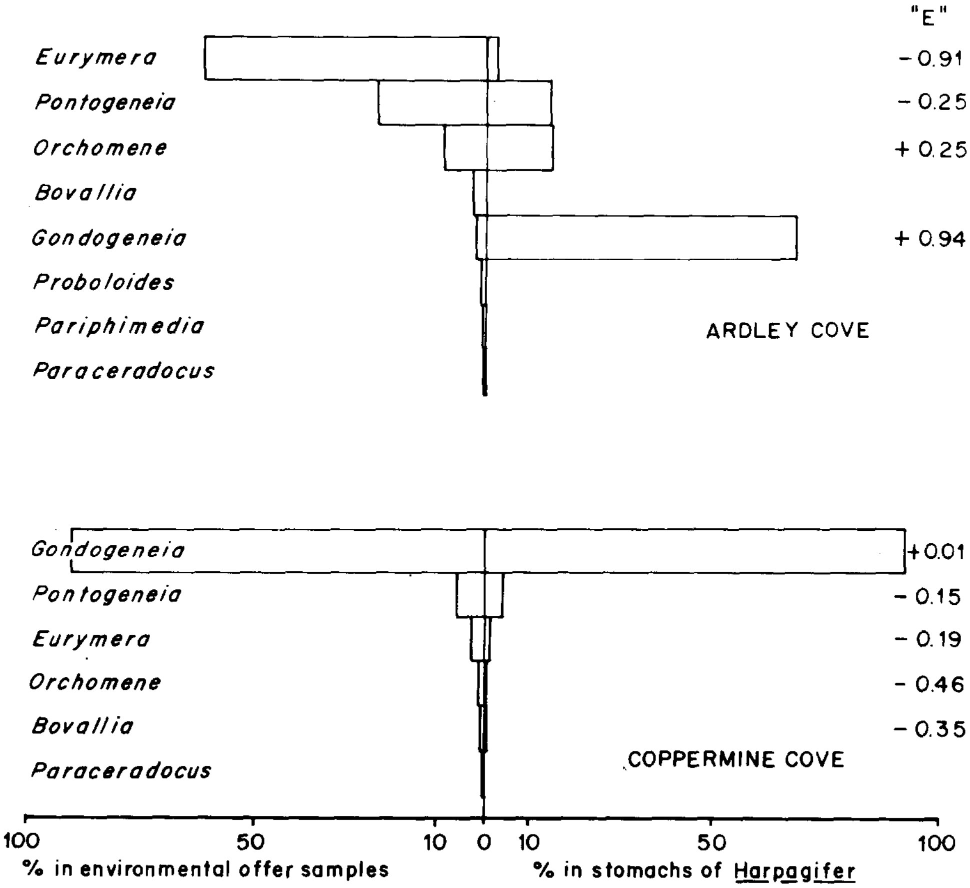

Fig. 2. Percentage of amphipods in the environmental samples and in the stomachs of *Harpagifer bispinis* for both sites. On the right hand side the values of E correspond to Ivlev's index of electivity.

and its weight represented 28.4% of the total prey weight for that stomach.

Amphipods represent the entire prey weight in 30% of the stomachs under analysis and in the other 70% they range from 62.9% to 99.8% having an average of 96.1%. Other prey items are very poorly represented.

When analyzing data of fish size with the average of prey size and establishing a product-moment correlation, we found non significant values of $r = 0.055$ ($N = 20$) for Coppermine and $r = 0.422$ ($N = 20$) for Ardley. From these data we can establish that at least for the size range of prey consumed by *H. bispinis* there is no relation between fish and prey size.

When examining availability samples of the benthos (0.10 m^2 each) from the rubble bottom community (Table 2) for both sites, we can appreciate that the amphipod fraction consists of 8 species for Ardley Cove and 6 for Coppermine cove. The most conspicuous amphipod of Ardley Cove is *Eurymera monticulosa* with an average of 26.7 individuals per sample, followed by *Pontogeneia sp.* (18.5 individuals per sample). *Gondogeneia antarctica* is poorly represented poorly represented. There are some species which are very well represented numerically such as *Laevilitorina cf. umbilicata* ($\bar{x} = 17.5$ individuals per sample), and *Gaimardia sp.* ($\bar{x} = 18.8$ individuals per sample), but which are not significant in weight.

At Coppermine Cove the principal amphipod is *Gondogeneia antarctica* with an average of 187 individuals per sample, followed by *Pontogeneia sp.* (12.1 per sample). Other animals have a very small representation.

When the information of Tables 1 and 2 is compared it is easily deducible that the availability of potential prey numerically duplicates what is consumed. On the other hand, of those that are consumed, there is a clear domination of species that have some degree of mobility, specially amphipods. This agrees with the behaviour of this fish as an ambush feeder (Daniels 1978). The high consumption of species from the amphipod fraction of the community permits a much more detailed study concerning food electivity of *H. bispinis*. In fact, the representation of these results (fig. 2) shows that it prefers *Gondogeneia antarctica* even when it is poorly represented in the environment, as at Ardley Cove. This supports the criticisms of Jacobs (1974) and Paloheimo (1979), that the electivity index of Ivlev is not always a good indicator of electivity. The high electivity over *Gondogeneia* is only explained by the combination of great prey mobility and the ambush feeding behaviour of *H. bispinis*. This is reinforced at Ardley Cove by the low consumption of *Eurymera monticulosa*, an amphipod that falls within the size range of the prey captured by *H. bispinis*, but which moves slowly over the bottom. The absence of *Bovallia gigantea* in the stomachs could be a consequence of size selection of food (fig. 3).

Fig. 2 show a clear difference in the abundance of the amphipod guild at the two sites, though the physical environments are similar and the tidal pools that were sampled seem identical and have a high faunistic similarity. Nevertheless, the relative abundance of *Harpagifer* is very different. At Ardley Cove density was 4 to 8 individuals/m^2 of tidal pool during low tide period, and at Coppermine Cove the values fluctuated between 0.5 and 1 individual/m^2.

The difference in the density of predators suggests that the 'predation pressure' can be influencing the numerical representation of the different species belonging to the amphipod fraction of the benthic community. *Gondogeneia* is consumed at Ardley until its level is depleted. This would permit an increase in the species less consumed. In other words, there could be a competitive hierarchy between the amphipod species controlled by the predator, *Gondogeneia* being the dominant species when there is a very low predator density or when the predator is not present. If this is so, we would expect an influence of *Harpagifer* over the diversity of the amphipod fraction of the benthic samples obtained, analogous to that shown by Porter (1972) for the effect of predation by *Acanthaster* on coral species diversity.

Table 3 shows that there are significant differences in diversity and evenness of the amphipods of 7 samples for both localities. Species diversity and species evenness are higher in the area of higher density of *Harpagifer*. Nevertheless, a doubt persists. Is the difference in the index of diversity more influenced by the number of species of each locality than by its evenness?

To clarify this doubt we correlated diversity (H′) v/s number of species and also with its evenness value (fig. 4). It clearly appears that for Ardley and

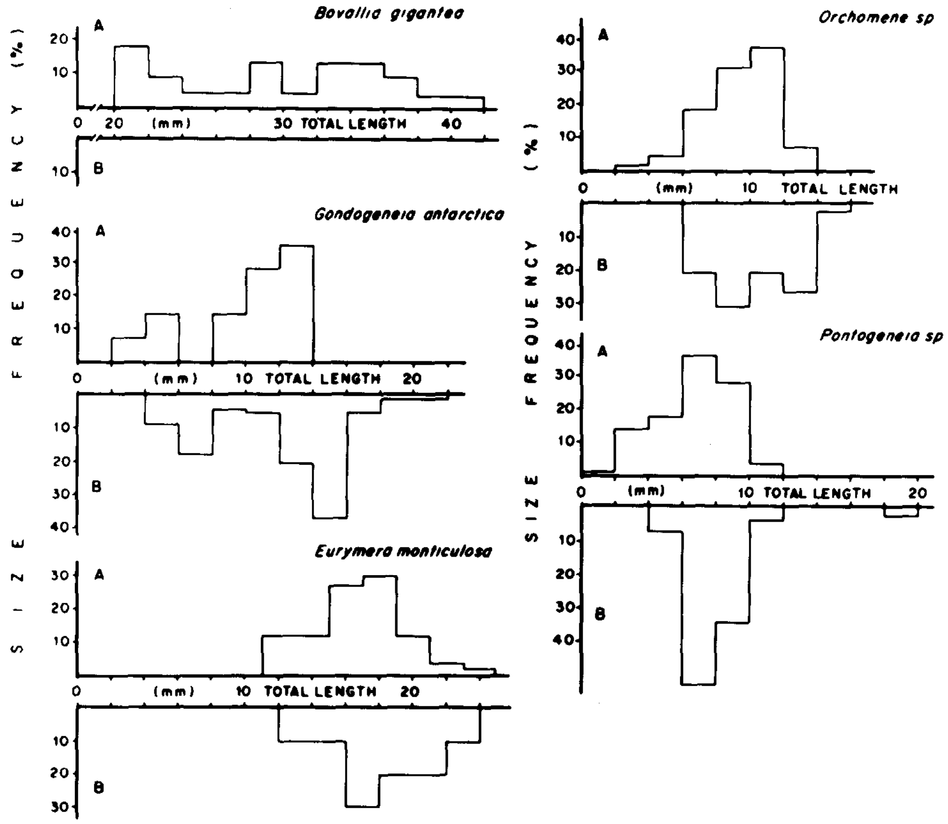

Fig. 3. Size selection of food by *Harpagifer bispinis* at Ardley Cove. A represents the available sizes of amphipod species in the environment and B represents the sizes of the consumed organisms. Notice that for *B. gigantea* the scale is different from the others.

for Coppermine the value of diversity (H′) is highly correlated with species evenness. This suggests that the difference in diversity is due to the effect of predation which levels off the numerical representation of each species, increasing the value of species evenness.

Discussion

Diet characteristics of *H. bispinis* in our study agrees strongly with the results obtained by Moreno (1971), Richardson (1975), Showers *et al.* (1977) and Daniels (1980), especially in the high representation of amphipods. This suggests an alimentary specialization in this species. The study of availability of food reinforces the conclusion obtained by the preceding authors concerning the trophic specialization of this fish.

However, the comment made by Arnaud (1977) dealing with the possibility that the apparent specialization of *H. bispinis* can reflect the absence of rarity of any other prey in the habitat, has to be reconsidered. In fact, this problem has to be limited to the 'real availability of prey' and not only to the 'potential availability', since Daniels (1978, 1980) has shown that this fish behaves as an ambush feeder. Thus the only available prey for this fish are species that have high mobility, that is those that are able to switch on its capture reflex.

Therefore, only *Gondogeneia antarctica,* the most active amphipod of our study area represents the most adequate prey for the behavioural requirements of *H. bispinis.* This is supported by the fact that it is consumed even when its representation in the environment is minimal. We state that the small number of prey species found in *H. bispinis,* if compared to the majority of antarctic fishes, is the result of an adjustment between prey accessibility and the specialization of the method used to capture them.

This interaction between amphipods and their

Table 3. Number, diversity and evenness of the amphipod species of intertidal pools from two isles from the South Shetland Archipelago, Antarctica (samples of 0.10 m^2).

- COPPERMINE COVE, ROBERT ISLAND (density of *H. bispinis* 0.5 to 1 indiv./m^2)

Sample number	Number of species (S)	Diversity (H')	Rank (R_1)	Evenness (H'/H'_{max})	Rank (R_2)
1	4	0.26	3	0.13	3
2	5	0.83	6	0.35	4.5
3	3	0.09	1	0.06	1
4	4	0.70	5	0.35	4.5
5	4	0.91	7	0.45	7.5
6	2	0.46	4	0.46	9
7	6	1.01	8	0.39	6
			Σ = 34		Σ R = 35.5

- ARDLEY COVE, KING GEORGE ISLAND (density of *H. bispinis* 4 to 8 indiv./m^2)

Sample number	Number of species (S)	Diversity (H')	Rank (R'_1)	Evenness H'/H'_{max})	Rank (R'_2)
1	4	1.92	14	0.96	14
2	4	1.52	11	0.76	11
3	4	1.66	12	0.83	12
4	4	1.72	13	0.86	13
5	5	1.05	9	0.45	7.5
6	4	1.09	10	0.54	10
7	4	0.22	2	0.11	2
			Σ R = 71		Σ R = 69.5

R_1 v/s R'_1 Wilcoxon's two-sample test. Us = 6 $P < 0.001$ (one way)
R_2 v/s R'_2 Wilcoxon's two-sample test. Us = 7.5 $P < 0.001$ (one way)

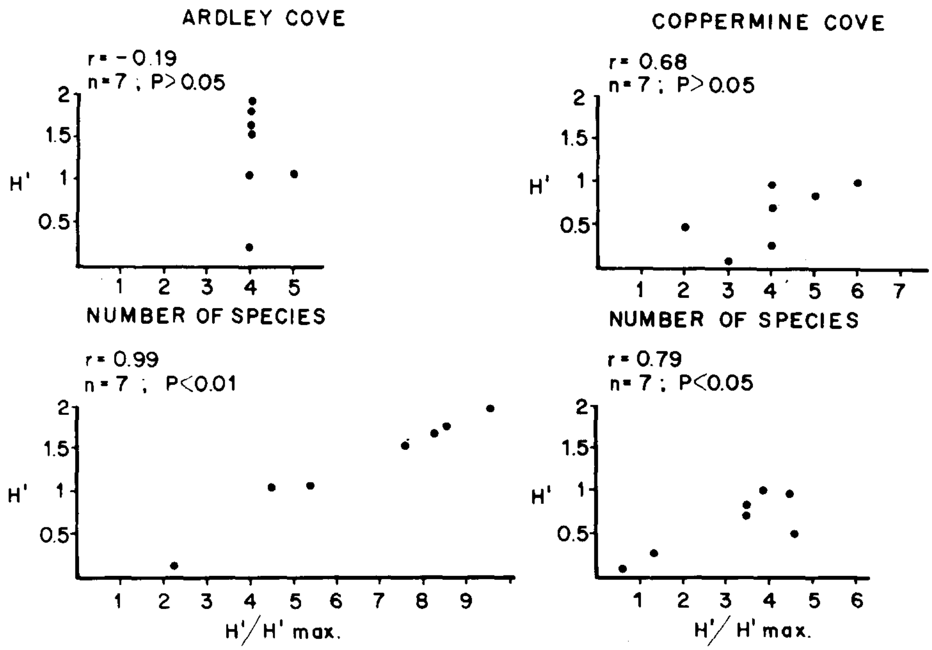

Fig. 4. Correlation between the diversity (H') value of the intertidal benthic samples v/s the number of species and species evenness at both sites.

predator in the intertidal pools seems to have consequences in the organization of the structure of the amphipod guild. A greater predation pressure, when the density of *H. bispinis* is high, can diminish consistently the abundance of its preferred prey and increase the local species diversity. Paine (1966) has shown that the absence or low density of a predator can switch competitive interactions between co-existing species that have similar requirements of space and/or food, inducing great changes in the local abundance of certain populations.

In this case, where similar intertidal pools had different predator densities, we are facing a 'natural experiment' in which it is appropriate to know something about the structure of the antarctic intertidal communities. It was not possible to conduct a field experiment (Connell 1974) in this habitat due to strong logistic restrictions.

The results of our 'reading' of the natural experiment favours the hypothesis that a higher predation intensity of *Harpagifer* on amphipods can not only increase the number of species, but also influence the numerical representation of each. This means accepting the fact that among amphipods of the antarctic intertidal pools there are competitive dominance hierarchies, though it is yet not clear which is the limiting factor of the interactions between amphipods. Another implication of these results is connected with the fact that the antarctic intertidal zone is permanently subjected to physical stress due to the constant impact of brush-ice and small icebergs over rocks and intertidal pools, therefore there should exist a higher physical control on this community (Sanders 1969). Nevertheless it is clear that the trophic specialization of *Harpagifer* can introduce a biological factor in the regulation of the mobile epibenthic communities of the intertidal zone in the West-Antarctica.

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Summary

Food electivity in *Harpagifer bispinis* (Pisces, Nototheniidae) from two localities of the South Shetland Archipelago, Antarctica was studied. For this purpose samples of 0.10 m^2 of the benthos from the intertidal zone were obtained to reveal prey availability together with the specimens of *H. bispinis*.

The density of *Harpagifer* for both localities was estimated.

In relation with the diet of *Harpagifer* it was found that the 75% of the analyzed specimens had only fed on amphipods of which *Gondogeneia antarctica* was the principal component. In the rest of the stomachs amphipods represented between 81.4% and 99.6% of the prey by weight.

The analysis of the food availability samples reflects an availability of several species at much higher densities than the fraction that is consumed. Nevertheless, *H. bispinis* due to its behaviour as an ambush feeder selects mainly those amphipod species that display great mobility, even when their representation in the environment is very low.

These facts suggest that this predator has a great impact in the abundance of the different amphipod species. This was analyzed in the availability samples obtained from the intertidal communities of two isles of the South Shetland Archipelago, West Antarctica which had quite different densities of *H. bispinis.*

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