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Vertebral Variation in Notothenioid Fishes from McMurdo Sound, Antarctica

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Summary. Vertebral variation was studied in eight species (299 specimens) of notothenioid fishes from McMurdo Sound, Antarctica. McMurdo Sound is one of the most physically stable marine environments in the world, with a nearly constant mean annual temperature. As measured by the coefficient of variation, McMurdo Sound species were slightly less variable than the temperate and arctic species used for comparison. When the F-distribution was used to test the significance of differences between mean variances of species from different localities, McMurdo Sound species were significantly different ($0.01 < P \leqslant 0.05$) in four of the six comparisons. Variance values indicated that McMurdo Sound species were less variable than arctic and temperate species in three out of the four significant comparisons. Although it can not be proven that the stable water temperature of McMurdo Sound contributes to reduced vertebral variation, this is certainly a plausible hypothesis. Vertebral variation is discussed with reference to the biology of notothenioid fishes.

Introduction

At 77° south latitude, McMurdo Sound, Antarctica is one of the most unique marine habitats in the world. Its waters have a nearly constant mean annual temperature (−1.87 °C), salinity and density and there is no vertical thermostratification (Littlepage 1965). Representatives of a highly endemic group of perciform fishes, the Notothenioidei, are found in this environment (DeWitt 1971). The 12 species inhabiting McMurdo Sound (Eastman and DeVries 1982) are permanent residents, specialized for feeding and reproduction in this environment. The constancy of McMurdo Sound is evidenced by the fact that these species are extremely stenothermal and have undergone an evolutionary reduction in their capacity to acclimate to thermal change (DeVries 1980).

It has long been known that meristic characters in fishes are influenced by environmental conditions. Vertebral number, for example, is related to water temperature (Jordan 1891) during embryonic development. Low water temperatures retard growth more than differentiation, thereby promoting the development of a greater number of vertebrae (Hubbs 1922, 1926). The number of vertebrae is determined during a short sensitive period early in development and it is during this period that vertebral number is most susceptible to environmental influence (Tåning 1952). Although the genotype determines a range of vertebral numbers, there have been few experimental studies defining the interaction of the genotype and the environment in setting vertebral number (Fowler 1970).

That fishes experience direct modification of vertebral number by water temperature is most graphically demonstrated by experiments using clones of self-fertilizing *Rivulus marmoratus* raised at different temperatures. Lindsey and Harrington (1972) found that the genotype did not restrict vertebral number in these genetically uniform fish. In experimental groups of *Rivulus* reared at 19.5° and 31.2 °C, the difference between vertebral means was 2.37 vertebrae. When expressed as a percentage of the overall mean count, Lindsey and Harrington noted that this response of 7.0% was greater than that of any species studied previously.

In this paper I will: 1) present data on vertebral variation for a sample of 299 notothenioids representing eight species from McMurdo Sound; 2) compare data from these species to that from the literature for other antarctic, arctic and temperate fishes; a 3) discuss vertebral variation with reference to the biology of notothenioid fishes.

Materials and Methods

McMurdo Sound

This study was conducted at the U. S. McMurdo Station (77°50′S, 166°40′E) on Ross Island in the southwestern corner of the Ross Sea.

Fishes were collected in McMurdo Sound, a 72 km by 81 km body of water between Ross Island and the Antarctic mainland (Littlepage 1965). The Sound is over 1000 m deep and is covered by a 2 – 3 m thick layer of sea ice for about 10 months a year (Littlepage 1965).

McMurdo Sound seawater at depths of 3 – 275 m is characterized by nearly constant mean annual temperature (– 1.87° C; SD = 0.09), salinity (34.70‰, SD = 0.29) and density (Sigma-t = 27.96; SD = 0.15) (Littlepage 1965). Furthermore, there is no vertical thermostratification and dissolved oxygen is high (73.5 – 104.7% saturation) throughout the year (Littlepage 1965). There are, however, seasonal variations in the amount of ice cover, light and productivity, although these parameters are diurnally stable during much of the year.

Collection of Fishes

Within 8 km of McMurdo Station, I collected 299 specimens (8 species) in October to early December, 1978 and 1979. Additionally, 12 *Notothenia kempi* and 26 *N. larseni* were collected near Sabrina Islet, Balleny Islands in February, 1974. They were captured at a depth of 100 m in a trawl pulled by an icebreaker.

Collecting sites in McMurdo Sound were holes drilled in the sea ice over various water depths. Wooden huts, used as fishing stations, were periodically moved to holes over 40, 70, 100, 200 and 550 m water depths in the Sound. The majority of specimens collected were adults in the size range 140 – 250 mm TL.

Benthic and benthopelagic species were taken in conical, wire mesh bottom traps. The traps were baited with beef, attached to the cable of an oceanographic winch and lowered in place to remain for 24 – 36 hours. Scavenging amphipods were attracted to the meat and the fishes followed the amphipods into the traps. Cryopelagic species were hand jigged with artificial lures immediately beneath the platelet ice. Bottom jigging was effective in capturing *Gymnodraco acuticeps.* Normal fish habitats in McMurdo Sound are illustrated by Eastman and DeVries (1982).

It is very difficult to collect pelagic fishes, other than the large *Dissostichus mawsoni,* in ice-covered McMurdo Sound. Specimens of pelagic *Pleuragramma antarcticum* were taken from the stomachs of *Dissostichus* (Eastman and DeVries 1981). Additional specimens of *Pleuragramma* were obtained from jellyfish tentacles which became tangled in winch lines.

Radiography and Counting Vertebrae

Vertebral counts were taken from radiographs produced with a Hewlett-Packard Faxitron soft X-ray machine (model 43805N). The settings on the machine were 30 kV and 2.75 mA with an exposure time of 2 – 8 min, depending on the size of the specimen. Radiographs were made on Kodak Type M Industrial X-ray Film. Notothenioids have one urostylar centrum, and this was included in the vertebral count. Specimens with abnormal vertebral columns were not encountered in this sample.

Statistical Analysis

The data were analyzed on an IBM 370/158 computer at the Ohio University Computer Center. I used statistical programs provided by the SAS Institute (1979 edition).

This study was designed to evaluate the relative amount of vertebral variation in McMurdo Sound fishes as compared to fishes from other locations, both polar and temperate. Therefore, the null hypothesis to be tested is H_0: there is no difference in the magnitude of vertebral variance in McMurdo species compared to that of species in other locations. This is a two-tailed test since the alternative hypothesis is $H_1: \sigma_1^2 \neq \sigma_2^2$ (Sokal and Rohlf 1981). The F-distribution was used to test the significance of differences between: variances (Simpson et al. 1960; Sokal and Rohlf 1981), natural logarithms (to the base e) of variances (Lewontin 1966) and squared coefficients of variation (Lewontin 1966).

Results

Table 1 and Fig. 1 display descriptive statistics for McMurdo Sound species. Vertebral data for a variety of species from other locations are also included for comparison. These data are from the literature. Figure 1 demonstrates that the samples of McMurdo Sound species approach statistical adequacy in terms of the ratio of dispersion (SD) to reliability (SEM) (Hubbs and Hubbs 1953). Seven of the eight McMurdo Sound species had moderately right-skewed distributions of the type common in zoology (Simpson et al. 1960). The mean coefficient of skewness for the eight species was + 0.24. The coefficient of kurtosis ranged from + 2.92 to – 2.07 with a mean of – 0.07.

Relative amounts of variation may be compared utilizing the coefficient of variation (V) which expresses the standard deviation as a percentage of the mean. Although not suitable for statistical testing, V provides a quantitative impression of the relative amount of intraspecific vertebral variation. Values of V are low in all species indicating that vertebral number is a good taxonomic character (Simpson et al. 1960). McMurdo Sound species, with a mean V of 1.19, are slightly less variable than the temperate and arctic species used for comparison. Species from antarctic locations other than McMurdo Sound also have lower values of V than spe-

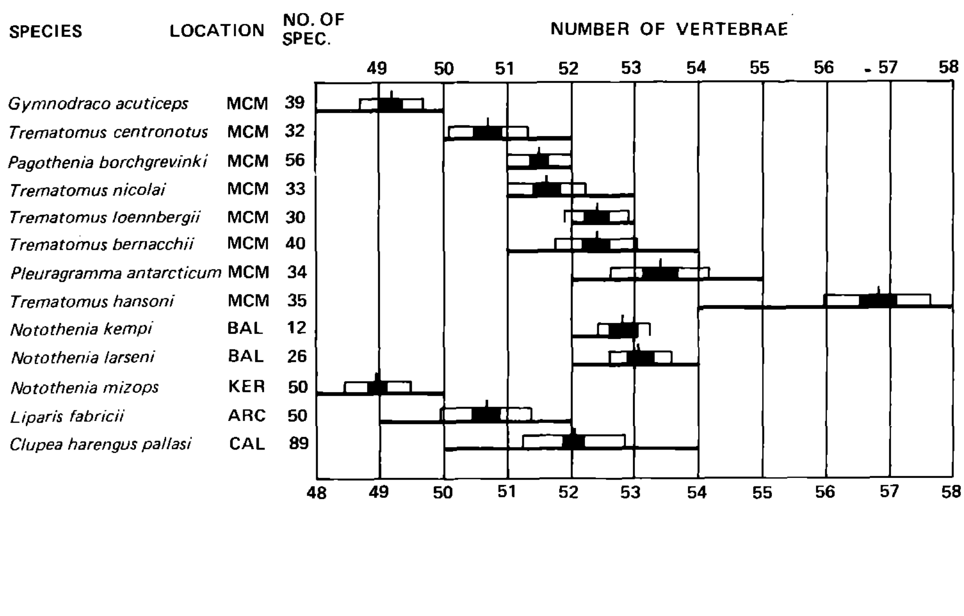

Fig. 1. Dice-Leraas diagram (modification of Hubbs and Hubbs 1953) comparing vertebral variation among antarctic and two non-antarctic species with approximately the same number of vertebrae. Heavy horizontal line is range; short vertical line is mean; black rectangle is two SEM on each side of the mean; one-half of each black rectangle plus white rectangle is one SD on each side of the mean. See Table 1 for location key

Table 1. Vertebral variation in McMurdo Sound species compared to fishes from other antarctic, arctic and temperate locations. Location key: MCM = McMurdo Sound (77 °S); BAL = Balleny Is. (67 °S); KER = Kerguelen IS. (49 °S), Andriashev (1959); ART = Western Canadian Arctic (75 °N), Able and McAllister (1980); CAL = California, Hubbs (1925); MIS = Mississippi, Chernoff et al. (1981); FRW = Freshwater: *Coregonus* – Minnesota, Eastman (unpublished); *Percina* – Michigan, Bailey and Gosline (1955)

Species	Location	N	$\bar{X}$	SD	SEM	V
Gymnodraco acuticeps	MCM	39	49.15	0.49	0.078	0.99
Trematomus centronotus	MCM	32	50.72	0.63	0.112	1.25
Pagothenia borchgrevinki	MCM	56	51.48	0.50	0.067	0.98
Trematomus nicolai	MCM	33	51.55	0.62	0.107	1.20
Trematomus loennbergii	MCM	30	52.37	0.49	0.090	0.94
Trematomus bernacchii	MCM	40	52.38	0.63	0.099	1.20
Pleuragramma antarcticum	MCM	34	53.41	0.78	0.134	1.47
Trematomus hansoni	MCM	35	56.80	0.83	0.141	1.47
Notothenia kempi	BAL	12	52.83	0.39	0.112	0.74
Notothenia larseni	BAL	26	53.08	0.48	0.095	0.91
Notothenia mizops	KER	50	48.98	0.52	0.073	1.05
Liparis trunicatus	ART	39	47.54	0.91	0.146	1.92
Liparis fabricii	ART	50	50.66	0.72	0.102	1.42
Clupea harengus pallasi	CAL	89	52.03	0.80	0.085	1.54
Menidia beryllina	MIS	30	39.60	0.77	0.141	1.94
Coregonus artedii	FRW	28	58.36	0.95	0.180	1.63
Percina caprodes semifasciata	FRW	33	41.97	0.59	0.102	1.40

cies from non-antarctic locations. For example, in Andriashev's (1959) sample of *Notothenia mizops* from Kerguelen, a subantarctic island, V = 1.05. Values of V for *Notothenia kempi* and *N. larseni* from the Balleny Islands are also low (<1.0), although sample size is small. These species are included because they inhabit a relatively constant (but >0 °C) water layer, at a depth of 100 m, throughout the year (DeVries and Eastman 1981).

The F-distribution was used to test the significance of differences between two location variances, ln variances and $(V)^2$. Table 2 presents the results of F-tests comparing the mean variance of the McMurdo Sound species to that of species or species groups from two other antarctic and four non-antarctic locations. F-tests of the ln variance and $(V)^2$ resulted in identical levels of significance and are therefore not shown in Table 2.

In four of the six comparisons the vertebral variance of McMurdo Sound species is significantly different at the level $0.01 < P \leqslant 0.05$. The null hypothesis is, therefore, rejected and it may be concluded that the vertebral variances are different. Inspection of the variance values in Table 2 indicates that McMurdo Sound species are less variable than arctic and temperate species in three out of the four significant comparisons. Although the McMurdo Sound species appear to be more variable than the Balleny Islands species, the small size of the Balleny sample casts some degree of uncertainty on this conclusion.

Table 2. Mean variance comparison of McMurdo Sound species with those from six other locations. (* denotes $P < 0.05$; n.s. denotes $P > 0.05$). F-tests of ln mean variance and $(V)^2$ comparisons resulted in identical levels of significance

Location	Mean variance	df	F
McMurdo Sound	0.4022	291	–
Balleny Islands	0.1927	36	2.09*
Kerguelen Islands	0.2649	49	1.52 n.s.
Canadian Arctic	0.6744	87	1.68*
California	0.6466	88	1.61*
Mississippi	0.5931	29	1.48 n.s.
Freshwater	0.6238	59	1.55*

Discussion

There is very little information on vertebral number and variation in notothenioid fishes and no data for McMurdo Sound species. Andriashev (1959) surveyed vertebral number in some notothenioids and DeWitt and Hureau (1979) detected a difference in vertebral counts for populations of *Chionodraco hamatus* from East and West Antarctica. They attributed these differences to development in waters of different temperatures. Based on significant differences in vertebral number, Freytag (1980) recognized distinct populations of *Notothenia rossii marmorata* from South Georgia and the South Shetlands.

The Nototheniidae is the most numerous and diverse family of the suborder Notothenioidei (Marshall 1964). All McMurdo Sound species in this study, except *Gymnodraco,* are nototheniids. Vertebral counts for McMurdo Sound nototheniids, including two not utilized in the current study, are: *Trematomus* (5 species) – 50–58; *Pagothenia borchgrevinki* – 51–52; *Pleuragramma antarcticum* – 52–55; *Aethotaxis mitopteryx* – 52–53 and *Dissostichus mawsoni* – 53 (Eastman, unpublished observations). The similarity of these counts is unusual since the average *D. mawsoni* is 250 times heavier and 6 times longer than average species of the other four genera. This is an apparent exception to the Pleomeristic Rule (Lindsey 1975), the tendency among related fishes for vertebral number to be positively correlated with maximum body length.

Although there is probably no single explanation for pleomerism, it is possible that swimming efficiency and hydrodynamics could influence pleomerism (Lindsey 1975). Lindsey suggests that large individuals may require more vertebrae for flexible swimming movements than do small individuals. In this regard, nototheniids may not exhibit pleomerism because the vertebral column is not involved in normal swimming movements. Most species are labriform swimmers and row themselves through the water with their pectoral fins (Eastman and DeVries 1981, 1982).

Most McMurdo Sound species are small sedentary fishes with life cycles that are confined to the Sound. Wohlschlag (1961) reported that *Trematomus bernacchii* was active and feeding all winter while Dearborn (1965) found that this species spawned on the bottom in December and January. Most species in McMurdo Sound are ecologically similar to *T. bernacchii* (Eastman and DeVries 1982) and probably do not migrate in or out of the

Sound. Thus, the eggs of these species develop in the thermally stable waters of the Sound.

Pleuragramma is pelagic (DeVries and Eastman 1978) and it is possible that this species may move in and out of McMurdo Sound. Its eggs may be subject to a slightly different thermal regime. It is also possible that large *Trematomus hansoni* (>300 mm TL) migrate in and out of the Sound as these individuals are never captured until late in the austral spring (A. L. DeVries, personal observation). Most McMurdo Sound species, however, experience no temperature shifts or shocks during their life in one of the most physically predictable natural environments in the world.

Although vertebral number is the least variable meristic character in fishes (Bailey and Gosline 1955), a variety of environmental factors, especially temperature, are known to influence vertebral number within the limits allowed by the genotype (Fowler 1970). My study of McMurdo Sound fishes was designed to examine the magnitude of vertebral variation in a group inhabiting a thermally stable body of water. The fact that these fishes exhibit significantly less vertebral variation than most of the temperate and arctic species used for comparison may or may not be related to temperature. In an observational study of a natural population, it is impossible to prove that stable water temperature is responsible for a reduction in vertebral variation. Thus any explanation for reduced vertebral variation in the McMurdo Sound species is conjectural, although the thermal constancy of the environment is certainly a plausible suggestion.

It is also possible that the genotype of McMurdo Sound species restricts the amount of vertebral variation. My data provide no information on genotypic variability of these fishes, however, Somero and Soulé (1974) studied protein polymorphism in three species of *Trematomus* from McMurdo Sound. They sought to test an aspect of the niche-variation hypothesis predicting that fishes from stable thermal habitats would exhibit less protein polymorphism than fishes from thermally variable habitats. Using estimates of mean individual heterozygosity, they found that fishes from stable thermal habitats (range $<5\,^{\circ}$C) did not differ significantly from fishes with a thermal range of $5\,^{\circ}$C or greater.

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