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Reproductive strategies and early development of three freshwater gobies

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Three species of gobiid fish inhabit the freshwater Lake Trichonis of western Greece. Two of these species, *Economidichthys pygmaeus* and *E. trichonis* are endemic, and the third is the widespread *Knipowitschia caucasica*. There are habitat separations between the three species. *E. pygmaeus* and *E. trichonis* prefer vegetated areas, the first being fully demersal at all stages of development and the second being semi-demersal. *Knipowitschia caucasica* prefers sandy bottoms and is distributed in shallower waters. Female *E. pygmaeus* and *E. trichonis* spawn in nests prepared by the males in the cavities of broken reeds. The males subsequently guard the eggs until they hatch, with females playing no role in parental care. *Economidichthys trichonis* is probably the smallest freshwater European species. Its eggs are ovoid, measuring about 0·64 × 0·58 mm, from which tiny, unpigmented and incompletely developed pelagic larvae hatch out after an incubation period lasting less than 1 day at a water temperature of 19·5° C. The eggs of *E. pygmaeus* are cylindrical and larger, measuring about 2·38 × 0·89 mm, from which relatively large, strongly pigmented and ontogenetically more advanced larvae hatch out after a longer incubation period. Both species reproduce only once in their lifetime, at the age of 1 year, and die shortly after spawning, but the breeding season involves several spawnings by each individual fish. These biological, developmental and reproductive characteristics are discussed in relation to current theories on evolution of life-histories.

Key words: Gobiidae; *Economidichthys pygmaeus*; *E. trichonis*; *Knipowitschia caucasica*; reproduction; nests; eggs; larvae; habitat separation; Greece.

I. INTRODUCTION

Of the five gobiid species inhabiting freshwater bodies of Greece, two species belonging to the endemic genus *Economidichthys* (Bianco *et al.*, 1987) are now recognized as the most distinctive components of the freshwater Greek ichthyofauna (Economidis & Miller, 1990). *Economidichthys pygmaeus*, originally described as *Gobius pygmaeus* by Holly (1929) (=*G. martensii prevesicus* Stephanidis, 1939) is a small freshwater goby of western Greece, commonly found in streams, the Rivers Louros and Arachthos, and in Lake Trichonis (local populations in small freshwater bodies of the mainland and in the Lefkas island seem to be extinct now) (Economidis, 1973, 1991). Until recently it was of uncertain taxonomic status, but Bianco *et al.* (1987) set this taxon as a type species of the new genus *Economidichthys*. This genus is also represented by a species recently described by Economidis & Miller (1990) as *E. trichonis*, restricted to Lake Trichonis, and is probably the smallest freshwater European teleost at maturity (Economidis & Miller, 1990; Miller, 1990). Both species have a dermal perianal organ, unique among teleosts, which may represent a level of specialization higher than that of other teleosts (Bianco *et al.*, 1987; Economidis & Miller, 1990; Miller, 1990). The function of this organ remains unclarified and, according to these

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authors, the special circumstances that led to its evolution may be revealed when the life-history of the species concerned is better known.

The widespread Ponto–Caspian species *Knipowitschia caucasica* (Kawrajsky) has been reported from the Caspian, Azov, Aral and Black Seas, several localities of northern Greece (Macedonia and Thrace), and Turkey (Sea of Marmara) (Miller, 1972, 1990; Georghiev, 1964; Kevrekidis *et al.*, 1990). A *Knipowitschia* form was recently discovered in Lake Trichonis and was provisionally attributed to *K. caucasica*. However, the taxonomic status of this local population is doubtful (Economidis & Miller, 1990). According to Kalinina (1976), *K. caucasica* is a euryhaline species able to live in fresh as well as in hypersaline waters.

We have examined aspects of the reproduction and larval development of these gobies in the framework of a broader study on the early ontogeny and reproductive biology of the fish species inhabiting Lake Trichonis (Economou *et al.*, 1991). This lake is the largest (97 km^2) and deepest (max. depth 58 m, average depth 30·5 m) natural freshwater body of Greece. It was initially an oligotrophic lake, but is now mesotrophic (Overbeck *et al.*, 1982). The study aimed at the two species of the genus *Economidichthys*, but when the presence of *K. caucasica* in our samples was later confirmed, aspects of its larval development were included in the investigation. Of the other 17 fish species which are known to inhabit Lake Trichonis, larvae and juveniles of the following five were commonly represented in our samples for gobies: *Tropidophoxinellus hellenicus* (Stephanidis); *Scardinius acarnanicus* (Stephanidis); *Atherina boyeri* (Risso); *Salaria fluviatilis* (Asso); *Cobitis trichonica* (Stephanidis).

II. MATERIAL AND METHODS

SAMPLING INSTRUMENTS AND PROCEDURES

Fish were collected during routine visits to Lake Trichonis from September 1988 until April 1991. The interval between sampling periods was 5–30 days. Initial investigations on the early life history of the fish species inhabiting the lake involved ichthyoplankton sampling using two conical tow nets. One net was of 1 m diameter, fitted with a gauze of 0·5 mm mesh size, and the other was of 0·5 m diameter, fitted with a gauze of 0·25 mm mesh size, ending in detachable cod-ends. Both nets were supplied with flow-meters and were towed from a fishing boat either obliquely or horizontally at various depths from the surface at a speed of approximately 1·5–2 knots. The larvae were preserved in 4% formalin neutralized with sodium phosphate.

Later, the sampling methodology was modified and improved because experience showed that most fish species of the lake either lack a planktonic phase or have a very short period of planktonic existence. Therefore it became necessary to deploy bottom-towed gear in order to catch benthic larvae. The instruments used had a rectangular iron frame, and one of their sides scraped along the substrate during towing. One, 75 × 30 cm, was fitted with a net of 0·5 mm mesh size, 1·85 m long, and another, 50 × 30 cm, was fitted with a net of 0·2 mm mesh size, 1·60 m long. Flow-meters were not employed. These instruments were used from June 1989. After each haul, the larvae and juvenile fish were preserved in 4% neutralized formalin. However, despite considerable effort, a variable and perhaps significant proportion of the sampled population escaped our attention during the sorting procedure. This was because the samples contained enormous quantities of aquatic plants, sand and debris, to which the larvae tended to stick and go unnoticed. From April 1990 this sorting bias was reduced by soaking the plants and debris, piece by piece, in a bucket of water. The larvae were liberated into the bucket and they were picked up with forceps or small vials. However, this improvement reduced comparability with the results of previous samplings.

Some tows with the rectangular nets were conducted parallel to the coastline at various depths in order to assess the species distribution in relation to depth and distance from the shore. To determine the substratum preference of the species, sampling in specialized microhabitats took place on days when the visibility through the water column allowed the type of bottom to be distinguished by dropping and towing the rectangular nets on the desired substratum (weeds, mud, sand or gravel).

Supplementary sampling was performed close to the shore with scoop-nets and a fry net (7 m long, 2 m deep, 1 mm mesh), sometimes combined with electrofishing. Day and night sampling with a fry net took place in order to assess diel migrations to and from the coast. A commercial beach-seine fitted with a cod-end (5 mm mesh) was also used for catching adult and juvenile fish.

In the laboratory the fish larvae were identified to species, counted and measured to the nearest 0·1 mm [notochord length (N.L.) for preflexion larvae, standard length (S.L.) and total length (T.L.) for post-flexion specimens].

Male-guarded nests of both species were collected from the field for determining the characteristics of the eggs and rearing the larvae hatched out from these eggs. Drawings of the various developmental stages of embryos and larvae were made using a binocular microscope fitted with a camera lucida.

When it is not otherwise stated, only standard lengths are given. Measurements always refer to larvae preserved in formalin. In the descriptions of larvae, terminology of the structural characters and the pigmentation patterns follows Russell (1976). The first appearance of scales was taken to mark the onset of metamorphosis.

REARING EXPERIMENTS

Reeds bearing nests of the two *Economidichthys* species, along with the guarding males, were collected at various times during March 1990 (water temperature ranged between 16·1 and 20·2° C in the different localities and sampling periods). The reeds were placed in polyethylene plastic bags half-filled with lake water, with the remaining space filled with oxygen, and were transported to the laboratory. The eggs were at various stages of development, and hatching was observed immediately after collection and continued for several hours or days. Batches of larvae of the two species that were hatched over a time interval of 8 h were transferred to separate glass aquaria of 22-l volume, and kept at a room temperature (about 19° C). From the second day of development, and until day 10, the larvae were offered zooplankton collected from Lake Trichonis with a plankton net (0·2 mm mesh) and transported alive to the laboratory. Dead larvae, unused food and debris were pipetted off, and part of the water was replaced daily.

Rearing was successful for *E. pygmaeus*, the larvae of which were relatively large at hatching (over 4 mm N.L.) and could accept the food offered. However, many larvae failed to establish exogeneous feeding and ultimately died. After day 10 from hatching, natural zooplankton was no longer available, and dried *Daphnia* was offered as food. Unlike the larvae of other freshwater species that were successfully reared by us on this diet, the larvae of *E. pygmaeus* refused this food, and mortality after 5 days was very high. Live *Artemia salina* (L.) nauplii were then provided as food to one group of larvae. Some larvae began feeding but mortality remained high for another 5 days, probably owing to the delayed provision of *A. salina* nauplii after the stock of natural zooplankton had been depleted. Larvae that died during this period had a degenerated digestive system and were retarded both in growth and in ontogenetic development in comparison with fed larvae. There were, however, about 50 survivors, which were subsequently reared with relatively high mortalities. Later in ontogeny, the fish were fed with commercial food, such as frozen *Chironomus* larvae and dried krill, and occasionally with chopped freshwater shrimps *Atyaephyra desmarestii* (Mill.) transferred from Lake Trichonis. At approximately 5-day intervals during the first 2 months and subsequently 10-day intervals, samples from this surviving population were taken and preserved in 4% neutralized formalin for observations on development.

We attempted to rear several batches of *E. trichonis* larvae hatched from eggs in guarded nests following similar techniques. None of them survived long after yolk absorption because live food of suitable small size was not available at the time of transition to

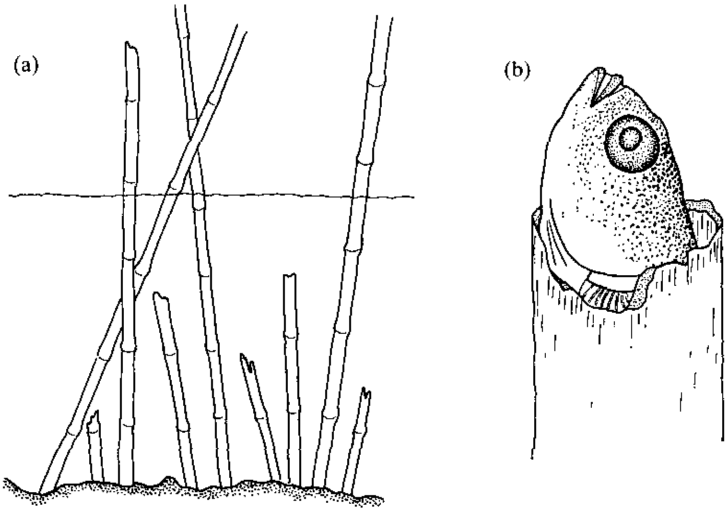

FIG. 1. (a) Spawning sites of *Economidichthys pygmaeus* and *E. trichonis* in a typical reedstand; (b) a male *E. pygmaeus* guarding the nest.

TABLE I. Egg dimensions (mm) of the two *Economidichthys* species

	Longer axis	Shorter axis	Number
E. pygmaeus	2·38 ± 0·13	0·89 ± 0·04	50
E. trichonis	0·64 ± 0·03	0·58 ± 0·02	50

exogeneous feeding. The larvae hatch at an extremely small size by freshwater standards (between 2 and 2·4 mm preserved N.L.), and the coarse meshes of the plankton net (0·2 mm) did not efficiently retain suitable microorganisms for feeding these larvae. Investigation of the gut contents of field-caught pelagic *E. trichonis* at around the stage of yolk absorption and little afterwards revealed that these larvae feed on non-crustacean prey, and probably on phytoplankters, ciliates and rotifers. However, the experiment was useful in defining early pigment patterns.

III. RESULTS

REPRODUCTIVE BEHAVIOUR AND SPAWNING CHARACTERISTICS

Spawning of the two *Economidichthys* species takes place between late February and the middle of May in the cavities of broken reeds (*Phragmites australis* Can.), which abound on the banks of the lake (Fig. 1). During reproduction the male assumes breeding colours, establishes a territory over a reed and prepares the nest by cleaning the opening of the reed; males were often observed to carry mouthfuls of debris and put them outside the nest. After spawning, he guards the eggs until they hatch, remaining either inside the nest, head half out, or in the vicinity of the nest. Presumably, he also defends the nest and aerates the eggs. The males do not

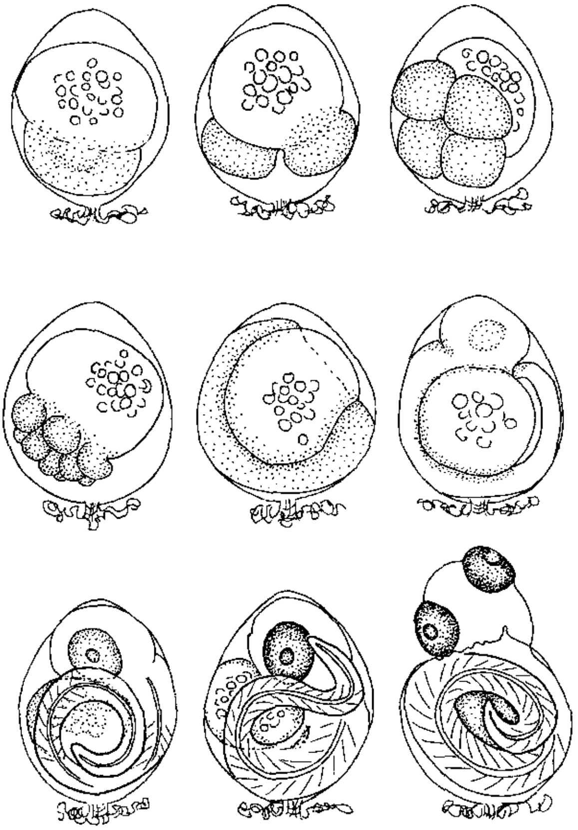

FIG. 2. Development of *Economidichthys trichonis* eggs.

feed during parental care activities. The females play no role in parental care. Nests abandoned by the male soon became full of debris and fungi. Almost invariably, the males entered the nest tail first, swimming backwards by undulating movements of the body in the anguilliform technique. In a few instances, however, small *E. trichonis* nesting in large reeds entered the nest head first, but they turned around immediately to take the upright position. Nests were also constructed in pieces of reed lying on the bottom, in empty shells of gastropods and even in plastic tubes. Few such nests were recovered with the rectangular nets towed on the bottom, however, and these seem to be atypical nest sites for the two species.

The nests were clear to see, not only because the top opening of the reed occupied was free of silt and debris, but also by the presence of the guarding male. When disturbed by our approach, some fish left the nest but remained in the vicinity, ready to return when the disturbance was over, while others withdrew inside the reed. Very rarely were females found near the reedstands during the day. It is likely that spawning takes place mainly at night, and afterwards the females leave the reedstands. During the period of reproduction, adult fish of both species were placed in glass aquaria to observe their spawning behaviour. The males almost immediately entered pieces of reed or plastic tubes that had been placed inside the aquaria. However, females were reluctant to enter the nest, and mating was not observed.

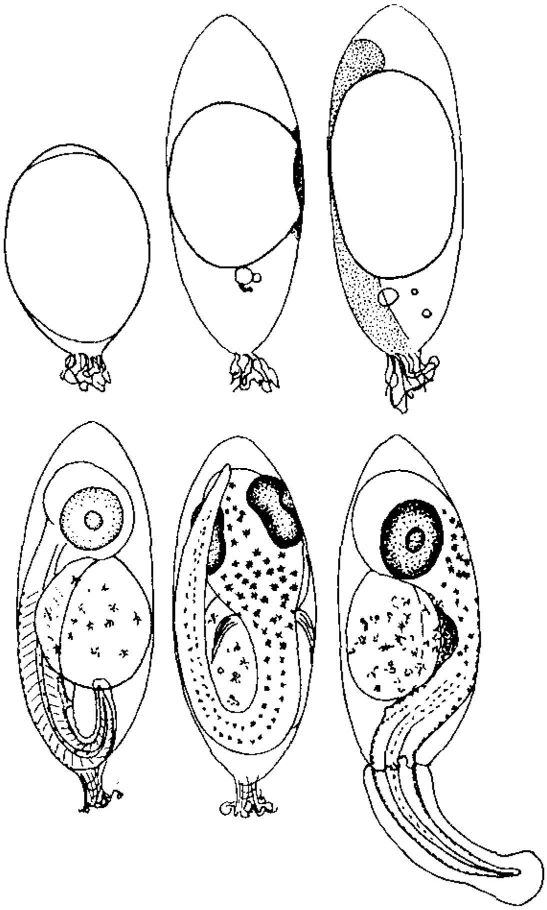

FIG. 3. Development of *Economidichthys pygmaeus* eggs.

The eggs of both species were laid uniformly in a single layer in the hollow cavity of the reeds, and were attached firmly to the substratum. The eggs of *E. pygmaeus* covered the whole inner surface of the reed, whereas the eggs of *E. trichonis* were usually found in discrete patches, with empty intervals between them. Egg size and morphology greatly differed between the two species. The eggs were spherical at spawning but soon they became ovoid in *E. trichonis* and cylindrical in *E. pygmaeus* (Table I, Figs 2 and 3). Unfertilized eggs maintained their spherical shape. Table II summarizes the information on the characteristics of some nests. In the nests of both species, discrete stages of egg development could usually be recognized, which probably reflected successive depositions of eggs by different females in the same nest. Pieces of clean reeds were placed in the reedstands and inspected regularly for newly constructed nests. Nests of *E. trichonis* containing eggs with well-formed embryonic discs or embryos at the beginning of the eye-pigmentation stage, attended by a male, were found in two instances in reeds left overnight and recovered 16 h later (Table II); a rapid embryonic development and an incubation period not exceeding 1 day at a water temperature of 19·5° C can be deduced from this evidence. Given that a typical nest of *E. trichonis* contains several hundreds or even

TABLE II. Characteristics of some *Economidichthys* nests

Nest number	Body characteristics of males (mm)			Reed opening dimensions (mm)	Eggs per nest	Unfertilized eggs	Development stages*		
	Total length	Body height	Head height				Blastula-morula	Embryonic disk	Eyed embryos
E. pygmaeus									
1	47·1	9·5	8·8	11·1 × 10·0	564	4	37 (75)	2 (25)	422 (3)
2	51·0	9·5	9·3	9·6 × 8·3	425	2	(9)	317	97
3	47·5	7·9	6·8	9·1 × 8·0	407	50			349 (8)
E. trichonis									
1†	27·2	5·0	4·0	10·0 × 9·0	244			244	
2†	24·7	4·3	4·2	9·1 × 6·5	16				16
3	25·2	5·0	4·6	8·7 × 8·0	1937			1517	420
4	39·5	5·2	5·1	9·0 × 8·0	1980		110	1815	55
5				8·5 × 7·8	1419				1419
6	26·5	4·5	3·9	8·0 × 7·8	1520		560	280	680
7	28·0	4·9	4·0	9·1 × 8·0	608			608	
8				10·5 × 9·6	1722		210	1344	168
9				8·0 × 7·8	1260			490	770

*Dead eggs in parentheses. †Nests constructed overnight in pieces of reeds placed on the previous evening.

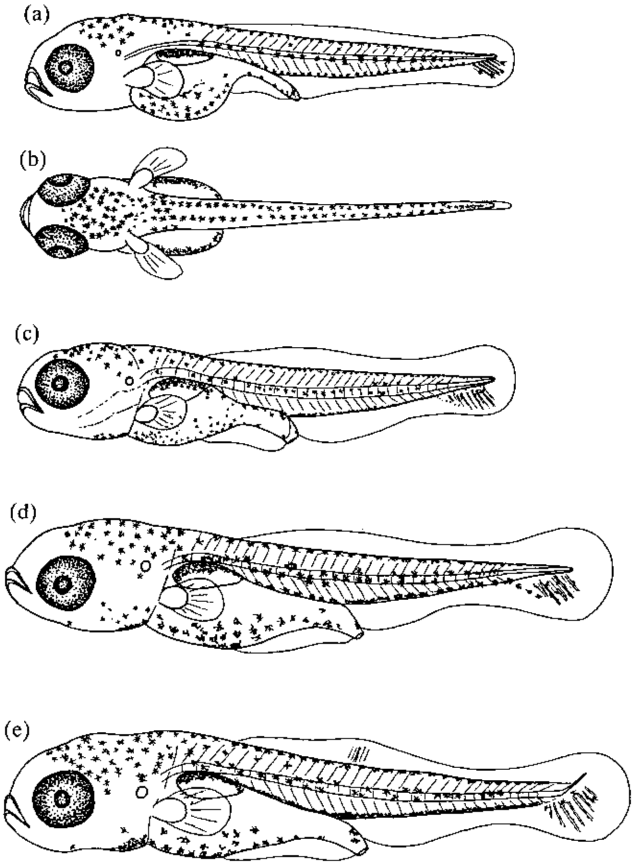

FIG. 4(a–c).

FIG. 4. Morphological development of *Economidichthys pygmaeus* larvae. (a), (b) day 0 (hatching), 4·1 mm; (c) day 1, 4·4 mm; (d) day 6, 5·0 mm; (e) day 7, 5·4 mm; (f) day 10, 6·0 mm; (g) day 13, 6·6 mm (detail of the perianal organ: pf, primordial fin; po, perianal organ; a, anus; up, urogenital papilla; af, anal fin); (h) day 34, 7·6 mm; (i) day 43, 8·4 mm; (j) day 55, 11·5 mm; (k) day 62, 13·8 mm.

thousands of eggs, and that the ovaries of the female fish of this species contain only a few hundred vitellogenetic oocytes (unpublished data), the participation of eggs from several females in each nest is implied from these data.

We made no observations on the spawning behaviour and the egg and nesting characteristics of *K. caucasica.* According to Koblitskaya (1961), in the Volga delta this species lays down cylindrical eggs 1·75–2·6 × 0·7–0·9 mm, in empty mollusc shells, under stones or in aquatic vegetation in shallow waters, and the male attends the eggs. Up to four discrete patches of eggs were observed per nest and an incubation period of about 2 weeks at an unspecified water temperature was stated.

MORPHOLOGY AND ONTOGENETIC DEVELOPMENT

Economidichthys pygmaeus

The descriptions that follow present the morphological development of *E. pygmaeus* larvae based on preserved material from the rearing experiments (Fig. 4).

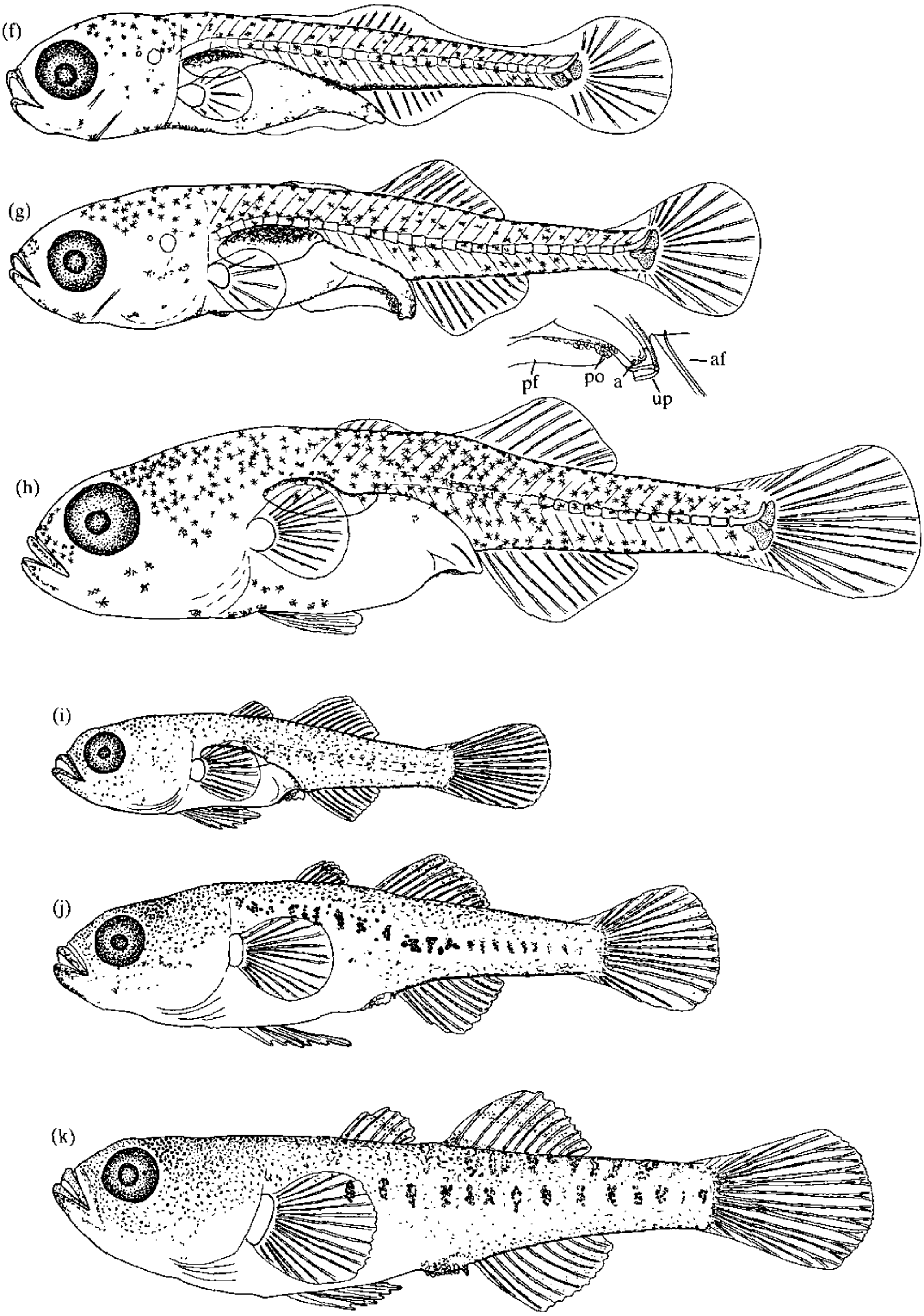

FIG. 4(f–k).

Day 0. Hatching length 4·1–4·4 mm N.L.; the body is divided into 30–32 myomeres; the larvae are strongly pigmented; the yolk sac is large and the yolk is granular with a yellowish hue; the sagitta is clearly visible; the eyes are dark but not yet black; the mouth is open; there are well differentiated rays in the pectoral fins emerging from relatively large fleshy lobes.

Day 1. Length 4·3–4·7 mm; the eyes are black; the swimbladder is partially inflated in some larvae, marked by the presence of brownish pigment on its dorsal side; cartilaginous elements appear in the suborbital region; a second otolith becomes evident in the otocyst region; the notochord is distinctly segmented; most larvae initiate exogenous feeding.

Day 2. The urostyle is straight, but hypourals and interspine rays begin to form in the caudal region; the yolk sac is small and variable in size among larvae; larvae with small yolk volumes are longer, capable of feeding, having larger otoliths and generally are more advanced in ontogenetic development than larvae with large yolk volumes.

Day 3. The yolk is absorbed in some larvae but remnants persist in other larvae.

Day 4. Length 4·7–5·2 mm N.L.; the yolk sac is absorbed in all larvae.

Days 5–6. Length 4·9–5·3 mm; the urostyle begins to flex.

Days 7–9. Length 5·1–5·6 mm; following a thickening of the primordial marginal fin, interspine rays appear in the regions where the second dorsal and anal fins will be formed; caudal fin rays are present.

Days 9–10. Ray development begins in the anal fin, and almost immediately in the second dorsal fin.

Days 12–14. Length 5·5–6·6 mm; the caudal fin is fully developed and the tail has almost taken its final form; the perianal organ is rudimentary present in a larva 6·6 mm, 12 days old; it is clearly seen in all larvae after day 34.

Days 16–20. Length 6·0–6·8 mm; the first dorsal fin bases begin to form; in some larvae the fin-ray development is complete (six rays invariably occur in the first dorsal fin, and 11 (rarely 10) rays in the second dorsal and in the anal fins); budding of pelvic fins starting; caniniform teeth form in the jaws; scales appear in the posterior part of the trunk.

Days 34–40. The fleshy pectoral lobes are reduced in size and become progressively shorter during subsequent development; ctenoid scales cover the sides of the body, being larger in the caudal region.

Pigmentation

At hatching the pigmentation pattern is well developed. It consists of scattered melanophores over the whole body, as well as groups of melanophores of which the following are the most important: branched melanophores on the yolk sac, a double dorsal row of large stellate melanophores, a double ventral row of smaller stellate or punctate melanophores running postanally up to the tail, a mediolateral single row, a group of head melanophores extending from the occipital to the

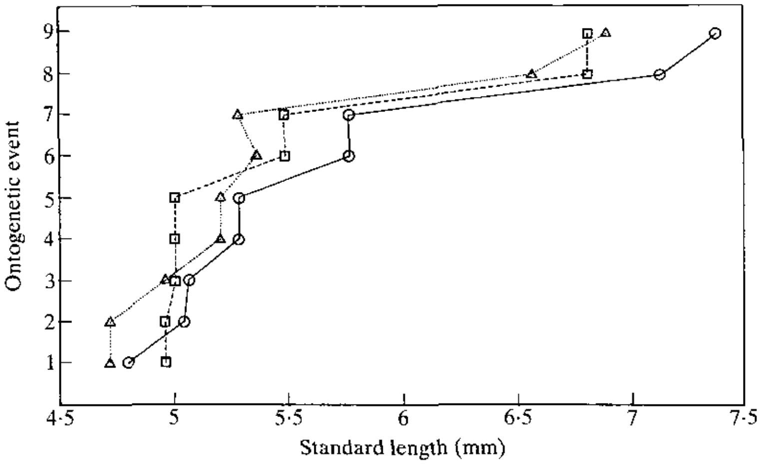

FIG. 5. Size-related ontogenetic events in *Economidichthys pygmaeus* larvae caught in three sampling periods of 1990: —O—, 18.4.1990; – – □ – –, 09.5.1990; · · △ · ·, 18.5.1990. (1) Interspine rays in caudal fin; (2) flexion; (3) true rays in caudal fin; (4) interspine rays in second dorsal fin; (5) interspine rays in anal fin; (6) true rays in second dorsal fin; (7) true rays in anal fin; (8) pelvic fin budding; (9) rudimentary appearance of first dorsal fin.

shoulder region, and aggregations of melanophores in the throat, the tail and the pectoral fins.

The pigmentation pattern shows little change during the first 8 days of development, except that there is an addition of new melanophores, especially in the dorsolateral region. By day 10 the mediolateral row is no longer apparent and the lateral side of the body is uniformly covered by branched brownish melanophores, which progressively increase in size and become more diffuse. The melanophores on the head and throat regions and on the pectoral fins increase in number and progressively show characteristic arrays. In a larva 8·4 mm, 43 days old, some lateral aggregations of melanophores can be distinguished with difficulty. In subsequent life stages these aggregations become progressively more intense. In a larva sampled on day 55 (11·5 mm) they had taken the form of the short transverse lateral bars, which characterize the juvenile and adult morphology. The other major changes in pigmentation that occur between days 43 and 69 are that vertical striated bars appear on the caudal fin and horizontal bands on the dorsal fins. In some individuals, a dark spot forms on the rear part of the first dorsal fin. The body is now densely pigmented with small punctate melanophores lying directly on the epidermis and larger stellate melanophores located on the dermis. The abdominal region is pale yellow and the pelvic fins remain unpigmented. No other important changes in pigmentation occurred until day 249, when the last survivor (19·7 mm) was killed.

Wild specimens

Three groups of larvae sampled during April and May 1990, totalling about 50 individuals each, were examined for assessing the size at which some morphological characters were differentiated in about 50% of the individuals in each group (Fig. 5). The results indicate that most differentiation events occurred at a larger

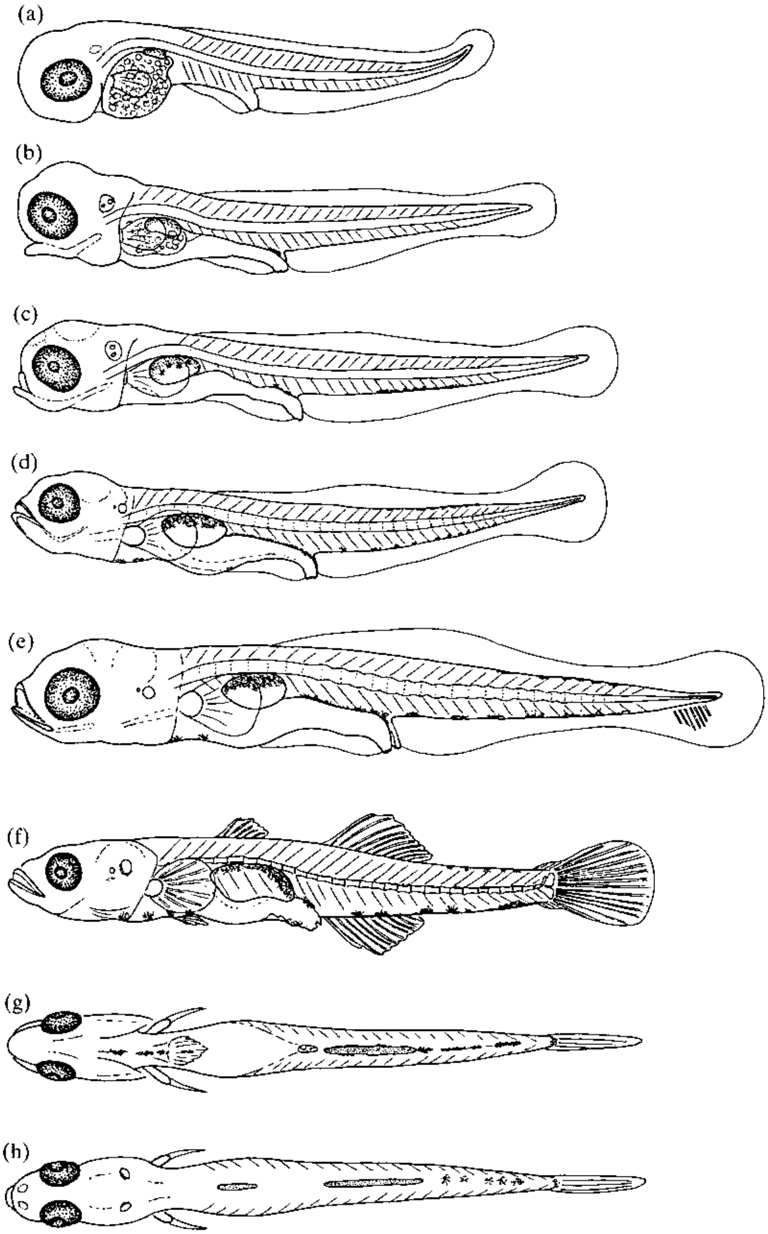

FIG. 6(a–h).

size in larvae hatched earlier in the season. In another group of larvae consisting of 35 individuals larger than 6·7 mm, sampled on 12 June 1990, all studied characters were already differentiated.

Comparing reared and wild larvae, most characters early in ontogeny (up to the stage of formation of true rays in the anal and second dorsal fin) differentiated at comparable sizes in the two groups. However, it should be noted that some shrinkage due to net capture may have taken place in the wild larvae, in addition to that

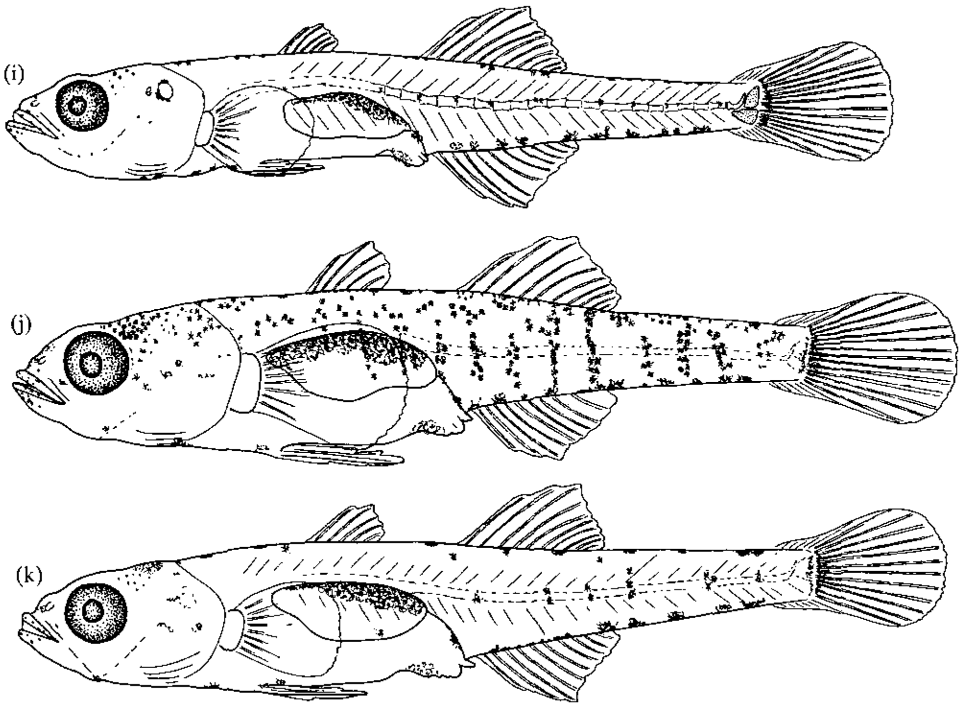

FIG. 6(i–k).

FIG. 6. Morphological development of *Economidichthys trichonis* larvae from laboratory rearing (a–c) and field collections (d–k). (a) day 0 (hatching), 2·1 mm; (b) day 1, 2·2 mm; (c) day 3, 2·6 mm; (d) 4·8 mm; (e) 6·4 mm; (f), (g), (h) lateral, ventral and dorsal view of a larva 10 mm; (i) 13·9 mm, male, caught in June 1989; (j) 14·8 mm, male, caught in October 1989; (k) 14·8 mm, female, caught in October 1989.

due to preservation, and this shrinkage could have affected that smallest specimens more strongly (Hay, 1981, 1982). Characters appearing later in ontogeny, i.e. first dorsal fin rudiments and pelvic buds, were present at larger sizes in the wild than in the reared larvae. Furthermore, the field-caught larvae were generally darker than the reared ones, probably reflecting an effect of the darker background in the field or of the stronger illumination in the laboratory (see Mooij, 1989).

Economidichthys trichonis

The development of *E. trichonis* larvae from rearing experiments (up to the stage of yolk absorption) and field collections (post yolk-sac stages) is described below and illustrated in Fig. 6.

Day 0. Hatching length between 2·1 and 2·5 mm N.L.; the eyes are dark; the body typically devoids pigment except some brownish melanophores present in the region where the swimbladder is to be developed; occasionally, a very weak and diffused trace of pigment is present in the ventral side of the body, midway between the anus and the urostyle; the yolk sac is relatively small, yellowish in colour, containing a variable number of oil globules; the mouth is closed but opens within few hours from hatching; the pectoral buds are well developed but fin rays are not yet differentiated; the otocyst is visible but the sagitta is hardly distinguishable; the swimbladder fills and becomes functional within one day from hatching.

Day 1. Length between 2·2 and 2·7 mm; the yolk sac is greatly reduced in size; the eyes are already black; the diffused trace of post-anal ventral pigment is now more prominent and takes the form of a weak branched melanophore; another weak melanophore appears on the ventral side of the trunk just above the anus; both melanophores are visible only under a suitable combination of reflected and translucent light.

Day 2. The yolk sac is fully absorbed in most larvae; tiny otoliths are visible in the otocyst; more pigment, still diffused, appears along the ventral side of the body, both preanally and postanally; small occipital melanophores are present.

Day 3. Post-anal ventral pigmentation takes the form of a single row of melanophores not extending up to the tail. Diffused pigment is present above the gut, extending to the swimbladder.

Day 4. Mass mortality of larvae, continuing on the following day.

Wild specimens

The description of post yolk-sac *E. trichonis* larvae is based on relatively few specimens caught with the bottom-towed instruments, probably on their way up during hauling. The larvae of this species generally resemble those of *K. caucasica* but are more lightly pigmented at comparable stages of development. Up to a size of 7 mm, the pigmentation pattern is characterized by a single row of ventral post-anal melanophores, a single row of dorsal branched melanophores situated posteriorly near the tail, and few large melanophores preanally extending from the throat to the position where the ventral fins are to be formed. There are also dense aggregations of overlapping melanophores above the digestive tract and on the dorsal side of the swimbladder.

In a larva of 10 mm, internal melanophores on the vertebral column appear. The perianal organ is hardly distinguishable. The dorsal and anal fins are well developed, the pectoral fin contains true rays, and the pelvic disc starts to form. Teeth are evident on the jaws. At about 11 mm, scalation has started, and small melanophores can be seen on the head and on the lower jaw, and a larger one on the base of the second dorsal fin. At this size, lateral pigmentation in the form of few stellate melanophores develops on the sides of the body near the tail region; with the growth of larvae, these melanophores progressively increase in number, finally forming the transverse bars which characterize the adult morphology. At about 13–14 mm the body is still transparent and sex determination is possible, based on external morphology and the pigmentation pattern (see Economidis & Miller, 1990, for characters distinguishing male and female fish). In general, the male fish present a more advanced pigmentation pattern, more pigment on the lower jaw, and a larger ventral fin in comparison with females. At 14·7 mm, the formation of the lateral bars is almost complete in males.

Knipowitschia caucasica

According to Koblitskaya (1966: in Kalinina 1976), hatching of *K. caucasica* larvae takes place at a size of 3–3·5 mm and the larva only has pigment on the yolk sac and the ventral post-anal region. In this respect, the newly-hatched larvae of *K. caucasica* differ from those of *E. trichonis* in that the larvae of the later species are smaller at hatching, have no pigment on the body but possess some pigment on the swimbladder region. The yolk is absorbed after 3–4 days at a size of 4–5·5 mm at an unspecified temperature. According to Koblitskaya (*op. cit.*), dorsal pigment and rays on the second dorsal and anal fins develop at a larval size of 5–6 mm.

As no *K. caucasia* larvae were available from rearing experiments, the descriptions that follow refer to wild specimens (Fig. 7). The smallest larva available was 5 mm. This was a post-flexion larva with already formed hypourals, interspine rays on the second dorsal and the anal fins, teeth on the jaws, well-developed dorsal and ventral rows of melanophores, preanal pigment, and few melanophores in the otocyst region and on the swimbladder. By the time that the size of 6·9 mm had been reached, melanophores had been added on the lower jaw, above the digestive tract and on the swimbladder. The second dorsal and anal fins were now well formed. At 7·2 mm, new melanophores had been added on the head, the snout and the caudal fin rays. In a larva of 8·7 mm, the first dorsal and pelvic fin buds were apparent, and scales could be observed scattered over the body, mostly in the tail region. Up to the size of 10 mm, the pelvic disc was developed, the first dorsal fin was formed, the scales covered the whole surface of the body and the pigment was thickening with the addition of new melanophores on the head, the jaws, the dorsal and lateral sides of the body. The lateral melanophores formed aggregations which finally take the form of bars. Subsequent development stages differ from the stages described only in the intensity of pigmentation.

With careful examination, distinction between *K. caucasica* and *E. trichonis* larvae species is possible at all stages of development, based on morphology and the pigmentation pattern (compare Figs 6 (f, g, h) and 7 (j, k, l)). In general, the *K. caucasica* larvae are more robust and more heavily pigmented than the *E. trichonis* larvae at comparable sizes.

THE LARVAL AND JUVENILE HABITATS

Sampling with planktonic instruments at or close to the surface layers from February to April in 1989 and 1990, yielded enormous numbers of tiny larvae at the yolk-sac stage or little beyond. These larvae presented the characteristics of gobiid larvae, as known from published descriptions of marine fish larvae, but only after the rearing experiments were conducted could they be positively identified as *E. trichonis*. They occurred everywhere in the lake, but their density diminished with distance from the shore. As the majority of hauls were taken with nets of 0·5 mm mesh, significant escape through the meshes of this net must have taken place, thus affecting both the estimated densities and the apparent size distribution of larvae. However, a few hauls conducted with the net of 0·2 mm mesh size revealed densities often approaching 70 individuals m^{-3}. The length–frequency distribution of these pelagic larvae from a number of hauls conducted in 1989 during the course of the spawning season is presented in Fig. 8.

Hauls taken with plankton nets failed to catch large numbers of post yolk-sac larvae of *E. trichonis*. Of the few caught, most were sampled at night. A greater number of post yolk-sac larvae were sampled in deeper layers or just above the bottom with the rectangular nets. We hypothesize that the larvae leave the upper layers of the water column shortly after yolk absorption and assume a semi-demersal mode of life, but migrate upwards at night. Post-metamorphozed larvae, juveniles and adults were caught with the rectangular nets towed on or above the

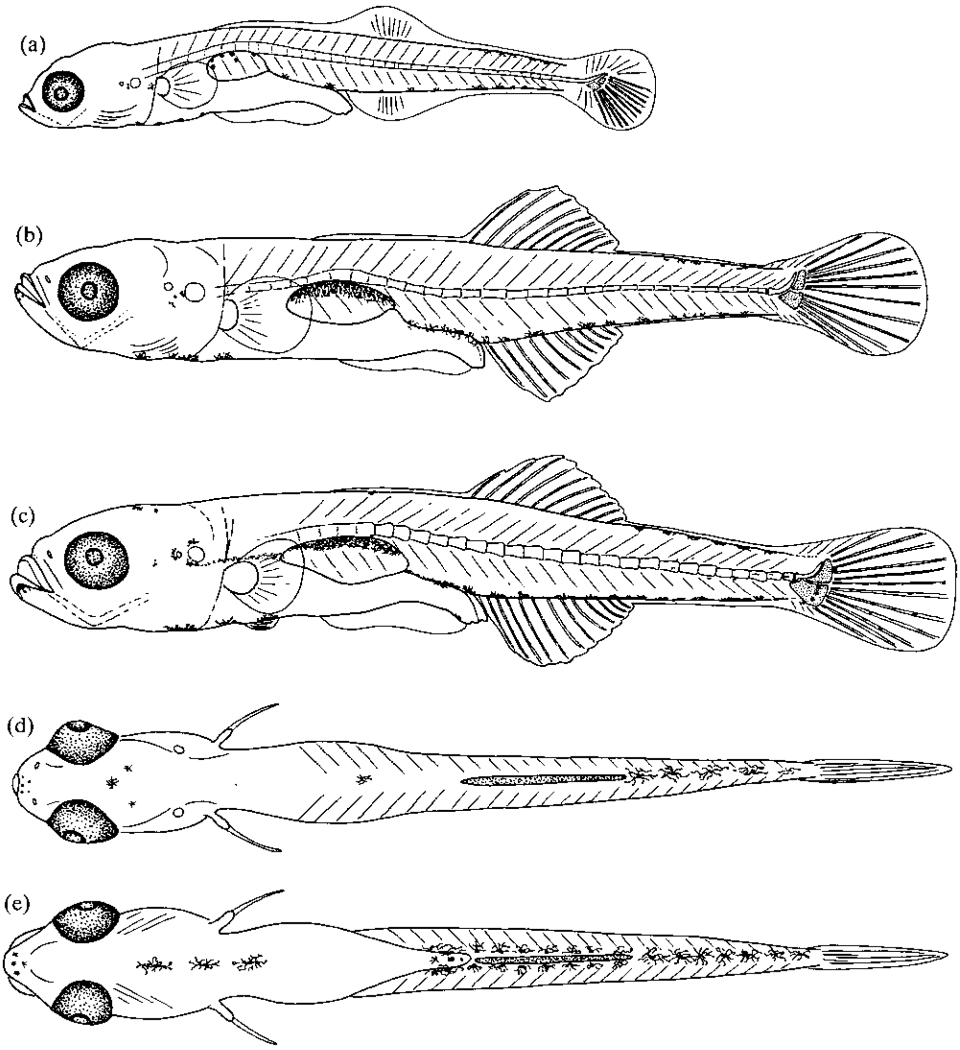

FIG. 7(a–e).

FIG. 7. Morphological development of *Knipowitschia caucasica* larvae from field collections. (a) 5·0 mm; (b) 6·9 mm; (c), (d), (e) lateral, dorsal and ventral view of a larva 7·2 mm; (f) 8·7 mm; (g) 9·2 mm; (h) 10 mm; (i) 13·5 mm; (j), (k), (l) lateral, ventral and dorsal view of a larva 10 mm.

bottom, especially in areas covered by aquatic vegetation. Juveniles and adults were also frequently caught with scoop-nets in reedstands and protected bays.

Larvae of *E. pygmaeus* were more rarely present in the plankton. All developmental stages, even the newly-hatched larvae, were in most cases encountered on the bottom, and were sampled with the rectangular nets predominantly in areas covered with aquatic vegetation. Late larvae and juveniles were also sampled with scoop-nets in small harbours, protected bays and in estuaries of tributaries that discharged into the lake. Probably, there is a pelagic period during the early ontogeny of this species, albeit very short, which permits dispersal from the reedstands to the vegetated areas of the lake. Thus, the larvae of *E. trichonis* appear

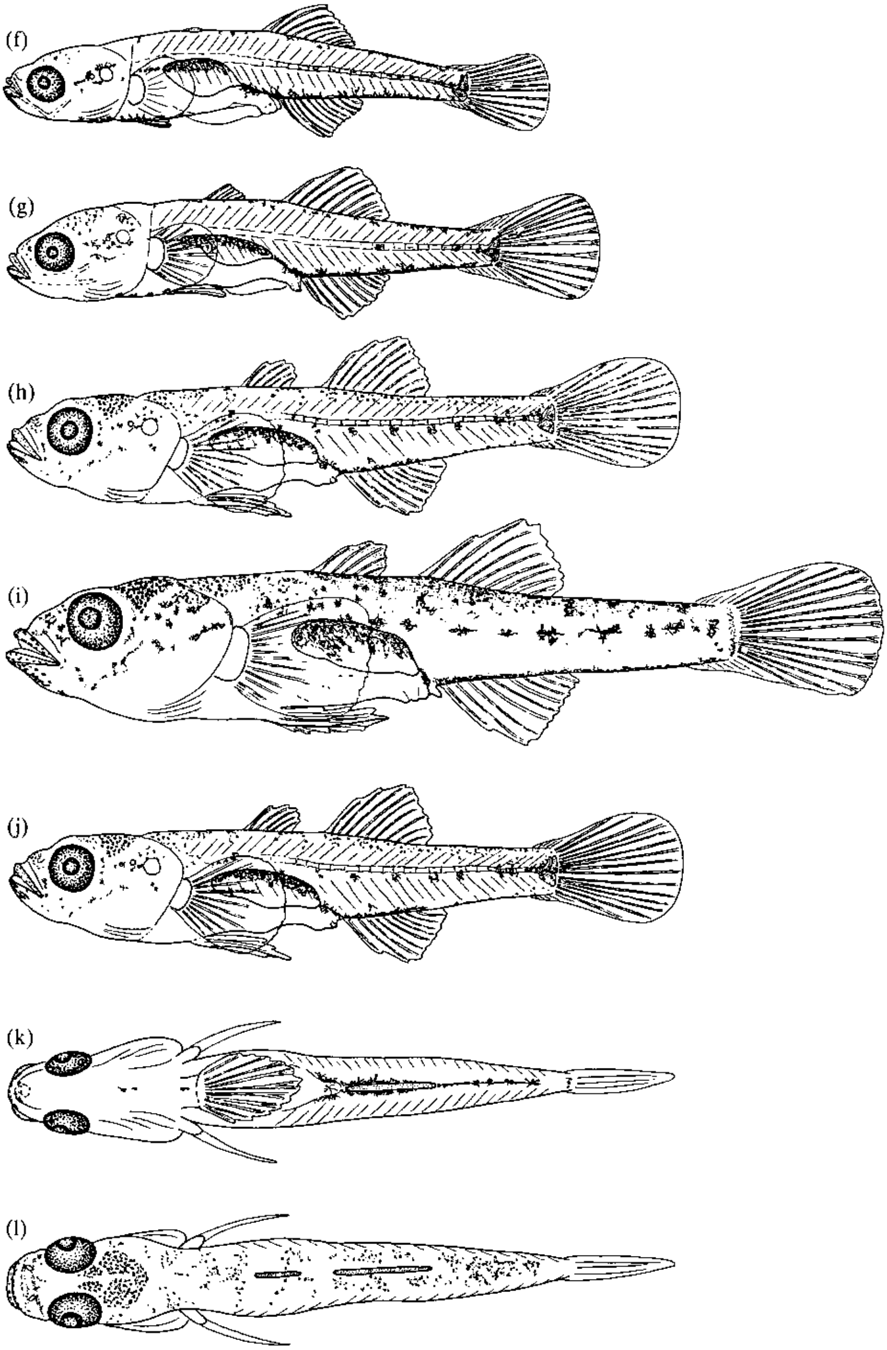

FIG. 7(f–l).

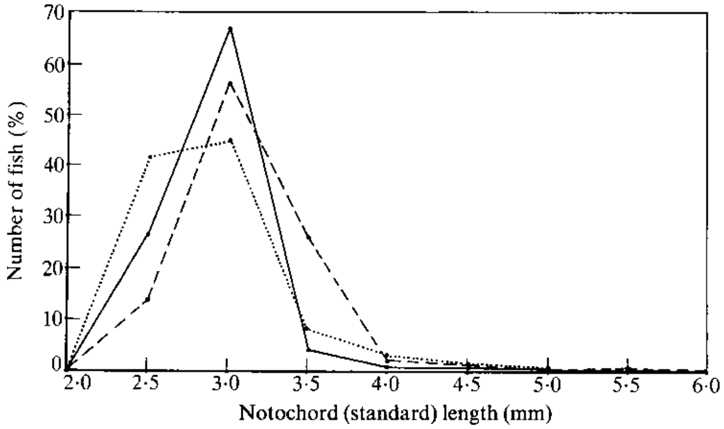

FIG. 8. Size distribution of *Economidichthys trichonis* larvae caught with plankton nets during daytime in different sampling periods. —, 22 March (381); – – –, 13 April (139); · · ·, 5 May (217).

TABLE III. Number of fish larvae caught with a fry net during day and night (20–21 November 1990) in a sandy area at a depth of 1 m

Species	Day	Night
E. trichonis	4	218
E. pygmaeus	1	0
K. caucasica	56	52
S. fluviatilis	8	13
A. boyeri	138	105
C. trichonica	1	0

to have a relatively longer period of planktonic existence than the larvae of *E. pygmaeus*.

The larvae of *K. caucasica* were found among aquatic vegetation and occurred in the same hauls as the *E. pygmaeus* larvae. However, later in life, the two species showed increasingly different habitat preferences. Larvae at around the time of metamorphosis and juveniles of *K. caucasica* preferred sandy, muddy or gravel substrata close to the shore, whereas *E. pygmaeus* were distributed in deeper areas and occupied mainly weed-covered substrata.

Table III presents the combined results of separate samplings performed in November 1990 during day-time and night-time using a fry-net in a sandy area near the shore. There is evidence that *E. trichonis* performed nocturnal migrations, moving close to the shore at night. Table IV shows the results of samplings conducted with the rectangular nets towed parallel to the shore at fixed depths during different periods of the year. Of the three gobiid species, *K. caucasica* showed the more shallow distribution, and *E. trichonis* was the most deeply distributed.

TABLE IV. Numbers of fish caught at different depths in Lake *Trichonis*

Species		21 November 1990			
	Depth (m)	1–2	4–5	8–10	15
E. trichonis		4	56	28	22
E. pygmaeus		7	9	6	0
K. caucasica		2	0	0	0
S. fluviatilis		33	37	13	1
		13 February 1991			
	Depth (m)	1–2	4–5	8–10	15
E. trichonis		20	35	40	14
E. pygmaeus		15	11	1	0
K. caucasica		6	0	0	0
S. fluviatilis		6	19	30	3
T. hellenicus		1	0	0	0
		20 March 1991			
	Depth (m)	1–2	4–5	8–10	15
E. trichonis		9	27	11	2
E. pygmaeus		10	1	0	0
K. caucasica		3	0	0	0
S. fluviatilis		11	32	0	0
C. trichonica		0	1	0	0
		25 April 1991			
	Depth (m)	1–2	4–5	8–10	15
E. trichonis		4	5	13	4
E. pygmaeus		15	46	1	0
K. caucasica		6	0	0	0
S. fluviatilis		25	11	15	0
S. acarnanicus		0	1	0	0

BIOLOGICAL OBSERVATIONS

All three gobiid species share a number of common life-history characteristics: they are small-bodied; short-lived; mature early and reproduce serially during only one breeding season in their lifetime (abbreviate iteroparous *sensu* Miller, 1984). Their length–frequency distribution was estimated by grouping the catches of the bottom nets and the beach-seine over monthly intervals (Figs 9, 10 and 11). Considerable increase in size occurred during the first few months of life, but the growth rate decreased after the onset of maturity in autumn. At age 6 months, sexual dimorphism is well expressed in both *Economidichthys* species. Spawning occurs in spring, and as the new generation enters the population, the old generation disappears. Most *E. pygmaeus* die shortly after spawning, but some

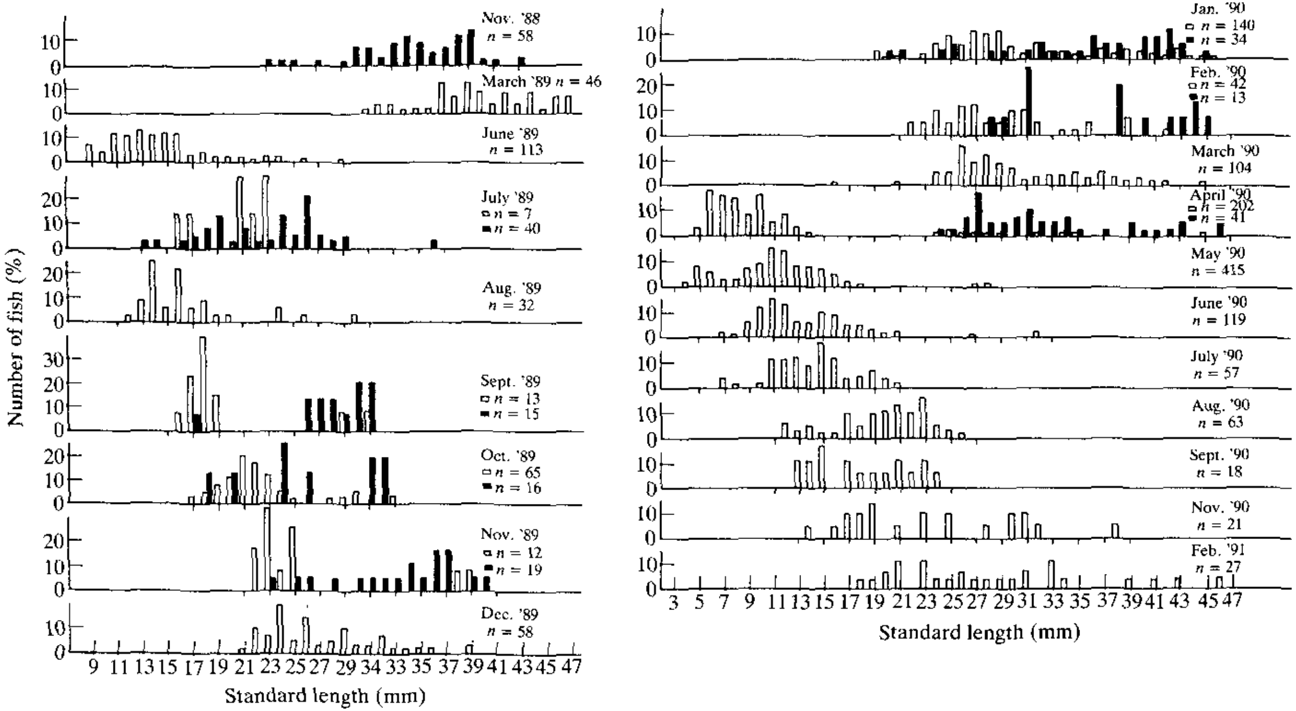

FIG. 9. Seasonal variation of the size distribution of *Economidichthys pygmaeus* larvae caught with the rectangular nets (white columns) and a commercial beach-seine (black columns).

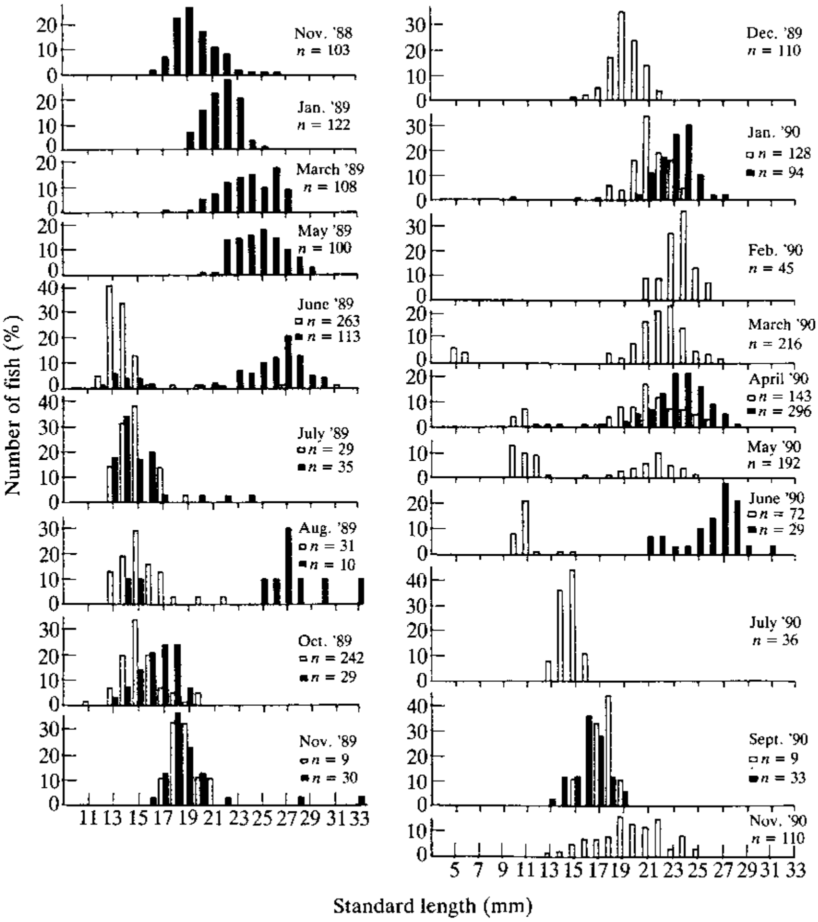

FIG. 10. Seasonal variation of the size distribution of *Economidichthys trichonis* larvae caught with the rectangular nets (white columns) and a commercial beach-seine (black columns).

E. trichonis live longer. The oldest individual found in our samples was an *E. trichonis* of 33 mm, caught in November 1989, aged approximately 18–21 months (Fig. 10). There was also a prominent difference in size between sexes, males being the largest in both species (Fig. 12).

Lake Trichonis seems to support large populations of *E. pygmaeus* and *E. trichonis*, but the population of *K. caucasica* is relatively small. Comparing years, *E. trichonis* was very abundant during 1988 and the early part of 1989, but declined considerably thereafter. In contrast, *K. caucasica* was extremely rare in 1988 and early 1989 but increased in abundance in 1990. Such fluctuations of abundance are to be expected in short-lived species, in which the spawning population consists of only one year-class and population size is determined primarily by the strength of individual year-classes.

Preliminary observations on the stomach contents of the three gobiid species indicate that they feed primarily on crustaceans and benthic invertebrates (Table V). The food of *E. pygmaeus* consists mainly of copepods and amphipods and that of *E. trichonis* contains a higher and seasonally variable proportion of

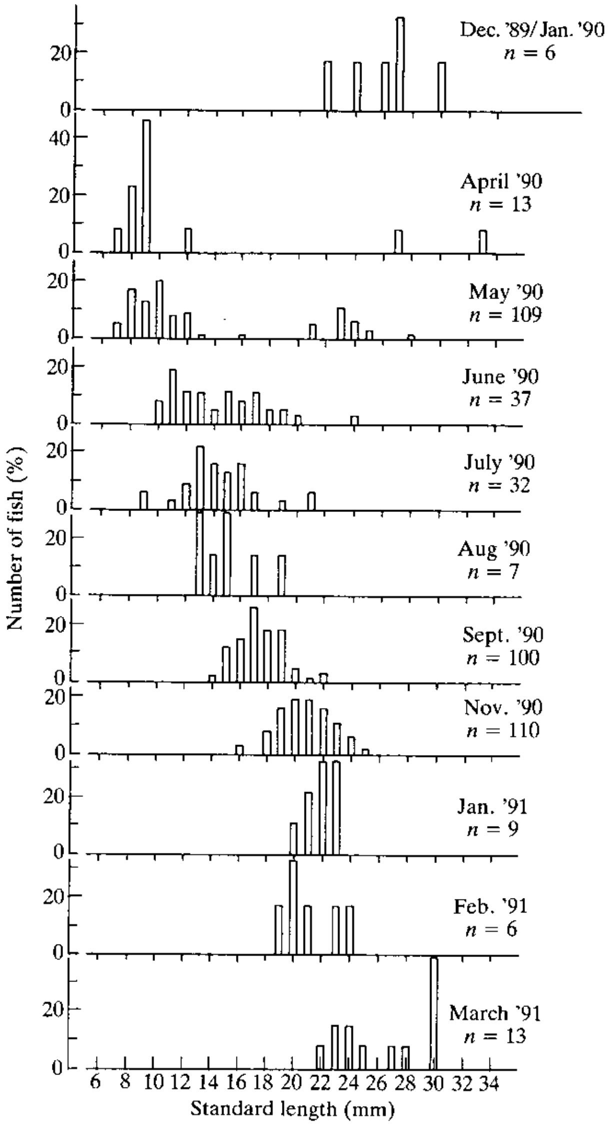

FIG. 11. Seasonal variation of the size distribution of *Knipowitschia caucasica* larvae caught with the rectangular nets.

cladocerans and *Dreisseina polymorpha* (Pallas) larvae at the settlement stage. The diet of *K. caucasica* consists mainly of copepods and *D. polymorpha* larvae. A more planktivorous feeding behaviour of *E. trichonis* than of *E. pygmaeus* is indicated from these data.

IV. DISCUSSION

Both *E. pygmaeus* and *E. trichonis* are polygynous with male parental care and can be characterized as guarding hole nesters, according to Balon's (1975, 1981,

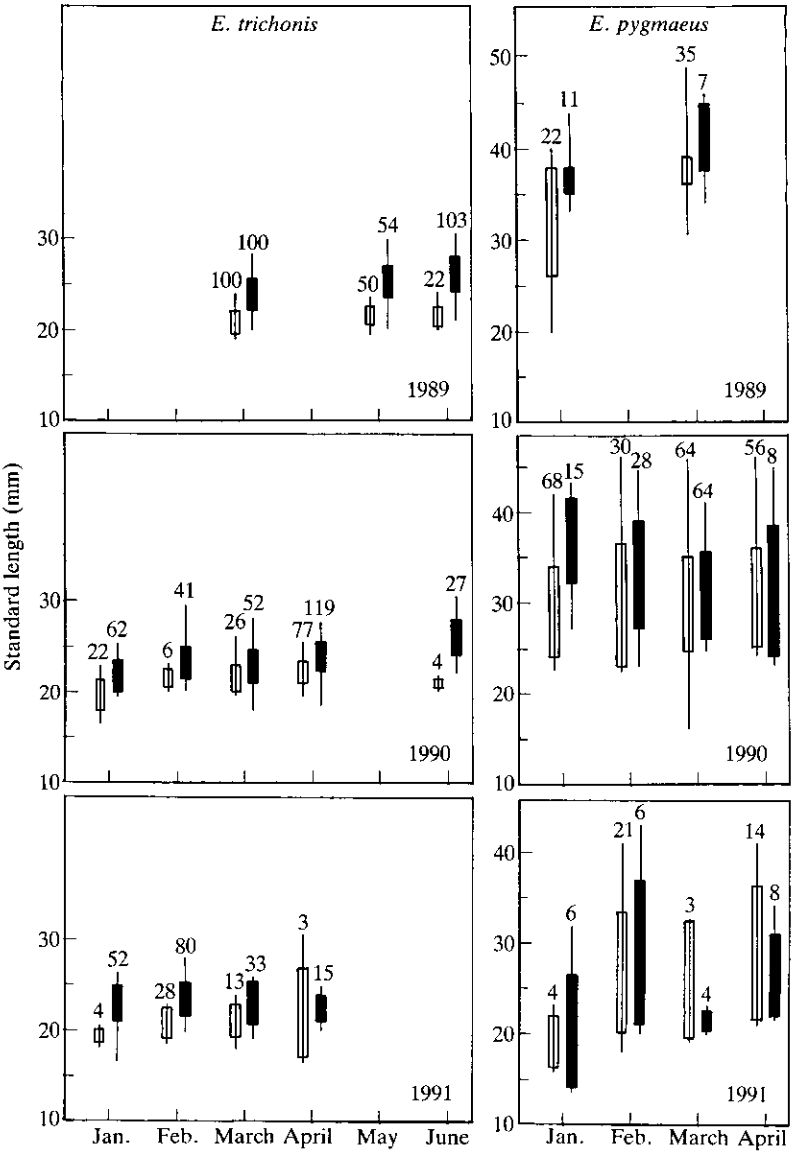

FIG. 12. Size distribution of male and female *Economidichthys trichonis* and *E. pygmaeus* before and during the period of reproduction. Bars represent the standard deviation and lines show the range of lengths. Numbers denote sample size. White bars: females, black bars: males.

1984; see also Flegler-Balon, 1989) classification of reproductive guilds. Their peculiar reproductive behaviour, i.e. deposition of the eggs in the cavities of reeds, deserves special attention. Although gobioid fishes have repeatedly been reported to lay their eggs in holes (empty shells of molluscs, crevices between stones or rocks, beneath stones, burrows excavated in the sand, nests built by the male out of leaves, etc.) (see Petersen, 1919; Breder & Rosen, 1966; Kalinina, 1976; Russell, 1976), we found in the literature only one record of a spawning site selection similar to that of the two *Economidichthys* species; Dotu & Fujita (1959; cited by Breder & Rosen,

TABLE V. Qualitative seasonal composition of the diet of the gobioid fishes of Lake Trichonis

Main prey types	*E. pygmaeus*				*E. trichonis*				*K. caucasica*	
	23.3.89	11.7.89	18.10.89	17.1.90	23.3.89	11.7.89	18.10.89	17.1.90	19.9.90	21.11.90
Cladocerans (*Bosmina*, *Daphnia*, *Moina*)			+	+	+++	+	+	++		+
Copepods (*Diaptomus*, *Cyclops*)	++	+	+++	+++	++	+++	+	+++	+++	++
Amphipods (*Gammarus*)	++	+	+	+						+
Isopods (*Aselius*)	+									+
Larval insects (*Chironomus*)		+				+	+		+	
Larval molluscs (*Dreisseina**)							+++	+	++	+++
Larval fishes		+								

*Larvae at the settlement stage.
+, Relative abundance.

1966) described a nest of an eleotrid fish (*Eleotris oxycephala* Temminck & Schlegel) as occupying the inner surface of an old piece of bamboo.

The life pattern of the two *Economidichthys* species, and probably of *K. caucasica* as well, is characterized by early onset of maturity, small final body size, short life-span and high reproductive effort concentrated early in life. Under the assumption that stable and competitive conditions favour growth and ability to compete, while unstable conditions favour reproductive activities at the expense of growth, general theory on life-history variation predicts that the life pattern of the gobies of Lake Trichonis should dominate under unstable, density-independent or colonizing conditions (Adams, 1980; Balon, 1983; Bruton, 1989; MacArthur & Wilson, 1967; Pianka, 1970) or under a large component of density-independent and non-selective, or unpredictable and variable adult mortality (Murphy, 1968; Stearns, 1976; Mann & Mills, 1979; Mann *et al.*, 1984). Given the relative stability of the environment in Lake Trichonis, the schedules of age-specific growth, survival and investment on reproduction of these gobies do not entirely fit the predictions of the theory for stable environments. Therefore, in agreement with other investigators (Armstrong & Shelton, 1990; Whitfield, 1990), we suggest that environmental stability, predictability and density dependence are insufficient to describe the selective forces shaping life-history variation.

It is not being argued that stability and density dependence, and other factors of the external environment, do not play a key role in the evolution of life-history patterns. Instead, we argue that a large portion of the existing life-history variation may be independent of the external components of the species environment, and is generated by internal components alone, and more specifically the feeding habits and risk-avoidance patterns that label the characteristic ecological role of each species in the community. The influence of the internal components of the species environment on the evolution of life histories is a poorly explored area. Gunderson (1980) argued that body size represents an adaptation to the level of resources posed by the feeding niche occupied by an organism. Miller (1979, 1984) suggested that adaptiveness of body size helps the organisms to assess the carrying capacity of their environment, and that a small size is energetically advantageous for organisms feeding on small prey. As body size is the main covariate of other life-history traits in fishes and other animal groups (Paine, 1990; and references therein), it is likely that sets of life-history traits which covary with body size arise by adaptiveness of body size. Therefore, the small size of the two *Economidichthys* species may be an adaptation to their trophic niche, while other characters that may co-evolve with small size (early maturity, high reproductive effort, short reproductive life span) may represent solutions of coping with the high rate of adult mortality posed by the living habitat and body size limitations. According to this view, the smaller adult size of *E. trichonis* may be a character derived from its planktivorous food habits and its distribution in the more exposed nectonic habitat in comparison with the more epibenthic *E. pygmaeus* (Economidis & Miller, 1990).

Part of the theory of life-history variation deals specifically with the relationship of the environment and reproductive characteristics. It is generally assumed that in unstable environments, where there is a large component of density independent mortality and an abundant food resource for the larvae, selection is likely to favour high fecundity, a small egg size and altricial larvae at hatching (*sensu* Balon, 1983). But in stable, and presumably more competitive environments, selection should favour a high investment on individual offspring, and hence a low fecundity, a large egg size and more precocious larvae, often associated with some degree of parental care (Bruton & Merron, 1990). Despite their sympatric occurrence, the two *Economidichthys* species lay eggs differing in size and shape, from which larvae differing in morphology and developmental characteristics are produced. *Economidichthys trichonis* produces unusually small, slightly ovoid, eggs, resembling in appearance the pear-shaped or bulb-shaped eggs of gobiid species belonging to the genera *Aphya* and *Pomatoschistus*. After a short incubation period (partly attributable to their small size, and partly to the high temperature), the eggs hatch out to extremely small and incompletely developed larvae, as indicated by their closed mouths and undifferentiated organs. These larval characters, along with transparency and the absence of pigmentation on the body, may reflect adaptations to the pelagic mode of life. The eggs of *E. pygmaeus* are more elongate, larger, and take longer to develop. The larvae hatch at an ontogenetically more advanced stage of development in comparison with *E. trichonis* larvae, and are more adapted to the demersal mode of life. Their cryptic pigmentation, already present at hatching, may serve as protection against predators and may reflect the fact that they do not pass through a long planktonic stage.

If egg size has evolved in response to the conditions of survival of larvae in the current environment, the interspecific variation in egg size between these two species should be minimal. But if egg size has evolved primarily in past environments, one would expect that the most fluvial (unstable) environment in the historical habitats of the distribution of *E. pygmaeus* (see Introduction), should have favoured an egg size smaller than that of *E. trichonis*, which might have evolved in relation to the more lacustrine (stable) environment of the lake. Such an association between stability and density dependence is not confirmed by our data. Similar discrepancies between natural observations and predictions of the general theory have been reported by Whitfield (1990) and Goto (1990) and raise doubts about the validity of the widely held assumption that precocity is the only evolutionary pathway against local competition (Economou, 1991).

Regarding the evolution of the unique dermal perianal organ possessed by these hole-nesting fish, we believe that it must be related to reproduction. Potts (1984) noted that the more sheltered the spawning site, the greater the vulnerability of eggs to bacterial, protozoan and fungal infections. The infection danger is greater in the two *Economidichthys* species than in other nesting species, first because the eggs are deposited in narrow and not well-aerated holes, and second because the nesting substratum is of organic origin where infections are more likely to develop. Therefore, it is a possibility that the perianal organ has a secretory function and produces substances against infections. According to this explanation, the perianal organ may be a character derived from the particular mode of reproduction of the two *Economidichthys* species, and may also be present rudimentarily in other hole-nesting species as well. If so, its presence does not necessarily indicate a close taxonomic affinity between the two species, as is also implied by the important differences in their egg and larval morphology. Such morphological characters could be used in future work for clarifying their phylogenetic relationships, also elucidating affinities with marine gobioid taxa of common ancestry.

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