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Feeding ecology of two nototheniid fishes, *Trematomus hansonii* and *Trematomus loennbergii*, from Terra Nova Bay, Ross Sea

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Abstract A study of feeding ecology in *Trematomus hansonii* Boulenger 1902 and *Trematomus loennbergii* Regan 1913 was carried out from samples collected in the austral summer 1990–1991 off Terra Nova Bay, Ross Sea. *T. hansonii* was caught between 35 and 566 m and *T. loennbergii* between 311 and 543 m. Stomach contents analysis shows that *T. loennbergii* relies on a wider range of prey than *T. hansonii*. Fish and decapods are the main food resources of *T. loennbergii*, which feeds also on epifaunal and tube-dwelling polychaetes. *T. hansonii* mostly relies on fish resources that are made up of juvenile stages of fish and eggs. Despite the common area occupied by the two species, the interspecific competition is mostly mitigated due either to taking different prey or to taking different amounts of the same prey.

Introduction

The striped notothen, *Trematomus hansonii* Boulenger, and the deepwater notothen, *Trematomus loennbergii* Regan, are widely distributed in the continental waters of the Southern Ocean and occur at 5- to 550-m and 65- to 832-m depth range, respectively (DeWitt et al. 1990).

At Terra Nova Bay *T. hansonii* is one of the most common nototheniid fishes, inhabiting shallow as well as deep waters, whereas *T. loennbergii* is commonly found at depths over 300 m (Vacchi et al. 1991).

Based on measurements of buoyancy and on morphological and ecological observations, Eastman and

DeVries (1982) found that *T. loennbergii* had a lower specific weight in seawater and showed more spontaneous swimming activity than other benthic nototheniids of McMurdo Sound, and they consider it to be a benthopelagic species. However, *T. hansonii* was considered the most active benthic species as indicated by greater swimming activity in aquaria (Eastman and DeVries 1982).

The trophic ecology of *T. hansonii* is well documented by several studies carried out all around the Antarctic Continent, e.g. in the Weddell Sea (Schwarzbach 1988), in the Cosmonaut Sea (Naito and Iwami 1982; Pakhomov and Tseitlin 1991), in the D'Urville Sea (Arnaud and Hureau 1966; Hureau 1970) and in the Ross Sea (Eastman 1985; Foster and Montgomery 1993; Montgomery et al. 1993), as well as off South Georgia (Linkowski and Rembiszewski 1978; McKenna 1991; Targett 1981). However, only a few studies have concentrated on the feeding habits of *T. loennbergii* (Eastman 1985; Schwarzbach 1988). From these studies, it seems that both species are probably opportunistic feeders, with diet related to the local abundance of prey organisms.

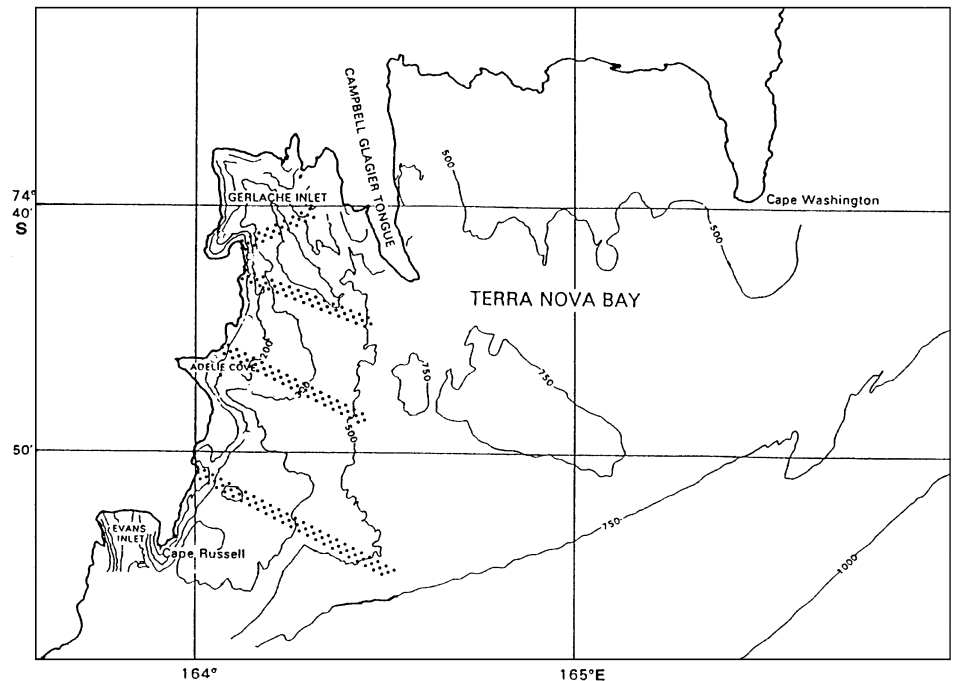
The present study provides additional knowledge of the feeding ecology of the latter species and also reports on some feeding strategies adopted by the two species that allow them to live in the same area without strong food competition.

Materials and methods

This study was conducted off the Italian Terra Nova Station (74°41'42" S and 64°07'25" E) from the Gerlache Inlet to Cape Russell in the northwestern Ross Sea during the Sixth Italian Antarctic Expedition. Fishes were collected by trammel and gill nets, lines and traps from 19 December 1990 to 9 February 1991. The hauls took place along four transects located from the coast towards the open sea and ranged between 16 m and 682 m depth (Fig. 1). Hauling time was, on average, 4–5 h and the fishing operations were mainly carried out during the day. All the specimens caught were

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Fig. 1 The study area of Terra Nova Bay showing the sampling transects (*grid stripes*)



stored deep frozen (-25°C) or in 10% buffered formalin (only three specimens of *T. hansonii*).

For the stomach contents analysis, each fish was sexed and staged according to Everson (1977), measured as TL and weighed to the nearest gram below. After dissection, the stomach contents were weighed and washed out into a petri dish for microscope examination. The sorting allowed us to count and weigh to the nearest milligram each prey item. Individual prey were identified as far as possible to species level.

Following the recommendation of the BIOMASS Programme (Anonymous 1981), the coefficient of emptiness $V = N_e/N_s$, where N_e is the number of empty stomachs and N_s is the total number of stomachs examined, as well as the Index of stomach fullness $I = W_{sc}/W_f \times 100$ where W_{sc} is the wet weight of stomach content of an individual and W_f is the wet weight of that individual, were calculated.

Moreover, data on food composition were processed according to the mixed method of Hureau (1970). The diet is expressed in terms of a dietary coefficient "Q", which is the product of the percentage by weight and the percentage by number of each prey type. To describe the uniformity with which groups of fish select their diet (Bowen 1983), the frequency of occurrence, that is, the number of stomachs containing a particular prey item as a percentage of the total number of stomachs examined, was also recorded. To evaluate the trophic overlap between the species we used the percentage diet similarity index $S = 100(1 - \frac{1}{2}\sum Px_i - Py_i)$, where Px_i and Py_i are the proportions by weight or by number of the *i*th prey in the diet of the species *x* and *y* (Linton et al. 1981). Finally, dietary diversity was expressed either by the number of taxa *P* present in the stomach contents or by the diversity index $H = -\sum p_i \ln p_i$, where p_i is the percentage by number of the *i*th prey in the sample (Shannon and Weaver 1949).

Results

Overall, 1758 fish belonging to 20 species were collected (Vacchi et al. 1991). Except for *Trematomus*

bernacchii, which is the most common species obtained at Terra Nova Bay using this type of gear (60% of the total catches), the two species selected for this study were the most abundant nototheniid fish sampled. One hundred and twenty-two specimens of *T. hansonii* and 94 specimens of *T. loennbergii* were caught, representing about 6.9% and 5.3% of the total samples, respectively. *T. hansonii* was caught in all the hauls where *T. loennbergii* was sampled.

Trematomus hansonii

T. hansonii was caught in all the transects from 35- to 566-m depth. However, more than 50% of the specimens were sampled below 300-m depth. One hundred and nine specimens were analysed, of which 56.9% and 43.1% were caught by the trammel and gill nets, respectively. The sizes ranged from 195 to 357 mm TL (mean length 252 mm and modal length 235 mm) and weights were between 69 and 615 g. The sex ratio between males and females was 1:1.4. Throughout the sampling period we found this species in spawning condition, the females having ovaries filled with large yolky eggs (up to 3.6 mm).

The stomachs of 58 specimens were empty ($V = 53.2\%$). The stomach fullness, *I*, ranged from 0.1 to 16.9%. Overall, 70 food items belonging to 18 taxa were identified and the dietary diversity index was 2.13 (Table 1). Stomach contents analysis revealed that *T. hansonii* was mainly piscivorous. Fishes, which were mainly juveniles and in most cases appeared as unidentifiable remains (vertebrae, crystalline lens, scales,

flesh), showed a *Q* value about 10 times higher than the second prey item in order of importance, i.e. fish eggs. Polychaetes (mostly tube-dwelling e.g. Maldanidae) and decapods (*Chorismus antarcticus* and *Notocrangon antarcticus* together) were secondary food items. The other taxa identified, i.e. algae, bivalves, amphipods, pycnogonids, echinoids and crinoids, were eaten only incidentally by *T. hansonii*.

Table 2 shows the food composition of females and males expressed as frequency of occurrence (%). The diet of females was more diversified than that of males and it was composed mostly of fishes and polychaetes, followed by fish eggs and crinoids. Males were more piscivorous than females, and frequently they relied on polychaetes, decapods and fish eggs.

In Table 3 the food composition of three size categories (small, medium and large) of *T. hansonii* is given.

Specimens of medium size fed on a wider range of prey than other size categories. Moreover, of the food items more frequently consumed, fishes and polychaetes were mostly eaten by small-sized fish, whereas fish eggs were consumed mostly by large specimens. Decapods were found only in the stomach contents of small- and medium-sized specimens. The other taxa of prey, such as algae, bivalves, amphipods and pycnogonids, were eaten less frequently, often by only one size category.

The dietary composition of *T. hansonii* in relation to depth of catch revealed some differences (Table 4). Some taxa of prey, such as algae, bivalves and pycnogonids, were consumed only by the specimens caught in shallow waters (below 300-m depth); some, such as amphipods, were eaten only by the specimens caught in deep waters (above 300-m depth). Polychaetes, as well as decapods, were more diversified in

Table 1 Diet composition of the fish species studied (*F* frequency of occurrence; *N* percentage by number; *W* percentage by weight; *Q* dietary coefficient; main food $Q > 200$; secondary food $200 > Q > 20$; accidental food $Q < 20$)

Prey taxon	<i>Trematomus hansonii</i>				<i>Trematomus loennbergi</i>			
	F	N	W	Q	F	N	W	Q
Algae	0.9	1.4	0.2	0.28				
Polychaetes	9.2	18.6	3.4	63.24	53.8	37.9	4.1	155.39
Epifaunal								
<i>Antinoella setobarba</i>					3.3	1.7	0.1	0.17
<i>Barrukia cristata</i>					1.1	0.6	0.003	0.002
<i>Eucranta mollis</i>					2.2	1.1	0.1	0.11
<i>Eunoe anderssoni</i>					15.4	8.0	0.8	6.40
<i>Eunoe</i> sp.					5.5	2.9	0.3	0.87
<i>Harmotoe</i> sp.					6.6	3.5	0.3	1.05
<i>Polyeunoa laevis</i>					2.2	1.7	0.1	0.17
Polynoidae	1.8	2.9	0.01	0.03	9.9	5.2	0.4	2.08
Syllidae					1.1	0.6	0.03	0.02
Tube-dwelling								
Maldanidae	1.8	2.9	0.2	0.58	2.2	1.1	0.4	0.44
<i>Flabelligera gourdoni</i>	0.9	1.4	0.3	0.42				
Ampharetidae					1.1	0.6	0.03	0.02
<i>Pista cf cristata</i>					1.1	0.6	0.2	0.12
<i>Pista</i> sp.					1.1	0.6	0.2	0.12
Terebellidae	5.5	8.6	2.6	22.36	12.1	6.3	0.4	2.52
Polychaetes unidentified	1.8	2.9	0.3	0.87	6.6	3.5	0.7	2.45
Bivalves	0.9	1.4	1.0	1.40				
Amphipods	1.8	2.8	0.9	2.52	16.5	8.6	1.5	12.90
<i>Epimeria</i> spp.					2.2	1.1	0.1	0.11
<i>Eusirus perdentatus</i>	0.9	1.4	0.7	0.98	1.1	0.6	0.1	0.06
<i>Eusirus</i> spp.	0.9	1.4	0.3	0.42	9.9	5.2	1.3	6.76
<i>Liljeborgia</i> sp.					2.2	1.1	0.02	0.02
<i>Tryphosella</i> sp.					1.1	0.6	0.02	0.01
Isopods					2.2	1.1	0.2	0.22
<i>Dolichiscus</i> sp.					1.1	0.6	0.2	0.12
<i>Mixarcturus</i> sp.					1.1	0.6	0.03	0.02
Decapods	5.5	11.4	3.6	41.04	51.6	35.0	29.9	1046.5
<i>Chorismus antarcticus</i>	1.8	5.7	2.3	13.11	24.2	14.9	9.9	147.51
<i>Notocrangon antarcticus</i>	3.7	5.7	1.3	7.41	34.1	20.1	20.0	402.00
Pycnogonids	0.9	1.4	0.04	0.06				
Echinoids	1.8	2.9	0.8	2.32				
Crinoids	4.6	7.1	2.6	18.46				
Fishes	21.1	41.4	68.0	2815.2	26.4	15.5	63.9	990.45
Channichthyidae	0.9	1.4	2.4	3.36	2.2	1.1	6.1	6.71
Nototheniidae	1.8	8.6	31.5	270.9	5.5	3.5	31.0	108.50
Fish remains	18.3	31.5	34.1	1074.15	18.7	10.9	26.8	292.12
Fish eggs	7.3	11.4	19.3	220.02	3.3	1.7	0.3	0.51

Table 2 Diet composition for female and male specimens of the fish species studied expressed as frequency of occurrence (%)

Prey taxon	<i>Trematomus hansonii</i>		<i>Trematomus Ioennbergii</i>	
	Females	Males	Females	Males
Algae	1.7			
Polychaetes	10.0	6.8	48.3	59.2
Bivalves	1.7			
Amphipods	1.7	2.3	15.0	18.5
Isopods			1.7	
Decapods	5.0	6.8	53.3	55.5
Pycnogonids	1.7			
Echinoids	1.7	2.3		
Crinoids	6.7	2.3		
Fishes	15.0	27.3	26.7	22.2
Fish eggs	8.3	6.8	1.7	7.4

Table 3 Diet composition for three size categories of the fish species studied expressed as frequency of occurrence (%)

Size TL (mm)	<i>Trematomus hansonii</i>			<i>Trematomus Ioennbergii</i>		
	Small 190–240	Medium 241–290	Large 291–350	Small 150–210	Medium 211–270	Large 271–330
Algae		2.6				
Polychaetes	10.0	5.3	9.5	56.2	47.4	56.7
Bivalves		2.6				
Amphipods	4.0			12.5	18.4	16.2
Isopods					2.6	2.7
Decapods	6.0	7.9		43.7	47.4	59.4
Pycnogonids			4.8			
Echinoids		2.6	4.8			
Crinoids	2.0	7.9	4.8			
Fishes	30.0	15.8	14.3	25.0	21.0	32.4
Fish eggs	4.0	5.3	19.0	6.2	2.6	2.7

Table 4 Diet composition of *Trematomus hansonii* according to its depth distribution (*F* frequency of occurrence; *N* percentage by number; *W* percentage by weight; *Q* dietary coefficient)

Prey taxon	<300-m Depth				>300-m Depth			
	F	N	W	Q	F	N	W	Q
Algae	2.2	4.2	0.6	2.52				
Polychaetes	2.2	4.2	3.4	14.28	19	26.1	3.5	91.35
Epifaunal								
<i>Antinoella setobarba</i>								
<i>Barrukia cristata</i>								
<i>Eucranta mollis</i>								
<i>Eunoe anderssoni</i>								
<i>Eunoe</i> sp.								
<i>Harmotoe</i> sp.								
<i>Polyeunoa laevis</i>								
Polynoidae					3.2	4.3	0.02	0.09
Syllidae								
Tube-dwelling								
Maldanidae					3.2	4.3	0.4	1.72
<i>Flabelligera gourdoni</i>					1.6	2.2	0.6	1.32
Ampharetidae								
<i>Pista cf cristata</i>								
<i>Pista</i> sp.								
Terebellidae	2.2	4.2	3.4	14.28	7.9	10.9	2	21.8
Polychaetes unidentified					3.2	4.3	0.5	2.15
Bivalves	2.2	4.2	2.3	9.66				
Amphipods					3.2	4.3	1.7	7.31
<i>Epimeria</i> spp.					1.6	2.2	1.2	2.64
<i>Eusirus perdentatus</i>					1.6	2.2	0.5	1.1
<i>Eusirus</i> spp.								
<i>Liljeborgia</i> sp.								
<i>Tryphosella</i> sp.								
Isopods								
<i>Dolichiscus</i> sp.								
<i>Mixarcturus</i> sp.								
Decapods	2.2	4.2	0.7	2.94	7.9	15.2	5.9	89.68
<i>Chorismus antarcticus</i>					3.2	8.7	4.2	36.54
<i>Notocrangon antarcticus</i>	2.2	4.2	0.7	2.94	4.8	6.5	1.7	11.05
Pycnogonids	2.2	4.2	0.1	0.42				
Echinoids	2.2	4.2	0.7	2.94	1.6	2.2	0.8	1.76
Crinoids	8.7	16.7	4.7	78.49	1.6	2.2	0.9	1.98
Fishes	13	37.5	45	1687.5	27	43.5	86	3741
Channichthyidae	2.2	4.2	5.4	22.68				
Nototheniidae	2.2	12.5	25.9	323.75	1.6	6.5	35.8	232.7
Fish remains	8.7	20.8	13.6	282.88	25.4	36.9	50.1	1848.69
Fish eggs	10.9	20.8	42.5	884	4.8	6.5	1.2	7.8

the latter group, whereas crinoids and fish eggs were eaten more frequently and largely by the former group. Fishes represented, by far, the main food item of both groups, but particularly of the specimens caught in deep waters.

Trematomus loennbergii

This species was collected in all the transects between 311 and 543-m depth (50% of the specimens above 500-m depth). Ninety-one specimens of *T. loennbergii* were analysed for stomach content. The percentages of fish sampled by the trammel and gill net were 64.8% and 35.2%, respectively. The size range of *T. loennbergii* was 155–330 mm TL (mean length 256 mm and modal length 285 mm) and weight was 25–359 g. The sex ratio between males and females was 1:2.2. Almost all *T. loennbergii* specimens were in a developing stage of maturity (stage III).

Of the 91 fishes examined, 12 of the stomachs were empty ($V = 13.2\%$). The stomach fullness, I , was between 0.5 and 15.2%. Table 1 summarises the diet composition. In this species the dietary diversity index was higher than in *T. hansonii* ($H = 2.72$). A total of 174 food items belonging to 28 taxa were identified, most of which were polychaetes (53.6%). These organisms were the most common prey found in the diet of *T. loennbergii*, occurring in 53.8% of the stomachs examined. Despite this, they appeared to be only a secondary food because of their low weight. The epifaunal *Eunoe anderssoni* and tube-dwelling Terebellidae were the most common polychaetes consumed. The decapods *C. antarcticus* and *N. antarcticus*, as well as fishes, represented the main food. The other crustaceans, constituted by amphipods (mainly *Eusirus* spp.) and isopods (*Dolichiscus* sp. and *Mixarcturus* sp.), as well as fish eggs, were seldom eaten, forming incidental food.

In Table 2 the food composition of females and males expressed as frequency of occurrence (%) is summarized. The diet was in general similar in both sexes, although males fed on fish eggs much more frequently than females (7.4% and 1.7%, respectively).

Table 3 shows the food composition of the three size categories (small, medium and large) of *T. loennbergii*. As for food items more frequently consumed, polychaetes, decapods and fishes were mostly eaten by large-sized fish. Fish eggs were more frequently found in the stomach contents of small-sized specimens, whereas isopods were eaten only by medium and large specimens.

The diet similarity between all the specimens of *T. hansonii* and *T. loennbergii* was 43.3% by number and 65.6% by weight. Conversely, the diet similarity between *T. hansonii* sampled below 300-m depth (see Table 4) and *T. loennbergii* was 27.3% by number and 49.0% by weight, whereas between *T. hansonii* sampled above 300-m depth (Table 4) and

T. loennbergii the diet similarity was 48.6% by number and 65.9% by weight.

Discussion

The coastal area of Terra Nova Bay is characterized by shallow hard bottoms up to 20-m depth, which are inhabited by a benthic association dominated by two macroalgal species (*Iridaea cordata* and *Phyllophora antarctica*) and a few animal taxa (mainly polychaetes, molluscs and peracarid crustaceans) (Gambi et al. 1994). For the soft bottoms, which appeared at about 20-m depth and extended down to 600-m depth, the benthic assemblages are represented by single species (e.g. facies of *Adamussium colbecki*) as well as by groups of species (sponges and cnidarians, bryozoans and polychaetes) (Di Geronimo et al. 1992).

Among nototheniids, *T. hansonii* and *T. loennbergii* are two of the most common fish species inhabiting the coastal waters of Terra Nova Bay (Vacchi et al. 1991). As some part of the spatial distribution of the two species in the study area overlapped (namely, above 300-m depth), it was interesting to detect the degree of food overlap between them and the possibility of the existence of some resources partitioning to mitigate interspecific competition.

The food spectrum of the two species of nototheniids mainly comprised benthic organisms that are more or less associated with the substrate. The stomach contents analysis showed that *T. loennbergii* fed on a wider range of prey than *T. hansonii*, at least at specific level (28 and 18 taxa of prey determined, respectively). In general (Table 1), the amount of the same prey consumed by both fishes was frequently very different. A high proportion of stomachs of *T. hansonii* were found empty (about 53%). Some of these specimens (28%) were females in spawning condition with very large ovaries that filled up the body cavity (Vacchi et al. 1995). This behaviour, however, seems frequent in other Antarctic fishes when they are in the spawning period (Kock 1990).

In both species, the polychaetes were the most diversified taxon as number of species. These prey have been subdivided into two groups in relation to their usual habitat. The first group comprises epifaunal polychaetes that crawl on the sea floor, whilst the second group consists of sessile or sedentary species that are generally exposed on the bottom. In general, *T. loennbergii* fed on more species of polychaetes than *T. hansonii*, which almost exclusively relied on tube-dwelling polychaetes. The lack of burrow-dwelling polychaetes in the diet of both species was noteworthy, considering that other *Trematomus* species commonly prey on such organisms in Terra Nova Bay (Vacchi et al. 1994). Burrow-dwelling polychaetes such as Orbiniidae, Opheliidae, Nephtyidae and Glyceridae were indeed commonly found in the stomach contents of

both *Trematomus centronotus* and *Trematomus bernacchii* (mostly in the former species) (Vacchi et al. 1994). The importance of polychaetes as food for *T. loennbergii* and *T. hansonii* has been shown in other Antarctic sites, such as the Ross Sea (Eastman 1985), the Weddell Sea (Schwarzbach 1988) and the Adélie coast (Hureau 1970).

For crustaceans, *N. antarcticus* and *C. antarcticus* represented some of the most common prey in the diet of both fishes, although *T. loennbergii* fed on them more frequently and in greater amounts than *T. hansonii*. Besides these quantitative differences, it was clearly shown that *T. loennbergii* mostly consumed *N. antarcticus*, while *T. hansonii* preferentially preyed on *C. antarcticus*. This was probably related to the bathymetric distribution of the two decapods. *N. antarcticus*, indeed, is a demersal prawn more commonly taken between 300 and 600-m (the same depth range where *T. loennbergii* has been caught at Terra Nova Bay), while *C. antarcticus* is most common sampled in near-surface waters of 15- to 300-m depth (Kirkwood 1984). Also gammarid amphipods were more frequently found in *T. loennbergii* than in *T. hansonii*, although in both species they represented incidental food. Fishes, mostly represented by juvenile nototheniids and unidentified fish remains, along with fish eggs were the most common prey of *T. hansonii*, while they ranged second in the diet of *T. loennbergii*. The piscivorous feeding habit of *T. hansonii* found in Terra Nova Bay has been often reported in other Antarctic localities, such as the Ross Sea (Eastman 1985; Montgomery et al. 1993), the Weddell Sea (Schwarzbach 1988) and the Cosmonaut Sea (Pakhomov and Tseitlin 1991).

The other taxa of prey, namely algae, bivalves, isopods, pycnogonids, echinoids and crinoids, were eaten only incidentally and taken by only one species.

The food composition of each sex, expressed as frequency of occurrence of major taxa of prey, is similar in *T. loennbergii*, whereas in *T. hansonii* the diet of females was more diversified than that of males.

As for the prey shift with fish size, the specimens of medium size of *T. hansonii* fed on a wider range of prey than other size categories, whereas all the specimens of *T. loennbergii* relied on the same number of taxa. However, it is noteworthy that the most common prey, such as polychaetes, fishes, decapods and fish eggs, were eaten alternatively by different size categories of the two species. So the first three food items were mostly eaten by small-sized specimens of *T. hansonii* and by large-sized specimens of *T. loennbergii*, whereas fish eggs were consumed mostly by large specimens of *T. hansonii* and by small specimens of *T. loennbergii*.

Data on food composition of *T. hansonii* in relation to depth of catch showed some differences, mostly related to the shift of the benthic fauna with depth. This fact greatly affects the value of food similarity between the two fishes, which increases in the comparison be-

tween *T. loennbergii* and the specimens of *T. hansonii* sampled below 300-m depth. This value of food similarity is, however, rather low and close to the value obtained in the comparison between *T. loennbergii* and all the specimens of *T. hansonii* sampled.

Finally, our results show that *T. hansonii* is an euryphagic species, which feeds heavily on juvenile fish and on several benthic organisms, as suggested in other studies (Arnaud and Hureau 1966; Hureau 1970; Pakhomov and Tseitlin 1991). We did not find planktonic prey in the diet of *T. hansonii*. This mode of feeding was observed in other sites, mostly at South Georgia where this fish fed almost exclusively on krill (McKenna 1991; Targett 1981), and at McMurdo Sound (Foster and Montgomery 1993).

At Terra Nova Bay, *T. loennbergii* relies on several species belonging to relatively few taxa of benthic prey. However, planktivory was recorded in this species in the Weddell Sea (Schwarzbach 1988).

We conclude that the examination of the diet of the two species at a low taxonomic level allows to state that, despite the common area occupied by the two species at Terra Nova Bay, the interspecific competition is mostly mitigated either by taking different prey or by taking different amounts of the same prey. Moreover, often the same prey was eaten by different size categories of the two species. From other studies, both fish species appear to be opportunistic feeders, carrying out occasional vertical migrations along the water column to exploit some locally and seasonally important planktonic prey.

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