Reproductive Guilds of Fishes: A Proposal and Definition

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Abstract

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The emergence of efficient ecosystem modelling is severely hampered by the need for an ecological classification of fishes. An earlier concept of ecological groups is here expanded to cover all living fishes. This ecological classification is based mainly on form and function in early developmental intervals, on preferred spawning grounds, and on features of reproductive behavior. Within the adaptations for reproduction and embryonic development two factors prevail — predators and the oxygen regime; consequently, spawning behavior and spawning grounds determine ensuing respiratory conditions and available protection from predators. The remaining factors are more or less associated with those two. From the point of view of resource exploitation, factors other than feeding habits governing density, biomass, and production are more important. In this sense reproductive guilds are more meaningful than feeding strategies, to which one usage of "guild" was limited.

Thirty-two guilds putatively encompass all the 30,000 living fish taxa (or about 20,000 species) and form an ecological classification unrelated to the Linnean classification. The guilds retain phyletic significance in respect to reproductive systems and form a basis for the construction of models on natural and cultural succession. Number of guilds and frequency of taxa within guilds in a given area reflect geochronological sequences and invasion abilities of members of different guilds.

Résumé

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Le manque d'une classification écologique des poissons nuit grandement à l'élaboration de modèles d'écosystèmes efficaces. L'auteur se sert d'un concept existant déjà et le développe pour englober tous les poissons vivants. Cette classification est fondée surtout sur la forme et la fonction aux premiers stades du développement, sur les frayères préférées et sur le comportement reproducteur. Parmi les adaptations visant la reproduction et le développement embryonnaire, deux facteurs prédominent — les prédateurs et le régime d'oxygène; en conséquence, le comportement reproducteur et les frayères déterminent les conditions subséquentes pour la respiration et les abris disponibles contre les prédateurs. Les autres facteurs sont plus ou moins liés à ces deux-là. Du point de vue de l'exploitation des ressources, des facteurs autres que les habitudes alimentaires contrôlant la densité, la biomasse et la production ont une plus grande importance. Dans ce sens, les gildes reproductrices ont une signification plus grande que les stratégies alimentaires, auxquelles on avait limité un usage du terme « gilde ».

Trente-deux gildes englobent putativement tous les 30,000 taxons de poissons vivants (ou environ 20,000 espèces) et forment une classification écologique indépendante de la classification linnéenne. La gilde conserve une signification phylétique en rapport avec les systèmes reproducteurs et sert de base à l'élaboration de modèles de successions naturelles et culturelles. Le nombre de gildes et la fréquence des taxons au sein des gildes dans une aire donnée reflètent les séquences géochronologiques et le pouvoir d'invasion de gildes différentes.

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> *". . . the Coelacanth doubtless sheds its eggs inside a special case, quite possibly like those produced by some sharks and rays. Who will be the first to find one?"*
>
> J. L. B. SMITH (1957)

> *"Son abdomen, dilaté, recelait une vingtaine d'oeufs sphéroïdes d'un beau rouge sombre, dépourvus d'enveloppes protectrices. Leur taille égalait celle d'une orange . . ."*
>
> J. MILLOT AND J. ANTHONY (1974)

It is generally agreed that the distribution, survival, density, and vulnerability of fish populations is limited by a complex of ecosystem factors, and a classification of fishes on an ecological basis would be most desirable. To construct an ecological organization of fishes based on the morphophyletic classification would be impossible, as the ramifications of evolution have resulted in an enormous number of morphologically distinct taxa. This is further complicated by convergence and parallelism, with the result that ecological and ethological characters are hopelessly intermingled and irretrievable at the familial and ordinal levels. An ecological classification based on reproductive strategies appears promising, however.

The difficulty in constructing an ecological classification based on reproductive strategies was well expressed by Breder and Rosen (1966): of just under 20,000 known species of fishes (Cohen 1970; Weitzman 1974) arranged in some 600 families and 30 orders (or 495 families and 62 orders according to Lindberg 1971, or 390 families, 3,713 genera, and 18,220 species according to Bailey 1971) "breeding habits" are well described for only 300 species, plus another hundred or so that are imperfectly known. Thus, any system based on reproductive strategies is, for the time being, incomplete and highly tentative. This paper should therefore be regarded as a preliminary proposal of such a system and a review of the present knowledge.

An ecological taxonomy of fishes should be simple enough to build from bits and pieces of available information about reproductive strategies. The categories should be low in number to permit ecosystem analyses, but broad enough to encompass all known species. The classification should group similar ecosystem users irrespective of phyletic origin, with the adaptations to similar ecosystems possibly reflected in convergent behavioral, morphological, and physiological characters.

My concept will be built on the basis of Kryzhanovsky's (1949) reasoning that "adaptations of fishes for spawning and development reflect not only the essential ecological factors of the embryonic period, but also the essential factors of all the other intervals of life. These adaptations mark the biology of adults, and define the type of migrations, invasion abilities, and limits of distribution" (p. 237, my translation). Some salmonids offer a good illustration. Their eggs require a high oxygen supply and, therefore, they must be hidden in the gravel of swiftly flowing streams, in clean lakes within springs, or in a substrate bathed by water currents. In the tidal zone the eggs would be destroyed by wave action and exposure; further from shore the sea bottom would provide few hiding places from the heavy predation; and at greater depths the eggs would perish from lack of oxygen. Consequently all salmonids, even those feeding in the sea or in open lakes, have to return to their special spawning grounds where the fate of the population will be decided (Kryzhanovsky 1956; Balon 1968). It is obvious that reproductive strategies *sensu lato* will be the most important characters on which the ecological classification should be built. However, if left closely related to the present morphological classification, similar ecological adaptations would be scattered throughout the present categories of more than 30 (Greenwood et al. 1966, 1967; Gosline 1971; Rosen 1973) or at best 7 "major analytic categories" (Breder and Rosen 1966) and an immense number of lower taxa. In the construction of an ecological classification a complete divorce from a Linnean classification seems to be inevitable.

Historical Review

Attempts to group fishes into other than morphological categories are only just over a quarter century old. The basic concept was, to my knowledge, formulated first by S. G. Kryzhanovsky in 1948. Although it was later repeated in detail at least twice, it somehow escaped the attention of scholars who have been active in this field. My plans 10 years later to work out a broader system with the founder never materialized.

Kryzhanovsky's (1948, 1949) hypothesis which is here used as a definition of his ecological groups has already been given in the previous section. "Two factors [writes Kryzhanovsky (1949) further] play leading roles during embryonic development: predators and availability of oxygen. All other factors are associated with these two and create together an extraordinary variety of adaptations associated with early development. However, the various reproductive strategies and spawning grounds predetermine the respiratory conditions and the potential for defense against predators. Hence, to a considerable degree, they predetermine the nature of adaptations associated with early development. Therefore, the astounding multitude of adaptations associated with development reveal the ecological patterns which reflect the essential relations of fish in nature."

To provide a better explanation of his principles for early fish development, Kryzhanovsky formulated ecological groups, all named after respective spawning grounds; for example: 1) lithophilous, 2) phytophilous, 3) psammophilous, 4) pelagophilous, and 5) ostracophilous.

All fishes belonging to the lithophilous groups deposit their eggs on a rock or gravel bottom, and on this substrate the embryos and larvae develop. This occurs in streams and rivers as well as oligotrophic lakes. Some hatch early and have a photophobic escape reaction, enabling them to scatter and hide under the stones. In this group embryonic respiratory organs are moderately developed. In all species there are segmental vessels in the ventral and/or dorsal fin fold; in some, there is also a subintestinal vein.

Fishes of the phytophilous group are adapted to develop within or on live or dead vegetation, above a muddy or silted bottom, and under conditions of very low oxygen. Larvae of this group are not photophobic and are more pigmented than the lithophils. Their embryonic respiratory organs are well, to exceptionally well, developed. They consist of the *ducti Cuvieri*, the caudal vein in the ventral fin fold, the segmental vessels in the dorsal fin fold, and in some larvae, the pectoral and gill cover vessels. Since the embryos and larvae do not hide, fecundity of the members of this group is usually very high to compensate for the high mortality caused by predators or water level fluctuations.

Some fishes, which Kryzhanovsky termed as intermediate, form a sort of transition between these two groups (e.g. *Alburnus alburnus*, *Rutilus rutilus*, *Leuciscus*, *Perca*, *Gymnocephalus*, *Stizostedion lucioperca*, *S. volgense*) and he admitted that no clear-cut division would be possible even in the best constructed system (Holčík and Hruška 1966).

Psammophilous fishes spawn on roots or grass above the sandy bottom or on the sand itself, where their embryos are adapted to develop. They are not photophobic and in contrast to phytophilous fishes, lack cement glands and cannot hang on plants. In response to moderately high oxygen availability the embryonic respiratory organs are usually limited to the *ducti Cuvieri* and the caudal vein; the gills become functional relatively late.

Fishes in the pelagophilous group scatter their eggs in the water column and the eggs are usually free floating; neutral or positive buoyancy is achieved by a very large perivitelline space and/or by numerous small oil globules or one large oil globule in the yolk. Embryos and larvae are normally not pigmented. The lack of pigment serves as a cryptic protection against predation. Embryonic respiratory organs are absent in this well-oxygenated habitat. Many of the freshwater pelagophils are of marine origin and some, such as *Lota lota*, display characteristics of a condition called semipelagophilous. One of these characteristics is a secondary loss of buoyancy in fresh water which has a lower density.

The last ecological group was called ostracophilous by Kryzhanovsky. It encompasses specialized fishes (Acheilognathinae) that deposit their eggs in the gill cavity of mussels. Not only does the adult female possess a special ovipositor for placing the eggs into the proper position in the live mollusc, her eggs are also elongated ovals that have only a barely visible perivitelline space. Consequently, more eggs can be deposited within the limited space between the gill filaments of the mussel (Balon 1962a). Embryos are especially adapted to the possibly low oxygen content of this confined environment. They have dense respiratory nets formed by the subintestinal vein on the yolk and by vessels in the dorsal and ventral fin folds. Their development is very slow and they retain the embryonic respiratory organs until they are ready to leave the mussel as advanced larvae. Prior to this, and soon after the first appearance of the eye pigment, they become extremely photophobic. This is a protective mechanism that prevents premature expulsion from the protection of the shell.

The system of ecological groups, proposed and used by Kryzhanovsky (1949; Kryzhanovsky et al. 1951), can be summarized as follows:

Fishes that scatter their eggs
— lithophilous
— intermediate
— phytophilous
— pelagophilous
— semipelagophilous
— psammophilous

Fishes that hide their eggs
— ostracophilous
— lithophilous

Fishes that guard their eggs
— lithophilous
  — adhere to the substrate in a single layer
  — in clumps
— phytophilous
— psammophilous
— nest building
  — in hollows
  — on the surface of the bottom
— brooders
— livebearers, and

fishes of unknown character (my arrangement and translation).

When this classification was applied to the members of freshwater fish families of a limited geographical area, little if any correspondence with morphological (Linnean) classification was demonstrated. Although Kryzhanovsky tried to prove that his groups were homogenous within families and with a few exceptions lacked parallelism, he also tried to prove that heterogeny with parallelism is limited to carps. However, if form and ecological function are closely related, then there should be more parallels between the ecological and Linnean taxonomy based on adult morphology. Lack of these parallels might imply that from an ecological viewpoint the Linnean taxonomy is highly artificial.

Then followed several attempts to improve the original ecological classification of fishes (Holčik and Hruška 1966; Balon 1966). Its use was extended to other geographical areas (Balon 1962b, 1964b, 1965) or applied to qualitative or quantitative values of fish populations. Basically, the latter was an extension of Swingle's (1950) concept of "balance" into a ratio of phytophils to lithophils (F/L, Balon 1962b, 1964a, 1964b), lithophils to indifferents (L/I, Holčik 1966), or biomass of lithophils to ichthyomass (L_s) and phytophil biomass to ichthyomass (P_s, Balon 1966).

To my knowledge only two independent systems were developed after Kryzhanovsky's. Breder and Rosen (1966), in an attempt to classify the data on reproduction in their giant compendium on reproduction of fishes, devised special analytic categories called "Division," seven of which encompassed all the available data. These categories "mean an assemblage of fishes that may conveniently be treated together from the standpoint of reproduction." However, their divisions retain a close relationship to the Linnean taxonomic arrangement and encompass various aspects of reproductive behavior and ecology. For example, their Division I is fairly monotypic and "the most characteristic reproductive feature of the members of this division is polyandrous mating in breeding aggregations, ... , nonadhesive pelagic eggs and virtual absence of parental care." This division consists of five primitive teleost orders. Division II, conversely, encompasses only one order, but fishes arranged in it mate in pairs or small polyandrous groups, eggs are mostly demersal and adhesive, and "may be buried, cast loose, or, in one case, actually laid out of water. Internal fertilization accompanied by an oviparous habit is reported. Parental care extends from none to cases of elaborate nest building or the carrying of the eggs in the mouth or adherent to the ventral surface of the body." Division III, which encompasses two orders, is in its reproductive characteristics very similar to Division I. Division IV includes the single order Gasterosteiformes which comprises fishes that "possess a variety of spectacular reproductive habits." Some of these habits include parental care in nests or brood pouches or hiding of eggs in the peribranchial cavity of ascidians. Breder and Rosen's system displays in some orderly fashion "trends in reproductive activities that are associated with morphology or phylogenetic relationship," but does not provide a basis for an adequate ecological grouping of fishes. However, my reorganization of Kryzhanovsky's concept was considerably facilitated by the information compiled by Breder and Rosen (1966).

A recent attempt by Nakamura (1969) to group fish ecologically is again based on early development. His categories A to F are based mainly on the spawning grounds and breeding behavior of Japanese cyprinid fishes. From the description given, his categories are similar to Kryzhanovsky's ecological groups and he quotes at least one of Kryzhanovsky's studies. Category A more or less equals phytophils, B has no equivalent in Kryzhanovsky's groups but is equal to my guarding speleophils (see later), C = lithophils, D = ostracophils, E = pelagophils, and in F, Nakamura arranges fishes of unknown spawning habits.

The behavioral groups of cichlids described by Wickler (1962, 1966) or by Fryer and Iles (1972) will also have some application in the following ecological classification. However, the reasons for not using Wickler's classification of "concealment" and "open" breeders are self-evident (see also Barlow 1974). The same applies to familial groups of Mochek (1972). A close relationship is to be remembered between guarding speleophils and bearing mouthbrooders, as illustrated by *Pelmatochromis taeniatus*, which starts off by guarding the eggs in a hole "but completes it by mouth brooding" or by *Geophagus jurupari* which has similar habits.

In the second edition of Webster's New International Dictionary of the English Language (1960) the ecological meaning of guild is defined as "an ecological group of plants distinguished from the ordinary herbs, shrubs, and trees by a special mode of life. ... The species of each of these, though unrelated, have specialized and sometimes similar physiological requirements."

The term guild was applied by Root (1967) in an attempt to arrange bird niches into "groups of species having very similar ecological roles within a community." Root wrote that "A guild is defined as a group of species that exploit the same class of environmental resources in a similar way." This can be interpreted that the primary characteristic for classification is the diet. But he implied, for *Parus inornatus*, that "while belonging to the foliage-gleaning guild with respect to its foraging habits, [it] is also a member of the hole-nesting guild by virtue of its nest-site requirements." The diet concept alone may be incomplete even in bird ecology, since Root then states "that the population's initial breeding effort will be concentrated in most favorable habitats" (p. 342). In short, the guild concept as formulated by Root (1967) may be congruent with my extended concept of Kryzhanovsky's ecological groups. In higher vertebrates the determining characters can nevertheless differ from those of fishes by reflecting the evolutionary pattern of morphological adaptations replaced by behavioral adaptations, in the same way as "the critical dimensions of the niche may be not food resources but other limiting factors" (Whittaker et al. 1973). In this sense, guilds should group quantitatively "species' niches."

According to Kryzhanovsky's hypothesis, the adaptations for spawning and early development are reflected in the biology (form and function) of adults, including their feeding habits. Therefore, the reproductive strategies of fishes may better define the ecological guilds. A good example is the case of *Alestes lateralis* in Lake Kariba. This species invaded the lake from above Victoria Falls and in a very short time replaced the abundant and indigenous *Brachyalestes imberi*. *Alestes lateralis* became the most abundant species in the lake in less than two years and exactly at a time when the reproductive conditions changed unfavorably for *B. imberi* and in favor of *A. lateralis*. The same food resources are used by both species (Balon 1971a, 1974). It is obvious, at least in fishes, that the successful existence of a certain guild depends on spawning grounds, predators, and oxygen and that these are resources that are exploited in a way similar to the universally recognized food resource.

Barlow (1974) accepted feeding guilds in Root's sense, admitting at the same time that "in both the cichlids and surgeon fishes, nonetheless, the social systems are seen ultimately as consequences of their feeding behavior, but other factors have a profound and sometimes more proximate influence. In this paper, the physical environment and the effect of predation were seen as the most important proximate modulators of the reproductive behavior in the Cichlidae." In surgeon fishes "the evidence suggests a range of reproductive behavior from group spawning through harem formation and leks, and even enduring pairs. There are some suggestions of ecological correlations with breeding strategy, but the relationships are not clear." This can merely mean that the densities and ecological production of pelagophils, "the largest single category of fishes in Hawaii" (Gosline in litt.; Jones 1968) for example, is regulated within this guild by the timing of spawning and reproductive behavior. This can be "viewed as an adaptation to avoiding egg predators" (Barlow 1974), and consequently determine acceptable densities, while it is doubtful whether the diversity of feeding habits and habitats can limit densities effectively.

"Ecological" grouping of fishes by Lowe-McConnell (1964) and Postel (1973) was limited to distribution and habitats and has no application in the present concept. The same applies to the "ecological" groups of Papadopol (1970) which were based on sexual maturity, fecundity, and egg laying frequency.

Ecological Classification

None of the previous systems fulfill the requirements called for in the Introduction, yet all provided useful information and insights. I have retained the nomenclature essentially as proposed by Kryzhanovsky and have extended it to encompass all living fishes. The Greek prefixes refer mainly to the character of usual type of spawning grounds, though other factors, such as breeding behavior, morphology of early respiratory organs, type of respiratory pigments, and behavior of embryos and larvae, are equally important in the definition of a given guild.

Thirty-two guilds putatively encompass all the living forms of fishes and form an ecological classification not related to the Linnean classification, although the current generic and specific names as well as the names of lower taxa had to be retained. The guilds are grouped into three major sections, each of which has two subsections. These are rather closely related to topics of reproductive behavior and define the ethological part of the guilds (Table 1). Hence, for example, there will be an A.1.3 guild of nonguarding, open substratum spawning lithophils and a B.2.1 guild of guarding, nest spawning lithophils.

The way the sections and their guilds have been arranged seems to indicate a direction for the evolution of reproductive details. Furthermore, diversity of guilds decreases gradually with the increased specialization. I shall return to this aspect in the discussion.

CHARACTERISTICS OF GUILDS

Only the most basic characteristics of each guild will be mentioned. For brevity, examples will be limited to freshwater fishes of Canada and

TABLE 1. Ecoethological guilds of fishes.

Section			
Subsection		Guild	
A. Nonguarders			
A.1	Open substratum spawners	A.1.1	Pelagophils
		A.1.2	Litho-pelagophils
		A.1.3	Lithophils
		A.1.4	Phyto-lithophils
		A.1.5	Phytophils
		A.1.6	Psammophils
A.2	Brood hiders	A.2.1	Lithophils
		A.2.2	Speleophils
		A.2.3	Ostracophils
		A.2.4	Aero-psammophils
		A.2.5	Xerophils
B. Guarders			
B.1	Substratum choosers	B.1.1	Lithophils
		B.1.2	Phytophils
		B.1.3	Aerophils
		B.1.4	Pelagophils
B.2	Nest spawners	B.2.1	Lithophils
		B.2.2	Phytophils
		B.2.3	Psammophils
		B.2.4	Aphrophils
		B.2.5	Speleophils
		B.2.6	Polyphils
		B.2.7	Ariadnophils
		B.2.8	Actinariophils
C. Bearers			
C.1	External	C.1.1	Transfer brooders
		C.1.2	Forehead brooders
		C.1.3	Mouth brooders
		C.1.4	Gill-chamber brooders
		C.1.5	Skin brooders
		C.1.6	Pouch brooders
C.2	Internal	C.2.1	Ovi-ovoviviparous
		C.2.2	Ovoviviparous
		C.2.3	Viviparous

Europe, or, in guilds with no representatives in those areas or only with rare forms, to other fishes whose reproductive characteristics, developmental characteristics, and breeding habits are known. The availability of current catalogues (Scott and Crossman 1973; Ladiges and Vogt 1965; Banarescu et al. 1971) facilitated the selection. The European fishes, however, are given in a corrected version of Banarescu et al., based mainly on my own studies. For Canadian fishes the data compiled by Scott and Crossman (1973) were used mainly for the allocation of species into guilds. The work of Breder and Rosen (1966), especially on rare and odd species, was a constant source of inspiration and an invaluable source of data. Their text is frequently paraphrased and all unidentified quotations should be attributed to Breder and Rosen (1966).

A. Nonguarders

OPEN SUBSTRATUM SPAWNERS (A.1)

Pelagophils (A.1.1) are usually related to the sea, though sometimes only by their origin. There are, however, some known forms that are of entirely freshwater provenance like the cyprinids from the large Chinese rivers north to the Amur. Nonadhesive eggs are released and scattered in open waters, in areas where the direction of the water current is favorable to their distribution and survival. The eggs are usually spherical or elliptical, 0.5–1.9 mm in diameter without the egg membrane and 2–6 mm with the membrane. Pelagophils produce eggs in large quantities, presumably to compensate for high mortality of the larvae (*Mola mola* was estimated to have 300 million eggs). Often the eggs develop while being carried along by the current. In rivers, pelagophils may migrate several hundred kilometers upstream to spawn.

Near-neutral or positive buoyancy is achieved in several ways. In freshwater members of this guild (i) the eggs absorb water into the perivitelline space which expands after fertilization 2–5 times its size, stretching the egg membrane and enlarging the egg size (Fig. 1a, 2a) accordingly, or, (ii) water is absorbed into the egg membrane which swells into a gelatinous substance leaving the perivitelline space relatively small. This gelatinous mass of many eggs forms a compact veil in which the eggs are embedded, and the whole structure then floats like a raft on the surface of the sea (*Ophidium barbatum*, *Carapus*, *Scorpaena*, *Histrio histrio*, *Antennarius marmoratus*). The veils of *Lophius americanus* are often 9 m long and 80 cm wide (Agassiz 1882). Some freshwater pelagophils have a higher content of water in the yolk than the substrate spawners, a buoyancy adaptation which prevails in marine pelagophils (Fig. 2b) where the water content in the yolk reaches ~ 95% as compared to ~ 65% in eggs deposited on the bottom. In marine members of this guild, however, the perivitelline space rarely swells (Ehrenbaum 1964) and usually there is a high content of water in the yolk, an ineffective adaptation in fresh water (Stokes' law).

In both marine and freshwater pelagophils, the oil globule, which is greatly oversized in some freshwater forms (Fig. 1b), forms an additional hydrostatic organ effective in later phases of development (Kryzhanovsky 1960). Probably a centrally located cluster of oil globules (Nose 1971, 1972) causes eggs of the eel to ascend at an optimum rate. All these buoyancy adaptations frequently assure, in a most delicate way, optimal conditions for the developing eggs (Alderdice and Forrester 1971). For example "the eggs of *Argentina silus* may sink in sea water with a specific gravity of 1.02738 but float in sea water with one of 1.02870. Since surface water ... had the first-mentioned density and the deeper water was more dense, it follows that these eggs are bathypelagic under such conditions."

Instead of or in addition to the oil globule, marine species have a special sinus in the anterior part of the enlarged dorsal fin fold into which water gradually moves as the yolk is absorbed (Fig. 2c, d). In *Loweina rara* both dorsal and ventral fin folds develop into extremely large inflated and translucent sinuses (Fig. 2f), larger than in other known lanternfish larvae (Moser and Ahlstrom 1970). This sinus acts as a form of hydrostatic organ but its main function is to take up surplus water from the absorbed yolk when that water cannot be excreted through membranes, blood vessels, or excretory organs. Later when these organs develop, water can be expelled from the fin-fold sinus (Kryzhanovsky et al. 1953).

Some larvae develop special temporary appendages to achieve a higher volume to surface ratio and near-neutral buoyancy (Fig. 1d, e, 2e). Egg membranes of some exocetids, for example, are equipped with long filaments (Fig. 1c) with which the eggs can attach to a variety of floating objects (*Fodiator acutus*, *Parexocoetus brachypterus*, *Cypselurus californicus*).

Pelagophils are adapted to develop in waters well saturated with oxygen. Usually no special embryonic respiratory organs are formed or such organs, if present, are poorly developed. The blood vessels do not come near the surface of the body. As a special protection against oxygen poisoning, erythrocytes do not appear for a long time and plasma alone is driven along the vessels by heart beats. In addition, a lack of blood pigment, melanophores, and chromatophores makes the embryos and larvae less visible and, therefore, affords protection against predation. Because of the low nutrient content in the watery yolk, eggs of pelagophils have less vegetative plasma than do members of the other guilds, which in turn results in the formation of a relatively small embryo and larva. This small size, in the early stages of development, facilitates absorption of oxygen by the entire body surface. Formation of gills is nearly always delayed; in some, erythrocytes and gills are missing during the whole larval period. In eels the larval period can be extremely prolonged.

Embryos and larvae of pelagophils swim constantly. Strong phototropism keeps them in the open and away from shaded areas. Cement glands do not develop and thus relaxation is impossible. If an individual sinks, at first contact with the bottom it immediately swims up again. As a rule, pigment appears late in development and to a lesser degree than in other guilds; melanophores form a single ventral row and yellow pigment develops early in the eyes, yolk, and ventral row (Breder 1962).

The following Canadian freshwater fishes belong to this guild: *Anguilla rostrata*, *Alosa sapidissima*, *Coregonus alpenae*, *C. nigripinnis*, *C. reighardi*, *C. zenithicus*, *Notropis atherinoides*, *Aplodinotus grunniens*.

In Europe, excluding Asia Minor and the area east of the Sea of Azov, the following freshwater fishes putatively belong to this guild: *Anguilla anguilla*, *Alosa alosa alosa*, *A. a. bulgarica*, *A. a. macedonica*, *A. caspia nordmani*, *A. maeotica*, *A.*

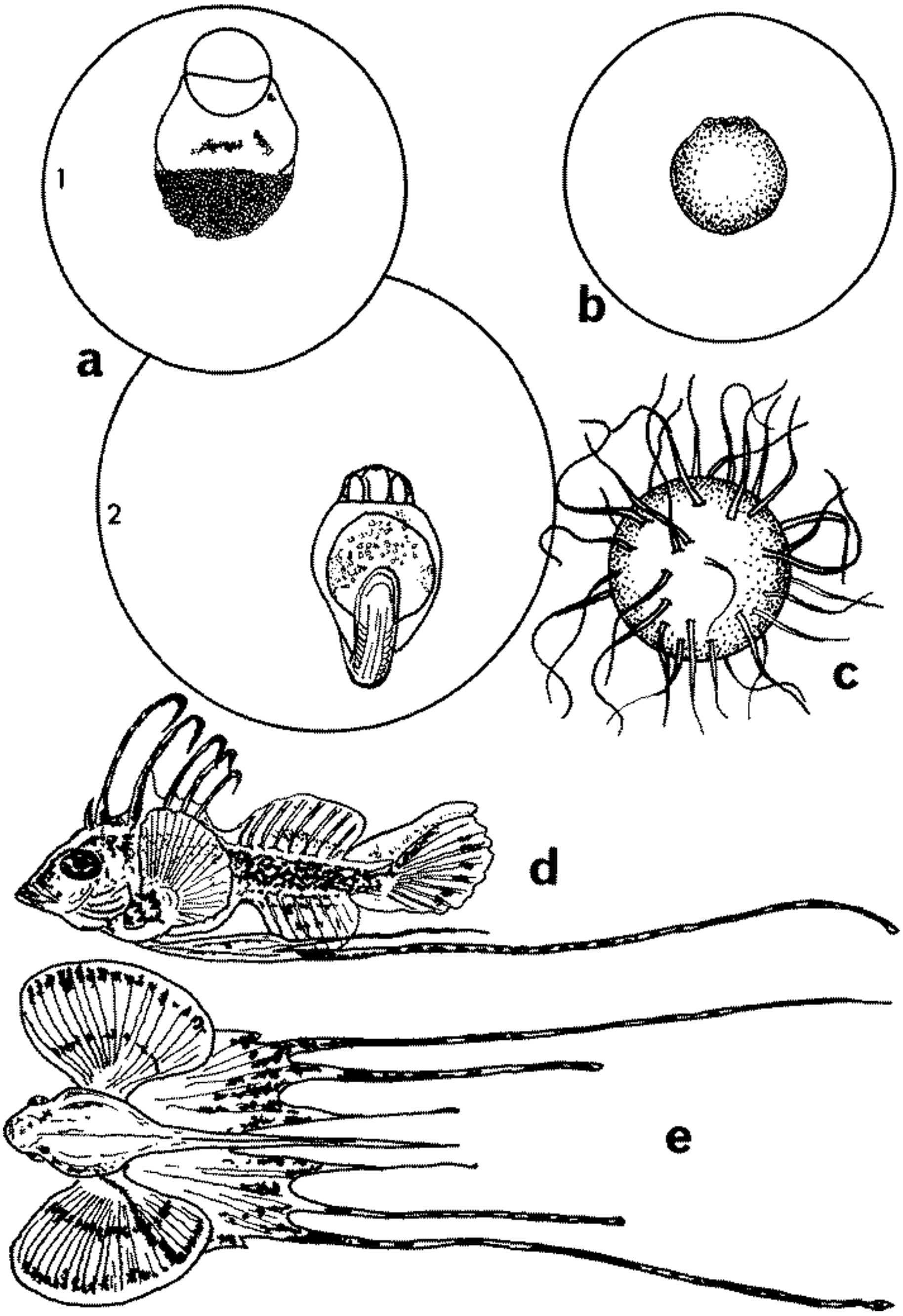

FIG. 1. a, Pelagic egg of the marine *Clupeonella delicatula* adapted for buoyancy in fresh water (diameter of yolk 0.59, of oil globule 0.32, and of egg membrane 1.3 mm); 1 = in cleavage phase, 2 = embryonic phase with increased size of perivitelline space; b, pelagic egg of the freshwater *Sarcocheilichthys sinensis* (diameter of yolk 1.9, of the egg membrane 5.3 mm); c, *Belone* sp. with tendrils for attachment to floating objects; d, e, *Lophius* sp. larva 30 mm long, lateral view (d) and dorsal view (e). After (a) Kryzhanovsky 1956, (b) Kryzhanovsky et al. 1951, (c) Bertin 1958, and (d, e) Agassiz from Ehrenbaum 1964.

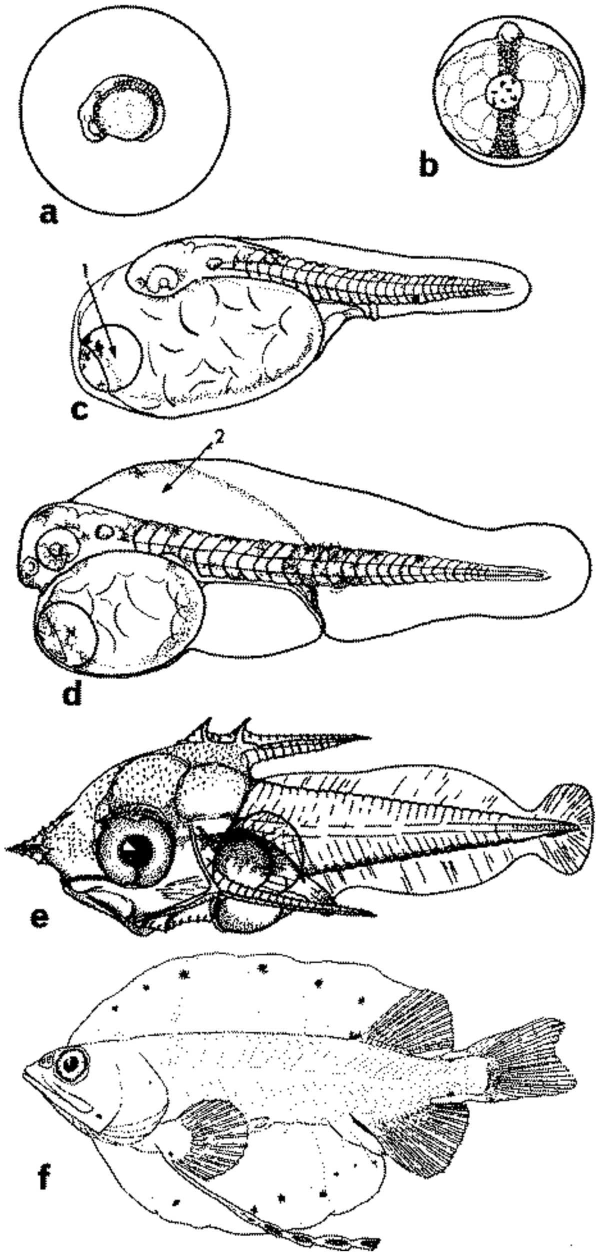

FIG. 2. a, Freshwater pelagic embryo of *Ctenopharyngodon idella*; b, marine pelagic egg of *Caranx* (watery yolk and an oil globule instead of perivitelline space); c, eleutheroembryo of *Caranx* just after hatching (1 = oil globule); d, same, at the beginning of the formation of the dorsal sinus (2); e, pelagic larva of *Adioryx vexillarius* with appendages for buoyancy; f, larva of *Loweina rara* (17.6 mm long) with dorsal and ventral fin fold sinuses. After (a) Nakamura 1969, (c, d) Kryzhanovsky et al. 1953, (e) McKenney 1959, and (f) from Moser and Ahlstrom 1970.

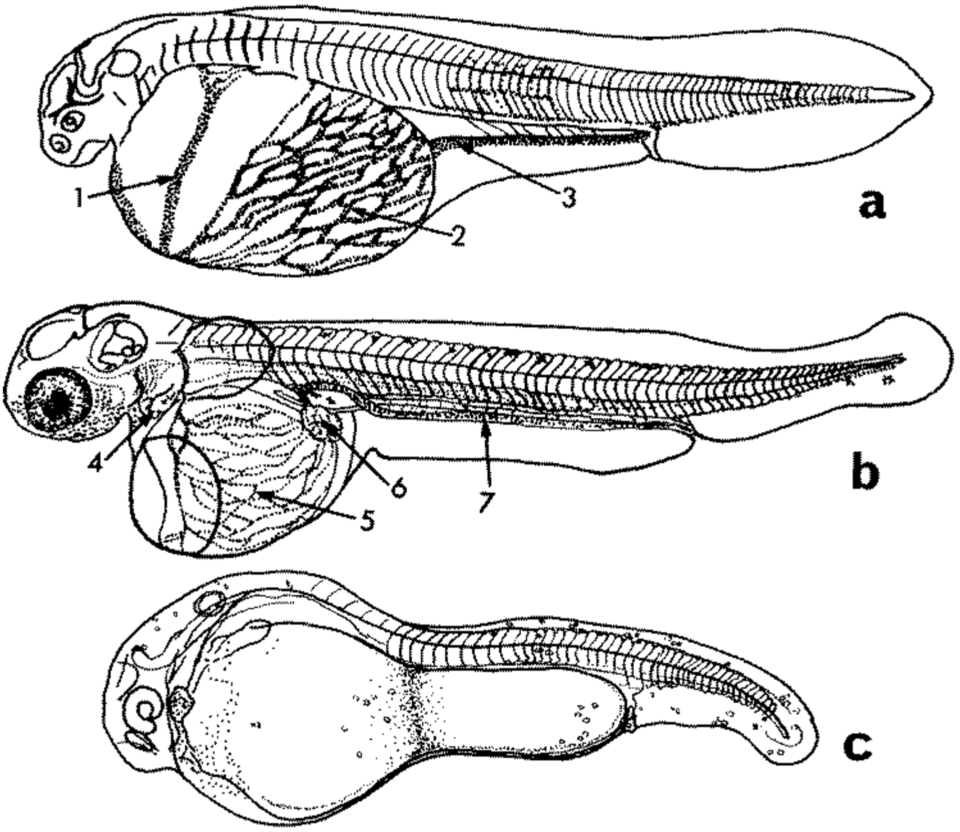

FIG. 3. a, Newly hatched eleutheroembryo of *Acipenser stellatus* 9 mm long (1 = Cuvier's duct, 2 = yolk respiratory vessels, 3 = subintestinal vein); b, eleutheroembryo of *Stenodus leucichthys* 9.4 mm long (4 = heart, 5 = respiratory branches of hepato-subintestinal veins, 6 = liver, 7 = subintestinal vein); c, eleutheroembryo of *Abramis ballerus* 3.8 mm long. After (a) Detlaf and Ginzburg 1954, (b) Smolyanov 1957, and (c) Balon 1959a.

pontica pontica, A. fallax fallax, A. f. killarnensis, A. f. lacustris, A. f. nilotica, Clupeonella cultriventris, Coregonus nasus, Pelecus cultratus, Dicentrarchus labrax, D. punctatus, Liopsetta glacialis, Platichthys flesus.

Litho-pelagophils (A.1.2) were considered by Kryzhanovsky to belong to lithophils with which they share numerous common characters. This guild encompasses fishes that go through a full range of transition from lithophils to pelagophils. Although their eggs are deposited on rocks and gravel, in some the eggs, in others the eleutheroembryos[1] and larvae become buoyant and water currents usually carry them away from spawning substrate, because they are not much heavier than the surrounding water. Sturgeon eggs adhere to the gravel and because the embryos hatch early, they are little developed but have a rich network of branches of subintestinal vein which are situated on a large yolk and form the main respiratory organ (Fig. 3a). In spite of a negative buoyancy the wide fin fold enables the embryo to make jumps towards the surface, resulting in a zigzag drift with the current. Embryos are not photophobic but there is no conclusive proof of phototropism. Some coregonids, which can also be fitted into this guild, spawn during winter in very cold waters. Their egg membranes remain slightly adhesive for only a short time; their larvae are semibuoyant and do not seek concealment on the bottom but swim immediately after hatching and display no photophobia. It is not known whether or not they are

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[1] Eleutheroembryo = yolk-fed embryo free from egg membranes (after hatching), and larva = the following period of exogenous nutrition with numerous temporary organs (see Balon 1971b).

actually attracted to light. Burbot eggs are semibuoyant due to a large oil globule in the yolk and the slightest water movement can lift them from the bottom. The eleutheroembryo looks like a typical pelagophil as it has no embryonic respiratory organs.

Canada: *Acipenser brevirostrum, A. fulvescens, A. medirostris, A. transmontanus, Dorosoma cepedianum, Coregonus artedi, C. hoyi, C. johannae, C. kiyi, Hiodon alosoides, H. tergisus, Lota lota, Morone saxatilis.*

Europe: *Huso huso, Acipenser nudiventris, A. ruthenus, A. güldenstaedti, A. naccari, A. stellatus, A. sturio, Coregonus albula, C. baunti, C. oxyrhynchus, C. peled, C. pidschian, Osmerus eperlanus, Lota lota.*

Lithophils (A.1.3) deposit eggs on a rock, rubble, or gravel bottom where their embryos and larvae develop. These sites can be in streams and rivers as well as in mesotrophic lakes. Usually embryos hatch early and are highly photophobic which helps them to scatter and hide under stones. Cement glands do not develop. Fishes of this guild are adapted to well-oxygenated waters and have moderately developed embryonic respiratory organs — *ducti Cuvieri, vena caudalis inferior* in the ventral fin fold, and later segmental vessels with loops at the base of the dorsal fin fold. In some, the subintestinal vein also functions as a respiratory organ. Black and yellow pigments appear relatively late (Fig. 3b, c).

Canada: *Coregonus autumnalis, C. laurettae, C. sardinella, C. clupeaformis, C. nasus, C. canadensis, Prosopium coulteri, P. cylindraceum, P. williamsoni, Thymallus arcticus, Osmerus mordax, Spirinchus thaleichthys, Acrocheilus alutaceus, Clinostomus elongatus, Couesius plumbeus, Mylocheilus caurinus, Notropis anogenus, N. blennius, N. dorsalis, N. rubellus, Platygobio gracilis, Ptychocheilus oregonensis, Rhinichthys atratulus, R. cataractae, R. falcatus, R. osculus, Semotilus margarita, Catostomus catostomus, C. columbianus, C. commersoni, C. platyrhynchus, Hypentelium nigricans, Minytrema melanops, Moxostoma anisurum, M. carinatum, M. duquesnei, M. erythrurum, M. hubbsi, M. macrolepidotum, M. valenciennesi, Percopsis omiscomaycus, Stizostedion canadense, S. vitreum.*

Europe: *Stenodus leucichthys leucichthys, S. l. nelma, Coregonus lavaretus, Abramis ballerus, A. sapa, Alburnoides bipunctatus, Aspius aspius, Aulopyge hügeli, Barbus barbus barbus, B. b. bocagei, B. b. plebejus, B. b. sclateri, B. albanicus, B. comiza, B. cyclolepis, B. euboicus, B. graecus, B. meridionalis meridionalis, B. m. petenyi, B. m. graellsi, B. microcephalus, B. prespensis, B. steindachneri, Chalcalburnus chalcoides, Chondrostoma nasus, C. genei, C. phoxinus, C. polylepis, C. soëtta, C. toxostoma toxostoma, C. t. arrigonis, Leuciscus svallize, L. cephalus, L. illyricus, Paraphoxinus alepidotus, P. adspersus, P. croaticus, P. epiroticus, P. ghetaldi, P, metohiensis, P. pstrossi, Phoxinellus hispanicus, Phoxinus phoxinus, Vimba vimba, V. elongata, V. melanops, Caspiosoma caspium.*

Phyto-lithophils (A.1.4) deposit eggs in relatively clearwater habitats on submerged plants, if available, or on other submerged items such as logs, gravel, and rocks. Relatively late hatching and the presence of cement glands makes some members similar to members of the next guild. Moderately developed embryonic respiratory organs and photophobia make others similar to lithophils (Fig. 4a, b).

A small controversy developed over this group when Holčik and Hruška (1966) found *Rutilus rutilus* and *Abramis brama*, originally assigned as phytophils by Kryzhanovsky and me, spawning on rocks and gravel. As a consequence, a group of indifferent (= Kryzhanovsky's intermediate) fishes was created. However, as already explained elsewhere (Balon 1966), when allocation was based only on spawning grounds, it was wrong. This should serve as a warning that for many species, arrangement into given guilds has to be tentative until there is evidence to make a categorical assertion. Holčik and Hruška's argument, nevertheless, led to the creation of this and two other, even more intermediate guilds (Table 1).

The true intermediate character of this guild can be best illustrated by the common herring. The Atlantic subspecies *Clupea harengus harengus* usually deposits adhesive eggs on a gravelly or rocky sea floor. However, there are records of eggs deposited on seaweeds, logs, and even man-made floating objects. This fish should then be considered as a true phyto-lithophil. The Pacific subspecies *C. harengus pallasi* spawns in much shallower waters than its Atlantic congener and prefers to deposit eggs on plants like *Zostera, Cystophilum, Ptilota,* and to a lesser degree on *Laminaria,* probably because of its slimy surface. Only a limited number of eggs are found on gravel or sand, and such cases are the result of violent spawning activity rather than a deliberate deposition. Some eggs are known to adhere even to living shrimps (Kryzhanovsky 1956). Therefore, this subspecies should be a phytophil rather than an ill-defined intermediate. The proper fit of this subspecies into a correct guild is further complicated by the pelagophilous structure of the embryos which have no special respiratory vessels and lack erythrocytes. The embryos' slower development, extended time of hatching, and early

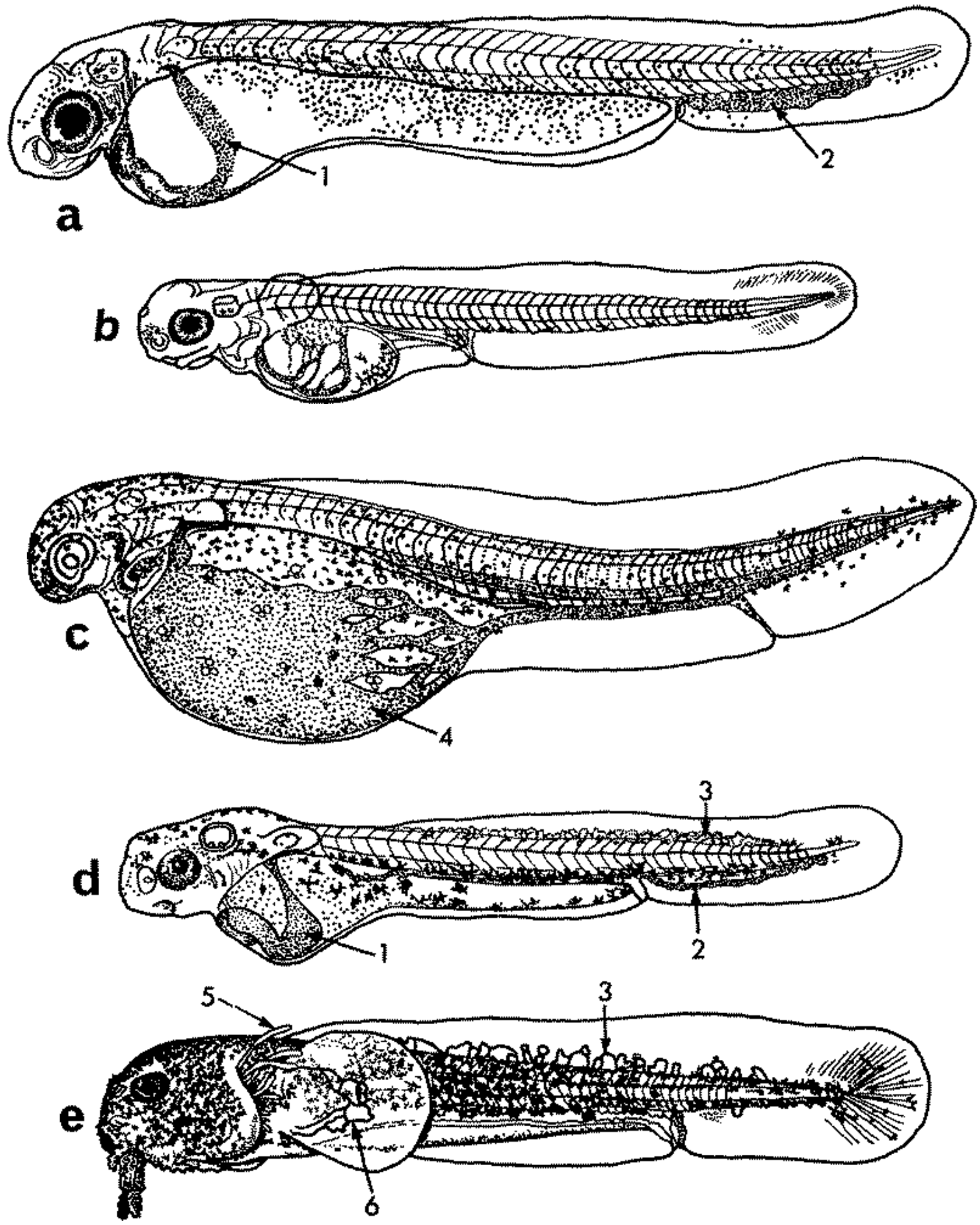

FIG. 4. a, Eleutheroembryo of *Rutilis frisi*, 8.5 mm long (1 = Cuvier's duct, 2 = lower caudal vein, points on the body surface are hatching glands); b, *Perca fluviatilis* 5.3 mm long; c, *Esox reicherti* 8 mm long (4 = respiratory organ of subintestinal vein on the yolk); d, *Cyprinus carpio* 6.7 mm long (3 = respiratory segmental vessels in dorsal fin fold); e, *Misgurnus fossilis* 5.6 mm long (5 = external gill filaments, 6 = respiratory vessels in the pectoral fin). After (a) Smirnova 1957, (b) Kryzhanovsky et al. 1953, (c) 1951, and (d, e) Kryzhanovsky 1949.

occurrence of yellow pigment (Kryzhanovsky 1956) reflects the poor oxygen conditions to which they are exposed.

The eggs of perches (*Perca* sp.) are not deposited simply but in long ribbons with a system of interior passages and a special water-pumping apparatus enhanced by the vibratory consistency of the whole egg mass. The substratum, in this case, is of little classificatory value and is more a matter of availability than selection. The same may apply to the wolffishes (*Anarhichas* sp.) whose eggs form compact balls that adhere as a whole to gravel, rocks, or plants.

Canada: *Acipenser oxyrhynchus, Alosa aestivalis, A. pseudoharengus, Hypomesus olidus, Phoxinus neogaeus, Hybognathus hankinsoni, H. nuchalis, Hybopsis storeriana, H. x-punctata, Notropis spilopterus, N. umbratilis, N. volucellus, Richardsonius balteatus, Fundulus heteroclitus, Microgadus tomcod, Labidesthes sicculus, Morone americana, M. chrysops, Perca flavescens, Etheostoma exile.*

Europe: *Abramis brama, Alburnus alburnus, A. albidus, A. charusini, Leuciscus leuciscus, L. idus, L. borysthenicus, L. microlepis, L. polylepis, L. soufia, L. tueskyi, L. ukliva, Pachychilon pictum, Rutilus rutilus rutilus, R. r. caspicus, R. r. carpathorossicus, R. r. heckeli, R. frisi frisi, R. f. meindingeri, R. f. velencensis, R. lemmingi, R. macedonicus, Perca fluviatilis, Gymnocephalus acerina, G. cernua, G. baloni, G. schraetser, Percarina demidoffi.*

Phytophils (A.1.5) scatter or deposit eggs with an adhesive membrane that sticks to submerged, live or dead, aquatic plants, or to recently flooded terrestrial plants; sometimes they deposit eggs on logs and branches but never on the bottom. Occasionally the eggs fall on stones, a type of replacement substrate where habitats have been altered by man. However, some such as most *Esox* sp. and *Cyprinus carpio* are adapted to spawn only on freshly flooded plants. If flooded vegetation is not available, spawning cannot take place.

Fishes in this guild are adapted to survive in habitats with dense plant growth and muddy bottoms and, therefore, with very low oxygen concentration. Embryos normally hatch later than those of lithophils. They have no photophobic reaction and cement glands are always present on their heads. This enables them to rest and take cover by attaching themselves to plants before they can swim actively and avoid hypoxic conditions on the bottom. Eggs and larvae are very small. In general, the postanal part of the eleutheroembryo is bent upwards to facilitate uplift and to prevent fish from falling to the bottom after hatching, before they are able to hang on plants (Fig. 4c, d). This is contrary to the larvae of lithophils which have downward-bent tails and are bottom dwellers.

In those fish that live in very poorly oxygenated waters, embryonic respiratory organs are extremely well developed (Fig. 4c, d, e), develop early, and last longer than those of embryos from well-oxygenated waters and consist primarily of the *ducti Cuvieri* and dense nets of vessels in the dorsal fin fold. The former are wide and long on the especially enlarged anterior part of the yolk and the latter last into the larval period and remain functional even at the beginning of gill function. In more highly oxygenated waters, duration of use and degree of development of respiratory organs decreases.

Canada: *Lepisosteus oculatus, L. osseus, Dallia pectoralis, Umbra limi, Esox americanus americanus, E. a. vermiculatus, E. lucius, E. masquinongy, E. niger, Chrosomus eos, Notemigonus crysoleucas, Notropis bifrenatus, N. emiliae, N. heterodon, Erimyzon sucetta, Ictiobus cyprinellus, Fundulus diaphanus, Etheostoma blennioides, E. microperca.*

Europe: *Esox lucius, Cyprinus carpio carpio, Blicca bjoerkna, Carassius carassius, C. auratus gibelio, Phoxinellus minutus, Rutilus alburnoides, R. macrolepidotus, R. pigus pigus, R. p. virgo, R. rubilio rubilio, R. r. arcasi, Scardinius erythrophthalmus, S. graecus, Tinca tinca, Cobitis taenia, C. calderoni, C. elongata, Sabanejewia aurata, S. bulgarica, S. conspersa, S. larvata, S. romanica, Misgurnus fossilis, Aphanius fasciatus, A. iberus, Valencia hispanica, Atherina hepsetus, A. boyeri, A. presbyter.*

Psammophils (A.1.6), characteristics for which are also taken from Kryzhanovsky (1949), hatch on the surface of sandy bottoms and are mainly adapted to life in running waters. Their eggs are scattered directly on the sand or near fine roots of plants that hang over the sandy bottom. In the latter case, eggs adhere to the roots and embryos fall to the bottom only after hatching. The eggs have an adhesive membrane, but no cement glands are present in embryos. Eggs of psammophils, like those of phytophils, are frequently small but the psammophils' spawning season is somewhere between that of lithophils and phytophils. The embryos become active immediately after hatching. This immediate activity facilitates emergence from the plant roots and enables them to drift towards the sandy bottom. Soon afterward all activity ceases. The embryos are phototropic which enables avoidance of crevices and other shady areas with a disadvantageous oxygen content.

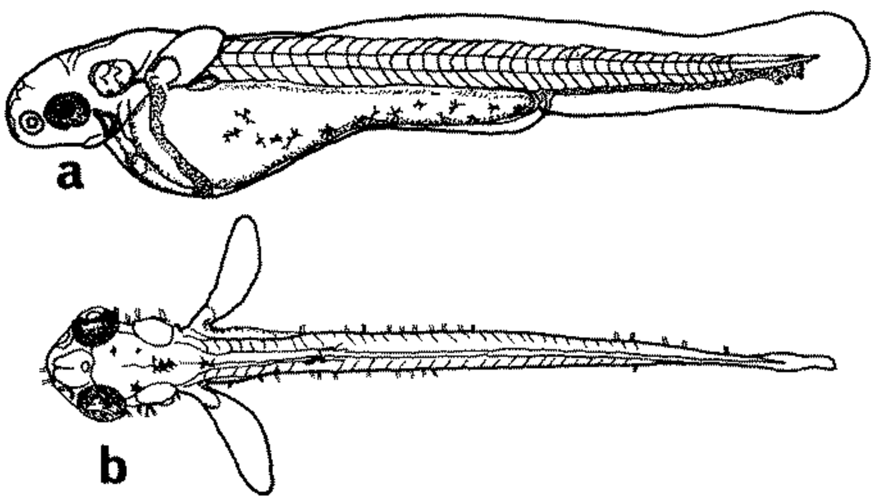

FIG. 5. a, Eleutheroembryo of *Gobio gobio* 4.7 mm long; b, the same 6.4 mm long from above (notice the sensory cupulae and large pectorals). After Kryzhanovsky 1949.

Adaptation to highly oxygenated waters is reflected in respiratory organs limited to the *ducti Cuvieri* which become shorter relatively early and to the little developed *vena caudalis inferior* (Fig. 5a). Pectoral fins appear very early and develop into large appendages that, when they are spread, enable the embryos and larvae to remain at the bottom in a vertical position (Fig. 5b). In view of this mode of life the swimbladder is reduced in size. Only in some members of this guild do the pectoral fins develop simple respiratory vessels as do the dorsal and ventral fin folds; gills also become functional early, with water entering wide-open gill apertures before the mouth is functional.

Canada: *Thaleichthys pacificus, Notropis heterolepis, N. hudsonius, N. stramineus, Carpiodes cyprinus, Catostomus macrocheilus, Ammocrypta pellucida,* and *Percina caprodes.*

Europe: *Gobio gobio, G. albipinnatus, G. kessleri, G. uranoscopus, Nemacheilus barbatulus, N. angorae, Mugil cephalus, M. auratus, M. labeo, M. labrosus labrosus, M. l. septentrionalis, M. ramada, M. saliens.*

BROOD HIDERS (A.2)

Most authors consider the preparation of redds and other similar constructions as nest building. After depositing eggs in such constructions, the fish abandon them immediately. Consequently, a subsection for nonguarding nest spawners seems appropriate. In general, however, some degree of preparation and protection of hiding places or objects hardly equals nest building and is common to all guilds in this subsection. I am inclined to consider as true nests only those places or constructions in which parental care extends beyond initial egg deposition.

Lithophils (A.2.1) of this subsection hide their eggs in natural or specially constructed places. None guard the deposited eggs, although the hiding place can be guarded throughout the spawning period, and *Oncorhynchus nerka* is known to remain with the eggs for up to 3 weeks until flushed away. In most cases the hiding places (called redds in salmonids) are excavated in gravel by the female, well in advance of the mating act. One fish can dig more than one hiding place. Generally, eggs are buried under gravel about twice the height of the body of the digging parent. In such hiding places oxygen conditions are much less favorable than on the open substrate and members of this guild are extremely limited in their choice of spawning grounds. Clean gravel or rocks and cold, clean, fast flowing water or springs are almost essential to assure at least some exchange of water around the eggs and to provide sufficient oxygen. Hidden eggs are better protected and are more likely to survive than exposed eggs. Therefore, the female can channel her reproductive energies into making fewer large eggs instead of many small ones. In Salmonidae, eggs are about 5 mm in diameter. A large, dense yolk with a membrane impermeable to water forms an enormous surface for a special embryonic respiratory organ (Fig. 6a, b). This organ is a rich network of vessels branched over the entire yolk surface (Olko 1955) between the liver and a collecting vitelline vein. Furthermore,

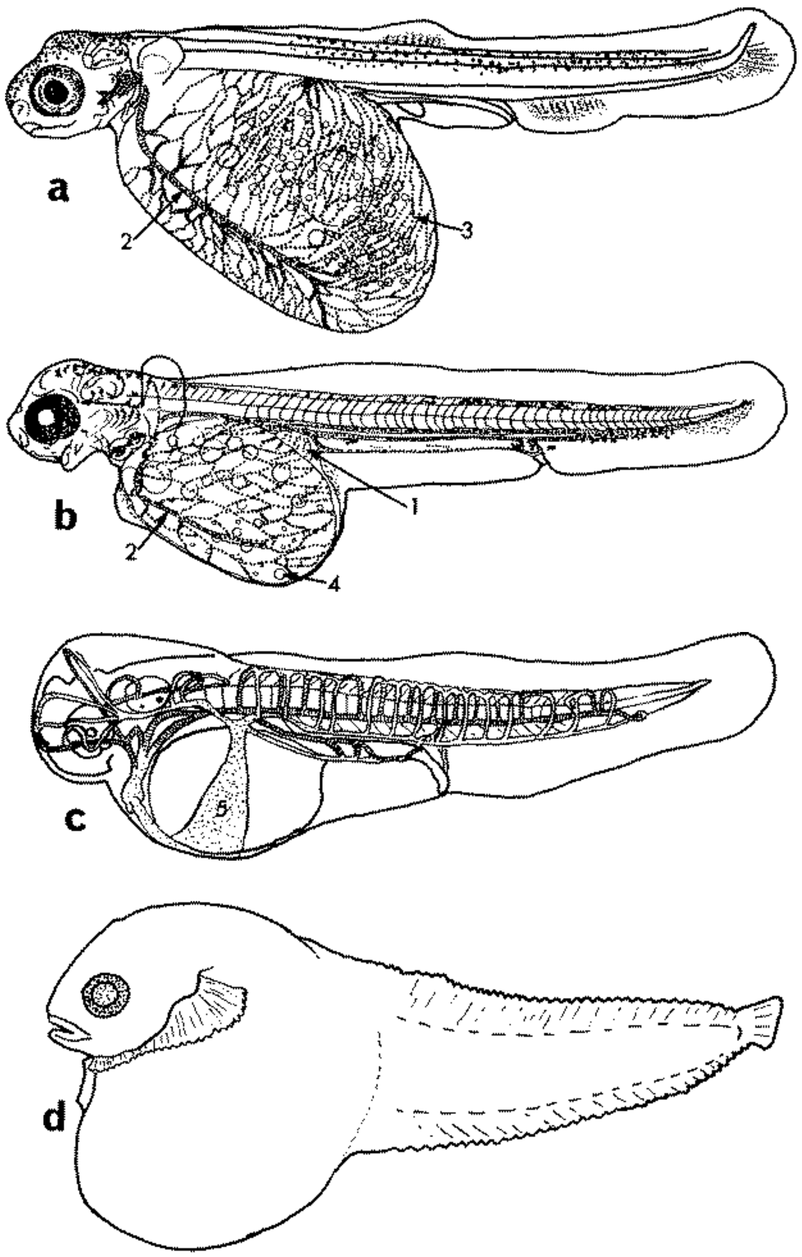

FIG. 6. a, Eleutheroembryo of *Oncorhynchus keta* 20.5 mm long (2 = vitelline vein, 3 = hepato-vitelline respiratory vessels); b, *Thymallus thymallus* 24 mm long (1 = liver, 4 = oil globule); c, *Anoptichthys jordani* 3.4 mm long (5 = Cuvier's duct); d, embryo of *Careproctus melanurus* (?). After (a) Disler 1957, (b) Balon 1967a, (c) Frank 1961, and (d) Peden and Corbett 1973.

the embryos hatch very early, and this facilitates absorption of oxygen. Since they are strongly photophobic they remain hidden under the gravel even after hatching and until most of the yolk is digested. The eleutheroembryo can roll and push itself away from the original place of incubation in a drive toward better oxygen conditions. Before eleutheroembryos emerge they disperse under the surface of the bottom. Later they emerge as large, fully formed, active alevins. This further decreases their mortality from predators.

Some, for example *Salvelinus namaycush*, dig no redds but spawn over a rocky bottom where the eggs settle in crevices and "honeycomb" cavities. This is generally considered a secondary adaptation. The eggs of most fishes in this guild are nonadhesive, but *Hucho taimen*, *Brachymystax lenok* and, to some lesser extent, *Thymallus arcticus* are reported to have adhesive eggs; this can represent an adaptation for spawning without a previously prepared hiding place for the eggs. The eggs of *Procatopus similis* or *Hesperoleucus symmetricus*, the female of which squirts her eggs into a deep crack in the rocks, are strongly adhesive. *Hybopsis micropogon* constructs redds of singly picked pebbles and after each mating adds more pebbles to cover the eggs.

Canada: *Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, *O. tshawytscha*, *Salmo clarki*, *S. gairdneri*, *S. salar*, *Salvelinus alpinus*, *S. fontinalis*, *S. malma*, *S. namaycush*, *Stenodus leucichthys*, *Nocomis biguttatus*, *N. micropogon*, *Semotilus atromaculatus*, *S. corporalis*, *Etheostoma caeruleum*, *Percina copelandi*, *P. maculata*, *P. shumardi*.

Europe: *Salmo salar*, *S. trutta*, *Hucho hucho*, *Salmothymus obtusirostris*, *S. ohridanus*, *Salvelinus alpinus*, *Thymallus thymallus*, *Zingel zingel*, *Z. asper*, *Z. streber*.

Speleophils (A.2.2) are a peculiar guild that could have been placed in the previous subsection. Even though the rare troglodytes *Caecobarbus geertsi* and *Anoptichthys jordani* expel their eggs in a more or less haphazard fashion, the substrate on which they spawn must have crevices and pores into which the adhesive eggs can roll and be hidden so they will not be eaten by their parents or other cave inhabitants. No parental care has been observed and the fish presumably follow the reproductive habits of their predecessors (*Astyanax mexicanus*) which live above ground (Cahn 1958). Nonetheless, the specialized morphophysiological adaptations of the adults are paralleled by characteristic adaptations in egg number and size, and in length of embryonic development. Only a few large eggs are produced and the embryonic period is extended, much as in the preceding guild. Well-developed larvae or juveniles probably emerge from these large eggs. The large size of larvae and ability to feed on larger items guarantees good survival for those few needed to keep the population at a constant density (Mohr and Poulson 1966). The large yolk can also serve as a surface for expanded embryonic respiratory organs (Fig. 6c) which are so essential in the hypoxic cracks where the eggs develop, and when fanning action of the guarding parents is not available. Nothing, however, is as yet known about the spawning habits of these fishes in nature (Lüling 1954).

Provisionally another species can be included here. According to Hayley (1957) captive *Rasbora trilineata* spawns only in darkened aquariums and deposits adhesive eggs under an object on the bottom. However, this has not yet been confirmed by other authors, and variation in egg number and size of eggs is unknown. It is likely that the South African *Clarias cavernicola* Trewavas, 1936 belongs in this guild, but nothing is known of its breeding habits and development (Jubb 1967). Probably other fishes belong to this guild and will be discovered later (Riedl 1966). *Stygichthys typhlops* is such a recent discovery.

There is no representative of this guild within the freshwater fishes of Canada and Europe.

Ostracophils (A.2.3) have already been well defined by Kryzhanovsky (1949), although he considered them a homogenous group of the subfamily Acheilognathinae (Rhodeinae) only. We now know that a similar strategy is used by some Gobioninae, liparids, and at least one aulorhynchid.

Fishes of this guild hide their eggs in the gill chambers of live mussels (*Unio*, *Anodonta*, *Cristaria*, etc.), crabs (*Paralithodes camtschatica*, *Lopholithodes foraminatus*), or ascidians (*Cynthia roretzi*). Species of different phyletic lines have developed this ability and represent a remarkable case of convergence. All females of this guild grow an ovipositor used to introduce eggs through the excurrent or incurrent siphon, or through the gill apertures of the host. As a rule it is the males that select the host. They eject their sperm before or after the eggs have been deposited (Wickler 1973, p. 34–35). The sperm is inhaled by the host which facilitates fertilization of the eggs.

Fecundity of members of this guild is low since the host, in which the eggs are hidden and incubated, protects them efficiently from predators. However, one host can harbor some 100 or more eggs deposited by different females (Balon 1962a, 1967a, Photograph 91) or even by one female only (Peden and Corbett 1973). Furthermore, there is a higher proportion of yolk in their eggs, relative to vegetative plasma, than in other fishes. The yolk is also more concentrated, which prolongs the time of embryonic development and enables the larva to leave the host in a well-advanced state. Special adaptations were necessary to enable incubation in such a strange environment (inside another animal). Adaptation to a possibly low oxygen content probably causes an extremely slow pace in the early stages of development. This adaptation is irreversible, because eggs extracted from the mussel and incubated in clean, well-oxygenated water develop no faster than those within the host's body, and most of them die.

Very strong embryonic respiratory organs develop, and a dense net of capillaries from the subintestinal vein forms on the surface of the yolk. Long, numerous loops of segmental vessels and of *vena caudalis inferior* form dense respiratory areas in the dorsal and ventral postanal fin fold (Fig. 7). These temporary respiratory organs are retained until the larva leaves its host.

In some species special temporary structures develop to oppose the possible premature expulsion from the host (Fig. 7a, b). Eggs of acanthorodeinids, which are reported to be more numerous but smaller than eggs of rhodeinids, hatch very early and become covered with spine-like epidermal scales (Fig. 7c). The premature eleutheroembryos are capable of moving in a worm-like manner and crawl away from the initial, closely packed group in an attempt to reach better oxygen conditions. Eggs of rhodeinids, which number less than 100 in one female, are larger than those of acanthorodeinids and are deposited individually within the gill lamellae of the host; the eleutheroembryos cannot crawl and develop no spiny scales but the anterior part of their yolk forms a pair of folds, bordered by glands of an unknown function (Fig. 7b). These folds may fix the eleutheroembryo inside the mussel. However, as soon as the first pigment appears in the eyes, all embryos of this guild become highly photophobic, which presumably prevents a premature departure.

Eggs of liparids are deposited in a densely packed group in one of the gill cavities of the king or box crab. The mass of eggs causes a collapse of the host's gills (Peden and Corbett 1973, Fig. 1 and 2). While the yolk is still very large, the embryos have fully differentiated fins (Fig. 6d) and are, in this respect, similar to other members of this guild.

Cyprinid fishes, like *Rhodeus sericeus*, *R. ocellatus*, *R. atremius*, *Acheilognathus moriokae*, *A. tabira*, *A. cyanostigma*, *A. rhombea*, *A. longipinnis*, *A. lanceolata*, *A. limbata*, *Tanakia tanago*, and *Pseudoperilampus typus* deposit their eggs in the suprabranchial cavity of mussels; *Sarcocheilichthys variegatus* in the mantle cavity or in the incurrent siphon of mussels (Nakamura 1969); the aulorhynchid *Aulichthys japonicus* in the peribranchial cavity of ascidians; and the liparids *Careproctus* spp. in the gill chamber of the king and box crabs (Rass 1950; Vinogradov 1950; Hunter 1969; Parrish 1972; Peden and Corbett 1973). Kryzhanovsky et al. (1951) indicated that *Sarcocheilichthys nigripinnis czerskii* (syn. *Chilogobio soldatovi*) may be an ostracophil, but Banarescu and Nalbant (1973) and Banarescu (1974) concluded that females of all species and subspecies of the East Asian cyprinid genus *Sarcocheilichthys*, except *S. sinensis* (Fig. 1b), have long ovipositors and "lay the eggs in the branchial cavity of living fresh-water mussels." However, there is neither convincing evidence of this available nor any data on their development.

A species from Lake Tanganyika may also belong to the same guild. Vanderplank (1941) found eggs in the mussel of the genus *Spatha* in the resting phase during the dry season. A similar phenomenon was reported recently by Able and Castagna (1974), who found *Fundulus heteroclitus* eggs in the shells of *Modiolus demissus*, exposed to desiccation at low tides in Virginia. The latter would be the first such case reported from the North American continent. Both the Virginia and Tanganyika reports have to be investigated further; in the end it may be found that the two species of fish are closer to one of the following two guilds than to ostracophils.

No Canadian species belong to this guild. *Rhodeus sericeus amarus* is the only European representative.

Aero-psammophils (A.2.4) bury their eggs out of water in the sands of sea beaches. Their eggs are incubated in the damp sand until the returning high tide washes them back to sea. The timing of the spawning act is surprisingly perfect. It occurs only during a single hour or so during consecutive days of a single week and at extremely high tide followed 14 days later by another slightly higher tide.

Only three unrelated species of this guild have been studied in detail. *Leuresthes tenuis* (night spawner) and *L. sardina* (day-time spawner) have pink, nonadhesive, hard eggs 2 mm in diameter. When the female reaches the highest point of the surf with one of the farthest running waves

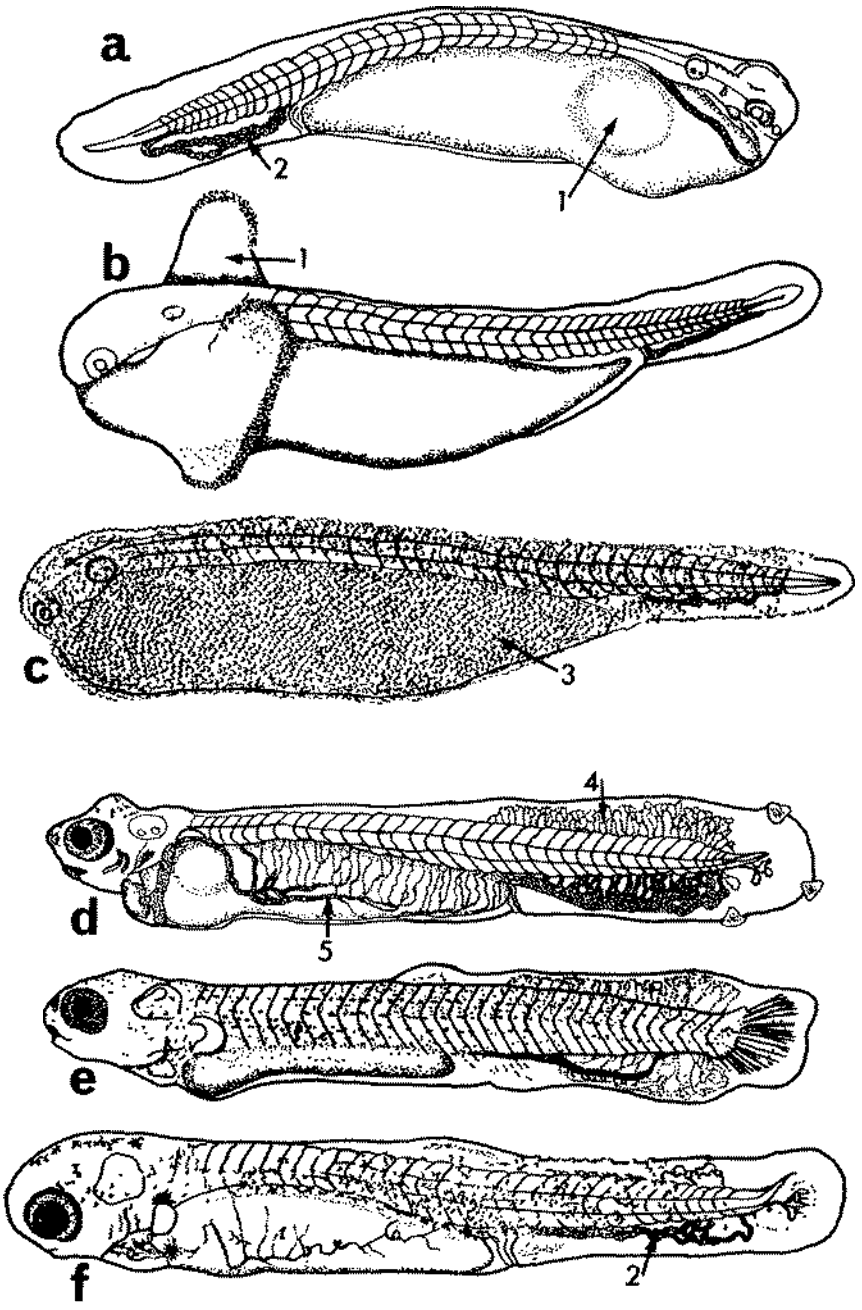

FIG. 7. a, Embryo of *Rhodeus sericeus amarus* 6 mm long; b, *R. sericeus sericeus* 5 mm long, and c, *Acanthorhodeus asmussi* 3 mm long (1 = folds of yolk, 2 = lower caudal vein); d, older embryo of *R. s. amarus* 8 mm long; e, *R. s. sericeus* 8 mm long and f, *A. asmussi* 6 mm long (4 = segmental respiratory vessels in dorsal fin fold, 5 = respiratory extension of subintestinal vein on the yolk). After Kryzhanovsky 1949 and Kryzhanovsky et al. 1951.

and if there are males close at hand, she buries herself out of water, tail first, in the sand. The males release sperm in the sand next to the female while she deposits her eggs. After approximately 2 weeks a new high wave with multiple receding wavelets uncovers the embryos (Fig. 8d) which hatch as they are freed. The Japanese fugu puffer, *Spheroides niphobles*, spawns in much the same way but the eggs are deposited not so far out of the water and measure only 1 mm in diameter. They hatch in less than 1 week (Uno 1955) only if appropriate rolling motion triggers the hatching. In both cases the ability of eggs to develop in damp air was reported independently; in water and under different temperatures no changes in the rate of development were demonstrated, which led to the conclusion that the peculiar and elaborate spawning habit "serves merely to give protection to the egg" (David 1939).

Xerophils (A.2.5) are a specialized guild of fishes with a short life span adapted to the seasonal desiccation of their habitat. These fishes inhabit, almost exclusively, small intermittent water bodies, i.e. isolated pools and swamps in the African savannah or the South American llanos and pampas that dry up completely during the dry season. Eggs are deposited in the bottom sod, sand, or most frequently, mud (e.g. Wickler 1973, p. 106) and they survive the several months of dry season under the cracked dry crust of the damp sod or mud. In extremely dry years the embryos of xerophils can survive as long as 18 months and more in the egg membranes lodged in the dry mud. Eggs of *Cynolebias elongatus* survived this period in dry peat under laboratory conditions and I was able later to induce hatching of viable fish. When the pools refill after the first rains, the embryos hatch and grow so rapidly that within several weeks they are able to reproduce. When the water begins to recede at the beginning of a new dry season, a large number of eggs have already been deposited along the subsequently exposed shore line and egg laying continues almost until the pool dries up and all adult fishes die. Myers (1952) characterized these species as "annuals." The whole population survives only in the egg membranes, as hibernating embryos. The embryonic period lasts nearly as long as the remaining larval, juvenile, adult, and senescent periods together.

In members of this guild the adaptations for survival rest mainly with some unique embryonic characteristics. The eggs can arrest their development at three different times. The first resting time (diapause I), usually facultative, occurs early in the cleavage phase (Fig. 8a). The cells disperse and rest for several weeks. Later embryogenesis commences from their reaggregated mass. The two other resting periods (diapause II and III) are usually obligate (Fig. 8b, c). During the time of developmental arrest, yolk reserves remain intact and blood circulation stops entirely. Heart contractions are occasional and feeble (Peters 1963, 1965; Wourms 1967, 1972a, b, c). Oxygen presumably reaches the eggs through pores in the dry soil and is considered the main regulating factor for the resting periods. Hatching is induced by reduction of oxygen occurring when rain water clogs the pores in the mud, and by the pressure of the water column above the eggs (Morenski 1974).

To date, xerophils are known only from cyprinodontid fishes of Africa and South America. The following "have been shown to have a dispersion–reaggregation pattern of development and the ability of diapause" (Wourms 1967): *Aphyosemion arnoldi*, *A. caeruleum*, *A. nigerianum*, *A. seymouri*, *A. walkeri* (names not updated), *Austrofundulus myersi*, *A. transilis*, *A. dolichopterus*, *Cynolebias bellotti*, *C. nigripinnis*, *C. whitei*, *C. melanotaenia*, *C. wolterstorffi*, *Nothobranchius guentheri*, *N. melanospilus*, *N. orthonotus*, *N. palmquisti*, *N. rachovi*, *N. taeniopygus*, *N. furzeri*, *N. kirki*, *Pterolebias longipinnis*, *P. peruensis*, *P. zonatus*, *P. maculipinnis*, *Rachovia brevis*, *R. hummelincki*, etc.

B. Guarders

SUBSTRATUM CHOOSERS (B.1)

Guarding is a solely ethological aspect of guilds. It has, however, profound ecomorphological consequences. Better protected from enemies, guarded eggs need not be numerous to assure survival of the species. Consequently, eggs can often be larger and result in more viable offspring with less food specialization. (Incidentally, external food independence is known to be assured by other means also.) Furthermore, spawning sites with low oxygen content can be used because the guarding parents clean the eggs and produce a flow of water around them by fin-fanning and oral ventilation. "In all known fishes that are parental, outside of the Cichlidae, the male is the parent. The evolutionary progression has been from (i) an exclusively parental male, to (ii) shared parental care by the male and female, to (iii) a division of roles with the female as the direct parent and the male as guardian, to (iv) polygyny (Barlow 1964). This is clearly a forward progression resulting in a more efficient division of labor between the male and female" (Barlow 1974).

Fishes that do not build the complicated struc-

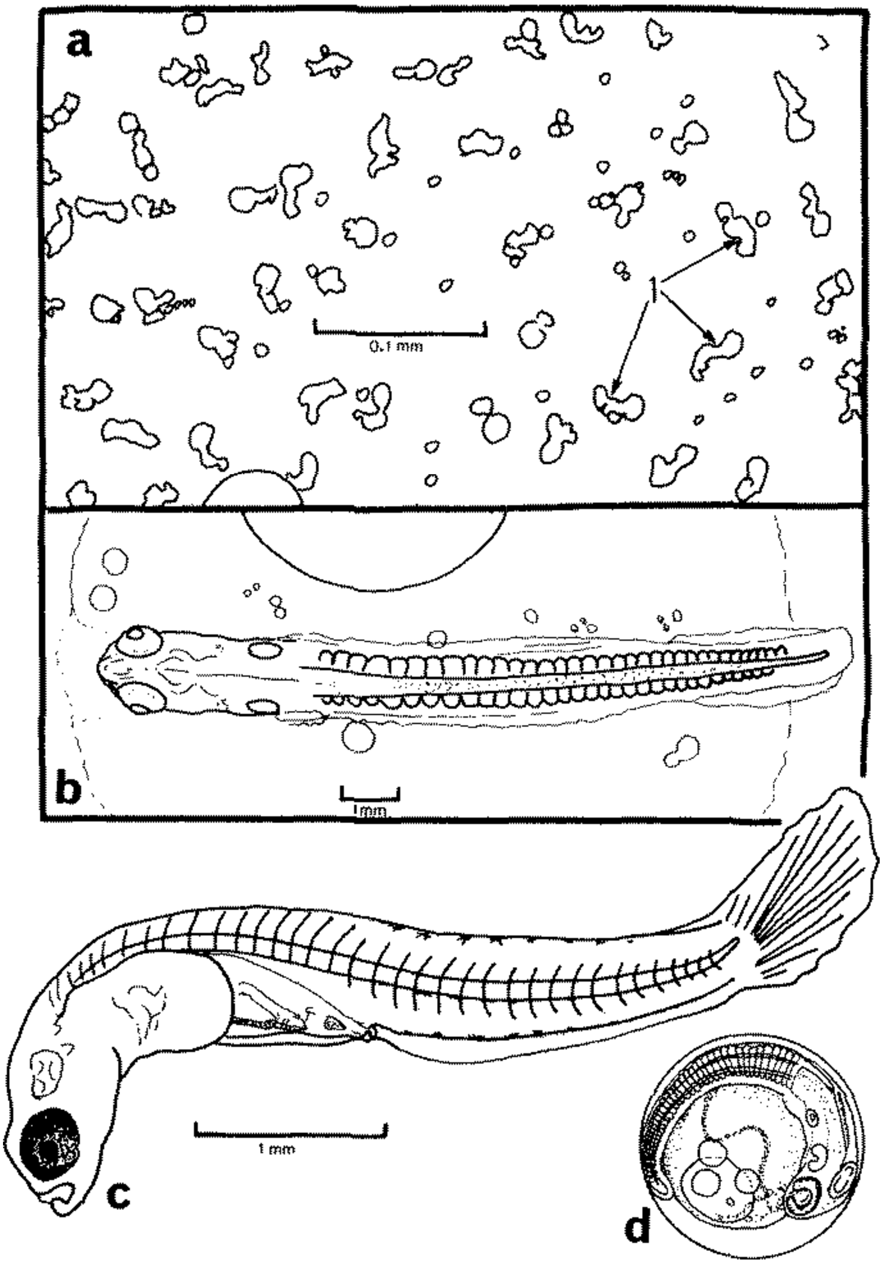

Fig. 8. a–c, Resting times in annual fishes: a, diapause I in dispersed cell phase of *Rachovia brevis* (1 = dispersed cells), b, diapause II during the long somite embryo phase of *Austrofundulus myersi*, and c, diapause III in *Pterolebias longipinnis* just before hatching, 6 mo after fertilization; d, Embryo of the grunion *Leuresthes tenuis* 60 h after fertilization. After (a, b) Wourms 1972c, (c) own unpublished material, and (d) David 1939.

tures, subsequently called nests, but that deposit their eggs on top of a selected object, are included in this subsection. The surface chosen for egg attachment may be cleaned and guarded in advance of the spawning act.

Lithophils (B.1.1) choose rocks for attachment of their eggs. The eggs are often more or less cylindrical and one pole is equipped with fibers that firmly adhere to the rock (Fig. 9a). Males of *Loricaria parva* and *L. macrops*, however, sit on their eggs like hens, cleaning them with a mouth-sucking motion and fanning them with a swinging motion of their whole body. Their eggs are spherical and have an adhesive membrane but no fibers. *Chromis chromis* of the Mediterranean deposits its eggs on slanting rock surfaces in spawning colonies, and the male fans them with his tail (Abel 1961). *Cyclopterus lumpus*, which can also be fitted into this guild, deposits a massive, spongy cluster of pink eggs over 20 cm in diameter. The female attaches them to rocks and until they hatch 2 months later, the male fans and ventilates them with jets of water from his mouth (Mochek 1973). *Tetraodon cutcutia* and *T. fluviatilis* are reported to do the same, but the eggs hatch in a week.

Europe: *Gobius melanostomus*, *G. gymnotrachelus*, *G. batrachocephalus*, *G. cephalarges*, *G. kessleri*, *G. ratan*, *G. syrman*, *Benthophilus stellatus*.

Phytophils (B.1.2) in this subsection scatter their eggs or attach them to submerged plants. The males guard and fan them. The place of egg attachment is sometimes selected and cleaned in advance of the spawning act and sometimes not. A variety of aquatic plants, with no marked preference, are used by *Polypterus*, *Paracheirodon innesi*, *Silurus glanis*, *Jordanella floridae*, *Labrus herggylta*, *L. turdus*, and *Sardelia capensis*. *Archoplites interruptus*, *Pomoxis annularis*, *Elassoma zonatum*, and *Clinus testudinarius* deposit their eggs in algal growth. Fishes of the genus *Pyrrhulina* prefer broadleaved plants and *Leucaspius* attach ribbon-like threads of eggs to broad leaves or around stems. The male of *Polypterus* also guards the larvae and in *Sardelia capensis* both sexes are reported to guard the eggs.

No cement glands are known in the members of this guild. So that the eleutheroembryos avoid contact with the hypoxic muddy bottom, the embryonic period is prolonged and the newly hatched larvae swim instantly. Probably as a result of the parents' fanning activity (Mertz and Barlow 1966) the embryonic respiratory organs are feeble, a characteristic of nonguarded lithophils (A.1.3) (Fig. 9e, f, g) also. Guarded phytophils developed this characteristic possibly as an adaptation to lentic conditions (Kryzhanovsky 1949). In other members of this guild with bottom-dwelling larvae (Fig. 9c, d) the development of external gills and large pectorals (Kerr 1907) compensates for the lack of oxygen.

Canada: *Pomoxis annularis*.

Europe: *Umbra krameri*, *Leucaspius delineatus*, *L. marathonicus*, *L. stymphalicus*, *Silurus glanis*, *S. aristotelis*.

Aerophils (B.1.3). So far as is known, this unique adaptation is exhibited by a single species, *Copeina arnoldi*. The eggs are not deposited in water but on undersides of broad leaves or rocks that overhang the water. The eggs are attached during the spawning act, when female and male leap out of the water together and cling upside-down to the chosen substrate, usually about 10 cm above the surface of the water. Every 20 minutes or so the male splashes the eggs by swishing his tail, using the edge of the egg attachment substrate as an aiming cue (Krekorian and Dunham 1972). Three days later the embryos hatch and drop into the water. Like phytophils, the embryos have cement glands and attach themselves for a short time to plants near the surface of the water. As a result of good oxygen conditions embryonic respiratory vessels are probably not well developed. Mating out of water occurs in *Aphyocharax rubripinnis* (Innes 1935) and in some *Glandulocaudines*. Aerophilous reproduction could have developed from this aerial mating which initially facilitated fertilization only (Nelson 1964). Protection from enemies seems to be the reason for this adaptation.

Pelagophils (B.1.4) in this subsection are a specialized guild, which includes to my knowledge, only *Ophiocephalus* spp. and *Anabas* spp. (Barlow et al. 1968). Their eggs are nonadhesive and positively buoyant. Deposited on the surface of the water in openings between vegetation growing in the shallows, they float in a cluster; and propelled by wind, they often drift into remote places. Both the male and female guard the eggs and larvae. Judging from data on development (Soin 1960) and from the need of the adults for complementary aerial respiratory organs, having pelagic eggs seems to be an adaptation to hypoxic conditions. As these pelagic eggs are, at the same time, vulnerable to predation, guarding evolved to ensure protection against enemies living in such habitats.

NEST SPAWNERS (B.2)

Some members of this subsection build more and some less elaborate structures for egg deposition or for guarding the hatched offspring, whereas

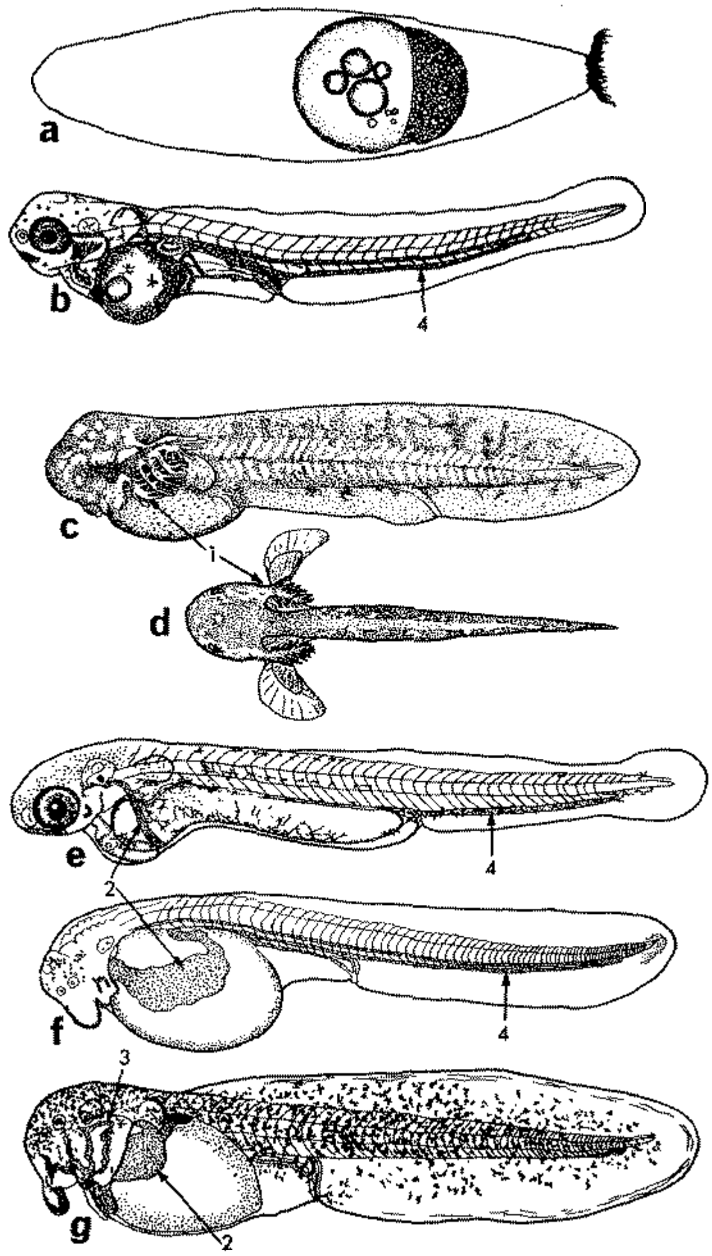

FIG. 9. a–b, Guarding lithophil *Rhinogobius similis*: a, cylindrical eggs in cleavage phase with attachment tendrils at one pole; b, eleutheroembryo 3.2 mm long; c, Eleutheroembryo of *Polypterus senegalus* 7.3 mm long; and d, larva 9 mm long with supporting wide spread pectorals, from above (1 = external gills); e, Eleutheroembryo of *Leucaspius delineatus* 5.3 mm long; f, *Silurus glanis* 7.4 mm long; and g, *Parasilurus azotus* 6.3 mm long (2 = ducti Cuvieri, 3 = respiratory vessels on the gill cover, 4 = lower caudal vein). After (a, b) Kryzhanovsky et al. 1951, (c, d) Kerr 1907, and (e, f, g) Kryzhanovsky 1949.

some only clean the place of the future egg attachment. Some clean by sandblasting, whereas others are less thorough. Eggs are guarded though this is not always the case with the hatched offspring (Mochek 1972). But if the offspring are guarded they are also herded, e.g. into bottom pits, for some time.

Lithophils (B.2.1) represents a polyphyletic guild and their eggs are deposited in single-layer or multilayer clutches on cleaned areas of rocks or in pits dug in gravel. Numerous deviations from this simple scheme have been recorded in the mode of nest construction and parental care. For example, males usually guard only the eggs deposited in gravel nests built in shallow running waters. The nest of *Myoxocephalus quadricornis* is built as a large pit in a soft mineral bottom or on a flat circular clearing amid algae and the male guards the egg cluster for an extended period of time (Westin 1970). The nest of *Leporinus affinis* is formed as a cavity in sand paved with pebbles. *Notropis cornutus* sometimes builds its own nest in the gravel but prefers to occupy, in cuckoo–cowbird fashion, those of *Hybopsis micropogon*, *H. biguttatus*, *Semotilus corporalis*, *S. atromaculatus*, *Exoglossum maxillingua*, *Campostoma anomalus*, or *Micropterus dolomieui* if available. A number of males may eventually spawn over one nest. In *Hexanematichthys australis*, eggs are buried under a mound of gravel. *Dormitator maculatus*, *Mogurnda mogurnda*, and *Crassiops gali* attach their eggs to cleaned rock surfaces. All these nests are guarded.

In cichlids parental care is usually extended and includes care of the offspring after hatching. Frequently both parents guard, but "the female does most of the direct parental care while the male guards the territory or remains nearby until the fry begin swimming. Then both sexes guard them. There is evidence of an inclination toward polygyny, but this is counteracted by selective pressure from predators, requiring both parents for protection of the fry" (Barlow 1974).

Eggs are attached to cleaned places on rocks, and one or more pits are dug on the bottom, to which the offspring are transferred by mouth after hatching. At nightfall, the swimming larvae and juveniles are often herded into these pits. This applies to *Aequidens pulcher*, *Astronotus ocellatus*, *Cichla ocellaris*, *Cichlasoma facetum*, *C. severum*, *C. nigrofasciatum*, *C. cyanoguttatum*, *C. biocellatum*, *Pelmatochromis arnoldi*, and many others. The females of *Cichlasoma aureum*, *C. tetracanthum*, *C. cutteri*, *C. haitiensis*, and *C. meeki*, do most of the egg incubating and the males most of the pit digging. The eleutheroembryos of *C. bimaculatum* and *C. festivum* are not placed in the pits but are hung on plants. In *Heterotilapia multispinosa*, plants or vertical surfaces of submerged objects are used if mud and detritus make the use of bottom pits impractical (Baylis 1974).

"Not only do the parents defend the fry, but in many species they also help provide food. In some species the parents turn over leaves for the offspring ... When the fry are extremely hungry in almost any Central American species they will begin to graze on the mucus on the sides of their parents (*C. nigrofasciatum*, *C. spilurum*, *C. macracanthum*, *C. friedrichstahlii*, *C. beani*, *C. longimanus*). In *C. citrinellum* the response is apparent even when the fry are only modestly hungry (Noakes and Barlow 1973), as is also true of *C. labiatum*" (Barlow 1974). *Geophagus brasiliensis* picks up its offspring by mouth more readily and after less provocation than most cichlids, whereas the eggs of *G. jurupari* and *G. balzani* are actually guarded by both parents in the nest for 1 day only; then the female collects them into her mouth and broods them in a regular bearers' (C.1.3) manner. This mouth-bearing phenomenon occurs several times in different guilds of this subsection and clearly indicates the polyphyletic evolution of mouth-brooding habits (Breder 1933).

The eggs are always spherical or elliptical and stick firmly to the substrate. Size varies greatly, as does color. *Pylodictis olivaris* eggs are deposited in a thick adhesive mass that "shake[s] like a bowl of jelly" when the male fans them, whereas individual eggs of *Pelmatotochromis subocellatus* and *Mogurnda mogurnda* are attached to the substrate by short stalks that wave under the influence of fanning.

In some members of this guild the photophobic reaction of A.1.3. lithophils is retained and the eleutheroembryos hide under the gravel of their nests and are guarded. But in the majority, the need to hide is replaced by parental care. Some that build their nests in running water have moderately developed embryonic respiratory organs; others from lentic nest sites have highly developed yolk and fin fold vessels (Fig. 10a). Most eleutheroembryos have cement glands (head glands) and swing their tails rapidly while attached to the substrate.

Canada: *Notropis cornutus*, *Exoglossum maxillingua*, *Ictalurus melas*, *Ambloplites rupestris*, *Lepomis auritus*, *L. cyanellus*, *L. macrochirus*, *L. megalotis*, *Micropterus dolomieui*, and *Myoxocephalus quadricornis*.

Europe: *Benthophiloides brauneri*, *Myoxocephalus quadricornis*.

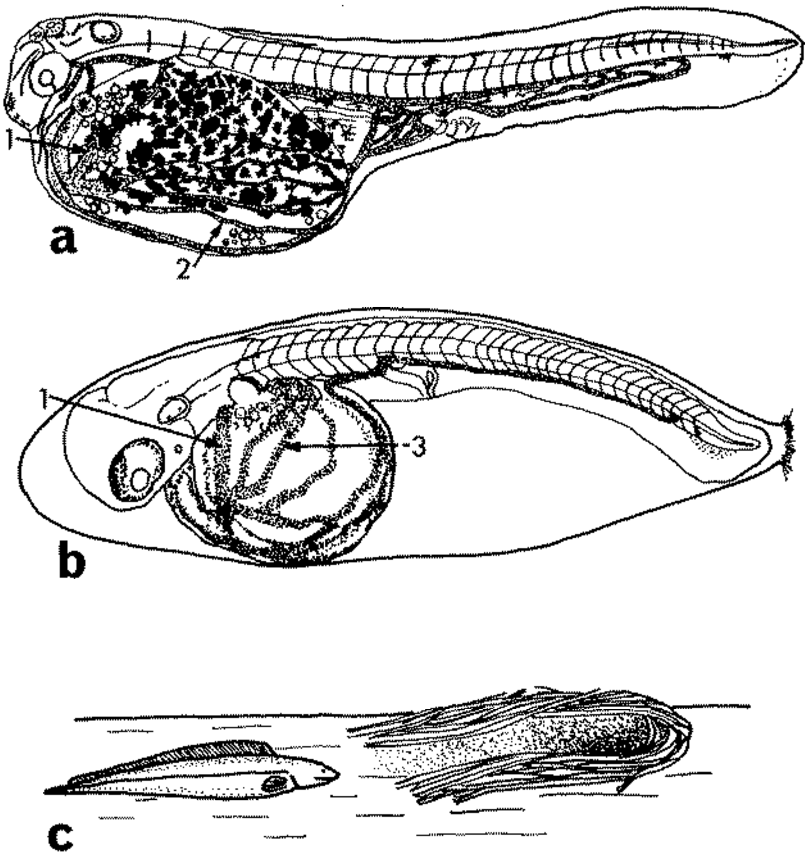

FIG. 10. a, Eleutheroembryo of *Cichlasoma cyanoguttatum* 4.2 mm long (1 = ducti Cuvieri, 2 = respiratory branches of subintestinal vein); b, embryo of *Percottus glehni* 3.7 mm long (3 = respiratory branches of hepatic vein); c, floating nest of *Gymnarchus niloticus*. After (a) Balon 1959b, (b) Kryzhanovsky et al. 1951, and (c) Daget 1952.

Phytophils (B.2.2) in this subsection are a polyphyletic guild very much like the preceding one. Its members, however, are adapted to nesting above or on a soft muddy bottom. For example, *Amia calva*, *Clarias batrachus*, *Enneacanthus gloriosus*, *Pomoxis nigromaculatus*, *Elassoma zonatum*, *E. evergladei*, *Etheostoma blennioides* and *Stizostedion lucioperca*, *S. marinum*, and *S. volgense* construct circular nests on the bottom amid algae and vascular plants whose roots are often exposed (Dmitriyeva 1973); nests are built and eggs are guarded by males. *Etheostoma microperca* and *Perccottus glehni* most often attach their elliptical eggs to stems of plants, whereas the female of *Heterostichus rostratus* constructs a nest in the kelp and lays eggs that are bound together with adhesive threads and defended by the male. *Pterophyllum scalare* and *P. eimekei* attach their eggs to a thoroughly cleaned surface on a broad leaf and immediately transfer the newly hatched eleutheroembryos to another cleaned leaf. Several cleaned "nursery areas" on a number of leaves are maintained simultaneously. If the young get detached and fall while swinging their tails too vigorously during respiratory movements, each is picked up and returned in their parents' mouths to the plants where they hang by means of cement glands. The same behavior is reported for *Nannacara taenia*, but in addition, the guarding parents can signal danger by quivering their fins and bodies. At this the young hide on the bottom or remain motionless close to their parents. *Amblydoras hancocki* builds a nest of detached leaves, in which a flat cluster of eggs is covered by more leaves and guarded by both parents. "*Aequidens coeruleopunctatus* breeds in streams in Panama where there is little hard substrate on which they can deposit their eggs. The female selects a relatively rare rubbery leaf from among the litter on the bottom and carries it past the male during courtship. Later she spawns on the leaf. ... When danger threatens she grasps the leaf in her mouth and pulls it back under the bank of the stream or into shallow water" (Barlow 1974).

Perccottus glehni attaches cylindrical eggs to stems by threads on one pole (Fig. 10b). A more refined type of attachment occurs in *Monocirrhus polyacanthus*. "The eggs when first laid are close to the leaf to which they are attached, and the supporting threads are tightly coiled into a fine spiral. As development proceeds, this sags down so that, by the time of hatching, the eggs hang farther from the leaf on a straight thread."

The male of *Gymnarchus niloticus* builds a floating nest of plants approximately 90 × 65 cm (Fig. 10c) in dense swamps. Amber-colored, spherical eggs, 10 mm in diameter (sic) hatch in 5 days and after 18 days the larvae are ready to leave the nest. The guarding male is very vicious. *Polycentropsis abbreviata* attaches its eggs to the underside of cleared areas on a broad leaf, but in addition the male surrounds them with bubbles of air fetched from the surface. A bottom pit is then prepared under this leaf into which the hatched eleutheroembryos drop. They soon leave this pit to hang briefly on plants. *Osphronemus goramy* builds its nest of plant fibers in midwater, and incorporates some mucous air bubbles in the construction. The eggs and young are positively buoyant and have to be kept under the nest canopy by the guarding parents. The froth nest builders (B.2.4) may have evolved from here.

Canada: *Amia calva*, *Micropterus salmoides*, *Pomoxis nigromaculatus*.

Europe: *Gobius ophiocephalus*, *Stizostedion lucioperca*, *S. marinum*, and *S. volgense*.

Psammophils (B.2.3) in this section form a guild for which relevant data are available for only a single noncichlid fish and one cichlid fish. *Abbottina rivularis* males "build special nests on the bottom; of [sic] shallow water (no deeper than 40 cm, at about 1 m from the shore); the nests are circular, their upper diameter is 12–43 mm, their depth 5 mm. [Nest photograph in Nakamura 1963, fig. 47c.] A female spawns several times in a season. The males guard the nest. The diameter of the egg is about 2–2.5 mm. The larvae hatch out in 6–8 days (at 18°C); they lay [sic] usually on the bottom and move very little" (Banarescu and Nalbant 1973). The eggs have a thick secondary membrane and cover the entire bottom of the nest in a layer over 2 cm thick (Nakamura 1969). At first, each egg is completely covered with sand grains, but during incubation the egg membrane loses its adhesiveness and the sand is gradually washed off. After hatching, the eleutheroembryos and larvae remain in the nest and maintain a standing position while leaning on their wide pectorals (Fig. 11a–c). Embryonic respiratory organs are feebly developed (Kryzhanovsky et al. 1951). *Abbottina rivularis*, like the A.1.6 psammophils, has long *cupulae* at the beginning of exogenous feeding (see possible significance in Balon 1960).

Cichlasoma nicaraguense "digs a remarkably deep hole in the sand by a rock ... The eggs are not only large but rather buoyant, bouncing around in the bottom of the nest. The absence of adhesive threads, large size, and buoyancy are adaptations to prevent loss of the eggs in the sand. While the female does some fanning of the eggs, she also does an inordinate amount of taking the eggs into her mouth and spitting them out (Stratton, 1968). Apparently this species is but one step away from becoming a mouthbreeder" (Barlow 1974).

Aphrophils (B.2.4). A unique habit among characids was reported for *Hepsetus odoe*. This common African pike-like fish builds nests of floating froth, 5 cm deep and about 20 cm in diameter, usually placed in grass or reeds along the shores. The eggs, 2.5 mm in diameter, are mixed with the froth and after hatching, the eleutheroembryos leave the froth to hang from the water surface by their cement gland. The froth nest is built by both parents and is maintained and guarded by one or the other, or by both (Svensson 1933; Jubb 1967).

In *Callichthys callichthys* a floating nest of froth "is constructed by the male who takes the air into his subterminal mouth in an inverted position and emits mucus-covered bubbles from his gill cleft." Only the male maintains and guards the nest. The froth nest of *Haplosternum* sp. is placed under a floating raft constructed of aquatic plants. The female practices an oral transfer of sperm, and deposition of egg groups "cupped between her ventral fins."

Among anabantids a surface froth nest is built by *Macropodus opercularis*, *Trichogaster trichopterus*, *T. leeri*, *Trichopodus pectoralis*, *Parasphromenus deissneri*, *Colisa labiosa*, *C. lalia* and *Betta splendens*. The floating or sinking eggs (presumably according to the different structure of the eggs, Soin et al. 1973) are picked up, blown

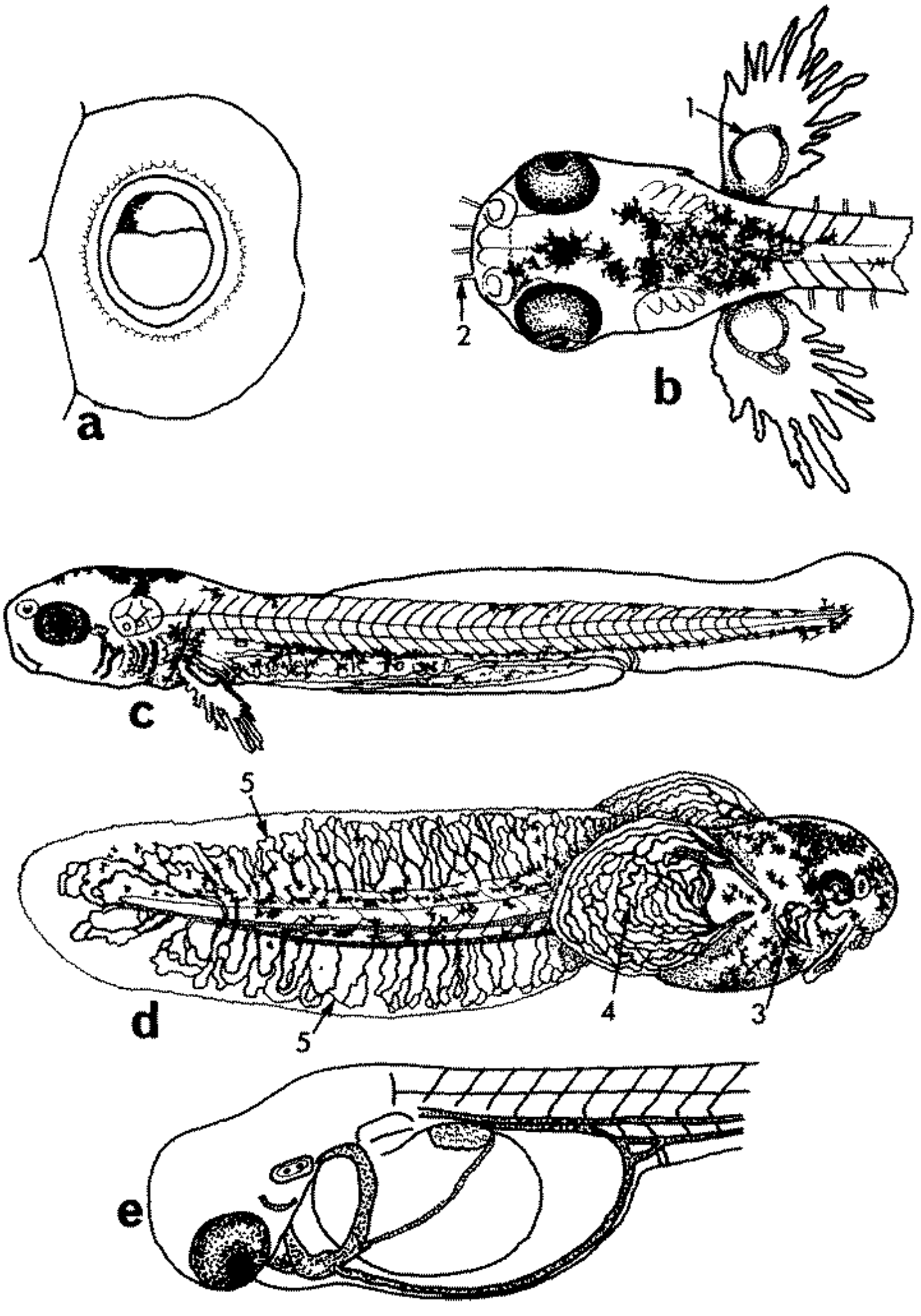

FIG. 11. a–c. Psammophilous nest spawner *Abbotina rivularis*: a, egg in gelatinous secondary membrane, b, protopterygiolarva 5.1 mm long from above (1 = respiratory snares of vessels in pectorals, 2 = cupula), c, same, from the left side; d, eleutheroembryo of *Haplosternum* sp. 6.5 mm long (3 = respiratory vessels in gill cover, 4 = respiratory vessels in pectorals, 5 = respiratory vessels of segmental and caudal veins in embryonic fin fold); e, anterior part of *Macropodus* sp. with respiratory vessels (see Fig. 10b for explanations). After (a) Nakamura 1969, (b, c) Kryzhanovsky et al. 1951, (e) 1953, and (d) Kryzhanovsky 1949.

into the bubble nest, and cared for by the male. *Sphaerichthys osphromenoides* and *Betta brederi* have been reported to build froth nests while keeping some of the eggs in the mouth or sometimes even practicing mouthbreeding (Kühme 1962). Sometimes the female blows a few mucous bubbles and cares for some of the eggs; more often, however, she is driven away by the male. *Macropodus cupanus* builds a less substantial bubble nest that is often in midwater among plants, or even in a shell on the bottom. *Colisa fasciata* reinforces its froth nest with small plant fragments. The floating eggs of *Belontia signata* and *Ctenops vittatus* are placed in a few bubbles only.

"The froth nests of these fishes are considered of importance as a depot for the eggs, protection from suffocation, protection from sunlight, attractant for microorganisms on which the fry can feed, an oxygen reservoir for the developing fry, and as an anchor for the eggs amid plants. To this list might be added a protective effect against small marauders, such as other small fishes and aquatic insects." The embryonic respiratory organs on the yolk are known to be well developed (Kryzhanovsky et al. 1953) in spite of good oxygen conditions within the froth nest (Fig. 11d, e).

Speleophils (B.2.5) are a large polyphyletic guild of fishes guarding their spawn in natural holes and cavities or in specially constructed burrows. The majority simply deposit their eggs on a cleaned area of the undersurface of flat stones and the male guards the eggs. The eggs can be in a single layer or in two, as well as in a multilayered mass. The eggs will, in general, have good oxygen conditions during their incubation (Morris 1954), and thus, the embryonic respiratory organs are only moderately developed (Fig. 12a). Many fishes can be fitted in this guild, as for example, *Pimephales notatus*, *Noturus flavus*, *Astroblepus chatae*, *Therapon jarbua*, some *Etheostoma* spp., some *Gobius* spp., *Sicydium japonicum*, *Ernogramus hexagrammus*, *Ophidion elongatus*, *Artedius fenestralis*, and *Cottus* spp.

Eupomacentrus leucorus builds its nest in similar holes under rocks; however, the cavity is first thoroughly sandblasted. Egg attachment on a vertical rock surface was reported in captive fish (Breder and Coates 1933), and this indicates the possible origin of the strategy to guard spawn in natural cavities which give more protection than an exposed substrate. The related *E. leucostictus*, as well as *Abudefduf zonatus* and many other members of this guild guard their spawn inside empty shells or under stones or shells (Keenleyside 1972). In some, the eggs are spherical, in others, more or less elliptical or cylindrical (Breder 1943); some of them have special adhesive threads at the pole of attachment. Others are glued together by a sort of secretion (*Ancistrus anisitsi*). In the last mentioned example strong embryonic respiratory adaptations to hypoxic conditions are present.

In *Anoplarchus purpurescens* and *Macrozoarces americanus* the female guards the adhesive eggs under stones and often she can be found coiled around them. *Eleotris oxycephala* has pear-shaped eggs with a short stem that attaches to the inner surface of an old piece of bamboo. The male of *Opsanus tau* guards large adhesive eggs 5 mm in diameter in a nesting cavity, for which human artifacts are preferred if available. The eggs are glued to an adhesive disc, produced before they are attached. Even after hatching, the eleutheroembryo can free itself only when the yolk is nearly absorbed, because the yolk is attached to the inner side of the egg membrane. *Paraclinus marmoratus* uses the inside of the sponge *Verongia fistularis* as spawning cavities and a few other fishes are reported to do the same. *Chaenogobius castanea* "deposits its eggs in the nearly vertical burrows of the shrimp *Upogebia*."

Other members of this guild build more or less elaborate burrows of their own. *Steatocranus casuarius* dig holes under stones; others dig them in sand or clay (*Cichlasoma maculicauda*) and may use an empty shell as a roof (*Gobius niger*, *G. minutus*). *Ancistrus anisitsi* digs tunnels in banks at the edge of a swamp, as does *Symbranchus marmoratus*. *Fluta alba* builds a U-shaped hole in a muddy bottom and is reported to have strongly developed embryonic and larval pectoral fins and fin folds with respiratory blood vessels. These fins are later fully absorbed and are absent in adults. *Pseudobagrus fulvidraco* builds vertical nest-burrows 9–14 cm deep in the bottom and the male guards the eggs (Fig. 12b). Recently *Acarichthys heckeli* was discovered to excavate tunnels in the bottom (Cichocki 1974). *Acanthogobius flavimanus* excavates Y-shaped burrows. More complex burrows are built by *Protopterus* sp., the male of which digs a long tunnel and an oval-shaped chamber, sometimes with more than one entry. The eggs are deposited inside the chamber, probably by more than one female. The oxygen concentration is very low in such a nest, where there are as many as 500 larvae at one time. The young commence air breathing only after 50 days, while still returning into the nest,

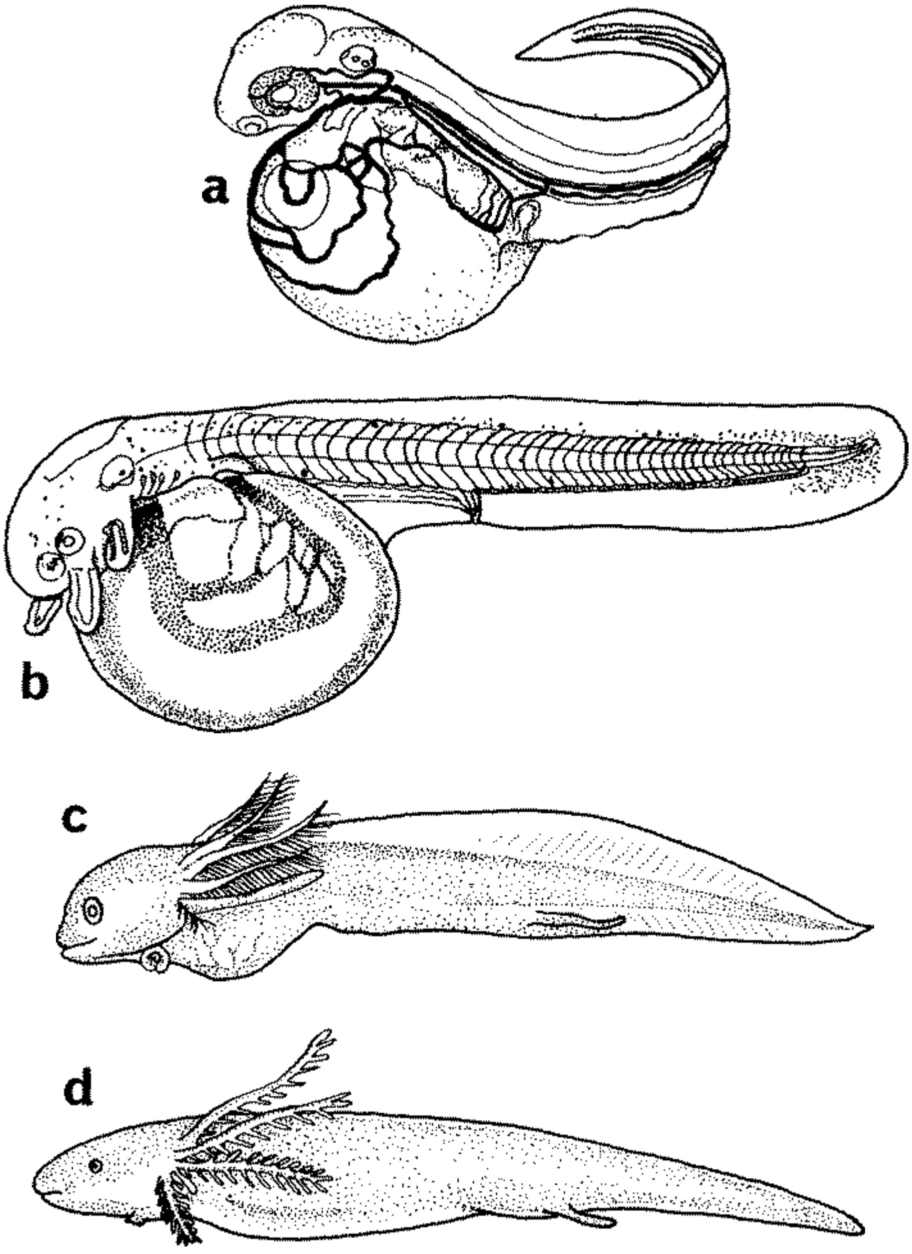

FIG. 12. a, Embryo of *Cottus* sp., b, eleutheroembryo of *Pseudobagrus fulvidraco* 5 mm long, and larvae c, of *Protopterus* and d, *Lepidosiren*. After (a) Portmann 1927, (b) Kryzhanovsky et al. 1951, and (c, d) Kerr 1910.

and when about 23 mm long (Greenwood 1958). The well-developed embryonic respiratory organs are assisted by the large external gills (Fig. 12c).

Some differences are reported in the construction of burrow-nests and in the development of eggs in different species (Brien and Bouillon 1959). Hibernation in a parchment cocoon in the dry season is in some species reported to be facultative. Adaptations for incubation under hypoxic conditions are even more elaborate in

Lepidosiren paradoxa. A long tube-like burrow with an entrance 10–12 cm in diameter is excavated on the bottom of a swamp. The burrow leads a short distance down but after an abrupt turn continues to lead for over 1 m horizontally directly to the nesting chamber. The pelvic fins of the guarding male change at nesting time into broom-like, highly vascularized organs that are able to release oxygen inside the hypoxic chamber and supply the much needed oxygen to the developing offspring (Fig. 12d).

Because of a large variety of adaptations for incubation in cavities and holes, I feel this guild is too broad to serve its purpose. Barlow's (1974) conclusion "that virtually all of the Central American cichlids are concealment breeders" expresses best the existing confusion. Fishes excavating special burrows and those guarding spawn in shallow and existing cavities, i.e. undersides of rocks and inside of shells and sponges, as well as in human artifacts (tin cans, boards, boxes) should be classified as belonging to separate guilds. However, not enough data are available on embryonic respiratory organs of either group to characterize with confidence two such separate guilds.

Canada: *Pimephales notatus*, *P. promelas*, *Ictalurus natalis*, *I. nebulosus*, *I. punctatus*, *Noturus flavus*, *N. gyrinus*, *N. miurus*, *Etheostoma flabellare*, *E. nigrum*, *Cottus aleuticus*, *C. asper*, *C. bairdi*, *C. cognatus*, *C. confusus*, *C. rhotheus*, *C. ricei*.

Europe: *Romanichthys valsanicola*, *Blennius fluviatilis*, *Padogobius nigricans*, *P. panizzai*, *Pomatoshistus canestrini*, *P. caucasicus*, *P. longecaudatus*, *P. microps*, *Proterorhinus marmoratus*, *Cottus gobio*, *C. poecilopus*.

Polyphils (B.2.6) are fishes that are not particular in the selection of nest building material and substrate. Some attach their adhesive, spherical, or cylindrical eggs to any cleaned surface (gravel, sand or sod) and subsequently guard the clutch (*Notopterus chitala*, *Badis badis*); others build nests of seaweeds or stones. The eggs form tough and rubbery masses that are, for example, red or yellow in *Myoxocephalus scorpius* and "maroon to bright crimson" in *Scorpaenichthys marmoratus*. *Hoplias malabaricus*, *Lepomis gibbosus*, *Enneacanthus chaetodon*, and *Taudanus taudanus* build circular nests (Clark and Keenleyside 1967), usually leaving sticks and rootlets in place. These nests are among or next to plants growing in muddy or sandy shallows of slow rivers or lagoons. The last species also uses its mouth to carry gravel and sticks in its nest. In all species the male guards the eggs (Fig. 13a).

Both males and females of *Arapaima gigas* build nest-holes, 60 cm in diameter and 20 mm deep, in the bottom where there is a current. The young accompany their mother, while the male guards them from some distance. White tubercles on the head of the guarding female are said to provide some kind of food for the young. In *Symphysodon discus* the nest is built or a nesting area is cleaned on rocks, sand, or plants with exposed rootlets. The mucus covering the body changes into a whitish, granular, and adhesive substance on the dorsal parts of both guarding parents and the young feed on this (Wickler 1973). In other cichlids this phenomenon occurs to a lesser degree (e.g. Noakes and Barlow 1973).

Heterotis niloticus builds a circular nest about 1 m in diameter and 20 to 60 cm deep in swamps. The rim of the nest is a high wall formed out of plant chunks. This wall is about 15–20 cm thick and projects above the water surface. The bottom is a clean platform of clay or mud. After the spawning act the fish leave by way of a hole in the wall, through which, 5 days later, the young leave the nest and are guarded by the male. For example, the nest of *Crenilabrus quinquemaculatus* "of fibrous plant material mixed with sand and gravel, was described as hemispherical in shape and exceeding 20 cm in diameter, with an opening near the bottom." The courtship and guarding of *Crenilabrus* is very similar to that of the stickleback.

Canada: *Lepomis gibbosus*.

Ariadnophils (B.2.7) are, with some exceptions, a monophyletic guild. Skill in nest building and parental care are remarkably developed. The nest building male has the ability to spin a viscid thread from a kidney secretion, which binds the nest of different material together. More than one female may lay eggs in the nest of one male, but only the male remains to guard. The nests are built of various materials and differ in shape and position (Wunder 1930; McInerney 1969; Rowland 1974a). Different species build their nests in a variety of habitats and different species deposit their eggs in a variety of places within it. In order to survive the eggs have to be constantly ventilated by the guarding male. The male guards the young after they hatch (Fig. 13b) until he can no longer orally return the wandering offspring back in the nest. Up to 200 eggs from 5 to 7 females were reported in one nest. One male sometimes guards several nests, skillfully rotating the order of ventilation. This makes the male of the stickleback "about the busiest thing among fishes that can well be imagined." Ventilation is achieved by fanning with the pectoral fins, or by

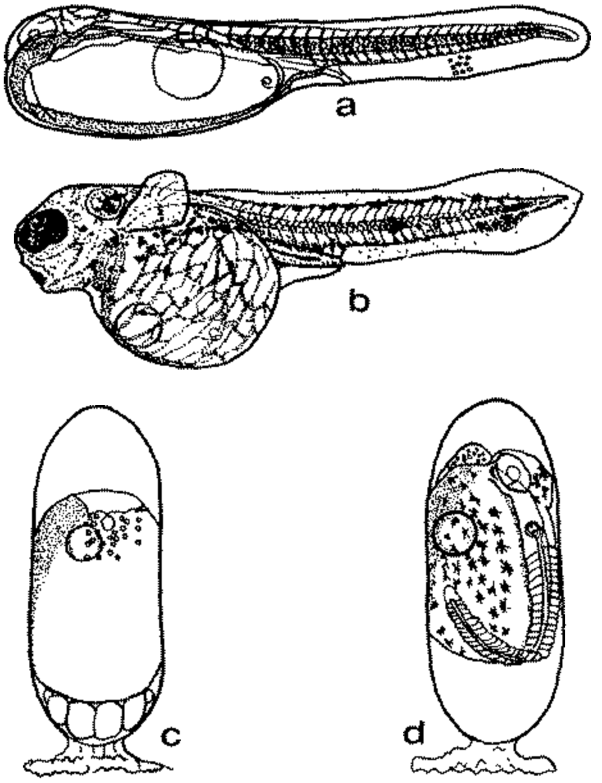

FIG. 13. a, Eleutheroembryo of *Lepomis gibbosus* 3.1 mm long, b, *Gasterosteus aculeatus* 4.3 mm long and eggs of *Amphiprion chrysopterus*, c, after 3 h of incubation in early cleavage phase, d, after 48 h in the middle of embryonic phase. After (a) Balon 1959c, (b) Kuntz and Radcliffe 1918, and (c, d) Allen 1972.

pumping water through the openings of the nest with the mouth, in a sort of speeded-up respiration. The male of *Apeltes quadracus* is reported to ventilate the eggs "by placing his snout into the hole [in the side of the nest] and sucking water through the nest by beating movements of his opercula" (Rowland 1974b).

The only non-stickleback with a similar ability is *Aulorhynchus flavidus*, which utilizes "algal fronds [which it binds] by means of a thread-like secretion in such a fashion that the growing frond tips point downward. ... The eggs are then placed above the place of binding, an activity that would seem to be derived from a former nest-building habit." The eggs, 2 mm in diameter, ranging in color from red to tan, are deposited in more than one cluster and are guarded by the male. Possibly other non-sticklebacks should be included in this guild. The British wrasse, *Crenilabrus melops*, was reported to build elaborate nests of algae (Potts 1973), and can be considered as a potential member of ariadnophils if the use of thread-like secretion is proven.

Canada: *Apeltes quadracus, Culaea inconstans, Gasterosteus aculeatus, G. wheatlandi*, and *Pungitius pungitius*.

Europe: *Gasterosteus aculeatus, Pungitius pungitius*, and *P. platygaster*.

Actinariophils (B.2.8) nest under the active protection of the tentacles of sea anemones (e.g. *Radianthus*). An area next to the pedal disc of an actinarian is cleaned, and cylindrical eggs (Fig. 13c, d) are attached to it. Both parents guard intermittently, fan with their pectoral fins and occasionally with their caudal fins, mouth the eggs, and exhibit substrate nibbling at the periphery of the egg clutch, similar to the initial cleaning activity. Dead eggs are eaten. Mouthing may involve coating the eggs with a mucus that protects the eggs against nematocysts. The tentacles of the anemone frequently brush the egg clutch without harming it. Hatching occurs in a week and during the night. The eleutheroembryos first sink to the bottom but then immediately swim up in zigzag fashion to the surface. A phototropic reaction has been observed. Larvae swim near the surface during the daytime and lie on the bottom at night. Soon after this short pelagic mode of life, early juveniles 6–8 mm long select their host anemone and begin their acclimation by careful and brief contacts. At this time they are promptly stung but they dart away. After 24 hours, however, they are able to enter the oral disc of the anemone without harm. Probably in different species (Allen 1972) either the fish or the actinarian becomes acclimated.

Only 26 species of the pomacentrid genus *Amphiprion* are presently known to have this nesting dependency on actinarians.

C. Bearers

EXTERNAL BEARERS (C.1)

External bearers carry their developing eggs on the surface of their bodies or in externally filled body cavities or special organs.

Transfer brooders (C.1.1) encompass fishes that carry their eggs for a certain time before depositing them. In some members of this guild only two to four large, adhesive eggs are released at a time into a "basket" formed by the cupped ventral fins (see photographs in Axelrod 1971, p. 28–34). Female *Callichthys fasciatus* and *Corydoras* sp. carry the spherical eggs in their fins during a prolonged search for a suitable place to attach them. Other members of this guild such as *Cubanichthys cubensis* and *Oryzias* spp. have 20–40 eggs, about 1 mm in diameter, hung in a cluster from the genital pore of the female (see photograph in Axelrod and Shaw 1967, p. 385). Yamamoto (1967) described this condition in *O. latipes* as follows: "After the ova are expelled *en masse* at the time of mating, a cluster of eggs remains attached to the belly of the female for some hours, suspended from the oviduct pore by fine threads attached to the chorion." Some observers noted that the eggs were carried by the female until they hatched; others found that the female sought out convenient notches between a plant leaf and stalk in which to catch and tear off the egg cluster. Nevertheless, in *Corydoras* and *Oryzias* these procedures seem to be an adaptation to removing the eggs from the spawning site, because the attention of predators drawn by the spawning act endangered the eggs. This guild has probably less phyletic significance for the guilds that follow it than has, for example, the hen-like guarding in *Loricaria* (B.1.1) for the skin brooders (C.1.5) and pouch brooders (C.1.6), or the mouth-transfer of eggs by nest spawners (B.2.1) for the mouth (C.1.3) and gill-chamber brooders (C.1.4). However, the possible relationship of the second type of transfer brooders with the forehead brooders cannot be denied.

Forehead brooders (C.1.2) are a unique monophyletic guild. Maturing males of *Kurtus gulliveri* and *K. indicus* gradually develop a hook on the superoccipital region. This hook juts forward and out from the forehead and the tip is bent downward (Fig. 14a). In the spawning season, this appendage is covered with a thick layer of skin. A cluster of eggs, attached by a thread looped through the hook, is carried on the forehead (Fig. 14b). When the eggs are hanging from the oviduct pore, they are probably collected by the male. This situation is similar to that described for the previous guild.

Mouth brooders (C.1.3) incubate their eggs in the buccal cavity and form a diverse polyphyletic guild. Mouth brooding evolved from the substrate guarders' practice of cleaning and taking eggs into the mouth during hatching, and of transferring the brood orally from incubation substrate to nursery pits. Transfer brooders could also have contributed to the development of mouth brooding (Oppenheimer 1970). The female of *Tachyrus argyropleurodon* deposits her eggs in a basket formed by the pelvic fins from which she transfers them directly to the mouth of the male. In *Apogon imberbis* "eggs are cast in a single mass of material bound together by tendrils arising from one pole of the eggs. The male immediately takes them in his mouth. ... The eggs are spat out by the male near the time of hatching." In *Apogon semilineatus*, which practices a similar egg transfer, both sexes brood the eggs orally. The female of *Glossamia gilli* releases her eggs grouped in a thin membrane. The male tears this apart immediately and takes the eggs, one at a time, into his mouth. Evolutionarily, probably only the males developed this habit, and it is still restricted to males among such species as *Bagre marinus*, *Galeichthys felis*, *Netuma commersoni*, *Arius falcarius*, *Potamarius nelsoni*, and *P. izabalensis*.

In true nesting fishes, however, first "both sexes take part in excavating a nest hole for the reception of the eggs, after which the female takes them into her mouth." This is also the case with *Pelmatochromis* spp. In more advanced brooding

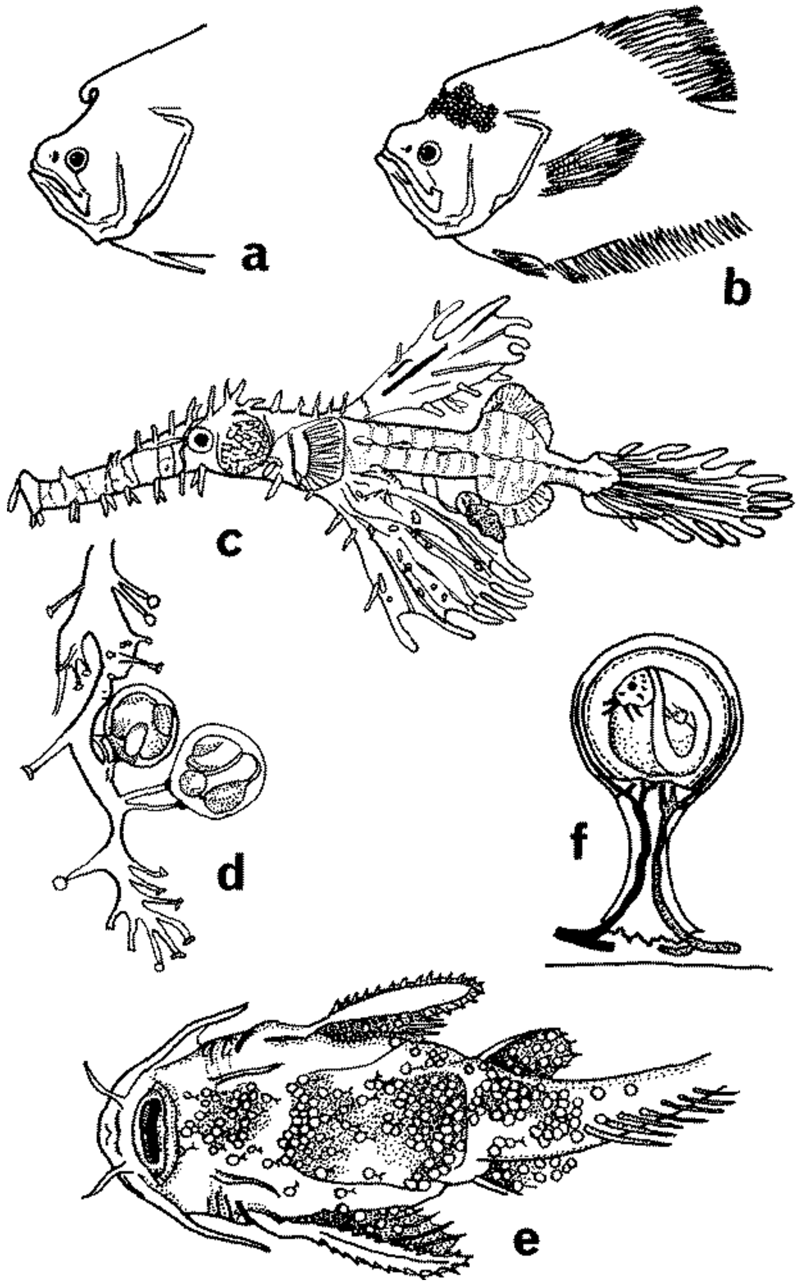

Fig. 14. a, b, Foreheads of *Kurtus gulliveri* males with bare hook (a) and with lodged egg cluster (b); c, d, female of *Solenostomus* (c), detail of pelvic fin of female with attached eggs (d); e, f, ventrum of *Aspredo* female with attached eggs (e) and detail of an egg on stalk within vascularized skin capsule (f). After (a, b) Guitel 1913, (c, d) Willey 1910, and (e, f) Wyman 1859.

strategies in *Haplochromis* spp., *Tylochromis* spp., and some *Sarotherodon* spp., the protective collection of eggs is carried out immediately after deposition, and fertilization is ensured within the buccal cavity. Even then sometimes elaborate, closely guarded sand nests are built (*Haplochromis heterodon*, *Sarotherodon karomo*) by the male. These nests are usually species-specific, circular depressions in the sand ranging from 0.3 to 1 m in diameter. They have conical mounds and various types of rims and eccentric grooves. Smaller nests are excavations produced by fin and body movements. "... the nest is built up by the laborious process of moving mouthfuls of sand into the correct position, and by this method some of the most elaborate and beautiful nests are constructed" (Fryer and Iles 1972).

Males of these species possess bifid genital tassels or pigment egg-dummies on the anal fin, which stimulate females to inhale sperm before and after egg laying and egg pickup. The same is true for the free spawning (without a nest) *Tropheus* whose eggs can be moved immediately to the protection of the mouth without losing time in depositing them in a nest for external fertilization. This is vital in a crowded habitat, or where egg-eating specialists are never far away (Fryer and Iles 1972).

Mouth-brooding individuals can usually be recognized by a marked downward deflection of their buccal cavity. The eggs are few but large. *Tropheus moori* and *Labeotropheus trewavasae* in my aquaria carried only two to eight eggs per female and it is unlikely that in nature they can brood more than 20 eggs. The eggs are spherical or elliptical, with a maximum length of only 3 mm in some species but as large as 7 mm in *T. moori* and *Hemibates stenosoma*. *Osteoglossum bicirrhosum* carries about 20 eggs 6 mm in diameter, whereas males of *Bagre marinus* carry over 50 eggs of about 20 mm in diameter, a size also reported for *Arius dispar*.

The yolk in the eggs of most mouth brooders is very concentrated; water content is only 50–60%. Early in the embryonic phase a strong blood circulation develops with networks of respiratory vessels spread out in the dorsal and anal fin folds and on the yolk. After hatching, the egg membranes are usually swallowed by the brooding parent. Except in *A. imberbis*, the larvae are brooded to the end of larval period (if such exist), and only the relatively large, free swimming pterygiolarvae or juveniles (like those in salmonids) are released from the mouth. With some exceptions, the young periodically seek refuge in their mothers' or fathers' mouths, and they are herded for some time. No cement glands are present.

None are known from freshwaters of Canada or Europe.

Gill-chamber brooders (C.1.4) may be derived from mouth brooders; they include, so far as is known, only the North American cavefishes. *Typhlichthys subterraneus*, *Amblyopsis spelaea*, *A. rosae*, *Speoplatyrhinus poulsoni*, *Chologaster agassizi*, and *C. cornuta* incubate their eggs in their gill chambers. The female probably takes the eggs into her mouth and subsequently passes them into the gill cavity, where they go on developing until some time after hatching. In the end, the gill cover muscles usually slacken and the young fall out. About 70 eggs 2.3 mm in diameter are reported per female.

Skin brooders (C.1.5) are a specialized guild. Females in some species or males in others carry the eggs attached to the ventral surface of their body. Females of a group of South American catfishes, which includes *Bunocephalus* spp., *Aspredo* spp., *Platystachus* spp., and *Loricaria piracicalae* develop a special, differentiated, spongy skin on their ventrum. These females roll on the eggs after they have been fertilized and the eggs adhere to the skin. After some time a cup with a stalk envelops each egg. This cup, which grows from the skin, is vascularized (Fig. 14e, f) and performs some kind of gas and nutrient exchange. This type of reproductive strategy is also used by some pipefishes, in which females loosely attach groups of eggs or single eggs to the ventral surface of the male during copulation. The eggs become embedded in a spongy mass on the males' ventrum (*Entelurus aegnoreus*, *Nerophis*, *Phyllopteryx*) or attached singly to special stalks. Skin incubation probably gave rise to the next guild (Fig. 14c, d).

Pouch brooders (C.1.6) encompass the same phyletic lines as skin brooders. The eggs, similarly incubated on modified skin, are enveloped by specially transformed structures, or covered with a membrane or plates, thus forming a marsupium. In *Loricaria vetula* and *L. anus* the pouch is formed by an enlarged and everted lower lip of males. In females of *Solenostomus* spp. the very large ventral fins "with their inner margin adnate to abdomen, their outer margins united at their base for a short distance, [form] a large pouch for the reception of the eggs, which are fastened by peduncles on threadlike filaments of the abdominal skin" (Weber and de Beaufort 1922). In pipefishes and seahorses (*Syngnathus*, *Siphistoma*, *Penetopteryx*, *Stigmatophora*, *Hippocampus*) a special marsupium is formed on the ventrum of the males. The brood pouch can be membranous or covered by protective bony plates. In some, the eggs are embedded in a spongy skin covered only by lateral protective plates (see photograph in Axelrod and Shaw 1967, p. 86). The eggs are deposited in the pouch during mating when both partners embrace face to face. The protruding oviduct of the female is "thrust into the buttonhole-shaped opening at the anterior end of the marsupium"; the eggs are fertilized as they pass into the pouch. About 150 eggs can be incubated. One female fills up the pouches of more than one male, or one male collects eggs from several females if his pouch has not been filled by the first female. The male is capable of pushing eggs to his pouch by peristaltic motions. The same mechanism is also used to flush out the empty pouch before new eggs are accepted. The offspring leave the pouch late, as juveniles.

None occurs in freshwaters of Canada; in Europe: *Syngnathus abaster* and *S. nigrolineatus.*

INTERNAL BEARERS (C.2)

The eggs are fertilized internally before they are expelled from the body cavity. Special organs are sometimes (or ? usually) developed to facilitate sperm transfer. Mating does not necessarily coincide with fertilization. After an initial copulation, sperm can be stored for a lifetime. After fertilization the eggs can be expelled and incubated externally or retained in the body cavity of the female, after which full-grown juveniles are born. Because an excellent review has recently been published by Hoar (1969), only the most basic data will be given in the following text.

Ovi-ovoviviparous (C.2.1) fishes, which form this intermediary polyphyletic guild, lay eggs fertilized internally. Egg expulsion can take place at the moment of fertilization, at the beginning of cleavage, or at any time during the embryonic phase. Internal fertilization is effected by special, often complicated, organs. In *Corynopoma riisei, Glandulocauda inequalis, Coelurichthys microlepis, C. tenuis,* and *Gephyrocharax valencia,* it has been suggested that "sperm vesicles are lodged in the female's oviduct" without a copulatory organ and "spawning occurred in the absence of males" (Nelson 1964). In elasmobranchs the eggs are internally fertilized with the help of large mixopterygia. After fertilization the eggs are coated in a durable horny case. In *Heterodontis francisi* and *H. galeatus,* for example, the eggs have the shape of a capsule with a double spiral; *Rhincodon typus, Scyliorhinus canicula, Galeus melanostomus,* and *Raja* spp. produce squarish eggs with long spiral tendrils at each corner. In some species these tendrils entangle objects and assist in further expulsion of the egg. In *Ginglymostoma cirratum* the horny egg capsule ruptures long before the expulsion of the embryos. The embryos have external gill filaments and can develop normally in sea water if surgically taken out of the female. Incubation is usually long, 10 or so weeks, and the number of eggs very low. Twenty-six young were reported from a female of *G. cirratum. Chimera* spp., *Callorhynchus,* and *Hydrolagus* have an additional frontal clasper and eggs in a horny case with two lateral fins.

Males of *Trachycorystes striatulus, Asterophysis* spp., and *Tatia* spp., for example, have a fleshy intromittent organ. Eggs are fertilized after ovulation and before they are extruded. *Phenacostethus smithi* has a complicated fleshy copulatory organ called a priapium, which in *Gulaphallus mirabilis* is assisted by special grasping organs, the toxactinium and the ctenactinium. Recently, an entirely different copulatory organ has been described in *Pantodon buchholzi,* a fish that has for some time been known to deposit internally fertilized eggs (Lastein and van Deurs 1973). *Tomeurus gracilis* has an elaborate gonopodium. The female deposits eggs, always attaching them to some object by long filaments on the chorion. The eggs can also be incubated internally. In either external or internal incubation, the embryos of this species develop a normal pericardial serosa that completely envelops the head and that is similar to the true livebearing *Xiphophorus* or *Gambusia. Horaichthys setnai* produces similar embryos from eggs 0.21 to 0.35 mm in diameter after 10–20 days of incubation. The genital pore of the female, however, is deflected to one side matching a similar deflection of the gonopodium in the male.

Ovoviviparous (C.2.2) fishes incubate their eggs in the body cavity where they grow by utilizing the yolk. Fertilization is internal and is usually facilitated by intromittent organs. "*Latimeria* lacks pelvic claspers or anal fin specialized as an intromittent organ ..., but males do possess modifications of the cloacal region, which are possibly developments for internal fertilization. These are the extension of the cloaca into a tubercle, and a series of surrounding erectile caruncules" (Griffith and Thomson 1973).

The deposition of eggs or embryos in members of this guild is delayed until hatching or even beyond that. Radioisotope studies have proved that nutriments are not taken by embryos from the female (*Scyllium*) during incubation and gestation in her body. Well-formed egg cases with rudimentary tendrils are often incubated in the female body for a year or up to 22 months

(*Chlamydoselachus anguineus*, *Hexanchus griseus*, *Notorynchus maculatus*, *Scapanorhynchus owstoni*, *Squalus* spp., etc.). It is reported that a female elasmobranch can have from 2 to over 100 embryos. The eggs are large and single or up to four or five per case, and the case is sometimes divided into chambers (*Pristis* sp.).

On January 5, 1972, a female of *Latimeria chalumnae*, 1.63 m and 78 kg, was landed at Anjouan with 19 eggs 85–90 mm in diameter (Anthony and Millot 1972). "We agree that this evidence makes the occurrence of viviparity in *Latimeria* unlikely, but we feel that there is a strong possibility that the living coelacanth is ovoviviparous, providing an ample supply of nourishment prior to fertilization but maintaining the embryo internally during early development. ... Finally, we note that the very size of *Latimeria* eggs is a strong argument that this species has a high degree of parental care, involving either ovoviviparity or guarding a cluster of eggs. It is difficult to believe that *Latimeria* could survive at all unless the small number of eggs were protected from predation" (Griffith and Thomson 1973).

Sebastes marinus expels the embryos just before or after they hatch from eggs 0.18–0.38 mm in diameter. The eleutheroembryos are poorly developed. The deep water brotulid *Cataetyx memorabilis* hatches at the time of parturition (Meyer-Rochow 1970), while another brotulid *Dinematichthys ilucoeteoides* was reported to hatch within the ovary long before parturition (Wourms and Bayne 1973). *Xenopoecilus poptae* from Celebes (= Sulawesi) lakes is an exemplary type for this guild. "As soon as the eggs are extruded, the young fry is hatched and swims with the mother. In the period of [parturition], broken egg membranes, rising to the surface, cover extensive stretches" (Weber and de Beaufort 1922). Another pelagic genus *Comephorus* of Lake Baikal has very similar parturition. In contrast to the other members of this guild, and the members of the following guild, *Comephorus* is known to produce large quantities of eggs per female.

Viviparous (C.2.3) fishes produce embryos whose partial or entire nutrition is supplied by the female via special absorptive organs (Turner 1940a, b, c, d), i.e. endogenous nutrition from the yolk is supplemented already in the prenatal phase by exogenous nutriments from the mother (Amoroso 1960; Hoar 1969). Fertilization is internal, but one group of these fishes lacks intromittent organs. *Carcharias taurus* seems to produce one young at a time, which is free within the body cavity and feeds on eggs gradually produced by the female. A large experienced predator is born. In general, however, an intimate association develops between the uterine wall of the female and embryos and 10–70 placental young per litter are born. An extended gestation period of up to 12 months was reported in elasmobranchs (Matthews 1950) that have these adaptations: *Carcharhinus milberti*, *Prionace glauca*, *Galeocerdo cuvieri*, *Mustelus canis*, *Eulamia floridana*, to mention only a few.

No more than 50 young in a litter are born to livebearing teleosteans and gestation does not, in general, take longer than a month. Males of many species including *Goodea luitpoldi*, *Neotoca bilineata*, and *Hubbsina turneri*, do not possess intromittent organs, whereas all the other members of this guild have claspers, clasper-like penises, or complicated gonopodia. Nutriment absorption and gas exchange from the female is achieved through the transformed embryonic fin fold or special processes (trophotaeniae), which the embryos develop for this purpose (Fig. 15a, b, c). The poeciliids are best known for having unchorionated eggs and superfetation, i.e. eggs without egg membranes, and the ability to carry several litters at different stages of development instead of a single litter at a time. Here, also, a special pericardial serosa (*Poecilia*, *Xiphophorus*, *Gambusia*, etc.) replaces the absorptive processes (*Parabrotula plagiophthalmus*) for the absorption of nutriments from the mother (Fig. 15d). This serosa can, in some, completely envelop the head. Fishes of different phyletic origin and with different adaptations for embryonic exogenous nutrition belong to this guild.

Discussion and Conclusions

The exploitation of ecosystem resources is dependent entirely on the density of each exploiting fish taxon. In a natural multispecies system, the available food resources, if left unutilized by the disappearance of one taxon, are eventually utilized by another. This is, in the long run, reflected in much the same total production within the same nutrient load, irrespective of the fate of single fish taxa (Balon 1974). Furthermore, a single taxon of fish can change readily from one feeding habit to another, which is known as changes from one type of "population dynamics" to another as reported earlier (Balon 1963). Even changes in skeletal structures are reported to accompany changes in food (Greenwood 1965) and extreme specialists like eye-biters, fin-eaters, or scale-eaters (Roberts 1970; Fryer and Iles 1972) are now known to be exceedingly inconsistent in their food preference. In my aquaria they in general

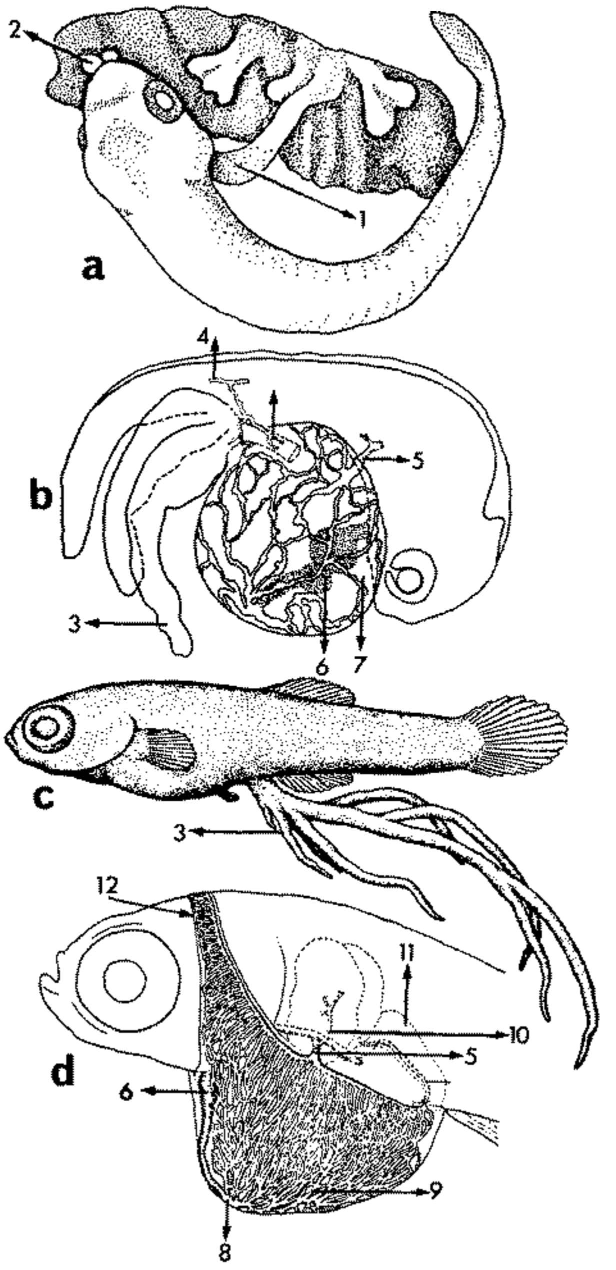

FIG. 15. a–d, Embryos and larvae of livebearing fishes with absorptive organs for "placental" nutrition: a, larva of *Jenynsia lineata.* Ovarian flap, extending through gill slit into the pharyngeal and buccal cavities, protrudes from the mouth (1 = trophonema, flap of ovarian tissue, 2 = tip of the ovarian flap), b, embryo of *Girardinichthys innominatus* 2.5 mm long with a combination of pericardial network and trophotaeniae (3 = trophotaenia, 4 = caudal vein, 5 = ductus Cuvieri, 6 = heart, 7 = pericardial sac), c, larva of *Zoogonecticus cuitzooensis,* after recession of the pericardial network accompanying the yolk sac absorption, uses highly vascularized trophotaeniae for respiration and absorption of the ovarian secretion, d, embryo of *Poecilia reticulata* with fully developed pericardial serosa and neck strap for absorption of ovarian secretion (8 = sinus venosus, 9 = portal system, 10 = hepatic vein, 11 = intestine, 12 = neck strap). From (a) Turner 1940d, (b, c) Turner 1940c, and (d) Turner 1940a.

TABLE 2. Number of indigenous freshwater fish species per guild in different faunae. References at right are the sources of the primary faunal lists and numbers of species.

	A.								B.									C.	
Guilds	1. 1	1. 2	1. 3	1. 4	1. 5	1. 6	2. 1	2. 3	1. 1	1. 2	1. 4	2. 1	2. 2	2. 3	2. 5	2. 6	2. 7	1. 6	
Arctic Basin	3	3	15	6	3	2	4	—	—	—	—	1	—	—	4	—	2	—	Scott and Crossman 1973
Pacific Basin	1	3	22	3	2	2	10	—	—	—	—	—	—	—	6	—	1	—	
Hudson Bay Basin	4	5	20	8	7	5	10	—	—	—	—	8	2	—	10	1	3	—	
Atlantic Basin	8	11	25	18	17	6	11	—	—	1	—	10	3	—	13	1	5	—	
Canada	8	13	43	20	18	8	21	—	—	1	—	10	3	—	17	1	5	—	
British Isles	5	5	4	6	5	5	4	—	—	—	—	—	—	—	2	—	2	—	Maitland 1972
Vistula River	4	4	10	7	10	3	3	1	—	2	—	—	1	—	2	—	2	—	Balon 1964b
Danube River	5	7	11	11	13	5	5	1	4	3	—	1	2	—	2	—	2	1	Balon 1967b
Europe	13	14	41	23	29	12	10	1	8	6	—	2	4	—	11	—	3	2	Banarescu et al. 1971
Amur River	20	2	9	—	9	8	6	3	—	3	1	—	—	1	7	—	2	—	Kryzhanovsky et al. 1951

take any available food; thus, any given feeding habits seem to be retained only within a given taxocene (Chodorowski 1959), density, and environmental conditions. Therefore, from the point of view of resource exploitation, factors other than the feeding habits are more important in governing density, biomass, and production. In this sense reproductive guilds of fishes are more meaningful than feeding strategies or trophic guilds (Root 1967, 1973), the latter being actually a supplement to and a part or reflection of the first. Accordingly, sex ratio as well as occasional hermaphroditism, protandry, and protogyny will be additional adaptations related in a more important way than feeding to reproductive strategies and potential population density (Warner 1975a, b).

Most likely the importance of reproductive guilds in other animals will be similar in importance to the reproductive guilds in fishes. A convincing example is the increase of the Canada goose density by the construction of man-made breeding platforms in the prairie provinces (A. Macpherson personal communication). Largest mortality has been reported to occur during the early life of fishes, in the embryonic and larval periods (Marr 1956; Vladimirov and Semenov 1959; Balon 1960). This leaves us, at least in fishes, with the periods of life where the density is decided, and only these periods should be essential for ecological classification.

The ideal situation would now be to use the proposed concept in quantitative ratios between single guilds, in aggregated values of density, biomass or, ultimately, ecological production, similarly to earlier attempts (Balon 1966). A valid pattern should emerge, and if related to known stresses, could uncover important features of ecosystem dynamics (Smith 1968; Christie 1974), and may facilitate better (Ryder et al. 1974) understanding and construction of predictive models (Regier and Henderson 1973; Regier 1974). While data needed for such an approach are very scarce, let me in this introductory paper apply the guild concept again only qualitatively (Kryzhanovsky 1949; Balon 1962b).

The 32 guilds presented here encompass all reproductive systems known in fishes at the present time. Some unknown systems may still be discovered and the number of guilds increased, or a better understanding of some ecomorphological and physiological features of early development may cause a split in present guilds and have the same effect ultimately. In single ecosystems we shall always deal with a much lower number of guilds.

Marine systems are very different from freshwater ones. In marine systems more fishes represent guilds of guarders, bearers, and nonguarding pelagophils, whereas the majority of freshwater fishes are concentrated in guilds of nonguarders excluding pelagophils (Kryzhanovsky 1949). Similar differences seem to apply to fluvial versus lacustrine systems and to temperate versus tropical systems.

In a number of guilds (Table 2) the freshwater faunae of Europe and Canada are very much alike. The lowest number — nine guilds — occur in the British Isles and the Pacific Basin of Canada. Of the 15 guilds representing the fishes of the whole of Europe, the Vistula River has 11 and the Danube River has 14 guilds. The Arctic Basin has 10, the Hudson Bay Basin 13, and the Atlantic Basin 14 of the 14 guilds that encompass the whole freshwater fauna of Canada.

Canadian and European pelagophils are fish mainly of marine origin, whereas those in the Amur River (selected for contrast and available data) are of freshwater origin; the ratio is 8 Canadian to 12 European to 19 Amurian. Most likely geochronological sequences are reflected in these differences. Invasion routes and the different histories of survival in the geological succession of ecosystems probably played a no less important role. The evolutionary significance, for example, of the very high number of open substratum spawning and hiding lithophils in Canadian (Table 2) as compared to European waters has as yet to be understood. The same applies to guarding speleophils and the reversed numbers to guarding lithophils. All these highly significant differences certainly have a historical meaning (McPhail and Lindsey 1970) and will hopefully be correctly interpreted when more ecosystems are analyzed and compared from an historical point of view.

I have no doubt that the species in guilds of guarders and especially of bearers evolved from species with much simpler nonguarding systems. Obvious examples of such evolution in more advanced guilds were given previously. For each of them special ecosystem conditions must have been available, but the length of geological time available seems to be important. The species in the more complex guilds of guarders and bearers had to have a longer time to achieve their level of adaptation and, in general, are limited to more specific ecosystems and taxocenes (Hutchinson 1967). This availability of evolutionary time applies to the consecutive guilds along each section in the ecological classification, as well as to the entire classification. Specialization to a limited ecosystem and taxocene is also reflected in decreased ability to invade new areas. The "primitive" species in section A are the first to follow the retreat of the ice sheet; livebearers never managed to move far from very old biotopes. But in this respect ariadnophils form an exception to the rule.

The terms "primitive" and "complex," however, are rather conjectural. The morphophysiological adaptations in reproductive systems of species in A are as complex as those of species in B and C. The functions of a morphological isolatory mechanism (gonopodium) in C has a counterpart in A in the elaborate prespawning and spawning rituals (Balon 1956; Fabricius 1959; Fabricius and Gustafson 1958). The ecomorphological adaptations are interwoven with ethological adaptations throughout all reproductive systems. Where the one is missing the other is more intense.

For most species, placement in a certain guild is highly conjectural because of lack of relevant data. For some faunae placement is presently impossible. However, the needed data are accumulating rapidly and I intend, in the years to come, to elaborate further upon this ecological classification of fishes.

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