

Behavioural Strategies for Feeding of Six Species of the Antarctic Fish Family Nototheniidae (Pisces, Notothenioidei) in a Tank

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ノトセニア科魚類（魚類：ノトセニア亜目）に属する
6種の魚の水槽中における摂餌戦略

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要旨： 温度、光条件を制御した水槽を用いて6種のノトセニア科魚類、*Notothenia coriiceps*, *Notothenia neglecta*, *Trematomus bernacchii*, *Pagothenia borchgrevinki*, *Lepidonotothen nudifrons*, *Pleuragramma antarcticum* の摂餌戦略の観察を行った。観察に用いた魚は、夏季、キングジョージ島、アドミラルティ湾で採取した。*P. antarcticum* は水中でだけ摂餌したが、他の5種は水中と底とで餌を摂った。*T. bernacchii*, *L. nudifrons*, *N. neglecta*, *P. antarcticum* は餌魚に対する攻撃行動を示した。*P. antarcticum* と *N. coriiceps* を除き、一連の摂餌行動は常に、休止状態から始まった。*N. neglecta*, *T. bernacchii*, *P. borchgrevinki* の場合、一度の摂餌行動で一匹の魚を捕食したが、*N. coriiceps* の場合、1回の摂餌行動に際して、あちこち泳ぎ廻りながら数匹の魚を食うという動作を示した。総ての魚種がナンキョクオキアミ、端脚類を摂餌した。*T. bernacchii* は魚、端脚類を一旦口に入れた後、はき出した。水槽中での食物に対する競争は摂餌行動の違いによって緩和されているようである。

Abstract : The feeding strategies of six Nototheniid fishes, *Notothenia coriiceps*, *Notothenia neglecta*, *Trematomus bernacchii*, *Pagothenia borchgrevinki*, *Lepidonotothen nudifrons* and *Pleuragramma antarcticum*, were studied in tanks, under controlled environmental conditions. These fish were caught in Admiralty Bay, King George Island, during the Antarctic summer. Although *P. antarcticum* preyed only in the water column, the remaining five species fed not only in the water column but also at the bottom. Persecutions of prey were observed in *T. bernacchii*, *L. nudifrons*, *N. neglecta* and *P. antarcticum*. The sequence for feeding always started from resting except for *P. antarcticum* and *N. coriiceps*. Each feeding sequence lead to the ingestion of one fish each time by *N. neglecta*, *T. bernacchii* and *P. borchgrevinki*, but *N. coriiceps* was able to catch and ingest several fish during one period of random swimming. Many krill and/or amphipods were usually ingested by all predators during one feeding action, but *T. bernacchii* also caught them one by one. *T. bernacchii*, *N. coriiceps*, *N. neglecta* and *P. antarcticum* sometimes rejected fish and/or amphipods after apprehension. The competition for food in the tanks seemed to be minimised by differences in feeding strategies.

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1. Introduction

Feeding is one of the most important activities of fish. Antarctic fish live in an environment with seasonally variable light conditions, inducing changes in food resources during the year. In order to cope with this situation most Nototheniidae are catholic, and although most species are demersal in habit, they feed opportunistically on pelagic prey (EVERSON, 1984). Behavioural and morphological adaptations are related to different habitats and to preferable or available food (EKAU, 1991; FANTA, 1994; FANTA *et al.*, 1994; GRÖTZNER and FANTA, 1998; MEYER and FANTA, 1998; RIOS and FANTA, 1998).

Fish use a variety of mechanisms to assure the necessary food supply, generalists may switch prey types and feeding strategies (DANIELS, 1982; FANTA *et al.*, 1994). Thus, when fish of different species share the same environment, with the same food resources, diversification in their feeding strategies will minimise competition for the available food (FANTA *et al.*, 1994; GRÖTZNER and FANTA, 1998).

Therefore, the aim of this study was to observe the feeding strategies of six species of Nototheniidae that might possibly share food items such as fish, krill, and amphipods in Martel Inlet. Aquarium observations can greatly contribute to the understanding of some trophic relations among those organisms and will raise questions to be solved through field observations and morphological, physiological and behavioural studies in the laboratory.

2. Material and Methods

The following fishes were studied: *Notothenia coriiceps* RICHARDSON, 1844 ($n = 15$; 16.5–19.5 cm TL), *Notothenia neglecta* NYBELIN, 1951 ($n = 30$; 17.5–35.0 cm TL), *Trematomus bernacchii* BOULENGER, 1902 ($n = 15$; 25.0–25.5 cm TL), *Pagothenia borchgrevinki* (BOULENGER, 1902) ($n = 15$; 10.0–15.0 cm TL), *Lepidonotothen nudifrons* (LÖNNBERG, 1905) ($n = 30$; 11.3–15.5 cm TL), and *Pleuragramma antarcticum* BOULENGER, 1902 ($n = 30$; 6.5–7.5 cm TL). All specimens were identified according to FISHER and HUREAU (1985). Genera names of *Lepidonotothen nudifrons* and *Pagothenia borchgrevinki* were according to KOCK (1992).

For this study *N. neglecta* described by NYBELIN (1951) and recently considered to be *N. coriiceps* as described originally by RICHARDSON (1844) were not considered to be one single species belonging to different geographical regions (KOCK, 1992) but as two different species according to the characteristics considered by FISCHER and HUREAU (1985).

The following organisms were offered as food: fish such as *Gobionotothen gibberifrons* (9.0–17.0 cm TL), *L. nudifrons* (8.5–11.7 cm TL), *Trematomus newnesi* (8.0–15.0 cm TL), *N. neglecta* (5.0–15.0 cm TL), *P. antarcticum* (6.5–8.0 cm TL); krill *Euphausia superba* DANA (3.5–5.5 cm TL); and amphipods such as *Bovallia gigantea* PFEFFER, 1888 (0.4–0.8 cm TL), *Gondogeneia antarctica* (CHEVREUX, 1906) (0.5–1.3 cm TL) and *Waldeckia obesa* (CHEVREUX, 1905) (0.2–0.3 cm TL).

Fish were caught at Martel Inlet in Admiralty Bay, King George Island, during the Antarctic summer. All species were captured with gill nets, from 40 to 80 m depth, except for *P. antarcticum* and *L. nudifrons*, which were caught by mid water trawl. Small fishes, amphipods and krill were obtained with traps, mid water trawl and krill nets and used as prey. In a 0°C laboratory at the Brazilian Antarctic Station Comandante Ferraz, all species were maintained in separate tanks for acclimation.

Observations were made in 150×150×50 cm tanks, containing 1000 L of sea water. Soft upper light was provided at a constant photo period of 20 hours light and 4 hours darkness. The light intensity at the bottom of the tanks was kept between 9 and 15 lux during the light period. The pH of the water was maintained between 7.5 and 7.8, the salinity at 33 ppt and the temperature between 0 and 1°C.

Four test designs were used: 1) 5 individuals of each species were kept separately in the test tank and potential food items were offered separately; 2) 5 individuals of each species were kept separately in the test tank and potential food items such as 5 fish, 20 krill and 20 cm³ of amphipods were presented all together; 3) 3 individuals of all fish species were kept together and food items were offered separately; 4) 3 individuals of all fish species were kept together and potential food items were all together, continuously present in the tank.

For each predator at least 10 individuals were observed and for each individual at least 50 feeding actions were registered.

Detection and apprehension of food was observed and described for each individual of each species. Behaviour was observed directly behind protective shields and the feeding process was always observed and/or filmed until it came to an end.

3. Results

Each species had standard patterns in feeding behaviour, though individual variation was observed. All fish received fish, krill and amphipods as potential prey.

3.1. *Notothenia neglecta*

N. neglecta reposed most of the time at the bottom, often grouped. Approaching *N. neglecta* provoked frontal display reactions (slow mouth opening and raising of pectoral and dorsal fins in alert of both fish) of members of the group, but these actions were not followed by persecutions. Only 4.34% of the aggressive acts were performed against conspecifics.

N. neglecta preyed on fish, krill and amphipods.

Feeding always started from repose at the substrate, occurring preferably in the water column but also at the bottom.

In the water column, the strongest stimuli to initiate feeding behaviour were sudden sinusoidal swimming movements of potential fish prey, usually when small fish like *L. nudifrons* recognised *N. neglecta* as predators, reacting by fleeing at high speed. Escaping fish were persecuted for periods up to 5 min, with 92% success in capture. If persecuted fish swam to the bottom to rest close to other individuals of

the same species or to become part of multi-species groups they were no longer identified as prey and the persecutions ceased.

Active fish like *P. antarcticum*, swimming in the water column, stimulated *N. neglecta* to perform feeding behaviour. Success in capture was lower, around 75%, because *P. antarcticum* swam at high speed, escaping from the persistent but slower *N. neglecta*. When capture failed, *N. neglecta* returned to the bottom, ingesting some resting *G. gibberifrons*, *T. newnesi* or *L. nudifrons* and even small isolated *N. neglecta*, and so fulfilling the feeding action that had already started.

When preying at the bottom, *N. neglecta* performed a sudden fast swimming movement apprehending a prey located within an angle of 90° of the front direction, with 95% success.

Apprehensions of fish prey occurred from the head or, preferentially, from the tail and ingestions took from 2 s up to 2 min. When capturing fish by their lateral region, what happened rarely, after shaking the head, immobilising and releasing the prey, they were apprehended again by the tail or the head and ingested. After ingestion, chasing continued until satiation. Prey were usually ingested entirely but sometimes remained out of the mouth for up to 24 hours. In such cases, *N. neglecta* remained at rest and other individuals tried to remove the part of the prey that protruded from the mouth, sometimes succeeding in removing the whole prey.

Fish up to 1/2 of *N. neglecta* body length were ingested with success. If the prey size was 80% of the predator's size, stimulation and persecutions occurred but apprehensions were not possible.

The most sought fish prey were *L. nudifrons*, *G. gibberifrons* and *P. antarcticum*.

N. neglecta fed on krill with 100% success. It seemed easier to catch as it was

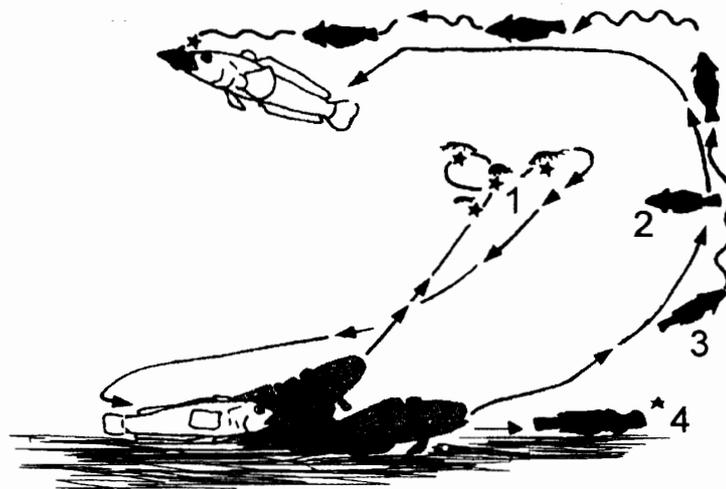


Fig. 1. Feeding movements of *N. neglecta*. 1: feeding on krill or amphipods and taking various prey during one feeding action; 2: resting prey in mid water does not stimulate feeding behaviour; 3: prey detects the predator *N. neglecta* and tries to escape being persecuted and finally ingested; 4: resting prey at the bottom weakly stimulates feeding behaviour but is sometimes captured when apprehension of other prey failed. Stars: apprehensions; black arrows indicate the direction of the movements of the predator; white arrows indicate the direction of the movements of the prey; prey are represented in black.

Table 1. Feeding patterns of the Nototheniidae fish *N. neglecta*, *N. coriiceps*, *T. bernacchii*, *P. borchgrevinki*, *L. nudifrons* and *P. antarcticum*. Food items are fish (F), krill (K) and amphipods (A). The numbers in the table indicate the sequence of actions for feeding. Repeated numbers mean that in the sequence of actions fish may choose between two or more options.

Species		<i>N. neglecta</i>					<i>N. coriiceps</i>							
Food		F		K	A	F			K		A			
FEEDING SEQUENCE	rest at bottom	1	1	1	1	1	1	1	1		1		1	
	rest at midwater													
	random swimming									1		1		1
	detection	2	2	2	2	2	2	2	2		2	2	2	2
	contact									2				
	alert													
	positioning						4		3					
	slow approach						3		4					
	attack	3	4	3	4	3	5	3	5	3	3	3	3	3
	persecution		3		3									
	apprehension	4		4	5	4	6	4		4	4	4	4	4
	failure		5	5					6	4				
	prey escapes			5					7					
	feed on other species			6										
	selection	5				5	7	5					5	5
	ingestion	6			6	6	8	6			5	5	6	6
	rejection	6			6	6	8	6					6	6
	continue feeding		6		7	7				5		6		7
return to rest position	7		7	7	7	9	7	8		6		7		
random swimming								8	6		6		7	
start feeding sequence	8		8	8	8	10	8	9		7		8		

Species		<i>T. bernacchii</i>			<i>P. borchgrevinki</i>			<i>L. nudifr.</i>		<i>P. antarcticum</i>			
Food		F	K	A	F	K	A	K	A	K		A	
FEEDING SEQUENCE	rest at bottom	1	1	1	1	1	1	1	1	1			
	rest at midwater										1	1	1
	random swimming										2		1
	detection	2	2	2	2	2	2	2	2	2	2	3	2
	contact												
	alert	3	3							3			
	positioning	4	4	3	3				3	4			
	slow approach	5	5		4								
	attack	6		4	5	5	3	3	3	3	5	3	4
	persecution		6							4			3
	apprehension	7		5	6	6	4		4	4	5	6	4
	failure		7		7		4	4					
	prey escapes				7			5				6	
	feed on other species		8					6					
	selection	8			7								5
	ingestion	9		6	8		5		5	5	6	7	5
	rejection	9			8								6
	continue feeding	10					5		6	6	7	8	6
return to rest position	10	9	7	9	8	6	5	7	6	6	7	6	
random swimming										8			
start feeding sequence	11	10	8	10	9	7		8	7	7	8	9	

slower than a fleeing fish, and therefore persecutions were shorter. During each feeding action several krill individuals were ingested before the fish returned to repose at the bottom.

Amphipods were ingested usually in the water column, but also at the bottom. They were taken mainly in the absence of fish or krill. Once satiation was reached *N. neglecta* followed the movements of amphipods with their eyes but did not perform any feeding action.

The movements for feeding are schematically represented in Fig. 1 and some feeding patterns in Table 1.

3.2. *Notothenia coriiceps*

N. coriiceps and *N. neglecta* are morphologically similar but their feeding behaviour was, in some aspects, different.

N. coriiceps remained resting at the bottom and also grouped and often mixed with *N. neglecta*. But when resting isolated, they established a territory mainly when in the presence of *N. neglecta* and *G. gibberifrons*, and displayed frontally mainly to *N. neglecta*. Aggressions in the water column were observed against *G. gibberifrons*.

They fed on fish, krill and amphipods, preferentially in mid water, starting from the resting position at the bottom but also from random swimming. They preyed also at the bottom.

When feeding started from the bottom, after detection of prey the first action was slow swimming and change of the body axis toward the prey, followed by a fast attack movement, capture of the prey and return by the same route to the resting position.

Often the typical feeding movements of other species, mainly *N. neglecta*, induced the beginning of random swimming and search for food by *N. coriiceps*. On the other hand, a group of fish swimming or motionless in the water column, as for example *P. antarcticum*, inhibited *N. coriiceps*' feeding activity. In such a situation they searched for food, mainly amphipods, only close to the substrate. When *N. coriiceps* were actively feeding in the water column, ingesting a sequence of prey in one feeding action, all other species stopped feeding, including *N. neglecta*.

N. coriiceps did not persecute prey. Therefore, even being attracted to fish prey the success of captures was low. This was probably one of the reasons for their preference for krill, which were slower than *N. coriiceps* and were easily caught.

Krill were immediately recognised as prey and the feeding success was 100% even if some individuals were apprehended and released two or three times before ingestion. After feeding on some krill they eventually ingested also amphipods. The intensity of feeding activity in the presence of krill showed that this was the preferential food of *N. coriiceps*. Even competition for food was observed when food was krill and when satiated, the mouth and the stomach replenished with food, they were still stimulated by the presence of krill. *N. coriiceps* even tried to catch them but had to abandon the action after noticing that there was no more space in the mouth for further ingestions.

Amphipods were immediately detected and sometimes apprehended and

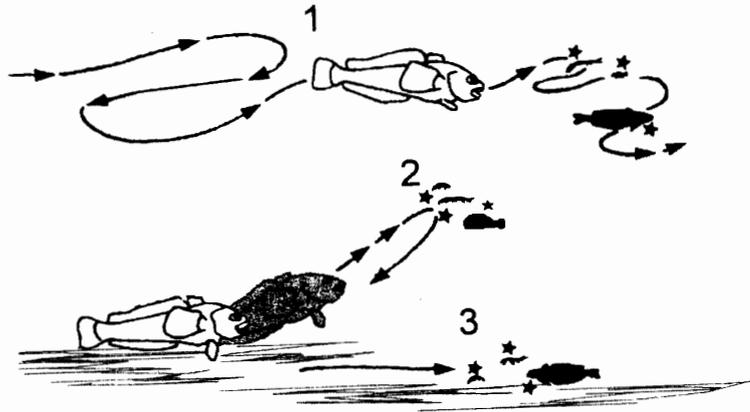


Fig. 2. Feeding movements of *N. coriiceps*. 1: feeding from random swimming for fish, krill or amphipods; 2: feeding in the water column, starting from resting at the bottom; 3: feeding at the bottom. Stars: apprehensions; arrows indicate the direction of the predator movements; prey are represented in black.

ingested, but only *G. antarctica*. *W. obesa* was 100% rejected. Many times they failed in apprehensions, biting wrongly or often performing up to 3 trials on the same prey. Thus, the feeding success was only 25%. Simultaneous feeding on krill and amphipods was not observed. However, after having captured krill, they ingested some amphipods.

A diagram of the feeding pattern and behaviour can be seen in Fig. 2, and different sequences of actions for feeding in Table 1.

3.3. *Trematomus bernacchii*

T. bernacchii rested most of the time at the bottom. Of all aggressive acts, 13.04% were against conspecifics and 56.52% against *N. neglecta*. *T. bernacchii* preyed on small fish, krill and amphipods.

Fish were detected by focusing on them with both eyes when they were inside the cone of binocular vision. The sequence of movements for feeding did not start immediately after detection but only as the fish to be preyed upon approached. Sometimes prey changed swimming direction and their movement was followed with one eye by *T. bernacchii*, then the prey was attacked from the side. Success was around 65%.

P. antarcticum were identified as prey by *T. bernacchii* because of their swimming movements. The feeding pattern started with slow swimming toward the prey in the water column, followed by body positioning and only then an attack. *P. antarcticum* are grouped like a swarm and as soon as the first attack occurred all fish dispersed in different directions and the *T. bernacchii* was then unable to capture any other individuals. During each feeding action, *T. bernacchii* did persecute up to 7 fish before returning to rest positions at the bottom, but success in capture was low (14.6%). When failure in apprehension occurred, *T. bernacchii* swam back to the original position at the bottom, apprehending a resting small individual to fulfill the feeding action that was already started. They never fed on resting fish at the bottom spontaneously.

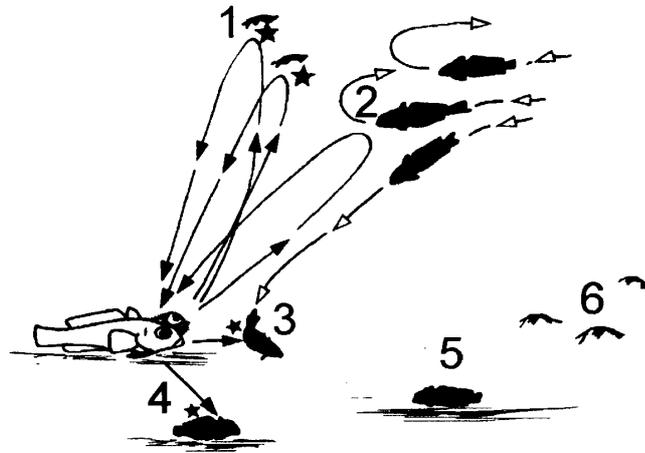


Fig. 3. Feeding movements of *T. bernacchii*. 1: feeding on krill in mid water, from resting, apprehending one individual during each feeding act; 2: trying apprehension of fish in a swarm; 3: trying to capture an approaching individual fish; 4: feeding on a fish at the bottom after a failure in apprehending a prey; 5: fish resting at the bottom and 6: krill, close to the bottom do not stimulate predators to feed. Amphipods are captured in the same regions as krill. Stars: apprehensions; arrows indicate the direction of movement of the predator; prey are represented in black.

When preying on krill, detection was immediate, followed by positioning of body axis and high speed swimming toward the prey. Ingestion was successful in 100% of the trials and the fish always returned to the former resting position at the bottom, starting from there for new captures.

T. bernacchii fed on Amphipods, but only on *G. antarctica* and *B. gigantea* in a proportion of 5 : 1. *W. obesa* were persecuted but apprehensions did not succeed.

When resting in alert for food detection, *T. bernacchii* moved the snares like two antennae, probably to optimise chemical prey detection. They also have independently moving eyes.

Movements for feeding are summarised in Fig. 3 and sequences of attitudes for feeding in Table 1.

3.4. *Pagothenia borchgrevinki*

P. borchgrevinki remained resting at the bottom for most the time. They preyed on fish, krill and amphipods.

Usually, motionless fish at the bottom or in the water column did not provoke a feeding reaction in *P. borchgrevinki*. They were only stimulated by fish swimming actively, like *P. antarcticum*. Several trials for capture were always made but were often not successful. After some failures they quickly ingested fish resting at the bottom, even those that were up to 60% of their total body length, like *N. neglecta*, *L. nudifrons*, *T. newnesi* or *G. gibberifrons*, to fulfill the feeding action. After a sequence of feeding actions, part of the last preyed fish could remain hanging out from the mouth of *P. borchgrevinki* for periods as long as 48 hours.

Feeding behaviour for krill and amphipods was voracious but always for very short periods. After an alert repose, attacks were certain and apprehensions had a success of 100%. One swimming action led to the intake of one or more prey. All

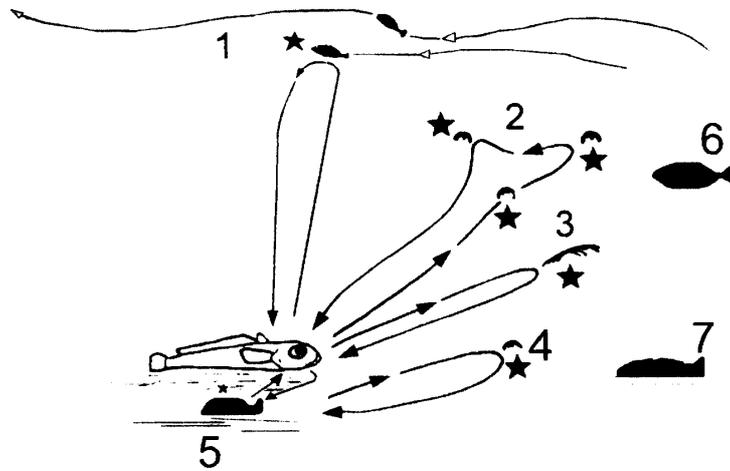


Fig. 4. Feeding movements of *P. borchgrevinki*. 1: trial to capture active fish, often without success; 2: capture of several krill and/or amphipods during one feeding act; 3: capture of one krill or 4: one amphipod during one feeding act; 5: feeding on a resting fish at the bottom after failure to capture fish in the water column; 6: resting fish in the water column or 7: close to the bottom do not stimulate predators to feed. Stars: apprehensions; black arrows indicate the direction of the movements of the predator; prey are represented in black; white arrows indicate the direction of the movements of the prey.

captures were in the lower or higher water column. As their eyes are laterally positioned, prey coming from behind were detected, followed with one of the eyes before the attack.

The typical movements for feeding are in Fig. 4 and the sequences of actions for feeding are summarised in Table 1.

3.5. *Lepidonotothen nudifrons*

L. nudifrons rested at the bottom. They seem to have a wide vision field, improved by the eyes' movements upwards, toward the frontal region or backward, when in alert. Their feeding behaviour changed not only with the type of prey but also when in the presence of conspecifics, when alone or in the presence of *T. newnesi*, *T. bernacchii*, *N. neglecta* or *N. coriiceps*. These species were always recognised by *L. nudifrons* as potential predators. The first reaction was paleness, and they remained at rest in a shelter. Several tried to escape, swimming toward the water column. Their fast swimming movements immediately provoked an alert reaction of the predators, and *L. nudifrons* were often captured. On the other hand when resting grouped, side by side with conspecifics or other species, mainly *G. gibberifrons* and *T. newnesi*, they became protected against their predators.

L. nudifrons did not show aggressiveness against conspecifics. Often they remained resting and moving their eyes, looking in alert to each other, without undertaking any action. *L. nudifrons* remained in shelters when with conspecifics, leaving the repose place for feeding. As soon as prey were detected the first reaction was to open the mouth, as for biting, before any swimming action started.

They fed on amphipods and krill.

Amphipods were chosen by size, and mainly small individuals were ingested. When amphipods were introduced into the aquarium the movements of the prey

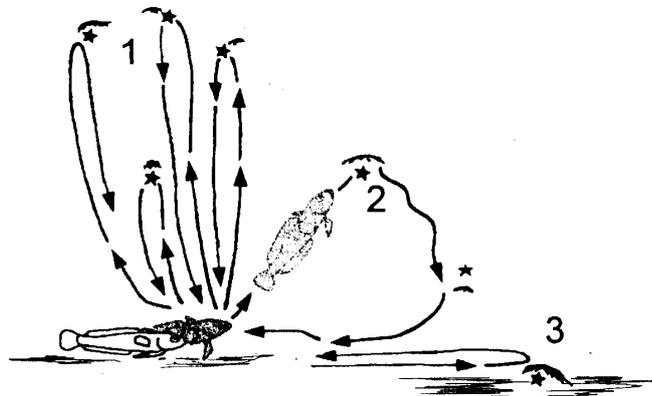


Fig. 5. Feeding movements of *L. nudifrons*. 1: feeding on krill and/or amphipods high in the water column; 2: chasing and apprehending krill; 3: feeding on krill and amphipods close to the bottom. Stars: apprehensions; arrows indicate the direction of the movements of the predator; prey are represented in black.

were followed with eyes or head movements of *L. nudifrons* before the feeding action started. Amphipods arriving from behind the fish were detected, but capture only took place when they reached the binocular vision cone in front of the fish.

In the presence of krill, however, chasing actions were undertaken, apprehensions and ingestions being immediate, always in the water column, rarely close to the bottom. Feeding success for krill was 100%.

The typical movements for feeding are in Fig. 5 and the sequences of actions for feeding are summarised in Table 1.

3.6. *Pleuragramma antarcticum*

P. antarcticum established no contact with the bottom, being pelagic, swimming and resting only in the water column, and remaining mostly grouped as a swarm. They were initially studied as prey, but as they are predators of krill and amphipods, both food items tested for other fish, their feeding behaviour was also observed.

Different feeding patterns could be used by these fish, starting from swimming or from repose.

P. antarcticum recognised the presence of potential benthic predators like *P. borchgrevinki*, *N. neglecta*, *N. coriiceps* or *T. bernacchii* what induced a higher level of swimming activity. They also became very active as soon as their prey, amphipods and krill, were present in the water.

They were stimulated by the presence of krill, but apprehensions and ingestions were successful for krill as small as half their body length. Even so, they tried to catch krill of their own size. In such cases the apprehended krill individuals were strong enough to pull *P. antarcticum*, swimming in spiral movements, until being released.

Success in feeding amphipods was 100%. They were not attracted by *B. gigantea*, but chased *G. antarctica*. Small *W. obesa* were apprehended but rejected quickly and bigger *W. obesa* were not identified as prey.

The typical movements for feeding are in Fig. 6 and the sequences of feeding

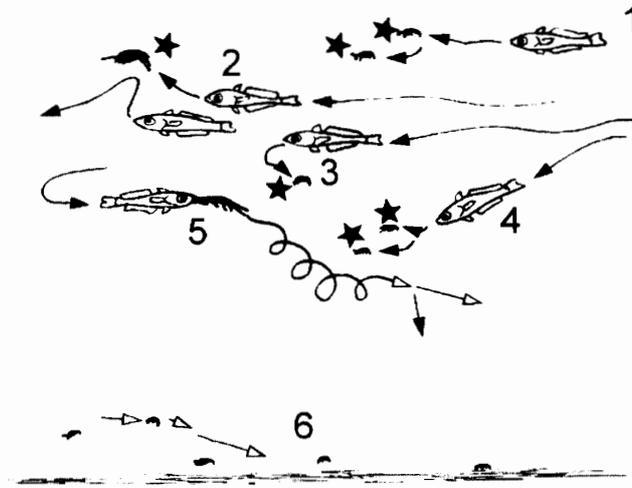


Fig. 6. Feeding movements of *P. antarcticum*. 1. Ingesting various krill individuals during random swimming; 2. persecuting krill and competing for food; 3: ingesting one amphipod during one feeding action; 4: ingesting various amphipods during one feeding action; 5: feeding on too big krill that has to be released; 6: amphipods or krill close to the bottom do not stimulate predators to feed. Stars: apprehensions; arrows indicate the direction of movements of the predator; white arrows indicate movements of prey; prey are represented in black.

attitudes are summarised in Table 1.

4. Discussion

In Admiralty Bay, a fjord of King George Island (South Shetlands), fishes belong to the Antarctic coastal fauna that inhabit shelves of islands of the Scotia Arch (KOCK, 1992; RAKUSA-SUSZCZEWSKI, 1993). Admiralty Bay has some ecological niches in the coastal ecosystem of the bay where 11 fish families with 39 species were identified (SKÓRA, 1993). In places like Martel Inlet, different Nototheniidae species like *N. neglecta*, *N. coriiceps*, *T. newnesi*, *L. nudifrons*, *G. gibberifrons*, *P. antarcticum*, *P. borchgrevinki*, *T. bernacchii*, besides the Channichthidae *Chaenocephalus aceratus* and the Harpagiferidae *Harpagifer antarcticus* (personal observations), share the environment and potential food items, facing inter and intraspecific competition for resting places and feeding grounds. They inhabit areas with or without algae, on a muddy or sandy muddy bottom, at depths that vary from the surface down to 80 m.

Species assemblages are found in many places in Antarctica, as for example in other regions of Admiralty Bay like McKellar Inlet where *Notothenia rossi* and *Trematomus newnesi* and the Bathyrachonidae *Parachaenichthis charcoti* are mainly associated with algae banks (our own observations), or in some areas of the Weddell Sea shallow shelf, or in the higher Antarctic Zone, associated with drifting ice or even under the permanent ice shelf (KOCK, 1992).

The herein studied species *N. coriiceps*, *N. neglecta*, *L. nudifrons*, *T. newnesi*, *P. borchgrevinki* and *P. antarcticum* were chosen for the tests because they were caught in the same area of Admiralty Bay. In the natural environment they might occupy

different niches in the same geographical area, but in any case they ingest the same group of prey.

Fish tests have been conducted before on Antarctic fish (FANTA, 1994; FANTA *et al.*, 1989a, b, 1994, 1995; GRÖTZNER and FANTA, 1998; MEYER and FANTA, 1998; RIOS and FANTA, 1998), and are useful to simulate in tanks, under controlled environmental conditions, situations that fish could face in the natural environment. Besides controlled environmental conditions like salinity, temperature, oxygen levels and photoperiod, the same food items were presented to all species in order to minimise the number of variables.

It is noticed that in the Bay, different fish are always captured in restricted areas and not spread equally throughout all regions. Thus, even considering that the available area for food search and capture as well as for escaping is smaller in a tank than in the natural environment, the relation among the individuals could be observed, helping to interpret some aspects of the community in nature.

The feeding behaviour of fish is related to multiple factors such as food availability, food preference, presence of other species, density of population, the morphofunctional capacity of food detection, ingestion and digestion, among many others (FANTA *et al.*, 1994; RIOS and FANTA, 1998) and coastal fish species are known to have a catholic diet (EVERSON, 1984).

The daily consumption rates of fish are small, about 2% of the body weight in plankton and benthos feeders and 3 to 4% in predators and euryphages (PAKHO-MOV and TSERTLIN, 1993). Therefore it is observed that the proportion of time in feeding activity is short. This was also observed for *T. newnesi* and *G. gibberifrons* (FANTA *et al.*, 1994). The proportional shortness of feeding activity is probably related to the sufficient amount of available food, a situation that was presented to all fish in this study. Normally, after satiation, they did not react any more to the presence of food. Even so, it was observed that *P. borchgrevinki* and *N. neglecta* still react to the presence of prey even when unable to ingest them because they are full.

Notothenioids generally move at low speed, using labrifrom swimming. High-powered tail fin propulsion or subcarangiform swimming is only of short duration and is reserved to capture prey or to avoid predators (MONTGOMERY and MACDONALD, 1984; JOHNSTON, 1989). Even at maximum speed *P. borchgrevinki* are slower than tropical fish, and escape responses are rarely sustained for more than 3 or 4 tail-beat cycles (MONTGOMERY and MACDONALD, 1984). It was observed that even when feeding on preferential food like krill and amphipods, the intense swimming action was always for a very short period. As was seen, some species such as *T. bernacchii* show two phases, slow swimming and fast swimming for feeding. Others like *N. neglecta* perform only fast swimming and *G. gibberifrons* (FANTA *et al.*, 1994) only slow swimming. Subcarangiform swimming is also used for persecutions and escape, and signalling to other fish in the area that a predator is feeding, eliciting a generalised feeding activity and prey to hide or escape (MONTGOMERY and MACDONALD, 1984). So, it was observed that as a consequence of the activity of *N. neglecta*, *N. coriiceps* were stimulated and started to search for food, and on the other hand, their prey such as *L. nudifrons* tried to hide or escape, as well as *P. antarcticum* that increased swimming activity in order to

escape.

Size selective predation is suggested by ELLIS and GIBSON (1995) and by RIOS and FANTA (1998). But, we could observe that fish can also be attracted to prey that are beyond their capacity to ingest. So, *P. antarcticum* chased and apprehended adult krill but was not able to ingest them. *N. neglecta* on the other hand tried to capture fish that were bigger than 2/3 of their own size without success.

Movement, shape, colour and taste of potential prey are also of great importance. So, *P. antarcticum* apprehended the amphipod *Waldeckia obesa*, but rejected it as soon as it was tasted inside the mouth. A similar act by *T. newnesi* was also observed; it apprehended but rejected the same amphipod (MEYER and FANTA, 1998). Also *G. gibberifrons* captured very small *N. neglecta* but rejected them immediately after apprehension (our own observation).

The identification of food often takes place after visual stimulation, mainly caused by movements of the prey. Strategies may vary, as *N. neglecta* may follow a prey for a long time but *N. coriiceps* were never observed to persecute prey.

Failure of visual detection may occur and prey are often not taken or even the wrong organisms are apprehended then rejected after touching the lips or the inside of the mouth (GRÖTZNER and FANTA, 1998; MEYER and FANTA, 1998). Certainly, an aquarium without cover for prey simplifies detection and location of prey (FANTA *et al.*, 1994). When shelters were provided by algae or stones, some fish like *T. newnesi*, *N. neglecta*, *L. nudifrons* and *Harpagifer antarcticus* acted mainly as ambush feeders (FANTA and GRÖTZNER, in preparation; FANTA and FREIBERGER, in preparation).

Based on morphological criteria, EKAU (1991) established the position of fish between pelagic and demersal. So, *P. borchgrevinki* is considered the less demersal and the most pelagic, being zooplanktivorous (EKAU, 1991; FOSTER *et al.*, 1987). But it was observed that *P. borchgrevinki* fed also on fish if they were available, showing even overfeeding. Ingestion of *P. antarcticum* was reported in McMurdo Sound (EASTMAN, 1985). It seems that this species is ecologically plastic, the components of the diet varying with water depth (EASTMAN, 1993). *P. borchgrevinki* fed also at the bottom, where they rested most of the time. *T. bernacchii* is considered to be the more active swimmer and feeding seems to be directed upward. They prey on benthic animals and are attracted by amphipods (EKAU, 1988, 1991) but feed also on pelagic euphausiids (MORENO, 1980). It was noticed here that higher feeding activity occurred in the water column and only sporadically at the bottom. While feeding they were active swimmers but most of the time they rested at the bottom. *P. antarcticum* is considered pelagic and migratory (EKAU, 1991), eating euphausiids and amphipods but also small pelagic fish (LINKOWSKI *et al.*, 1983; EASTMAN, 1993). In this study they fed on krill and amphipods, but were selective as they rejected *W. obesa* and were not attracted to *Bovalia gigantea*.

W. obesa was also rejected by *N. coriiceps* and by the amphipod feeder *T. newnesi* (MEYER and FANTA, 1998), and not caught by *T. bernacchii*.

L. nudifrons stomach content indicates preferential feeding of amphipods, some fish showing a diversified diet in Admiralty Bay (LINKOWSKI *et al.*, 1983) but here they fed also on krill when available.

Differences in feeding strategy seem to be more important than rhythms of activity to minimise mutual interference as was seen in *G. gibberifrons* and *T. newnesi* (FANTA *et al.*, 1994).

Behavioural types for feeding were described (KEENLEYSIDE, 1979; GEHRKE, 1988) as basal behaviour, orientation, positioning, attack and ingestion. Basically all fish perform this way but differences were observed according to the habitat, to the prey to be ingested, to the presence of other individuals or of other species. Some species use completely different tactics depending on the situation, as *G. gibberifrons* for example (FANTA *et al.*, 1994) and also *N. coriiceps*, *N. neglecta*, *L. nudifrons* and *T. bernacchii*. Slight variations of the basic pattern were observed for *P. antarcticum* and *P. borchgrevinki*.

Nototheniids use variations of four basic feeding behaviours: ambush feeding, bottom slurping, grazing and water column feeding (DANIELS, 1982), adapting to a variety of benthic subhabitats (ROBERTS, 1982). It has been observed that, with the exception of *P. antarcticum*, all other species herein studied fed on both, the water column and the bottom, if necessary.

Water column feeding is characteristic of not only the pelagic *P. antarcticum* and *P. borchgrevinki*, that show specialisation for life in the water column (EASTMAN and DEVRIES, 1985), but also of many Nototheniids which exhibit regular vertical migrations to take advantage of the locally and seasonally abundant prey in the water column, such as krill or *P. antarcticum*.

According to DANIELS (1982) ambush feeding is probably the strategy most frequently utilised by fish feeding on the bottom; *T. bernacchii*, *N. coriiceps* and *G. gibberifrons*, for example, perch among the rocks or wait motionless for prey organisms to approach. This was also observed for other Nototheniids like *N. neglecta* (RIOS and FANTA, 1998) and *T. newnesi* (MEYER and FANTA, 1998) and the Harpagiferidae *Harpagifer antarcticus* (FANTA *et al.*, in preparation).

Although necrophagy has been described as locally common among Nototheniids (ARNAUD, 1970), many species have been observed by diving and in aquaria, to take only moving organisms, ignoring readily visible but stationary prey organisms (DANIELS, 1982; HUBOLD, 1991). This was also observed for *T. bernacchii* and *P. borchgrevinki*. *P. borchgrevinki* can even recognise low frequency vibrations emitted by crustacean limb movement with their lateral line system (MONTGOMERY and MACDONALD, 1984). Others, like *N. neglecta*, *N. coriiceps*, take mainly moving organisms, but also resting ones. Some fish such as *N. neglecta* can even recognise the prey chemically, without visual or mechanical stimulation (FANTA *et al.*, in preparation), *T. newnesi* (MEYER and FANTA, 1998; FANTA and DONATTI, submitted for publication) or the Zoarcidae *Ophthalmolycus concolor* (FANTA *et al.*, submitted for publication), which may become important in low light conditions (FOSTER *et al.*, 1987).

Territory maintenance or defence can be seen in *L. nudifrons* (HOURIGAN and RADTKE, 1989) and *T. bernacchii* (MORENO, 1980), which also show parental care. In the tanks, neither of these species established a territory, but *N. coriiceps* did, in certain circumstances.

According to FISCHER and HUREAU (1985) and based on stomach content

analysis the feeding habits of some Nototheniidae were established. The segregation of fish according to their diet into five categories (KOCK, 1992) seems to be certain for several species but not for all of the Nototheniids: *L. nudifrons* feeds on small benthic invertebrates and together with *G. gibberifrons* are considered benthos feeders (KOCK, 1992), but may also feed on plankton or organisms in the water column; *T. bernacchii* feed on polychaets, gastropods, isopods, amphipods and a few algae; *P. borchgrevinki* on copepods, young krill and macrozooplankton (FOSTER *et al.*, 1987; MONTGOMERY *et al.*, 1989); *N. neglecta* and *P. antarcticum* on small pelagic organisms, krill and other euphausiids, copepods and post larval fish; *P. antarcticum* and *P. borchgrevinki* are considered plankton feeders but the last one named can feed also on fish and, eventually, at the bottom. They all belong to nearshore feeding communities (HUREAU, 1994), where resource partitioning seems to be the rule (KOCK, 1992).

However, it was observed that, even feeding mostly on certain food items in the natural environment, fish might have other preferences or choices once different food items are available and depending on the existing concurrence for food.

Not only the choice of food items but also a high variability of strategies for feeding, depending on the type of food, was observed for some species like *N. coriiceps* and *N. neglecta*.

In this study, *N. coriiceps* and *N. neglecta* were considered as two different species, as it was possible to distinguish them slightly morphologically, using the data presented in FISCHER and HUREAU (1985), in spite of the great morphological variability of *N. neglecta*. They also performed slightly different feeding behaviour and apparently preferred different food items when maintained under identical conditions. On the other hand they occurred at the same depth and region in Admiralty Bay, being caught in the same nets. If they were only one species with variations caused by geographical distance, it will be necessary to investigate more deeply, at molecular biology level, many individuals that are identified as *N. neglecta* and/or *N. coriiceps* in Admiralty Bay, in order to clarify whether they are the same species or not.

If they are not two valid species but different populations of one single species, specifically *N. coriiceps* (EVERSON, 1969; KOCK, 1992), the variability in strategies and food preferences is even higher. This might be useful to the species, increasing their adaptability to the varied food supply available during the year, multiplying their survival chances.

KOCK (1992) considered *N. coriiceps* a coastal nearshore species, *N. gibberifrons* and *L. nudifrons* oceanic, and *T. newnesi* high Antarctic. But they occur in the same geographical area of Admiralty Bay, at least during the summer. In this area, they might choose different niches and hiding places, as well as substrates or depths.

One can conclude from this study that the species herein observed interact if kept in a relatively small area, but avoid excessive interference in their feeding activities by adapting feeding behaviour and patterns to the local and momentary composition of the community. This flexibility in the choice of strategies and ingestion of available food, within limits, increases their possibilities of survival in the highly variable Antarctic environment.

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