

# Aspects of the ecology of two nototheniid fish species in the inshore zone of the sub-Antarctic Marion Island

O Gon

J L B Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140

D Mostert

Department of Zoology, University of Stellenbosch, Stellenbosch 7600

*The nototheniid species Notothenia coriiceps and Paranotothenia magellanica are able to coexist in the inshore zone of Marion Island by way of resource partitioning along the axes of spatial distribution, substrate, occurrence of life history stages, diel activity and diet. N. coriiceps was very scarce and the few specimens sampled were all adult fish four to six years old (determined from scales). P. magellanica was much more abundant and its population was composed of immature fish one to three years old. Resource partitioning also forms the spatial distribution within the latter species. Fingerlings transforming to benthic life were the highest off the bottom and were loosely associated with Desmarestia. Juveniles were found on red algae between and under bushes of Desmarestia on the upper half of boulders, or inside masses of detached algal fronds. Sub-adults were found on the bottom, near or under large boulders.*

*Deur die gesamentlike hulpbronbenutting deur middel van onder andere ruimtelike verspreiding, verskillende substraatgebruik, voorkoms van verskillende stadia in die lewensiklus, daaglikse aktiwiteit en dieët is die nototheniidae-spesies, Notothenia coriiceps en Paranotothenia magellanica in staat om saam te leef in die kussone om Marion-eiland. N. coriiceps was baie skaars en die klein hoeveelheid monsters wat versamel is, was almal volwasse vis met ouderdomme wat wissel van vier tot ses jaar (bepaal deur skublesings). P. magellanica was volopper en het bestaan uit onvolwasse vis, een tot drie jaar oud. Hulpbronverdeling was verantwoordelik vir die ruimtelike verspreiding binne laasgenoemde spesies. Vingerlinge, wat na 'n bentiese leefwyse oorgeskakel het, is hoofsaaklik met die bodem en die alge Desmarestia geassosieer. Jong visse het voorgekom op rooi-alge tussen en onder bosvormige Desmarestia op die boonste helfte van rotse. Hulle het ook voorgekom binne los blare van alge. Onvolwasse visse is gevind op die seabodem, onder of naby groot rotse.*

## Introduction

The islands of Marion and Prince Edward are situated in the West Wind Drift of the South Indian Ocean (46°45' S, 37°55' E), close to two major oceanic frontal systems: the Antarctic Polar Front and the sub-Antarctic Front (Lutjeharms & Valentine 1984). The islands are of volcanic origin and are estimated to be 0.25 to 0.50

million years old (McDougal 1971).

The 72 km long coastline of Marion Island is dominated by vertical cliffs, up to 30 m in height, frequently interrupted by (usually) short stretches of boulder beaches. Depending on their size, the boulders form various beach types, from stoney beaches to large boulder beaches with rocks of several meters in diameter (De Villiers 1976). With the exception of Ship's Cove (see below), there are no sheltered bays or beaches on the island. The island is exposed to strong winds, usually from the west, that reach gale force speeds on more than 100 days a year. The oval shape of the island refracts the waves in such a way that the north and south coasts also receive heavy swell. Therefore, most of the coastline is exposed to powerful surf and wave action.

The fish fauna of the Prince Edward Islands consists of 33 species of which 20 species are benthic (Gon & Klages 1988). Most of the benthic species occur beyond the *Macrocystis* forest, a 50 to 100 m wide zone of giant kelp at about 50 m offshore, in water deeper than 50 m. A photographic survey of the benthic invertebrates of the shelf (depth range 50 to 500 m) between the two islands (Branch *et al* 1992) implies that most of the fish biomass is likely to be found at 100 to 250 m depth. Three species inhabit the inshore zone, i.e. the sea area between the shore and the *Macrocystis* forest. They are *Paranotothenia magellanica* (Foster in Bloch & Schneider 1801), *Notothenia coriiceps* (Richardson 1844) and *Harpagifer georgianus* (Nybelin 1947). The first two species are probably the largest of the species found around the islands and were the subject of this study.

*P. magellanica* is distributed in the sub-Antarctic region of the Southern Ocean, from South America through the Indian Ocean to the south islands of New Zealand. Several catches of pelagic fingerlings were reported from south of the Antarctic Polar Front (DeWitt *et al* 1990). However, Balushkin (1990) related these to his new species, *P. dewitti*. Around Marion Island, *P. magellanica* is the most abundant inshore species and thus plays an important role in the ecology of this zone (Gon & Klages 1988). Little is known on the biology of this species. Hureau (1970) studied aspects of its growth, food habits and reproduction in the Kerguelen Islands; Moreno & Jara (1984) investigated aspects of spatial distribution, abundance and diet in the Fuegian Islands, Chile; and in Marion Island, Blankley (1982) studied the food habits of this species. *P. magellanica* is preyed on by imperial cormorants (Blankley 1981, Espitalier-Noël *et al* 1988) and

penguins (Brothers 1985, Brown & Klages 1987, Williams 1988).

*N. coriiceps* is a widely distributed species known from the Scotia Sea Islands, the Antarctic Peninsula, several localities on the Antarctic continent, and the sub-Antarctic islands of the Southern Ocean (DeWitt *et al* 1990). It had been the subject of several studies, in South Georgia (White *et al* 1982, Burchett *et al* 1983), South Orkneys (Everson 1970a, b) and Adelie Land (Hureau 1970), including its early life history, growth, reproduction, diet, behaviour and ecology. The study of the diet of this species in Marion Island (Blankley 1982) is the only published work on the biology of *N. coriiceps* in the sub-Antarctic region.

## Material and methods

The study was conducted during three visits to Marion Island in winter and late summer/autumn 1988/1989. The behaviour of the fish was observed in a series of 15 scuba dives from the shore to the kelp zone during day and night. Diving with hand nets proved to be the most efficient way of collecting specimens, but several were also collected by gill nets. The sea around and between the islands was surveyed for larvae and pelagic fingerlings during summer and winter visits. Sampling below the surface to about 30 m depth was done using an RMT 2 net; a neuston net was employed for fishing between 0 to 1 m. The samples used in the study of age, growth and reproduction included eight specimens of *Notothenia coriiceps* and 48 specimens of *Paranotothenia magellanica*.

The age of both species was determined from scales.

Scales were removed from the left mid-body area about two to three rows below the lateral line, and from above the anal-fin base of fresh as well as preserved specimens. The scales were immersed for two to six hours (depending on size) in a 10% solution of a commercial dishwashing detergent. After removing the remaining epidermal tissue they were mounted between glass slides and dried. Generally, scales taken from above anal-fin base were easier to read.

Otoliths were used to determine the relationship of otolith to body size in *P. magellanica*. Otolith length was measured between the antirostrum and the posteroventral margin of the otolith using an ocular graticule. Graticule units were converted to millimetres for data analysis. Data analysis was performed on the Rhodes University mainframe computer using BMDP Statistical Software (PAR — derivative-free nonlinear regression).

Gonads were removed from several specimens of each species and fixed in formalin. Small blocks of tissue from these organs were then embedded in parafin wax, sectioned, and stained with hematoxylin/eosin. The gonad state of development was assessed using the schemes of Yamamoto (1956), Davis (1977) and Dipper & Pullin (1979).

## Results

### The study area

The inshore zone of Marion Island is defined as the sea area between the shore and the *Macrocystis* forest. Two study sites were selected on the north-east side of the island where sea conditions are favourable compared with



Fig 1: Marion Island coastline showing the position of the study sites, Transvaal Cove and Ship's Cove (modified from De Villiers 1976)

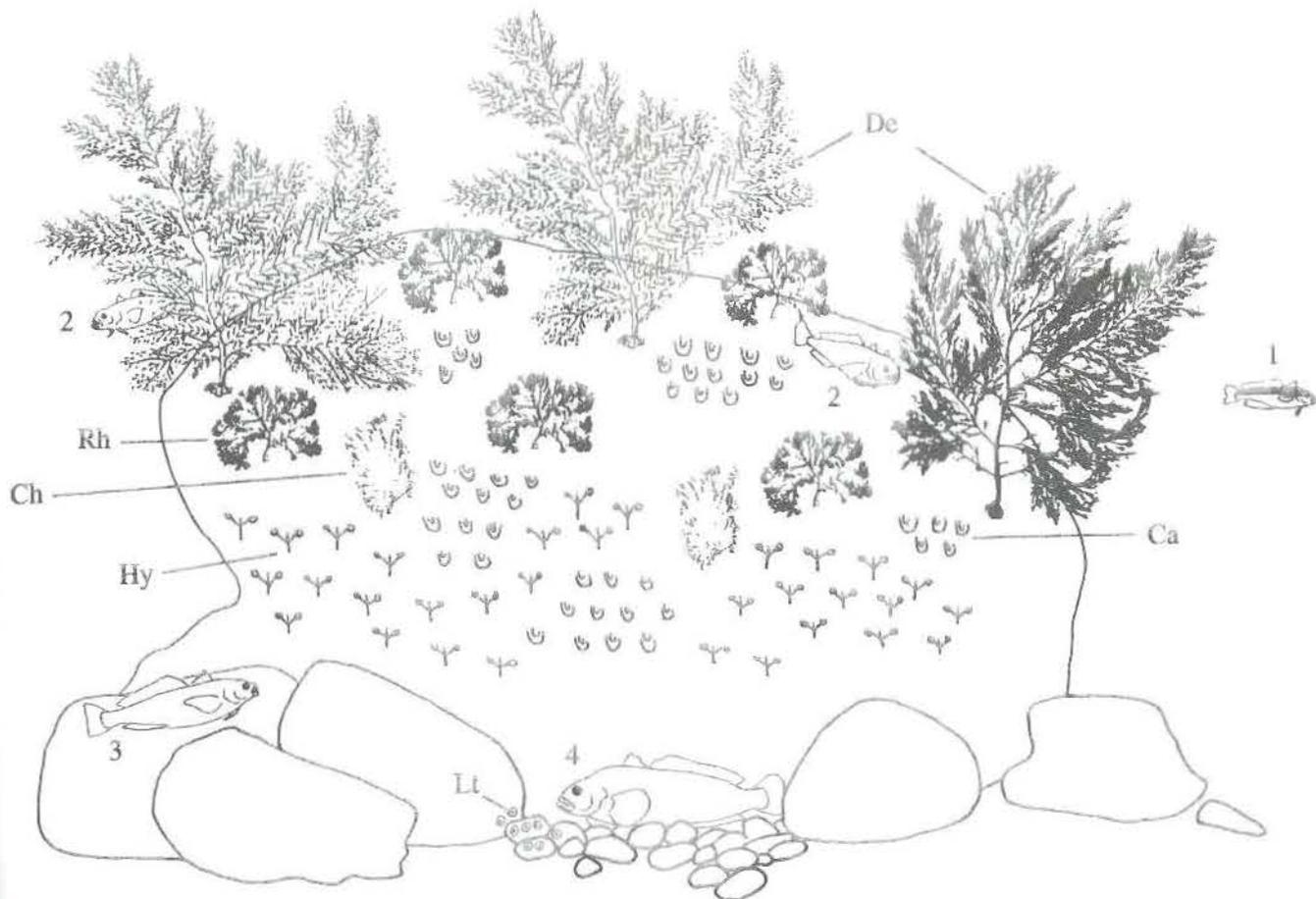


Fig 2: Diagrammatic representation of the rocky substrate of the inshore zone of Marion Island, its nototheniid fishes, and the dominant taxa that cover large boulders at 3 to 6 m depth. *P. magellanica*: (1) transforming fingerling; (2) benthic juvenile; (3) benthic sub-adult. *N. coriiceps*: (4) adult. Ca — coralline algae; CH — Chlorophyta; De — *Desmarestia* spp.; Hy — hydrozoans; Lt — limpets; Rh — Rhodophyta

the rest of the island's coastline. The sites (Fig 1), selected to represent the extremes of the habitat range of the inshore zone, were:

**Transvaal Cove** — A boulder beach, about 50 m long, located directly below the island's research station. The exposed boulders of the littoral zone are about 70 cm in diameter, becoming larger in the sublittoral zone and reaching 1 to 3 m size at a depth of 3 to 6 m. In the sublittoral zone, the boulders between the shore and the *Macrocystis* forest are covered with a variety of algae, dominated by corallines, several rhodophyte species and large and bushy *Desmarestia*, as well as hydrozoans. The coverage of a typical boulder at a depth of about 4 to 5 m is shown in Fig 2. The varied size and shape of the rocks give rise to a diverse habitat rich with benthos.

**Ship's Cove** — Situated about 2.5 km north-west of Transvaal Cove, this site has the only sandy beach on Marion Island. At times, storms erode the sand, exposing the underlying rock. Ship's Cove is an embayment surrounded by high, vertical cliffs. The sandy section of the beach is composed of a short stretch of fine, black sand that gradually changes to a pale yellow sand offshore. On each side the sand is flanked by a small area of large boulders extending into the water no farther than the breaker zone or to about 6 m depth. Owing to the lack of hard substrate in a suitable depth, there are only a few *Macrocystis* plants in Ship's Cove. This site constitutes a more uniform habitat than Transvaal Cove, with

much less abundance, and probably lower diversity, of marine life.

### Ecology

*Notothenia coriiceps* — Six large (> 300 mm SL) specimens were sighted under water. Of these, five were observed and collected in Ship's Cove. No larvae or pelagic fingerlings were found in the RMT 2 survey around the islands.

All sightings were during daylight hours of single fishes and in shallow water, 2 to 6 m depth. None were seen within the *Macrocystis* forest. A search of the immediate area around a sighting point failed to reveal other individuals. The fishes were always resting motionless on the rocky (small rocks, usually less than 50 cm in diameter) bottom, near a large boulder or under a ledge, and their colour was similar to that of the substrate, i.e. dark grey or black. They were usually exposed and near concentrations of the limpet *Nacella delesserti* on which they feed.

The fish did not react to the presence of divers around them, unless approached in a threatening manner, indicating strong affinity to the substrate. Indeed, even when chased these fishes do not rise more than a few centimetres off the bottom. They are poor swimmers and move short distances before settling down again, or will dive under the nearest rock that offers adequate protection. No fishes were seen on the sandy bottom or in al-

gal debris, even though both were sometimes only a few metres away.

The five captured fishes were kept alive for several days. All regurgitated their stomach contents that contained only whole, or partially digested limpets, a major food item in the diet of this species at Marion Island (Blankley 1982). The limpets are often found in clusters of individuals irregularly piled one on top of another. In such clumps the top individuals apparently do not develop full suction and are therefore an easy prey that does not require the fish to develop special means to detach them from the substrate.

*Paranotothenia magellanica* — Fishes of this species were sighted at 4 to 12 m depth. A great difference in abundance between day and night has been found. During daylight fish were observed in or near refuges and were very alert. In several day dives not a single fish has been sighted. At night, on the other hand, they were out in the open, slow to react, and many were sighted on each dive.

The inshore habitat is shared by a number of size-classes representing several life-history stages of *P. magellanica*. A distinct habitat partitioning was apparent between the various size-classes in terms of the space utilised and association with the substrate (Fig 2). Fingerlings (about 50 to 70 mm SL) were observed hovering in the open about 1 m off the algae. If approached, they would dive head first into the bushy growth, but would emerge a short while later. The colour of this size group (dark brown on the back and silvery on the lower half of the body) and their emarginate caudal fin indicate that they were in the process of transforming from pelagic to benthic life. Fishes fully transformed to benthic life have truncate caudal fins. Juveniles (70 to 150 mm SL) were more closely associated with *Desmarestia* and the rhodophyte species that cover the rock surface between and under the large bushes of the former algae (Fig 2). They were always within the algal cover, usually on the

upper half of boulders, either perching on their pelvic fins, or darting from one perching post to another or browsing on algae. These fishes had a similar colour to the algae in which they were living, i.e. either scarlet red or reddish dark brown, with some silver on the abdomen, the upper pectoral-fin base and along the dorsal-fin base. Several individuals of the larger end of this size group were associated with large masses of broken fronds of *Durvillaea* or *Macrocystis* found on the bottom. These fishes were brownish green in colour, similar to the kelp they inhabited.

Sub-adults (> 150 mm SL) were seen only at night on the rocky bottom, on boulders and on rocks with little or no algal growth. During daylight hours they are probably hiding under rocks and boulders.

#### Age determination, growth and reproduction

*Notothenia coriiceps* — Age was estimated from the scales (Fig 3) of eight specimens, including three from previous collections in Transvaal Cove. These fishes were found to be four to six years old (275 to 398 mm SL). Males apparently grow more slowly and hence are smaller than females. A six-year-old male measured about 300 mm SL whereas a female of the same age was about 350 mm SL.



Fig 3: Scale of a six-year-old male *N. coriiceps*

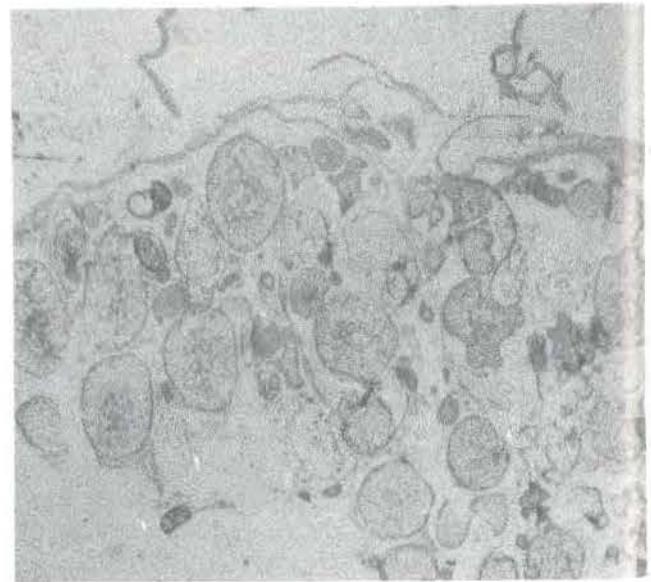


Fig 4: Ripening ovary of *N. coriiceps* with ova at an advanced state of vitellogenesis

Seven of the specimens were sexed and the sample was found to include two males and five females. Oocytes in the ovaries of the females were in various stages of vitellogenesis (Fig 4), indicating that all were adults. One male and one female collected in May had ripe gonads. The ova in the females' (357 mm SL) ovary were about 1.7 mm in diameter (preserved), loose and ready for spawning. Females collected in September had no ripe ova.

*Paranotothenia magellanica* — The age estimate for the inshore specimens of *P. magellanica* was one to three years old ( $n = 30$ ; 72 to 295 mm SL). In 1989, August and September were the coldest months of the year, with mean temperatures of 4.2 and 4.0 °C, respectively. Scales



**Fig 5:** Scale of a juvenile *P. magellanica* collected in September, showing the winter growth zone at the edge of the scale

taken from fish collected during this period all showed a distinct band of narrowly spaced sclerites on the outer edge (Fig 5), thus establishing that such a band represents a winter growth period. On the other hand, scales of fishes collected during April 1989 (monthly mean temperature 5.9 °C) had widely spaced sclerites at the edge (Fig 6), representing a period of summer growth. In Antarctic fishes each type of growth zone is deposited once a year and thus subsequent summer and winter zones con-



**Fig 6:** Scale of sub-adult *P. magellanica* collected in April, showing the summer growth zone at the edge of the scale and the first annulus with two slow growth subzones

stitute an annulus (Shcherbich 1975, North 1988).

The first well-expressed winter growth zone, representing the first annulus, was at a distance of 20 to 34 sclerites from the centre of the scale. This zone was highly variable in width, with six to 27 sclerites. In most specimens it appeared as two subzones of narrowly spaced sclerites separated by several more widely spaced ones (Fig 6). In other fish it appeared as a single, continuous zone of narrowly spaced sclerites. The meaning of the variable expression of the first winter growth zone is discussed below.

In the analysis of the relationship between the otolith length (OL) and the body length (SL), the model that showed the best fit with the data is expressed by the following power curve:

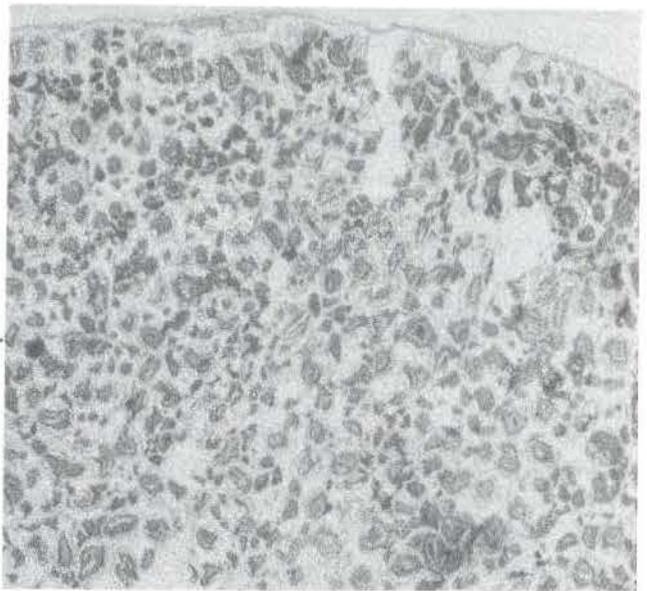
$$SL = 35.1 \times OL^{2.12} \text{ (r-square} = 0.79; n = 30; \text{ mean length } 148.4 \text{ mm SL)}$$

The exponent value calculated by Hecht & Cooper (1986) was 1.8 (n = 82).

The relationship between the body weight (WT) and the body length (SL) is described by the following power curve:

$$WT = 1.05 \times 10^{-4} \times SL^{2.75} \text{ (r-square} = 0.95; n = 48; \text{ mean length } 174.9 \text{ mm SL)}$$

The exponent value calculated by Hecht & Cooper (1986) was 3.0 (n = 133), which they interpreted as an indication of isometric growth.



**Fig 7:** Immature ovary of a sub-adult *P. magellanica* showing previtellogenic ova

All the specimens of *P. magellanica* collected during this study were sexually immature. The ovaries contained only oogonia (stage 1 of development) or primary growth oocytes in a previtellogenic state (stage 2) (Fig 7). Two adult females collected at the end of April (1983) beyond the kelp bed (about 200 m offshore) had gonads in stages 3 and 4; the ova measured about 0.5 mm (preserved in alcohol).

One fingerling transforming to benthic life was kept alive in a cold-water tank at the J L B Smith Institute of Ichthyology for a year. Water temperature was maintained at 5 °C and during most of the period the fish was fed with Antarctic krill pieces. The specimen was about 50 mm SL when collected in April 1989. In 12 months, during which it displayed a healthy rosy and shiny colour, it more than doubled its length, reaching 107 mm SL by April 1990.

## Discussion

### Ecology

The small number of adult *N. coriiceps* sightings, the absence of juveniles from the study sites and the absence of pelagic fingerlings from the sea around the island in winter as well as summer is unclear. In the South Orkney Islands, fingerlings migrate inshore and transform to benthic life in the second year of their life (Everson 1970a). The pelagic phase is therefore long, possibly over a year.

The colour phases of the young of this species are similar to those of *P. magellanica* and can be misidentified underwater, but the elusive juveniles were not present in collections from this research either. Several small, red fishes were photographed in deep water during a survey of the benthos of the Prince Edward Islands; they could be this species. One hypothetical explanation for the low number of sightings is that the population of adult *N. coriiceps* in the inshore zone of Marion Island may be declining with little recruitment into the inshore zone due to avian predation pressure on fingerlings. As recently as the early 1980s, anglers at Transvaal Cove were able to land a dozen large specimens in a short space of time (Dr G Kerley, Department of Zoology, University of Port Elizabeth, pers comm). Attempts with hook and line at this site produced no fish. A possible cause for such a decline may be the growing population of resident fur seals on the island. Two species of fur seal reside on the Prince Edward Islands, namely *Arctocephalus tropicalis* and *A. gazella*. At Marion Island, the populations of both species were expanding at a rate of 15% per year in the early 1980s (Kerley 1983) and about 12% in the late 1980s (Wilkinson & Bester 1990).

Larvae of *P. magellanica* proved to be as elusive as those of *N. coriiceps* and only one fingerling was collected in pelagic surveys of the water around Marion Island. Larvae of both species were also absent from the samples of several ichthyoplankton surveys in Kerguelen (Koubbi *et al* 1990). These authors suggested that both species spawn nearshore, in the area where they live. Observations indicate that at least *P. magellanica* does not spawn in the inshore zone. It is possible, however, that predation pressure forces the adults to spawn not far off the *Macrocystis* forest, which can then be used as a shelter by the larvae and the fingerlings.

The absence of adult *P. magellanica* from the study area is not incidental. In the Fuegian Islands, Chile, the largest specimen collected by Moreno & Jara (1984) in the *Macrocystis* forest was 24 cm TL, a sub-adult size. In Kerguelen Islands, Hureau (1970) also found that only

immature *P. magellanica* is present in the inshore zone and concluded that the adults migrate to spawn. The authors think that important inferences can be drawn from these observations. The colour of four adult specimens collected on the sea side of the kelp forest of Marion Island in previous years was dark blue to dark grey on the upper part of the body and pale ventrally, suggesting that these fishes returned to a pelagic life, though probably not far off land (De Witt *et al* 1990).

*N. coriiceps* and *P. magellanica* of Marion Island utilise a different ecological niche than their conspecifics in the Scotia Sea Islands and South America, respectively. In South Georgia, Burchett (1982) found that *N. coriiceps* was more active at night and preferred shallow areas with dense growth of macroalgae. The different habitat preference in South Georgia was also reflected in the food habits with amphipods, isopods and algae being the major food items (Burchett *et al* 1983). Similar food habits were found in fishes from the South Sandwich Islands (Targett 1981). In Marion Island, this species was observed only during the day, always on rocky substrate devoid of macroalgae and fed mostly on limpets.

In the Chilean Fuegian Islands, Moreno & Jara (1984) found that *P. magellanica* inhabits the *Macrocystis* forest, but visits the intertidal zone at high tide. Fishes were usually observed on the stipe and lower fronds of the kelp. In Marion Island, hardly any fishes were observed within the kelp forest. However, the diet of the fish in Chile was similar to that of the Marion Island population (Blankley 1982). Moreno & Jara (1984) also reported a migration of large individuals (15 to 24 cm TL) from the kelp bed, which they attributed to sexual maturity. In Marion Island, fishes of this size range included immature juveniles and sub-adults, both of which were present in summer as well as in winter catches and sightings. Since adult *P. magellanica* revert to pelagic life and assume pelagic colours, it is suggested that the Chilean fishes of the above size range do not migrate to spawn, but move from the kelp to a different substrate, i.e. to the bottom, under rocks.

*N. coriiceps* and *P. magellanica* of Marion Island are able to coexist in the inshore zone by way of resource partitioning along the axes of spatial distribution, substrate, occurrence of life-history stages, diel activity and food habits (Table 1). Resource partitioning also forms the pattern of spatial distribution of the different size-classes observed in *P. magellanica* (Fig 2). Fingerlings transforming to benthic life were always the highest off the bottom and were loosely associated with *Desmarestia*. Juveniles were usually within this bushy algae, on tufts of rhodophytes on the face of the rock near *Desmarestia*, or inside large masses of detached *Macrocystis* and *Durvillaea* fronds. Sub-adults were found on the bottom near or under large boulders. In addition, a certain degree of resource partitioning in the diet of these size-classes is inevitable if only because of different mouth sizes. Unfortunately, in the three published studies on the diet of *P. magellanica* (Hureau 1970, Blankley 1982, Moreno & Jara 1984) the data were not segregated by size-classes.

The greater abundance of *P. magellanica* at night indicates nocturnal activity. Activity may be limited to

Table 1

Resource partitioning between *N. coriiceps* and *P. magellanica* in the inshore zone of Marion Island

	<i>N. coriiceps</i>	<i>P. magellanica</i>
Depth range	2 to 6 m	4 to 12 m
Substrate	Small rocks without macroalgae	Large rocks with macroalgae
Life-history stages	Adults	Juveniles & sub-adults
Diurnal activity	Day	Night
Most important prey organisms (Blankley 1982)	Limpets	Isopods and amphipods

a short period of time after dark and possibly another period before sunrise. The fishes observed and collected during night dives were found in the open but seemed to be inactive. They were indifferent to divers around them and reacted visibly only when touched or when lights were pointed directly at them. Feeding probably takes place immediately after dark when amphipods migrate into the water column. They occur in such an abundance that the fish can feed to satiation in a very short time. Since there is no danger from avian predators during the night and no large predatory fish inhabit the inshore zone and the kelp forest of the island, *P. magellanica* can remain in the open till dawn. This is corroborated by the observation that the imperial cormorant, *Phalacrocorax atriceps*, one of the principal predators of *P. magellanica* (Blankley 1981, Brothers 1985), is more active at sunset and sunrise.

Only two studies on the abundance of nototheniid fishes in the sub-Antarctic region are known and both reported very low fish counts per transect. In southern Chile *P. magellanica*, Moreno & Jara (1984) counted  $8 \pm 2.16$  SD specimens per 500 m<sup>2</sup>. In the Auckland Islands, New Zealand, Kingsford *et al* (1989) counted  $2.6 \pm 0.8$  SE specimens of *Notothenia angustata* and  $3.8 \pm 2.2$  SE specimens of *N. microlepidota* per 250 m<sup>2</sup>. Unfortunately, logistic problems prevented the undertaking of a quantitative survey of abundance in Marion Island waters. However, it is thought that these studies underestimated the real abundance of nototheniids in their respective localities. In Marion Island daylight encounters agree with these studies, but estimates from night diving are much higher. Two divers of the research team were able to collect over 20 fishes in a single dive over an area smaller than 250 m<sup>2</sup> and others were sighted but not collected.

## Age, growth and reproduction

*Notothenia coriiceps* — The inshore population of this species is composed only of adults, four to six years old. *N. coriiceps* seems to grow more rapidly in the relatively warmer water of the Prince Edward Islands than elsewhere. In Adelie Land, on the Antarctic coast, Hureau (1970) determined that females 300 mm long were 11 years old. In the authors' study fishes of similar lengths (300 to 350 mm SL) were only five to six years old.

The presence of ova in advanced vitellogenesis (stage 4 to 5) in the ovaries of females collected in April, and the capture of a gravid female in May, imply that *N. coriiceps* spawns in May and possibly June. In the colder water of the Scotia Arc Islands, the spawning season is also in May and June (White *et al* 1982, Burchett *et al* 1983, Kock 1989).

*Paranotothenia magellanica* — The first annulus may appear on the scales of this species as either a single zone or two close zones of narrowly spaced sclerites. This is corroborated by the much wider summer growth zone that separates this annulus from the next one (Fig 6). The variable structure of the first annulus was interpreted as a reflection of different timing of growth events in the ontogeny of individual fish, namely the transformation from pelagic to benthic life and the winter effect on the growth of the scales. If these events take place simultaneously, they are likely to appear on the scale as a normal winter growth zone. But if they are separated by a short period of time of a different growth rate, they will probably be manifested as two close, but clearly disconnected growth zones. It follows that if these events are subsequent to each other, the first annulus will be expressed as a wider zone of narrowly spaced sclerites. The time of spawning (i.e. the beginning, middle or end of the spawning season) determines the time interval between the change in habitat and the effect of winter on growth, and their subsequent expression in the scales of individual fishes.

In Kerguelen, *P. magellanica* spawns during March/April. Ripe eggs are apparently pelagic and measure 0.8 mm in diameter (Hureau 1970). Nototheniid species with small eggs have a relatively short period of incubation. For example, the eggs of *Gobionotothen gibberifrons* from South Georgia are 1.5 to 2.5 mm and the incubation period is 1.5 months (Sil'yanova 1980, Kozlov 1982); the eggs of *Lepidonotothen larseni* from South Georgia and Elephant Islands are 1.6 to 2.0 mm and the incubation period is 2 to 2.5 months (Permitin & Sil'yanova 1971, Sil'yanova 1981, Kellermann 1989, Kock 1989). It is, therefore, reasonable to postulate that the small pelagic eggs of *P. magellanica* will incubate in the warmer water of the sub-Antarctic islands of the Indian Ocean sector over a period of about  $2 \pm 1$  months.

In Marion Island, the smallest fingerling transforming to benthic life was observed at the end of April. Its length was about 50 mm SL, and it still had dark dorsal and pale silvery ventral colours. A similar size specimen that was collected during the same expedition (1989) and another specimen, 66 mm SL, collected in the same month of 1985, were completely scaled and already had the scarlet colour characteristic of benthic juveniles associated with the substrate of brown and red algae. As-

suming that *P. magellanica* of Marion Island spawns over the same period of time as that of Kerguelen, the eggs probably hatch over May/June, i.e. the beginning of winter. The larvae develop into fingerlings which, together, spend  $10 \pm 2$  months in the pelagic zone. At the end of the following summer, the fingerlings transform to benthic life. The change in diet involved in this transformation produces the first zone of narrowly spaced sclerites in the first annulus. Once the transformation is completed, the benthic juveniles are able to maintain high growth rate until winter conditions prevail. This short period of rapid growth is expressed in the scales as the few widely spaced sclerites that separate the transformation zone from the second zone (winter growth) of narrowly spaced sclerites in the first annulus.

Juveniles of *P. magellanica*, which showed their first annulus in August/September 1989, measured 72.4 to 101.9 mm SL. The above hypothesis implies that this size range represents a growth period of 12 to 15 months. This conclusion was supported by the live specimen, which grew from about 50 mm SL to 107 mm SL when cultured in a tank over a period of one year. Hureau (1970) obtained a similar growth estimate for young *P. magellanica* in Kerguelen.

In the growth equation of length-weight relationship, the exponent (E) represents dimensional growth and its value ranges between 2 and 4. In isometric growth  $E=3$ , and in allometric growth  $E \neq 3$  (Tesch 1968). In view of the life-history cycle of *P. magellanica*, including transformations from pelagic to benthic life as juveniles and sub-adults, and back to pelagic life as adults, allometric growth pattern may be hypothesised for this species. The real value of E for *P. magellanica* probably falls somewhere between the authors' ( $E=2.75$ ) and that of Hecht & Cooper (1986) ( $E=3$ ). The samples of both studies are biased due to the length-frequency distribution of the specimens. Although the size range (82 to 333 mm SL) of the sample of Hecht & Cooper (1986) is similar to this study (72 to 370 mm SL), a greater mean length of the former sample will result in a higher value of E. Unfortunately, Hecht & Cooper (1986) did not provide the mean length of their sample. However, the lower value of the exponent in their body-length to otolith-length relationship (1.8 versus 2.12 in this study) implies a greater component of larger specimens in their sample.

## Acknowledgements

The authors wish to thank the South African Department of Environment Affairs for the funding and the logistical support of this project. We are grateful for the assistance and cooperation of the captian, officers and crew of the SA *Agulhas*, and the helicopter pilots and crews during our expeditions to Marion Island. We also thank the 1989/90 island team members, particularly D Baker, for assisting us with diving operations on Marion Island. A Robertson of the Sea Fisheries Research Institute, Cape Town, kindly provided a portable laboratory cooler for our expeditions. A Barkai of the University of Cape Town kindly provided cold room facilities in Cape Town and R Anderson of the University of Cape Town identified

samples of algae. We are grateful for the frozen Antarctic krill kindly given to us by J Cooper and S Jackson of the University of Cape Town. Special thanks are due to our diving assistants L Burger, R Bills and O Greenberg.

## References

- BALUSHKIN AV 1990. Review of blue notothenias of the genus *Paranotothenia* Balushkin (Nototheniidae) with description of a new species. *Vop. Ikhtiol.* 30 (5): 752-763
- BLANKLEY WO 1981. Marine food of Kelp Gulls, Lesser Shearwaters and Imperial Cormorants at Marion Island. *Cormorant* 9: 77-84
- BLANKLEY WO 1982. Feeding ecology of three inshore fish species at Marion Island (Southern Ocean). *S. Afr. J. Zool.* 17: 164-170
- BLOCH ME & SCHNEIDER JG 1801. *M.E. Blochii Systema ichthyologiae iconibus ex illustratum*. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit JG Schneider, Saxo. Berolini, lx + 584 pp, 110 pls
- BRANCH ML, GRIFFITHS CL, KENSLEY B & SIEG J 1991. The benthic Crustacea of subantarctic Marion and Prince Edward Islands: Illustrated keys to species and results of the 1982-1989 University of Cape Town surveys. *S. Afr. J. Antarct. Res.* 21(1): 3-44
- BROTHERS NP 1985. Breeding biology, diet and morphometrics of the king shag, *Phalacrocorax albiventer purpurascens* at Macquarie island. *Aust. Wildl. Res.* 12: 81-94
- BROWN CR & KLAGES NT 1987. Seasonal and annual variation in diets of macaroni *Eudyptes chrysolophus chrysolophus* and southern rockhopper penguins *Eudyptes chrysocome chrysocome* at sub-Antarctic Marion Island. *J. Zool. Lond.* 212: 7-28
- BURCHETT MS 1982. The ecology of some coastal fish populations at South Georgia. *Prog. Underwater Sci.* 7: 15-20
- BURCHETT MS, SAYERS PJ, NORTH AW & WHITE MG 1983. Some biological aspects of the nearshore fish populations at South Georgia. *Br. Antarct. Surv. Bull.* 59: 63-74
- DAVIS TLO 1977. Reproductive biology of the freshwater catfish, *Tandanus tandanus* Mitchell, in the Gwydir River, Australia. 1. Structure of gonads. *Aust. J. Mar. Freshwater Res.* 28: 139-158
- DE VILLIERS AF 1976. Littoral ecology of Marion and Prince Edward Islands. *S. Afr. J. Antarct. Res. Suppl.* 1: 1-40
- DEWITT HH, HEEMSTRA PC & GON O 1990. Nototheniidae (pp 279-331). In: *Fishes of the Southern Ocean*, eds O Gon & PC Heemstra. J L B Smith Institute of Ichthyology, Grahamstown xviii + 462 pp, 12 pls
- DIPPER FA & PULLIN RSV 1979. Gonochorism and sex-inversion in British Labridae (Pisces). *J. Zool. Lond.* 18: 97-112
- ESPITALIER-NOEL G, ADAMS NJ & KLAGES NT 1988. The diet of the imperial cormorant *Phalacrocorax atriceps* at Marion island. *Emu* 88: 43-46
- EVERSON I 1970a. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull.* 23: 25-50
- EVERSON I 1970b. Reproduction in *Notothenia neglecta* Nybelin. *Br. Antarct. Surv. Bull.* 23: 81-92
- GON O & KLAGES NT 1988. The marine fish fauna of the sub-Antarctic Prince Edward Islands. *S. Afr. J. Antarct. Res.* 18 (2): 32-54
- HECHT T & COOPER J 1986. Length/mass relationships, energetic content and the otoliths of Antarctic cod *Paranotothenia magellanica* (Nototheniidae: Pisces) at sub-Antarctic Marion Island. *S. Afr. J. Zool.* 21 (4): 294-296
- HUREAU J-C 1970. Biologie comparée de quelques Poissons antarctiques (Nototheniidae). *Bull. Inst. océanogr. Monaco*, 68 (1391): 1-244
- KELLERMANN A 1989. The larval community in the zone of seasonal pack ice cover and its seasonal and interannual variability. *Arch. FischWiss.* 39 (1): 81-109
- KERLEY GIH 1983. Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. *S. Afr. J. Zool.* 18: 388-392
- KINGSFORD MJ, SCHIEL DR & BATTERSHILL CN 1989. Distribution and abundance of fish in a rocky reef environment at the subantarctic Auckland islands, New Zealand. *Polar Biol.* 9: 179-186

- KOCH K-H 1989. Reproduction in fish around Elephant Island. *Arch. Fischwiss.* 39 (1): 171-210
- KOUBBI P, DUHAMEL G & CAMUS P 1990. Early life stages of *Notothenioidei* from the Kerguelen Islands. *Cybium* 14 (3): 225-250
- KOZLOV AN 1982. Seasonal dynamics of the morphophysiological and biochemical indices of *Notothenia gibberifrons*. *J. Ichthyol.* 22 (1): 101-106
- LUTJEHARMS JRE & VALENTINE HR 1984. Southern Ocean thermal fronts south of Africa. *Deep-sea Res.* 31: 1461-1475
- MOCDUGAL I 1971. Geochronology. In: *Marion and Prince Edward Islands*, eds EM Van Zinderen Bakker et al. A A Balkema, Cape Town
- MORENO CA & JARA HF 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegian Islands, Chile. *Mar. Ecol. Prog. Ser.* 15: 99-107
- NORTH AW 1988. Age of Antarctic fish: validation of timing of annuli formation on otoliths and scales. *Cybium* 12 (2): 107-114
- NYBELIN O 1947. *Antarctic fishes*. Scientific results of the Norwegian Antarctic Expedition 1927-1928 et Sqq., no 26, 76 pp
- PERMITTIN YU YE & SIL'YANOVA ZS 1971. New data on the reproductive biology and fecundity of fishes of the genus *Notothenia* Rich. in the Scotia Sea (Antarctica). *J. Ichthyol.* 11 (5): 693-705
- RICHARDSON J 1844. Ichthyology of the voyage of H M S 'Erebus' and 'Terror' (viii + 139 pp). In: 1844-1848 *The zoology of the voyages of H M S "Erebus" and "Terror"*, 2. eds J Richardson & JE Gray (1844: 1-16; 1845: 17-52; 1846: 53-74; 1848: i-viii, 75-139)
- SHCHERBICH LV 1975. Methods of determining age and onset of sexual maturity in the marbled Antarctic cod *Notothenia rossi marmorata*. *J. Ichthyol.* 15 (1): 82-88
- SIL'YANOVA ZS 1980. Gametogenesis of some West Antarctic fish species. In: An ecological and biological description of some species of Antarctic fishes. *Trudy VNIRO* 80: 52-57. (In Russian)
- SIL'YANOVA ZS 1981. Oogenesis and stages of maturity of fishes of the family Nototheniidae. *J. Ichthyol.* 21 (4): 81-89
- TARGETT ET 1981. Trophic ecology and structure of coastal Antarctic fish communities. *Mar. Ecol. Prog. Ser.* 4: 243-263
- TESCH FW 1968. Age and growth (pp 93-123). In: *Methods for assessment of fish production in fresh waters*, ed WE Ricker. Blackwell Scientific Publications, Oxford and Edinburgh. xiii + 313 pp
- WHITE MG, NORTH AW, TWELVES EL & JONES S 1982. Early development of *Notothenia neglecta* from the Scotia Sea, Antarctica. *Cybium* 6 (1): 43-51
- WILKINSON IS & BESTER MN 1990. Continued population increase in fur seals *Arctocephalus tropicalis* and *A. gazella*, at the Prince Edward Islands. *S. Afr. J. Antarct. Res.* 20 (2): 58-63
- WILLIAMS R 1988. The nearshore fishes of Macquarie Island. *Pap. Proc. R. Soc. Tasm.* 122 (1): 233-245
- YAMAMOTO K 1956. Studies on the formation of fish eggs. *J. Fac. Hokkaido Univ. Ser. 5, Zool.* 12 (3) 32-400