

# Interpopulation relationships in two species of Antarctic fish *Notothenia rossii* and *Champscephalus gunnari* from the Kerguelen Islands: an allozyme study

GUY DUHAMEL<sup>1</sup>, CATHERINE OZOUF-COSTAZ<sup>1</sup>, GHISLAINE CATTANEO-BERREBI<sup>2</sup> and PATRICK BERREBI<sup>2</sup>

<sup>1</sup>Museum national d'histoire naturelle, Laboratoire d'ichtyologie générale et appliquée, 43 rue Cuvier, 75231 Paris Cedex 05, France

<sup>2</sup>Université Montpellier II, Laboratoire Génome et Populations, CNRS URA 1493, case 063, place E. Bataillon, 34095 Montpellier Cedex 05, France

**Abstract:** Enzymatic polymorphism was used to detect variability within *Notothenia rossii* from two sites on the Kerguelen Plateau and *Champscephalus gunnari* from the same sites and the South Orkney Islands. No polymorphism was found in the second species and it was low but not statistically significant in the first. This apparent homogeneity does not substantiate suggestions from other results that the populations can be separated, especially in the case of *C. gunnari*. Other approaches will be necessary to solve definitively the question of population separation.

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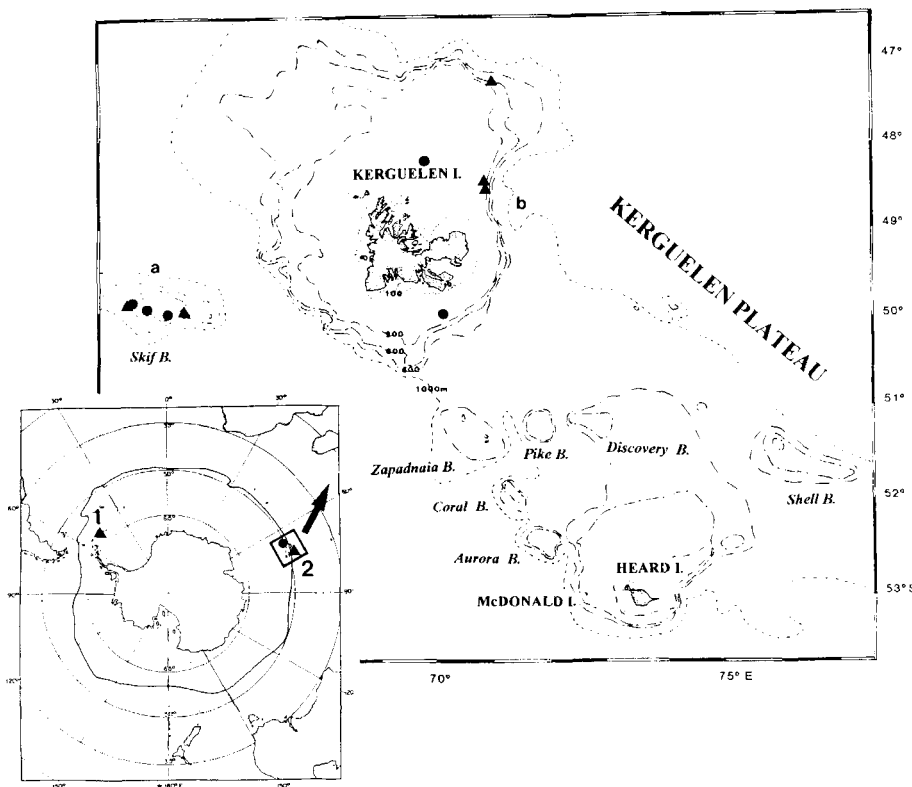
## Introduction

The Kerguelen Plateau, the largest shelf in the Southern Ocean, is located in the Indian sector and has a north-west/south-east orientation. It nearly reaches the Antarctic continental shelf in its southern extent. The Kerguelen Islands in the north (49°S) and Heard and McDonald islands (53°S) are the only islands to emerge from the shelf. Among the 61 fish species known to inhabit the shelf, diversity is low with only 19 endemic (Duhamel 1993). Of these, the order Notothenioidae dominates both in number of species (58%) and in biomass. Four species of this group have been exploited during the last 25 years, mainly off the Kerguelen Islands on the shelf break and the surrounding banks. Seven banks (named Skif, Shell, Coral, Aurora, Discovery, Pike and Zapadnaia) occur at various distances and depths (Fig. 1). They are populated by most of the species found on the shelves, but whether or not the populations are isolated from those on the shelves has not been resolved. Because of their relative proximity exchanges between the peri-insular and bank fish within each species cannot be precluded. For instance, a semi-pelagic behaviour could facilitate migration of shelf fish towards the ocean and the banks for trophic or reproductive reasons, or a population could disperse geographically during the larval stage.

For *Champscephalus gunnari* and *Notothenia rossii*, elucidating whether or not the bank and peri-insular shelf populations are separated would help both our understanding of their biological cycles whilst also increasing our knowledge of the stock dynamics of these two heavily exploited species.

*C. gunnari*, of the family Channichthyidae, is the most abundant species on the Kerguelen Shelf. Analyses of

length/frequency distributions of this species for the whole area have been analysed for over 25 years (Duhamel 1987a, 1991, 1993, Gerasimchuck 1993). The data reveal an apparently distinctive demographic structure for the species with cyclic appearances of size groups identified as cohorts or age classes. These cohorts are often characteristic of individual islands and banks. An icefish group on the Skif Bank, 225 km south-west of the Kerguelen peri-insular shelf, never shows any common length distributions with the Kerguelen peri-insular group (Duhamel 1987a). This lack of common population features suggests that individuals from both sites are reproductively isolated. Furthermore, the existence of a spawning ground specific to Skif Bank and bathymetrically isolated from that of the islands, and where fish spawn at different times (Duhamel 1987b), shows that the brood stock from both groups do not spawn at the same time. Observations made on the shelf of Heard and McDonald islands and its related banks (R. Williams, personal communication 1992) have shown the same phenomenon. It has previously been shown from analysis of morphological and meristic characters (Kock 1981, Gubsch 1982, Sosinski 1985), from parasite infestation rate (Siegel 1980) and from differences in biological characteristics (Kock 1992) that populations from the Atlantic sector of the Southern Ocean (i.e. South Georgia, South Orkney Islands, South Shetland Islands and Bouvet Island) are distinct from the populations of the Indian sector. The aim of our study is to determine whether distinct populations of *C. gunnari* also exist in various parts of the Kerguelen Plateau. Population genetics methods will test for the existence of an independent population on the Skif Bank.



**Fig. 1.** Sampling sites for the isoenzymatic study of *Champsocephalus gunnari* (triangles) and *Notothenia rossii* (circles). 1. South Orkney Islands (Atlantic sector of the Southern Ocean). 2. Kerguelen Plateau (Indian sector of the Southern Ocean). a. Skif Bank, b. peri-insular shelf of the Kerguelen Islands.

The second species, *N. rossii* of the family Nototheniidae, has a characteristic biological cycle in the Indian and Atlantic sectors of the Southern Ocean (Olsen 1955, Burchett 1983a, Duhamel 1987a). Juveniles grow exclusively in the coastal zone of the subantarctic islands amongst the giant kelp (*Macrocystis* spp.) and, as adults, disperse to become semi-pelagic outside this zone. Reproduction is annual, occurs in winter and takes place in deep water on the slope. In the Indian sector of the Southern Ocean only one spawning ground has so far been identified, on the south-east side of the Kerguelen shelf (Duhamel 1982). The regular presence of only adults on the Skif Bank suggests that migration occurs between the shelf and the bank and that these individuals all originate from the only known spawning ground. However, an independent brood stock might exist on the bank, producing post-larvae that reach insular coastal areas with the West Wind Drift and settle there before returning as adults. The hydrology of the area (Murail *et al.* 1977, Park *et al.* 1993) would allow this. It would be useful to test this hypothesis and determine if the Skif Bank fish can be discriminated from that on the peri-insular shelf. This might also help to explain the origin of adults of this species (Meisner & Kratkii 1978, Chechun 1984, Tankevich 1994) on the Ob (52°20'S–41°20'E) and Lena (52°50'S–44°30'E) banks which are even more isolated from shelf coastal zones in the Indian sector of the Southern Ocean.

With these objectives in mind, we have tested the degree of genetic differentiation between samples taken in different parts of the Kerguelen Plateau in the Indian sector and elsewhere (Atlantic sector: South Orkney Islands).

## Materials and methods

During the last phase (February–April 1988) of the French-USSR oceanographic cruises SKALP (Duhamel 1993) around the Kerguelen Islands, the ships *Skif* and *Kalper* trawled specimens of *C. gunnari* and *N. rossii* in the north-east and south-east areas of the Kerguelen Islands shelf and the Skif Bank (Fig. 1). Tissue samples were dissected from the fresh fish and immediately frozen at -20°C in Eppendorf tubes. The samples ( $n = 123$  and 100 for *C. gunnari* and 102 and 75 for *N. rossii* from the peri-insular shelf and the Skif Bank respectively) were shipped back to France for electrophoresis. For comparison 14 similar samples of *C. gunnari* were taken, in February 1989, west of the South Orkneys (60°38.9'S–49°56.7'W) during the EPOS Islands cruise of the RV *Polarstern*.

Muscle and liver samples were analysed for 13 enzymes (Berrebi *et al.* 1986). The number of specimens subject to electrophoresis was 44 of each species from the Kerguelen Islands shelf, 42 *C. gunnari* from the Skif Bank and seven from the South Orkneys, 32 *N. rossii* from the Skif Bank.

Approximately 1.5 g from each sample were homogenized in equal amounts of Tris-HCL-EDTA-NADP pH 6.8 buffer, in the presence of  $\text{CCl}_4$  to eliminate lipids from the extract. Centrifugation for 30 min at 15 000 g cleared enzyme extracts which were then kept at -70°C until electrophoresis. For details of the starch gel (12%) electrophoresis see Pasteur *et al.* (1987). Table I indicates the buffer-organ combination used for each enzyme. Staining was according to Shaw & Prasad (1970) and Harris & Hopkinson (1976).

**Table I.** Details of the enzymes, organs and buffers used for both species. Active loci in the liver and muscle are only indicated once in the organ that showed the best resolution. When two figures appear, they correspond to *Champscephalus gunnari* and *Notothenia rossii*, respectively. A dash indicates no data.

Enzyme systems	Number of loci per organ		Number of polymorph loci per organ		Buffer
	muscle	liver	muscle	liver	
AK	1	-	0	-	TC 6,7
AAT	2	1	0	0	PC 6,3
CK	1	-	1	-	PC 6,3
GDA	-	1	-	0	TC 6,7
GLO	-	1	-	0	Poulik
IDH	1	1	0/1	0/1	Poulik
LDH	1	1	0	1	Poulik
MDH	3	1	0	0	TC 6,7
ME	-	1	-	0	TC 6,7
6PGDH	-	1	-	0	TC 6,7
PGI	2	-	1/2	-	Poulik
PGM	1	-	0/1	-	Poulik
SOD	-	1	-	1/0	Poulik

The index of genetic diversity (H) used follows the formula  $H = \sum_{i=1}^r S_i^2 h/r$  (r: number of locus, h: heterozygosity index to each locus and  $h = 1 - \sum_{i=1}^r S_i^2$ ,  $q_i$ : ith allele frequency of the locus under consideration).

## Results

Tables II and III show the allelic frequencies for each of the sites of both species. Enzyme heterozygosity was low: for *C. gunnari*  $0 < H < 0.006$  and for *N. rossii*  $0.029 < H < 0.039$ . Mean heterozygosity (criterion 95%) was 0% for *C. gunnari* and  $9.5 < P < 14.3\%$  for *N. rossii*. The only loci which could be used for meaningful comparative tests were IDH-F\*, PGI-1\* and PGM\* in *N. rossii*.  $\chi^2$  tests were performed on these three loci but no significant differences were detected between the Kerguelen Islands shelf and the Skif Bank groups. In the case of *C. gunnari*, loci for each of the three localities (Indian and Atlantic sectors of the Southern Ocean) were not significantly different.

From all analyses performed, a clear intraspecific statistical homogeneity was demonstrated.

## Discussion

Results from the isoenzyme study show polymorphism ranging from a low level to zero in both species. In marine teleosts, mean genetic variability lies between 0.051 and 0.060 (Powell 1975, Nevo 1978, Smith & Fujio 1982) whereas in our study the value never exceeds 0.039 and is frequently well below this value. However, other cases of low level of heterozygosity have been detected elsewhere (Blanquer *et al.* 1992).

Various models have been proposed in the literature to explain different levels heterozygosity. Kimura & Ohta (1971) suggest a direct correlation between heterozygosity

**Table II.** Allelic frequencies for three loci analysed for two different sites on the Kerguelen Plateau and in South Orkney Islands for *Champscephalus gunnari*.

Loci	Alleles	Skif Bank	South Orkney Islands shelf	Kerguelen Island shelf
LDH-F*	110	0.00(32)	0.00(7)	0.03(32)
	100	1.00	1.00	0.97
PGI-1*	100	0.98(41)	1.00(7)	1.00(44)
	90	0.02	0.00	0.00
SOD*	100	1.00(32)	1.00(32)	0.97(32)
	10	0.00	0.00	0.03

Figures in brackets indicate the number of specimens analysed per locus. The monomorphic loci AK\*, AAT-1\*, AAT-2\*, AAT-3\*, CK\*, GDA\*, GLO\*, IDH-F\*, IDH-M\*, LDH-M\*, MDH-F\*, MDH-1\*, MDH-2\*, MDH-3\*, ME\*, 6PGDH\*, PGI-2\*, PGM\* are not presented.

**Table III.** Allelic frequencies for five loci analysed in two different sites of the Kerguelen Plateau for *Notothenia rossii*.

Loci	Alleles	Skif Bank	Kerguelen Island shelf
IDH-F*	100	0.97(18)	0.95(33)
	90	0.03	0.03
	65	0.00	0.02
IDH-M*	120	0.03(30)	0.04(38)
	100	0.97	0.96
PGI-1*	110	0.03(29)	0.04(44)
	105	0.05	0.05
	100	0.92	0.89
	90	0.00	0.01
	80	0.00	0.01
PGI-2*	100	1.00(24)	0.98(30)
	90	0.00	0.02
PGM*	105	0.25(32)	0.27(37)
	100	0.73	0.73
	90	0.02	0.00

Figures in brackets indicate the number of specimens analysed per locus. The monomorphic loci AK\*, AAT-1\*, AAT-2\*, AAT-3\*, CK\*, GDA\*, GLO\*, GLO\*, LDH-M\*, MDH-F\*, MDH-1\*, MDH-2\*, MDH-3\*, ME\*, 6PGDH\*, SOD\*, X\* are not presented. The locus named X\* represents an unknown enzymatic activity, precisely localized enough in the gel to be considered as a presumptive locus.

and population size (neutralist theory). Somero & Soulé (1974) point to the importance of the date of the last "bottleneck" (drastic loss of polymorphism). Ayala *et al.* (1975) suggest that since polar species produce fewer eggs than temperate species, the low level of polymorphism would be consistent with the fact that the polar species cannot afford the luxury of producing many genotypes for selection as in temperate species. Nevo (1978) links a high heterozygosity to biotic and abiotic environmental heterogeneity, which he defines as being proportional to the surface area of the geographical zone considered. Smith & Fujio (1982) link a high polymorphism to a specialized habitat containing a small number of prey species.

From these hypotheses it seems that the notion of population

size influencing the degree of polymorphism can be rejected. This is because the populations of *C. gunnari* are quite large: several hundred millions for each abundant age class on the Kerguelen Shelf and several tens of millions on the Skif Bank (Duhamel & Agnew 1990, unpublished). For *N. rossii*, the estimated biomass on the Kerguelen shelf is >20 000 t (Duhamel 1988). In addition the fecundity rates are not very low compared to many temperate species (Kartas & Quignard 1984) even if Antarctic fish produce large eggs in small numbers (Marshall 1953). *C. gunnari* produces between 1300 and 31 000 eggs (absolute fecundity) depending on the adult size and the spawning area, with a mean diameter of 3.2 mm and a relative fecundity rate of 8–45. *N. rossii* produces between 12 200 and 130 000 eggs with a mean diameter of 5.0 mm and a relative fecundity rate of 6–23 (Duhamel 1987b, Kock & Kellerman 1991).

Both species are widely distributed in the Southern Ocean. *C. gunnari* ranges from the tip of Antarctic Peninsula to the Kerguelen Plateau (60°W–80°E) in the vicinity of the Antarctic Polar Front. *N. rossii* is practically circum-Antarctic in the subantarctic zone. The distribution is mainly governed by the latitudinal frontal system but the habitat is longitudinally homogeneous between fronts. Numerous species are common to shelves of Atlantic and Indian sectors of the Southern Ocean and others are vicariant sibling species or can be assigned to ecotypes. *C. gunnari* has a restricted bathymetric distribution throughout its life cycle. *N. rossii*, on the other hand, lives in the coastal inshore areas (kelp belt) and has a demersal behaviour when juvenile, but when adult becomes benthic-pelagic and moves offshore with an annual winter spawning migration towards deeper habitats in c. 500 m, which supposes certain physiological adaptations. *C. gunnari* has only two main types of prey which compose 85% of its diet (Permitin & Tarverdieva 1972, Duhamel 1981, 1987a, Kock, 1981, Chechun 1984); *N. rossii*, shows a greater prey diversity in all geographical sectors dependent on the different habitats this species occupies throughout its life cycle (Hureau 1970, Tarverdieva 1972, Permitin & Tarverdieva 1972, Tarverdieva & Pinskaya 1980, Duhamel 1981, 1987a, Burchett 1983b, Chechun 1984). These observations agree with the hypotheses of Nevo (1978) and of Smith & Fujio (1982) in that the low polymorphism of both species is explained by environmental homogeneity, and the higher heterozygosity of *N. rossii* can be ascribed to the differences in the biology between the two species.

Finally, the origin of these populations must also be considered. Although it is known that fish inhabited Antarctic freshwaters some 400 Ma, fossils of modern notothenioids have not been found, even in the youngest known fossils of the late Eocene (Eastman 1993). One may suppose that the zoogeographical isolation of the Southern Ocean occurred c. 25 Ma, when hydrological boundaries became effective and the circum-antarctic current appeared, thus preventing most exchanges, at least in shallow waters. Eastman (1993) supposes that endemic species of fish, in particular the

notothenioids, have been associated with the Gondwanan shelf since the late Tertiary period. Most phylogenetic divergence occurred between 25 and 2 Ma after the total isolation of the Antarctic continent, the formation of the Southern Ocean, the increase in biological productivity and the appearance of cold conditions. Once species were well established, separate populations could then develop. If the geographical isolation was of long duration and the populations abundant, the appearance of great depths preventing migrations of adults between shelf areas and of great distances between areas of distribution, making larval dispersal impossible, would have favoured the emergence of a strong heterozygosity. This, however, does not seem to be the case. Long-term geographical isolation might also have drastically reduced the size of the populations which, although substantial and isolated on the shelves and banks, might not have been sufficient for polymorphism to emerge and one might consider these populations as relicts. In this case, the low level polymorphism is homogeneous in all the populations and the emergence of genetic differentiation using enzymatic markers might take much longer to become noticeable. If, however, this isolation was more recent, genetic exchanges between populations might have occurred for a long time in shallow waters between the Antarctic shelf and the Kerguelen Plateau, via the Kerguelen-Gaussberg ridge in the Indian sector or the Scotia Arc in the Atlantic sector. Such a possibility could be the reason for homogeneity between populations.

From our data, one cannot conclude whether the distant groups of fish of both Antarctic species are differentiated at the population level or not. The only suspected positive conclusion suggesting the existence of distinct populations, as a result of electrophoretic analysis of enzyme polymorphisms in an Antarctic fish, has been reported (Schneppenheim *et al.* 1994) for *Lepidonotothen squamifrons* between individuals from the Kerguelen Islands and Atlantic sector (South Georgia, South Orkney Islands, Elephant Island). The present results for *C. gunnari* do not corroborate the above conclusion. Indeed, the data do not substantiate any of the conclusions set forth by different authors on the population separation inside the Kerguelen Plateau area. The distinction, even at a population level, between *N. rossii* from various distant shelves and Banks of the Indian sector of the Southern Ocean is still open. In view of the low level of polymorphism the following three points might help to resolve this:

- 1) a greater range of sampling sites to find polymorphic populations thus proving the bottleneck,
- 2) an increase in the number of fish sampled to several hundreds to focus only on the polymorphic loci: *IDH-F\**, *PGI-1\** and *PGM\** of *N. rossii* to confirm or reject,
- 3) use of certain genetic markers known to evolve more rapidly such as restrictive fragments of mitochondrial



DNA or nuclear DNA microsatellites. According to Brown *et al.* (1982), mitochondrial DNA evolves 5–10 times faster than nuclear DNA. This last point has recently been studied (Williams *et al.* 1994) with samples of *C. gunnari* originating from the Kerguelen shelf (same area as the present study), the Heard/McDonald shelf and outlying banks (Shell and Discovery). The analysis of the nucleotide sequence diversity of mitochondrial DNA was coupled and compared between sectors but produced statistically insignificant low inter-population diversities which concurs with our preliminary results. The authors conclude that the mtDNA data do not support the existence of genetically separate populations on the Kerguelen Plateau, but neither do they preclude the existence of isolated stocks.

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