Antarctic Science 4 (4): 421–430 (1992)

Reproduction and larval growth of *Harpagifer antarcticus* Nybelin (Pisces, Notothenioidei)

M. G. WHITE[1] and P. J. BURREN[2]

[1]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[2]*Macfish Ltd, Watermill Road, Fraserborough, Grampian AB43 5HA, UK*

Abstract: The spiny plunder-fish, *Harpagifer antarcticus*, is a common shallow-water demersal species distributed along the southern limb of the Scotia Arc. A year round study was made of its reproductive biology at Signy Island, South Orkney Islands, for comparison with populations from the Antarctic Peninsula and with *H. georgianus* at South Georgia. Adult *H. antarcticus* inhabit rubble substrata and spawn 300–1500 eggs into a nest during May/July. The nest is guarded by both male and female fish during an incubation period of up to 150 days. After hatching during November/December the larvae grow at a rate of 0.082 mm d^{-1} (summer), 0.049 mm d^{-1} (winter) and 0.067 mm d^{-1} (annual), calculated from a time-series of samples collected from the field. This rate of growth is slow even among Antarctic species but is similar to the closely related species *H. georgianus*. Adult male and female *H. antarcticus* at the South Orkney Islands attain a maximum standard length of 88 mm and 85 mm respectively.

Received 10 April 1991, accepted 30 October 1991

Key words: Harpagiferidae, Notothenioidei, growth, reproduction, Antarctic, fish

Introduction

Harpagifer antarcticus is a small demersal notothenioid fish reported to be distributed in shallow neritic habitats along the southern limb of the Scotia Arc (Hureau 1990). The systematic status of the genus *Harpagifer* has been recently revised. Until the review of *Harpagifer* by Hureau *et al.* (1979) the genus was accepted to be a single species, *Harpagifer bispinis* (Schneider), with several sub-species distributed from southern South America, the Falkland Islands and the peri-Antarctic islands to the Antarctic Peninsula. Hureau *et al.* (1979) divided *H. bispinis* into five species but did not achieve a satisfactory definition of the species at the South Orkney Islands because of the lack of suitable material. We subsequently collected samples at Signy Island, South Orkney Islands, and on the basis of these specimens Hureau was able to demonstrate that the population at the South Orkney Islands was morphologically indistinguishable from *H. antarcticus* (Hureau 1990). Therefore *H. antarcticus* appears to have a continuous distribution from the Antarctic Peninsula to the South Sandwich Islands and includes the South Orkney Islands. However, the exact systematic status of this species at the South Sandwich Islands requires further investigation because its identification there is based on a very small sample (J-C. Hureau, personal communication 1991).

Aspects of the biology of *H. antarcticus* have been described at the South Shetland Islands (Moreno 1971), Antarctic Peninsula (Daniels 1978, 1983, Duarte & Moreno 1981, Tomo 1981) and South Orkney Islands (Burren 1988, North 1989). The larval stages have been described by Everson (1968), North & White (1982) and Kellermann (1990) as well as larval temporal and spatial distribution (Everson 1968, Daniels 1978, Balbontín *et al.* 1986, Kellermann 1989, 1990). Diet and feeding behaviour has been described by Richardson (1975), Duarte & Moreno (1981), Tomo (1981), Wyanski & Targett (1981), Daniels (1982), and Balbontín *et al.* (1986). The osteology and phylogenetic relationships have been discussed by Eakin (1981). Early life-history of the closely related species from South Georgia, *Harpagifer georgianus* Nybelin, has been described by White & North (1987) and North (1989). In common with many other Antarctic fish, especially those inhabiting shallow water, *Harpagifer antarcticus* has anti-freeze protection (Tradatti *et al.* 1983).

Adult *H. antarcticus* are commonly found in shallow coastal rocky habitats. At the South Shetland Islands and Antarctic Peninsula the adults occur from intertidal rockpools to a depth of 18 m (Daniels & Lipps 1982) while at the South Shetland Islands Wyanski & Targett (1981) report a distribution of 15–90 m. Harpagiferidae use nests for egg incubation and the brooding behaviour and incubation of *H. antarcticus* has been described by Daniels (1978, 1979) from observations at Arthur Harbour, Antarctic Peninsula.

The presence of a readily accessible population of *H. antarcticus* in nearshore shallow water habitats on Signy Island, South Orkney Islands (60°45'S, 45°36'W) allowed a year-round study on the reproductive biology of this species. The nesting behaviour, incubation, growth and the development of newly hatched larvae were investigated. The development of the newly hatched larvae has been inferred from an incomplete data set (Burren 1988, North 1989). A year-round series of samples is now available and so the initial growth of *H. antarcticus* at the South Orkney Islands can be presented. Additional information was collected on the habitat preference and distribution of *H. antarcticus*.

Materials and methods

The behaviour of *H. antarcticus* at nest sites, spawning, incubation and hatching were observed by diving in Factory Cove and Borge Bay, Signy Island, at approximately weekly intervals during 1986. In subsequent years the occurrence of nests was recorded by divers during the course of their normal research activities.

To investigate development and duration to hatching, fertilized eggs were acquired by stripping ripe adults the procedure described by White *et al.* (1982). In addition, observations were made on the development of eggs from spontaneous spawning in the laboratory and from translocation of 'wild' nests to the laboratory (Burren 1988). Nests, with adults were kept in an open-circuit aquarium system. Stripped ova were maintained in an accessory circulation of filtered sea-water until hatching occurred. Development of ova in the laboratory and field was followed by weekly sampling.

Collection of larvae and juvenile *H. antarcticus* was undertaken by hand while diving and by the use of 1 m 500 μm mesh plankton ring-net tows in Factory Cove and Borge Bay from March 1986 to January 1988. '0' group and '1' group fish were caught using a 1 m Agassiz trawl with fine mesh liner.

Adults were collected during monthly dives with additional samples from the intermittent use of a 1 m Agassiz bottom trawl. Individuals were identified, sexed and their reproductive condition assigned using a five point scale (after Everson 1977). Measurements of total length (TL), standard length (SL), total weight (tw), eviscerated weight (ew) and gonad weight (gw) were made and the ovaries of selected adult females were examined to determine egg diameter and fecundity. *H. antarcticus* have two generations of ova present in the ovaries and the larger series was counted to determine fecundity.

Collections of larval and '0' group fish, scheduled for each month of the year to establish a time-series were intermittently interrupted during periods of instability in the seasonal fast-ice which persists for an average of 149 days at Signy(White 1977, Clarke *et al.* 1988). Fish were preserved in formaldehyde solution in diluted sea-water (1:9 by volume) and later transferred to Steedmann solution (Steedmann 1976) for storage. Linear measurements, recorded to the nearest millimetre and rounded down, are likely to reflect some shrinkage because the specimens were measured after fixation. The gonadosomatic index was calculated using the equation: (gonad weight ÷ eviscerated weight) x 100.

For calculations of growth rate, a standard hatching date was set at 15 November. An average hatching size of 7 mm standard length (SL) was used; the mean post-fixation length of newly hatched larvae observed in this study. Estimates of growth rate were calculated by least-squares regression analysis using mean standard length values for samples of larvae captured in the field. 'Summer' growth rates were estimated from mean lengths from December–March and 'winter' rates from April–October. All statistical analyses used the MINITAB package (Pennsylvania State University).

Demersal fish were sampled at Signy Island from 1984–1988 to provide samples for physiological and ecological studies. The species composition and specimen biometry was recorded (White, BAS unpublished data), and used to provide additional information about the distribution and life history of *H. antarcticus*.

Results

Distribution of adults and larvae

Harpagifer antarcticus at the South Orkney Islands occurs most frequently from the immediate sub-tidal zone to a depth of 12 m, but extends to 100 m. The preferred habitat of adult fish was among rubble bottoms where macroalgae are sparse. Adults were usually found in cavities beneath rocks or in crevices and most commonly occur in refuges adjacent to sandy or gravel areas. Adults were rarely observed in exposed positions during the day but occasionally individuals were observed on the top of prominent rocks. This was presumed to be a feeding position but may also be a territorial display.

Early larval stages were found in the nearshore plankton at 15–20 m depth from November–May. They were most readily captured at night either in the surface layer or close to the sea-floor. This distribution pattern is consistent with our observations made in aquaria where the newly hatched larval stages either rested on the tank floor or repeatedly swam vertically towards the surface and then passively descended to near the bottom.

The demersal stage 0- and 1-group fish occurred on shallow sandy substrata and were first sampled from these localities in Factory Cove and Borge Bay during May.

Maturation

Both males and females were in spawning condition (stage 4) during April–June and post-spawning condition (stage 5) in June and July indicating that spawning was confined to a 2–3 month period in early winter.

Examination of the ovaries demonstrated that ova of two sizes were present and of these the larger were those that would complete maturation to spawning in each year. Egg diameter of the larger series was 0.5–1.0 mm between July–December followed by a rapid increase in diameter to 2.0–2.6 mm by May/June. (Fig. 1). The gonadosomatic

https://doi.org/10.1017/S0954102092000622 Published online by Cambridge University Press

index (GSI) followed a similar cycle with the GSI in females being 5% for the period July–December and rising to 55–60% by May–June (Fig. 2). A similar cycle was exhibited by the males but the increase was less extreme and GSI only rose to about 10% by spawning time.

Estimates of fecundity were derived by examination of the ovary of the near-spawning female and by counting eggs deposited in nests. The two methods produced very similar results with a relative fecundity of 76–87 eggs g^{-1} female total weight from ovaries and 76–99 eggs g^{-1} female total weight from nests. Estimates of absolute fecundity varied between 579–993 eggs per female (using data derived from nests) and 1113–1522 eggs per female (using data from examination of ovaries of near-spawning females).

Spawning

In the field, nests were usually found on the floor of cavities under rocks while in the aquaria adult fish spawned spontaneously and deposited eggs on whatever substrata were provided. Female *H. antarcticus* produced a single clutch of eggs as a discoid single layer. In this study, females spawned during late May and June with a peak of hatching 5–6 months later during mid-November. Fertilized eggs

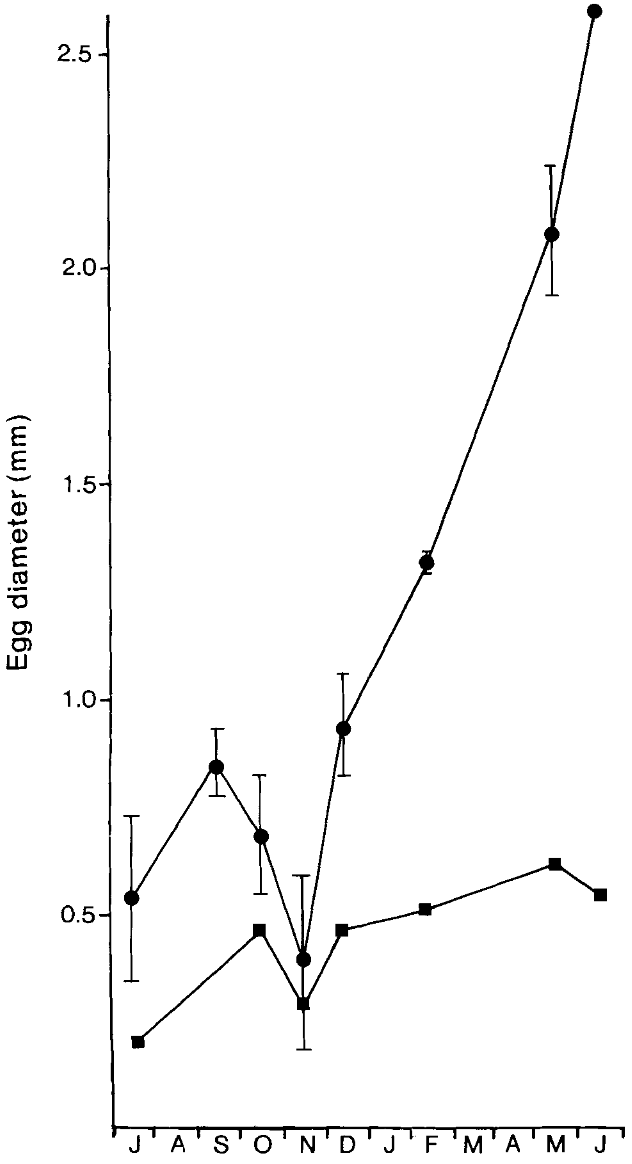

Fig. 1. *Harpagifer antarcticus*: seasonal changes in ova diameter. ● = large ova, ■ = small ova, bar = one standard deviation.

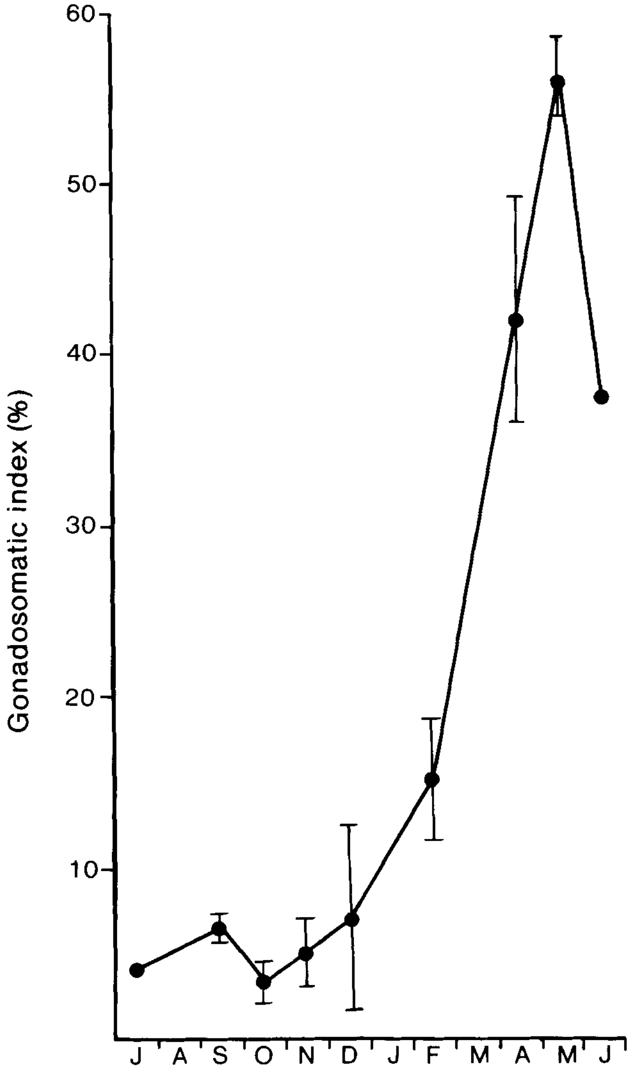

Fig. 2. *Harpagifer antarcticus*: seasonal changes in gonadosomatic index of females. Bar = one standard deviation.

https://doi.org/10.1017/S0954102092000622 Published online by Cambridge University Press

were highly adhesive but this property was lost after about 24 h. Observations by divers has shown that the first nests are usually found during May (1988–1991) but can be delayed in some years until July (1987) (BAS unpublished records).

Nest guarding

Both male and female fish were observed to guard the nest in the field and the aquaria. The presence of a nest guard appeared to provide a major role in protecting the eggs from predation and disease because unguarded eggs were subject to fungal infection and predation. Echinoderms, amphipod and isopod crustaceans and opisthobranch molluscs were observed on infected and unguarded nests and among these the echinoderm, *Odontaster validus* Koehler, and the amphipod, *Pariphimedia integricaudata* Chevreux, were observed feeding on *H. antarcticus* eggs.

Incubation

Eggs were sampled from nests in the field and aquaria at 6 h, 2 weeks and then weekly after fertilization, and the rate of development was observed directly. A few weeks after spawning, (Fig. 3) embryos became obscured because of a light covering of silt and epiflora but development could usually be followed by viewing through the 'window' where eggs had been in contact. The rates of development were found to be very similar in the field and laboratory (Table I). By combining the results from observations in the field and laboratory it was shown that *H. antarcticus* developed to

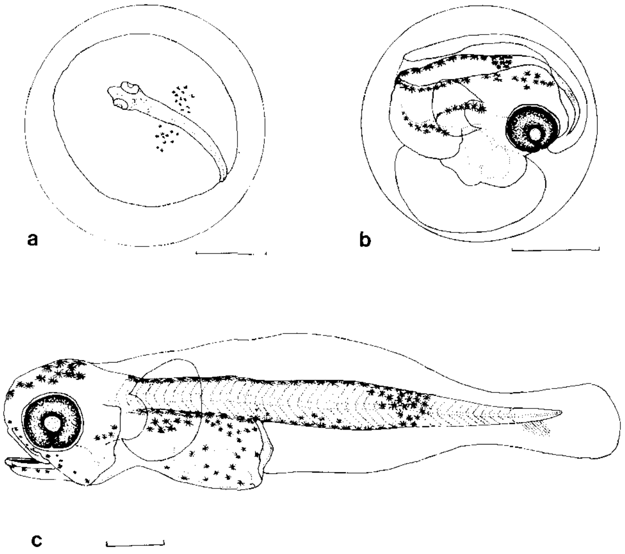

Fig. 3. *Harpagifer antarcticus*: development of embryo during incubation. **a.** 35 days, **b.** 105 days, **c.** 7 days after hatching. Scale bar = 1 mm.

Table I. Main stages of development observed during incubation of *Harpagifer antarcticus* at Signy Island, South Orkney Islands (vertical position of remark indicates relative period within month).

Month	Laboratory	Field
May	Artificial spawning	First nests observed (24/5/86)
June	Natural spawning Development of head	
July	Tail movements	
		Tail movements
	Eyes visible and pigmented	
August	Heart beat visible	
		Heart beat visible
Sept	Top of yolk pigmented First hatch 16/9/86 at 105 days, 8 mm TL	
		Eggs appear fully developed
October		Eggs hatch in sampling bag before reaching laboratory
	Eggs brought from field hatch immediately in laboratory	
November		First hatching observed in the field
	Naturally spawned eggs hatch 18/11/86	
		Peak hatching period
December		No nests present at obervation site (12/12/86)

hatching stage 105 days after spawning. However, hatching did not normally occur at this time unless the brood was disrupted by handling or a marked change occurred in environmental conditions. Hatching of undisturbed nests took place 140–150 days after fertilization. The eggs in a clutch usually hatched near-synchronously with 80% hatching within 24 h.

Natural hatching during the study period occurred during November and December 1986 and few nests remained occupied by mid-December. The larvae hatched at a length of 6–8 mm.

Growth

Samples size for each monthly collection ranged from 1–123 individuals. The standard length data in large samples was normally distributed and so the arithmetic mean was used to describe the average size of each sample.

When the mean size of each sample was plotted against time-since-hatching it was evident that growth occurred throughout the whole of the year (Fig. 4), but with a seasonally varying growth rate. The growth of fish is traditionally described by the use or modifications of the von Bertalanffy equation, although larval growth is not well described by this equation (Cushing 1975). Growth of larval and '0' group fish is frequently linear, (Hubold 1985, Penney & Evans 1985,

https://doi.org/10.1017/S0954102092000622 Published online by Cambridge University Press

Gutiérrez & Morales-Nin 1986, Victor 1986, Thorrold & Williams 1989, North 1990) and linear regression analysis of the increase in length with time (Table II) was found to provide a good fit (r = 0.98). The point-to-point curve for mean sample length with time showed a seasonal variation in growth rate. There appears to be slow initial growth, an acceleration during the summer, slower winter growth then an increase in rate during the second summer. Linear regressions fitted to the 'summer' and 'winter' segments of the growth curve indicate an approximate doubling in growth rate during the summer (Table II).

The overall daily growth increment for *H. antarcticus* was 0.067 mm d^{-1} resulting in an average annual growth increment of 24.5 mm, to a length of 31.5 mm (SL), during the first year. Daily growth increments for winter and summer were 0.049 mm d^{-1} and 0.082 mm d^{-1}, respectively (Table II).

The two samples of small larvae with markedly different average length collected only seven days apart (Fig 4) are likely to be a result of the extended hatching period. The late December 1987 sample was of recently hatched larvae while those from early January 1988 had resorbed yolk-sacs and may have hatched up to two months previously.

H. antarcticus metamorphosed to juvenile stage at 23–27 mm standard length (SL). Male fish grew to a maximum SL of 88 mm (TL = 108 mm) at the South Orkney Islands while the females were slightly shorter at 85 mm (TL = 104 mm). Adult fish became mature at similar sizes, 47 mm SL for males and 48 mm SL for females, a length which they can attain in three years (Burren 1988, White BAS unpublished data). Adult *H. antarcticus* at the South Orkney Islands have been aged at up to 11 years old using the otolith sectioning technique (Bedford 1983), (White, BAS unpublished data).

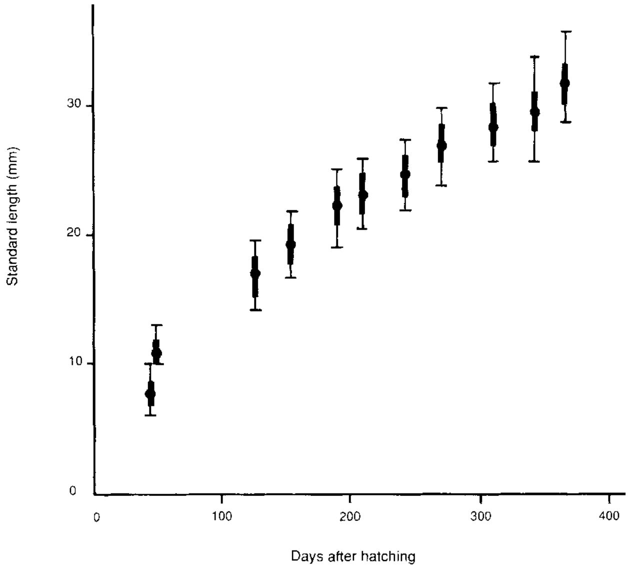

Fig. 4. *Harpagifer antarcticus*: growth of larvae during first year after hatching. Line = range, bar = one standard deviation.

Table II. Growth in standard length (SL) of larval *Harpagifer antarcticus* at Signy Island

a. Linear regression for SL y = a = bx

	a	sd	b	sd	r	p
Annual	8.26	0.65	0.067	0.003	0.985	<0.001
Summer	6.87	0.24	0.082	0.002	0.998	<0.001
Winter	13.1	1.17	0.049	0.004	0.980	<0.001

y = mm SL, a is intercept, b is slope mm/days^{-1}, x is time in days, r = correlation coefficient, sd = standard deviation

b. Increments for SL

	Daily	Calculated annual	Estimated length at 1 year
Mean daily	0.067	24.5	31.5
Mean summer daily	0.082	29.9	36.9
Mean winter daily	0.049	17.9	24.9

Annual increment = daily increment x 365; length at 1 year = annual increment + average length at hatching (7 mm).

Discussion

Distribution

The preferred habitat of adult *H. antarcticus* at the South Orkney Islands, in refuges among rubble bottom substrata in shallow water, is same as that reported for this species at the Antarctic Peninsula (Daniels 1983) and the South Shetland Islands (Duarte & Moreno 1981). However, the distribution pattern differs in that *H. antarcticus* is not found in intertidal rockpools at the South Orkney Islands but does extend to depths of 100 m. The absence of this species from the shallowest habitats may reflect the colder and more extreme meteorological conditions experienced at the South Orkney Islands (Pepper 1954, Jones & Limbert 1987) rather than a difference in preferred substrata. Comparison of seawater temperature between South Orkney Islands and Anvers Island is tentative because there is no complementary data set to compare with Clarke *et al.* (1988). However, records from Anvers Island (Shabica 1976) and Paradise Harbour (Tomo 1981) indicate that the lowest near-surface seawater temperatures are maintained for a shorter period during the winter and are higher in summer than Signy Island, probably because of the lower solar insolation levels at the South Orkney Islands and the influence of the Weddell Sea gyre. The greater depth distribution range at the South Orkney Islands is likely to be a result of more extensive local sampling and is similar to that (15–90 m) reported for the South Sandwich Islands by Wyanski & Targett (1981).

The habitats of juvenile fish and adults were distinct with the early juveniles occurring on open sandy and fine gravel substrata at depths of 5–15 m. Adult *H. antarcticus* are ambush feeders consuming amphipods and small fish (Richardson 1975, Tomo 1981, Daniels 1982, Duarte & Moreno 1981, Wyanski & Targett 1981) whereas the juvenile fish feed on small crustaceans such as harpacticoid copepods and small amphipods (White, BAS unpublished data). We consider that the distinct division of preferred habitat by adult and juvenile *H. antarcticus* is to avoid intraspecific competition for food and predation by the adult fish.

The larval stages of *Harpagifer georgianus* and *H. antarcticus* have been reported to be highly neritic (North & White 1987, North 1989). The greater abundance of the larval stages of *H. antarcticus* near to the coast over shallow depths was indicated by plankton sampling at Signy Island, where larvae were most commonly caught at night over depths of 15–20 m. Sampling from research vessels in the Bransfield Strait has captured larval *H. antarcticus* over deeper water but the distribution patterns remain essentially neritic (Balbontín *et al.* 1986, Kellermann 1989).

Confusion has arisen in respect of the occurrence and duration of the pelagic phase of *H. antarcticus* at different localities. Yolk-sac and small larvae have been observed in the Bransfield Strait and adjacent waters from October–January (Kellerman 1989, 1990), the Antarctic Peninsula in November (Marr 1944, Daniels 1978) and at the South Orkney Islands in November and December (this study). Small pelagic phase larvae of the closely related *H. georgianus* can be captured throughout the whole of the year at South Georgia (North & White 1987) and it is possible that *H. antarcticus* may adopt a similar strategy. However, the description of *H. antarcticus* as having an extended hatching season covering the winter and spring months at the South Orkney Islands (Kellermann 1990) is the result of an incorrect interpretation that the larvae described by Everson (1968) all came from the same locality and the incorrect report that the samples were collected in June 1944. The yolk-sac larvae were a description of J.W.S. Marr's collection from Port Lockroy, Antarctic Peninsula, while the remaining collections of post-larvae came from Borge Bay, Signy Island (January–March 1967) (Everson 1968). The single observation of newly hatched *H. antarcticus* yolk-sac larvae in June is wrong; reference to the original collections notes (Marr 1944) shows clearly that Marr collected eight adults, a nest of eggs and yolk-sac larvae of *H. antarcticus* from a rock pool at Port Lockroy on 1 November 1944.

Notwithstanding this erroneous observation in the literature, an extended period of hatching for *H. antarcticus* remains a possibility. The evidence for this appears to result from the occurrence of yolk-sac larvae of *H. antarcticus* in the Bransfield Strait from October to January/February; these observations are derived from collections in different years (Kellermann 1989) and the data implies that at a given locality in a specific year, hatching is more abbreviated and not spread over a five month period. When naturally spawned nests were monitored in detail at Signy Island, hatching was confined to a relatively brief six week period and this may be typical for most localities. The underlying reason for records of newly hatched larvae occurring in the ichthyoplankton at widely different periods during the austral spring and summer is likely to be a result of marked inter-annual variation in the timing of spawning (May–July in different years during this study) and the observation that development to hatching could be completed in 105 days but natural hatching may be delayed until as much as 150 days after spawning.

Development

The Antarctic marine environment has a very stable temperature but a pronounced seasonal production cycle. These characteristics have been suggested to be responsible for Antarctic marine organisms having slow but seasonal rates of development (White 1977, Clarke 1988). The mechanisms by which low temperature and seasonal variations in food supply may combine to control growth are not clear (Clarke & North 1991). Observations on *H. antarcticus* at the South Orkney Islands show distinct seasonal variations in maturation, spawning and early growth. Physiological experiments on *H. antarcticus* under controlled laboratory conditions by Targett *et al.* (1987) suggest that this species is very sensitive to temperature change. In these experiments, a small fall in temperature (< 3°C) and a reduction in photoperiod associated with changes in daylength from summer to winter conditions causes a marked reduction in feeding. However, further investigation is required to resolve the influence of temperature, photoperiod, diet and feeding behaviour in relation to seasonal growth in Antarctic fish.

Maturation and spawning

The maturation cycle and development of the ova to spawning condition is similar to that reported for many demersal Antarctic fish which spawn during the early winter (Kock & Kellermann 1991). The occurrence of two 'generations' of developing ova and the rapid increase in egg diameter and GSI before spawning in May and June are very similar observations to the development described by Everson (1970) for *Notothenia neglecta* Nybelin at the same locality and for many other Antarctic species of demersal fish (Kock & Kellermann 1991). It is accepted that the eggs of winter spawning notothenioid species are usually >2 mm (North & White 1987) and Antarctic fish usually spawn with a GSI >20% (Kock & Kellermann 1991). Tomo (1981), described the pre-spawning GSI values as 13.6–39.1% for *H. antarcticus* at Paradise Harbour, Antarctic Peninsula, and egg size as

https://doi.org/10.1017/S0954102092000622 Published online by Cambridge University Press

2–2.5 mm. These egg diameter results are very similar but the maximum GSI values are only about half those recorded at Signy Island. The much smaller egg size (0.6–1.0 mm) and lower GSI value (7.2%) reported by Daniels (1978) for a population of *H. antarcticus* just before spawning from Arthur Harbour, Antarctic Peninsula is difficult to explain especially as this is a locality near to that sampled by Tomo (1981). The conclusions of Kock & Kellermann (1991) would imply that Daniel's observations must have been derived from immature or spent fish.

Examination of mature ovaries in adult female *H. antarcticus* by Daniels (1978, 1983) show that the absolute fecundity varies between about 300 and 1000 mature eggs but this study suggests that *H. antarcticus* may spawn up to 1500 eggs. There was no evidence during this study of more than one female *H. antarcticus* spawning at the same nest site. The total number of eggs in the ovary is much higher due to presence of a 'generation' of eggs that will be spawned in subsequent years. When it is possible to distinguish between the ova to be spawned in each year, the relative fecundity of *H. antarcticus* is about 80 eggs g^{-1}, a value which is similar to that reported for other small Antarctic fish such as *Nototheniops larseni* (Lönnberg) (Permitin & Sil'yanova 1971). The value of 500 eggs g^{-1} in *H. antarcticus* reported by North & White (1987) is incorrect; this value was an estimate of mean absolute fecundity.

Spawning by *H. antarcticus* normally occurred during May and June at Signy Island and although a delay until July has been recorded. Spawning appears to occur slightly later at the Antarctic Peninsula with nest preparation reported in June and spawning continuing into August (Daniels 1978). Tomo (1981) reported spawning in *H. antarcticus* at a nearby locality in Paradise Harbour during spring with most spawning completed by November. This conclusion was inferred from the seasonal gonad maturation cycle and so must be considered less reliable than Daniels' direct observations using diving techniques. Nest site selection and clutch size of *H. antarcticus* at the South Orkney Islands are largely indistinguishable from the detailed description given by Daniels (1978).

Nesting behaviour

The construction and guarding of nests occurs in many species of non-Antarctic demersal fish (Potts 1984). This strategy has selective advantages among species that spawn a small number of eggs because of the protection offered from egg predators, dispersal to unsuitable habitats and adverse factors such as silting, infection and imperfect gaseous exchange.

Spawning behaviour and sites are not well known for Antarctic fish but Marshall (1953, 1964) concluded that the production of demersal eggs was typical in Antarctic species. The large size of the eggs of many species and the prolonged incubation period would imply that the spawning of demersal eggs should be an effective strategy in preventing them from being dispersed into the open ocean but exposes them to extended periods of being consumed by benthic predators.

The use of nests for incubation of eggs was first described for an Antarctic fish by J.W.S. Marr in 1944 (Marshall 1964) who observed nests of *Harpagifer* (*H. antarcticus*) at Port Lockroy. This behaviour was subsequently described in detail by Daniels (1978). Nesting has been observed in other members of the genus such as *H. georgianus* and it is likely that all species of the genus adopt the same mode of reproduction.

The fate of spawned eggs is not well documented for species other than *Harpagifer*. Hourigan & Radtke (1989) record nest building in *Nototheniops nudifrons* (Lönnberg), a small nototheniid with a similar geographical distribution but occurring at greater depths than *Harpagifer*. *Trematomus bernacchii* Boulenger deposit eggs in the cavities of sponges (Moreno 1980) and the bathydraconid *Pseudochaenichthys georgianus* Norman produces adhesive demersal eggs (White *et al.* 1982) but it is not known if either species produces discrete nests or guards the eggs during incubation. The eggs of liparid *Paraliparis gracilis* Norman have been found attached to hydroids at South Georgia (Marshall 1964). The nototheniids *Trematomus eulepidotus* Regan and *Nototheniops larseni* are reported to produce benthic egg masses (Ekau 1989, Konecki & Targett 1989). The conflicting factors of extended incubation, prolonged development periods and low relative fecundity, in relation to extended exposure to predation remain to be examined in detail among polar poikilotherms.

Laboratory studies and plankton sampling have demonstrated that some species of Antarctic fish have pelagic eggs. The closely related *Notothenia rossii* (Richardson) and *N. neglecta* spawn pelagic eggs (Camus & Duhamel 1985, North 1989, Kellermann 1990, White & North unpublished BAS Data) as do *Dissostichus eleginoides* Smitt and *Champsocephalus gunnari* Lönnberg (North 1988, Kellermann 1990). *Nototheniops larseni* has been reported to have pelagic eggs for part of the period of incubation (Kock 1989) but this is now thought unlikely.

Daniels (1979) reported the occurrence of altruistic replacement guards in *H. antarcticus* when the primary guard was lost or removed from a nest. This behaviour was not observed among this species at Signy Island in the field or laboratory, but guarding was observed to be undertaken by both male and female parents. This would imply that the altruistic guard recorded by Daniels (1978) was the other parent but it would not explain why all the alternative guards were male.

Incubation

The natural incubation duration was, on average, 23% less at the Antarctic Peninsula (98–126 days) (Daniels 1978) than at the South Orkney Islands (140–150 days). The difference is probably significant and could be attributed to lower

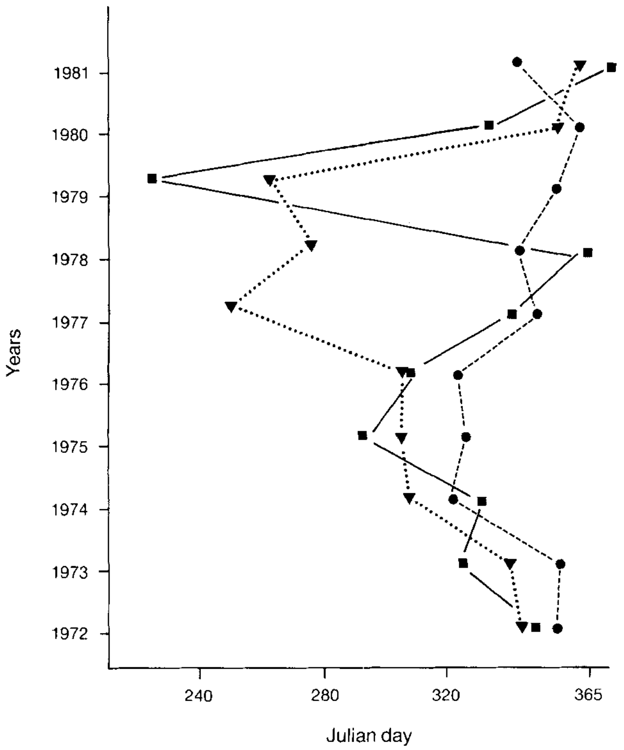

Fig. 5. Key events in marine parameters over series of years at Signy Island, South Orkney Islands to illustrate intra- and inter-annual variations (Data adapted from Signy Island seawater monitoring data-base.) ● = Temperature rise above -1°C, ■ = chlorophyll level above 1mg m^{-3}, ▲ = fast-ice break-out.

Table III. Growth rates of larval stages of Antarctic fish (mm d^{-1}) measured as increase in standard length (SL)

Species	Summer	Winter	Annual	Source
Harpagifer georgianus		-0.014	0.049	North 1989
Nototheniops larseni	0.068			Loeb 1991
Nototheniops larseni	0.08			Kellermann 1986
Pleuragramma antarcticum			0.08	Kellermann 1986
Harpagifer antarcticus	0.082	0.049	0.067	This paper
Parachaenichthys georgianus		0.014		North 1989
Trematomus scotti	0.11			Loeb 1991
Nototheniops nudifrons	0.122		0.046	North 1989
Pseudochaenichthys georgianus		0.044	0.103	North 1989
Notothenia neglecta	0.122	0.130	0.183	North 1989
Notothenia neglecta			0.195	White *et al.* 1982
Notothenia gibberifrons	0.139			Loeb 1991
Artedidraco georgianus	0.157			North 1989
Chionodraco rastrospinosus	0.21			Kellermann 1986
Chaenocephalus aceratus			0.221	North 1989
Chaenocephalus aceratus		0.13		Slosarczyk 1987
Pleuragramma antarcticum	0.24			Hubold 1985
Notothenia angustrifrons	0.251	0.121	0.139	North 1989
Notothenia gibberifrons	0.286	0.11	0.056*	North 1989
Pleuragramma antarcticum '0	0.32			Kellermann 1986
Champsocephalus gunnari	0.354	0.079		North 1989

* hatching size = 4.7mm, average SL after 365 days = 25.2mm.

seawater temperatures at the latter locality. However, close observation of development during incubation in the field and laboratory at Signy Island demonstrated that the larvae are fully developed after about 105 days but hatching was delayed. The hatching stimulus has not been identified but has been attributed to the break-up of sea-ice (Daniels 1978) or marked changes in the coastal seawater characteristics such as turbidity at the onset of spring bloom (this study).

The Antarctic marine environment is highly seasonal with respect to the light and primary production cycle. This seasonality is exacerbated by the sea-ice environment (White 1973) with the result that major events such as peak phytoplankton production, increase in sea temperature and sea-ice dispersal are not predictable events in the summer nor are the sequences regular. Observations of these phenomena over several years (Fig. 5) for Borge Bay clearly illustrates the highly irregular occurrence and sequence of the key features of the polar marine environment at a specific locality, probably the major limiting factor for the nearshore benthic communities.

The phenomenon of delayed hatching by *H. antarcticus* is thought to be an adaptation to the irregular coastal marine environment to ensure that the larvae are released at a time most suitable for early feeding. Thus the strategy to delay the release of larvae until suitable conditions occur in the environment is a most effective adaptation to maximize the survival of larvae in a species that has low absolute fecundity. This observation supports the hypothesis that reproductive strategies among Antarctic poikilotherms are closely linked to the manner and stage at which a species is dependent on the seasonal production cycle (White 1977).

Larval growth rates

An evaluation of available data on growth rates in larval fish from different marine habitats has been reviewed by Clarke & North (1991). They concluded that growth rates among Antarctic fish were slow when compared with temperate and tropical species and averaged 0.152 mm d^{-1}. The *H. antarcticus* growth rate of 0.067 mm d^{-1} is therefore slow even among Antarctic species (Table III) but is similar to the average daily increment of 0.049 mm d^{-1} for the closely related species, *H. georgianus* (North 1989). Such a growth rate may be typical for small demersal Antarctic Notothenioidei. More rapid growth rates during the first year, of up to four times that measured in *H. antarcticus*, are achieved by pelagic species such as *Champsocephalus gunnari* and

Pleuragramma antarcticum Boulenger (Table II). This may reflect an increased scope for growth among notothenioid species that have successfully adopted a pelagic niche at all stages in their life history. Research on the effect on larval growth of changes in environmental parameters such as temperature and food availability has yet to be undertaken on Antarctic species of fish. This field warrants investigation owing to the acknowledged responsiveness of larval development to small changes in temperature, the importance of larval biology to the recruitment of fish populations and the likelihood of the high latitudes being most subject to the impacts of global climate change (Manabe & Stouffer 1979, 1980).

Acknowledgements

We are gratefully acknowledge the help and encouragement offered by members of the BAS research station staff at Signy Island and in particular Richard Price, Julian Ashford and Greg Wilkinson. Our thanks are also owing to Andrew Clarke, Julian Priddle and two anonymous referees for offering constructive criticism and Kim Chiaverio for examining samples of larval *H. antarcticus*.

References

BALBONTÍN, F., GARRETÓN, M. & NUELING J. 1986. Composición del alimento y tamaño de las presas en larvas de peces del estrecho Bransfield (SIBEX-Fase II – Chile). *Serie Científica Instituto Antártico Chileno*, **35**, 125-144.

BEDFORD, B. 1983. A method for preparing sections of large numbers of otoliths embedded in black polyester resin. *Journal du Conseil permanent international pour l'exploration de la mer*, **41**, 4-12.

BURREN, P. J. 1988. *Reproductive biology of* Harpagifer *sp. at Signy Island, South Orkney Islands*. MSc Thesis, University of North Wales, 52pp. [Unpublished].

CAMUS, P. & DUHAMEL, G. 1985. Pont et developpement embryonnaire de *Notothenia rossii rossii* (Richardson 1844), Nototheniidae des Iles Kerguelen. *Cybium*, **9**, 283-293.

CLARKE, A. 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology*, **90B**, 461-473.

CLARKE, A., HOLMES, L.J. & WHITE M.G. 1988. The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands, 1969-82. *British Antarctic Survey Bulletin*, No. 80, 65-86.

CLARKE, A. & NORTH, A.W. 1991. Is the growth of polar fish limited by temperature? *In* DI PRISCO, G., MARESCA, B. & TOTA, B. *eds. Biology of Antarctic Fish.* Berlin: Springer-Verlag, 54-69.

CUSHING, D.H. 1975. *Marine ecology and fisheries.* Cambridge: Cambridge University Press, 277pp.

DANIELS, R.A. 1978. Nesting behaviour of *Harpagifer bispinis* in Arthur Harbour, Antarctic Peninsula. *Journal of Fish Biology*, **12**, 465-474.

DANIELS, R.A. 1979. Nest guard replacement in the Antarctic fish *Harpagifer bispinis*: possible altruistic behaviour. *Science*, **205**, 831-833.

DANIELS, R.A. 1982. Feeding ecology of some fishes of the Antarctic Peninsula. *Fisheries Bulletin of the United States*, **80**, 575-588.

DANIELS, R.A. 1983. Demographic characteristics of the Antarctic plunder fish, *Harpagifer bispinis antarcticus. Marine Ecology Progress Series*, **13**, 181-187.

DANIELS, R.A. & LIPPS J. 1982. Distribution and ecology of fishes of the Antarctic Peninsula. *Journal of Biogeography*, **9**, 1-9.

DUARTE, E. & MORENO, C. 1981. The specialized diet of *Harpagifer bispinis. Hydrobiologia*, **80**, 241-250.

EAKIN, R. 1981. Osteology and relationships of the fishes of the Antarctic family Harpagiferidae (Pisces, Notothenioidei). *Antarctic Research Series*, **31**, 81-147.

EKAU, W. 1989. Egg development of *Trematomus eulepidotus* Regan 1914 (Nototheniidae, Pisces) from the Weddell Sea. *Cybium*, **13**, 213-219.

EVERSON, I. 1968. Larval stages of certain Antarctic fishes. *British Antarctic Survey Bulletin*, No. 16, 65-70.

EVERSON, I. 1970. Reproduction in *Notothenia neglecta* Nybelin, *British Antarctic Survey Bulletin*, No. 23, 81-92.

EVERSON, I. 1977. *The Living Resources of the Southern Ocean*, GLO/SO/77/1. Rome: FAO, 156pp.

GUTIÉRREZ, E. & MORALES-NIN, B. 1986. Time series analysis of daily growth in *Dicentrarchus labrax* L. otoliths. *Journal of Experimental Marine Biology and Ecology*, **103**, 163-199.

HUBOLD, G. 1985. The early life history of the high Antarctic silverfish, *Pleuragramma antarcticum. In* SIEGFRIED, W.R. CONDY, P.R. & LAWS, R.M. *eds., Antarctic nutrient cycles and food web. Proceedings of the 4th SCAR Symposium on Antarctic Biology*. Berlin: Springer-Verlag, 445-451.

HUREAU, J-C. 1990. Harpagiferidae. *In* GON, O. & HEEMSTRA, P. C. *eds. Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 357-363.

HUREAU, J-C., LOUIS, J., TOMO, A. & OZOUF-COSTAZ, C. 1979. Application de l'analyse canonique discriminante la revision du genre *Harpagifer* (Teleostens, Notetheniiformes). *Vie et Milieu*, serie AB, **28/29**, 287-306.

HOURIGAN, T.F. & RADTKE, R.L. 1989. Reproduction of the Antarctic fish *Nototheniops nudifrons. Marine Biology*, **100**, 277-283.

JONES, P.D. & LIMBERT, D.W.S. 1987. *A data bank of Antarctic surface temperature and pressure data.* DOE/ER/60397-H2 Washington D.C.: United States Department of Energy, 52pp.

KELLERMANN, A. 1986. On the biology of early life stages of Notothenioid fishes (Pisces) off the Antarctic Peninsula. *Berichte zur Polarforschung*, **31**, 1-149.

KELLERMANN, A. 1989. The larval fish community in the zone of seasonal pack-ice cover and its seasonal and interannual variability. *Archiv für Fischereiwissenschaft*, **39**, 81-109.

KELLERMANN, A. 1990. Catalogue of early life stages of Antarctic notothenioid fishes. *Berichte zur Polarforschung*, **67**, 44-136.

KOCK. K-H. 1989. Reproduction in fish around Elephant Island. *Archiv für Fischereiwissenschaft*, **39**, 171-210.

KOCK, K-H. & KELLERMANN, A. 1991. Reproduction in Antarctic notothenioid fish – A review. *Antarctic Science*, **3**, 125-150.

KONECKI, J.L. & TARGETT, T.E. 1989. Eggs and larvae of *Nototheniops larseni* from the spongocoel of a hexactinellid sponge near Hugo Island, Antarctic Peninsula. *Polar Biology*, **10**, 197-198.

LOEB, V.J. 1991. Distribution and abundance of larval fishes collected in the western Bransfield Strait region, 1986-87. *Deep-Sea Research*, **14**, 1251-1260.

MANABE, S. & STOUFFER R.J. 1979. A CO_2-climate sensitivity study with a mathematical model of the global climate. *Nature*, **282**, 491-493.

MANABE, S. & STOUFFER R.J. 1980. Sensitivity of global climate model to an increase of CO_2 concentration in the atmosphere. *Journal of Geophysical Research*, **85**, 5529-5554.

MARSHALL, N.B. 1953. Egg size in Arctic, Antarctic and deep-sea fish. *Evolution*, **7**, 328-341.

MARSHALL, N.B. 1964. Fishes. *In* PRIESTLEY R, ADIE R.J. & ROBIN G DE Q, *eds, Antarctic Research*. London: Butterworths, 206-218.

MARR, J.W.S. 1944. *Operation Tabarin: Serial collecting notes, numbers 1071 to 1575, 1944.* Cambridge: British Antarctic Survey Archives, LS/REG1/2/2, 53pp. [Unpublished].

MORENO, C. 1971. Somatometria y alimentacion natural de *Harpagifer georgianus antarcticus* Nybelin, en Bahia Fildes, Isla Rey Jorge, Antarctica. *Boletin Instituto Antartico Chileno*, **6**, 9-12.

MORENO, C. 1980. Observations on food and reproduction in *Trematomus bernacchii* (Pisces, Nototheniidae) from the Palmer Archipelago, Antarctica. *Copeia*, No. 1, 171-173.

NORTH, A.W. 1988. Distribution of fish larvae at South Georgia, horizontal, vertical and temporal distribution and early life history relevant to monitoring year class strength and recruitment. *Scientific Committee for the Conservation for Antarctic Marine Living Resources Selected Scientific Papers 1987*, 105-141

NORTH, A. W. 1989. *Ecological studies of Antarctic fish with an emphasis on early development of inshore stages at South Georgia.* PhD Thesis, National Council for Academic Awards, 319pp. [Unpublished]

NORTH, A.W. & WHITE, M.G 1982. Key to fish larvae from the Scotia Sea, Antarctica. *Cybium*, **6**, 13-32.

NORTH, A.W. & WHITE, M.G. 1987. Reproductive strategies of Antarctic fish. *In* KULLANDER, S.O. & FERNHOLM, B. *eds., Proceedings of the Vth Congress of European Ichthyologists, Stockholm 1985.* Stockholm: Swedish Museum of Natural History, 381-390.

PENNEY, R.W. & EVANS, G.T. 1985. Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. *Canadian Journal Fisheries and Aquatic Science*, **42**, 1452-1464.

PEPPER, J. 1954. *The meteorology of the Falkland Islands and Dependencies 1944-1950.* London: Falkland Islands Dependencies Survey, 249 pp.

PERMITIN, Y.Y. & SIL'YANOVA, Z.S. 1971. New data on the reproduction biology and fecundity of fishes of the genus *Notothenia* (Richardson) in the Scotia Sea (Antarctica), *Voprosy Ikthiologij*, **11**, 806-819. [In Russian].

POTTS, G.W. 1984. Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. *In* POTTS, G.W. & WOOTTON, R.J. *eds., Fish Reproduction: Strategies and Tactics.* London: Academic Press, 223-244.

RICHARDSON, M.G. 1975. Dietary composition of some Antarctic fish. *British Antarctic Survey Bulletin*, No. 41, 113-120.

SHABICA, S.V. 1976. *The natural history of the Antarctic limpet,* Patinigera polaris *(Hombron and Jacquinot).* PhD Thesis, Oregon State University, 294pp. [Unpublished]

SLOSARCZYK, W. 1987. Contribution to the early life history of Channichthyidae from the Bransfield Strait and South Georgia (Antarctica). *In* KULLANDER, S.O. & FERNHOLM, B. *eds., Proceedings of the Vth Congress of European Ichthyologists, Stockholm 1985*, Stockholm: Swedish Museum of Natural History, 427-433.

STEEDMANN, H. F.(*ed*) 1976. *Zooplankton fixation and preservation.* Paris: UNESCO Press, 350pp.

TARGETT, T. E., YOUNG, K.E., KONECKI, J.T. & GRECAY, P.A. 1987. Research on wintertime feeding in Antarctic fishes. *Antarctic Journal of the Unites States*, **22**, (5), 211-213.

THORROLD, S.R. & WILLIAMS, D.M. 1989. Analysis of otolith microstructure to determine growth histories in larval cohorts of a tropical herring (*Herklotsichthys castelnaui*). *Canadian Journal of Fisheries and Aquatic Science*, **46**, 1615-1624.

TOMO, A.P. 1981. Contribucion al conocimiento de la fauna ictiologica del sector Antartico Argentino. *Contribucion Cientifica, Instituto Antartico Argentino*, No. 14: 1-242

TRADATTI, C.E., BADRAN, A.F. & BUSATTO, D. 1983. Anticongelantes biologicos en *Harpagifer antarcticus. Institito Antartico Argentino Contribucion* No. 301, 1-9.

VICTOR, B.J. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Science*, **43**, 1208-1213.

WHITE, M.G. 1973. Aspects of the biological significance of ice in the marine environment. *Proceedings of the Challenger Society,* **4**, 145-146.

WHITE, M.G. 1977. Ecological adaptations of Antarctic poikilotherms to the polar marine environment. *In* LLANO G., A. *ed., Adaptations within Antarctic Ecosystems, Proceedings of the 3rd SCAR Symposium on Antarctic Biology.* Washington, D C.: Smithsonian Institution, 197-208.

WHITE, M.G. & NORTH, A.W. 1987. Postlarval Nototheniodei and midwater fish collected during the SIBEX cruise by British Antarctic Survey, 1985. *In* KULLANDER, S.O. & FERNHOLM, B. *eds., Proceedings of the Vth Congress of European Ichthyologists, Stockholm 1985.* Stockholm: Swedish Museum of Natural History, 405-411.

WHITE, M.G., NORTH, A.W., TWELVES, E.L. & JONES, S. 1982. Early development of *Notothenia neglecta* from the Scotia Sea, Antarctica. *Cybium*, **6**, 43-51.

WYANSKI, D. M. & TARGETT, T.E. 1981. Feeding biology of fishes in the endemic Antarctic Harpagiferidae. *Copeia*, **3**, 686-693.