Reproduction in the live-bearing teleost *Clinus superciliosus*

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By studying embryonic mass increase, yolk availability and embryonic oxygen consumption, it was established that the embryos of *C. superciliosus* rely almost entirely on maternal secretions for their nutrients and the species therefore displays an advanced form of viviparity. They breed throughout the year and the species also exhibits superembryonation (superfoetation – *sic*) with as many as 12 broods developing simultaneously. Furthermore, it was found that the relationships between the body mass and the gonad masses and number of embryos produced, are linear. It was suggested that these phenomena, coupled to the territoriality exhibited by the species, are factors whereby the species overcomes the problem of a reduction in the number of embryos produced, a phenomenon normally encountered in viviparous fishes.
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By die bestudering van embrioniese massa-toename, dooierbeskikbaarheid en embrioniese suurstofverbruik, is vasgestel dat die embrios van *C. superciliosus* feitlik heeltemal staatmaak op moederlike sekresies vir hulle voedsel en daarom toon die spesies 'n gevorderde vorm van vivipariteit. Hulle broei dwarsdeur die jaar en die spesies toon ook superembrionasie (super-fetasie – *sic*) met soveel as 12 broeisels wat gelyktydig ontwikkel. Verder is ook gevind dat die verhoudings tussen die liggaamsmassa en die teelkliermassas en die aantal embrios geproduseer, liniêer is. Dit is voorgestel dat hierdie verskynsel, gekoppel aan die territorialiteit getoon deur hierdie spesies, faktore is waarby die spesies die probleem van 'n verlaging in die aantal embrios geproduseer oorbrug – 'n verskynsel wat normaalweg aangetref word by viviparige visse.
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Clinus superciliosus has been described by Gilchrist and Thompson (1908), Smith (1946, 1949) and Penrith (1969). According to Penrith (1970), the clinids are the dominant group of fishes living permanently around the shores of the Cape Province and the southern region of the West African coast. Clinid distribution has also been studied by Barnard (1927), Penrith (1965) and Gosline (1968).

C. superciliosus is the most common clinid found along the Cape coast and its distribution has been documented by Penrith (1969). *C. superciliosus* is a viviparous teleost and gestation is intrafollicular. There are numerous excellent reviews on viviparity in teleosts in which embryonic adaptations for nutrient uptake are discussed (Ryder 1885; Turner 1947; Bertin 1958; Hoar 1955, 1969; Amoroso 1960; Breder & Rosen 1966). In the case of *C. superciliosus* autoradiographic studies showed that the embryos absorb nutrients through the epidermis, the fins and the gut, and these structures have become extensively modified in order to act as absorptive tissues (Veith 1978). The bulk of nutrients required for embryonic differentiation are secreted by the ovarian epithelium in the form of embryotrophe which is particularly rich in amino acids and lipids (Veith 1979).

The protection of young in fishes increases the chance of survival, and some teleosts protect their young by a variety of means (Hubbs 1921): by burying the eggs, nest construction, laying them under plants or in bubbles, driving predators away, laying the eggs in tough capsules and by various means of gestation such as mouth, brood pouch and intraovarian gestation.

The purpose of this paper is not only to demonstrate the degree to which viviparity has developed in *C. superciliosus*, but also to show some of the ways in which the problem of reduced reproductive output have been circumvented by this species.

Procedure

Specimens were collected along the south coast from Gordons Bay to Onrust, most of which were, however, caught at Pringle Bay and Rooi Els. Smaller specimens were collected with a hand line, but larger specimens were caught with a rod. They were kept alive and subsequently transported to the laboratory, where they were kept in 140 *l* seawater tanks, fitted with undergravel filters, a Hykro protein skimmer and a Turbinette filter, all of which were found to be essential for the well-being of the fish. When fish were maintained in the laboratory for any length of time, they were fed on Tetra Min staple food. General observations on ecology and behaviour were made while snorkling, as well as in the laboratory. In order to establish the degree to which the embryos rely on maternal secretions for their nutritive requirements the embryonic mass increase, yolk availability and oxygen consumption of the embryos was studied.

Mass increase

The embryos were removed from the ovaries of gravid females, the smallest measured 2,2 mm and the largest 20 mm. The embryos were weighed as a group to the nearest 0,1 mg. Because of the very small mass individual weighing was not feasible. Embryos measuring 2,2 mm were the smallest that could be handled and 20 mm were prepartum embryos.

Yolk availability

In order to determine whether sufficient yolk was available in the embryos for completion of their embryonic development, the volume of yolk present in early embryos was determined by measuring the diameter of yolk within the spherical yolk sacs under the microscope and then calculating the volume with the formula for volumes of spheres. In view of the small amount of yolk present it was not possible to carry out any direct determinations of yolk mass and energy content and a theoretical approach was therefore employed. The values used for the specific gravity and the energy value of yolk can obviously not be assumed to be exactly the same in all fishes. For the purpose of this theoretical approach a certain amount of leeway can be allowed without altering the outcome substantially. The energy value of fish yolk was determined on the yolk of *Micropterus salmoides*. The yolked eggs were supplied by the Department of Inland Fisheries of the Jonkershoek research station. The energy value was determined on a IKA adiobatic bomb calorimeter. The energy value of clinid embryos was also determined.

Embryonic oxygen consumption

The oxygen consumption of 18 prepartum embryos (20 mm) was determined in a Gilson respirometer. Three reaction vessels, containing six embryos each, were used for the determination.

All determinations were carried out at 16 °C.

Reproductive cycle

The reproductive cycle was examined by noting changes in gonad mass throughout the year. Fish masses were determined to 0,1 g and gonad masses to 0,1 mg. All lengths were measured as standard length, as outlined by Day (1969).

Results

Embryonic mass increase

The mean mass of 2,2 mm embryos was found to be 1,3 mg (n = 12) and the mean mass of 20 mm embryos was found to be 46,3 mg (n = 12). This represents a mass increase of 45 mg.

Yolk availability

It was found that the mean diameter of yolk present in the yolk sacs of the smallest embryos in the ovary of a gravid clinid was 0,3 ± 0,08 mm (n = 64). From this it was possible to calculate the approximate volume of the yolk. It was found that the approximate mean volume of yolk was 0,13 ± 0,1 mm^3. Assuming that the specific gravity of yolk is 1,025 (Smith 1957), then the mass of yolk available to the embryos is 0,133 mg (wet weight) and further assuming a theoretical 65% water content, this would represent a dry mass of 0,047 mg.

The energy value of fish yolk was found to be 27,86 kJ/g (dry mass), as determined on the yolk of *M. salmoides*. If this value is applied to clinid yolk, then the yolk available for embryonic growth, would amount to 1,3 J per embryo. The energy value of prepartum embryos was found to be 22,95 kJ/g (dry mass) and as these embryos have a dry mass of 16,2 mg (46,3 mg wet mass), this would amount to an energy value of 371,8 J per embryo.

The disparity between 1,3 J (original yolk) and 371,8 J (prepartum embryo), great. Figure 1 shows a cross-section through the ovary of a gravid *C. superciliosus* and shows the increase in size achieved by the embryos during gestation. Figure 1 also shows that the species exhibits superembryonation and as many as 12 broods were found in the ovary of a single female.

Embryonic oxygen consumption

In the present investigation the oxygen consumption of 20 mm embryos was determined and it was found that the mean oxygen consumption was 473,48 ± 155,17 μ l/g/h. For a single embryo with a body mass of 46,3 mg, this would represent an oxygen consumption of 21,9 l/embryo/h. If we convert this to joules consumed (using the relationship 20,1 kJ = 1 *l* oxygen), then this would represent 0,44 J/h and would mean that a prepartum embryo would consume all the energy in the yolk (initially available) within 2,95 h.

The reproductive cycle

Body mass gonad mass relationship

C superciliosus breeds throughout the year. Mature females caught at any time during the year, were always gravid.

The body mass and gonad mass of 29 females were plotted and correlated and it was found that gonad mass increased linearly as the body mass increased (Fig. 2). The line was fitted by linear regression, using the method of least squares. It was found that r^2 = 0,76. In the current investigation it was found that a linear relationship is not only applicable to body mass and gonad mass, but that there is also a linear relationship between body mass and the number of embryos present (Fig. 3).

Discussion

The increase in mass achieved by the embryos during the course of gestation is a criterion often used to ascertain the degree to which viviparity has evolved in a species

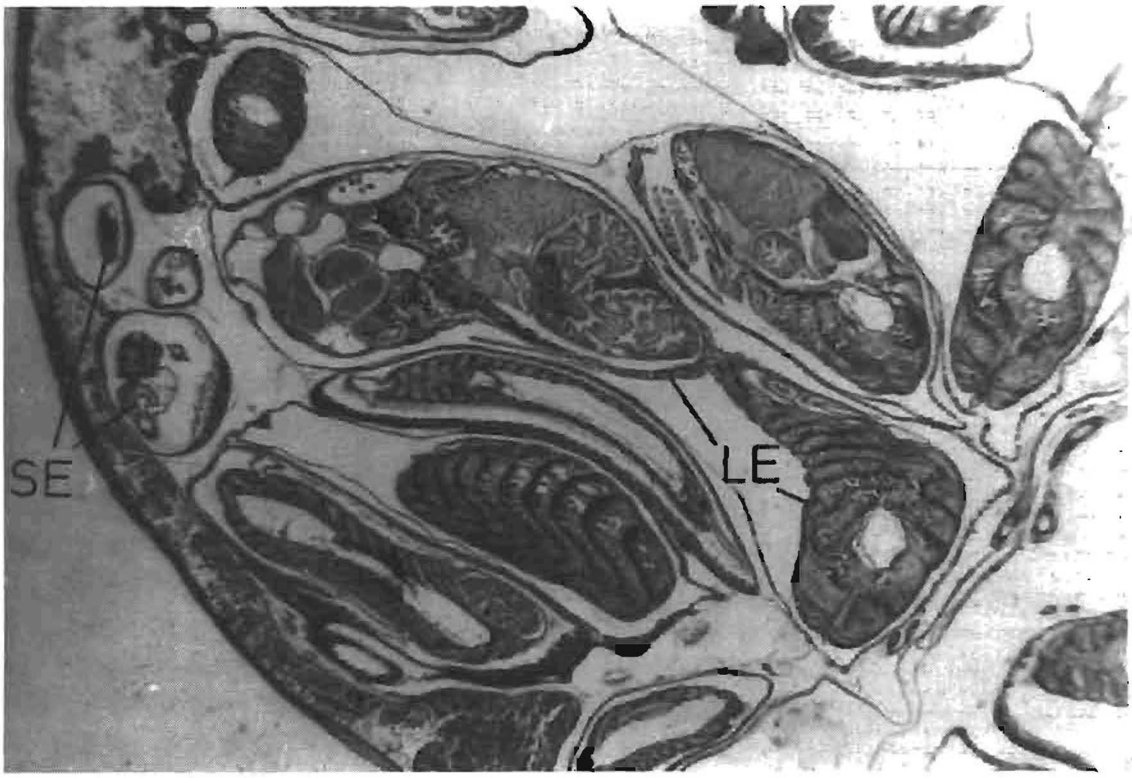

Fig. 1 Cross section through the ovary of *C. superciliosus* showing small and large embroyos. LE — large embryo; SE — small embryos. The section also demonstrates superembryonation. (X12).

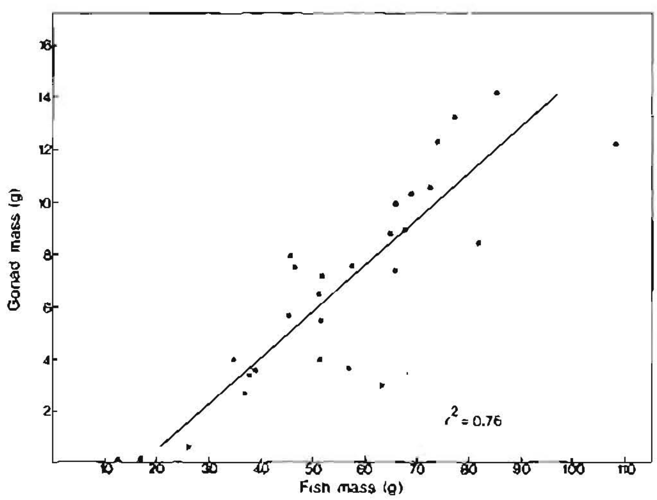

Fig. 2 The relationship between gonad mass and fish mass in *C. superciliosus*.

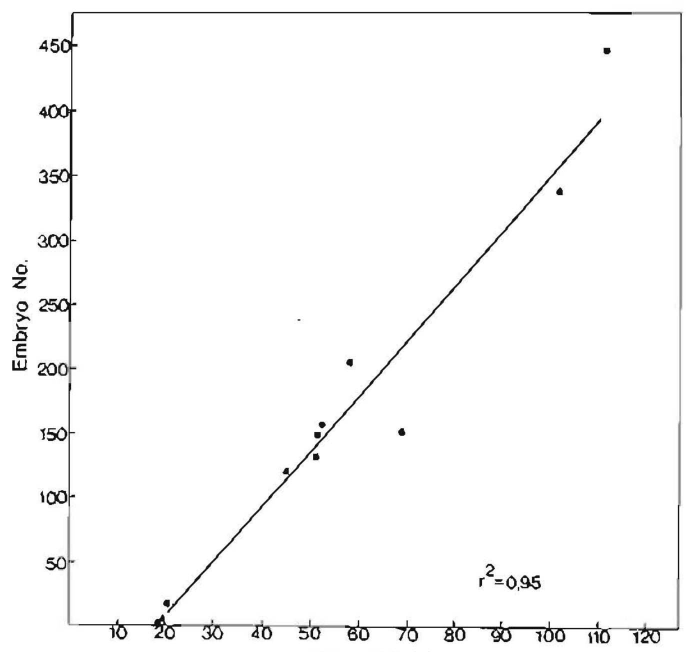

Fig. 3 The relationship between the mass of *C. superciliosus* and the number of embryos.

(Scrimshaw 1944, 1945). In the case of *C. superciliosus* the embryonic increase in conjunction with the hypothetical energy value of the yolk initially available to the embryos and the energy value of prepartum embryos indicates an advanced form of viviparity. If the metabolic rate of embryos is also taken into account then it can be assumed that the embryos must rely on nutrients absorbed from the embryotrophe for nearly all their metabolic requirements. The small amount of yolk is probably only important during initial development.

Studies on the oxygen consumption of the embryos of viviparous fishes are still relatively rare, but Webb and Brett (1972) carried out extensive metabolic rate studies on two species of viviparous seaperches. The oxygen consumption of *Clinus* embryos at term was approximately double that reported for *Rhacochilus vacca*.

The reduction in embryo numbers normally associated with viviparity is overcome by *C. superciliosus* in that it breeds throughout the year thus increasing the number of fish spawned per annum. According to Penrith (1970), conditions of temperature, normally one of the strongest factors influencing seasonal variation, tend to vary little at any given locality on the South African coast. Maximum and minimum temperatures rarely show differences greater than 6,5 °C. This condition would favour breeding all the year round. Indeed, some of the other clinid species like *C. cottoides*, *Blennioclinus brachycephalus* and *Pavoclinus* *mus* from localities in False Bay showed eggs and embryos in several stages of development throughout the year (Penrith 1970). By breeding throughout the year, *C. superciliosus* partly overcomes one of the problems of viviparity, namely reduced reproductive output.

Through superembryonation the embryos are not all spawned at the same time and this possibly decreases the chance of detection. (The term superembryonation is used in preference to superfoetation when referring to lower vertebrates as the term foetus should be confined to mammals.)

Superembryonation is not uncommon in teleost fishes. It occurs in poeciliid fishes (Turner 1947) and the ovary of *Heterandria formosa* can contain as many as nine broods all developing simultaneously (Turner 1937).

Gonad mass and embryo number increase linearly with increased body mass. The reason for the deviation from the line shown by some of the samples, might be that some of the embryos had been recently spawned. This would reduce the overall gonadal mass for a short period after spawning, and also account for the fact that large deviations are found below the line. That gonadal size and brood size increase with age, has been found in other viviparous teleosts (Mendoza 1939, 1956; Seal 1911; Hubbs 1921; Wilson & Millemann 1969). By becoming reproductively active at an early age the reproductive output of any one female throughout her lifetime can be increased significantly. By further ensuring (through territoriality) that the fish producing the greatest number of offspring are located in the most favourable areas, the viability of the species can probably be greatly increased.

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