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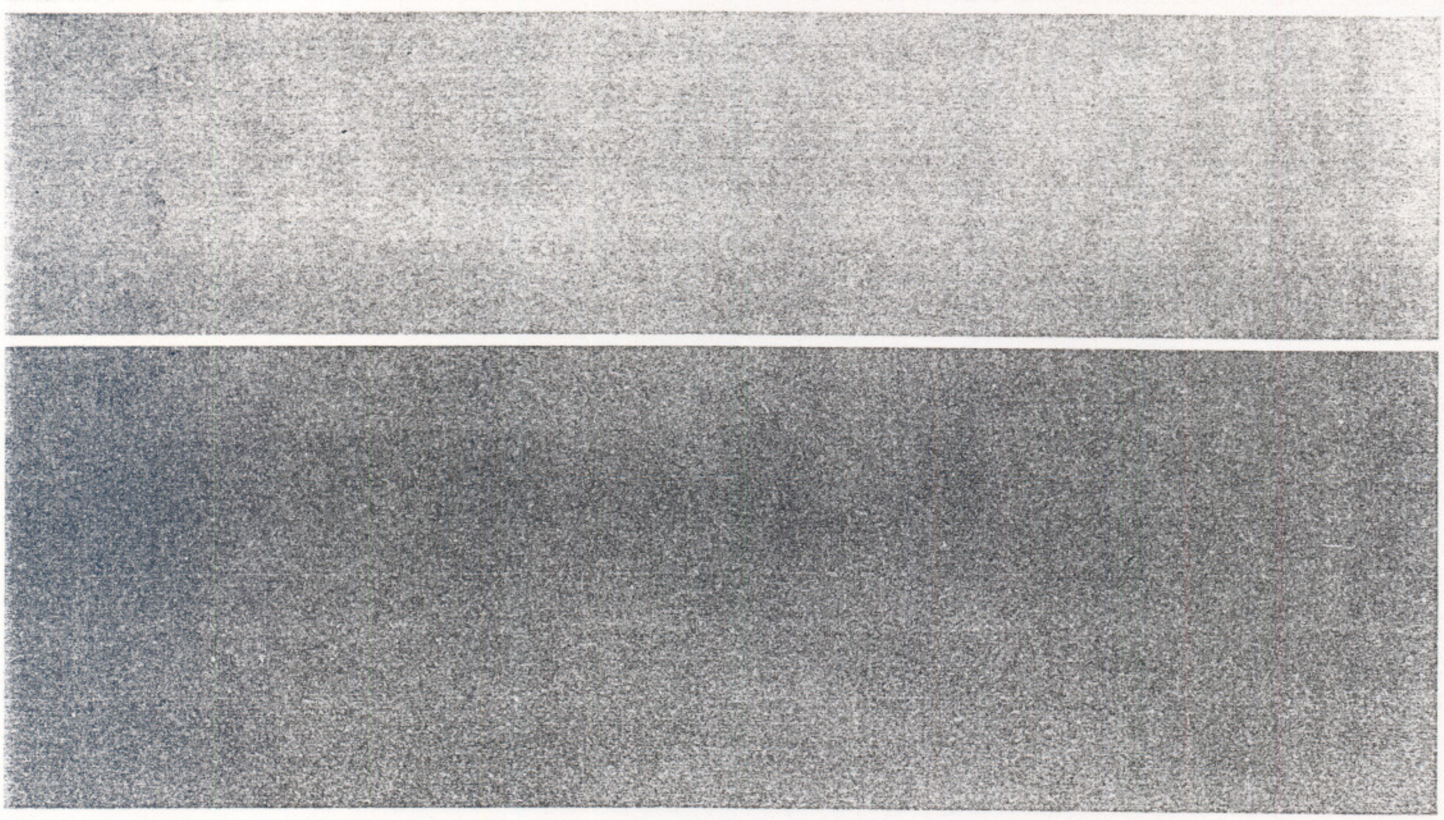
Fecundity, Egg Weight and Oocyte Development in Tilapias (Cichlidae, Teleostei)

Hans M. Peters

Translated from German
and edited by Daniel Pauly



INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

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Preface

Although published more than twenty years ago, this study by Professor H.M. Peters of the University of Tübingen, on the fecundity and related aspects of the biology of tilapias has remained the most detailed of its kind. Unfortunately, its publication in German has restricted its readership particularly in those tropical countries where tilapias are being cultured and are becoming extremely important food fishes.

Several problems occurred in the course of this translation, one of them being the narrative style used by the author. Some tightening up of the text was achieved here by drawing together all the comments and remarks on material and methods that were strewn throughout the text into an expanded 'material and methods' section, by incorporating all original footnotes into the text, and by creating, out of various bits and pieces a new 'acknowledgements' section. Also, the original tables, which had in the original neither numbers nor legends have been numbered consecutively and given appropriate legends. Some figures have been modified slightly to make them more readily intelligible, while all references, cited as "in press" in the original have been updated. It must be stressed, however, that despite these modifications, *all* of the original information is incorporated in the translation presented here, i.e., no attempts were made to shorten the text.

Another problem that occurred in the course of the translation pertained to the definition by Peters of certain concepts and terms. Thus, while the German word "Gelege" is well translated by "spawn", the problem remains that "Gelege/spawn" as used here has a number of meanings, not all of which are covered by the author's definition; the same problem applies to "oocyte" and "egg" which are sometimes used interchangeably, and sometimes with different meanings.

The future of tilapias as food fishes depends largely on the availability of suitable fry, obtained from rearing the eggs of selected broodstocks. Although a considerable amount of work has been done on the reproductive biology of tilapias since Peters' study (see reviews in Pullin and Lowe-McConnell 1982)[1] his work remains a most valuable series of observations. In tilapia hatcheries, the need for good estimates of the fecundity of broodstock is paramount. Peters' study indicates why such estimates are so difficult to obtain and clarifies the patterns of egg production for a variety of species.

Peters' brief reference to increased spawning frequency when eggs are removed from a mouthbrooding female is also important. This phenomenon was also noted by Dr. Jen-Chyuan Lee in doctoral thesis work at Auburn University (1979)[2] and is the rationale behind current work on egg removal and artificial incubation, which is already in limited commercial use in Taiwan. It merits much fuller investigation.

Peters also refers to resorption of unspawned eggs—a pointer to tilapia breeders that overripening of ovulated eggs can occur if oviposition is delayed. This is a key factor in determining egg quality in many species of cultured fishes and is likely to assume greater importance in tilapia culture if the use of manipulative techniques such as stripping and artificial incubation increases. Peters' study thus seems particularly relevant to present-day problems of tilapia culture.

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[1] Pullin, R.S.V. and R.H. Lowe-McConnell, Editors. 1982. The biology and culture of tilapias. ICLARM Conference Proceedings 7, 432 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

[2] Lee, J-C. 1979. Reproduction and hybridization of three cichlid fishes, *Tilapia aurea* (Steindachner), *T. hornorum* (Trewavas) and *T. nilotica* (Linnaeus) in aquaria and plastic pools. Auburn University, Auburn, Alabama. 83 p. Ph.D. dissertation.

The tilapiine fishes, formerly considered to belong to one single genus *(Tilapia)* containing more than 100 species, are now considered—at least by some authors—to consist of several genera. Dr. E. Trewavas, of the British Museum (Nat. History) has gone furthest in splitting the tilapias. A table is provided below which shows how her classification of the tilapias relates to the name originally used by Peters. This table also incorporates the names proposed by Thys van den Audenaerde, of the Tervuren Museum, Belgium, for the fishes used by Peters.

Names of the species of tilapias used in Peters' investigation.

Peters (1959)	v.d. Audenaerde (1968)[a]	Trewavas (1982)[b]
T. tholloni	*Tilapia tholloni*	*Tilapia tholloni*
T. guineensis	*Tilapia guineensis*	*Tilapia guineensis*
T. zillii	*Tilapia zillii*	*Tilapia zillii*
T. mossambica m	*Tilapia mossambica*	*Oreochromis mossambicus*
T. mossambica k	*Tilapia korogwe*	*Oreochromis korogwe*
T. macrocephala	*T. melanotheron*	*Sarotherodon melanotheron*
T. galilaea	*T. galilaea*	*Sarotherodon galilaeus*

[a]"An annotated bibliography of *Tilapia* (Pisces, Cichlidae)." Mus. R. Afr. Centr. Tervuren, Belg., Doc. Zool. No. 14, 406 p.

[b]Trewavas, E. 1982. Generic groupings of Tilapiini used in aquaculture. Aquaculture 27: 79-81.

The identity of the fish material used by Peters thus remains established, despite the change of names.

Although I never met Professor Peters, I received in the early seventies several letters from him in response to queries I had concerning my own work on tilapias. His answers were always friendly and helpful. I now hope that my translation will help make his work better known in English-speaking countries.

I would like to take this opportunity to thank R.S.V. Pullin (ICLARM) for reviewing the translated text, and suggesting various improvements.

Daniel Pauly
Manila, March 1983

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Abstract[1]

A study is presented of the fecundity, egg weights and oocyte development in tilapiine fishes, based mainly on data from 7 species of substrate-spawning and mouthbrooding tilapias.

The weight of single eggs in a tilapia spawn varies widely, and the average egg weight is higher in mouthbrooding than in substrate-spawning tilapias. In both groups, egg weight increases with body weight.

Weight differences of eggs are mainly due to differences in yolk quantity. Water content after fertilization amounts to 50-60% of egg weight; it is species-specific and higher in substrate-spawners than in mouthbrooders.

A tilapia spawn matures as a whole group of oocytes which are deposited as a whole, except for a number of "residual" eggs which remain in the ovary. There is a marked tendency to resorb ripe eggs, a feature which must be taken into account when determining the effective fecundity of tilapias.

The number of eggs per spawn tends to increase with body weight, but varies widely between fish of the same body weight. Egg number is inversely related to the average egg weight of a spawn, i.e., a tilapia produces either a large number of small eggs, or a small number of large eggs. The weight of a whole spawn is closely related to body weight, however.

The possible occurrence of such interrelationships in other fish groups is discussed, along with some of the ecological implications.

Introduction

Among tilapiine fishes, two behavioral types may be distinguished: the "substrate-spawners" and the "mouthbrooders". In the first type, both parents guard the brood; the young form a school, which follows the parents. In almost all mouthbrooding tilapias, on the other hand, only the female cares for the brood.

[1]Translator's note: Adapted from the author's English language summary.

She takes the freshly spawned eggs in her mouth and keeps them past hatching, until the time when the yolk sac is almost resorbed. Then, the female releases the young; these however remain close to their parents, as is the case with young of substrate-spawners. As opposed to the latter, however, the young of mouthbrooders seek refuge in their mother's mouth when afraid and at night. In only one species of mouthbrooder has it been conclusively demonstrated that it is the male that does the brooding. At first, everything happens as in the case of female brooders. However, a characteristic difference occurs in that once the young are released from the mouth of the brooding male, they form a school and swim away.

As shown by Dambach (1963), these behavioral traits are associated with type-specific egg sizes. The eggs of the substrate-spawners are small and their yolk supply limited, resulting in its rapid resorption. The young begin to swim about at an early stage of their development, i.e., in a phase of their ontogeny that is characterized by numerous larval features. However, they grow under the protection of their parents until they become self-sufficient.

The mouthbrooders, on the other hand, have larger eggs. In the case of the above-mentioned male mouthbrooding species, the eggs reach extreme sizes; it takes quite a while until the yolk is used up. Thus, when the young finally leave the mouth of the brooding male, they have developed so much that they apparently do not require further protection. The characteristic association between the parents and their young that occurs in substrate-spawners and in mouthbrooders with moderate-sized eggs may thus be bypassed in cases of extremely large eggs—this is in a nutshell how egg size and behavior are interrelated. However, this is a broad generalization of a set of very complex and little understood phenomena, which the author has been attempting to elucidate (Peters 1963). In the course of these investigations, the need became apparent to conduct a detailed comparative study of egg sizes. Such study would allow for a link-up of behavioral studies with physiological and ecological aspects of reproduction in teleosts.

The size of tilapia eggs is not constant; it varies rather widely within spawns, and is also related to the size of the spawning females in that larger fish generally produce larger eggs. Superimposed on these relationships, however, is the feature that egg sizes are inversely related to spawn sizes, such that a given tilapia produces either a large number of small eggs or a small number of large eggs. Such relationships have been discussed in Peters (1959)[2]. The aim of the present study is to expand on this earlier work.

There are in the literature several accounts of the fecundity of tilapias; the data presently rest on counts of eggs spawned, or of eggs removed from ovaries. These accounts are quite scattered, based on casual observations, and not on planned, larger-scale studies. This is generally so because their authors were interested, for practical purposes, only in preliminary estimates of fecundity. Also, these accounts did not take into consideration the interrelationships, discussed above, between egg numbers, egg sizes and body weight. For these reasons, these accounts cannot be used as a basis for the present investigations, which furthermore are based on species different from those from which earlier data are available. Finally, it seems that a number of the earlier data are unreliable, as will be shown below for a few cases. Mortimer (1959) and Lowe (McConnell) (1955) should be consulted for more details on this subject. Lowe (McConnell) came closest to the aim of the present investigation; she was the first to point out that mouthbrooders have fewer, but larger eggs than substrate-spawning tilapias. She also confirmed older studies suggesting that egg numbers increase with body weight and found that the egg sizes of various mouthbrooding species differ characteristically and lead to the conclusion that the evolution of mouthbrooding led to a reduction of fecundity.

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[2]Translator's note: This investigation pertained to *T. mossambica* and an unidentified herbivorous tilapia species.

Material and Methods

MATERIAL AND METHODS USED THROUGHOUT THE INVESTIGATION

The present investigation is mainly based on the 7 tilapia species listed in Table 1, where the origin of the various stocks—so far it is known—is given.

The egg[3] dimensions were determined with a micrometer and a binocular microscope. The measurements pertain to the egg itself, without the egg membrane. Egg "length" refers to the main axis of the egg; egg "width" refers to the maximum length that is perpendicular to the main axis. Egg "size" finally refers to the mean of egg length and egg width (as in Peters 1959).

The ovaries were weighed to one-hundredth of a gram, using analytic scales with a precision of one-tenth of a milligram. "Egg weight" is defined as in Peters (1959) and Dambach (1963) as the "weight of an egg from which adhering water has been removed" (prior to weighing, the eggs were separated and kept on blotting paper until all adhering water had been removed; complete removal of water was assessed by means of a binocular microscope, using the fact that the wet eggs tend to have a shiny surface which becomes dull when all adhering water is removed). Weighing was done in batches of 50 or 100 eggs, mean egg weights were then calculated. Table 2 shows that this method gives values which are largely reproducible.

The weighing of the eggs generally occurred a few hours after spawning. Because of water absorption, the eggs increase their weight after fertilization (leading to the appearance of a perivitelline space); however, this increase is so slight that it can be neglected. This absorption of water is completed 2-3 hours after fertilization. A weight increase of the eggs occurs later, when the embryo appears; as shown by Dambach (1963) in *T. tholloni,* egg weights change only very little within 4 days after spawning. Thus, weighing eggs within one day of spawning produces reliable values; this was the longest period occurring here, except in some cases involving *Tristamella simonis* (see below).

The term "weight of spawn" is here defined as the weight of the eggs in a given batch of eggs ready to be spawned. The term thus refers not only to eggs that are actually spawned, but also to "residual eggs" left in the ovary, and to eggs that may have been swallowed. The weight of spawn was determined by counting the eggs in a spawn and multiplying it by the mean egg weight as defined above, this method being the same as used earlier (Peters 1959).

In some cases, it was necessary to estimate egg weight from eggs preserved in 4% formalin. An assessment was made of the effect of preservation on egg weight, as follows. Batches of 100 eggs (80 eggs in one case) from 4 different, unfertilized spawns were weighed fresh, then weighed again after several weeks in formalin. It appeared (Table 3) that the changes in egg weights were so small as to be negligible.

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[3] Translator's note: Throughout this text, "egg" generally refers to "ripe" oocytes and/or oocytes that were extruded (fertilized or not); the term "oocyte" is generally used for "unripe" oocytes.

Table 1. Basic characteristics of fishes studied.

Behavioral type	Species	Origin of broodstock
Substrate-spawner	*Tilapia tholloni*	unknown
	Tilapia guineensis	unknown
	Tilapia zillii	Israel
Mouthbrooder I (female carries eggs)	*Tilapia mossambica*	unknown[a]
	Tilapia nilotica	part Israel (Tel Aviv), part unknown
	Tilapia galilaea[c]	Israel
	Tristamella simonis[d]	Israel
Mouthbrooder II (male carries eggs)	*Tilapia macrocephala*	Nigeria[b]

[a]According to Dr. E. Trewavas, British Mus. (pers. comm.), the *T. mossambica* material used here belongs to two populations, with one resembling the "korogwe" population (here: *T. mossambica k.)* and the second differing strikingly from the first in that, during courtship, the males become jet black, with the exception of the throat, which remains white (here: *T. mossambica m.).*

[b]These fishes were supplied by Dr. L. Aronson, New York Museum of Natural History.

[c]In this species, *both* parents mouthbrood (translator's note).

[d]This species is not a tilapia, but a closely-related mouthbrooding cichlid.

Table 2. Data for assessing the precision of weight estimates in tilapia eggs.

Species	No. eggs in spawn	No. eggs in first, second and third subsamples	Mean egg weight (mg) in first, second and third subsamples
T. tholloni	3,009	465/960/1,577	1.51/1.59/1.53
T. macrocephala	724	50/50/–	5.14/5.02/–
T. macrocephala	436	223/185/–	11.25/11.39/–
T. macrocephala	over 482	218/264/–	11.56/11.62/–

Table 3. Data for assessing the effects of 4% formalin preservation on tilapia egg weights.

Species	Mean egg weight (mg) fresh	preserved
T. nilotica	2.81	2.96
T. nilotica	3.08	3.21
T. nilotica	5.09	5.30
T. galilaea	5.44	5.44

MATERIAL USED FOR SPECIFIC PARTS OF THE INVESTIGATION[4]

Material Used for Fig. 1

The data for *T. tholloni* were provided by Mr. M. Dambach (pers. comm.) and are based on a spawn of 932 fertilized, unpreserved eggs. Of these, 16 were destroyed by handling. A few eggs from this spawn may have remained in the ovary, or been swallowed after spawning. Mean egg weight was 1.12 mg. The *T. macrocephala* eggs stem from a spawn of 345 unfertilized eggs, one of which was destroyed. Mean egg weight was 10.46 mg.

Material Used for Fig. 3

The substrate-spawner eggs used for deriving Fig. 3 were generally weighed 2-6 hours after spawning (in one case after 18 hours in *T. tholloni* and after 24 hours in one case involving *T. zillii).* Sample size was at least 100 eggs in *T. zillii* and *T. tholloni;* in the latter species, almost whole spawns were weighed. Sample size in *T. guineensis* was only 12 eggs each. The mouthbrooder eggs used for Fig. 12 stem from 18 *T. mossambica* spawn and 11 *T. macrocephala* spawns, respectively. In *T. mossambica,* 2 of the spawns were unfertilized; the eggs were weighed from 30 minutes to several hours after spawning (18 hours in two cases). Sample size was 19 eggs in one case (fish weight 13.2 g), and most of the spawn in the other cases. In *T. macrocephala,* 5 of the spawns were unfertilized. Earliest weighing was 1-1/2 hours after spawning; the latest weight obtained was 1 day after spawning. Sample size was 50 eggs in one case, and most of the spawn in the majority of the other cases.

Material Used for Fig. 4

The *T. macrocephala* eggs weighed were from 23 spawns, 5 of which were unfertilized. Weighing was done 1-1/2 hours after spawning (1 day in one case). Sample size was 50 or 100 eggs, most of the spawn in a number of cases.

The fertilized, unpreserved *T. nilotica* eggs ("Tübingen stock" of unknown origin) were weighed 3 to 24 hours after spawning. Sample sizes were 25 eggs (up to 97 g body weight) or 50 eggs (> 97 g). In the case of the "Tel Aviv stock" of *T. nilotica,* all weighing was done within 1 day after spawning. The eggs were fertilized and preserved; sample size was 100 eggs. The *T. galilaea* material consisted in one case of 25 eggs with embryos from the mouth of a female weighing 813 g; all other eggs were unfertilized; in 5 cases the eggs had been removed, after ovulation, directly from the ovaries. In 16 cases, these eggs had been extracted from females caught on their spawning ground in Lake Tiberias. All eggs had been preserved in formalin (see above). Sample size was 80-100 (22 in the case of a female of 343 g).

The *Tristamella simonis* eggs were from Lake Tiberias, and were removed from the mouth of brooding females; the eggs belonged to several early developmental stages. Two spawns consisted of eggs without embryos (body weight of females—135 and 715 g). The most advanced spawn consisted of early larvae with yolk-sacs and pigmented eyes (body weight of female—146 g). Sample size was 50 eggs (10 in the case of one spawn consisting of eggs in the process of hatching).

In Fig. 4, "body weight" refers to weight of the body inclusive of *spent* gonad, except in *T. galilaea* where body weight includes in several cases the weight of (parts of) the spawns.

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[4]Translator's note: This section is consolidated from various bits and pieces spread throughout the original text.

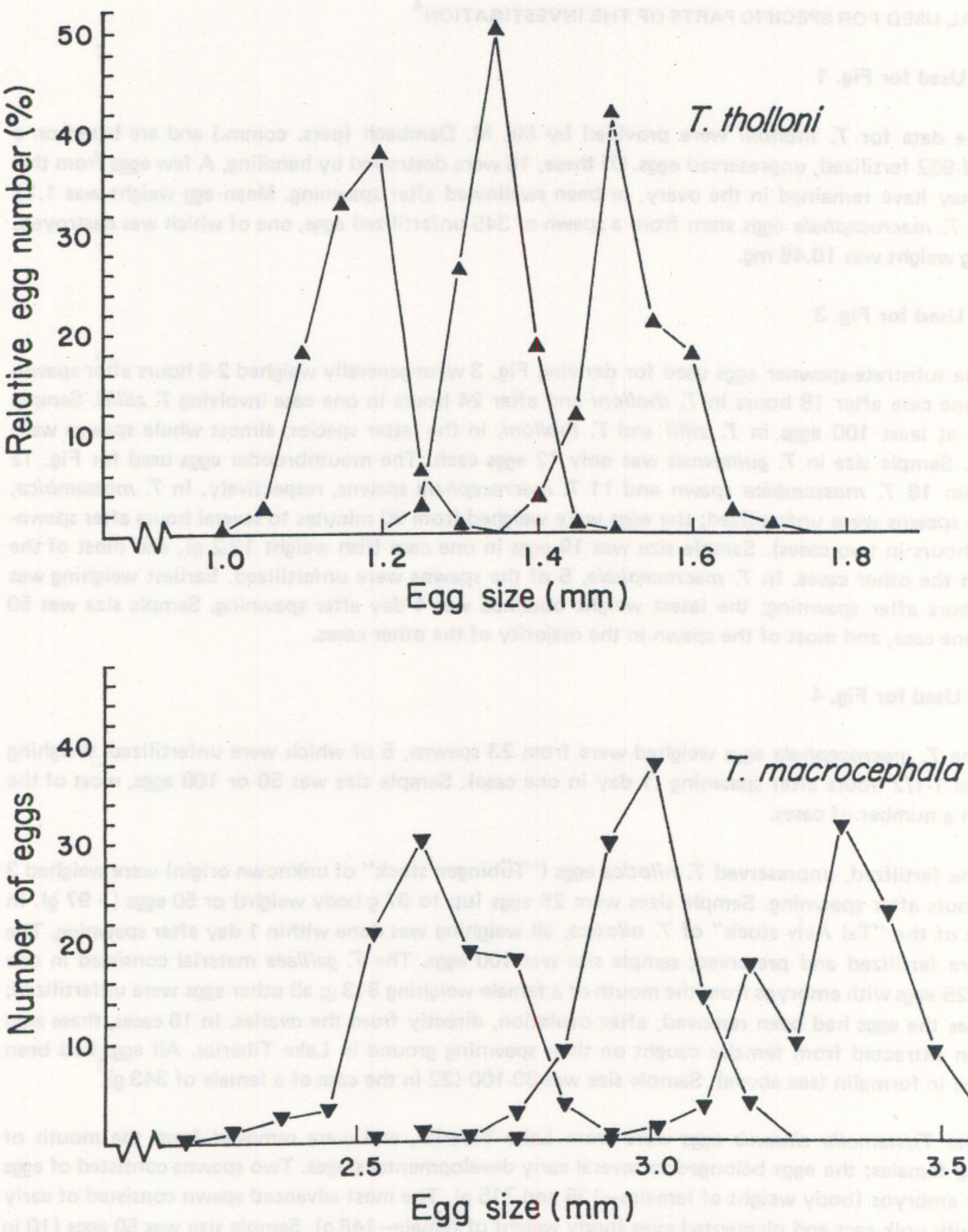

Fig. 1. Relative numbers of eggs of various size classes in a spawn from *Tilapia tholloni* and *Tilapia macrocephala*.

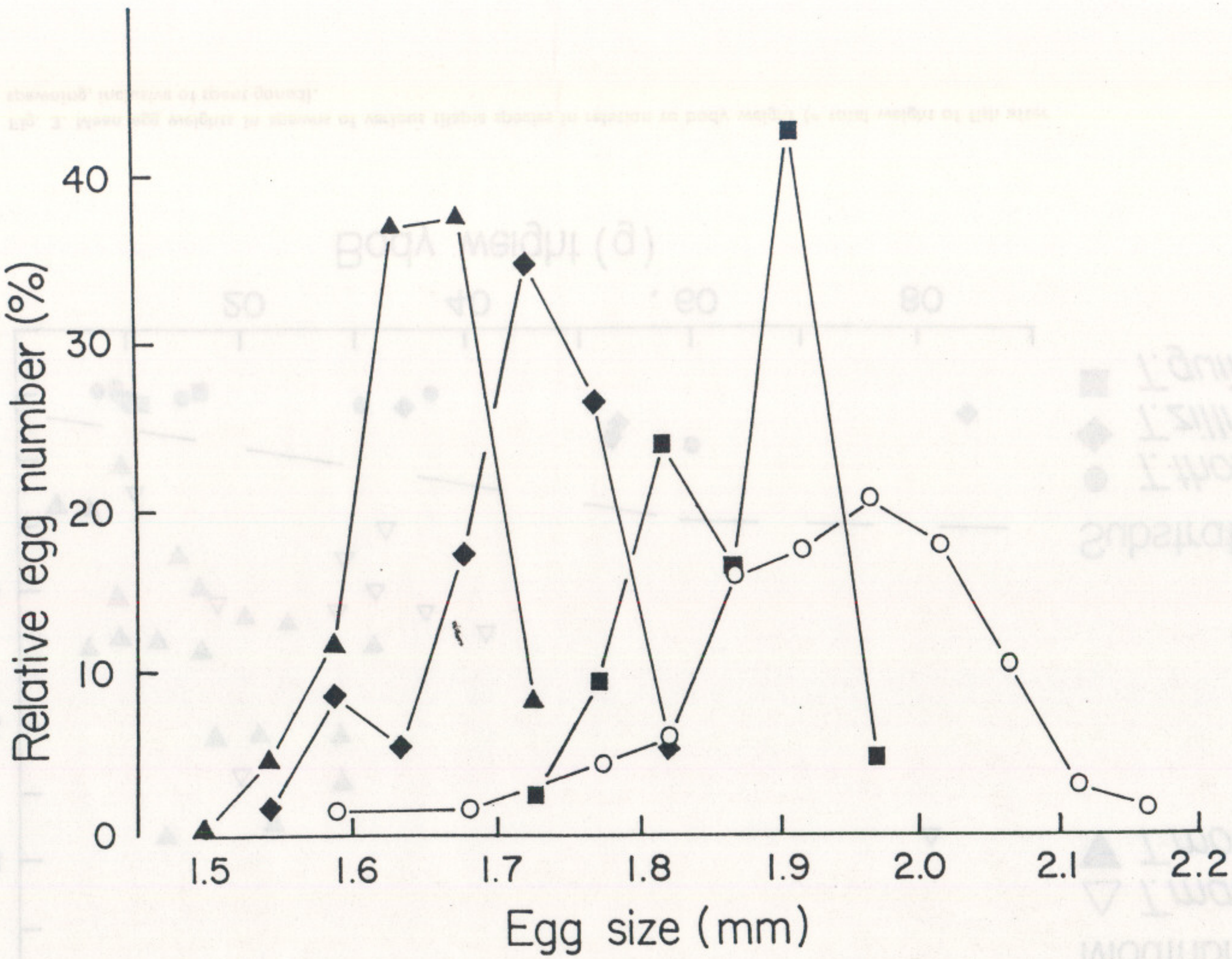

Fig. 2. Frequency distribution of egg "size" (= mean of egg width and egg length) in four different spawns of *T. mossambica*. ▲ eggs taken from mouth of female right after spawning; eggs preserved and measured in 70% alcohol; n = 192. ♦ eggs taken from ovary after ovulation; eggs preserved in Bouin's fluid and measured in 70% alcohol; n = 109. ■ eggs removed from mouth of female right after spawning, measured fresh; n = 42. ○ eggs removed from mouth of female right after spawning; preserved and measured in 70% alcohol; n = 68.

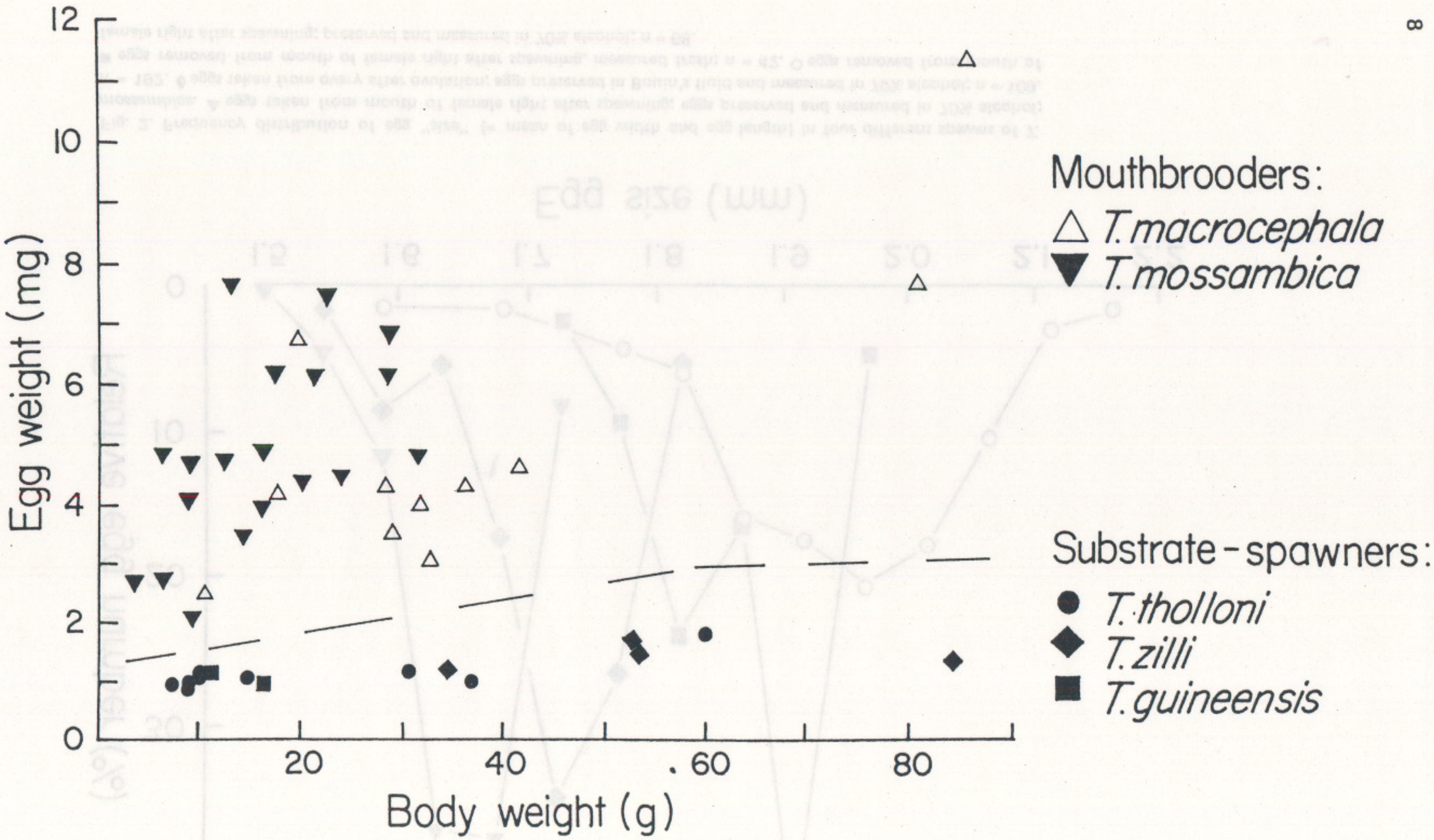

Fig. 3. Mean egg weights in spawns of various tilapia species in relation to body weight (= total weight of fish after spawning, inclusive of spent gonad).

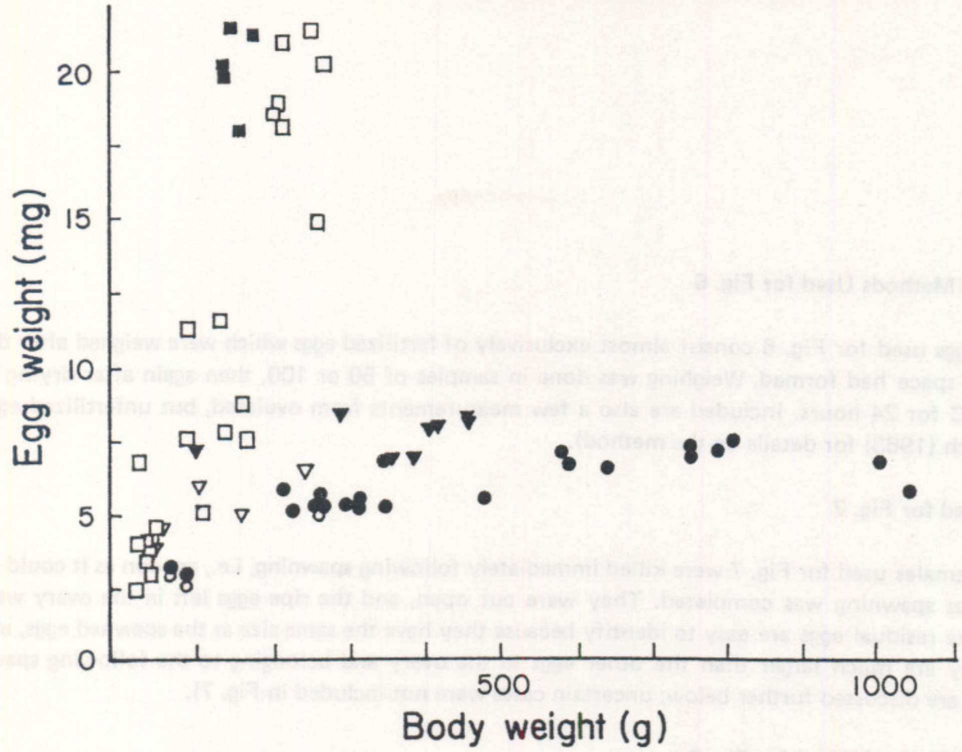

Fig. 4. Mean egg weights in various cichlids, in relationship to body weight. ● preserved eggs of *T. galilaea;* ○ fresh eggs of *T. galilaea;* ▲ preserved eggs of *T. nilotica;* △ fresh eggs of *T. nilotica;* ■ preserved eggs of *Tristamella simonis;* and □ fresh eggs of *T. macrocephala.*

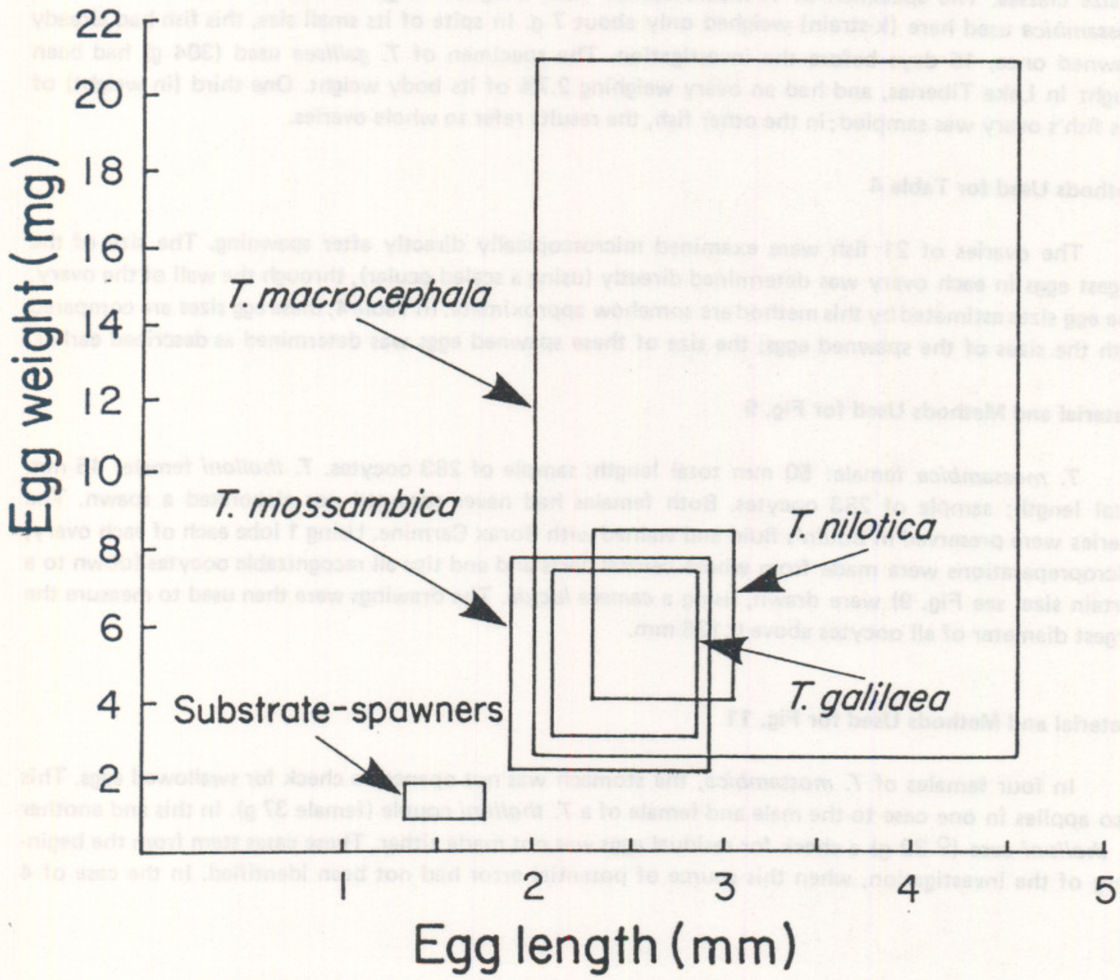

Fig. 5. Relationships between egg length and egg weight in tilapias, based on measurements of eggs in *T. tholloni, T. guineensis, T. mossambica, T. nilotica* and *T. macrocephala.* Boxes give observed ranges of *mean* weights per spawn, not ranges of single eggs, which may be considerably smaller or larger than shown here.

Material and Methods Used for Fig. 6

The eggs used for Fig. 6 consist almost exclusively of fertilized eggs which were weighed after the perivitelline space had formed. Weighing was done in samples of 50 or 100, then again after drying at about 110°C for 24 hours. Included are also a few measurements from ovulated, but unfertilized eggs (see Dambach (1963) for details on the method).

Methods Used for Fig. 7

The females used for Fig. 7 were killed immediately following spawning, i.e., as soon as it could be assumed that spawning was completed. They were cut open, and the ripe eggs left in the ovary were counted. The residual eggs are easy to identify because they have the same size as the spawned eggs, and because they are much larger than the other eggs in the ovary and belonging to the following spawn (exceptions are discussed further below; uncertain cases were not included in Fig. 7).

Material and Methods Used for Fig. 8

The ovaries used for this study were preserved mostly in Bouin's fluid. All eggs (down to a set minimum size) were then isolated from each other and measured. The measurements were then grouped in size classes. The specimen of *T. macrocephala* used weighed 15 g, and had never spawned. The *T. mossambica* used here (k-strain) weighed only about 7 g. In spite of its small size, this fish had already spawned once, 15 days before the investigation. The specimen of *T. galilaea* used (304 g) had been caught in Lake Tiberias, and had an ovary weighing 2.7% of its body weight. One third (in weight) of this fish's ovary was sampled; in the other fish, the results refer to whole ovaries.

Methods Used for Table 4

The ovaries of 21 fish were examined microscopically directly after spawning. The size of the largest eggs in each ovary was determined directly (using a scaled ocular), through the wall of the ovary. The egg sizes estimated by this method are somehow approximate. In Table 4, these egg sizes are compared with the sizes of the spawned eggs; the size of these spawned eggs was determined as described earlier.

Material and Methods Used for Fig. 9

T. mossambica female: 50 mm total length; sample of 283 oocytes. *T. tholloni* female: 45 mm total length; sample of 283 oocytes. Both females had never spawned nor elaborated a spawn. The ovaries were preserved in Bouin's fluid and stained with Borax Carmine. Using 1 lobe each of each ovary, micropreparations were made from whose central parts and end tips all recognizable oocytes (down to a certain size, see Fig. 9) were drawn, using a *camera lucida.* The drawings were then used to measure the largest diameter of all oocytes above 0.126 mm.

Material and Methods Used for Fig. 11

In four females of *T. mossambica,* the stomach was not opened to check for swallowed eggs. This also applies in one case to the male and female of a *T. tholloni* couple (female 37 g). In this and another *T. tholloni* case (♀ 39 g) a check for residual eggs was not made either. These cases stem from the beginning of the investigation, when this source of potential error had not been identified. In the case of 4

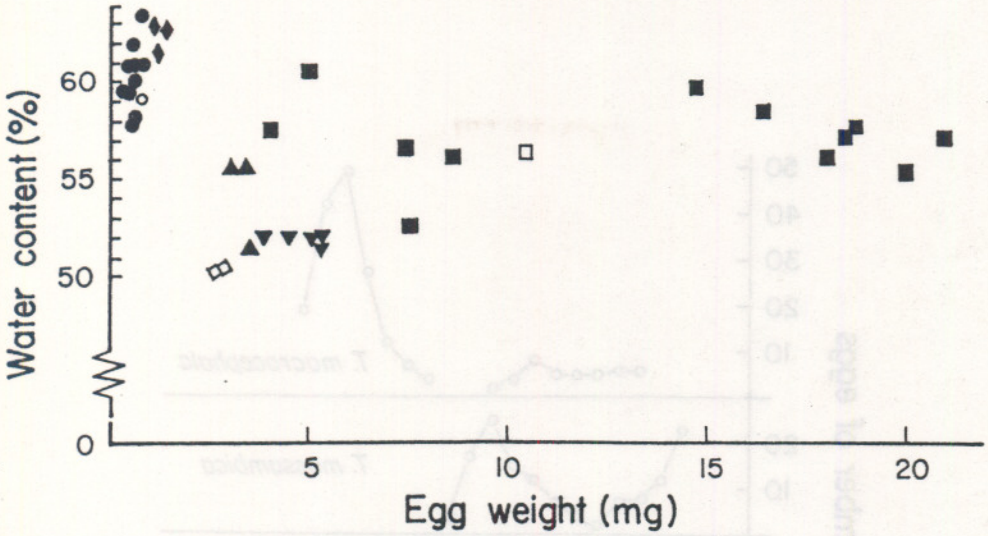

Fig. 6. Water content of tilapia eggs in relation to their weight. Based mainly on data obtained by Mr. M. Dambach (pers. comm.). Sample sizes: 50 or 100 eggs per point. ● fertilized and ○ unfertilized eggs of *T. tholloni;* ■ fertilized and □ unfertilized eggs of *T. macrocephala;* ▲ fertilized eggs of *T. mossambica m.;* ▲ fertilized eggs of *T. nilotica;* ♦ fertilized eggs of *T. zillii;* ◇ unfertilized eggs of *T. galilaea.*

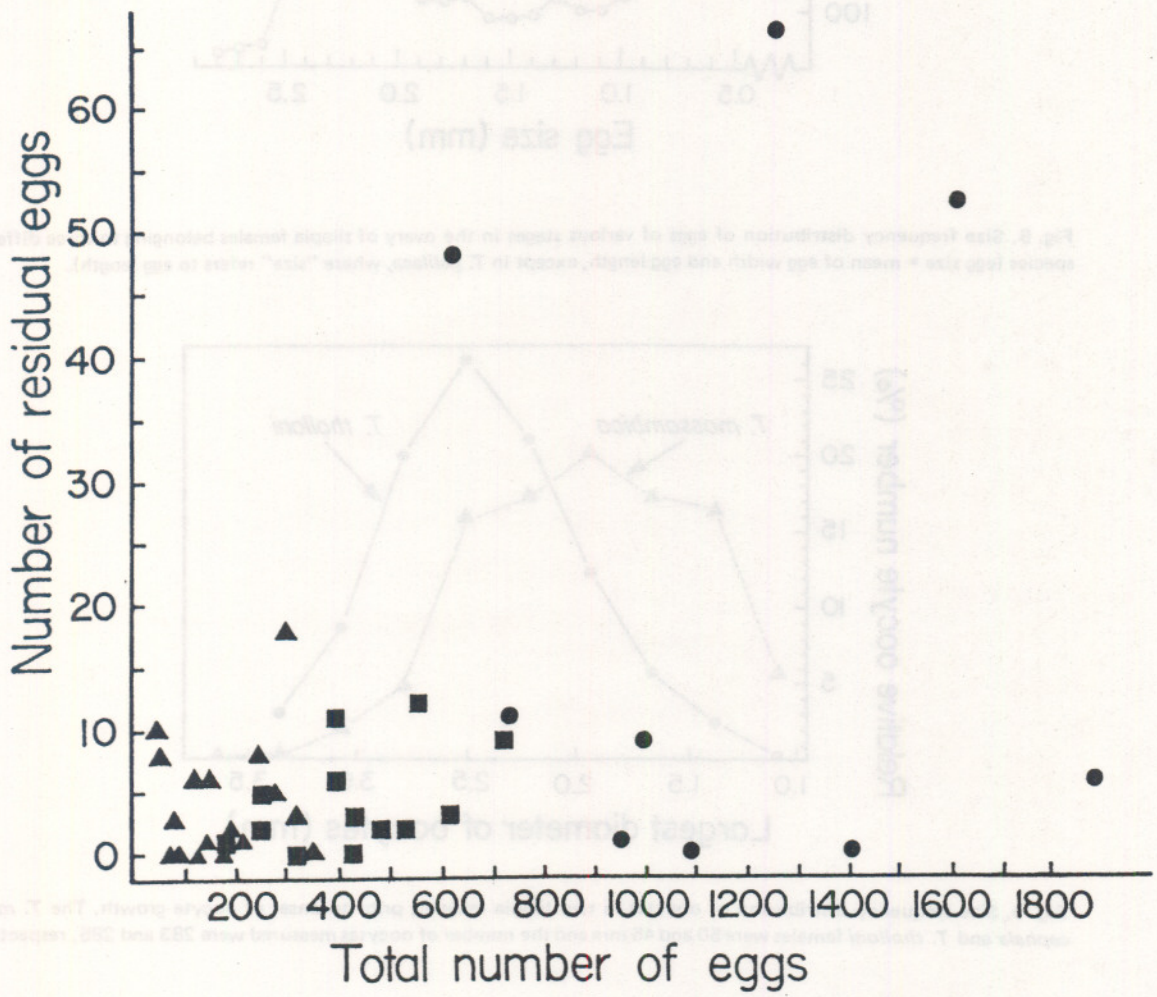

Fig. 7. Number of residual eggs in relation to total egg production (the spawning of a *T. tholloni* female with 624 eggs may have been interrupted, resulting in a smaller number of eggs spawned). ● *T. tholloni;* ▲ *T. mossambica;* ■ *T. macrocephala.* Translator's note: The original of Fig. 7 contains an inconsistency in that the abscissa scale reads "3,000" where it should read "1,800". The scale has been corrected on the assumption that the point on the extreme right pertains to approximately 1,800 eggs, and not to approximately 3,000 eggs.

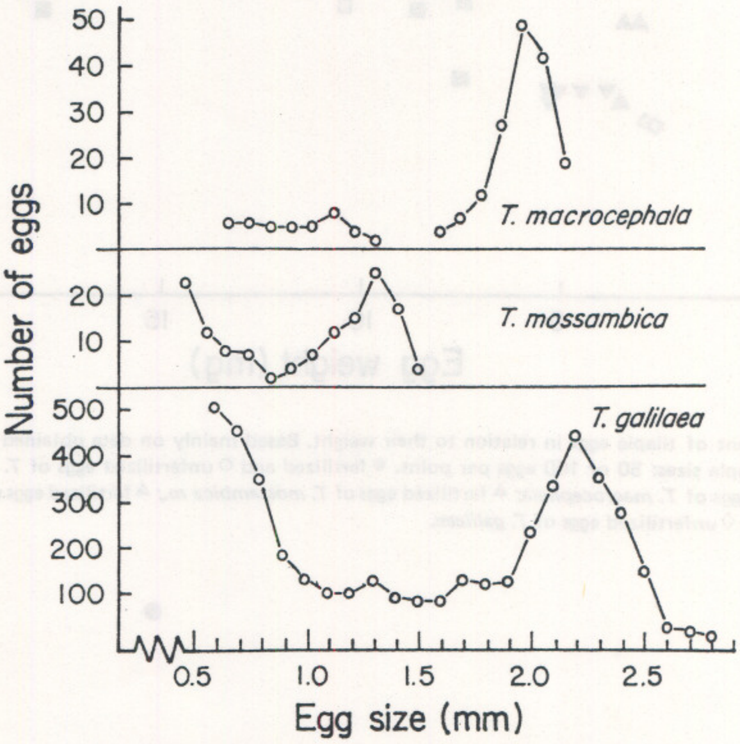

Fig. 8. Size frequency distribution of eggs of various stages in the ovary of tilapia females belonging to three different species (egg size = mean of egg width and egg length, except in *T. galilaea,* where "size" refers to egg length).

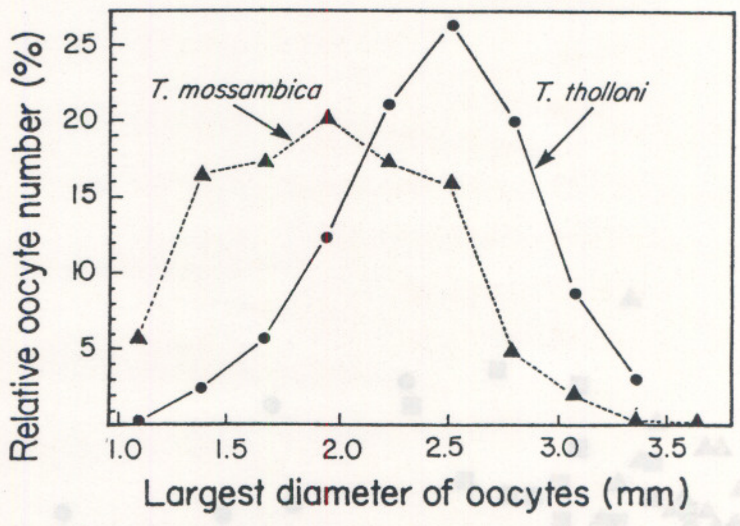

Fig. 9. Size frequency distribution of oocytes in two tilapia females, prior to onset of oocyte growth. The *T. macrocephala* and *T. tholloni* females were 50 and 45 mm and the number of oocytes measured were 283 and 285, respectively.

Table 4. Size characteristics of ovarian eggs.

Species	Size range of eggs in most advanced spawn (mm)	Size range of eggs in second most advanced spawn (mm)	Minimum size of yolked eggs[a]
T. tholloni	1.3 – 1.6	0.4 – 0.7	0.26
T. guineensis	–	–	0.26
T. mossambica k.	2.7 – 2.9	1.1 – 1.3	0.31
T. macrocephala	2.0 – 4.5	1.1 – 3.5	0.35

[a]Eggs preserved in Bouin's fluid.

Table 5. Frequency of egg occurrences in tilapia stomachs.

Species	No. of fish	Number of eggs in stomachs			
		0	1-10	11-20	>20
T. tholloni ♀	10	6	3	1	0
T. tholloni ♂	10	8	1	1	0
T. mossambica k. ♀	16	11	3	1	1 (74 eggs)
T. mossambica k. ♂	10	6	4	0	0
T. macrocephala ♀	18	12	5	0	1 (43 eggs)
T. macrocephala ♂	13	7	3	3	0

Table 6. Identification in *Tilapia galilaea* of the value of the gonadosomatic index (GSI) at which the gap in egg size distribution becomes apparent.

State of ovary	Fish weight (g)	GSI[a]
all eggs unripe, no size discontinuity apparent (n = 12)	141 – 827	1.0 – 3.9
largest eggs ripe, size discontinuity apparent (n = 7)	59 – 689	3.9 – 9.7
eggs ovulated (n = 2)	254 – 689	4.6 – 7.8

[a]GSI = gonad weight x 100/body weight.

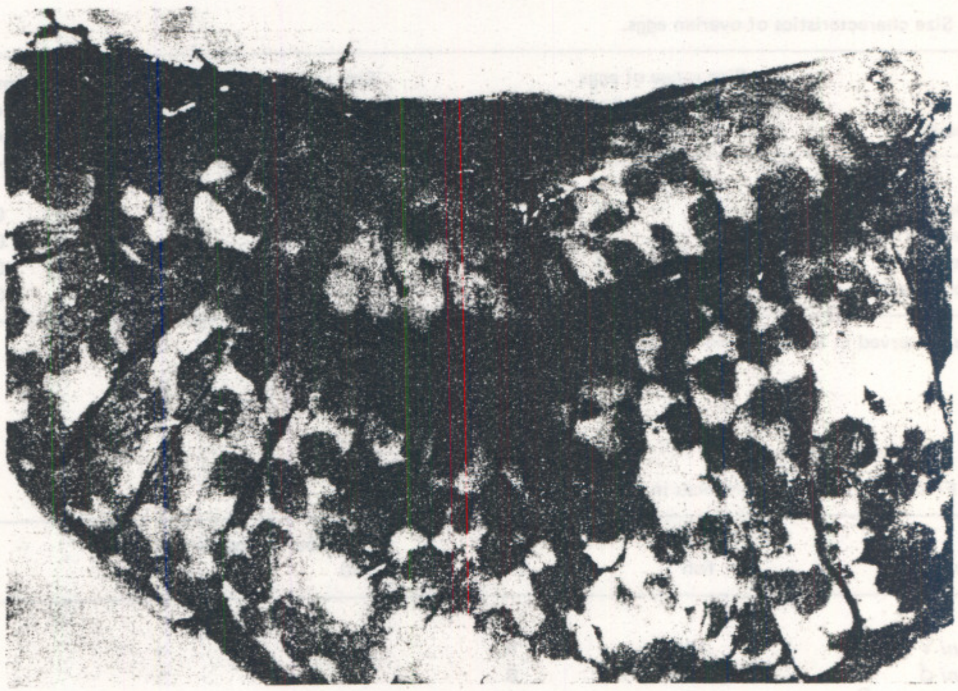

Fig. 10. Ovary (left lobe) of *T. tholloni,* showing advanced resorption of eggs. The light, irregular blotches are the atresic follicles; located in between are numerous intact eggs (dark, regular shapes). Based on fresh material, photographed through the transparent wall of the ovary.

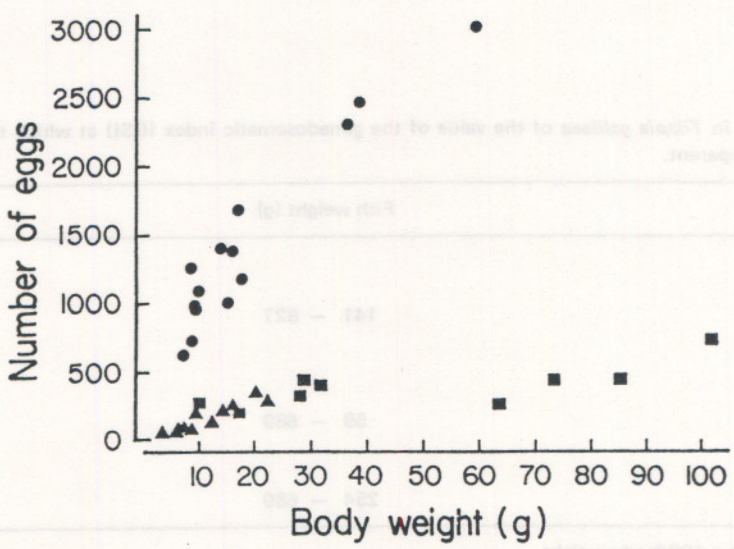

Fig. 11. Fecundity/body weight relationship in *T. tholloni, T. mossambica* and *T. macrocephala.* (Body weight refers to total weight of spent fish, i.e., inclusive of spent gonad, except in 4 *T. tholloni* specimens where the weight includes unspent gonads.) ● *T. tholloni;* ▲ *T. mossambica k.;* and ■ *T. macrocephala.*

T. tholloni females, the ripe eggs were taken from the ovaries and counted (body weights: 15.7; 16.8; 17.7 and 18.2 g). The other counts refer to spawns that were extruded.

Material and Methods Used for Fig. 12

The opportunity was taken to obtain, while in Israel, large specimens of *T. galilaea.* Nineteen ovaries were obtained which were considered "ripe" at the onset of the spawning season, from both Dor Fisheries Research Station and Lake Tiberias. Of these 19 ovaries obtained from fish ranging from 59 to 827 g, 12 turned out upon closer examination to contain spawns that were not completely elaborated; the ovaries were in a state similar to that depicted in Fig. 8 (below). Only 7 of the 19 ovaries were "ripe" in the sense that a gap in the size distribution of the eggs was apparent; 2 of these ovaries contained ovulated eggs.

Since only those ovaries should be used (for assessing fecundities) which have a gap in the egg size distribution, not enough ripe ovaries were available to establish an unclear relationship between egg number and body size in *T. galilaea.* For this reason, ovaries were also used in Fig. 12 in which the gaps in the egg size distribution were not completely formed; thus a small error had been introduced when estimating the egg number of the spawns. Degenerated eggs occurred in a number of ovaries. These eggs were counted and given separately in Fig. 12. However, these numbers are lower estimates since completely degenerated eggs cannot be counted reliably.

Methods Used for Table 7

"Ovary weight prior to spawning" is defined for most cases (i.e., in spent fish) as weight of spawn (see elsewhere for definition) plus weight of spent ovary (exclusive of "residual" eggs). In some cases, the ovary weight was obtained directly by weighing the ovary of a fish ready to spawn. Significant differences between the two methods for determining ovary weight did not occur. That a fish was ready to spawn was determined by observing its behavior; it was assessed to be ready when the characteristical preparations for spawning began—in such cases, the eggs had generally already ovulated. Before weighing the ovaries, adhering water was removed with blotting paper. The (very short) egg duct is not included in the ovary weight. Weighing of spent ovaries was done immediately after spawning.

Table 7. Gonadosomatic index (GSI) in ripe and spent tilapias.

Species	State	No. of fish	Body weight (g) min.	max.	mean	GSI[a] min.	max.	mean
T. tholloni	ripe	10	9.4	64.7	21.1	8.8	14.3	11.2
T. tholloni	spent	6	8.8	60.0	18.8	1.9	2.7	2.3
T. mossambica	ripe	5	3.7	24.6	13.4	4.9	10.2	7.0
T. mossambica	spent	6	3.6	24.1	14.5	1.0	3.0	1.7
T. macrocephala	ripe	15	7.4	316	107	4.3	11.6	8.1
T. macrocephala	spent	15	10.7	268	77.2	2.2	5.1	3.5

[a]GSI = gonad weight x 100/body weight.

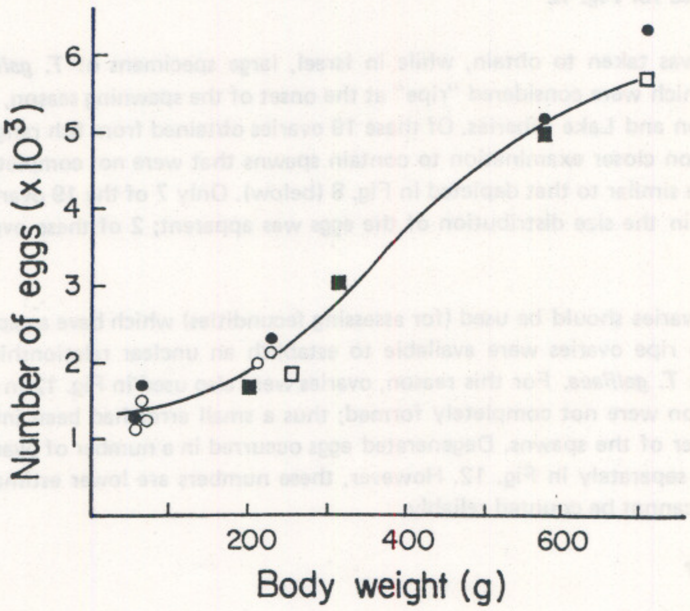

Fig. 12. Fecundity/body weight relationship in *T. galilaea.* ○ number of intact eggs; ● number of intact eggs plus number of atresic follicles; □ egg from ovulated ovaries; ■ estimated number of eggs (see text).

Results

PROPERTIES OF TILAPIA EGGS

With regard to the shape of the eggs, it may be mentioned here that those of the substrate-spawners are "ellipsoid", while those of the mouthbrooders are typically ovoid, with the blunt end toward the vegetative pole (see Dambach 1963 for illustrations).

SIZE DISTRIBUTION OF EGGS IN SPAWN

The sizes of eggs in the spawn of a tilapia are spread about a mean value, and the differences between smallest and largest eggs can often be considerable. Fig. 1 shows examples of the size distribution of eggs in a substrate-spawner *(T. tholloni)* and a mouthbrooder *(T. macrocephala)*. It will be noticed that the egg size distribution of *T. tholloni* spawn is nearly symmetrical, whereas the mode in

T. macrocephala is pushed to the right. This asymmetry is even stronger in *T. mossambica* (Fig. 2).

Fig. 2 also suggests that every tilapia spawn has its own characteristics, with different modes, ranges and overall shape of the size-frequency distribution.

EGG SIZE IN RELATION TO BODY SIZE

Lowe (McConnell) (1955) concluded "that the size of the eggs varies from species to species and not with the size of the female." This last point is erroneous and can be explained by the insufficiency of the material available to her. Cridland (1961) also observed no relationships between egg weight and body weight in *Tilapia esculenta*. However, his data on *T. zillii* agree with those obtained in the course of the present investigation.

Fig. 3 illustrates the feature that the mean egg weight per spawn is in substrate-spawners *(T. tholloni, T. guineensis, T. zillii)* much smaller than in the two representatives of the mouthbrooders *(T. mossambica, T. macrocephala)*. The figure, although it is based on a small range of body size (except in *T. macrocephala*), demonstrates further in both groups a marked tendency for egg size to increase with body size (weight).

Fig. 4 illustrates the direct relationship between egg weight and body weight. Here, eggs from very large fish were obtained only from *T. nilotica* and *T. galilaea*, while the eggs of *T. macrocephala* stem from specimen larger than those used in Fig. 3. Also included are data for *Tristamella simonis*. This fish which is closely related to the tilapias has extremely large eggs, a feature already noted by Ben-Tuvia (1960).

Here again, it clearly appears that the mean egg weight increases with the body weight of the fish. This is particularly evident in *T. macrocephala*, where the eggs rapidly reach a weight of about 20 mg. Unfortunately, the very large females did not spawn. It seems however that 20 mg represents a maximum value which is not markedly exceeded, even in large fish. The apparent maximum egg weights for *T. galilaea* (about 6 mg) and *T. nilotica* (about 7.5 mg) are much smaller. Also apparent is a great variability of the egg weights for equal or similar body weights.

THE RELATIONSHIP BETWEEN SIZE AND WEIGHT OF THE EGGS

The reason egg weights were preferred in this study are that weight may be expected to allow for quantitative inferences on the mechanism of egg growth; also egg weight can be easily estimated with great accuracy and precision for which reason it is a most useful measure in comparative studies. However, it may be useful to also know the relationship between egg weight and egg length. Fig. 5 illustrates this relationship, based on a large number of weight and size determination. Note that the ranges pertain to the *mean* sizes of various spawns, and not to the smallest and largest eggs observed in given species (c.f. Peters 1959). On the other hand, spawns were considered which in several cases came from very small females, i.e., of sizes much below sizes at first maturity such as occur in nature (this applies particularly to *T. mossambica)*. The data thus presented here should not be used to infer on the size of eggs spawned under natural conditions, except possibly as far as the upper ranges in *T. nilotica* and *T. galilaea* are considered.

WATER CONTENT AND OTHER EGG PROPERTIES

The size and thus the weight differences between different eggs are doubtlessly caused by differences in yolk content. A preliminary comparative study of the embryos (blastodiscs at the 4 cell stage) of large and small eggs within and between species revealed that the differences in the protoplasm weight are negligible.

On the other hand, water content of eggs is also important. This water can be viewed as: 1) water already present in the egg before spawning and 2) water absorbed after spawning and fertilization. Since neither the yolk nor the protoplasm seems to absorb water after fertilization, the water absorbed in (2) should predominantly consist of the water in the perivitelline space. The formation of the latter occurs 2-3 hours after fertilization. At this time, the egg shell is further removed from the egg proper. Still, the space between the chorion and the egg (i.e., the perivitelline space) is very small. Only near the animal pole does a small protuberance occur. This is illustrated in Dambach (1963) who compared the water content of ovulated, but unfertilized eggs of *T. tholloni* with fertilized eggs after formation of the perivitelline space (4 cell stage), and showed a difference of 7% (of the total water). (The perivitelline space thus contains about 7% of the total water of a fertilized egg.)

Fig. 6 summarizes the available data on the water content of tilapia eggs. As might be seen, inter-species differences do occur; also the values for the substrate-spawners seem higher than for the mouth-brooders. It appears finally—if it is at all legitimate to generalize from the data on *T. macrocephala*—that water content is independent of egg size.

DEVELOPMENT OF THE OOCYTES—PRELIMINARY REMARKS

"Spawn" as used in this paper refers to a batch of eggs that are ready to be spawned, as it seems inappropriate to limit the definition of a spawn to those eggs that are actually spawned. Not to make this difference would obscure features of the reproduction of fishes that are extremely important for a comparative analysis. In tilapias, "eggs that are ready to be spawned" are about equivalent to "eggs that are about to ovulate", since, as shown by Aronson and Tucker (1949) in *T. macrocephala,* the eggs leave their follicles immediately prior to spawning. The present investigation confirmed this feature not only in *T. macrocephala,* but also for all other tilapias that were examined (see Table 1). Only *T. galilaea* differs from this in that a longer period may occur between ovulation and spawning.

At spawning, most of the eggs of a given spawn are extruded. Often, however, a small fraction of these eggs remain in the ovary. These eggs are called "residual eggs" (Peters 1959); they are later resorbed. Residual eggs comprise both ovulated and non-ovulated eggs. Nothing suggests, however, that these eggs are in earlier developmental stages or damaged. For this reason, it may be assumed that mechanical effects determine whether eggs are extruded or not. In terms of their development, the residual eggs belong to the same batch as those that are extruded, for which reason they are here included in the "spawn".

Fig. 7 shows the number of residual eggs that were recorded in various tilapia species.

DEVELOPMENT OF THE OVARIAN EGGS

A tilapia spawn can be identified as such, in an ovary, well in advance of spawning. Fig. 8 illustrates 3 different stages in the development of a spawn. The examples are taken from 3 different species, but this does not affect the results, because the mechanism is the same in all species (see also Peters 1959). Also, the results would be the same if young fish were used which have matured prematurely, or old fish that have spawned repeatedly.

It will be noted that in *T. macrocephala* (Fig. 8 above) two size classes (between 1.3 and 1.6 mm) are empty; this size discontinuity can be explained by the fact that the eggs above 1.6 mm represent a well-differentiated spawn. However, the eggs in that spawn are not necessarily fully developed and they probably would have continued to grow, resulting—as observed in other cases—in an enlargement of the gap in the egg size distribution. It should also be noted that the overall shape of the egg size distributions generally correspond to the shapes observed from eggs in earlier stages of development. This becomes apparent when comparing Fig. 8 (above) with Figs. 1 and 2, where modes of the size frequency distribution are also on the right side of the graphs. Finally, it may be noted that in the *T. macrocephala* example of Fig. 8 (above), the eggs of size <1.3 mm (they were measured down to sizes of 0.65 mm) belong to the following spawn.

The *T. mossambica* example (Fig. 8, center) differs from the *T. macrocephala* example in that the spawn is in an earlier phase of its development. The larger eggs (> 0.85 mm) are not separated by a complete gap from the smaller eggs. The minimum at 0.85 mm suggests, however, the location of the gap that would have emerged, had these eggs been allowed to develop further, i.e., to a state where their size distribution would have resembled that in the example above. The *T. galilaea* example (Fig. 8 below) typifies a situation where the eggs are even less developed than in the *T. mossambica* example. The lack of a clear-cut gap between the eggs of the emerging spawn and those of the following spawn will be noted. It is obvious that in such a case, it is impossible to count the eggs that will be included in a future spawn, as opposed to the situation in the *T. mossambica* example where an approximate dividing line could be drawn separating the most advanced from the following spawn, and the situation in the *T. macrocephala* example, where the two groups of eggs are unequivocally separated.

The feature illustrated in Fig. 8 thus identifies the source of a number of errors made in previous studies of the fecundity of tilapias. Thus, one repeatedly reads in the literature that the number of eggs in a spawn was estimated by counting the number of "ripe eggs" in the ovaries; however, no criterion is given as to what "ripe eggs" are. Clearly, the number of eggs in a tilapia spawn can only be assessed reliably when the eggs of that spawn are separated from those of the next spawn by a gap in the size distribution—a feature which must be studied explicitly. A vague impression of "ripeness", caused by the presence of a number of ripe eggs is not sufficient.

The low fecundity in tilapias that are often reported in the literature thus may have possibly been caused by counting only the largest eggs of incomplete spawns.

REMARKS ON THE GAP IN THE EGG SIZE DISTRIBUTION

As mentioned above, residual eggs are generally easy to identify, a criterion being the size difference between the eggs of a ripe spawn and those of the following spawn. Only in some cases, in *T. macrocephala* did a smooth transition occur between the smallest eggs that were spawned and the largest of the eggs remaining in the ovaries. In such cases, it is not possible to identify residual eggs; otherwise, it can be easily done.

To assess the size distribution of the eggs immediately following those of a ripe spawn, 21 ovaries of fish that had just spawned were examined in some detail. The results are given in Table 4. These results, and others not presented here suggest that the eggs in the second most advanced spawn have, at the time of spawning, grown much more in mouthbrooders than in substrate-spawners. Further, the data confirmed earlier results (Peters 1959) suggesting that (especially in *T. macrocephala)* the eggs of the second spawn are the larger, the more the spawned eggs had grown. This, with reference to Fig. 8 can be also formulated as follows: in a tilapia ovary, the gap in the egg size distribution will tend to shift toward larger size classes as the eggs of the most advanced spawn develop and grow.

ONSET OF A SPAWN'S DEVELOPMENT

The beginning of the development of a spawn may be viewed as the time when the oocytes begin to grow markedly, i.e., when yolk begins to be accumulated by the oocytes. Von Kraft and Peters (1963) discuss the cytological aspects of this phase of oocyte development.

Table 4 (last column) gives the minimum oocyte sizes at which yolk accumulation becomes noticeable. These figures may be compared with those of the second column of Table 4. As might be seen, the oocytes in the second most advanced spawn of a given ovary here already accumulated a fair amount of yolk, particularly in the mouthbrooders. The size distribution of oocytes in the very early stages of their development is still largely unknown. It can be expected, however, that they are more or less normally distributed, as is the case with the oocytes that are more advanced. Moreover, there is direct evidence that the oocytes display a more or less normal distribution as shown in Fig. 9 which represents the size distribution of small oocytes in representative of two tilapia species.

REMARKS ON THE REPRODUCTIVE CYCLE/ATRESIA OF FOLLICLES

It has often been reported that tilapias, once they have begun reproducing, tend to spawn several times. Then, after a pause, spawning may be initiated again. In regions with strong seasonality, these cycles tend to occur seasonally, while strict rhythmicity does not seem to occur where the seasons are less pronounced. Since tilapia generally can reach several years, they are likely to go through several spawning periods. The average period between two spawnings is probably a few weeks. This period can be considerably shortened however by the loss of the brood, as illustrated by a *T. nilotica* female from the mouth of which the freshly spawned eggs were repeatedly removed with the result that this female spawned 11 times within 4 to 8 days (L. Fishelson, pers. comm.).

However, the spawning periodicity of tilapias is still little investigated (see Lowe 1955; Peters 1959; Cridland 1961, 1962). The most detailed investigations conducted to date have been conducted by Aronson (1945, 1951) who worked on *T. macrocephala.*

Certain difficulties in obtaining a reliable basis for an understanding of spawning cycles result from the fact, hardly ever considered by any author, that ripeness of the gonad (while being a necessary condition for spawning) needs to occur together with a number of other conditions (sufficient conditions). In tilapias, these sufficient conditions seem to be missing more frequently than in other fishes, with the result that ripe eggs fail to leave their follicles and are subsequently resorbed, with a new spawn being elaborated, which may again be resorbed. Or, in other words: it is not possible to directly derive, from the number of completed spawnings, the number of spawns which have been elaborated by a given fish. Also, the presence of maturing eggs in a fish cannot necessarily be used to infer that it will actually spawn.

The relative independence of the spawning cycle from the ovarian cycle is known from a number of fishes. This is the reason why MacGregor (1957) objects to indiscriminately using the number of maturing spawns in an ovary to estimate the number of spawning acts, since some of these spawns—in certain fishes at least—are resorbed regularly. Clark (1925) reports of *Leuresthes tenuis* that the eggs differentiate for a layer of yolk-rich oocytes, and are spawned at the peak of the spawning season, at regular intervals, but that this process is reversed near the end of the spawning season, at which point above-mentioned oocyte layer is resorbed. Useful information were also collected on gobiids; Miller (1961) reported, e.g., from *Gobius paganellus* that, at the end of the spawning season, the yolk-rich oocytes degenerate that were maturing hitherto.

In tilapias, the resorption of ripe spawns is a common phenomenon. The eggs at first become soft and of lighter color, while their shape become irregular. The yolk of each egg seemingly "liquefies", but the egg remains in its follicle. Subsequently, the eggs degenerate to small yellow bodies. At first, only a few degenerating eggs may be seen, but others follow, until the whole gonad is filled with atretic follicles. Fig. 10 shows a gonad with eggs in an advanced stage of degeneration.

It is interesting to note that the beginning of egg resorption not necessarily implies an end to the readiness to spawn. In tilapia, females have often been noted to spawn, although the degeneration of their spawn has already begun. In such cases, only the intact eggs were spawned, or those in which the degenerative processes had only begun. The latter eggs are readily identified by their softness, and by the fact that their outer membrane is very fragile. The mortality of embryos from such spawns—when embryos are formed—is generally very high.

The resorption of spawn in tilapias should not be seen as signalling the end of a spawning cycle, because new eggs may be elaborated during (?)[5] or at least shortly after the resorption of a spawn. A fish may thus be ready to spawn shortly after having resorbed a spawn. It has been suggested earlier (Peters 1959) that the tendency of tilapia spawns to be resorbed is related to the feature that the readiness to spawn can be maintained only for a short time, approximately one week. If after this time no suitable male is found, the spawn will be resorbed. Cases have been recorded, however, where a plausible reason for the egg resorption could not be found. Clearly, further investigations are required.

Another aspect of the phenomenon of egg resorption concerns the age at first maturity. The time at which a tilapia first spawns is not necessarily an index of attainment of first maturity, since several spawns may have been produced and resorbed before the first spawning act occurs. The phenomenon that "hidden spawns" are elaborated (not to complete maturity, however) then resorbed before sexual maturity has already been reported in other fishes, e.g., by Hickling (1935) working on *Merluccius.*

It should further be mentioned that egg resorption does not occur only in captive fish. Female *T. galilaea* specimens studied by the author in Israel at the Dor Fisheries Research Station and at Lake Tiberias always contained a number of degenerated eggs. The ovaries were studied at the onset of the spawning season, i.e., the spawns were the first that were produced after the winter pause. It is possible that the proportion of resorbed eggs would have been lower if sampling had been closer to the peak spawning season.

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[5] Translator's note: Question mark in original.

EGG NUMBERS, EGG WEIGHTS AND WEIGHT OF SPAWN

Preliminary Remarks

As stated above, the primary purpose of this investigation was the elucidation of the relationships between egg numbers, egg weights and spawn weight; thus, all previous considerations may be considered as preliminary to the following paragraphs. It should now be obvious that when estimating the number of eggs in a spawn, not only those eggs must be counted that have been actually spawned, but also those eggs which have remained in the ovary ("residual eggs"). In the following, all egg counts include residual eggs, except when otherwise noted. When estimating egg numbers, it is also important to account for egg resorption, since lower egg counts are obtained when an ovary has already been subjected to resorption of its eggs. Thus, when not stated otherwise, the data presented below pertain to females with intact ovaries, as assessed visually in every case.

Another feature which must be considered is the tendency of tilapias (females and males) to swallow a few eggs during the spawning act. Substrate-spawners particularly seem to prefer such eggs which float in the water rather than those which stick to the substrate. To assess the number of eggs that were swallowed, fishes were dissected in all cases where direct observations were lacking; this procedure is rather straightforward because the ingested eggs remain undamaged for quite a while. In the case of mouthbrooders, the stomach of the brooding parent was always opened, because such fish may at any time swallow eggs that are in their mouth. Table 5 gives the results of a number of stomach studies.

Egg Numbers

Fig. 11 shows the relationship between egg numbers and body weight in a substrate-spawning species *(T. tholloni)* and two mouthbrooding species *(T. mossambica k.* and *T. macrocephala).*

Fig. 12 gives the relationship between egg numbers and body weight in the mouthbrooder *T. galilaea.*

In the course of the work on *T. galilaea,* the weight of the ovaries was also determined, and related to the body weights (Table 6). The results suggest that the separation of a spawn from less-developed oocytes occurs when the gonadosomatic index (GSI) reaches about 3.9%. Thus, it can be recommended, when large-scale investigations of the fecundity of tilapias are conducted, to first estimate the GSI value from which the presence of a distinct spawn can be assumed, and to use for fecundity estimates only the ovaries of fishes with a GSI value higher than the critical value. This method is considerably simpler than that which involves the identification, through egg size measurements, of a gap in the egg size distribution. However, it is again stressed here that without using any of the critical methods presented here, fecundity estimates are likely to be erroneous.

The available data on the relationships between egg numbers and body weight in tilapias do not yet allow for unequivocal interpretation; Figs. 11 (especially *T. tholloni*), 12 and 14 suggest, however, that the curves tend to become flat when body weights reach very high values.

Egg Numbers and Spawn Weight

T. mossambica k. was used in an earlier investigation to demonstrate the existence of a relationship between egg numbers in a spawn and the weight of that spawn (Peters 1959). "Spawn weight" means here the weight of all eggs that ripened in a given fish, including "residual eggs" (see above) and eggs that were swallowed. The method to obtain the weight of a spawn is described above. Fig. 13 (dots) shows the rather close relationship between spawn weight and body weight in *T. mossambica k.* On the other hand, when egg weights are plotted on body weights, the relationship is less close (Fig. 13, triangles). This reflects the following phenomenon: either a fish produces many small eggs or a few large eggs; the number and size of the eggs are adjusted such that the relationship between spawn weight and body weight is a simple function of body weight.

Since this earlier investigation was conducted, additional data were gathered, especially from fishes whose ovaries were in the process of being resorbed. As is to be expected, these fishes provide values that are lower than for intact eggs (see Fig. 13, open dots and open triangles). This suggests, once again, that the tendency for tilapia eggs to be resorbed must be considered when assessing the fecundity of these fishes.

It must be considered, when assessing the results in Fig. 13 that they are based on small fish, i.e., on sizes at which *T. mossambica k.* does not spawn in nature. It may be assumed that the curve, had larger fish been considered, would display an inflection and tend to become horizontal, as is the case for *T. macrocephala* (Fig. 14). The relevant data could not be obtained, however, because the fish ceased growing and the whole stock subsequently died.

To date, only *T. macrocephala* could be studied over a wide range of sizes (Fig. 14). The data confirm that egg numbers and egg weight are inversely related; indeed the curves linking egg number and body size and those linking egg size and body weight are mirror images of each other (Fig. 14).

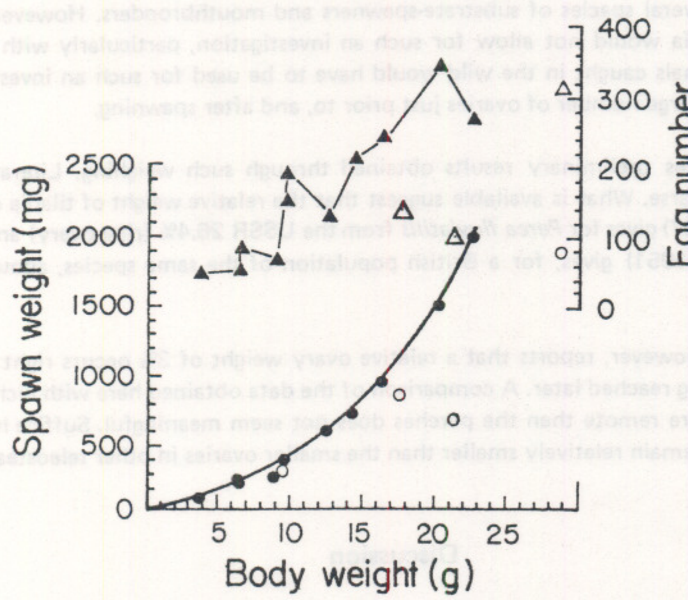

Fig. 13. Weight of ripe egg batch and number of eggs in batch in *T. mossambica k.* Partly based on data in Peters (1959). Body weight refers here to total fish weight after spawning (i.e., inclusive of spent gonad). ● weight of spawn; ○ weight of spawn, but ovary atresic; ▲ number of eggs in spawn and △ number of eggs in spawn, but ovary atresic.

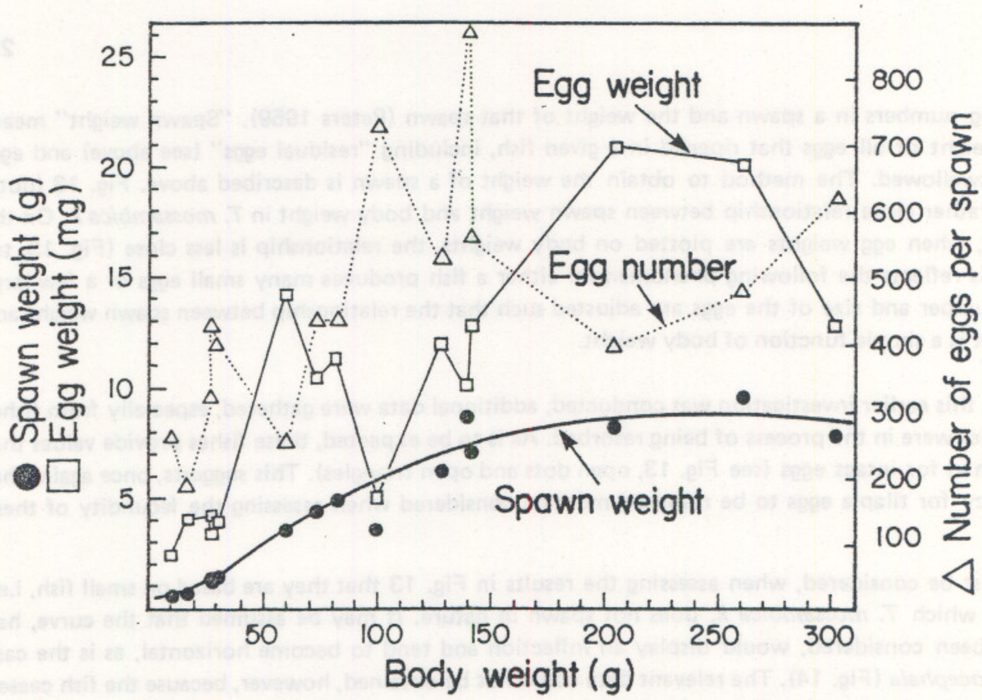

Fig. 14. Weight of ripe spawn, mean egg weight and number of eggs in spawn of *T. macrocephala.* Body weight refers here to total body weight minus gonad plus eggs that might have been swallowed. ● weight of ripe spawn; □ mean egg weight and △ number of eggs in spawn.

It was at first planned to obtain detailed information on the relationships between spawn weight and body weights in several species of substrate-spawners and mouthbrooders. However, it turned out that the available aquaria would not allow for such an investigation, particularly with regard to large specimens. Clearly, animals caught in the wild would have to be used for such an investigation. It was also planned to weigh a large number of ovaries just prior to, and after spawning.

Table 7 summarizes preliminary results obtained through such weighing. Literature data from other bony fishes are sparse. What is available suggest that the relative weight of tilapia ovaries is rather low. Thus, Mayenne (1927) gives for *Perca fluviatilis* from the USSR 26.4% (ripe ovary) and 0.78% (spent ovary), while Le Cren (1951) gives, for a British population of the same species, about 20% and 1%, respectively.

Le Cren (1951), however, reports that a relative ovary weight of 3% occurs right after spawning the low value of 1% being reached later. A comparison of the data obtained here with cichlids with other fishes taxonomically more remote than the perches does not seem meaningful. Suffice here to mention that ripe tilapia ovaries remain relatively smaller than the smaller ovaries in other teleosteans.

Discussion

1) Bertin (1958) distinguishes two modes of spawn elaboration, the "type unimodal" and the "type plurimodal", these names referring to the size distribution of the oocytes. Examples of the unimodal type are *Esox lucius* (Carbine 1943), *Limanda yokohamae* (Kiriya and Shirahata 1955), *Clupea*

harengus (Naumov 1959), and *Coregonus wartmanni* (Von Kraft et al. in press), although a large number of other teleosteans could be listed here. In these cases, a considerable layer of oocytes are held in reserve, at a stage prior to the onset of oocyte growth. These oocytes remain generally free of yolk (a few of them may initiate the accumulation of yolk, however). While these oocytes remain undeveloped, a group of eggs grow steadily; these are the eggs that will be spawned in the next spawning season.

In the plurimodal type, two or more groups of oocytes might be ripening at the same time, the eggs in each group being slightly larger than those of the following group. Examples of fishes with 3 groups of eggs (trimodal type) are *Gasterosteus, Syngnathus* and *Liparis* (Fulton 1898), with *Blennius pholis* (Qasim 1955) and *Scomberomorus* sp. (De Jong 1940) possibly also belonging to this group. The bimodal type, with two groups of egg sizes in the ovary, is best illustrated by *Etheostoma blennoides* (Fahy 1954).

In the last example, two distinct size groups of eggs may be found: a large number of oocytes that have developed but little, and a small number of very advanced eggs. The detailed investigation by Fahy (1954) leads to the conclusion that both groups of eggs are eventually spawned during the same spawning season.

The tilapias belong doubtlessly to the plurimodal type, as do many other cichlids (Peters 1957). However, it remains to be established, whether two spawns are elaborated at the same time (one closely following the other) or whether several spawns are elaborated at any given time. If the beginning of a spawn's elaboration is set at the time the yolk begins to be incorporated in the oocytes, then, it appears probable that the egg size distribution in the tilapia ovary is generally bimodal. This problem requires further investigation.

2) In general, egg numbers increase, in teleosteans, with body size. This rule applies *mutatis mutandis* in viviparous poecilids (Turner 1938). Often, egg numbers increase linearly with body weight (see, e.g., Bagenal 1957 on *Hippoglossoides*).

In tilapias, further work is needed involving very large specimens. The available data suggest, however, that with increasing body sizes, the egg sizes cease to increase as rapidly as with small body sizes. This could be an effect of ageing, similar to that reported by Liamin (1959) from certain populations of herrings.

3) The phenomenon that egg sizes at first tend to increase with increasing body sizes, then stabilize (as in *T. nilotica,* and *T. galilaea*) is certainly widespread, and was reported by Von Kraft et al. (in press) from *Coregonus wartmanii.*

4) The physiological mechanisms which determine egg numbers and egg sizes (egg weights) in bony fishes are to date still unknown. In this context, the finding of an inverse relationship between egg weight and egg number appears particularly valuable. What turned out to be important is the relationship between spawn weight and body weight, this relationship being itself a function of body weight. However, more work is needed, including studies on larger tilapia specimens. Also, these relationships should be compared among different tilapia species. It could be expected that the relatively small number and large size of eggs in mouthbrooders should result in spawn weights comparable to those of substrate-spawners of similar body sizes. This is, however, not the case, as mouthbrooders have spawns that are somewhat lighter than those of the substrate-spawners of similar body sizes. This might be due to the need of the spawn to fit inside the mouth cavity (see Reinboth 1956). This is also a question which has been but little investigated.

It can be assumed that tight relationships between egg numbers and egg sizes do not occur only in tilapias, but are very widespread, as suggested by the recent studies on this topic in which closely related teleostean species or different populations of the same species were investigated. Baxter (1959), for example, who studied different herring populations came to the conclusion that "in the groups under view, fecundity is inversely related to the size of the egg". The northern summer-autumn spawners have a relatively small egg and a high fecundity. Norwegian spawners have a relatively large egg and a low fecundity (see also Liamin 1959). Hempel and Baxter (1961) measured the dry weight of herring eggs, and so obtained a firm basis for the estimation of the yolk content of the eggs of different herring populations. The feature that different populations of fishes have different fecundities is however not limited to marine species. Thus, Rounsefell (1957) discussed the varying fecundity of fishes of same species and sizes, but belonging to different populations. Furthermore, the fecundity of salmonids fluctuates seasonally, as also shown in other fish groups. Hubbs (1958) also discusses differences in fecundity between different populations in certain perches, in which egg numbers and egg size are also inversely related.

The problem remains unsolved as to how, in such cases, relative spawn weights and egg numbers are interrelated. Thus, the question could be asked whether egg weight and egg numbers are inversely related in individual fish, as is the case in tilapias. Several authors have shown that egg numbers can differ widely between individuals, of similar sizes; Miller (1961) for example, demonstrated this in *Gobius paganellus.* In such cases a check should thus be made whether small spawns consist of relatively large eggs (and inversely) or not.

5) It would be premature to attempt to explain the physiology of the phenomena discussed here; a few aspects were presented earlier (Peters 1957, 1959). An ecological interpretation, similarly would be very general. Rounsefell (1957) points out correctly that "size [of the eggs; H.M.P.] can be attained only by the sacrifice of number. In each ecological situation, there is some point at which, on the average, the forces favoring size are exactly balanced by those favoring number." Svärdson (1949) similarly discussed the selective advantages of different egg numbers in fishes, yet in the face of the many unknown factors which would have to be considered here, it seems at present impossible to follow these thoughts further.

Also, broad generalizations should be avoided. Marshall (1953) discussed the selective value of egg size and proposed the rule "that coastal fishes from arctic and antarctic waters and deep-sea fishes have a marked tendency to produce relatively large, yolky eggs." He suggests that it is the relatively poor availability of food for the larvae which makes it adaptive for the eggs to be large and yolky, such that the larvae that hatch out of these eggs will be in advanced stages of development when they begin foraging. However, what seems to apply in some cases does not need to apply in others; thus, in tilapias, egg size is related primarily to the form that parental care takes, as discussed in the Introduction. Thus, in teleosts in general, it seems that there are a number of different causes for differences in egg sizes.

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