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Spawning behaviour and early development in the naked dragonfish *Gymnodraco acuticeps*

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Abstract: Nesting sites of the naked dragonfish *Gymnodraco acuticeps* have been identified in 15–35 m water under fast ice adjacent to McMurdo Station, making it possible to examine embryonic development and early larval growth. Egg-laying (predominantly in October) is preceded by a distinctive whirling behavioural pattern driven by the male prodding the side of the female's abdomen. The eggs (3.42 ± 0.19 mm in diameter) are laid on rocks as a single adherent layer (*c.* 2500 per patch). Development is unusually protracted, the first cleavage occurring after about 24 hr at about -1.9ºC. Hatching occurs about 10 months post-fertilization, beginning soon after the sun rises above the horizon. During this period one of the parents may act as a guard in an attempt to keep predators at bay. Upon hatching, the larvae (12.09 ± 0.36 mm long) swim towards the surface ice where they presumably seek refuge. Yolk absorption is complete in about 15 days. Larvae (grown in aquaria at a density of 0.7 larvae l^{-1}) display an average daily growth rate of 0.42% over nine weeks. Hatching in aquaria can occur up to 100 days in advance of that seen in the field, suggesting that under natural conditions hatching may be delayed until an appropriate stimulus (such as the return of the sun) is received.

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Introduction

The fish fauna of the Southern Ocean is represented by 322 currently known species (Eastman 2005). In the highest latitudes, members of the perciform suborder Notothenioidei account for about 77% of the species diversity and 91% of the fish biomass. The notothenioids evolved rapidly in Antarctic waters, adopting a variety of habitats left vacant by more temperate species, which failed to adapt as the waters began to cool in the Miocene (25–5 Ma). Eight families representing 101 Antarctic species are currently identified within this sub-order.

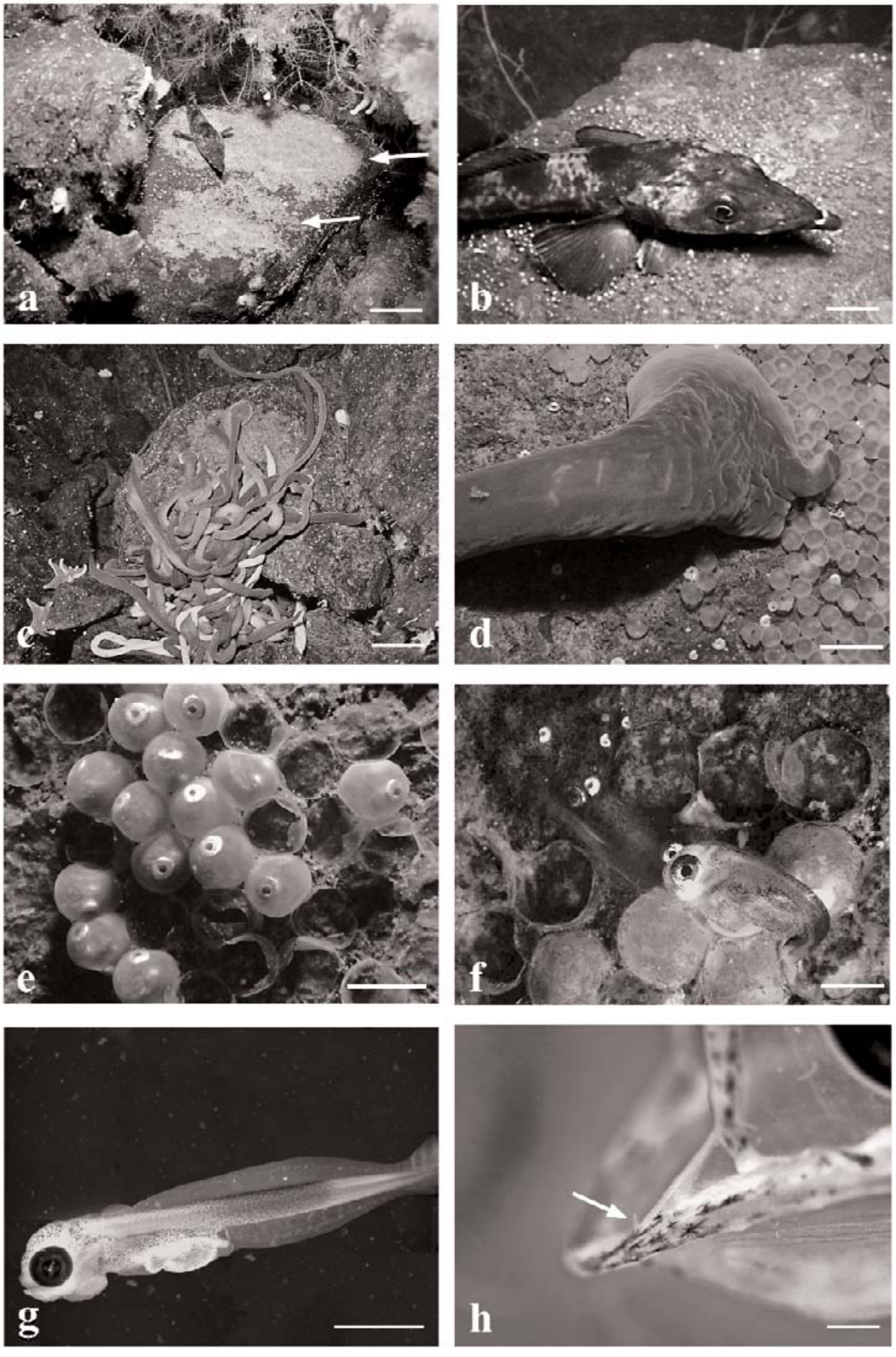
Although notothenioids have been the subject of a large number of scientific investigations, there remains a paucity of data in many aspects of their reproductive biology. In this report we describe features of the spawning behaviour and embryonic and larval development of *Gymnodraco acuticeps* Boulenger, 1902 (family Bathydraconidae). This circum-Antarctic notothenioid is generally found in relatively shallow water (< 50 m), although it has been collected at depths as great as 550 m (Gon 1990). Its common name, the naked dragonfish, stems from its lack of scales (except in the lateral line region) and the dragon-like form of its head, emphasised by a protruding lower jaw bearing prominent, exposed canines.

Adult dragonfish have been collected up to 34 cm total length (TL) (Gon 1990). They are predatory in nature, feeding on a variety of organisms including fish, amphipods and polychaetes. There are no apparent external characteristics to distinguish the sexes, although the female of a pair is typically larger. Little is known of the egg-laying behaviour and early development of the species. We have found gravid female dragonfish in the McMurdo Sound region near McMurdo Station and have been able to follow aspects of their spawning behaviour and early egg and larval development both in the field and under laboratory conditions.

Materials and methods

Naked dragonfish spawning site

A naked dragonfish spawning site has been identified at the McMurdo Station saltwater intake jetty on Ross Island (77º51.081'S, 166º39.821'E) following investigations by divers. The site consists of patches of flat, rocky substrate on which courting behaviour and egg-laying takes place. Divers undertook field observations at this site from late August through January (2001–03 seasons) in an attempt to monitor spawning behaviour, early embryonic development and hatching. Field observations involved twice-daily diver deployment so that newly-laid egg batches could be identified and the nests labelled for subsequent monitoring. Field estimates of the time of egg-laying were within 16 h accuracy, whereas aquarium estimates were more precise, particularly if video recordings were made or if fertilization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was artificially induced. Divers collected eggs of known age from nesting sites by gently scraping samples into a plastic bottle, which were then capped and returned to the McMurdo Station aquarium in an insulated container of local sea water (-1.9ºC).

Aquarium observations

Newly-laid eggs were collected and analysed for developmental stage from their time of fertilization in October. Eggs laid in the wild during the previous spring were collected in early September (*c.* 10 months post-fertilization) and returned to the aquarium where they were transferred to tanks with free-flowing sea water at ambient temperature (*c.* -1.6ºC). Most eggs hatched 12–24 h after collection and the larvae were then fed daily with fresh plankton collected from McMurdo Sound. The larvae were incubated in tanks of different sizes (*c.* 30 l and 1400 l) at different densities (*c.* 3 and 0.7 larvae l^{-1} respectively) using a flow-through seawater system.

Adult naked dragonfish (mature males and gravid females) were collected from the nesting site prior to egg-laying and returned to the aquarium at McMurdo, where they were introduced into a 680 l tank containing several large, flat rocks to facilitate spawning behaviour and egg deposition. The tank was partly shaded from natural (window) and fluorescent lighting and was supplied with flow-through seawater at about -1.6°C.

On one occasion egg fertilization took place naturally on a rock surface in the tank; otherwise spawning was induced by massaging the female's abdomen to promote egg release onto a ceramic tile submerged in a shallow pan of sea water. Artificial spawns were immediately fertilized by adding spermatozoa from an induced ejaculate or by smearing the eggs with the cut surface of an excised testis. Artificial fertilization resulted in virtually all the eggs being successfully fertilized, after which the ceramic tile was transferred to the tank.

A rock, bearing about 1000 fertile naked dragonfish eggs laid in the aquarium at McMurdo on 19 October 2002 was transported to Auckland, New Zealand on 21 December 2003 in an insulated container of cold, aerated seawater. The rock was then transferred to an aquarium at Kelly Tarlton's Antarctic Encounter and Underwater World and kept in flowing, filtered seawater. For practical reasons, the eggs were kept at about +1ºC to +1.4ºC, which is about 3ºC warmer than the ambient seawater temperature near McMurdo Station. It was not possible to control illumination to mimic natural Antarctic conditions, and the eggs were consequently exposed to intermittent fluorescent lighting on a daily basis.

Eggs, yolks, embryos and larvae were weighed wet (after blotting) or dry (2–3 d at 55°C) on a Sartorius Supermicro balance (± 0.1 µg accuracy). The yolk at hatching had hardened and was easily dissected as a single structure from each larva. Length measurements were made using a Zeiss Axiovert microscope fitted with an ocular reticle or with a ruler (larger larvae).

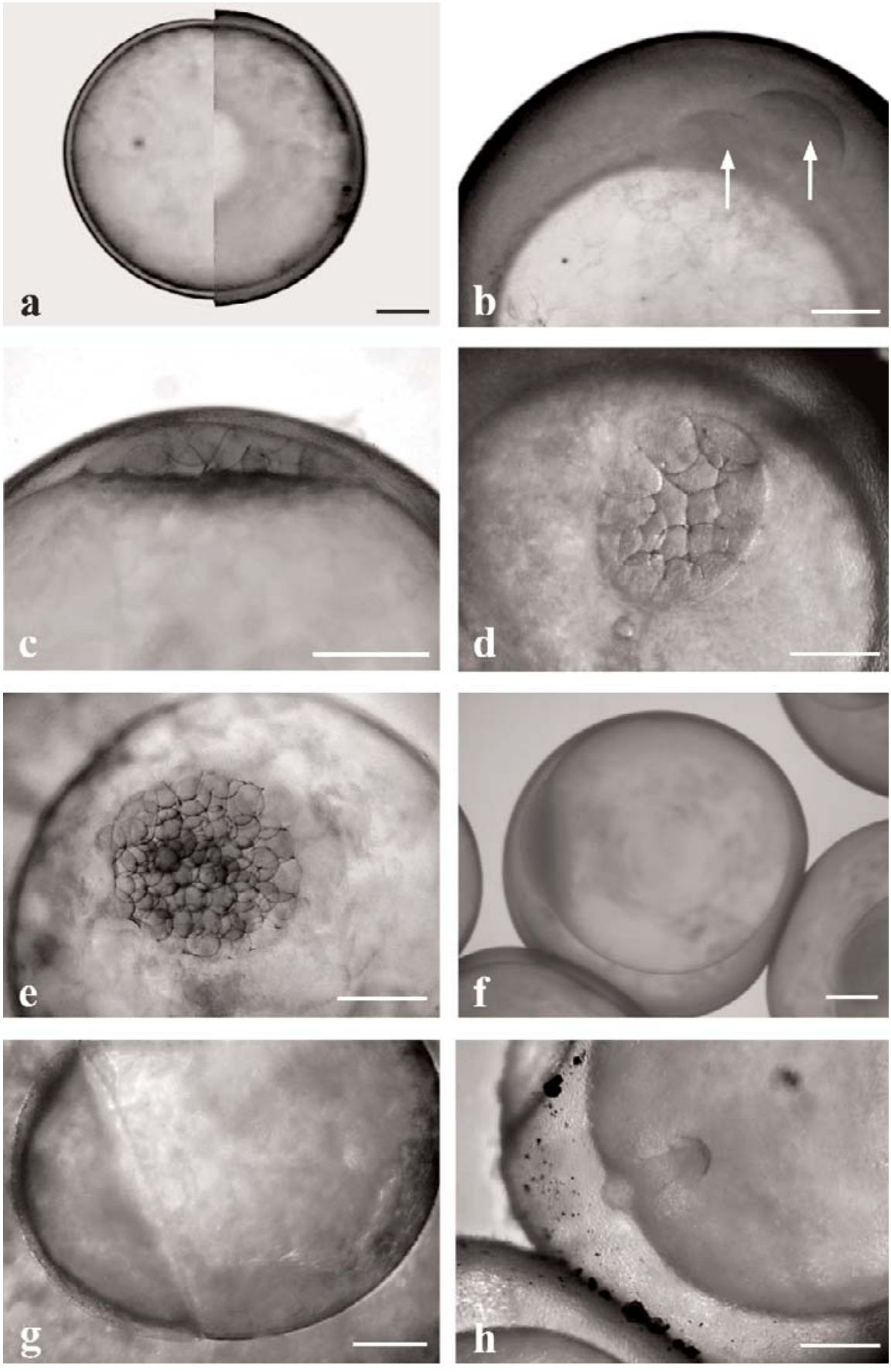
Results

Pre-spawning behaviour

Naked dragonfish nesting sites near McMurdo Station consist of patches of flat, rocky substrate (at 15–35 m depth) on which the eggs are laid, typically in mid-October but extending into the first week of November. Adults collected from this site and returned to McMurdo Station have spawned successfully under aquarium conditions, using large, flat rocks placed in their tank as surfaces for egg deposition. Both field and aquarium observations indicate that adult fish, at first typically males, seek out potential nesting sites and that they then spend significant amounts of their time at or near these nests. Initially, males and females may change places on the nest, but as spawning approaches a male and female pair increasingly cohabit the chosen site. On a single occasion we followed pre-spawning behaviour in an aquarium using time-lapse cinematography. The first sign of pre-spawning behaviour after nest selection involves gentle prodding of the swollen abdomen of the female by the male, using his snout (actually the protruding lower jaw). The female may respond with a small shift in position, so that with repeated actions a whirl-like effect may be observed with time-lapse enhancement, the female spinning in the plane of the nest with the male at right angles to her abdomen. This whirling behaviour was spread over a number of hours before the eggs were finally laid.

The eggs, which are negatively buoyant and sticky, average 3.42 ± 0.19 mm in diameter (measured within 24 h of laying) and are laid as an adherent monolayer. Eggs at the centre of the patch are contiguous, whereas those towards the edge are more scattered. Assuming a patch area of 625 cm^2 and taking an average of 4 eggs cm^{-2}, we estimate

Fig. 1. (opposite) Field observations of developing naked dragonfish eggs. **a.** Adult dragonfish guarding multiple spawns. Bar = 150 mm. **b.** Adult dragonfish on nest site. The prominent canines in the protruding lower jaw are obvious. Bar = 50 mm. **c.** Accumulation of nemerteans at a nest site. The asteroid *Odontaster validus* (Koehler, 1906) is also present. Bar = 300 mm. **d.** Nemertean feeding on early dragonfish embryos. Bar = 15 mm. **e.** Adherent dragonfish eggs just prior to hatching. The uppermost eye of each embryo is obvious. The embryos actively turn within their chorions, casts of which are visible where hatching has been completed. Bar = 5 mm. **f.** A larva emerging from its protective chorion, just prior to an energetic swim towards the surface. Bar = 5 mm. **g.** Newly hatched dragonfish larva showing gross morphology and pigmentation pattern. Bar = 130 mm. **h.** Tooth on the left lower jaw of a 70 day-old larva (arrow). Note pigmentation extending over the lips. Bar = 0.33 mm.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about 2500 eggs per patch.

Nest guarding

After the eggs have been laid, one of the pair will usually assume nest guarding responsibilities (Fig. 1a & b). Observations by divers suggest that at first this is usually, but possibly not exclusively, the female. Males may take over nest guarding at a later date, with some males being seen guarding nests 2–3 months after egg-laying. Occasionally nests are left abandoned. When present, the guard remains in the vicinity of the nest with occasional movement or fanning of its pectoral fins over the eggs, which may serve to keep debris from settling on the patch. From time to time the guard may leave to forage nearby or drive away intruders. Aggressive behaviour is displayed towards threatening species, which at this locality includes various fish species, asteroids, echinoids and nemerteans. The nemertean *Parborlasia corrugatus* (McIntosh, 1876) accumulates in the nesting region (Fig. 1c), presumably in response to odorant cues since they possess a highly developed chemosensory system (McDermott & Roe 1985, Thiel & Kruse 2001). It is not known to what extent nemerteans are kept at bay by the guarding individual, or whether they gather only on vacated nests or if they drive off the guard. Once a nest has been located, nemerteans can accumulate in numbers (as many as 20 per nest) to completely strip it of eggs (Fig. 1d). Many eggs remaining in nests from which nemerteans have been manually removed are non-viable, possibly as a consequence of exposure to toxins exuded with the nemertean mucus.

Fertilisation and early embryonic development

The development of naked dragonfish embryos was followed both in the field and in aquaria. The rate of development was broadly similar under both conditions, although temperatures in the aquaria were slightly warmer (typically -1.6ºC as opposed to -1.9ºC in the field, with some temporal variation). There was considerable variation between egg batches, especially as development proceeded, and therefore the timing reported in the following outline could not be determined precisely.

Soon after fertilization, the outer protective layers of the zygote thicken to form the fertilization membrane (Fig. 2a). The cleavage pattern is discoidal and meroblastic, and the embryo (even up to quite late stages) is fragile and cannot withstand opening of the chorion. The first cleavage (Fig. 2b) usually occurs around 24 h post fertilization (hpf) and yields two blastomeres which are not separate initially from the underlying yolk. More cleavages follow roughly once every 24 h, identifiable at least over the first week. A somewhat irregular tier of blastomeres is apparent by the 16–32 cell stage (Fig. 2c & d), *c.* 4–5 days post-fertilization (dpf). By way of comparison, an early tiered appearance arises in the zebrafish *Danio rerio* (Hamilton, 1822) as an artefact of blastodisc curvature in conjunction with embryo transparency, two true layers not developing until the 64 cell stage (Kimmel *et al*. 1995). In the naked dragonfish, stratification of the blastodisc as early as the fourth cleavage seems to arise from unevenness in the division planes. Cleavage continues (Fig. 2e) and the blastodisc increases in height to form a solid multicellular blastula in which a blastocoel is not readily apparent (Fig. 2f). The yolk cell then begins to bulge inwards towards the cleaving cells to take on a domed shape (Fig. 2g), which is readily apparent by 30% epiboly (26 dpf). Fifty percent epiboly is reached by 29 dpf, at which time gastrulation is underway. Germ ring swelling (marking formation of the embryonic shield) is readily obvious by 31 dpf. Convergent-extension cell movements continue within the embryonic shield and by 35 dpf the embryonic axis is apparent with rudimentary swellings at the extremes including optic primordia (Fig. 2h). At this stage the embryo extends over about 35% of the yolk circumference. The optic primordia in the zebrafish are first visible at the 4–5 somite stage, about 11–12 hpf (Westerfield 2000). Somite formation in the naked dragonfish has not been followed in detail because the embryos remain sensitive to manipulation and their transparency is clouded by substrate debris (eggs are returned to the laboratory with grains of rock remaining attached). By the completion of diving activities enforced by the break-up of sea ice in January (when the developing eggs are about 4 months old), the pigmented embryos extend over about 60% of the yolk circumference.

Natural hatching

Under natural conditions the eggs hatch in late August–early September (Fig. 1f) soon after the sun rises above the horizon (*c.* mid-August). The incubation time for eggs laid in their natural environment is in the order of 310 d (~10 months). Diver observations show that the hatchlings, on average about 12.09 ± 0.36 mm long (Fig. 1g) but with considerable batch variation, actively swim for the surface. At the time of hatching, the underside of the sea ice generally has a growing layer of loosely-packed platelets that may offer refuge from predators.

Fig. 2. (opposite) Microscopic observations of developing naked dragonfish eggs. **a.** composite image of two naked dragonfish eggs pre- and 4h post-fertilization (hpf). Note the thickening of the fertilization membrane. **b.** Two cell stage (arrows), 24 h. **c, d.** 16 cell stage, 60–96 hpf. Note the overlapping of the blastomeres. **e.** 64 cell stage with overlapping blastomeres, 144 hpf. **f.** 1–2000 cell stage prior to epiboly. The blastula flattens onto the yolk, 11 dpf. **g.** 25% epiboly. The yolk begins to bulge towards the animal pole. 25 dpf. **h.** Embryonic axis showing rudimentary head structures including prominent optic vesicles, 45 dpf. Bar = 1 mm

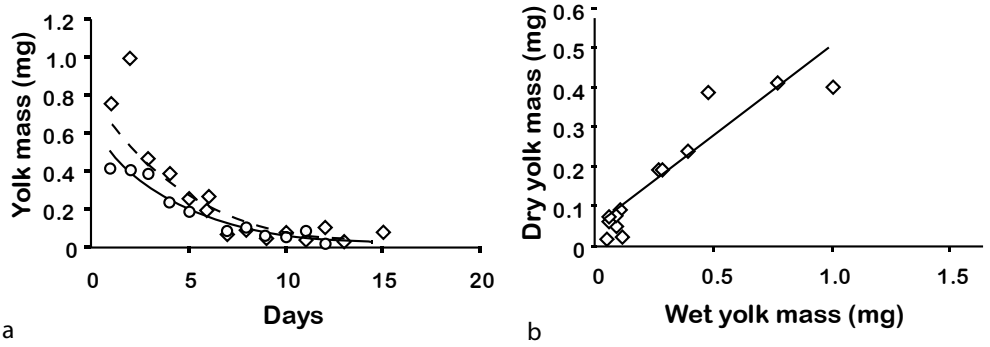

Fig. 3. Age-dependent change in yolk mass. **a.** Decrease in larval yolk mass with development. ◇ = wet mass (dashed regression curve), ○ = dry mass (solid regression curve). **b.** Relationship between wet and dry yolk masses.

Aquarium hatching

Egg samples near the time of hatching were collected by divers and returned to the laboratory for post-hatch analysis. The embryos were eyed (Fig. 1e) and actively turned within their chorions. Most eggs hatched 12–24 h after collection. New hatchlings swam vigorously upwards on freeing themselves from the chorion, and then swam continuously to maintain their position near the top of the water column. Swimming is primarily subcarangiform, with the head kept relatively stable and undulations passing along the body, beginning near the caudal end of the abdomen. The pectoral fins beat regularly in a labriform-like mode, presumably augmenting locomotion and assisting with manoeuvrability and stabilisation. Simple illumination experiments show the larvae are positively phototactic, and in aquaria most tend to swim and feed in the top half of the tanks (80 cm deep).

New hatchlings retain considerable amounts of yolk, which is utilized as the yolk sac larvae develop. The yolk mass was measured wet (YM_w) and after drying (YM_d) (Fig. 3a; $YM_w = 0.8098e^{-0.2149days}$; $r^2 = 0.76$; $YM_d = 0.6449e^{-0.2401days}$; $r^2 = 0.93$). A linear relationship was apparent between the yolk wet and dry masses (Fig. 3b; $YM_d = 0.4468YM_w + 0.0494$; $r^2 = 0.87$). A plot of the natural logarithm (Ln) of larval total length (TL) with time (Fig. 4a) showed a linear relationship (Ln TL = 0.0042days + 2.0425; $r^2 = 0.66$), as did the Ln of the larval wet mass (LM_w) (Fig. 4b; Ln LM_w = 0.0118days + 1.8129; $r^2 = 0.51$). An exponential curve was fitted to describe the relationship between LM_w and TL (Fig. 5a; $LM_w = 0.8547e^{0.267TL}$; $r^2 = 0.53$) and a linear relationship was determined between the larval wet and dry masses (LM_d) (Fig. 5b; $LM_d = 0.1497LM_w + 0.2648$; $r^2 = 0.76$). Larvae grown at lower density (0.7 larva L^{-1}) displayed an initial (7 day) growth rate of 1.94% (Fig. 6; Ln TL = 0.0194days + 2.1006; $r^2 = 0.71$), which slowed to an average daily growth rate of 0.42% over nine weeks (Fig. 4a). Larvae grown at higher density (3 larva L^{-1}) failed to thrive (Fig. 6; Ln TL = -0.00002days + 2.2114; $r^2 = 0.0002$). The stomachs of aquarium-reared larvae primarily contained calanoid copepods, although several examples of cannibalism were noted amongst older larvae (beginning around 127 days post-hatch).

Hatchlings bear a considerable number of melanophores with dense patches on the crown and in the post-anal trunk region where they extend to about 75% TL. The abdomen is pigmented with lighter shading ventrally. The mouth edge is angled backwards ventrally and the face is flattened, in complete contrast to the prognathic appearance of the adult. The three or four defining teeth on the lower jaw described in Kellermann (1989) are not apparent at the time of hatching. Seventy day-old larvae hatched in aquaria contain two teeth, one on each side of the lower jaw near the corner of the mouth (Fig 1h). The jaw elongates from about 70 dph to 154 dph, beyond which date further observations were not possible (Fig 7a–d). The larvae continue to gain teeth during this period, but the prominent canines of the adult are not yet present. The blood includes haemoglobin-containing erythrocytes at the time of hatching, easily visible through the heart wall.

For the rock bearing fertile native dragonfish eggs taken

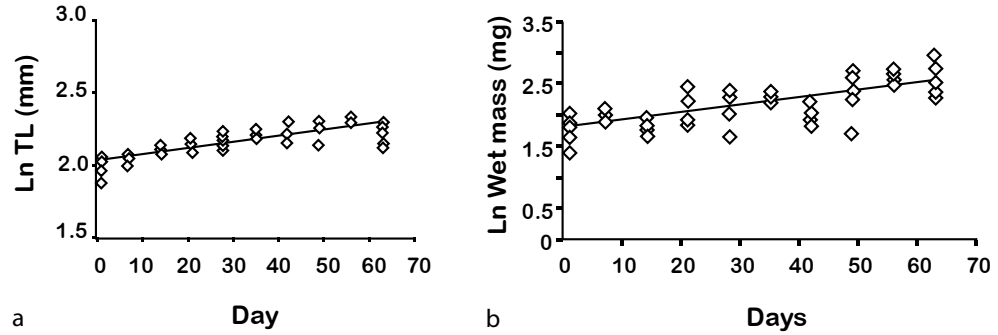

Fig. 4. Growth of larvae. **a.** Larval total length (natural logarithm) and age. **b.** Larval wet mass (natural logarithm) and age.

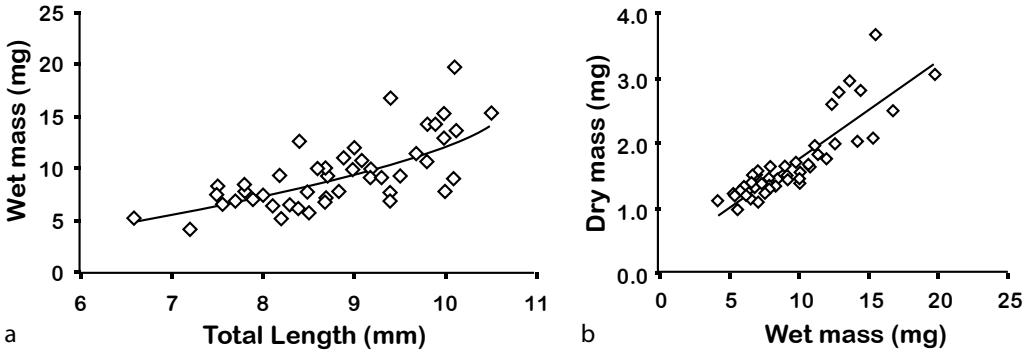

Fig. 5. Larval wet mass relationships. **a.** Larval wet mass as a function of total length. **b.** Relationship between larval wet and dry masses.

to Auckland, New Zealand first hatchlings were detected at 149 dpf (17 March 2003), probably as a consequence of removing fungal-infected eggs to limit the spread of disease. These larvae were viable, but obviously premature since they sank to the bottom of aquarium and moved only when prodded with a pipette. Another premature hatch occurred on 11 April 2003 (174 dpf), again in response to egg disturbance. Both of these premature releases failed to survive. The bulk of the eggs hatched without further interference on 16 May 2003 (209 dpf). This hatch, which yielded free-swimming larvae, took place in about two-thirds of the time observed in the wild. A few larvae were slower to hatch, perhaps reflecting difficulties in freeing themselves from their chorions. Like hatchlings under natural conditions, all these newly emerged larvae still contained significant amounts of yolk. The last larva survived until 18 June 2003. Because early- and late-hatching larvae could not be distinguished, this allows only an estimate of 33 days as the theoretical maximum larval survival time.

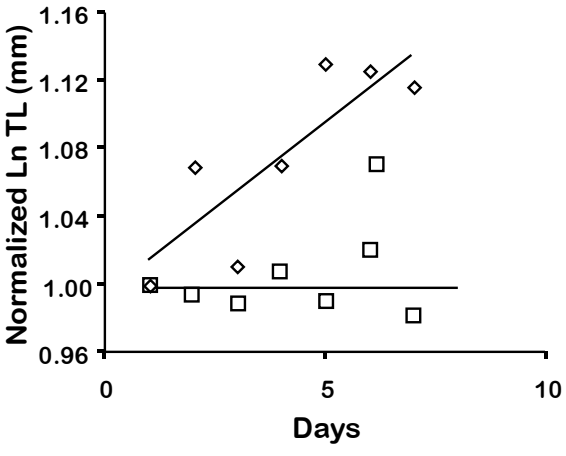

Fig. 6. Effect of larval density on the short-term growth (normalized natural logarithm) of aquarium-reared naked dragonfish larvae. Each point is the average of 10 individuals (see text for details). The data have been normalized to take into account differences in larval length between egg batches. ◇ = low density (0.7 larvae L^{-1}), □ = high density (3 larvae L^{-1}).

Discussion

Pre-spawning behaviour in Antarctic notothenioids has seldom been observed under either field- or laboratory-based conditions because of the logistical problems involved. The discovery of spawning *Gymnodraco acuticeps* adults as well as developing embryos near McMurdo provided an excellent opportunity to examine early development of this notothenioid species. The behaviour of pre-spawn naked dragonfish pairs typically

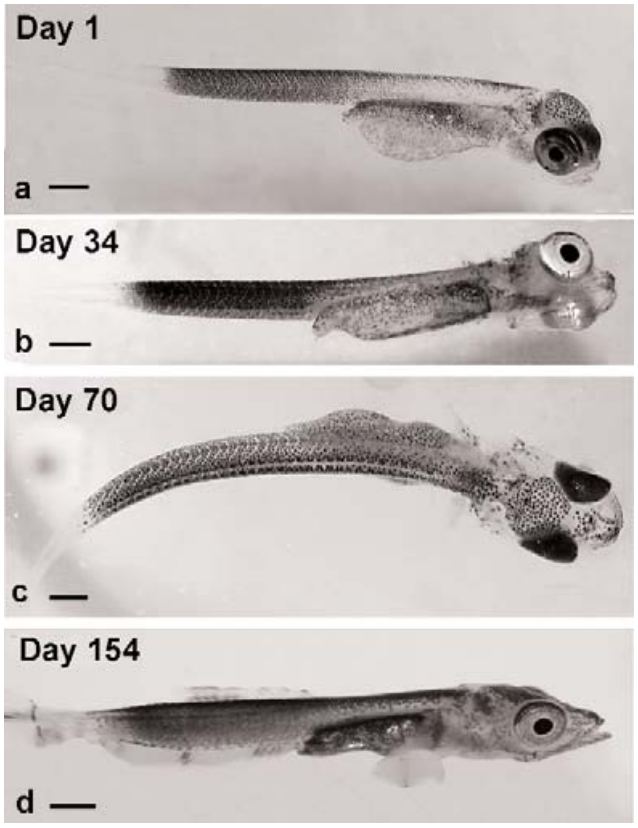

Fig. 7. Elongation of the jaw. Progression from the rounded jaw of a 1 day-old larva **a.** to the pointed jaw of a 154 day-old larva is evident (**d**.). **a**, **b** & **d** are from an oblique lateral perspective, whereas **c** tends towards dorso-lateral. Scale bars = 1 mm (**a**–**c**) and 2 mm (d).

involves intermittent prodding of the female's abdomen by the male, and a whirling movement that arises from this action. Egg-guarding behaviour (commonly fanning of eggs and aggression towards intruders) has been reported previously in just a few notothenioids. These include *Harpagifer* species, in which either or both sexes may be involved (Daniels 1978), the Antarctic nototheniid *Lepidonotothen nudifrons* (Hourigan & Radkte 1989), and the non-Antarctic nototheniid *Patagonotothen tessellata* (Rae & Calvo 1995). Additionally, egg-guarding behaviour has been observed in the channichthyid *Chaenocephalus aceratus* from near Bouvet Island by participants in ICEFISH 2004 (Eastman, personal communication 2005). Taken together with our observations in the bathydraconid *Gymnodraco acuticeps*, egg-guarding behaviour has now been observed in four of the five Antarctic notothenioid families.

Potential fecundity in Antarctic notothenioids ranges from a minimum of *c.* 400 eggs in *Harpagifer antarcticus* Nybelin, 1947 to a maximum of *c.* 1.3 x 10^6 eggs in *Dissostichus mawsoni* Norman, 1937 (Kock & Kellermann 1991). Citing Hureau (1963), Gon (1990) reports ripe ovaries in the naked dragonfish contain about 5000 eggs. Our estimates of clutch size are about half this number. However, the ovaries of notothenioids typically contain two size groups of oocytes representing two different levels of maturation (Everson 1977). The large, yolky oocytes of a developing (grade 2) ovary represent the pending season's spawn, whereas the smaller pre-vitellogenic oocytes presumably represent the subsequent season's spawn. In such a case, not all of the oocytes will be shed on maturation in a single season, and thus the number of eggs laid could be lower than the number estimated within the ovaries. Interestingly, we have noticed some naked dragonfish guarding more than one egg patch on the same rock, suggesting that multiple lays may occasionally take place if conditions (such as available nest area) permit. Genetic analysis could potentially resolve the maternal origin of adjacent egg patches.

Naked dragonfish eggs are typically laid in the McMurdo Sound area during the spring, usually in October or early November, on large flat rocks at a depth of 15–35 m. The eggs are usually guarded by one of the parents, often beginning with the female. One of the extraordinary features of the naked dragonfish is its protracted embryonic phase, extending to about 10 months in the wild, with egg hatching occurring in late August–early September. In marked contrast, development of the zebrafish through to hatching is achieved in as little as 48 h (Westerfield 2000). It is tempting to speculate that hatching of naked dragonfish eggs is initiated in response to daylight, since it begins almost coincidentally with the return of the sun. The yolk is absorbed over about 15 days (Fig. 3), but since aquarium observations show that yolk sac larvae can feed, the rate of yolk utilization may be a function of available food. The maximum survival period of starved naked dragonfish larvae hatched under aquarium conditions in Auckland (33 d) is a likely overestimate since the time of hatch could not be determined accurately for individual larvae. The majority of larvae died at 2–3 weeks of age. Larvae held in aquaria at McMurdo Station, which fail to eat, survive for an approximately equivalent maximum period of time. Published yolk absorption times for other notothenioids are in the order of 21–35 d, which is considerably longer than that for temperate fishes (Kock & Kellermann 1991). The switch from yolk-dependency to the free-living state appears to be a critical time for the larvae, with a proportion failing to thrive under aquarium conditions at McMurdo despite being provided with an abundance of plankton. Larvae which do survive this critical period have a much higher chance of continued survival under aquarium conditions, provided adequate nutrition is available.

The growth of Antarctic notothenioid larvae has been described in terms of an exponential model of the form $\log_e SL = \log_e SL_i + gt$, where SL is the standard length (mm), (SLi) is the initial standard length, g is the daily growth rate, and t is the time in days (Kellermann 1986). A plot of the Ln TL against time for naked dragonfish larvae yields Ln TL = 0.0042days + 2.0425 (r^2 = 0.66), which provides an instantaneous larval growth rate of 0.42% TL d^{-1} over a nine week period. This is within the range of the growth rates determined for a selection of notothenioid larvae reported by North (1998) based on SL data, but may be influenced by the unnatural conditions of growth in aquaria. Indeed, larvae grown at lower density in large tanks (0.7 larvae L^{-1}) can show an initial (7 day) growth rate of 1.23% TL d^{-1}, whereas larvae grown at higher density in smaller tanks (3 larvae l^{-1}) fail to thrive. The density of naked dragonfish larvae under natural conditions is unknown.

Although both the eggs and larvae of naked dragonfish are negatively buoyant, the larvae swim energetically towards the surface on hatching, apparently assisted by positive phototaxis. The platelet layer on the underside of the sea ice may offer crevices for protection from predators, but carries with it the not insignificant risk of death from freezing. Adult cryopelagic notothenioids such as *Pagothenia borchgrevinki* (Boulenger, 1902), which also inhabit the platelet layer, are adequately protected from freezing due to the presence of significant amounts of antifreeze glycoproteins in their blood and other extracellular fluids (DeVries 1988). Paradoxically, for the first few months from hatching naked dragonfish larvae possess inadequate concentrations of antifreeze glycoproteins to prevent freezing at ambient temperature (*c.* -1.9ºC) (Cziko *et al*. unpublished observations). This leaves unanswered questions concerning the mechanisms by which naked dragonfish larvae survive exposure to ice-laden seawater.

One of the key features in the morphogenesis of naked dragonfish larvae is the shape of the mouth. The adult is

characterized by an elongate snout-like face with a protruding lower jaw, whereas in newly hatched larvae the mouth is relatively rounded and the lower jaw does not protrude. Elongation of the jaw begins after 70 dph and continues through 154 dph, when observations ceased.

The incubation time for naked dragonfish eggs laid in their natural environment is in the order of 10 months (~310 d). Rombough (1997) reviewed the average incubation periods for eggs of various marine and freshwater fish species and derived the relationship $\log D = 1.20 - 0.0494T + 0.203\phi$, where D is the incubation period (days), T is the temperature (°C) and ϕ is the egg diameter (mm). Fitting the naked dragonfish data to this equation yields a predicted incubation period of about 97.3 d at -1.9°C, which is about one third of that actually observed in the field. Interestingly, viable larvae can hatch in aquaria as early as 209 dpf (about 100 days earlier than that expected under natural conditions), although even this is far slower than the predicted 66.9 days at the warmest aquarium incubation temperature (1.4ºC). These observations (along with the predicted incubation times) raise the possibility that embryonic development may be effectively complete well in advance of the time that natural hatching occurs. Significantly, Burren (1998) reported that the eggs of *Harpagifer antarcticus* maintained in an aquarium can hatch about a month earlier than under field conditions, even though the field embryos appeared fully developed by an equivalent time. As far as the naked dragonfish is concerned, it may be possible that developed embryos do not hatch immediately. Instead, they may wait (possibly in a quiescent state to minimise energy consumption) until triggered by some stimulus, such as the return of the sun. Experiments are planned to address these issues.

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