Spawning and early ontogenesis in channel bull blenny *Cottoperca gobio* (Notothenioidei, Perciformes) caught off the Falkland Islands and maintained in captivity

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Abstract The channel bull blenny *Cottoperca gobio* (Notothenioidei, Perciformes) is the largest species of the family Bovichtidae that inhabits both the shelf and upper slope around the southern tip of South America. It is a common non-retained bycatch species during finfish bottom trawl fisheries on the Patagonian Shelf in the Southwest Atlantic. The present study aimed to address previously unknown aspects of its spawning, egg development and early larval growth by maintenance of adults in an aquaculture facility. The fish spawned in the beginning of austral spring (early September), adhering the eggs to the wall of the tank in a band of about 120 cm long, and 20–25 cm wide, estimated to contain ∼170,000 eggs. Before and after spawning, the body colouration of both sexes changed displaying marked sexual dimorphism. The male did not guard the spawning site. Egg sizes varied between 2.1 and 2.4 mm. Eggs had a characteristic oil droplet inside. Embryogenesis lasted 50 days, constituting 305 accumulated degree-days. Newly hatched larvae were 7.8–8.1 mm total length, having the oil droplet inside their yolk sac. The yolk sac feeding period lasted approximately 9 days. Anterior part of the larval body was heavily pigmented such that pigmentation could be used for identification purposes. *C. gobio* occupied the very r-end of the r/K continuum among demersal notothenioid fish, characterised by high fecundities, small eggs and larvae, lack of parental care and high growth rates enabling it to populate the vast areas of the Patagonian Shelf whilst competing with other abundant large demersal fish predators.

Keywords *Cottoperca gobio* · Bovichtidae · Egg mass · Embryogenesis · Southwest Atlantic

Introduction

Antarctic and Sub-Antarctic areas of the Southern Ocean are the centres of speciation of perciform fish of the suborder Notothenioidei that evolved several physiological and biochemical features to live in cold water environments. Despite relatively small number of species (129 species belonging to eight families), notothenioids have developed a variety of life forms from benthic and nektobenthic to holopelagic (Eastman 2005). Among them, twelve species belonging to three small basal families, Bovichtidae, Pseudaphritidae and Eleginopsidae, are non-Antarctic with the exception of one species. These fish lack the genes for antifreeze glycoprotein production (Coppes Petricorena and Somero 2007) and have probably radiated in brackish cold waters before the isolation of Antarctica (Eastman and McCune 2000). Genetic data showed paraphyletic nature of the Bovichtidae within Notothenioidei (Lecointre et al. 1997). It was assumed that the Bovichtidae diverged from the rest of Notothenioidei due to fragmentation of Gondwana and cooling of Antarctica in Late Cretaceous–Eocene and then distributed widely in the southern South America, Australia and New Zealand (Miller 1987; Eastman 1993).

The largest bovichtid, channel bull blenny *Cottoperca gobio* (Günther 1861) inhabits cold shelf waters around the southern tip of South America from kelp forests of Chilean fjords in the Southeast Pacific (Vanella et al. 2007) to the

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Patagonian shelf in the Southwest Atlantic (Nakamura et al. 1986). This bottom dwelling fish occurs from shallow inshore waters to 200–300 m depths of the shelf break and slope. *C. gobio* does not aggregate in schools with adult males probably being territorial. The species is characterised by a marked sexual dimorphism both in size and body colouration. Mature males are larger attaining 50–80 cm total length (TL) and have much brighter colours of the body and fins than females, that attain 40–60 cm TL (present data). Similar to other blenny-like notothenioids, *C. gobio* is an opportunistic ambush predator with a wide niche breadth (up to 6.29) (Laptikhovsky and Arkhipkin 2003). Diets of both small (11–30 cm) and large (31–80 cm) *C. gobio* are dominated by the most abundant near-bottom notothenioid rock cod *Patagonotothen ramsayi* and Patagonian squid *Doryteuthis* (*Loligo*) *gahi* (Laptikhovsky and Arkhipkin 2003). Despite being a common bycatch during demersal trawl fishery for finfish in the Southwest Atlantic (Falkland Islands Government 2013), little attention has been paid to study the main population parameters of *C. gobio* such as age, growth and maturation (Eastman 1993), whereas reproductive biology is practically unknown.

In 2011, the Fisheries Department of the Falkland Islands established an onshore aquaculture facility to investigate the biology and behaviour of various fish inhabiting the Patagonian Shelf. The first experiment of the live maintenance of *P. ramsayi* lasted for more than a year and covered two winter spawning seasons. Many previously unknown aspects of *P. ramsayi* biology including brooding behaviour, structure of the egg mass, embryogenesis and early larvae were described (Arkhipkin et al. 2013). This paper presents the results of the second successful experiment of rearing of another notothenioid, *C. gobio* that aimed to address previously unknown aspects of its spawning, egg development and early larval growth.

Materials and methods

Five live adult specimens of *C. gobio* (45–60 cm TL) were collected from the catch of the last trawl of a survey carried out by the Fisheries Department onboard the chartered commercial trawler *Castelo* on 13 July, 2013. The trawl (St. 1140) was carried out in shallow waters (53 m depth) to the northeast of the Falkland Islands, Southwest Atlantic at 51°25′S, 57°42′W. After capture, the fish were kept onboard in 25 l plastic tanks with running sea water. Upon returning to Port Stanley within 2 h of the last trawl, the fish were transferred in large plastic bags filled with water into the Fisheries Aquaculture Facility located on a large floating barge (FIPASS).

The fish were placed into a 7,216-l circular tank with a bottom area of approximately 7.2 m² and 1 m water depth.

There was a mature biofilm/epizoan growth on the walls developed during the first experiment with rock cod. Several big rocks and halved large terracotta flower pots were placed on the bottom of the tank to create several shelters for the fish. Sea water was pumped into the tank directly from Stanley harbour with the total water turnover of 87 min. Temperature and salinity in the tank were monitored daily using a Valeport mini-CTD. The room with the tank was darkened by putting black semi-transparent shades onto the windows to minimise stress. Fluorescent lighting was used only when feeding the fish and cleaning the tank. Similar to the previous experiment with rock cod (Arkhipkin et al. 2013), *C. gobio* were fed every second day with defrosted squid *D. gahi*, pieces of rock cod and hoki *Macrouronus magellanicus* taken from commercial bycatch. Unfortunately, several days after the start of the experiment, three fish died of skin infection and barotrauma. The two surviving fish appeared to be a male and female. During the next 2 months (August–September 2013), fish behaviour was observed before feeding. After the spawning event had taken place, fish were photographed the same day by a diver submerged in the tank using a Nikon D90 digital camera with underwater housing and flash.

One egg mass was found attached to the side of the tank on 7 September, 2013. It was decided to leave the egg mass attached to the side. The whole egg mass was therefore only measured, but not weighed. Number of eggs in the egg mass was therefore only approximately estimated from the mean diameter of a single egg (estimated from a sample of 50 eggs), area covered by the egg mass and also approximate number of egg layers in the egg mass.

Samples of 10–15 eggs were taken from the egg mass daily during the first 10 days and then every other day until hatching and examined under a zoom microscope Olympus SZX12. Stages of embryonic development were assigned according to Kimmel et al. (1995). Eggs were measured and photographed using an Olympus DP70 digital camera attached to the zoom microscope.

Just before hatching, a portion of the egg mass was accurately scraped off the side of the tank and relocated to the Falklands Fish Farming Limited aquaculture facility for larvae rearing. At the same time, both parent fish were released back to sea. Details of the maintenance system can be found in Arkhipkin et al. (2013). After hatching, several *C. gobio* larvae and early juveniles were taken every second day for examination. Upon disappearance of the yolk sac, the larvae were fed with Otohime B1 Diet larval feeds (Japan), of 200–360 micron particle size. Larvae were fed three times per day at 08:00, 13:00 and 16:00, respectively. Feed quantities were gauged daily and adjusted to suit demand. Feeding was carried out by hand. The rearing experiment was terminated in the middle of December 2014.

Results

Environmental parameters

Water temperature and salinity in the broodstock tank reflected the varying parameters in Stanley Harbour. A positive trend was observed in water temperature that gradually increased from 4.3 to 8.2 °C (mean 6.0 °C) over the period from 7 September until 23 October. Apart from two significant dropouts in temperature that happened on 1 and 12 October, variability between close dates did not exceed 0.5 °C (Fig. 1a). Salinity had a slight positive trend during incubation (Fig. 1b), varying from 31.8 to 33.8 due to the halocline features of the surface water in Stanley Harbour and increased precipitation in the first half of September.

Water temperatures and salinities in the rearing tank were close to those observed in presumed spawning grounds of *C. gobio* on the shelf of the Falkland Islands. To the east of Port Stanley near the bottom at 50–100 m depths, water temperatures slightly increased from 6.5 to 6.9 °C, and salinity was almost stable at 33.67–33.71 between 21 September and 25 October, 2013 (Fig. 1).
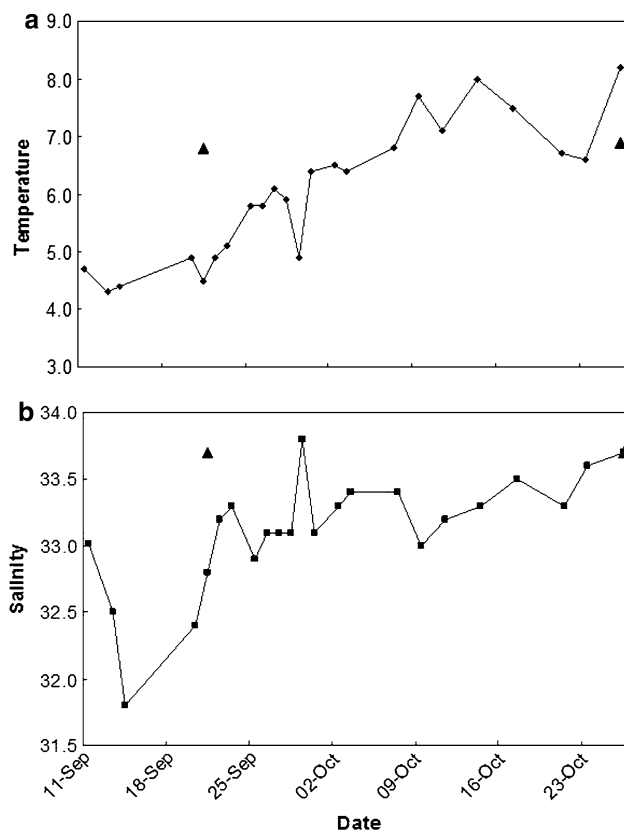

Fig. 1 Temperature (**a**) and salinity (**b**) profiles in the maintenance reservoir (*line* with rombuses) and in situ (*triangles*) near-bottom at 100 m depth on the shelf east of Port Stanley (Falkland Islands)

Fish behaviour in reservoir

During the first month of the maintenance, both fish were mainly hiding in their shelters made of terracotta pots (Fig. 2), occasionally leaving the shelters and searching for food. The food was distributed from the surface of the tank, and the fish acclimatised to feeding protocols within 1 week of entering the broodstock tank, swimming towards the feeding site and taking the food from the water column. In the beginning of the experiment, it was impossible to determine the sex of fish by colouration. Both fish had quite similar orange-brown stripes on their body with brownish fins, typical for adult specimens of this species (Nakamura et al. 1986). However, by the middle of August, the abdomen of one of them (female) started to extend.

By the end of August, the sides of the female abdomen were fully distended, possibly showing maturation of its ovary. The colouration of the body and fins of both fish also changed, displaying marked sexual dimorphism. The female acquired orange colour at the base and lower part of pectoral fins and also above the upper part of the jaw. Membranes between the first and fourth rays of the dorsal fin became white (Fig. 2a, c). The male changed in colouration more markedly than female. The head became bright yellow-greenish with white spots. Dorsal fin and caudal fin darkened acquiring almost black colour. The first six rays of the dorsal fin became white. The upper posterior part of the dorsal fin developed a longitudinal greenish band (Fig. 2a, b). Both sexes had flexible white appendages scattered along their body (Fig. 2a).

The spawning was not observed. After spawning, the female became much slimmer indicating the spawning incidence. After spawning, the male kept his sexual colouration for at least several days. The male did not display any aggressive behaviour to the female after spawning; however, the female preferred to stay in the shelter. The male cruised sometimes along the egg mass, but did not display any guarding behaviour when being photographed or disturbed. After spawning, both fish ate readily. The fish were kept in the tank until December 2013, but no further spawning and egg laying were observed.

Egg masses

One egg mass was found adhered to the wall of the tank on 7 September, 2013. The egg mass consisted of a band of eggs of about 120 cm long and 20–25 cm wide, tapered at both ends. The upper edge of the egg mass was about 40–50 cm from the surface of the tank. Eggs were laid in several layers, from one to two layers at proximal ends of the egg mass to five–six layers closer to the middle of the egg mass.
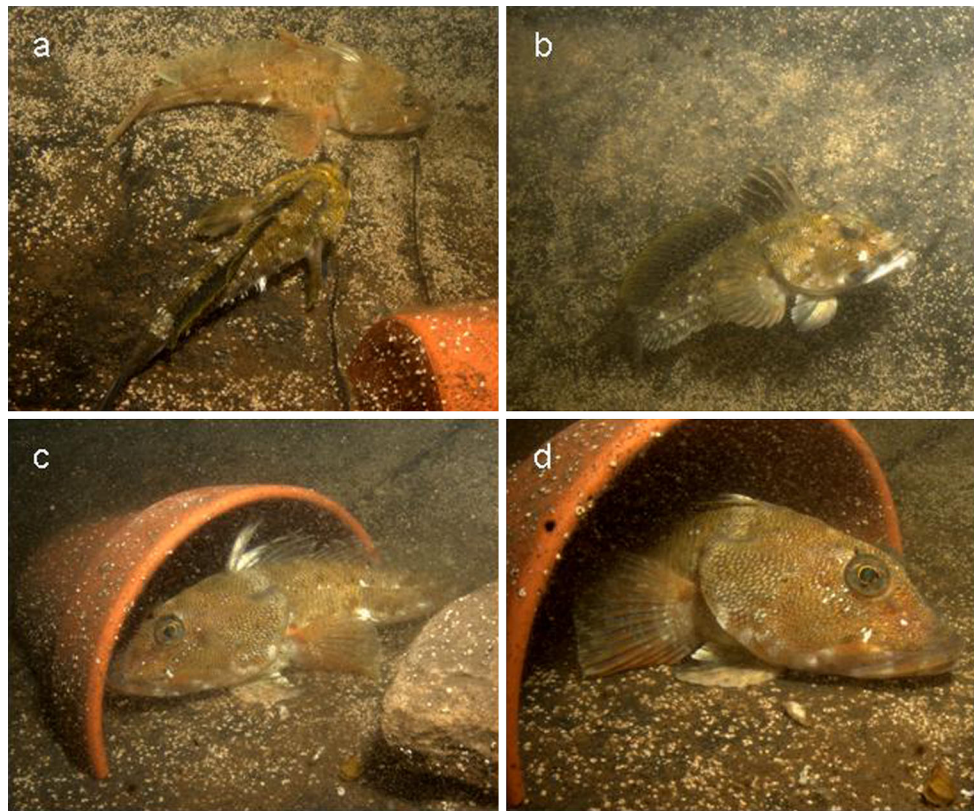
Fig. 2 *Cottoperca gobio*: male (*below*) and female (*above*) in breeding colouration after spawning (**a**); male in breeding colouration cruising along the egg mass adhered to the wall of the reservoir (**b**); female in breeding colouration (**c**) and female hiding in the shelter (**d**)

Eggs in the egg mass were adhered to each other in a honeycomb pattern leaving gaps between them to allow water circulation to the eggs inside (Fig. 3a). No unfertilised eggs were observed. Eggs were pale yellow, and they did not change their colouration during the whole embryogenesis. Egg diameters varied between 2.1 and 2.4 mm. There was a characteristic oil droplet inside each egg, about 0.5–0.6 mm in diameter. The cytoplasm contained a large agglomeration of dark granules (under transmitted light of the microscope), being much denser near the vegetal pole of the egg (Fig. 4). The total number of eggs was estimated to be about 170 thousand assuming the average of three egg layers eggs throughout the egg mass. After hatching of larvae, empty shells of eggs remained on the tank wall (Fig. 3b).

Embryogenesis

Description of the stages of the embryonic development with degree-days calculated to each stage is presented in Table 1. At the time when the egg mass was first observed on 7 September, the eggs were undergoing discoid cleavage that formed the spherical ball on the animal pole. This indicated that the embryos entered the blastula period. Continuous cleavage formed a multicellular layer and the

blastula began to flatten onto the yolk prior to epiboly. The epiboly started on the sixth day after fertilisation, when the blastoderm began to spread around the yolk towards vegetal pole (Fig. 4).

The embryonic axis formation, i.e. differentiation of primordial notochord, neuroblast and two parallel mesoblasts took place on the 8th day post fertilisation after the epiboly had been completed and therefore the embryos finished the gastrulation period (Fig. 4f). The segmentation period and formation of various organs of the embryo began on the 12th day after fertilisation with the appearance of primordial eyes and brain (Table 1; Fig. 5).

Early larval period

The first larvae started to hatch on 26 October, after 50 days post fertilisation. The hatching period was quite short and lasted about 2 days. The total length of newly hatched larvae ranged from 7.9 ± 0.2 mm, with the diameter of the yolk sac attaining 1.4 mm. The oil droplet was still visible inside the yolk sac. The primordial larval fin ran along the whole length of the body from the head to anus. The snout was flat. Two rows of melanophores formed along the body. The denser ventral row ran from the middle part of the body to the tail. Few much smaller
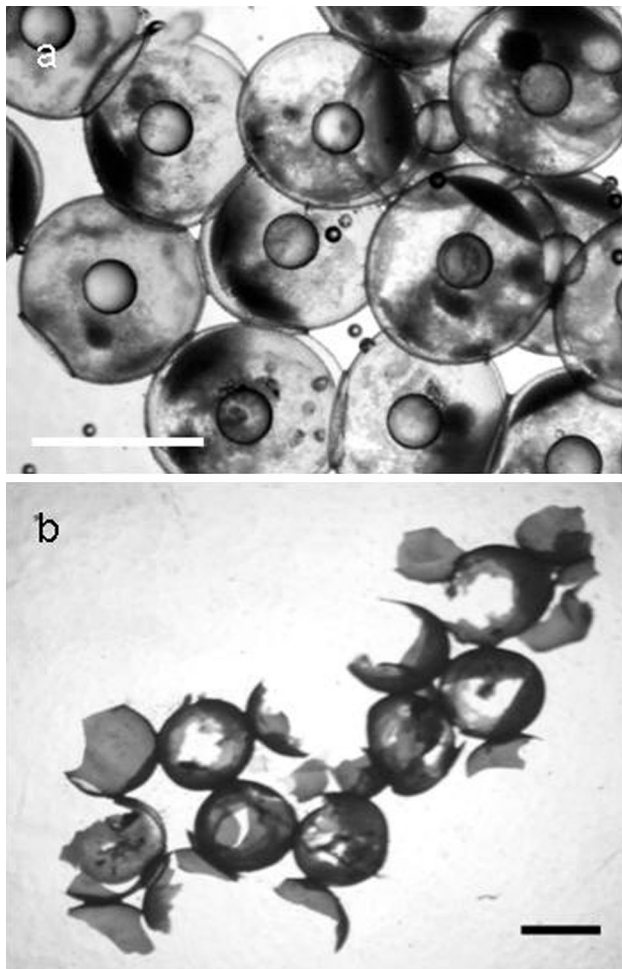
Fig. 3 Honeycomb cluster of *Cottoperca gobio* eggs with gaps that allow water circulation through the egg mass. The first day after egg laying (**a**) and after hatch of larvae after 50–52 days of incubation (**b**). *Scale bar* 2 mm

melanophores composed the middle row that ran along the middle lateral line. Dense aggregations of melanophores were observed on the yolk sac, dorsal side of the anterior part of the body, on the head and snout (Fig. 6a).

After hatching, the larvae moved actively in the water column. The yolk sac period lasted approximately 9 days. By the end of this stage, the larvae attained 8.9 ± 0.2 mm TL. General body morphology changed significantly when the larvae started to feed: the jaws became more pronounced, the dorsal and caudal fins more developed, with visible fin rays. Melanophores became more numerous and well resolved (Fig. 6b). At the end of the experiment 2 months after hatching, the young fry attained 1.5 cm TL. The dorsal and caudal fins became more pronounced, with visible fin rays in both fins. A third row of melanophores appeared on the dorsal side of the body close to the dorsal fin (Fig. 6c).

First feeding

Larvae were initially fed a mixture of the nauplii of *Artemia salina* and Otohime B1 Diet larval feeds (Japan), of 200–360 micron particle size. Observations of larva behaviour and microscope analysis showed that the gape of the jaws was not sufficient to consume the live food, as a consequence only the dry feed was used. Prior to first feeding during the yolk sac period, larvae avoided light and tried to swim to the bottom of the egg incubators or larval tank. In the 24 h before first feeding, larvae began to show active hunting behaviour within the water column and were positively phototaxic. 'Green water' in the form of concentrated *Nannochloropsis* sp. was used in the larval tank to promote hunting behaviour and to improve the success of feeding attempts.

Initial feeding response was poor in the larvae with eight out of ten attempts at consuming the feed failing. First feeding success was between 60 and 70 % of larvae added to the larval tanks. Three days after first feeding, larvae were able to consume the dry feed successfully with on average only two attempts out of ten failing. Larvae would sight a potential feed and fix their eyes upon it whilst circling it. They also formed the classic S-shaped posture. After a few seconds of circling behaviour, the larvae would straighten their body, pounce forward and swallow the feed. Feed size did not increase during the experiment.

Discussion

In vivo husbandry of *C. gobio* revealed for the first time some important aspects of its reproductive biology. *C. gobio* has many features characteristic to notothenioids living in the Sub-Antarctic waters including high fecundities, relatively small eggs and winter–early spring spawning (Kock and Kellermann 1991; Rae and Calvo 1995). Fish in our experiment spawned in early spring, when the water temperatures on the shelf (and fish tank) began to rise from 4.5 to 6 °C (Arkhipin et al. 2004). The spawning took place approximately 2 weeks later than the first spawning event observed in *P. ramsayi* (Arkhipin et al. 2013) and at least a month later than in *Patagonotothen tessellata* (Rae and Calvo 1995).

Similar to many demersal notothenioids, *C. gobio* displayed a marked sexual dimorphism in colouration of the body and fins both before and after spawning, with the male having brighter colours than the female. Both dorsal fins of male became black, whereas the first dorsal fin of female became white, possibly facilitating the recognition of sexes in twilight conditions near the bottom of the shelf. Similar change in colouration with darker fins and body of
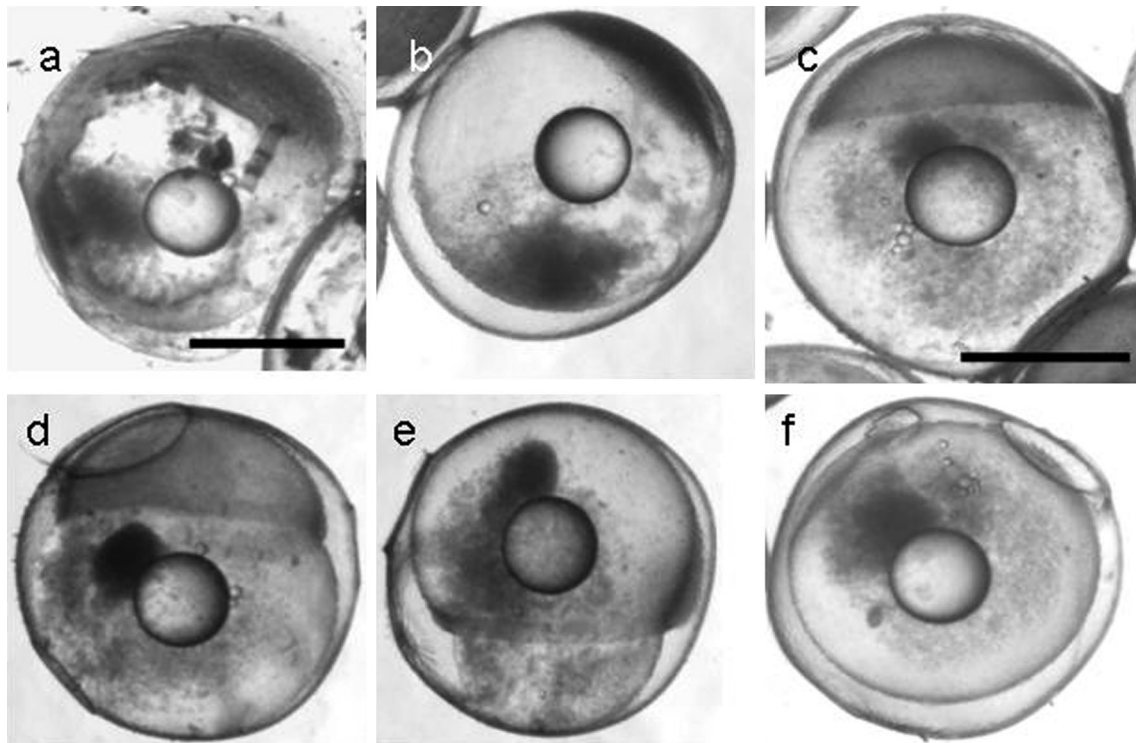
Fig. 4 Early embryogenesis in *Cottoperca gobio*: blastula as spherical ball (**a**) and flattens onto yolk (**b**), beginning of epiboly (**c**), 25 % of epiboly (**d**), 75 % of epiboly (**e**), full epiboly with embryonic axis formation (**f**). Note the presence of oil droplet inside the egg. *Scale bar* 1 mm

Table 1 Stages of embryonic development in *Cottoperca gobio*

Stage	Days	*C. gobio* degree-days	*P. ramsayi* degree-days	Description
Zygote and cleavage period	1 (dpf)	4.7	3.0	Zygote and early cleavage period were not observed
Blastula period spherical ball	2 (dpf)	9.4	6.8	Cleavage continues, the cells become spherical ball shape
Blastula flattens onto yolk	4 (dpf)	18.8		Cleavage continues forming multicellular layers prior to epiboly
25 % of epiboly	6 (dpf)	28.0	10.8	The blastoderm grows around the yolk towards the vegetal pole (25 % of epiboly)
Gastrula period			14.9	The blastoderm continues spreading around the yolk producing the primary germ layers and the embryonic axis
75 % of epiboly	7 (dpf)	32.3		
100 % of epiboly	8 (dpf)	36.7		Embryonic axis formation; notochord primordium, neuroblast, two parallel mesoblasts
Segmentation period	12 (dpf)	54.9	18.7	First somites form and optical vesicle becomes visible
	15 (dpf)	69.1	65.2	First heart beat noticeable
	19 (dpf)	90.3	42.3	First movement
	21 (dpf)	102.2	42.3	Otoliths become visible
	24 (dpf)	119.4	69.4	Melanophores appear on the belly, eyes pigmentation begins
	28 (dpf)	145.3	73.4	Pelvic fins develop
	31 (dpf)	165.3		Capillaries appear on the yolk sack
	33 (dpf)	180.2		Melanophores appear along the body and on the head
	50 (dpf)	305.5	143.3	Hatching

Dpf—days post fertilisation, degree-days in °C units. Degree-days of *Patagonotothen ramsayi* are presented for comparison and have been calculated from Arkhipkin et al. 2013

Fig. 5 Late embryogenesis in *Cottoperca gobio*: development of first somites (**a**) and eye balls (**b**), appearance of otoliths and eyes pigmentation (**c**), development of pelvic fins and appearance of capillaries before hatching (**d**). *Scale bar* 1 mm
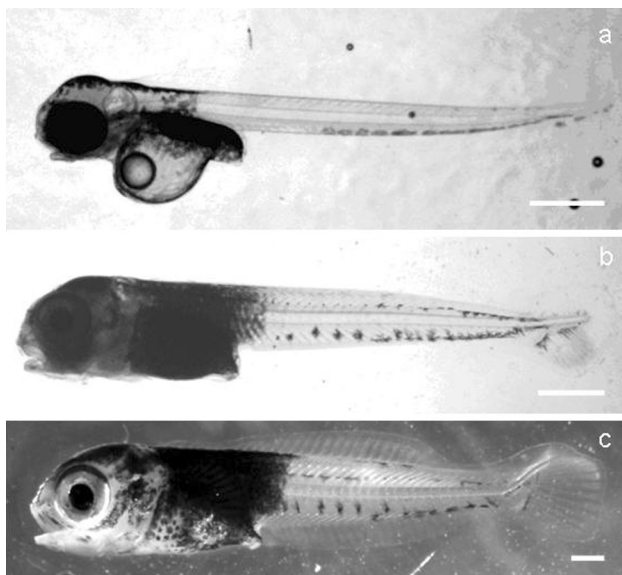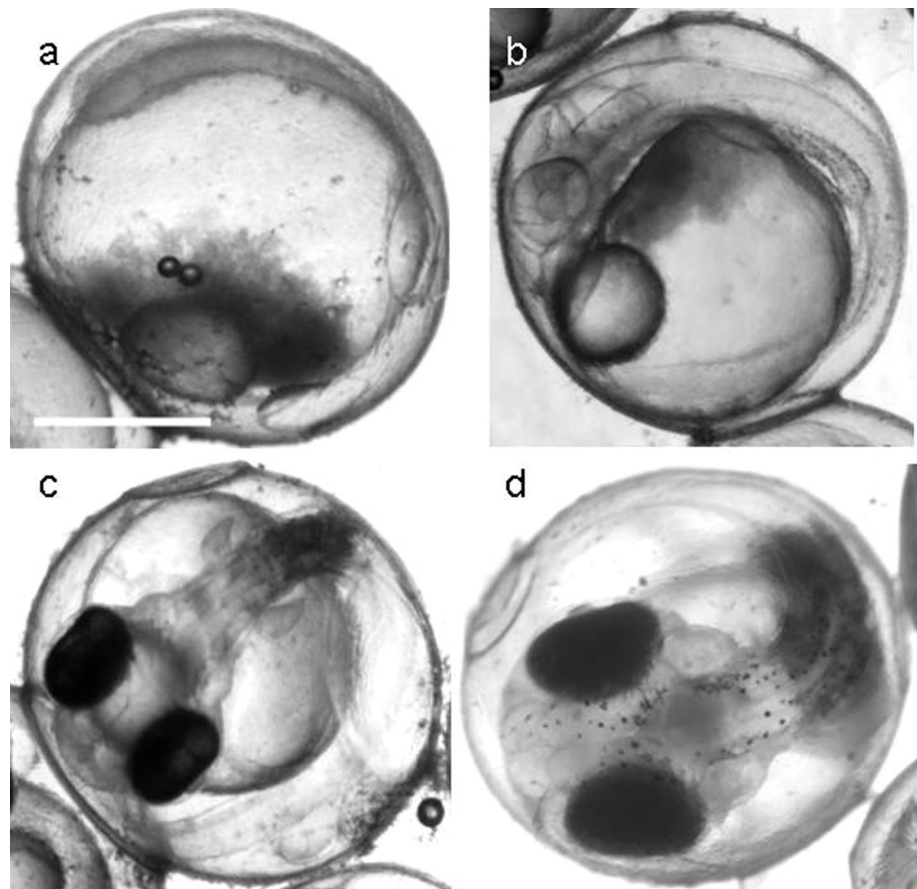

Fig. 6 Newly hatched larva with yolk sac and oil droplet (**a**), feeding 10-days old larva (**b**) and 2-months old young (**c**) of *Cottoperca gobio*. *Scale bar* 1 mm

males was observed in *P. ramsayi* (Ekau 1982; Arkhipkin et al. 2013). Males were known to change the body colouration in other notothenioid fish such as *Lepidonotothen*

nudifrons (Kock 1989) and *P. tessellata* (Rae and Calvo 1995).

Notothenioid fish exhibit an array of spawning patterns from pelagic spawning and eggs in *Notothenia rossi* and *Dissostichus eleginoides* (Camus and Duhamel 1985; Kellermann 1990) to benthic egg masses either unattached as in *P. ramsayi* (Arkhipkin et al. 2013) or attached to stones and sponges as in *L. nudifrons* (Hourigan and Radtke 1989). *C. gobio* had a sticky egg chorion and may attach their eggs onto hard substrate on the bottom like rocky outcrops or stones. Nevertheless, the structure of the egg mass was similar to that unattached sponge-like egg masses belonging to *P. ramsayi* (Arkhipkin et al. 2013) with eggs being stuck to each other in a honeycomb pattern with the gaps between eggs to facilitate ventilation. Quite unusually for demersal egg masses, eggs of *C. gobio* had a distinct and large oil droplet that obviously did not contribute to the buoyancy of the egg mass itself.

Neither sex of *C. gobio* displayed a guarding behaviour in the fish tank. The male cruised periodically along the egg mass but did charge neither female nor a scoop net that was immersed in the water during feeding, whilst the female hid in the shelter. Similar to many other bottom spawning notothenioids (Kock 1992), the egg masses of *C.*

gobio in situ are probably unprotected for the duration of incubation period, being therefore quite vulnerable to predation by benthic invertebrates.

C. gobio eggs are relatively small (2.1–2.4 mm in diameter), similar to other bottom spawning Sub-Antarctic and temperate notothenioids such as *P. ramsayi* (Arkhipkin et al. 2013) and *P. tessellata* (Rae and Calvo 1995). Due to the size of its egg mass, *C. gobio* has one of the largest fecundities among notothenioids (Kock 1992). There was no other spawning event from the same pair, indicating that only one portion of eggs has developed and matured in the gonad, and then has been spawned as a single egg mass similar to *P. ramsayi* (Arkhipkin et al. 2013). This was in contrast to the confamiliar *Bovichtus diacanthus*, whose mature females had two portions of yolk oocytes in the gonad and therefore might have batch spawning (La Mesa et al. 2010). Batch spawning might develop as an adaptation to more variable environmental changes in nearshore waters and intertidal pools inhabited by *B. diacanthus* in Tristan da Cunha, whereas total spawning was more characteristic for fish like *C. gobio* and *P. ramsayi* spawning in more stable environment of their offshore shelf spawning grounds (Brickle et al. 2006; La Mesa et al. 2010).

Despite similar egg size and higher incubation temperatures, the duration of embryogenesis in *C. gobio* ($\sim$50 days) was much longer than in *P. ramsayi* (28–32 days) and *P. tessellata* (28 days) (Arkhipkin et al. 2013; Rae and Calvo 1995). However, it was still shorter than in the Antarctic species *L. nudifrons* and *Harpagifer antarcticus* (about 120–150 days) that have similar egg diameters as *C. gobio* (2.2–2.5 mm) (Daniels 1978; Hourigan and Radtke 1989). The total amount of accumulated degree-days for the whole embryogenesis was three times greater in *C. gobio* than in *P. ramsayi*, indicating much slower development of embryos at all stages in the former species. Sizes of newly hatched larvae ($\sim$8 mm) corresponded well with the relationship between the egg size and larval size at hatch for notothenioid fish (Kock 1992). Despite similar egg size, newly hatched larvae of *C. gobio* were larger but had slightly shorter yolk resorption period (9 days) than those of *P. ramsayi* (6.2–6.7 mm TL and 11 days, respectively; Arkhipkin et al. 2013). Shorter yolk resorption period and rather small yolk supplies in spring-hatched larvae (such as *C. gobio* and *P. ramsayi*) would indicate their earlier exploitation of the spring zooplankton blooms (Boltovskoy 1999). Conversely, larvae of winter-hatched species have larger yolk supplies and longer yolk resorption period of up to 3 weeks, such as in *L. nudifrons* (Hourigan and Radtke 1989) and up to 5 weeks in *H. antarcticus* (Daniels 1978) enhancing their survival during periods of relative food scarcity before the spring peak of zooplankton.

The unusual oil droplet that is present throughout the embryonic stage could facilitate the newly hatched *C. gobio* larvae to vertically ascend from colder near-bottom waters to warmer and more productive superficial layers, thereby potentially accelerating their growth. Early larvae of *C. gobio* had not only head pigmentation like the larvae of *D. eleginoides* and *H. antarcticus* (Evseenko et al. 1995; White and Burren 1992), but they were also pigmented anteriorly, making the pigmentation pattern quite specific that could be used for identification purposes.

The blenny-like and sculpin-like notothenioid fish represent a good example of r/k strategy continuum that changes with the latitudes of their habitats. High latitude species living in Antarctic waters possess many K-selection features such as large eggs and larvae, territorial behaviour with nest guarding and parental care, slow development and growth rates (Kock 1992). Low-latitude species living in Sub-Antarctic and temperate waters are located at another side of that r/K continuum having smaller eggs and larvae, higher fecundities, lack of parental care and high growth rates (Kock and Kellermann 1991; Rae and Calvo 1995). Our data showed that *C. gobio* is placed at the very r-end of the r/K continuum among sculpin-like notothenioids, having demersal egg masses but the largest fecundities comparable to those of pelagic spawning notothenioids such as *Eleginops maclovinus* and *D. eleginoides* (Brickle et al. 2005; Laptikhovsky et al. 2006). These specific life history traits may have enabled *C. gobio* to populate the vast areas of the Patagonian Shelf and upper continental slope in the Southwest Atlantic, whilst competing with other abundant large demersal fish predators at the 4–5th trophic levels such as red cod *Salilota australis*, kingclip *Genypterus blacoides* and hakes *Merluccius hubbsi* and *M. australis* (Arkhipkin et al. 2012).

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