Review
Reproduction in Antarctic notothenioid fish

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Abstract: Gonad maturation in Antarctic notothenioid fish is a biennial process although spawning is likely to take place annually. However, part of the populations of *Champsocephalus gunnari* in the Atlantic Ocean sector do not spawn each year. Gonadosomatic index (GSI) of females is 15–40% at spawning. Apart from a few nototheniid species the GSI of males is much less and typically only 15–20% of that of females. Length at first spawning may be from 55% of L_{max} onwards, but in many species it is not attained until 70–80% of the maximum length. The only exception is *Champsocephalus gunnari* at South Georgia which may begin spawning at about 40% of L_{max}. Most species of the Seasonal Pack-ice Zone are autumn/winter spawners, whereas in the High-Antarctic Zone more species spawn in summer and autumn. Spawning time is remarkably constant among populations of some species, in others a latitudinal shift in spawning time is apparent. Fecundity is commonly positively correlated with fish length and weight. It exceeds 100 000 eggs only in a few nototheniid species and is commonly in the order of 1000 to 15–20 000 eggs. Ova diameter varies from 0.8 to 5.0 mm. Egg size distribution among fishes of the Seasonal Pack-ice Zone is bimodal. There is a general trend in nototheniids of increasing egg size and decreasing relative fecundity towards higher latitudes. Incubation time may be up to five months. Eggs of most species are probably left unattended for the long incubation period. Nest guarding has been observed in three species but may be more common in particular among the artedidraconids. A number of reproductive strategies associated with nest guarding, egg size and the duration of the pelagic phase have been identified.

Introduction

The prominent features of the Southern Ocean are its temperatures close to the freezing point of sea water and its extreme seasonality in ice cover and primary productivity. Annual variation in bottom temperatures decreases from 2–3°C in shelf waters at the northern margin of the Seasonal Pack-ice Zone (*sensu* Hempel 1985) to less than 0.1°C in parts of the High-Antarctic Zone close to the Antarctic continent.

The coastal fish fauna is much less diverse on a higher taxonomic level (order, family) than the boreal and Arctic ichthyofaunas. The shelf and upper slope waters are dominated both in terms of species and biomass by a single, endemic perciform suborder, the Notothenioidei. Lacking swim bladders they are considered to be primarily bottom-dwelling and only a few species have secondarily adapted to a more or less permanent pelagic mode of life. Notothenioids are thought to have evolved from a bottom-living ancestral group which became isolated from temperate waters after the establishment of the Antarctic Circumpolar Current some 23–28 m.y. ago (Eastman & Grande 1989). During their emergence they have radiated into the six families Nototheniidae, Channichthyidae, Bathydraconidae,

Artedidraconidae, Harpagiferidae and Bovichtidae with a variety of morphologies from small sculpin-like to large hake-like forms. Their evolution was associated with a number of specializations related to low temperature and trophic factors including the emergence of a unique family, the Channichthyidae (ice fishes). These lack the respiratory pigment haemoglobin (Ruud 1954) and their muscles contain only traces of myoglobin (Hamoir & Gerardin-Otthiers 1980). Notothenioids form two major ichthyofaunal groupings in the Southern Ocean: the less diverse fauna of the Seasonal Pack-ice Zone and around the islands north of it, and the more diverse fauna of the High-Antarctic Zone (Schwarzbach 1988, Tiedtke & Kock 1989, Ekau 1990). Both faunal groups overlap in the southern Scotia Arc and in the Antarctic Peninsula region.

Species of the Seasonal Pack-ice Zone and islands north of it have been commercially harvested since 1969/70. Exploitation of fish in the High-Antarctic Zone started in 1982/83 in the Indian Ocean sector (Kock & Köster 1989). Large-scale harvesting may entail adverse effects for the reproduction of some species.

Early observations on reproduction in notothenioids have already described some common characteristics: prolonged gametogenesis, low fecundity and relatively large yolky eggs (Andriashev 1965). Since then a large number of
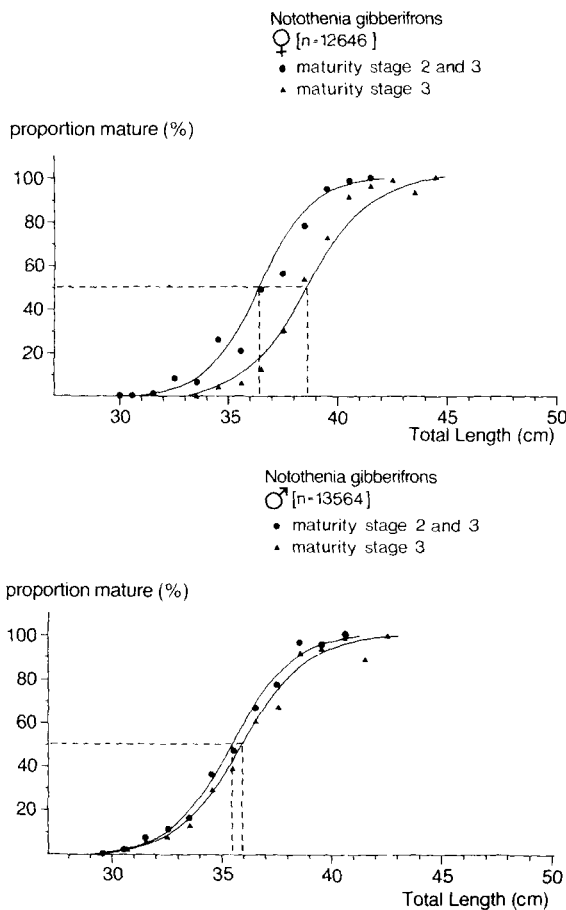
Notothenia gibberifrons
♀ [n=12646]
  • maturity stage 2 and 3
  ▲ maturity stage 3

proportion mature (%)

Notothenia gibberifrons
♂ [n=13564]
  • maturity stage 2 and 3
  ▲ maturity stage 3

proportion mature (%)

Fig. 1. Length at sexual maturity and length at first spawning in *Notothenia gibberifrons* around Elephant Island (from Kock 1989).

studies on Antarctic fish reproduction have been conducted, mainly during scientific activities concomitant to fishing operations or shore-based marine biological programmes. Consequently, most information on annual cycles, spawning and fecundity refers to harvested species in the Scotia Arc and the Kerguelen Islands regions and shallow-water species within easy reach of shore stations (reviews in Everson 1984, Kock 1985, Duhamel 1987a,b, Lisovenko 1987, North & White 1987). Information on High-Antarctic notothenioids has become available only recently and is still much less complete.

Our review summarizes existing information on reproduction as a key parameter in the adaptation of Antarctic notothenioids to the environment and addresses some implications for fisheries management in the Southern Ocean. Terms and definitions used are those given in Kock (1989).

Review of existing information on reproduction

Annual gonad cycle

The maturity scale currently in use for notothenioids is

provided in Table IX. Maturity is an ambiguous term in that it is used to denote two different stages in the life cycle: sexual maturity (often referred to as 'first maturity'), which is attained only once, and spawning maturity which is usually attained each year thereafter until senescence. Some authors, for example Kock (1981, 1989) and Hubold (1984) have classified females as being (sexually) mature (i.e. at least in maturity stage 2 of the scale), when oocytes were visible macroscopically. Others, for example Gubsch (1980 1982) and Sosinski (1981), classified fish as mature only when gonads were enlarged compared to the resting stage (i.e. in maturity stage 3). Fish in stage 2 include maturing virgins, which are unlikely to spawn in the current season, whereas stage 3 is exclusively comprised of current season's spawners (Kock 1989). Logistic curves fitted to data on fish length versus the proportion of fish in maturity stages 2–5 thus estimate length at sexual maturity, those of fish in maturity stages 3–5 estimate length at first spawning. Consequently length at sexual maturity is less than length at first spawning (Fig. 1). The confusion of both terms in a number of studies may explain the sometimes substantial differences in estimates of length at sexual maturity for the same population, for example in *Chaenocephalus aceratus* at South Georgia (Kock *et al.* 1985, table 2).

The development of mature ova is a biennial process, although spawning probably takes place annually thereafter (Everson 1977). Double spawning within a year has so far only been described from captive *Nototheniops nudifrons* (Hourigan & Radtke 1989) and may not reflect natural conditions. Maturing ovaries are typically filled with ova in two stages of maturation. Large yolky oocytes form the current season's spawn. Eggs are probably released as one batch. Intermittent spawning has not been observed and is unlikely given the presence of only one generation of oocytes, which are of very similar size. Ova of 0.5–0.7 mm diameter in various stages of pre-vitellogenic growth represent next year's spawn (Fig. 2).

Complete annual cycles have been described so far only for a few species:

Notothenia cyanobrancha	(Hureau 1970)
Notothenia neglecta	(Everson 1970)
Notothenia rossii	(Kozlov 1982, Kozlov & Silyanova 1983, Duhamel 1987a)
Notothenia squamifrons	(Duhamel 1987a)
Trematomus bernacchii	(Hureau 1970, Andriashev *et al.* 1979, Butskaya & Faleeva 1987)
Trematomus hansoni	(Hureau 1970)
Pagothenia borchgrevinki	(Andriashev *et al.* 1979, Butskaya & Faleeva 1987)
Champsocephalus gunnari	(Duhamel 1987a)

They all show the generalized pattern given by Everson

(1977) for *Notothenia neglecta* at the South Orkney Islands (Everson 1970): a 5–6 month period of recovery after spawning with a low gonadosomatic index (GSI) in females of 3–4 is followed by a steady build-up of the GSI within a few months, when gonads begin to mature again, to 15–40 at spawning. A high GSI of 20–30 in females at spawning is consistent for most of the species and also within populations of one species, for example *Notothenia neglecta* (Table I). This casts some doubts on observations on *Notothenia neglecta* off Terre Adélie and *Paranotothenia magellanica* at Kerguelen Islands: their GSI at spawning appear to be only slightly elevated compared to the remainder of the year (Hureau 1970, tables 1,5).

The GSI is different in males. In some nototheniid species, for example *Notothenia rossii, Notothenia gibberifrons* and probably *Dissostichus eleginoides*, GSI is almost as high as in females. In other nototheniids, channichthyids, the bathydraconid *Parachaenichthys georgianus* and the harpagiferid *Harpagifer antarcticus* GSI of males is typically only about 15–20% of that in females (Fig. 3).

Length and age at first spawning

Length at first spawning is commonly attained at 55–80% of L_{max}. The existing information does not indicate that the notothenioids of the High-Antarctic Zone begin to spawn at a higher value of their L_{max} than those of the Seasonal Pack-ice Zone (Fig. 4). Length at first spawning as a proportion of L_{max} is lowest at about 55–65% in some populations of *Champsocephalus gunnari* and in *Notothenia rossii* and highest at about 80% in *Chaenocephalus aceratus* and *Dolloidraco longedorsalis*. The only exception is *Champsocephalus gunnari* at South Georgia, which matures precociously and spawns at about 40% of L_{max} (Fig. 4). Length at first spawning (in relation to L_{max}) seems very similar in all populations of a species except in *Champsocephalus gunnari*. There is no evidence for delayed maturation in populations of the same species towards higher latitudes. Substantial differences, as observed in populations of *Nototheniops larseni*, are more likely to be caused by deficiencies in the data rather than reflect true differences between populations.

Length (and age) at first spawning in *Champsocephalus gunnari* at South Georgia has remained constant between 1976 and 1985, although the population has undergone considerable fluctuations both in size and composition due to heavy fishing during that period (Kock 1990a).

Age at sexual maturity and age at first spawning are far less well known than length. The main reasons are that growth has either not been studied or that age determinations and corresponding growth curves of one species or population exhibit considerable differences between investigators (Kock *et al.* 1985, Kock 1990b), thus leading to substantial differences in the determination of age at sexual maturity and age at first spawning. Existing information indicates that species which
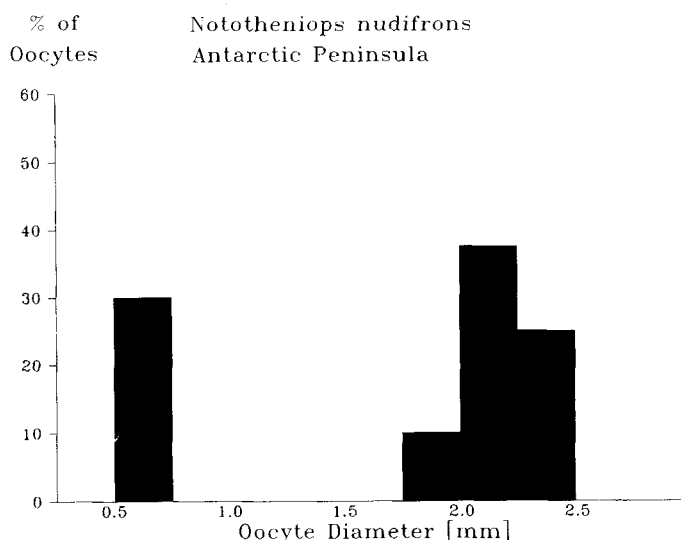

Fig. 2. Size-frequency distribution of pre-vitellogenic oocytes and vitellogenic oocytes in the ovaries of *Nototheniops nudifrons* at the Antarctic Peninsula (from Hourigan & Radtke 1989).
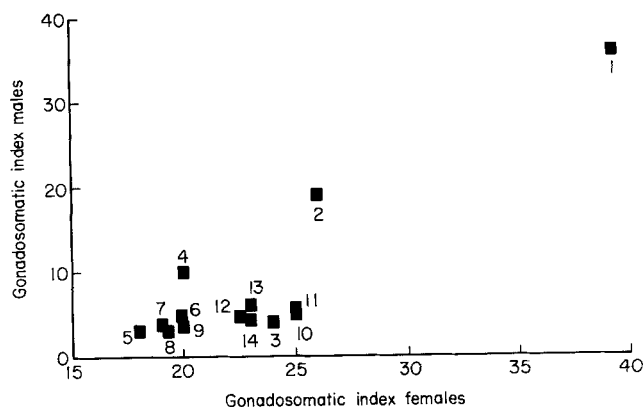

Fig. 3. Gonadosomatic Index (GSI) of males in relation to the GSI of females in 14 notothenioid species.

1. *N. rossii* SG	**2.** *N. gibberifrons* SG.
3. *N. cyanobrancha* Ke.	**4.** *N. neglecta* SO.
5. *T. bernacchii* TA.	**6.** *T. eulepidotus* WS.
7. *T. hansoni* TA.	**8.** *P. borchgrevinki* DS.
9. *C. gunnari* SG.	**10.** *C. aceratus* AP.
11. *Pseudochaenichthys georgianus* SG.	
12. *C. rastrosp.* AP.	**13.** *P. georgianus* SG.
14. *H. antarcticus* SO.	

AP: Ant. Peninsula. Croz: Crozet Is. DS: Davis Sea. Ke: Kerguelen Is. OLB: Ob and Lena Banks. SG: South Georgia. SO: S Orkney Is. TA: Terre Adélie. WS: Weddell Sea.

Table I. Gonadosomatic index (GSI) in females, diameter of oocytes or eggs spawning, incubation and hatching time, size at hatch and duration of larval and juvenile pelagic phase in nototheniids of the Seasonal Pack-ice Zone and around islands north of it.

Species	Locality	GSI	Egg* diameter (mm)	Spawning time	Est. time of incubation (days)	Occurrence of larvae	Size at hatch (mm)	Pelagic phase	Source
Dissostichus eleginoides	Burdwood Bank/ South Georgia	>15	**4.3-4.7**	July-Sept	60-90	November	14	long	Ciechomski *et al.* 1981 Kellermann 1990, Kock *et al.* 1985
Notothenia acuta	Kerguelen Is	-	1.2-1.6	September	-	-	-	-	Duhamel 1987b
Notothenia angustifrons	South Georgia/ S Sandwich Is		*1.6*	June/July?		Nov/Dec	5-7.5	long?	Permitin & Silyanova 1971, Kellermann 1990
Notothenia cyanobrancha	Kerguelen Is	18-24	1.3-1.6	end of Jan (first spawners) April/May	-	-	-	-	Hureau 1970
Notothenia gibberifrons	South Georgia	21-27	1.5-2.5	July/Aug	40-60	September	8.5-11.5	short	Efremenko 1979a, Silyanova 1980, Kozlov 1982, Kellermann 1990,
	Elephant Is/ Ant. Penins.	-	-	Aug/Sept	50-60	November	7.4-9.2	short	Kock 1989, Kellermann 1990
Notothenia kempi	S Orkney Is Ant. Penins.	-	1.2-1.6	Nov/Dec	60	Jan/Feb	7-10	long	Silyanova 1980, Kellermann 1986
Notothenia squamifrons	South Georgia		1.6-1.9	February	-	-	-	-	Silyanova 1980, 1981
	Kerguelen Is	20-30	1.4-1.7	Oct/early Nov	50-70		-	-	Duhamel & Ozouf-Costaz 1985
Notothenia neglecta =*N. coriiceps*[3]	South Georgia	-	**4.1**	April-June[2]	103[2]	early Nov[2]	-	long	White *et al.* 1982, Burchett *et al.* 1983,
	S Orkney Is	>16	>4.0	May	150	-	-	long	Everson 1970, White *et al.* 1982
	Elephant Is/ Ant. Penins.	21-27	**4.3-4.7**	May/June	150	Nov/Dec	12.2-16.3	long	Kock 1989, Kellermann 1990
	S Sandwich Is			May/June	-	-			Kock unpublished
Notothenia rossii	South Georgia	36.5	4.5-5.0	April-June	90-120	September	15	short	Sherbich 1975, Silyanova 1980, Kozlov & Silyanova 1983
	Elephant Is	-	-	May-June	-	-	-	-	Kock 1989
	Kerguelen Is	30-50	**5.0**	June-July	70-100	-		short	Duhamel 1982, Camus & Duhamel 1985

may live to at least 13–20 years old, such as *Notothenia rossii*, *Notothenia neglecta*, *Notothenia gibberifrons* and *Chaenocephalus aceratus*, do not spawn before they are 6–8 years old. *Dissostichus eleginoides*, which may live to 25–30 years old, may be more than 8–10 years old when spawning for the first time (Kock *et al.* 1985). The only exception is *Champsocephalus gunnari* at South Georgia and the Kerguelen Islands, which may spawn for the first time at an age of 2.8–3 years (Duhamel 1987a, Kock 1990a). Small-sized nototheniids in the Seasonal Pack-ice Zone, for

example *Nototheniops* spp. and *Patagonotothen guntheri*, which presumably have a life span of less than 10 years, probably spawn at ages 3 and 4 for the first time. Inserting data on length at first spawning into available growth curves of the High-Antarctic *Pleuragramma antarcticum* and *Trematomus eulepidotus* (Ekau 1988, Hubold & Tomo 1989) indicate that these species do not spawn before they are 7–9 years old.

Length at sexual maturity and length at first spawning are commonly determined by fitting logistic curves to length-

Table I. continued

Species	Locality	GSI	Egg* diameter (mm)	Spawning time	Est. time of incubation (days)	Occurrence	Size at of larvae (mm)	Pelagic hatch	Source phase
Nototheniops larseni	South Georgia	11	1.6-2.0	June/July	60-90	September	8.5-11.2	long	Permitin & Silyanova 1971 Efremenko 1979a, Silyanova 1981
	Elephant Is/ Ant. Penins.	12	**2.0**	July/Aug	60-90	Sept-Nov	7	long	Kellermann 1989, Kock 1989, Konecki & Targett 1989
Nototheniops larseni	Crozet Is	-	2.0	March-June	-	-	-	-	Duhamel & Pletikosic 1983
Nototheniops tchizh[3]	Ob and Lena Banks	11-20	2.2	July/Aug	-	-	-	-	Shandikov 1985
Nototheniops mizops	Kerguelen Is	-	**1.98**	June	-	-	-	-	Duhamel 1987a
Nototheniops nudifrons	South Georgia	17-20	2.0+	April/May	120	Sept/Oct	7	short	Marshall 1953, Silyanova 1981 Kellermann 1990
	Elephant Is/ Ant. Penins.	20-25	2.0-2.5	April/May[1]	120[2]	September	7	short	Kock 1989, Riehl & Kock 1989 Kellermann 1989, Hourigan & Radtke 1989
Paranotothenia magellanica	Kerguelen Is	3.2	0.8	April	-	-	-	-	Hureau 1970
Patagonotothen guntheri	South Georgia	16-18	1.0-1.2	July/Aug?					Lisovenko 1987
Trematomus bernacchii	Ant. Penins.		**4.1**	Nov	90-100				Moreno 1980
Trematomus hansoni	South Georgia	20	3.8	Feb/March	-	March-July	12	-	Burchett et al. 1983 Kellermann 1990, Kock unpubl.
	Ant. Penins.	22	3.5-3.7	February	-	-	-	-	Bellisio 1966
Trematomus newnesi	Ant. Penins.	-	2.5	March-April	-	Oct-Nov	9	short	Shust 1987, Kellermann 1990

[1] May/June in tank experiment   [2] in tank experiment   [3] =*N. larseni* (De Witt et al. 1990)

*Egg diameters marked in bold originate from eggs after fertilization
Egg diameters marked in italics originate from oocytes visually classified as ripe or estimated from the smallest observed yolk-sac larvae.

maturity data (see Kock 1989). In populations of *Champsocephalus gunnari* in the Scotia Arc area these data are distributed asymmetrically. There are more fish with ovaries in the resting stage (maturity stage 2) in the greater length classes than fish with developing gonads (maturity stage 3) in the shorter length classes (Fig. 5) (Lisovenko & Silyanova 1980, Kock 1981, Sosinski 1981, Balguerias & Quintero Perez 1987, Kock 1990a). It indicates that 15–25% of the population around South Georgia, and an unknown proportion of the other populations in the Atlantic Ocean

sector, do not spawn each year (Kock 1990a). A similar phenomenon has been observed in the two populations on the Kerguelen Plateau only once, in 1983, when spawning concentrations and aggregations of non-spawners were observed on the shelf at the same time (Duhamel, personal communication).

Spawning season and duration of spawning

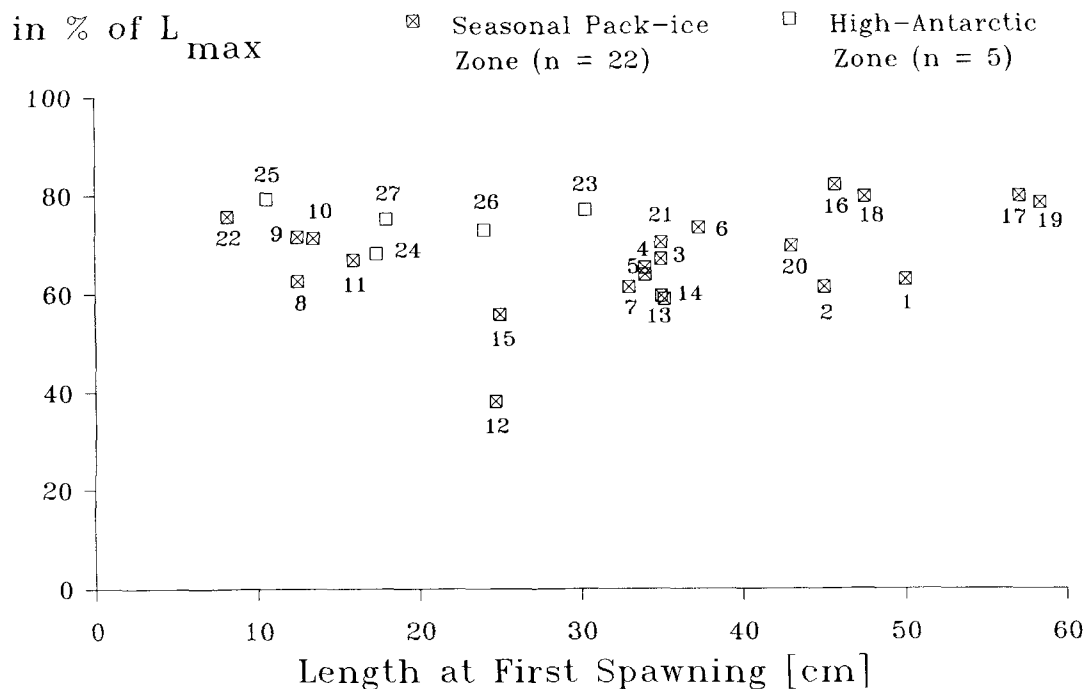Spawning time and the duration of spawning seem to be well

Fig. 4. Length at first spawning in relation to the maximum observed length L_{max} in 24 populations of 16 notothenioid species.

1. *N. rossii* SG.	**2.** *N. rossii* Ke.	**3.** *N. neglecta* SO.	**4.** *N. neglecta* AP.	**5.** *N. gibberifrons* SG.
6. *N. gibberifrons* AP.	**7.** *N. squamifrons* Ke.	**8.** *N. tchizh* OLB.	**9.** *N. larseni* Croz.	**10.** *N. nudifrons* AP.
11. *P. guntheri* SG.	**12.** *C. gunnari* SG.	**13.** *C. gunnari* SO.	**14.** *C. gunnari* AP.	**15.** *C. gunnari* Ke.
16. *C. aceratus* ♂ SG.	**17.** *C. aceratus* ♀ SG.	**18.** *C. aceratus* ♂ AP.	**19.** *C. aceratus* ♀ AP.	**20.** *Ps. georgianus* SG.
21. *C. rastrospinosus* AP.	**22.** *H. antarcticus* SO.	**23.** *C. myersi* WS.	**24.** *Pl. antarcticum* WS.	**25.** *D. longedors.* WS.
26. *T. lepidorhinus* ♀ WS.	**27.** *T. lepidorhinus* ♂ WS.		Localities see Fig. 3.	

known for a larger number of species and populations (Tables I,III,V,VII). However, these are often generalized from single observations of gravid individuals or extrapolations from GSIs. Catches of a larger number of running ripe males and females are scarce and confined to a few species in the Seasonal Pack-ice Zone and the islands north of it:

Notothenia rossii	Kerguelen Islands (Duhamel 1987a)
Notothenia neglecta	Elephant Island (Kock 1989)
Champsocephalus gunnari	Kerguelen Islands (Duhamel 1987a)
Harpagifer antarcticus	Signy Island (Burren 1988)

They indicate that peak spawning in these species, when 80–90% of a population is reproducing, occurs within a short period of 2–4 weeks. Unimodal and narrow length compositions of larvae in other species, for example *Notothenia gibberifrons* and *Nototheniops larseni,* may also argue for a short period of intensive spawning. Larval hatch extended over a period of several months, as in *Psilodraco breviceps, Trematomus hansoni* (North, personal communication) and *Chaenocephalus*

aceratus, gives evidence for a longer spawning season in these species. Two peaks in spawning time have been described for *Notothenia cyanobrancha* at Kerguelen Islands (Hureau 1970) (Table I).

The majority of species and populations in the Seasonal Pack-ice Zone and around the islands north of it are autumn and winter spawners. Existing information on spawning in the High-Antarctic Zone gives evidence for a higher proportion of spring and particularly summer spawners being present (Fig. 6).

Spawning times may be consistent within several populations of a species, e.g. *Notothenia neglecta, Nototheniops nudifrons, Trematomus hansoni* and *Pseudochaenichthys georgianus* in the Atlantic Ocean sector. They may indicate a latitudinal trend, at least in the Atlantic Ocean sector populations of the same species spawn about a month or two later in the more southerly South Orkney Islands or the Antarctic Peninsula region than around South Georgia (e.g. *Champsocephalus gunnari, Chaenocephalus aceratus, Notothenia rossii*) (Tables I,III). Given the unusual low peak GSI in *Notothenia neglecta* at Terre Adélie (Table V) the species probably does not spawn there in January (Kock 1989) as previously suggested by Hureau (1970).

Spawning areas

Information on spawning areas is often given only in very broad terms, for example 'inshore waters' or 'on the slope'. Accurate information on spawning localities, either from catches of spawning individuals or egg and larval surveys, is sparse and confined to some of the commercially exploited species, e.g. *Notothenia rossii*, *N. squamifrons*, *Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Pseudochaenichthys georgianus* around South Georgia and the Kerguelen Islands, or some shallow water species, e.g. *Harpagifer antarcticus*, in the vicinity of shore stations. Hardly any information exists on the spawning localities of fish of the High-Antarctic Zone.

Depending on species the notothenioids spawn in different parts of the continental shelf. Shallow water spawners are *Notothenia angustifrons*, *Nototheniops nudifrons*, *Parachaenichthys georgianus*, *Notothenia neglecta* at South Georgia, *Trematomus bernacchii* in the Antarctic Peninsula region and *Harpagifer* ssp. (Moreno 1980, Burchett *et al.* 1983, Daniels 1978, Burren 1988). The deeper (>80–100 m) inshore waters and fjords are spawning grounds for *Champsocephalus gunnari* at South Georgia and Kerguelen Islands, and *Chaenocephalus aceratus*, *Pseudochaenichthys georgianus* and *Trematomus hansoni* at South Georgia (Olsen 1955, Kock 1981, Burchett *et al.* 1983, Duhamel 1987a). Offshore shelf areas (>150m) are spawning grounds for *Notothenia rossii* and *Notothenia gibberifrons* at South Georgia, *Notothenia neglecta* at Elephant Island (Permitin & Silyanova 1971, North 1988, Kock 1989, Kellermann 1990a). Spawning on the slope is known for *Notothenia kempi* in the Antarctic Peninsula region, *Notothenia rossii* and *Notothenia squamifrons* in the Kerguelen Islands, and *Dissostichus eleginoides* on Burdwood Bank, off South Georgia and in the Kerguelen Islands (Duhamel 1987a, Kellermann & Kock 1989, Kellermann 1990a, Kock, unpublished).

Spawning of *Pleuragramma antarcticum* is likely to occur in front of the great ice shelves of Antarctica (Kellermann 1986). An egg mass of *Trematomus eulepidotus* has been collected at 200 m depth in the eastern Weddell Sea (Ekau 1989).

Spawning migrations

Spawning migrations have been described for a number of species in the Seasonal Pack-ice Zone and the islands north of it. All three icefish species present around South Georgia move inshore for spawning. Males start their spawning migration earlier than females (Kock 1981). *Notothenia rossii* migrate from their feeding grounds on the north eastern part of the Kerguelen Plateau to the south eastern shelf for spawning (Meissner *et al.* 1974, Duhamel 1987a). Inshore migrations associated with reproduction are also likely for *Nototheniops nudifrons* around Elephant Island
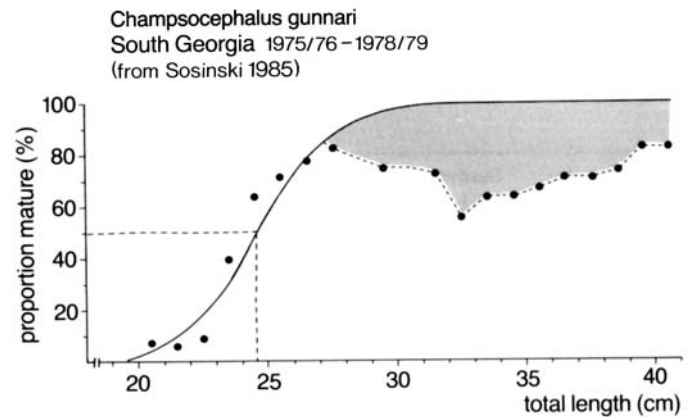

Champsocephalus gunnari
South Georgia 1975/76 – 1978/79
(from Sosinski 1985)

Fig. 5. Spawning maturity curve of *Champsocephalus gunnari* around South Georgia. The shaded area denotes the proportion of individuals which refrain from spawning in the current season (from Kock 1990a).
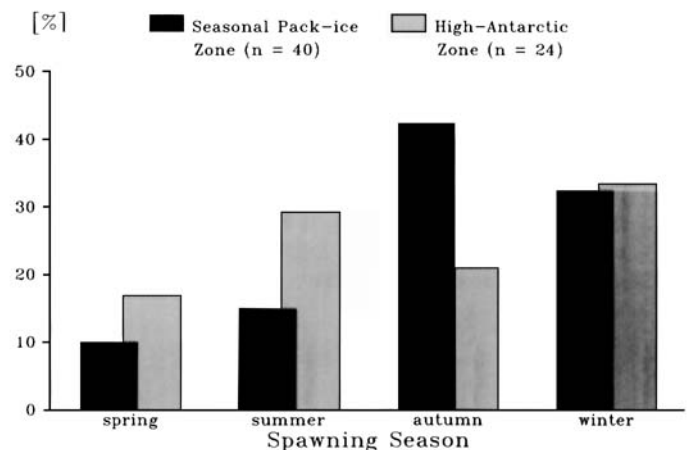

Fig. 6. The proportion of species or populations in each spawning season for notothenioids in the Seasonal Pack-ice Zone and around islands north of it, and in the High-Antarctic Zone.

(Kock 1989). In contrast, *Notothenia neglecta*, apart from the population at South Georgia, move from shallower inshore waters to deeper waters for spawning (Everson 1970, Hureau 1970, Kock 1989).

Fecundity

Estimates of fecundity sometimes originate from ovaries which have been collected several months before spawning. As a result, maturing ova forming the current season's spawn are still quite small and difficult to distinguish visually from ova which will mature in the following year. Apparent differences in relative fecundity at the same egg size between

Table II. Fecundity in nototheniids of the Seasonal Pack-ice Zone and the islands north of it.

Species	Locality	Nos. invest.	Length range (cm)	Potential fecundity min	Potential fecundity max	Relative fecundity	Fecundity in relation to length (cm)	Fecundity in relation to weight (g)	Source
Dissostichus eleginoides	Burdwood Bank	26	93-131	238314	545665	16.1-31.3	$F=2104.1 \cdot L^{1.088}$	$F=181041+10.29W$	Kock *et al.* 1985
Notothenia acuta	Kerguelen Is	8	23-27	41650	86580		-	-	Duhamel 1987a,b
Notothenia angustifrons	S Sandwich Is	5	13-17	5610	12900	250-352	-	-	Permitin & Silyanova 1971
Notothenia cyanobrancha	Kerguelen Is	-	-	20000	30000	c. 100	-	-	Hureau 1970
Notothenia gibberifrons	South Georgia	9	40.5-49.0	60610	106700	50-104	-	-	Permitin & Silyanova 1971
	South Georgia	63	35-52	30000	135000	48-130[1]	$F=0.54 \cdot L^{3.7}$	$F=35.8 \cdot W^{1.1}$	Lisovenko & Silyanova 1979, Silyanova 1982
	South Georgia	20	38-50	26349	113436	33.9-101.7	-	-	Kompowski 1985,
	S Orkney Is	4	35-42	23570	84660	59-120	-	-	Permitin & Silyanova 1971
	Elephant Is	41	34-47	21699	143620	36.8-100.0	$F=0.93 \cdot 10^{-5} L^{6.0899}$	$F=-31624+107.7W$	Kock 1989
Notothenia kempi	S Orkney Is	6	26.2-41.0	17500	161010	78-170	-	-	Permitin & Silyanova 1971
	S Orkney Is	12	26-38	25000	78000	78-193[1]	$F=0.01 \cdot L^{4.4}$	$F=37.3 \cdot W^{1.2}$	Lisovenko & Silyanova 1980 Silyanova 1982
Notothenia squamifrons	South Georgia	11	34-52	68000	180000	67-159[1]	$F=111.6 L^{1.8}$	$F=4517 \cdot W^{0.43}$	Lisovenko & Silyanova 1980 Silyanova 1982
	Kerguelen Is	134	27-48	40760	284610	133-226	$F=0.5781 \cdot L^{3.362}$	-	Duhamel & Ozouf-Costaz 1985, Duhamel 1987b
Notothenia neglecta = *N. coriiceps*[5]	South Georgia	9		36397	48383	-	-	-	Burchett *et al.* 1983
	S Orkney Is	19		7000	35000	7.5-15.5	-	$F=18.29+13.2 (W-1.578)$ [2]	Everson 1970
	S Orkney Is	1	43.2		12915	8	-	-	Permitin & Silyanova 1971
	S Orkney Is	6	36.3-47.3	15800	32700	18.3-31.0[3]	-	-	Bellisio 1964
	Elephant Is	2	35.8+40.7	10956	14710	10+16	-	-	Permitin & Silyanova 1971
	Elephant Is	36	34-55	6897	41024	6.6-17.3	$F=0.01026 \cdot L^{3.7969}$	$F=-2347+13.21 \cdot W$	Kock 1989
	S Sandwich Is	22	34-50	6719	33812	7.3-14.1	$F=0.0128 L^{3.7240}$	$F=4259.5+14.58 \cdot W$	Kock 1989
	Terre Adélie			20000	30000	13-20	-	-	Hureau 1970

Table II. continued

Species	Locality	Nos. invest.	Length range (cm)	Potential fecundity		Relative fecundity	Fecundity in relation to length (cm)	weight (g)	Source
				min	max				
Notothenia rossii	South Georgia	38	50-83	20137	94146	8-16	-	-	Permitin & Silyanova 1971
	South Georgia	101	52-84	20100	130000	12-24[1]	$F=0.23 \cdot L^{2.95}$	$F=13.5 \cdot W^{0.99}$	Lisovenko & Silyanova 1979 Silyanova 1982
	Elephant Is	40	51-78	19271	99330	6.1-22.6	$F=3.2459 \cdot L^{2.3114}$	$F=9240+12.22 \cdot W$	Kock 1989
	Kerguelen Is	83	47-77	12200	109710	9.9-20.4	$F=0.0073 \cdot L^{3.781}$	-	Duhamel 1987a
Nototheniops larseni	South Georgia	6	17-19	6200	9086	140-195	-	-	Permitin & Silyanova 1971
	South Georgia	48	14-25	2000	21000[4]	-	$F=0.086 \cdot L^{3.8}$	$F=47.3 \cdot W^{1.2}$	Lisovenko & Silyanova 1979
	S Orkney Is	25	14-21	2337	7127	76-92	-	-	Permitin & Silyanova 1971
	Elephant Is	23	15.6-21.1	1851	7070	56.3-105.4	$F=0.0728 \cdot l^{3.7734}$	$F= -124.2+80.4 \cdot W$	Kock 1989
Nototheniops tchizh =N. larseni[3]	Crozet Is	25	11.5-13.7	1600	3060	-	-	-	Duhamel & Pletikosic 1983
	Ob and Lena Banks	22	13.0-17.5	1041	4575	58-129	-	-	Shandikov 1985
Nototheniops mizops	Kerguelen Is Crozet Is	1	17	-	9350	-	-	-	Andriashev & Tokarev 1958
Nototheniops nudifrons	South Georgia	18	12-18	1646	6886	51-127	-	-	Permitin & Silyanova 1971
	South Georgia	10	14.5-18.5	2000	6800	74-123[1]	$F=0.0012 \cdot L^{5.3}$	$F=3.04 \cdot W^{1.8}$	Lisovenko & Silyanova 1979 Silyanova 1982
	S Orkney Is	17	12-22	792	6746	36-51	-	-	Permitin & Silyanova 1971
	Elephant Is	25	11.5-19.1	544	3110	8.0-57.2	-	-	Kock 1989
	S Shetland Is	16	11-17	110	3460	15-55	-	-	Hourigan & Radtke 1989
Paranotothenia magellanica	Kerguelen Is	-	-	60000	70000	100	-	-	Hureau 1970, Lisovenko 1987
Patagonotothen guntheri	South Georgia	-	-	8000	28000	200-280	-	-	Lisovenko 1987
Trematomus hansoni	South Georgia	26	26-41	8500	23000	27-32[1]	$F=1.98 \cdot L^{2.58}$	$F=18.9 \cdot W^{1.08}$	Lisovenko & Silyanova 1980 Silyanova 1982
	South Georgia	44	28-38	5851	19605	18.9-25.3	$F=0.164 \cdot L^{3.17}$	$F=540.9+20.9W$	Kock unpubl
Trematomus bernacchii	Ant. Penins.	1	-	-	1730	-	-	-	Moreno 1980

[1] fecundity in relation to viscera -free weight. [2] weight in kg. [3] doubtful, probably weight of alcohol or formaldehyde preserved specimens instead of fresh weight. [4] maximum value doubtful, see Lisovenko & Silyanova 1979 fig. 3a. [5] see DeWitt *et al.* 1990.

Table III. Gonadosomatic index (GSI) in females, diameter of oocytes or eggs, spawning, incubation and hatching times, size at hatch and duration of larval and juvenile pelagic phase in channichthyids, bathydraconids, artedidraconids and harpagiferids of the Seasonal Pack-ice Zone and islands lying north of it.

Species	Locality	GSI	Egg* diameter (mm)	Spawning time	Est. time of incubation (days)	Occurrence of larvae	Size at hatch (mm)	Pelagic phase	Source
Champsocephalus gunnari	South Georgia	20-27	3-4	March-May	120	Aug-Oct	12.5-15.3	long	Efremenko 1979b, North & White 1987 White 1987
	Elephant Is/ Ant. Penins	20	3.5-4.1	June-July	150-180	Jan-Feb	12	long	Kock 1989, Kellermann 1989
	Kerguelen Is	15	3.2	Aug-Sept	45-60?	October?			Duhamel 1987a
	Skif Bank	15-16	2.6	May-June	-	-	-	long	Duhamel 1987a
Chaenocephalus aceratus	South Georgia	20-27	4.4+	March-May	120	Aug-Dec	11-17	long	Permitin 1973, Lisovenko & Silyanova 1980, Kock 1981, North & White 1987
	Elephant Is Ant. Penins.	~25	4.4-4.7	May-June	90-120	Aug-Nov	15-19	long	Slosarczyk 1987, Kock 1989, Kellermann 1990
Pseudochaenichthys georgianus	South Georgia	>20	4.5	Feb-April	120-150	July-Sept	15-20	long	Lisovenko & Silyanova 1980, Kock 1981, Gubsch 1982
	S Orkney Is/ Ant. Penins.		4.2-4.8	March	-	-	-	-	Gubsch 1982
Chionodraco rastrospinosus	S Shetland Is	20-25	4.8-5.0	March-April	-	late winter/ spring	20-25	long	Kellermann 1989
Channichthys rhinoceratus	Kerguelen Is	11.6	4.5	February	-	-	-	-	Hureau 1966, Duhamel 1981, 1987b
	Heard Is	0.5-20.4		Feb-March	-	-	-	-	Williams 1983
Parachaenichthys georgianus	South Georgia	20-30	4.0	March-April	90-120	June-Sept	11-17	long	North & Ward 1989
Parachaenichthys charcoti	Ant. Penins.	~25	3.2+	March(?)	-	Aug-Sept(?)		-	Bellisio 1967, Kellermann 1990
Artedidraco mirus	South Georgia		3.0+	May-June	-	September?	7	-	Regan 1916, Kellermann 1990
Harpagifer antarcticus	S Orkney Is	>30	**2.2-2.6**	May-June	150-180	end Nov	8	long	Burren 1988
	Ant. Penins.	7.2-11.6	**2.5**	June-Aug	126	Oct-Jan	5-10	long	Daniels 1978, Kellermann 1990

* Egg diameters marked in bold originate from eggs after fertilization
Egg diameters marked by + signs originate from maturing oocytes

populations of the same species, for example *Nototheniops larseni* and *Nototheniops nudifrons* (Table II), may have been caused by inadvertently counting the oocytes responsible for two years spawn (see Everson 1984) and may not necessarily reflect a decrease in relative fecundity towards higher latitudes.

Potential fecundity is commonly estimated either by counting all ova (Kock 1981) or a weighed subsample of oocytes (Sosinski 1981) or oocytes in sections from the central part of the ovary (Lisovenko & Zakharov 1988). Although all

three methods lead to similar results, Kock (1990a) was able to demonstrate that observed differences in fecundity of *Champsocephalus gunnari* at South Georgia between the second half of the 1970s and the first half of the 1980s were most likely to be attributable to these methodological differences and did not reflect year-to-year variations in fecundity.

In the Seasonal Pack-ice Zone and around the islands north of it potential fecundity in nototheniids is highest in the large-sized *Dissostichus eleginoides* with 238 000–546 000

eggs and lowest in the small-sized members of the genus *Nototheniops* with some hundreds to 10 000 eggs (Table II). In channichthyids highest absolute fecundity is found in *Champsocephalus gunnari* with a maximum of 13 000–31 000 eggs. It is about half less in *Channichthys rhinoceratus* and *Chaenocephalus aceratus*, and 3–4 times less in the other two species *Pseudochaenichthys georgianus* and *Chionodraco rastrospinosus* (Table IV). Information on bathydraconids is available only for two species, *Parachaenichthys georgianus* and *Psilodraco breviceps*, with potential fecundities of 10 000–24 000 and 1300 eggs respectively (Table IV). Among the harpagiferids, *Harpagifer antarcticus* produce 400–1500 eggs (Table IV).

In the High-Antarctic Zone *Dissostichus mawsoni* is outstanding among the nototheniids and the other families in that it has a potential fecundity of 472 000–1343 000 eggs. Next are *Pleuragramma antarcticum* and a number of *Trematomus* species with up to 12 000–18 000 eggs. The lowest fecundity is found in *Trematomus bernacchii* and *Pagothenia borchgrevinki* with a few thousand eggs (Table VI). Potential fecundity in channichthyids is highest in *Chionobathyscus dewitti* and *Cryodraco antarcticus* with 10 000–15 000 eggs and lowest in *Chaenodraco wilsoni* with less than 1000 eggs. The other species typically produce 1500–6000 eggs (Table VIII). *Cygnodraco mawsoni* is the most fecund among the bathydraconid species with 3000–8000 eggs, whereas *Akarotaxis nudiceps* has the lowest fecundity with 200 eggs (Table VII). Artedidraconids of the genus *Artedidraco* obviously produce only a few hundred eggs per season, while fecundity in *Pogonophryne ventrimaculata* was 1000–2000 eggs (Table VII).

It is commonly accepted that potential fecundity is positively correlated with fish length and weight. Antarctic fish are no exception to this rule (Fig. 7a,b). Only in *Dissostichus eleginoides* does the poor fit of fecundity to length and weight data indicate that factors other than body size, such as age, may additionally influence fecundity (Kock, unpublished). Potential fecundity to length/weight relationships have been established for most of the exploited species and some of the common nototheniids in the Seasonal Pack-ice Zone and around the islands north of it, but are lacking for virtually all other species in particular in those in the High-Antarctic Zone (Tables II,IV,VI,VIII).

In some species, for example *Champsocephalus gunnari*, fecundity decreases with higher latitudes (Fig. 8), in others, such as *Chaenocephalus aceratus*, it increases (Kock 1982).

Relative fecundity is typically higher in the Seasonal Pack-ice Zone and around the islands north of it than in the High-Antarctic Zone, although there exists considerable differences among the families. More than 40% of the species and populations in the Seasonal Pack-ice Zone have relative fecundities of more than 50, whereas only one species (*Pleuragramma antarcticum*) has such a high fecundity in the High-Antarctic Zone (Fig. 9). The vast majority of the species in the Seasonal Pack-ice Zone and islands north of it
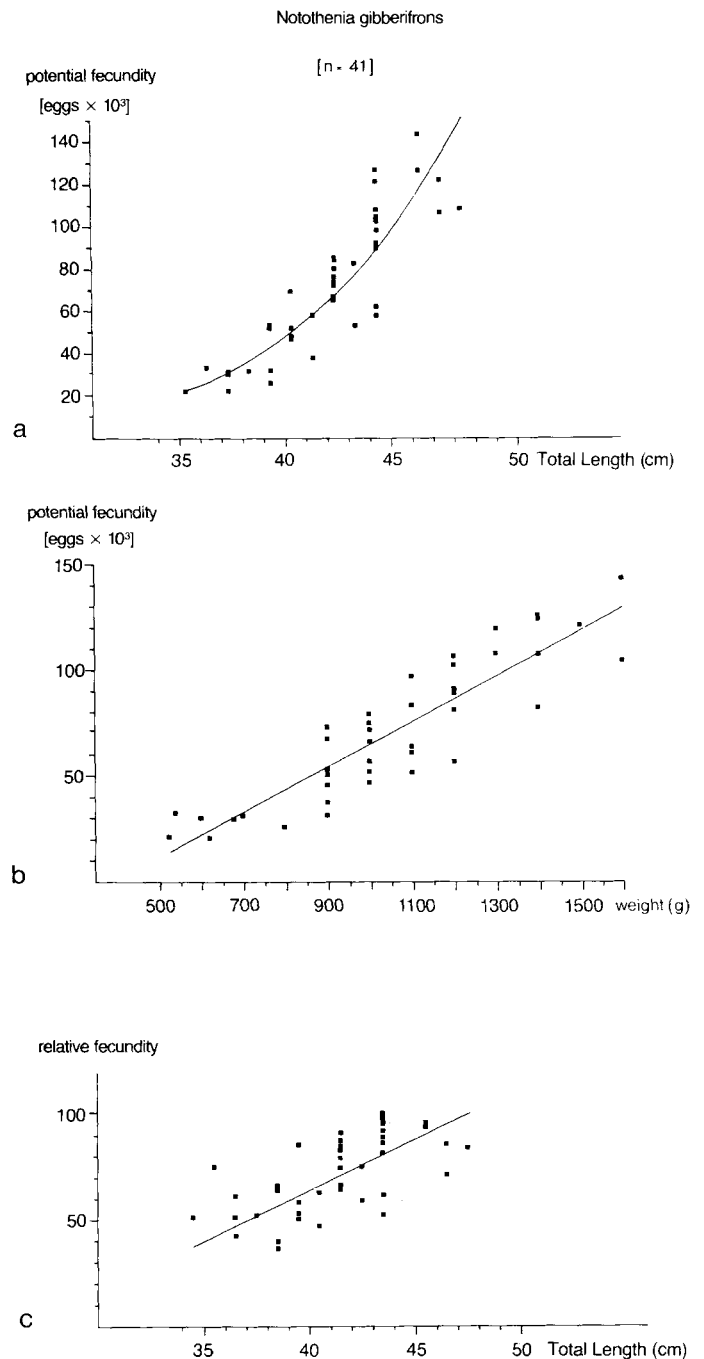

Fig. 7. Potential (absolute) fecundity in relation to length (a) and weight (b), and relative fecundity in relation to length (c) in *Notothenia gibberifrons* around Elephant Island (from Kock 1989).

are the late winter/spring spawning members of the genera *Notothenia* and *Nototheniops*, for example *Notothenia gibberifrons, N. squamifrons* or *Nototheniops larseni* (Table II). Considerable differences in relative fecundities in *Nototheniops* from the Atlantic Ocean sector (Table II) appear to indicate a decrease in relative fecundity towards higher latitudes.

Table IV. Fecundity in channichthyids, bathydraconids and harpagiferids of the Seasonal Pack-ice Zone and the islands north of it.

Species	Locality	Nos. invest.	Length range (cm)	Potential fecundity min	Potential fecundity max	Relative fecundity	Fecundity in relation to length (cm)	Fecundity in relation to weight (g)	Source
Champsocephalus gunnari	South Georgia	345	22-51	1700	17338	-	$F=0.2223.L^{2.8882}$	$F=801+16.02W$	Sosinski 1981, 1985
	South Georgia	138	22-57	1564	31045	13.7-30.6	$F=0.1292.L^{3.0145}$	$F=383+17.97\,W$	Kock 1981, 1989
	South Georgia	15	33-54	4050	23187	12-18	-	-	Permitin 1973
	South Georgia	-	25-43	2208	11126	-	$F=1.54.L^{2.29}$	$F=189.6\,W^{0.59}$	Lisovenko & Silyanova 1980
	South Georgia	158	22-58	1294	21932	-	$F=3.19.L^{2.08}$	$F=1.97.W^{0.58}$	Lisovenko & Zakharov 1988
	S Orkney Is	67	31-44	5169	9889	-	$F=0.2574\,L^{2.7744}$	$F=1753+10.14W$	Sosinski 1981, 1985
	S Orkney Is	1	43	-	8352	14	-	-	Permitin 1973
	Elephant Is	59	34-50	3094	11664	8.0-16.7	$F=0.1216L^{2.9177}$	$F=1523.1+8.55W$	Kock 1989
	S Shetland Is	61	36-47	5710	11753	-	$F=3.774.L^{2.0487}$	-	Sosinski 1981, 1985
	S Shetland Is	14	32-44	3388	9067	12.4-16.5	$F-0.0454.L^{3.2235}$	$F=128+14.45W$	Kock 1982
	S Sandwich Is	4	33-36	3264	4188	-	-	-	Kock 1981
	Skif Bnk/Kerg./Heard Banks.	80	26-38	2000	10645	-	$F=0.0055.L^{3.9498}$	$F=57.14+21.42W$	Sosinski 1981, 1985
	Kerguelen Is	277	26-37	2980	9060	24.2-45.4	$F=0.3027.L^{2.845}$	-	Duhamel 1987a
	Skif Bank	82	25-35	1750	5220	17.9-29.2	$F=0.20.L^{2.869}$	-	Duhamel 1987a
Chaenocephalus aceratus	South Georgia	16	47.7-73.0	7358	22626	5-9	-	-	Permitin 1973
	South Georgia	-	48-72	3082	22626	-	$F=0.93.L^{2.28}$	$F=83.5\,W^{0.65}$	Lisovenko & Silyanova 1980
	South Georgia	67	58-75	5898	18039	4.0-6.8	$F=0.1182.L^{2.7449}$	$F=-572+5.45W$	Kock 1981
	S Orkney Is	32	52-67	4499	15174	3.9-6.8	$F=0.0021.L^{3.7531}$	$F=340+5.52W$	Kock 1981
	S Orkney Is	2	58+60	9292	9425	4.8-5.8	-	-	Permitin 1973
	S Orkney Is	1	53	-	9284	6.3	-	-	Bellisio 1964
	Elephant Is	52	51-66	6711	19672	4.9-9.2	$F=0.0038.L^{3.6691}$	$F=1073.7+6.0W$	Kock 1989
	S Shetland Is	11	53-61	7375	12450	4.6-8.2	$F=0.0319.L^{3.0964}$	$F=408.9+5.98W$	Kock 1982, 1989
Pseudochaenichthys georgianus	South Georgia	92	46-58	4666	10746	4.3-7.1	$F-3.3985.L^{1.9620}$	$F=2151+4.13W$	Kock 1981
	South Georgia	25	47.8-56.5	5830	12970	4-7	-	-	Permitin 1973
	South Georgia	15	-	5880	17958	-	-	-	Lisovenko & Silyanova 1980
	S Orkney Is	5	45-52	5707	8860	5.3-6.1	-	-	Kock 1981
	Elephant Is	2	55+57	8775	12721	5.6+7.9	-	-	Kock 1981
Chionodraco rastrospinosus	S Orkney Is	7	37.2-42.0	2510	4094	4-5	-	-	Permitin 1973
	S Shetland Is	66	33-47	1464	5216	3.7-6.2	$F=0.232.L^{2.578}$	$F=744.4+3.68W$	Kock 1989
Channichthys rhinoceratus	Kerguelen Is	-	-	6000	14000	-	-	-	Hureau 1966
	-	18	31-57	2770	13920	10.2-13.7	$F=2.0277.L^{2.107}$	-	Duhamel 1987a
Parachaenichthys georgianus	South Georgia	25	-	19658	23910	-	-	-	Burchett et al., 1983
	South Georgia	1	58.7	-	14098	10.8	-	-	Permitin 1973
	South Georgia	6	52-58	8585	10130	8.9-12.8	-	-	Kock unpubl.
Psilodraco breviceps	South Georgia	1	14.7	-	1340	74	-	-	Permitin 1973
Harpagifer antarcticus	S Orkney Is	9	-	600	1500	76-100	-	-	Burren 1988
	Ant.Penins.	8	-	400	1000	-	-	-	Daniels 1978

However, given the similar egg sizes in all areas (Table I) and the greatly extended body cavity at spawning it seems unlikely that twice as many eggs could be produced for the same body size around the more northerly South Georgia. Data in Permitin & Silyanova (1971) indicate that the egg counts were from ovaries at an early stage of maturity and oocytes representing next year's spawn may have inadvertently been included in the egg counts (see Everson 1984).

Autumn and early winter spawning members of the genus *Notothenia*, for example *N. rossii* and *N. neglecta*, have relative fecundities of 10–25. *Trematomus* species range typically in the order of 15–50 (Tables II,VI).

The channichthyids *Champsocephalus gunnari*, *Channichthys rhinoceratus* and *Chionodraco myersi* have relative fecundities of 10–30 while all other channichthyids have a relative fecundity of less than 10, some (*Neopagetopsis ionah, Chaenodraco wilsoni*) even less than five (Tables IV, VIII).

Relative fecundities in five bathydraconid species were 10–25, those of the two other species *Bathydraco marri* (40–50) and *Psilodraco breviceps* (70) were higher (Tables IV, VII).

The few artedidraconids so far investigated exhibited relative fecundities of 6–16. Relative fecundity in the more northerly distributed harpagiferid *Harpagifer antarcticus* was 75–100 (Tables IV, VII).

Around Elephant Island relative fecundity decreased with size in *Champsocephalus gunnari* and *Chionodraco rastrospinosus*, but remained constant with size in *Notothenia rossii, N. neglecta, Chaenocephalus aceratus, Nototheniops larseni* and *N. nudifrons*, and increased with size in *Notothenia gibberifrons* (Fig. 7c) (Kock 1989).

Egg size and incubation time

Egg diameter after fertilization ranges from 2.0 mm in *Nototheniops larseni* and *Pleuragramma antarcticum* to 5.0 mm in *Notothenia rossii* (Camus & Duhamel 1985, Hubold 1990, Konecki & Targett 1989). Such data are available for a few species only. In most cases, however, egg size had been estimated from oocytes which had been
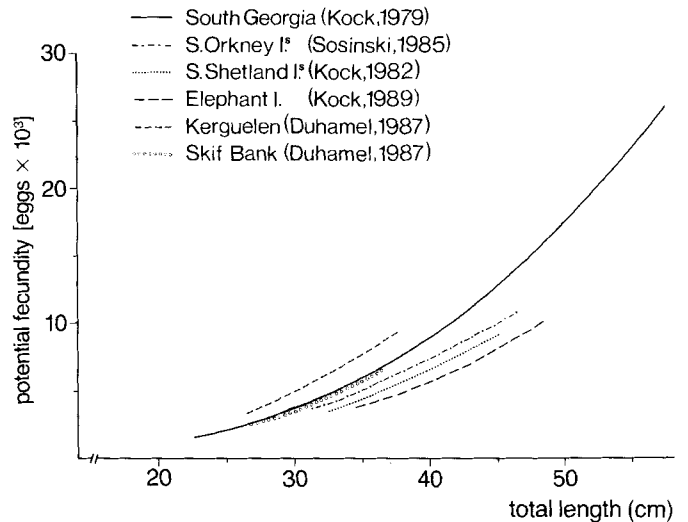

Fig. 8. Potential fecundity to length relationships in various populations of *Champsocephalus gunnari* (from Kock 1990a).

visually classified as ripe or from lengths of smallest observed yolk-sac larvae. If measurements had been clearly identified as being from maturing oocytes they should be regarded as minimum estimates (Tables I,III,IV,VII). An increase in egg volume prior to or after fertilization, due to the uptake of water, is reported for a number of species, such as *Trematomus eulepidotus* (Ekau 1989), *T. hansoni* (Hureau 1970) and *Parachaenichthys georgianus* (White *et al.* 1982) which may correspond to a gain in volume of a factor of 1.5–2.4. Eggs of other species, for example *Notothenia neglecta* (White *et al.* 1982, Kock & Kellermann unpublished) increase little in size after spawning. In other species there may be a shift of egg size during the spawning season. In *Notothenia cyanobrancha* first spawners reproduce about three month earlier than do older individuals (Hureau 1970) and a similar though less significant age-specific difference has also been observed in *N. neglecta* from the South Orkney Islands (Everson 1970). Hureau's data indicate that egg size is smaller in young females, which would lead to a seasonal increase in egg size. In the icefish *Champsocephalus gunnari*
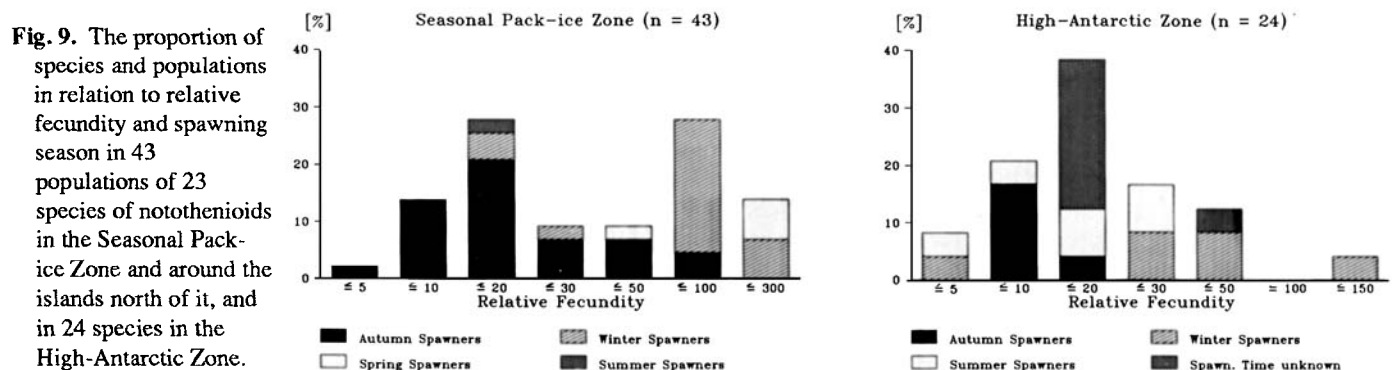

Fig. 9. The proportion of species and populations in relation to relative fecundity and spawning season in 43 populations of 23 species of notothenioids in the Seasonal Pack-ice Zone and around the islands north of it, and in 24 species in the High-Antarctic Zone.
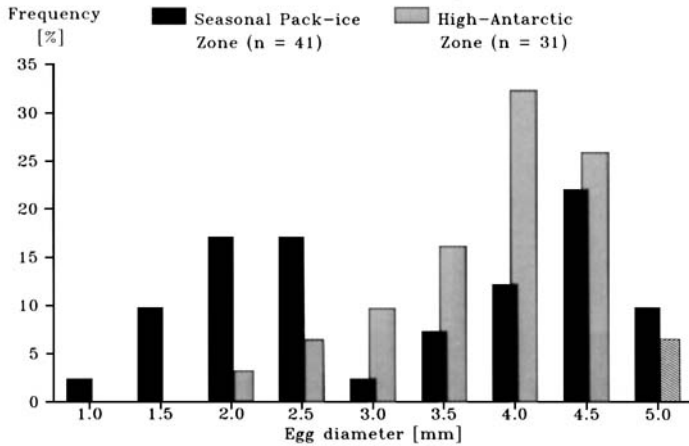
Fig. 10. The proportion of species and populations in relation to egg diameter in 46 populations of 38 notothenioid species in the Seasonal Pack-ice Zone and around islands north of it, and in the High-Antarctic Zone.

at South Georgia average oocyte dry weight was greatest in larger females, which indicates that these spawn earlier and/ or tend to produce larger eggs (Kock 1979,1981).

In the Seasonal Pack-ice Zone and around the islands north of it two groups of species can be discriminated with respect to egg sizes (Fig. 10): the first group exhibiting egg sizes of mostly 1.5–2.5 mm is comprised of species of the nototheniid genera *Notothenia, Nototheniops* and *Patagonotothen* which are late winter and spring spawners and the bathydraconid *Psilodraco breviceps* and the

harpagiferid *Harpagifer antarcticus* which have a high relative fecundity of more than 50. The second group is primarily made up by autumn-spawning members of the genus *Notothenia* and icefish. In the High-Antarctic Zone species with egg sizes of less than 2.5 mm are absent apart from *Pleuragramma antarcticum* which exhibits egg sizes of 2.0 mm (Hubold 1990). Members of the genera *Trematomus* and *Pagothenia* have egg sizes of about 2.5–4.3 mm. The largest egg sizes of 4–5 mm are again observed in channichthyids. Artedidraconids and bathydraconids produce eggs of 3–4 mm size.

Egg sizes are similar among separate populations of a species. Differences apparent in Tables I,III,V,and VII are most likely to be due to the methodological differences described above and may not indicate population differences. This casts further doubts on observations on *Notothenia neglecta* from Terre Adélie, which apparently have egg sizes of 1.2 mm at spawning (Hureau 1970) while all other populations exhibit egg sizes of at least 4.0 mm (Table I). Egg size is closely related to relative fecundity (Fig. 11) and accounts for about 80% of the variance in these data.

Due to their comparatively large size and the absence of oil droplets the eggs of most species were thought to be benthic. Direct evidence is recorded from fishes providing parental care such as *Nototheniops nudifrons* (Hourigan & Radtke 1989), *Trematomus bernacchii* (Moreno 1980) and *Harpagifer antarcticus* (Daniels 1978, Burren 1988) which attach their eggs either to stones or sponges. Egg masses of *Trematomus eulepidotus* (Ekau 1989) and *Nototheniops larseni* (Konecki & Targett 1989) were found in bottom trawl catches. Due to the relatively thin chorion and the
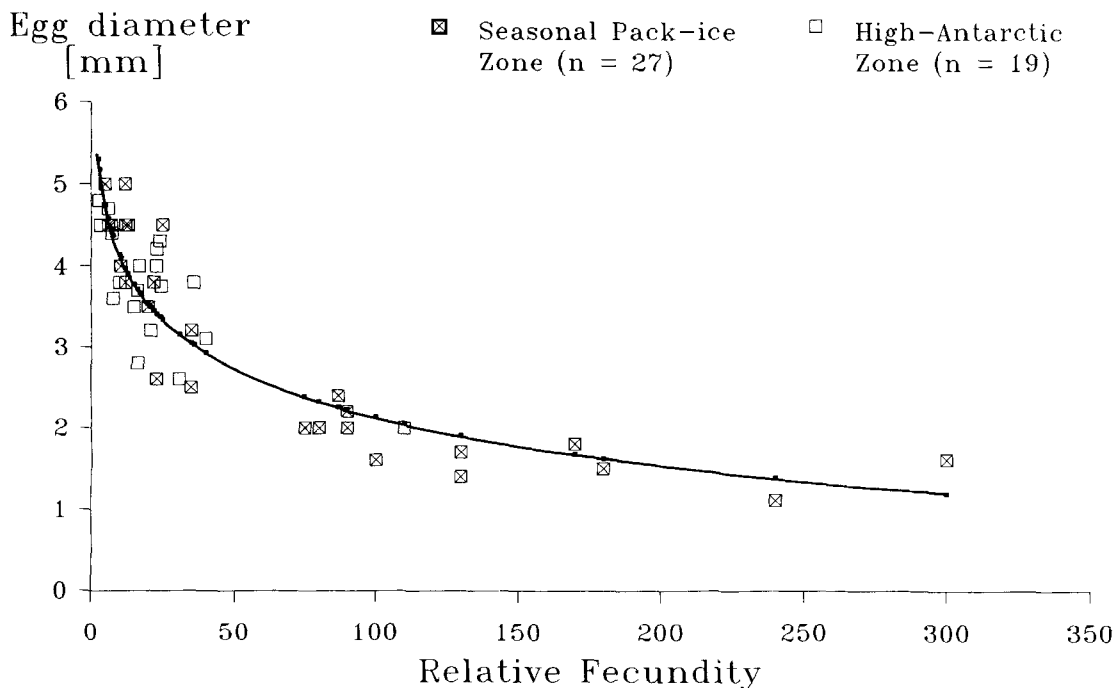

Fig. 11. Egg diameter in relation to relative fecundity in the Seasonal Pack-ice Zone and around islands north of it and in the High-Antarctic Zone (y = 6.383–2.127·logx, v²=0.799).

Table V. Gonadosomatic index (GSI) in females, diameter of oocytes or eggs, spawning, incubation and hatching times, size at hatch and duration of larval and juvenile pelagic phase in nototheniids of the High-Antarctic Zone

Species	Locality	GSI	Egg* diameter (mm)	Spawning time	Est. time of incubation (days)	Occurrence of larvae	Size at hatch	Pelagic phase (mm)	Source
Dissostichus mawsoni	Ross Sea	-	4.0-4.3	Aug/Sept	-	-	-	long	Yukhov 1982
Notothenia neglecta	Terre Adélie	2.1	1.2	January	-	-	-	-	Hureau 1970
Pleuragramma antarcticum	Weddell Sea	13-46	**1.8-2.0**	Aug/Sept	60-75	November	9	long	Shust *et al.* 1984 Hubold 1990, Hubold unpubl.
Pagothenia borchgrevinki	Davis Sea	> 20	2.4	June/July	-	-	-	long	Andriashev *et al.* 1979 Eastman & De Vries 1985
	Ross Sea	28.8	3.5-4.0	June/July	-	-	-	-	Butskaya & Faleeva 1987, Pankhurst 1990
Trematomus bernacchi	Davis Sea	> 19.5	3.6	Oct/Nov	-	-	-	-	Andriashev *et al.*, 1979
	Terre Adélie	18.5	4.0	Oct/Nov	-	-	-	-	Hureau, 1970
	Ross Sea	> 17	3.6-3.9	Dec/Jan	-	-	-	-	Dearborn 1965, Waite 1911
Trematomus eulepidotus	Weddell Sea	> 20	**4.3**	Dec-Feb	150	June	11-15		Lisovenko 1987, Ekau 1989
Trematomus hansoni	Ross Sea/ Terre Adélie	15-20	3.5	February	-	-	11-13	-	Hureau 1970 Haschemeyer 1981
Trematomus lepidorhinus	Weddell Sea	> 14	2.6+	winter	-	November	8.7-11	-	Kellermann 1990 Duhamel *et al.* unpubl. Ekau in press
Trematomus loennbergii	Weddell Sea	> 8.6	2.6-3.5	-	-	-	-	-	Ekau 1988
Trematomus nicolai	Weddell Sea		2.3+						Ekau 1988
Trematomus centronotus =T. pennellii	Mawson Sea Weddell Sea	> 15	3.0-3.8	Feb/March	-	October	16	-	Lisovenko 1987, Shandikov & Faleeva 1987, Kellermann 1990
Trematomus scotti	Mawson Sea Ant.Penins.	-	2.5	Aug/Sept	-	Jan/Feb	8-11	long	Shandikov & Faleeva 1987 Kellermann 1990
Trematomus tokarevi	Ross Sea	-	3.8	-	-	-	-	-	Lisovenko 1987

* Egg diameters marked in bold originate from eggs after fertilization
Egg diameters marked by + signs originate from maturing oocytes

Table VI. Fecundity in nototheniids of the High-Antarctic Zone.

Species	Locality	Nos. invest.	Length range (cm)	Potential fecundity min	max	Relative fecundity	Fecundity in relation to length (cm)	weight (g)	Source
Dissostichus mawsoni	Ross Sea	22	120-180	471900	1343380	14.5-31.3	-	-	Yukhov 1982
Pleuragramma antarcticum	Mawson Sea	30	15.4-25.6	4315	17774	67.7-156.8	$F=6.35.(S)L^{2.44}$	$F=252.14.W^{0.82}$	Gerasimchook 1987
Pagothenia borchgrevinki	Davis Sea	9	16.5-23.5	1500	3000	c. 20	-	-	Andriashev et al. 1979 Butskaya & Faleeva 1987
	Ross Sea	13	17.9-21.2	1100	2750	22.4-26.7	-	F=25.3 W-23.6	Pankhurst 1990
Trematomus bernacchii	Enderby Land	-	-	2166	2890	-	-	-	Benyazh et al. 1980
	Davis Sea	-	20-28	1200	3000	-	-	-	Andriashev et al. 1979
	Adélie Land	-	-	1500	2500	-	-	-	Hureau 1970
	McMurdo	-	20.4-23.1	1154	3123	c. 9-10	-	-	Dearborn 1965
Trematomus eulepidotus	Mawson Sea	3	26.5-30.5	5900	9800	-	-	-	Shandikov & Faleeva 1987
	Weddell Sea	22	-	1400	12300	12.3-35.5	-	-	Ekau 1988, 1989
	Weddell Sea	11	24.0-33.7	2548	19477	14.6-35.2	-	-	Duhamel et al. unpubl.
	Elephant Is	7	27-31	6043	12854	22.1-32.1	-	-	Kock 1989
Trematomus hansoni	Adélie Land	3	-	7000	12000	14.4-17.5	-	-	Hureau 1970
Trematomus lepidorhinus	Weddell Sea	34	-	2200	10800	12.0-50.8	-	-	Ekau 1988
Trematomus loennbergii	Weddell Sea	19	-	5900	13200	22.1-59.8	-	-	Ekau in press
Trematomus newnesi	Ross Sea	-	-	2300	12200	-	-	-	Shust 1987
Trematomus nicolai	Weddell Sea	1	-	-	8900	16.7	-	-	Ekau 1988
Trematomus centronotus	Ross Sea	-	-	2800	6600	14-23	-	-	Shust 1987
=T. pennellii	Weddell Sea	7	-	2500	6300	-	-	-	Ekau 1988

presence of oil droplets the eggs of *Nototheniops larseni* had previously been assumed to be pelagic (Kock 1989, Riehl & Kock 1989). The egg chorion of *Parachaenichthys georgianus* becomes sticky shortly after spawning (White *et al.* 1982).

Laboratory experiments and plankton tows provided direct evidence that eggs of *Notothenia rossii* at South Georgia, *N. neglecta* at the South Orkney Islands and in the Antarctic Peninsula region, *Dissostichus eleginoides* off South Georgia and *Champsocephalus gunnari* at South Georgia are pelagic

at least through parts of their incubation period (Camus & Duhamel 1985, North 1988, Kellermann 1990a).

Incubation took about 2.5–3 months for *Notothenia rossii* at Kerguelen Islands (Camus & Duhamel 1985, Tankevich 1986) and *N. neglecta* at South Georgia (White *et al.* 1982), but was prolonged in *N. neglecta* at the more southerly South Orkney Islands and the Antarctic Peninsula region to five months (White *et al.* 1982, Kock 1989, Kellermann 1990a). Development to hatching of an egg mass of *Trematomus*

eulepidotus collected from a bottom trawl catch in the Weddell Sea took at least five months (Ekau 1989). Egg sizes of these species are 4.1–5.0 mm (Tables I,III).

Incubation periods for the eggs of captive *Nototheniops nudifrons* and *Harpagifer antarcticus*, which guard a nest of eggs and both produce eggs of 2.2–2.5 mm, was about four months at and in the vicinity of Palmer Station (Antarctic Peninsula) (Daniels 1978, Hourigan & Radtke 1989) and five months at Signy Island (Burren 1988). Interestingly, the eggs of *Harpagifer antarcticus* which developed under quasi-field conditions in aquaria at Signy Island hatched about a month earlier than those in the field despite the fact that embryos in the field were already fully developed after four months (Burren 1988).

Egg surface structures were found to be species-specific and do not alter after fertilization. They can be utilized to identify fish eggs from plankton and benthos tows (Riehl & Kock 1989).

Sexual dimorphism

Sexual dimorphism has been observed in a number of species. This may be displayed by different colouration of the sexes when mating as in *Nototheniops larseni* (Shandikov 1985) and *N. nudifrons* (Hourigan & Radtke 1989, Kock 1989), differences in growth as in *Chaenocephalus aceratus* (Kock 1981) and larger fins in males, such as the first dorsal fin in *Champsocephalus gunnari* and *Chionodraco* spp. (Olsen 1955, De Witt & Hureau 1979, Iwami & Abe 1981) or the second dorsal fin in *Pogonophryne* spp. (Andriashev 1967).

Nest guarding

Nest guarding has been observed in *Nototheniops nudifrons* (Hourigan & Radtke 1989), *Trematomus bernacchii* (Moreno 1980) and *Harpagifer antarcticus* (Daniels 1978, Burren 1988). Eggs are deposited on stones or in burrows under stones or in sponges. Egg guarding until hatching is undertaken by the male in *Nototheniops nudifrons*, male and female in *Harpagifer antarcticus* and the female in *Trematomus bernacchii*. This is accomplished chiefly by fanning the eggs and aggressive behaviour towards intruders. An egg mass of *Nototheniops larseni* has been found in a spongocoel (Konecki & Targett 1989) but it is not known if the species guards its eggs.

Larval length at hatching

Since length at hatching has been observed so far only in *Notothenia rossii* (aquaria) (Camus & Duhamel 1985), *N. neglecta* (aquaria) (White *et al.* 1982), *Nototheniops nudifrons* (aquaria) (Hourigan & Radtke 1989), *N. larseni* (field) (Konecki & Targett 1989), *Trematomus eulepidotus* (aquaria) (Ekau 1989), *T. bernacchii* (field) (Moreno 1980)

and *Harpagifer antarcticus* (field and aquaria) (Daniels 1978, Burren 1988), existing data were supplemented by information on length of smallest field-caught yolk-sac larvae to demonstrate a relationship of larval length to egg size. It is evident from Fig. 12 that a close relationship exists between larval length at hatching and egg size. About 73% of the variance in observed larval length is explained by egg size (Fig. 12). Artificial rearing of eggs in some of the studies mentioned above, for example in *Notothenia rossii* at Kerguelen Islands, may have influenced larval length at hatching to an unknown extent and may have led to smaller length than could be expected from the relationship of size at hatch to egg diameter.

Discussion

Reproduction involves a cyclical demand for energy. Key elements in the dynamics of reproductive energy expenditure are:

(1) lifetime and annual reproductive effort, i.e. the quantity of energy devoted to reproduction;
(2) onset of sexual maturity and first spawning in relation to life span and size;
(3) fecundity, i.e. the allocation of reproductive output per egg;
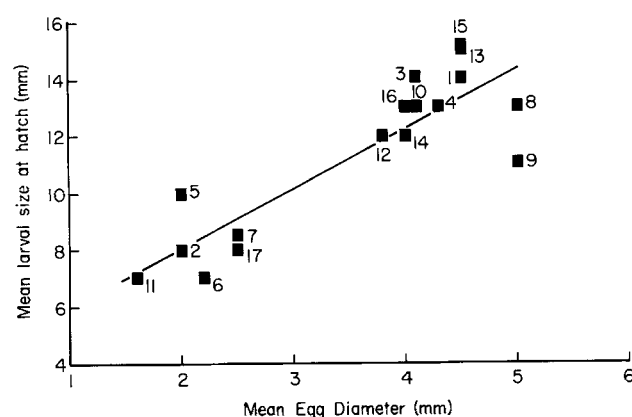(4) timing, i.e. the period of breeding and hatching in relation to environmental seasonality;

Fig. 12. Mean size at hatching in relation to mean egg diameter in 17 populations of 16 notothenioid species
$(y = 3.811 + 2.114x, v^2 = 0.733)$.

1. *D. eleginoides* SG.	**2.** *Pl. antarcticum* WS.
3. *T. bernacchii* AP.	**4.** *T. eulepidotus* WS.
5. *N. larseni* AP.	**6.** *N. nudifrons* AP.
7. *N. gibberifrons* SG.	**8.** *N. rossii* SG.
9. *N. rossii* Ke.	**10.** *N. neglecta* SO.
11. *N. kempi* AP.	**12.** *T. hansoni* SG.
13. *Ps. georgianus* SG.	**14.** *C. gunnari* SG.
15. *C. aceratus* SG.	**16.** *Pa. georgianus* SG.
17. *H. antarcticus* SO.	

Table VII. Gonado-somatic index (GSI) in females, diameter of occytes or eggs, spawning, incubation and hatching times, size at hatch (length of smallest recorded larvae) and duration of larval and juvenile pelagic phase in channichthyids, bathydraconids and artedidraconids of the High-Antarctic Zone.

Species	Locality	GSI	Egg* diameter (mm)	Spawning	Occurrence of larvae	Size at hatch (mm)	Pelagic phase	Source
Chaenodraco wilsoni	Cosmonaut Sea	> 25	4.5-5.0	Nov/Dec	winter	-	long	Pszeniczkov 1988, Gerasimchook & Trozenko 1988, Kellermann 1990
Chionobathyscus dewitti	Weddell Sea Bransfield Str	> 17	3.5-3.6	February	Oct-Feb	17	-	Duhamel et al. unpubl. Kellermann 1990
Cryodraco antarcticus	Weddell Sea Ant.Penins.	25	4.4	Feb/March	late winter	-	long	Ekau 1988, Kellermann 1990
Chionodraco hamatus	Mawson Sea	> 25	4.4-4.9	Feb/March	-	-	long	Shandikov & Faleeva 1987
Chionodraco myersi	Weddell Sea	> 18	3.8-4.2	winter/ early spring	-	-	long	Duhamel et al. unpubl. Ekau in press
Dacodraco hunteri	Weddell Sea	-	-	-	summer	16-20	long	Duhamel et al. unpubl. Kellermann 1990
Neopagetopsis ionah	Weddell Sea	-	> 4.0	winter	-	-	-	Lisovenko 1987
Pagetoptis macropterus	Weddell Sea		>4.0		winter	<20		Pappenheim 1912, Lisovenko 1887, Kellermann 1990
Pagetopsis maculatus	Weddell Sea		4.3-4.8	early winter	Jan/Feb	13-14	long	Kellermann 1990
Akarotaxis nudiceps	Weddell Sea	-	2.5+	autumn	winter/spring?	-	-	Lisovenko 1987, Kellermann 1990
Bathydraco antarcticus	Weddell Sea	-	-	-	early summer	15	-	Kellermann 1990

(5) detrimental effects of spawning.

The maturation of ova, i.e. the process of yolk deposition, takes two years and thus two distinct size groups of yolky oocytes are present in the mature ovary. Yolk deposition may occur throughout most of the year in both types of oocytes, although the greatest amount occurs in the larger oocytes in the months immediately prior to spawning. It is still not clear why the fish take two years to lay down yolk in the oocytes. There may be a link to seasonality which may permit rapid deposition prior to spawning (Everson 1984). This has also been suggested by Kozlov (1980) who found that final maturation in Notothenia rossii and Notothenia gibberifrons takes place when energy-rich food (krill) is available in abundance to the species.

Reproductive effort is commonly expressed by GSI. In female notothenioids GSI is 15–20 in the genus Nototheniops and 35–40 in Notothenia rossii. These values are high compared to, for example, gadoids in the North Atlantic which exhibit GSIs typically of about 10. Energy loss during spawning is obviously substantial and has been described as 50–60% in Notothenia rossii at South Georgia (Kozlov 1980), although this does not only include loss through the eggs.

With a few exceptions GSI in male notothenioids is much lower, which does not mean that reproductive effort is much less in males. It may be partly balanced by the spawning maturity kept over an extended period of 1–2 months. Furthermore secondary commitments such as territoriality, courtship and parental care may considerably increase reproductive effort in males. This is most obvious in the nest-guarding Nototheniops nudifrons in aquaria, where nest guarding is carried out only by the male. The earlier onset of the spawning migration in males of a number of species may indicate that males establish territories prior to spawning.

Part of the populations of Champsocephalus gunnari in the Atlantic Ocean sector do not spawn each year. This phenomenon, which is also not uncommon in fish outside the Southern Ocean, such as cod (Gadus morhua) (Thurow 1970), has not been reported for other species in the Southern

Table VII. continued.

Species	Locality	GSI	Egg* diameter (mm)	Spawning	Occurrence of larvae	Size at hatch (mm)	Pelagic phase	Source
Bathydraco marri	Weddell Sea	-	-	early winter	-	-	-	Duhamel *et al.* unpubl.
Cygnodraco mawsoni	Weddell Sea	> 25	3.5+	Nov/Dec	-	-	-	Ekau in press
Gerlachea australis	Weddell Sea	-	3.0+	-	late winter/ spring	< 20	long	Lisovenko 1987 Kellermann 1990
Gymnodraco acuticeps	Weddell Sea	-	-	-	spring	16	short	Kellermann 1990
Prionodraco evansii	Weddell Sea Ant.Penins.	-	3.7	autumn ?	spring	12	short	Kellermann 1990
Racovitzia glacialis	Weddell Sea Ant.Penins.	-	*3.9-4.3*	autumn/ early winter	spring	12-13	long	Kellermann 1990
Artedidraco loennbergii	Weddell Sea	-	3.7	-	spring	-	-	Duhamel *et al.* unpubl.
Artedidraco shackletoni	Weddell Sea	> 16	3.2+	-	-	-	-	Ekau in press
Artedidraco skottsbergi	Ant.Penins. Ross Sea	-	3.0+	-	Oct/Nov	10	-	Lisovenko 1987 Kellermann 1990
Dolloidraco longedorsalis	Weddell Sea	> 16	-	late summer/ autumn	-	-	-	Duhamel *et al.* unpubl.
Pogonophryne ventrimaculata	Weddell Sea	-	2.7+	autumn	-	-	-	Ekau in press

* Egg diameters marked by + signs originate from maturing oocytes
Egg diameters marked in italics originate from oocytes visually classified as ripe or estimated from the smallest observed yolk-sac larvae

Ocean. However, this may be more attributable to the scarcity of data rather than to the rarity of this phenomenon.

If the size and age at first spawning is largely determined by the natural mortality rate and by the size that has to be attained before a fish can exploit its final food niche most efficiently (Jones & Johnston 1977), it may offer an explanation why Antarctic fish do not spawn before they reach 55–80% of their maximum observed length L_{max}. Some species do not spawn until they have attained 70–80% of their final size. This indicates that, disregarding energy spent for maintenance and activity, energy expenditure is clearly partitioned between growth and reproduction in the life-span of a species. Producing ovaries of 20–30% of the total weight would mean a considerable loss of energy at each spawning. Thus energy is probably needed thereafter mostly for refuelling the stores for next year's spawning and little energy seems to be used for somatic growth. Euphausiids (primarily *Euphausia superba* and also *E. crystallorophias* in the High-Antarctic Zone) and fish to some extent are the final food organisms

exploited by many fish species in the Southern Ocean. Thus, postponing maturity until achieving a size large enough to exploit the most abundant food resources available in shelf waters seems to be a plausible reason for delayed maturity. Egg size in *Champsocephalus gunnari* seems to be smallest among the channichthyids and its potential and relative fecundity is highest. This may indicate that *Champsocephalus gunnari* is subject to a higher natural mortality which is balanced by a smaller length at first spawning and a higher fecundity.

The production of large yolky eggs has meant that fecundity must be quite low (Everson 1984). Potential (absolute) fecundity is exceeding 15 000–20 000 eggs only in *Dissostichus* spp. and a few larger-sized members of the genus *Notothenia*. Artedidraconids form the lower end of the scale, producing only 100–200 eggs. Consequently the investment of reproductive effort per offspring is much higher than, for example, in common gadoid and clupeoid species in boreal and Arctic waters. Egg dry weight (see Kock 1981) of late

Table VIII. Fecundity in channichthyids, artedidraconids and bathydraconids of the High-Antarctic Zone.

Species	Locality	Nos. invest.	Length range (cm)	Potential fecundity min	max	Relative fecundity	Fecundity in relation to length (cm)	weight (g)	Source
Chionobathyscus dewitti	Weddell Sea	1	60.8	-	15612	7.6	-	-	Duhamel *et al.* unpubl.
Chaenodraco wilsoni	Cosmonauts Sea	3	29.5-33.0	393	862	1.4-3.8	-	-	Gerasimchook & Trozenko 1988
Cryodraco antarcticus	Weddell Sea	1	41.5-56.8	3506	7239	7.1	-	-	Duhamel *et al.* unpubl.
	Weddell Sea	1	-	-	10700	7.4	-	-	Ekau in press
Chionodraco hamatus	Weddell Sea	3	37.1-43.0	3086	4571	5.4-8.6	-	-	Duhamel *et al.* unpubl.
	Weddell Sea	6	-	2900	4200	4.6-7.4	-	-	Ekau in press
	Mawson Sea	5	38-42	2728	4251	-	-	-	Shandikov & Faleeva 1987
Chionodraco myersi	Weddell Sea	1	-	-	6200	7.8	-	-	Ekau in press
	Weddell Sea	4	29.0-34.0	3033	4212	15.6-19.9	-	-	Duhamel *et al.* unpubl.
Neopagetopsis ionah	Mawson Sea	2	50-52	2200	3520	2.6-3.7	-	-	Shandikov & Faleeva 1987
	Lazarev Sea	31	38.9-49.7	1500	3400	2.5-4.7	$F=0.0011.L^{2.0}$	$F=0.052.W^{0.59}$	Lisovenko & Trunov 1988
Akarotaxis nudiceps	Weddell Sea	1	-	-	200	16.2	-	-	Ekau in press
Bathydraco marri	Weddell Sea	6	21-24	1549	2208	38.0-46.6	-	-	Duhamel *et al.* unpubl.
Cygnodraco mawsoni	Weddell Sea	4	-	3400	8500	9.5-10.9	-	-	Ekau in press
Gerlachea australis	Weddell Sea	1	24.5	-	1143	20.8	-	-	Duhamel *et al.* unpubl.
Racovitzia glacialis	Weddell Sea	1	-	-	1400	20.5	-	-	Ekau in press
	Weddell Sea	3	25.2-26.4	1612	1968	21.1-24.7	-	-	Duhamel *et al.* unpubl.
Artedidraco loennbergii	Weddell Sea	1	11.2	-	136	16.2	-	-	Duhamel *et al.* unpubl.
Artedidraco shackletoni	Weddell Sea	2	-	170	310	8.6-16.1	-	-	Ekau in press
Pogonophryne ventrimaculata	Weddell Sea	9	-	980	1800	6.7-11.3	-	-	Ekau in press

winter spawning notothenioids is 3–8 times higher, whilst that of autumn/early winter spawning notothenioids is 30–100 times higher than egg dry weight in herring and gadoids like cod or haddock. Total reproductive output (in egg dry weight) in the channichthyid *Chaenocephalus aceratus* and the nototheniid *Nototheniops larseni*, however, seems to be comparable to that of similar-sized Icelandic cod and North Sea herring (Schopka 1971).

A general trend is apparent in notothenioids in producing less but larger eggs towards higher latitudes. This shift in egg size and fecundity, however, is mostly confined to the family Nototheniidae. Smaller egg sizes of 1.2–2.5 mm are more common among the genera *Notothenia* and *Nototheniops* in the Seasonal Pack-ice Zone but is limited to only one species, *Pleuragramma antarcticum*, in higher latitudes. Nototheniids (*Trematomus* sp.) in the High-Antarctic Zone commonly produce eggs of at least 3.0–3.5 mm size. This trend is not evident in channichthyids which typically produce

eggs of 4–5 mm irrespective of the locality. The only exception is *Champsocephalus gunnari*, which shows an increase in egg size and a decrease in potential and relative fecundity towards higher latitudes. Bathydraconids and artedidraconids are represented in the Seasonal Pack-ice Zone by a few species only.

Eggs of the majority of species are probably left unattended for a relatively long incubation period. They have been reported as prey items in a number of fish species and also from seal stomachs. Parental care to minimize mortality on the egg stage has been reported for a few species only. However, nest-guarding until hatching, which has also been observed in *Patagonotothen sima* (Marshall 1953, Moreno & Jara 1984) outside the Antarctic, may be much more common in Antarctic notothenioids than indicated by the observations, in particular in artedidraconids which spawn relatively few eggs.

Incubation time of eggs is closely linked to egg size and ambient temperature. Larval length at hatch is directly related to egg size and accounts for almost 80% of the variance in these data. It is likely that yolk volume or the size of the yolk-sac accounts for the residual variability in larval length at hatch. Yolk resorption times reported from larvae of notothenioids are long compared with data from larvae of temperate or boreal fishes. It takes up to three weeks in larvae of *Nototheniops nudifrons* (Hourigan & Radtke 1989) and up to five weeks in *Harpagifer antarcticus* (Daniels 1978). Yolk-sac larvae of *Notothenia neglecta* can survive up to four weeks without food and maintain searching behaviour (Kellermann, unpublished). The maternal yolk reserves enable the larvae to cope with extended periods of food shortage.

Thus, it may suggested that starvation is a less important factor than predation in larval mortality . Natural mortality bears a decreasing relationship to body size (Ware 1975, Anderson 1988). Variation in egg size, and thus length at hatch, may therefore be considered as one important adaptation to join the general mortality process at different stages. If mortality rates of larvae of comparable size do not differ, increase in egg size would simply delay the point of entry (Kock 1989).

Both strategies have been embodied in that two groups of notothenioids can be discriminated between with respect to egg size. The first group comprises species with a moderately high relative fecundity which spawn numerous smaller eggs resulting in a large number of larvae. This strategy is common among late winter/spring spawners in the Seasonal Pack-ice Zone, e.g. *Nototheniops larseni*, *Notothenia gibberifrons*, *N. squamifrons* and *N. kempi*, and *Pleuragramma antarcticum* in the High-Antarctic Zone. Their larvae are small particle feeders which utilize mainly copepod eggs, nauplii and copepodite stages as well as pelagic molluscs, such as *Limacina* sp. (Balbontin *et al.* 1986, Hubold 1985, Kellermann 1987, 1990a,b). The second group produces fewer, larger eggs which release correspondingly large

larvae, e.g. icefishes, *Trematomus* and some larger-sized *Notothenia*. Most of these are large particle feeders. Icefish, for example, commence feeding on larval stages of euphausiids and fish larvae (Kellermann 1986).

The majority of species hatch in spring and early summer when zooplankton production is elevated following the onset of the spring phytoplankton bloom. Spring hatching larvae originate from eggs spawned from early autumn to late winter and exhibit a wide range of lengths at hatch of 5-17 mm, indicating that different food size spectra are utilized by the early feeding larvae. Though data on the food of larvae in spring are limited to a few species, the larger number of species investigated in summer suggest that interspecific overlap of prey species is balanced by the utilization of different size fractions (Williams 1985, Balbontin *et al.* 1986, Kellermann 1986). Interspecific egg size variation, although resulting in somewhat overlapping hatch periods due to increasing incubation time with egg size (North & White 1987, fig. 6, Kellermann 1989, fig. 9), allows for size-dependent resource partitioning by the abundant co-occurring larvae (Kellermann 1989). Similar observations were made in the mostly ice-free waters off South Georgia (North & White 1987, North & Ward 1989), but hatching periods there appear to occur earlier in the season, possibly due to the earlier onset of the production cycle. Delayed occurrence of early larvae compared to South Georgia is reported for *Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Notothenia gibberifrons* in the Antarctic Peninsula area (Kellermann 1989, 1990a). The peak hatching season of larvae in the High-Antarctic Weddell Sea appears to be further delayed compared with the Seasonal Pack-ice Zone (Hubold 1990).

A number of species hatch during winter. They all have large larvae emerging from large and yolky eggs of 4–5 mm in diameter. These larvae have lower relative food requirements and large search volumes so that they can cope with food scarcity under the winter sea ice cover. North & White (1987) noted that the species at South Georgia which occur far in advance of the onset of the production cycle have the largest larvae.

Besides the trophic niche segregation by larval size variation in spring there exists a temporal sequence of hatching periods by species throughout summer. This is thought to be related to the sequential occurrence of reproduction peaks of calanoid copepods (Kellermann 1986, 1989). Since these summer hatching fish species have a high relative fecundity, egg size variation as well as temporal and spatial niche segregation, for example in *Notothenia gibberifrons* and *N. kempi* in the Antarctic Peninsula region, probably preclude competition between the abundant larvae. Channichthyid larvae hatching in spring and summer match with the overwintering larval and juvenile krill or with the hatching periods of nototheniids, their other food resource. Winter hatching channichthyids probably feed on overwintering krill larvae.

Table IX. Maturity scale for nototheniids and channichthyids based on ovarian and testis cycles in *Notothenia coriiceps*, *Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Pseudochaenichthys georgianus* (from Everson 1977, Cielniaszek & Parkes 1989 in Anon. 1989).

Maturity Stage	Description
Females	
1. Immature	ovary small, firm, no eggs visible to the naked eye
2. Maturing Virgin or Resting	ovary more extended, firm, small oocytes visible, giving ovary a grainy appearance
3. Developing	ovary large, starting to swell the body cavity, colour varies according to species, contains oocytes of 2 sizes
4. Gravid	ovary large, filling or swelling the body cavity, when opened large ova spill out
5. Spent	ovary shrunk, flaccid, contains a few residual eggs and many small ova
Males	
1. Immature	testis small, translucent, whitish, long, thin strips lying close to the vertebral column
2. Developing or Resting	testis white, flat, convoluted, easily visible to the naked eye, about 1/4 length of the body cavity
3. Developed	testis large, white and convoluted, no milt produced when pressed or cut
4. Ripe	testis large, opalescent white, drops of milt produced under pressure or when cut
5. Spent	testis shrunk, flabby, dirty white in colour

Apart from the timing of spawning and hatching the duration of the pelagic phase is a further important factor within the reproductive strategy. Hatching in those species producing relatively small eggs of 2.0–3.5 mm is in spring, and the pelagic phase is completed before or at the onset of the following winter as in artedidraconids, harpagiferids, some bathydraconids and several nototheniids. Pelagic development is confined to the period of elevated plankton production. It is these species that agree with Marshall's (1953) earlier concept that larval occurrence is limited to the short austral summer. However, there is a second group of spring and summer hatching species such as *Nototheniops larseni* and *Notothenia kempi* with small eggs that extend larval development over the following winter. Their trophic niches are greatly expanded in time and are probably linked to cyclopoid copepods or seasonally non-migrating calanoids during winter. The delayed transition to demersal life may allow for a demersal settlement of juveniles when competition

in the new habitat is lowest (Kellermann & Schadwinkel in press).

Another group of fishes generates large eggs spawned throughout the year, thus including spring, summer and winter hatching larvae. This group includes the icefishes, in which hatching occurs independently of the seasonal zooplankton production cycle and is instead linked to the early ontogeny of krill and nototheniid fishes. With the exception of the nest guarding *Trematomus bernacchii* and of *Pagetopsis macropterus*, pelagic phases are extended over most of the summer and winter months.

An extended spawning or hatching season among nototheniid fishes is reported in the nest guarding *Harpagifer antarcticus* and *Nototheniops nudifrons*. The prolonged occurrence of early larvae in the plankton increases the chance of matching with the development of suitable food and may compensate for the variability of their nearshore nutritional environment.

Detrimental effects of spawning such as massive post-spawning mortality as reported in capelin (*Mallotus villosus*), have not been described for nototheniid fishes. However, a high post-spawning mortality has been discussed as one possible reason to explain virtual extinction of a yearclass of *Champsocephalus gunnari* at Kerguelen Islands after two or three spawning seasons only (Anon. 1989).

The reproductive characteristics of notothenioids have a number of implications for fisheries management in the Southern Ocean under the auspices of the "Convention on the Conservation of Antarctic Marine Living Resources" (CCAMLR). Spawning stock biomass (SSB) and SSB/Recruit calculations in Virtual Population Analysis (VPA) and Yield per recruit analyses are commonly based on sexual maturity ogives. Although spawning in *Champsocephalus gunnari* occurs each year it has been found that part of the populations of *Champsocephalus gunnari* in the Atlantic Ocean sector do not spawn each year. This phenomenon may also occur in other species. Present input parameters to the VPA may thus overestimate true spawning stock biomass. Maturity ogives should preferably be based on size and age at first spawning instead of at sexual maturity (Kock 1990a, Kock & Köster 1989).

Length at sexual maturity is a key parameter in establishing mesh size regulations. The rationale behind this is that the minimum mesh size should be large enough to let juvenile fish and first spawners escape. Due to the delay of one year between length at sexual maturity and length at first spawning the establishment of minimum mesh sizes should be based on the size at first spawning instead of size at sexual maturity.

Inshore spawning migrations in males of some of the exploited species, for example *Champsocephalus gunnari* and *Chaenocephalus aceratus* at South Georgia, tend to be earlier than in females. Thus, females stay longer on the fishing grounds and may suffer from a higher fishing mortality than males. The extension of closed seasons to protect

spawning of a species may be one option to overcome this problem (Kock 1990a).

Recruitment variability has been little investigated in Antarctic fish and is only known for a few of the exploited species. Recruitment (to the age of first capture) in *Notothenia rossii* and *N. gibberifrons* (Anon. 1989, Kock & Köster 1989) prior to the onset of large-scale exploitation shows a high degree of stability. Variation in the yearclass strength in *Notothenia rossii* was less than a factor of 2, which raises the question "has recruitment varied at all?". In contrast yearclass strength in *Champsocephalus gunnari* varied by a factor of 20 (Kock & Köster 1989), which is still in the range of many fish populations (Rothschild 1986). Exploitation and the resulting substantial decline in stock size has reduced recruitment in *Notothenia rossii* and *Chaenocephalus aceratus* considerably, whereas recruitment in *Champsocephalus gunnari* has obviously been less affected despite the substantial decline in spawning stock size in some years following heavy exploitation (Anon. 1989, Kock & Köster 1989). This may also argue for the higher resilience of this species already apparent in its smaller size at first spawning and its higher fecundity.

Knowledge of reproduction in Antarctic fish has increased considerably and a number of processes, including fecundity and reproductive strategies at least of species in the Seasonal Pack-ice Zone and around islands north of it, are much better understood than 10–15 years ago. However, other features, like the energetic costs of reproduction as an aspect of adaptation, are still little understood and offer a wide field for future research.

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