

Growth and Reproduction of the Antarctic Nototheniid Fish *Pagothenia borchgrevinki*

N. W. Pankhurst

Leigh Marine Laboratory, University of Auckland, Private Bag, Auckland, New Zealand

Received 12 March 1989; accepted 2 November 1989

Summary. Growth and reproductive parameters were recorded from *Pagothenia borchgrevinki* captured from beneath the sea ice in McMurdo Sound during October and November 1987. Fish were aged on the basis of unvalidated check rings in otoliths. Fish were estimated to be 2–7 years old. There was good correlation of estimated ages with length–frequency modes for a number of year classes. Growth was linear, and did not approach an asymptote with increasing age. Most females were in the early stages of vitellogenesis, however, 2 fish showed evidence of imminent or recent spawning activity. Males were all in the early stages of spermatogenesis. Relative fecundity was low, and this was associated with large egg size. Ovarian development was group synchronous, and it appears that spawning mainly occurs during winter.

Introduction

The characteristics of growth and reproduction of Antarctic fishes are known largely from studies of open water populations (North and White 1987). Growth in these species is typically slow, maturation delayed, and reproduction seasonal, with the production of large yolky eggs and hence large larval size at hatching. Owing to seasonal or permanent inaccessibility due to sea ice, there is less information on species or populations from continental regions. The proximity of a number of Antarctic bases to hard ice has, however, allowed a number of 'land-based' studies. Growth data for the nototheniid *Dissostichus mawsoni* from McMurdo Sound (Burchett et al. 1984) shows that here also, fish are slow growing, late to mature and have long life-spans. A year-round study of *Trematomus bernacchii* in McMurdo Sound (Dearborn 1965) established that reproduction was seasonal, with spawning occurring in late spring. The limited data available suggest that the characteristics of growth and reproduction in continental areas are similar to those reported for oceanic areas.

The cryopelagic *Pagothenia borchgrevinki* is a common species from continental coastal areas, and aspects of its physiology have been the subject of intensive study (reviewed by MacDonald et al. 1987). To date, however, there are no published data on growth and reproduction in high Antarctic populations of this species. There is some information on the reproductive biology of *P. borchgrevinki* from lower latitudes (Andriashev et al. 1979; Butskaya and Faleeva 1987). This study examines growth and reproductive parameters of fish from a population of *P. borchgrevinki* from beneath sea-ice in McMurdo Sound.

Materials and Methods

Specimens of *P. borchgrevinki* were captured from beneath the sea-ice off Scott Base, McMurdo Sound, during October and November, 1987, by jig-fishing through holes cut in the sea-ice. Two hundred and four fish were examined. Length, total body and gonad weight, and macroscopic condition were recorded at capture. Gonadosomatic indices (GSI) were calculated as gonad weight/total body weight $\times 100$. Saggital otoliths were removed for age estimation. Pieces of ovarian tissue were fixed overnight in Bouin's fixative, then stored in 70% ethanol. Ovarian fecundity was estimated from 13 females with ovaries containing vitellogenic oocytes. Approximately 0.5 g of fresh ovary was excised, weighed and placed in a small volume of teleost saline. Vitellogenic oocytes were dispersed from the ovarian stroma and counted. Fecundity was calculated as number of oocytes in the sub-sample \times total gonad weight/sub-sample weight.

Fixed tissue was dehydrated in an ethanol series, embedded in paraffin, sectioned at 7 μm , and stained with hematoxylin and eosin. Size frequency distribution of oocytes at different developmental stages was determined from ovarian sections using an ocular micrometer. Measurements were only made from oocytes in which the nucleus was visible. Proportions of gamete stages in testis sections were estimated by scoring the stage present under the intersects of an ocular grid (100 points) which covered an area of 0.063 mm².

Ages were estimated from otoliths that had been lightly burned, cracked across the nucleus and embedded in silicone on glass slides. A drop of glycerol was placed on the fractured face and otoliths were examined using a binocular microscope.

Differences in growth between the sexes were assessed using oneway ANOVA of log transformed data. Best-fit curves were fitted to growth data using the GRAPHER programme package.

Results

Otoliths of most fish were found to contain clear large check rings. A small number of fish had otoliths with rings that were incomplete or difficult to read. These fish were discarded from the analysis. The smallest fish examined (total length 84 mm) was estimated to be 2+ years old (i.e. 2 check rings) whereas the largest fish (total length 229 mm) was estimated to be 7+ years old. Growth in length was linear over the size range examined with linear regression of age on length giving an r value of 0.998. The relationship between mean weight and estimated age was best described by a second order polynomial (Fig. 1). There was no significant difference in size at age between the sexes. Asymptotic length was estimated from a Walford plot (Ricker 1958) at 531 mm, and used to calculate values of K for a range of measured values using the Von Bertalanffy growth function (VBGF). K ranged from 0.07–0.076. Asymptotic weight could not be estimated in the same way, as annual weight increments tended to increase with increasing age. Mean lengths at estimated age corresponded well with peaks in the size frequency distribution for fish estimated to be 4–7 years old (Fig. 2). Insufficient numbers of smaller fish were captured for adequate comparison of length frequency modes, and estimated gas.

The majority of female fish captured had ovaries that were dominated by oocytes in endogenous or early exogenous vitellogenesis (Stages 2 and 3, Table 1). There were smaller numbers of females with only previtellogenic oocytes in the ovary (Stage 1), and only 2 fish showing evidence of imminent or recent spawning activity (final oocyte maturation (Stage 4) and spent (Stage 6) respectively). There was a clearly identifiable clutch of maturing oocytes (group synchrony) at all stages of vitellogenesis (Fig. 3a). Measurement of the fresh hydrated oocytes from

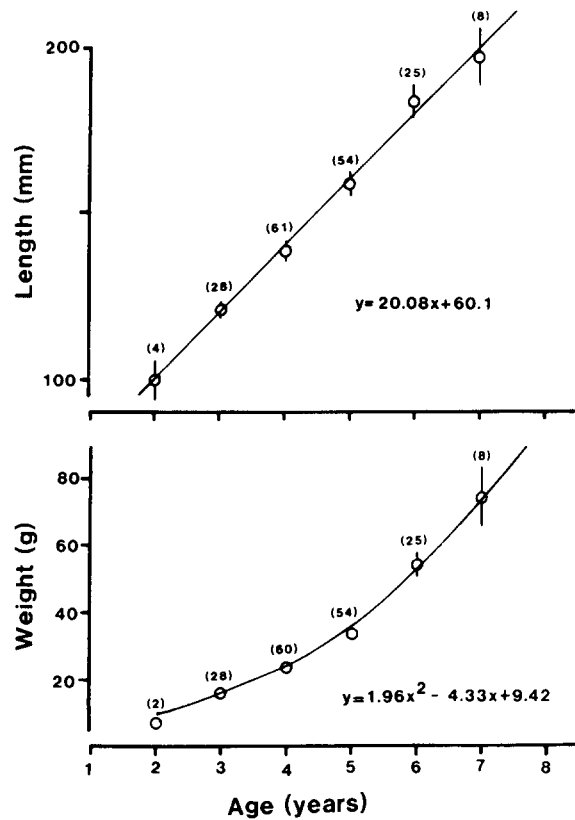


Fig. 1. Change in length and weight with presumptive age in *Pagothenia borchgrevinki* captured from McMurdo Sound during spring 1987. Values are mean \pm SE(n)

the single Stage 4 female captured (oocyte diameter 3.5–4.0 mm) confirmed this.

Absolute fecundity ranged from 1100 in a 179 mm (49 g) fish to 2750 in a 212 mm (103 g) fish. There was a linear relationship between weight (x) and fecundity (y) (y

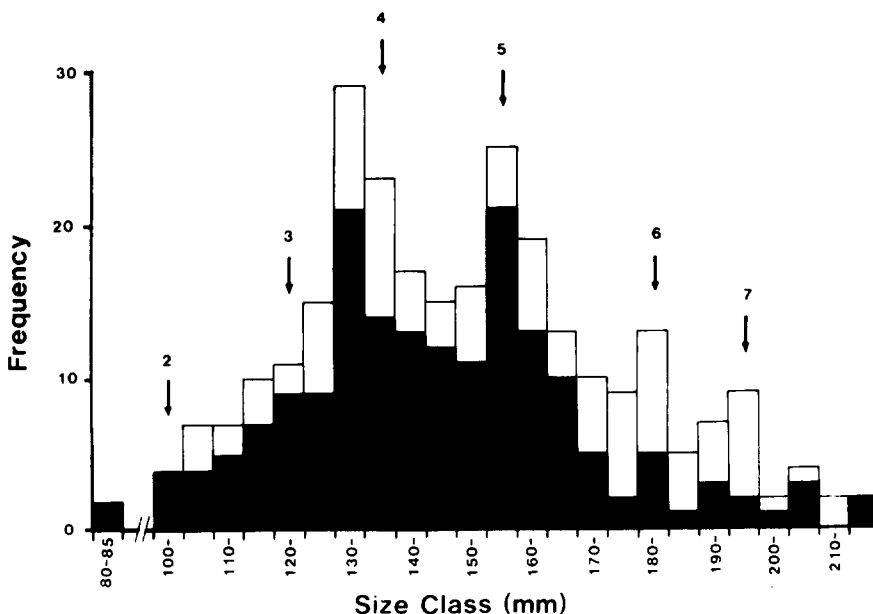


Fig. 2. Size frequency distribution of *Pagothenia borchgrevinki* captured from McMurdo Sound during spring 1987. White bars = all fish; black bars = males only. Numbered arrows show the mean length at age (years)

Table 1. Macroscopic and histological characteristics of gonads of *Pagothenia borchgrevinki* captured from McMurdo Sound during spring 1987

Stage ^a	Macroscopic appearance	Histology	GSI (mean ± SE)
Males			
1 (1)	Small threadlike testis	spermatogonia only	0.05 ± 0.003 (n = 101)
2. (2)	Testis enlarged but no milt in cut testis	Primary spermatocytes dominate; small numbers of secondary spermatocytes and spermatogonia	0.90 ± 0.16 (n = 24)
Females			
1. (1)	Small clear ovary, oocytes not visible	Oocytes previtellogenic	0.99 ± 0.08 (n = 18)
2. (2-3)	Clear ovary with small clear oocytes visible	Previtellogenic, endogenous and early exogenous vitellogenic oocytes	1.79 ± 0.14 (n = 31)
3. (2-3)	Opaque ovary with maturing yolky eggs	Previtellogenic, endogenous and exogenous vitellogenic oocytes	3.52 ± 0.15 (n = 28)
4. (2-3)	Opaque ovary with hyaline mature oocytes	Final oocyte maturation of leading clutch of vitellogenic oocytes	28.80 (n = 1)
5. (4)	Ovulated		
6. (5)	Spent; ovary flaccid and bloody	As for stage 2 but post-ovulatory follicles present	5.09 (n = 1)

^aStages of Everson (1977) are given in parentheses for comparison

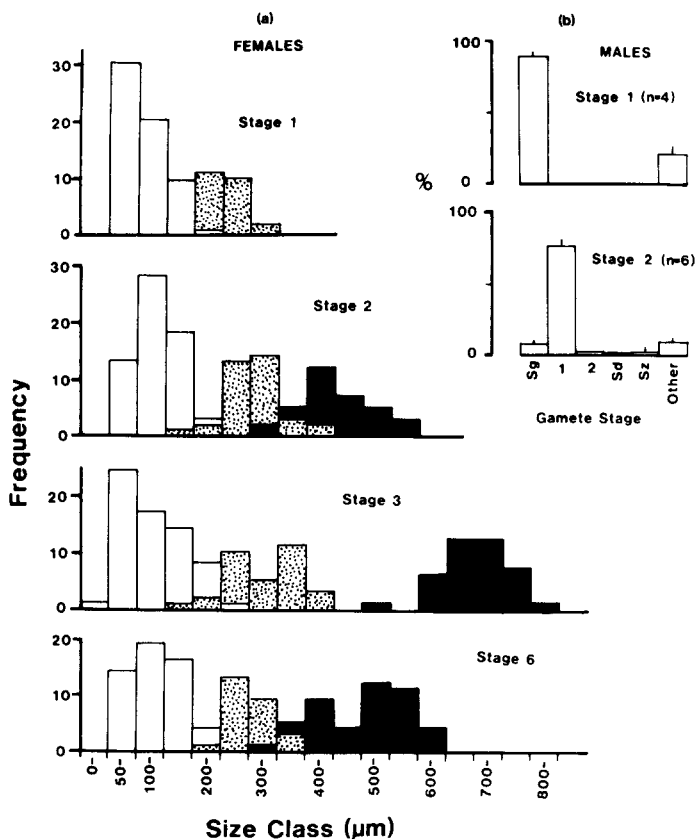


Fig. 3. Size-frequency distribution of oocytes (a) and proportions of gametes present in testes (b) from representative gonad stages of *Pagothenia borchgrevinki* captured from McMurdo Sound during spring 1987. Females; clear bars = previtellogenic oocytes, stippled bars = endogenous vitellogenesis, black bars = exogenous vitellogenesis. Males; sg = spermatogonia, 1 = primary spermatocytes, 2 = secondary spermatocytes, sd = spermatids, sz = spermatozoa

= 25.3x - 23.6, $r = 0.90$, $n = 13$) giving a calculated relative fecundity value of 25,300 eggs.kg⁻¹ body weight.

Most males had small regressed or immature testes (Stage 1) containing spermatogonia only. A smaller number of males had enlarged testes in which most of the gametes were primary spermatocytes (Table 1, Fig. 3b).

Females with developing vitellogenic oocytes (Stage 3) were found among age classes from 4+ years onwards (Table 2) whereas younger fish were Stages 1 or 2. A number of 4+ and 5+ fish were also classified as Stage 1. The Stage 4 and 6 females were both 6+ years old. Males up to 5+ years old were predominantly Stage 1 although Stage 2 males as young as 3+ years were found.

Discussion

P. borchgrevinki aged on the basis of the unvalidated technique presented here showed no evidence of decreasing growth rates with advancing age. This is in contrast to the growth pattern often found in fish where growth is initially rapid, then slows usually at or near the onset of sexual maturity, to approach an asymptotic value (von Bertalanffy 1938). *P. borchgrevinki* from the present study were sexually mature within the size-range sampled, so the near linear growth is not due to the fish not having reached sexual maturity. It is possible that the unvalidated ageing technique underestimates the age of larger fish, however there is good correlation between estimated ages and the length frequency modes found among the fish sampled. It is acknowledged that sampling by angling may produce biased samples, and it is possible that larger fish in the population were not sampled. If this is the case, then

Table 2. Presumptive age (years) and macroscopic gonad stage of *Pagothenia borchgrevinki* captured from McMurdo Sound during spring 1987

Age	Stage								
	Males			Females					
	i ^a	1	2	i	1	2	3	4	6
2	1	1		1	1				
3	2	16	2	2	5	1			
4		39	1		6	11	2		
5		28	6		1	9	10		
6		4	9			2	9	1	1
7			3			1	4		

^ai = sexually immature

it is likely that growth does slow in fish older than those sampled here. It is considered less likely that the asymptotic size of 531 mm predicted from the Walford plot is approached (maximum reported size for *P. borchgrevinki* is 280 mm, Foster et al. 1987).

Other Antarctic species show both strongly asymptotic growth curves, and growth curves with long linear portions. Asymptotic growth has been reported for the nototheniids *Notothenia rossii* (Shust and Pinskaya 1978; Burchett 1983), *N. gibberifrons*, *N. kempfi*, *N. larseni*, *Trematomus hansonii* (Shust and Pinskaya 1978), *T. bernacchii* (Wohlschlag 1961), *N. squamifrons* (Shust and Pinskaya 1978; Duhamel and Ozouf-Costaz 1985), and *N. ramsayi* (Ekau 1982) from Antarctic or sub-Antarctic waters, with the point at which growth slows generally corresponding with the onset of sexual maturity. In contrast, growth of *Dissostichus mawsoni* from McMurdo Sound (Burchett et al. 1984) is approximately linear for the first 15–20 years of life. Growth rates of *D. mawsoni* do slow at ages greater than about 20 years, however, this is well past the estimated age at sexual maturity of 8 years (Burchett et al. 1984). Similarly, *D. eleginoides* also mature at 7–8 years but have essentially linear growth for up to 21 years (Hureau and Ozouf-Costaz 1980). Size of both species of *Dissostichus* at age 8 is about 60% of maximum recorded length, and in this respect both are similar to other Antarctic species in which first spawning occurs when 60%–80% of maximum length is attained (Kock 1989). It is not clear, however, why *P. borchgrevinki*, *D. mawsoni* and *D. eleginoides* do not show a marked fall in growth rate after the attainment of sexual maturity. All three species can apparently meet the increased energetic demands of reproduction at small cost to somatic anabolism, and this may be a consequence of the generally low growth rates displayed by these species.

The results of the present study indicate that *P. borchgrevinki* have group synchronous ovarian development in which only one clutch of eggs is matured during a reproductive cycle. Butskaya and Faleeva (1987) also identified a single maturing clutch of oocytes in the ovaries of *P. borchgrevinki* sampled from the Davis Sea. Group

synchrony is typical of polar species (Permitin and Sil'yanova 1971; Duhamel 1982), and is also common among fish from the cool waters of the mid-continental slope (Pankhurst et al. 1987). The functional significance of this type of reproductive pattern may be related to the highly seasonal production peaks associated with higher latitudes (Clarke 1988), and the need for synchronised reproduction to coincide with, or anticipate these peaks.

The predominance of single gamete stages in the testes of *P. borchgrevinki* found in this study, and also by Butskaya and Faleeva (1987) supports the idea that spawning is synchronized within the population, and probably of short duration. Males of other species with group synchronous ovarian development and one spawning per year, typically show sequential dominance of testis sections by a single gamete stage (Pankhurst et al. 1987), whereas males of repeat spawning species tend to have a wide range of gamete stages present in the testis at all times of the year (Pankhurst and Conroy 1987).

Absolute fecundity of *P. borchgrevinki* ranged in the present study from 1100–2750 and is similar to that found in fish from the Davis Sea (1500–3000, Butskaya and Faleeva 1987). Maximum oocyte diameter was, however, greater in the present study (3.5–4.0 mm) than reported earlier (1.9 mm). This is probably due to the fact that the most mature fish sampled by Butskaya and Faleeva (1987) were at the end of the vitellogenic phase, and the oocytes had not begun hydration (GSI maximum of 19.3 versus 28.8 in the present study).

Low absolute fecundity and large egg size are also found in the Antarctic nototheniids *T. bernacchii* (Dearborn 1965), and *Notothenia nudifrons* (Permitin and Sil'yanova 1971; Kock 1989). *D. mawsoni* (Yukov 1971), *N. rossii* and *N. neglecta* (Permitin and Sil'yanova 1971; Kock 1989) have egg-size and relative fecundity similar to that of *P. borchgrevinki*, but higher absolute fecundity by virtue of large body size. A third group (*N. gibberifrons*, *N. larseni*, *N. kempfi* and *N. anqustifrons*) produce smaller eggs and have correspondingly higher relative (and in the case of large-bodied species higher absolute) fecundity (Permitin and Sil'yanova 1971; Sil'yanova 1981; Kock 1989). Species such as *P. borchgrevinki* with large eggs, have larvae that hatch at a large size enabling them to utilise larger prey whose abundance may not be directly associated with production peaks. In consequence, reproduction may not be acutely synchronised with the production cycle (North and White 1987). In contrast, small larvae tend to be produced by species that have reproductive cycles that are more closely matched to the production cycle.

Previous work suggests that spawning of *P. borchgrevinki* occurs during the austral winter. Female *P. borchgrevinki* captured from McMurdo Sound from January to March had oocytes that were only part way through vitellogenesis (J. A. MacDonald, personal communication), and Eastman and DeVries (1985) reported the capture of 'gravid females' from bottom traps set in McMurdo Sound in July. Butskaya and Faleeva (1987)

found females captured from the Davis Sea in July to have 'well-preserved empty follicles', at the same time males with freely running milt occurred. The capture of two females in the present study that had hydrated oocytes and post-ovulatory follicles respectively indicates that at least a small proportion of fish spawn later in the spring. Sampling in the period August–September is required to determine how well spawning is synchronised within the population.

The large eggs of Antarctic species are thought to take 3–5 months to hatch, and may survive for a further 2 months on nutrients from the yolk-sac (North and White 1987). There are no data on the incubation time of *P. borchgrevinki* eggs; however, application of a model developed for forecasting hatching time on the basis of egg size and incubation temperature (Pauly and Pullin 1988) predicts a hatching time of 65 days. If as suggested, spawning occurs in July, and hatching takes 2 months as predicted, then a further 2 months period of dependence on yolk nutrients would take *P. borchgrevinki* larvae into the December primary production peak in McMurdo Sound (Bunt and Lee 1970) at first feeding. A similar situation occurs among the winter spawning fish species from around South Georgia, with larvae from species with large eggs generally hatching from June to November, and zooplankton biomass increasing from about November (North and White 1987).

Acknowledgements. Thanks are extended to John Cargill and Heiko Weix for assistance with fish capture, and to Georgina Andersen for the preparation of histological material. This study was funded by the University Grants Council of New Zealand, and logistic support was provided by the Antarctic Division of the Department of Scientific and Industrial Research. Thanks also to John Montgomery and Malcolm Francis for a critical review of the manuscript.

References

- Andriashev AP, Butskaya NA, Faleeva TI (1979) Sexual cycles of Antarctic fishes *Trematomus bernacchii* and *Pagothenia borchgrevinki* (Nototheniidae) in connection with adaption to living conditions. Dokl Acad Nauk SSSR 248:499–502
- Bertalanffy L von (1938) A quantitative theory of organic growth. Hum Biol 10:181–213
- Bunt JS, Lee CC (1970) Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. J. Mar Res 28:304–320
- Burchett MS (1983) Age and growth of the Antarctic fish *Notothenia rossi* from South Georgia. Br Antarct Surv Bull 60:45–62
- Burchett MS, DeVries A, Briggs AJ (1984) Age determination and growth of *Dissostichus mawsoni* (Norman 1937) (Pisces, Nototheniidae) from McMurdo Sound (Antarctica). Cybium 8:27–31
- Butskaya NA, Faleeva TI (1987) Seasonal changes in the gonads and fecundity of Antarctic fishes *Trematomus bernacchii*, *Trematomus hansonii* and *Pagothenia borchgrevinki* (Nototheniidae). J Ichthyol 27:27–36
- Clarke A (1988) Seasonality in the Antarctic environment. Comp Biochem Physiol 90B:461–473
- Dearbon JH (1965) Reproduction in the nototheniid fish *Trematomus bernacchii* Boulenger at McMurdo Sound, Antarctica. Copeia 3:302–308
- Duhamel G (1982) Biology and population dynamics of *Notothenia rossi* from the Kerguelen Islands (Indian sector of the southern ocean). Polar Biol 1:141–151
- Duhamel G, Ozouf-Costaz C (1985) Age, growth and reproductive biology of *Notothenia squamifrons* Gunther, 1880 from the Indian sector of the southern ocean. Polar Biol 4:143–153
- Eastman JT, DeVries AL (1985) Adaptations for cryopelagic life in the Antarctic nototheniid fish *Pagothenia borchgrevinki*. Polar Biol 4:45–52
- Ekau W (1982) Biological investigations on *Notothenia ramaysi* Regan 1913 (Pisces, Notothenioidei, Nototheniidae). Arch Fischereiwiss 33:43–68
- Everson I (1977) The living resources of the southern ocean. Southern Ocean Fisheries Survey Programme GLO/SO/77/1. FAO Rome, 156 pp
- Foster BA, Cargill JM, Montgomery JC (1987) Planktivory in *Pagothenia borchgrevinki* (Pisces: Nototheniidae) in McMurdo Sound, Antarctica. Polar Biol 8:49–54
- Hureau JC, Ozouf-Costaz C (1980) Age determination and growth of *Dissostichus mawsoni* Smitt, 1898 from Kerguelen and Crozet Islands. Cybium 8:23–32
- Kock K-H (1989) Reproduction in fish around Elephant Island. Arch Fischereiwiss 39:171–210
- MacDonald JA, Montgomery JC, Wells RMG (1987) Comparative physiology of Antarctic fishes. Adv Mar Biol 24:321–388
- North AW, White MG (1987) Reproductive strategies of Antarctic fish. Proc Vth Congr Europ Ichthyol, Stockholm 1985, pp 381–390
- Pankhurst NW, Conroy AM (1987) Seasonal changes in reproductive condition and plasma levels of sex steroids in the blue cod, *Parapercis colias* (Bloch and Schneider) (Mugiloididae). Fish Physiol Biochem 4:15–26
- Pankhurst NW, McMillan PJ, Tracey DM (1987) Seasonal reproductive cycles in three commercially exploited fishes from the slope waters off New Zealand. J Fish Biol 30:193–211
- Pauly D, Pullin RSV (1988) Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ Biol Fish 22:261–271
- Permitin 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 11:693–705
- Ricker WE (1958) Handbook of computations for biological statistics of fish populations. Bull Fish Res Board Can 119:1–300
- Shust KV, Pinskaya LA (1978) Age and rate of growth of six species of Notothenid fish (family Nototheniidae). J. Ichthyol 18:743–749
- Sil'yanova SZ (1981) Oogenesis and stages of maturity of fishes of the family Nototheniidae. J. Ichthyol 21:81–89
- Wohlschlag DE (1961) Growth of an Antarctic fish at freezing temperatures. Copeia 1961:11–18
- Yukov VL (1971) The range of *Dissostichus mawsoni* Norman and some features of its biology. J Ichthyol 11:8–18