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Sammendrag:

Dette er er i stor grad det selvvalgte foredraget jeg holdt til prøveforelesningen min. Det er i hovedsak bygget på E.K. Balons arbeider og tar for seg hvilken fasinerende og komplisert prosess fisks reproduksjon er.

Emneord - norsk:	Emneord - engelsk:
1.	1.
2.	2.
3.	3.

.... Prosjektleder

.... Seksjonsleder

PREFACE

I wan´t to dedicate this article to the memory of a young friend of mine, Kristoffer who was killed in an accident when I was preparing this work. He was an aquarist like myself with a strong interest for his fishes. The memory of him has been very present during the preparation of this work.

ABSTRACT

This lecture is the chosen one given in connection to my Dr. phil. dissertation in December 1994. It is to a large extent built upon the work of E. K. Balon particularly ; Balon (1975a), Balon (1975b), Balon (1981), Balon (1984), Balon (1985), Balon (1986). The intention is to show what a fascinating and diverse process fish reproduction is. According to Balon fish species are put into 32 different guilds, separated into three different ethological sections; nonguarders, guarders and bearers. Examples from most of the different guilds are presented in this talk. In addition to this intervals in fish development are defined, and saltatory ontogeny and a hierarchical life history model are explained. Examples on indirect (with metamorphosis), transitory and direct development are given.

SAMMENDRAG

Dette er det selvalgte emnet gitt som ble gitt som prøveforelesning i forbindelse med forsvaret av doktoravhandlingen min. Arbeidet er i stor grad bygget på E. K. Balons arbeider. Hensikten har vært å vise hvilken fasinerende og komplisert prosess fisks reproduksjon er. I følge Balon kan reproduksjonen til alle arter og underarter deles inn i 32 forskjellige «laug». Navnet på disse «laugene» er til en stor grad knyttet til valg av substrat. I tillegg kan gyteadferd, larvenes adferd og pigmentering og de tidlige respirasjonsorganenes morfologi ha betydning. Disse «laugene» er samlet i tre forskjellige ethologiske seksjoner, ikke beskyttende, beskyttende og bærende arter. Eksempler fra de fleste «laugene» er vist i denne artikkelen. Videre blir de forskjellige intervallene i fisks liv og utvikling definert. At fisk utvikler seg i «rykk og napp» nødvendiggjør en hierarkisk livshistoriemodell, og dette blir nærmere forklart i dette arbeidet. Artikkelen avsluttes med eksempel på arter med indirekte utvikling (med metamorfose), direkte utvikling og en overgangsform.

INTRODUCTION

The answer to the title is both yes and no, it depends first of all what we mean with many , and if we define many several thousand, and if its egg production of marine pelagic species or economically important fish species we talk about, the answer is yes. If its egg production in the about 8000 fresh water species, 12000 species in the sea and 120 anadromous or catadromous species living today (Cohen 1970) the answer is perhaps no. If its tropical freshwater species the answer is certainly no. Among animals, bony fishes (Osteichthyes) exhibit perhaps the greatest range in clutch size. From the ovoviviparous coelacant (*Latimera chalumna*) producing a single neonate measuring a third of the females body length (Balon 1984), to the ocean sunfish (*Mola mola*) producing tiny pelagic eggs that can number over 200.000.000 per clutch (Itô 1978). In inshore fish, coral reef fish and in many freshwater species there is often evolved some kinds of guarding and bearing reproductive styles as an answer to high predation risk and to eliminate advection away from their habitat, therefore these fish often produce fewer eggs each with large amount of yolk. In this talk I will try to explain how extreme diverse fish reproduction is, I will present examples of different reproductive styles in fish, and talk about ontogeny and life history models with reference to the work of E. K. Balon.

According to Balon at the beginning, through juvenilisation, a ciliated auricularia-like larva probably became a fish-like creature. The sessile lophophore-feeding adult interval was eliminated and the first pelagophilous fish appeared (Garstang 1928, 1962; Young 1978), its entire ontogeny adapted to planktonic life (Schmalhausen 1968). In the silurian the planktonic fish-like chordates reinvaded benthic habitats and most likely evolved some kinds of guarding and bearing reproductive styles (Moy-Thomas & Miles 1971). Nevertheless, pelagophilus reproduction and pelagophilus early ontogeny have predominated throughout the ages (Johannes 1978, Balon 1978, Barlow 1981, Baylis 1981) and prevail amongst extant fish-like chordates.

An effort to make an ecological classification of the reproductive biology of fishes is made by Balon(1975, 1981) who puts the different fish species into 32 different guilds. 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». The names of the guilds refer mainly to the character of usual type of spawning ground, through other factors, such as breeding behaviour, morphology of early respiratory organs and pigments and behaviour of embryos and larvae, are equally important. 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.

The guilds are separated into three different ethological sections; nonguarders, guarders and bearers. The nonguarders is divided into two ecological groups; open substratum spawners and brood hiders. The guarders is divided into substrate choosers and nest builders and the bearers into external bearers and internal bearers (Tab. 1).

Table 1. Classification of reproductive styles of fish in ethological sections and groups (after Balon 1975a,1981).
(Inndeling av fisk med forskjellig gyteadferd i økologiske grupper, etter Balon 1975a,1981)

ETHOLOGICAL SECTION	ECOLOGICAL GROUP
Nonguarders	1) Open substratum spawners 2) Brood hiders
Guarders	1) Substrate choosers 2) Nest spawners
Bearers	1) External bearers 2) Internal bearers

NONGUARDERS

Open substratum spawners

The first nonguarding guild is the pelagic spawners (Tab. 2; Fig. 1), they are usually related to the sea, but forms of entire freshwater origin are known. They release clutches of nonadhesive buoyant eggs with a diameter between 0.5-6 mm in open water.

Table 2. The different guilds of nonguarding open substratum spawners (after Balon 1981).
(De forskjellige «laugene» som fisk som gyter fritt uten noen form for yngelpleie kan deles inn i)

GUILD	EXAMPLES
Pelagic spawners	Cod, Mackerel, Shad(maisild), Floodcarp(flodkarpe)
Rock and gravel spawners with pelagic larvae	Sturgeon(stør), Burbot(lake)
Rock and gravel spawners with benthic larvae	Minnow(ørekyt), Whitefish(sik)
Nonobligatoty plant spawners	Herring, Perch(abbor), Roach(mort)
Obligatory plant spawners	Pike(gjedde), carp(karpe), Pacific herring
Sand spawners	Gudgeon(grundling), Mullet(multe)
Terrestrial spawners	Brown mudfish, *Brycon petrosus* (Characid)

To keep buoyant the eggs absorb water and free amino acids are the active osmotic agents, many pelagic eggs contain oil globules and they can have tendrils for attachment to floating objects (Fig. 2). Another way to be buoyant is when the egg membrane swells into a gelatinous substance. This

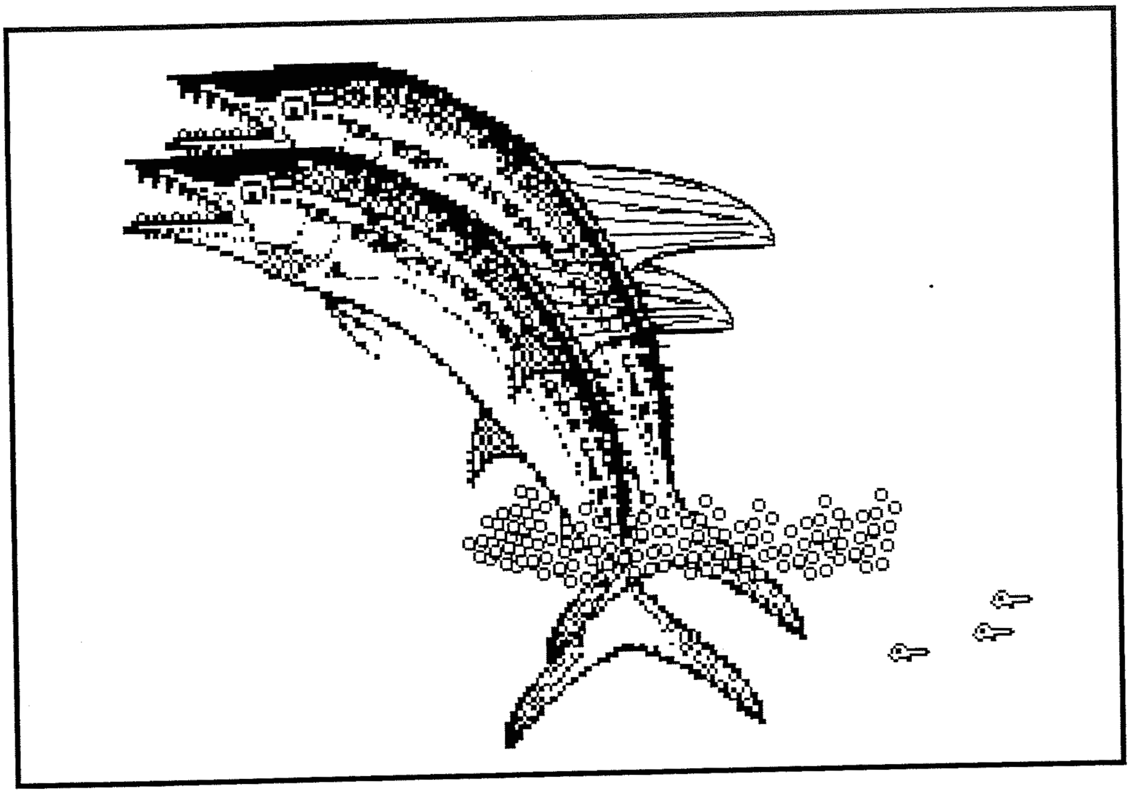


Fig. 1. A nonguarding open substratum pelagic spawner.

(Eksempel på en fisk som gyter fritt i de åpne vannmassene)

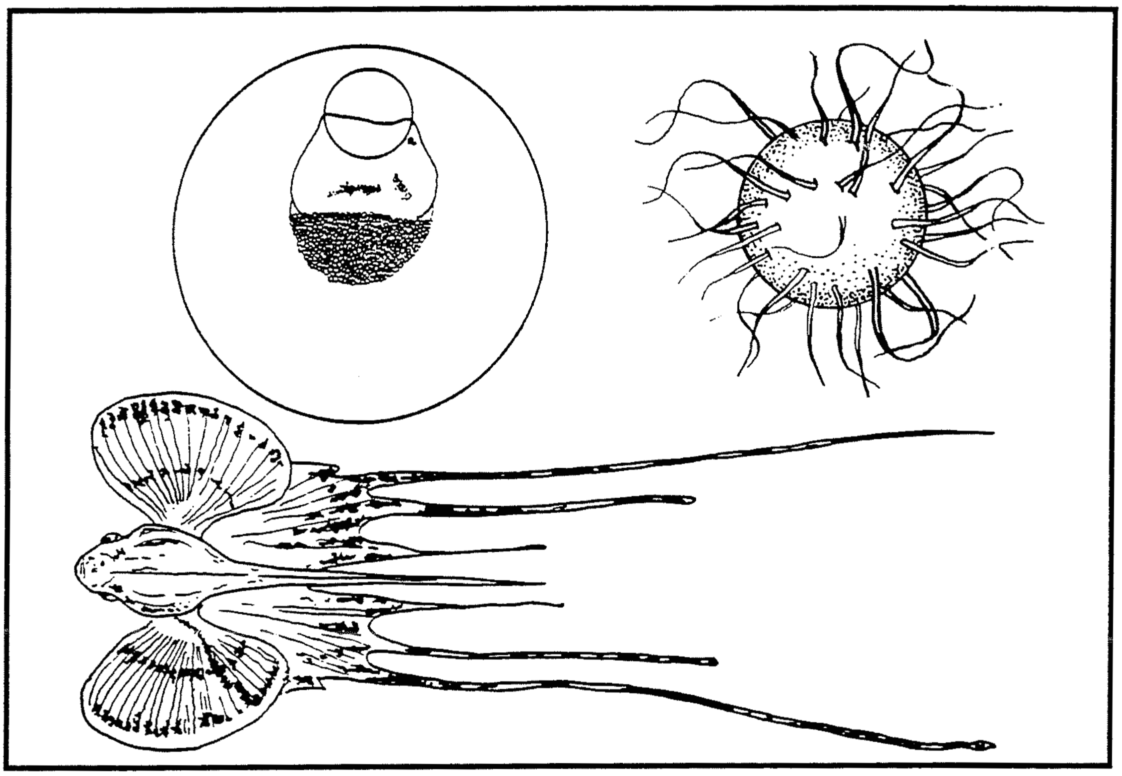


Fig. 2. Various adaptations to pelagic life during the egg and larval phase (after Balon 1975a).

(Forskjellige tilpassninger til livet som egg og larve i de fri vannmassene, etter Balon 1975a)

gelatinous mass can form a veil in which the eggs are embedded, floating like a raft in the surface layers of the sea.

Pelagic spawners have a higher content of water in the yolk than substratum spawners (≈95% compared to 65%). The embryos and larvae lack special respiratory organs and erythrocytes do not appear for a long time. Oxygen is absorbed by the whole body surface and plasma alone is driven along the vessels by heart beats. The lack of blood pigments make the larvae and embryos less visible, an adaption to reduce predation. The relative small egg with high water content in the yolk result in the formation of a relative small embryo and larvae, therefore the larval period can be prolonged. In some species even extreme prolonged and it have been found eel larvae with total length of 1.8 m. Pigments appears late in the development, an exception is the eyes.

Pelagic spawning is an good adaption for survival in the marine pelagic ecosystems containing a prey rich «soup». In addition little extra energy is used in the reproduction process and the energy gained by this can be used by the adults to feed and migrate.

However, lots of fish species pay much more concern and energy in reproduction and different hiding, guarding and bearing techniques have evolved.

The next guild of open substratum spawners are rock and gravel spawners with pelagic larvae (Fig. 3). The eggs are deposited on rocks and gravel, in some species the eggs become buoyant in others the eleutheroembryo and larvae become buoyant and water currents carry them away from the spawning ground. The eleutheroembryo look like a typical pelagic spawned one .

The next guild is rock and gravel spawners with benthic larvae (Fig. 4) they deposit eggs on rock, rubble or gravel where their embryos and larvae develop. Embryos hatch early and are highly photophobic which helps them to hide

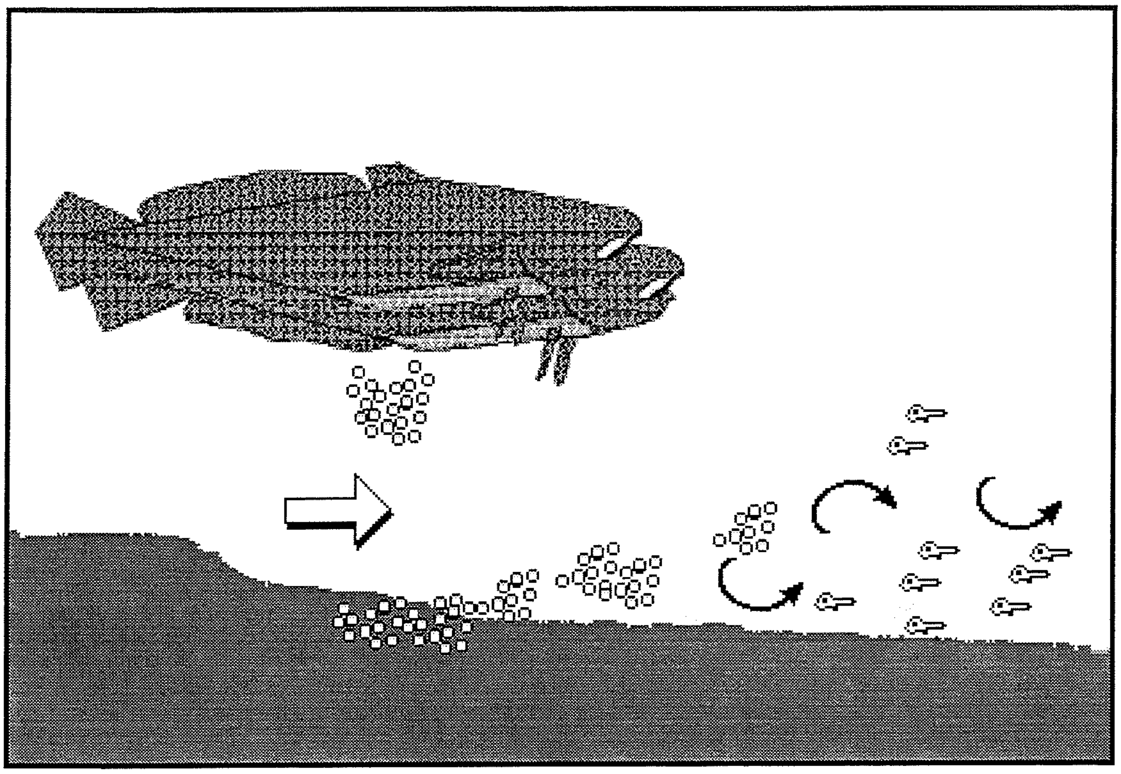


Fig. 3. A nonguarding open substratum rock and gravel spawner with pelagic larvae.
(eksempel på en fisk som gyter fritt over stein og grus med pelagiske egg og/eller larver)

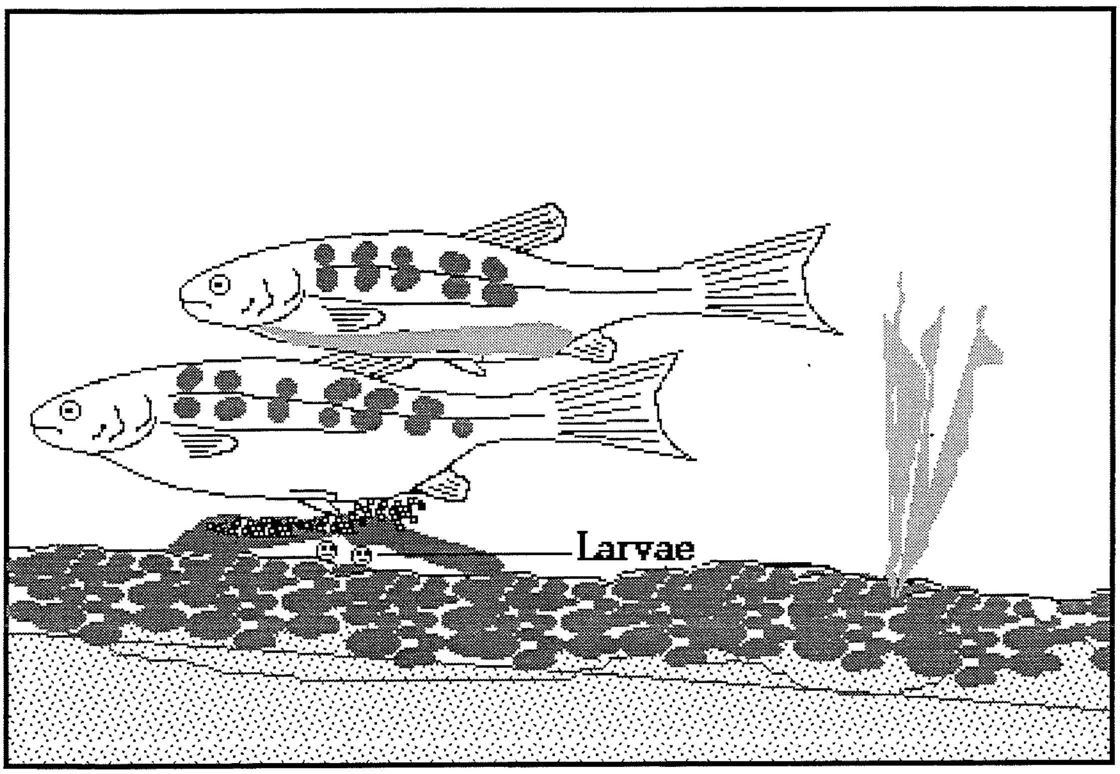


Fig. 4. A nonguarding open substratum rock and gravel spawner with benthic larvae.
(eksempel på en fisk som gyter fritt over stein og grus og der larvene gjemmer seg på bunnen)

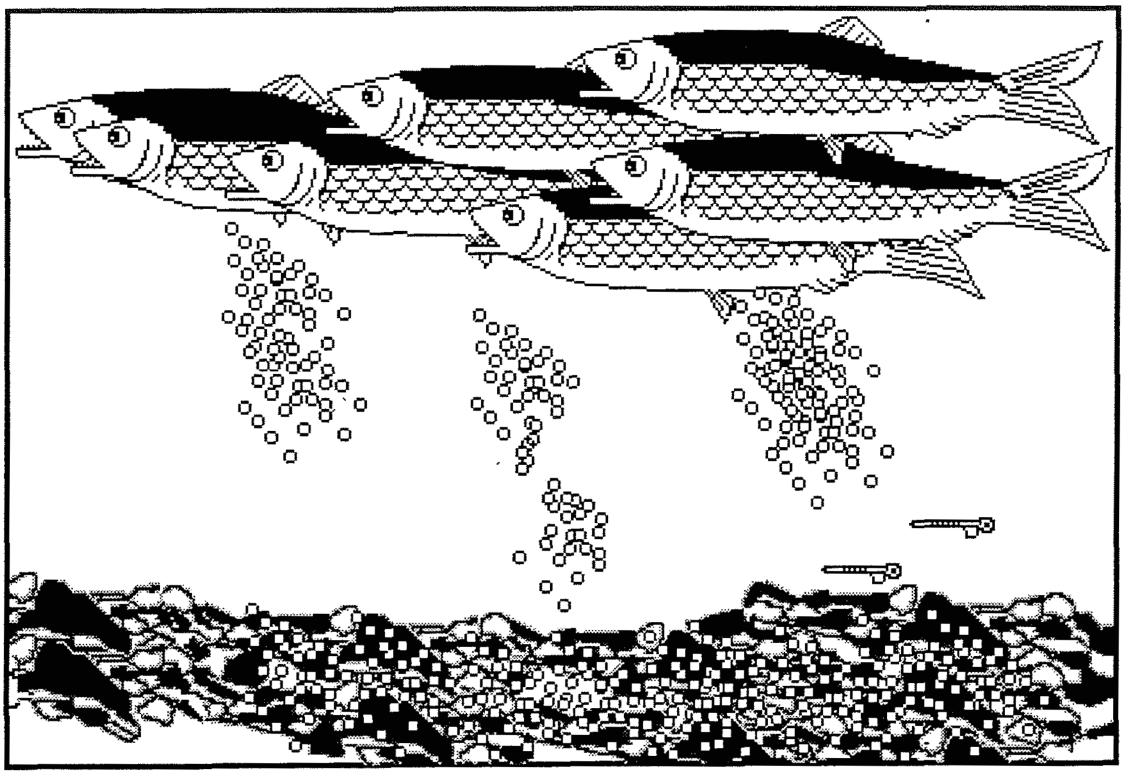


Fig. 5. A nonguarding open substratum nonobligatory plant spawner.
(eksempel på en fisk som gjerne gyter på planter, men der eggene også i stor grad gytes over annet substrat)

under stones.

Nonoblogatory plant spawners is the next guild (Fig. 5). It can be looked upon a transition between the previous and the next guilds. The true intermediate character of this guild is best illustrated by the herring. The Atlantic subspecies a nonobligatory plant spawner usually deposit adhesive eggs on a gravelly and rocky sea floor. However, there are records of eggs deposited on seaweeds, logs, and even manmade floating objects. The Pacific subspecies belong to the next guild (Fig. 6) the obligatory plant spawners and spawns in much shallower waters and prefers to deposit eggs on plants like *Zostera* (eel grass), *Cystophilium,* and to a lesser degree on Laminaria probably because of its slimy surface.

The two last guilds of the open substratum spawners are the sand spawners and the terrestrial spawners, the sand spawners (Fig. 7) deposit their adhesive

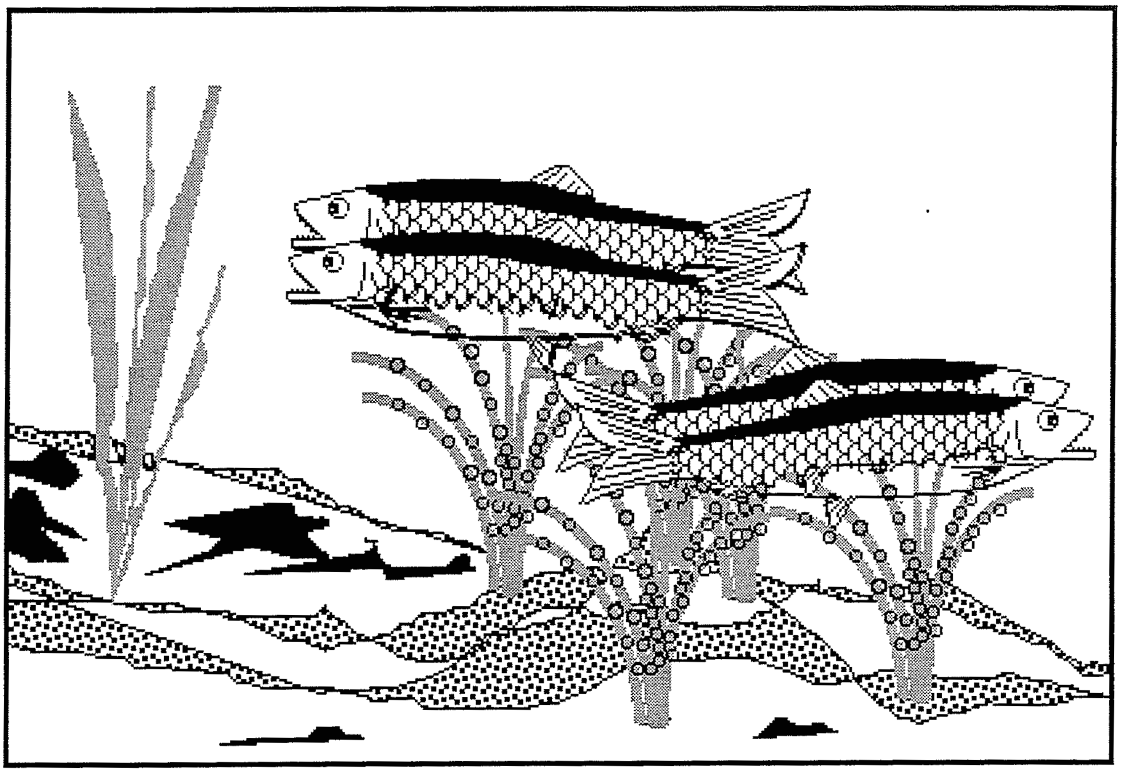


Fig. 6. A nonguarding open substratum obligatory plant spawner.
(eksempel på en fisk som gyter fritt over planter)

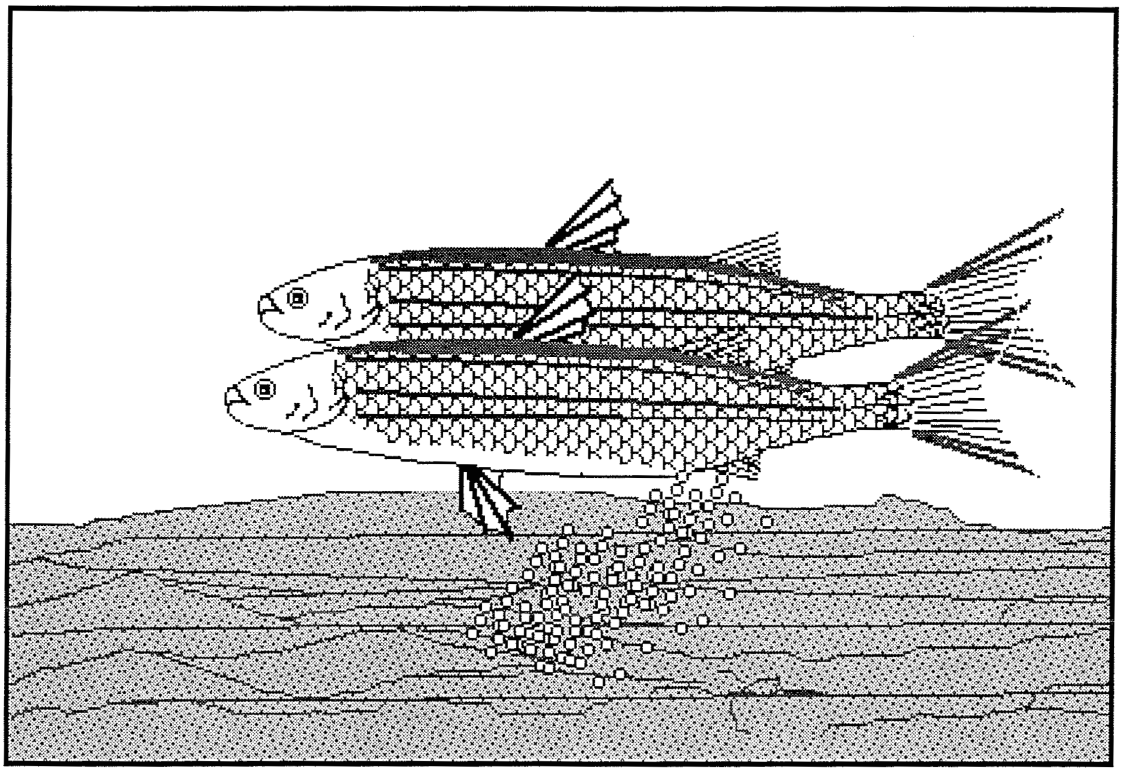


Fig. 7. A nonguarding open substratum sand spawner.
(eksempel på en fisk som gyter fritt over sand)

Fig. 8. A nonguarding open substratum terrestrial spawner.
(eksempel på en fisk som gyter ute av vannet uten noen annen form for yngelpleie)

eggs in running water on sand or on fine roots over sand, the embryos are free and have no cement glands. In the last guild relative small eggs are scattered out of the water in damp sod (Fig. 8).

Brood hiders

The next ecological group is the brood hiders (Tab. 3) where some degree of preparation of hiding places or objects takes place, but no parental care extends beyond initial egg deposition.

The first guild is the beach spawners (Fig. 9), where eggs are buried out of water in the sand of sea beaches at extreme high tide. The eggs are incubated in the damp sand until the returning high tide 14 days later washes them back to sea.

Annual fishes are a specialized guild of fishes with a short lifespan (Fig. 10) adapted to the seasonal desiccation of their habitat. They live in small isolated

Table 3. The different guilds of nonguarding brood hiders (after Balon 1981).
(De forskjellige «laugene» fisk som gjemmer eggene sine uten noen annen form for yngelpleie kan deles inn i)

GUILD	EXAMPLES
Beach spawners	*Leurestes tenui, Leurestes sardina*
Annual fishes	Killifish(sessongfisk)
Rock and gravel spawners	Salmon, Trout(ørret), Char(røye, Greyling(harr), Capelin (lodde)
Cave spawners	Troglodytes
Spawners in live invertebrates	*Rhodeus sericeus*(bitterling)

pools and swamps in the African savanna or the South american pampas that dry up completely during the dry season. Eggs are deposited in the bottom mud and in extreme years the embryos can survive as long as 18 months or more in the egg membranes lodged in the dry mud.

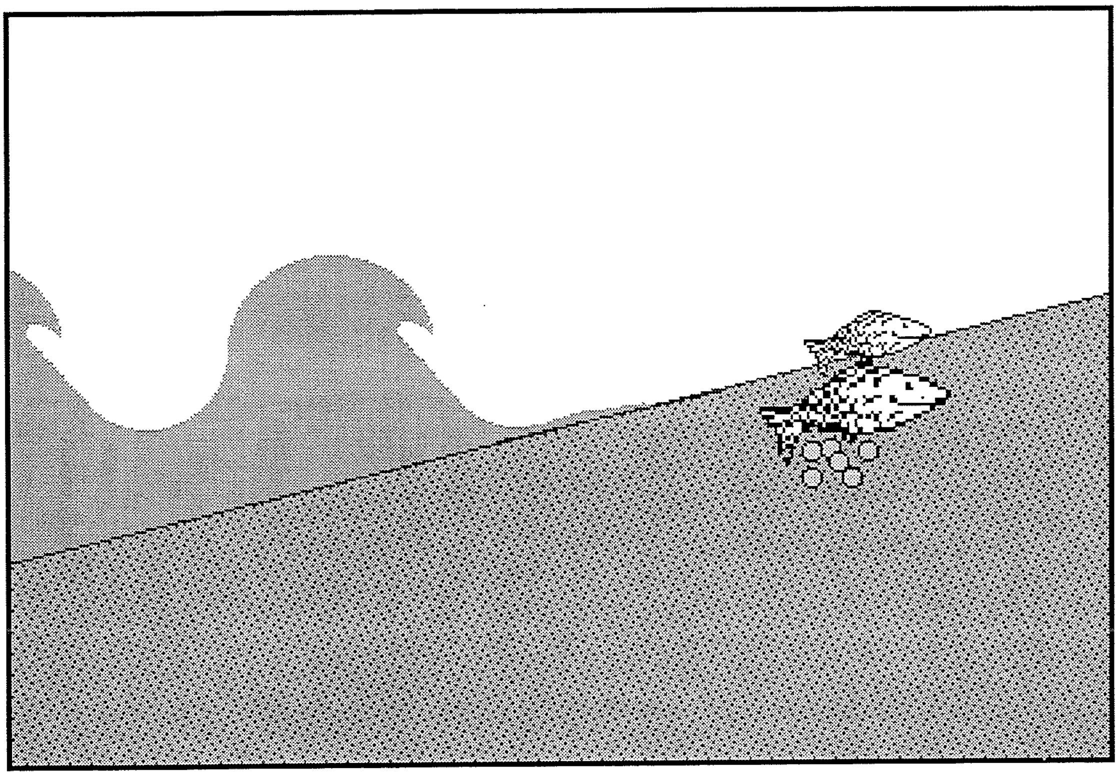


Fig. 9. A nonguarding brood hiding beach spawner.
(Eksempel på en art som gyter i våt sand ved ekstremt høyvann)

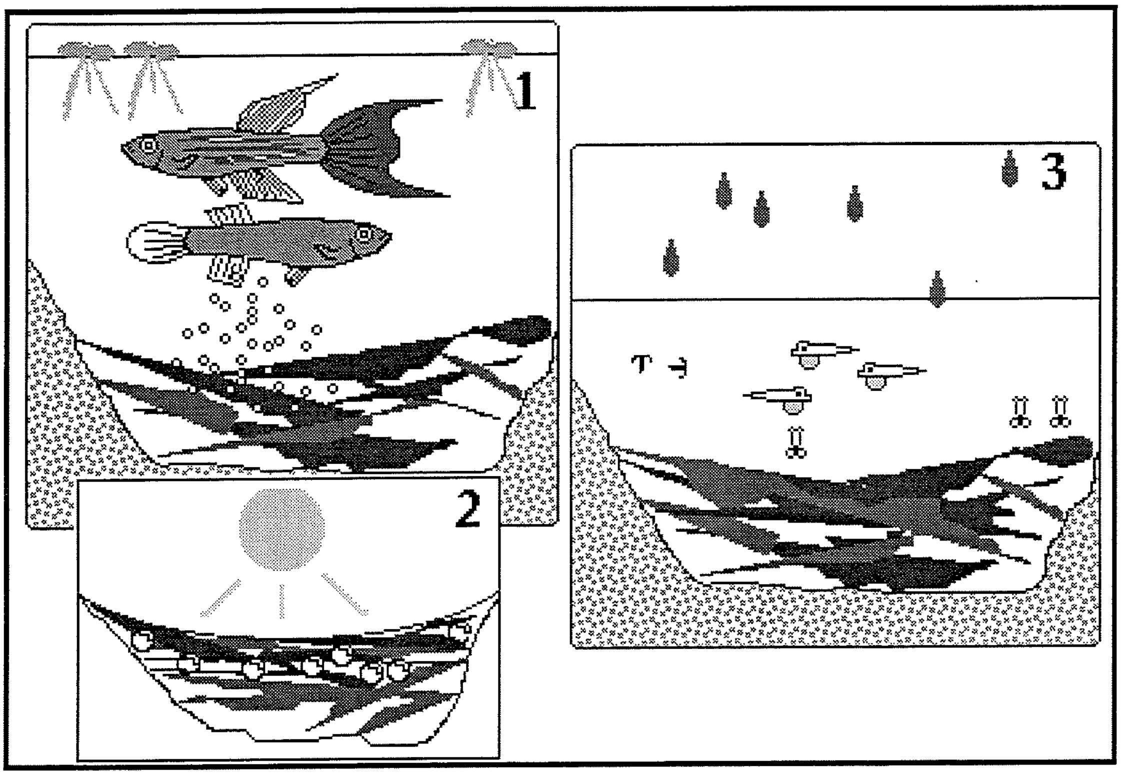


Fig. 10. Nonguarding brood hiding annual fish.

(Eksempel på en sessongfisk som er tilpasset til å leve i vannhull som tørker helt inn)

The eggs can arrest their development in three different diapauses. When the pools refill after the first rain the embryos hatch and grows so rapidly that within several weeks they are able to reproduce. In these fishes the embryonic period lasts nearly as long as the remaining larval, juvenile, adult and senescent periods together.

Rock and gravel spawners of this subsection hide their eggs in natural or specially constructed places called redds in salmonids (Fig. 11). Generally eggs are buried under gravel about twice the body height of the digging parents. Clean gravel or rocks and cold, clean fast moving water are almost essential to provide sufficient oxygen to the developing embryos. The embryos hatch early, they are photophobic and remain hidden under the gravel. They merge as large, fully formed active alevins.

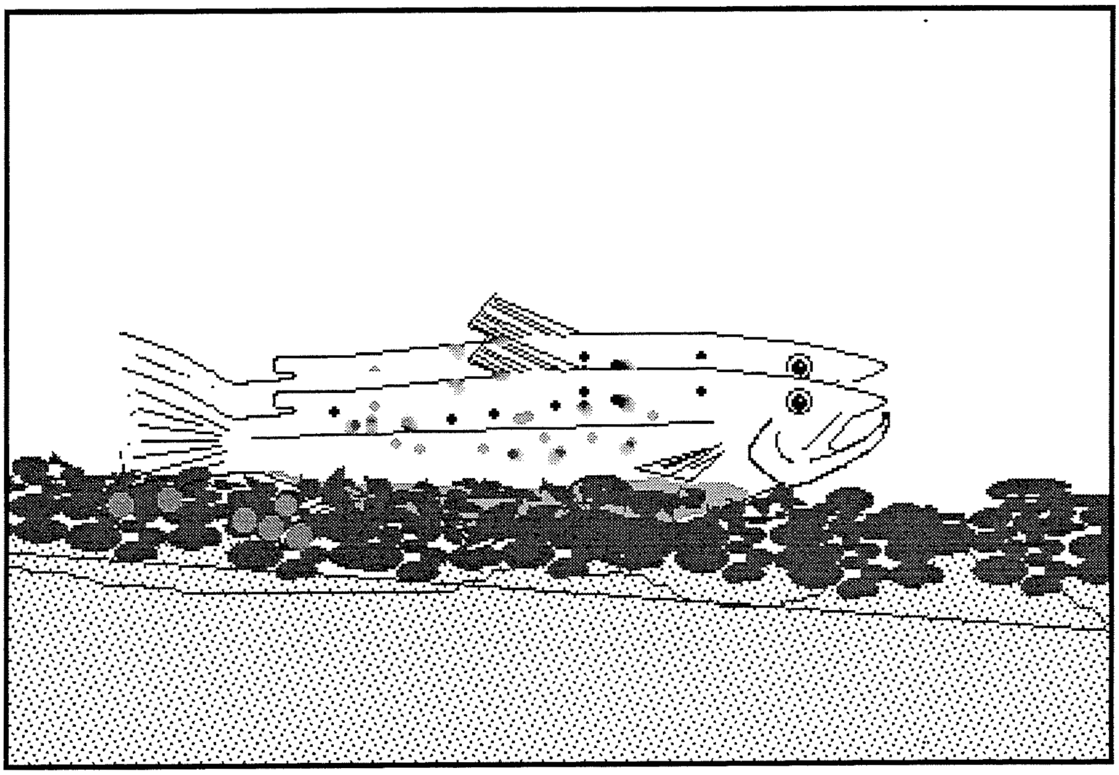


Fig. 11. A nonguarding brood hiding rock and gravel spawner.

(Eksempel på en art som graver ned eggene sine uten ellers å vise noen form for yngelpleie)

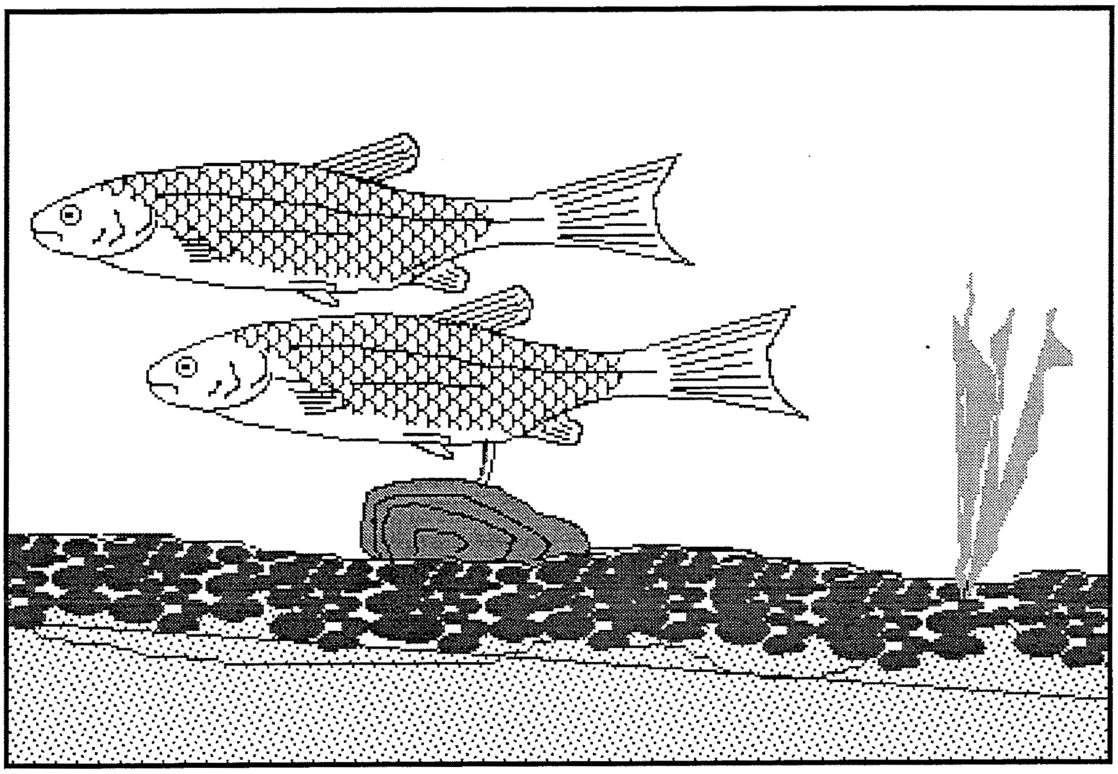


Fig. 12. A nonguarding brood hiding fish, which hide the eggs in live invertebrates.

(Et eksempel på fisk som gyter inne i en evertebrat)

Spawners in live evertebrates hide their eggs in the gill chambers of live mussels, crabs or ascidians (Fig. 12). All females of this guild grow an ovipositor used to introduce eggs through the hosts siphon. One host can harbour some 100 or more eggs deposited by different females. Eggs with a large proportion of yolk enables the larvae to leave the host in an advanced stage. The eggs are adapted to low oxygen concentrations, they are often covered with spines to prevent premature expulsion and they are able to withstand the immunic reaction of the host.

GUARDERS

The next ethological section is the guarders, better protected from enemies, guarded eggs need not to be so numerous to assure survival of the species. Furthermore spawning sites with lower oxygen content can be used, because the guarding parents clean the eggs and produce a water flow around them by fin-fanning and oral ventilation. In all known fishes that are parental outside the cichlidae, the male is the parent. The evolutionary progression in cichlidae has been from an exclusively parental male to a shared parental care by the male and the female to a division of roles with the female as the direct parent and the male as guardian and at last to polygyny.

Substrate choosers

The first ecological group is the substrate choosers (Tab. 4) which consists of pelagic spawners, above water spawners, rock spawners and plant spawners. The pelagic spawning guild (Fig. 13) guard a cluster of free floating buoyant eggs that are deposited between vegetation.

The splash-tetra is the single member of the above water spawners (Fig 14). They deposit eggs in the spawning act appr. 10cm out of water on broad leaves that overhangs the water. Every 20 minutes the male splashes water on the eggs by swishing the tail. After three days the eggs hatch and the embryos falls into the water. This guild is evolved to ensure protection against predators.

Table 4. The different guilds of guarders that choose their spawning substrate (after Balon 1981).

(De forskjellige «laugene» fisk som vokter eggene sine og velger gytesubstrat kan deles inn i)

GUILDS	EXAMPLES
Pelagic spawners	*Ophiocephalus*(slangehodefisk), *Anabas*
Above water spawners	Splash tetra(sprøytetetra)
Rock spawner	Lumbsucker(rognkjeks), Gobies(kutlinger)
Plant spawners	Bichir(bikir), European Catfish(europeisk malle)

The rock spawners fans and ventilate a cluster of eggs that are attached to rocks (Fig. 15). The incubation time of the lumbsucker is as long as two months.

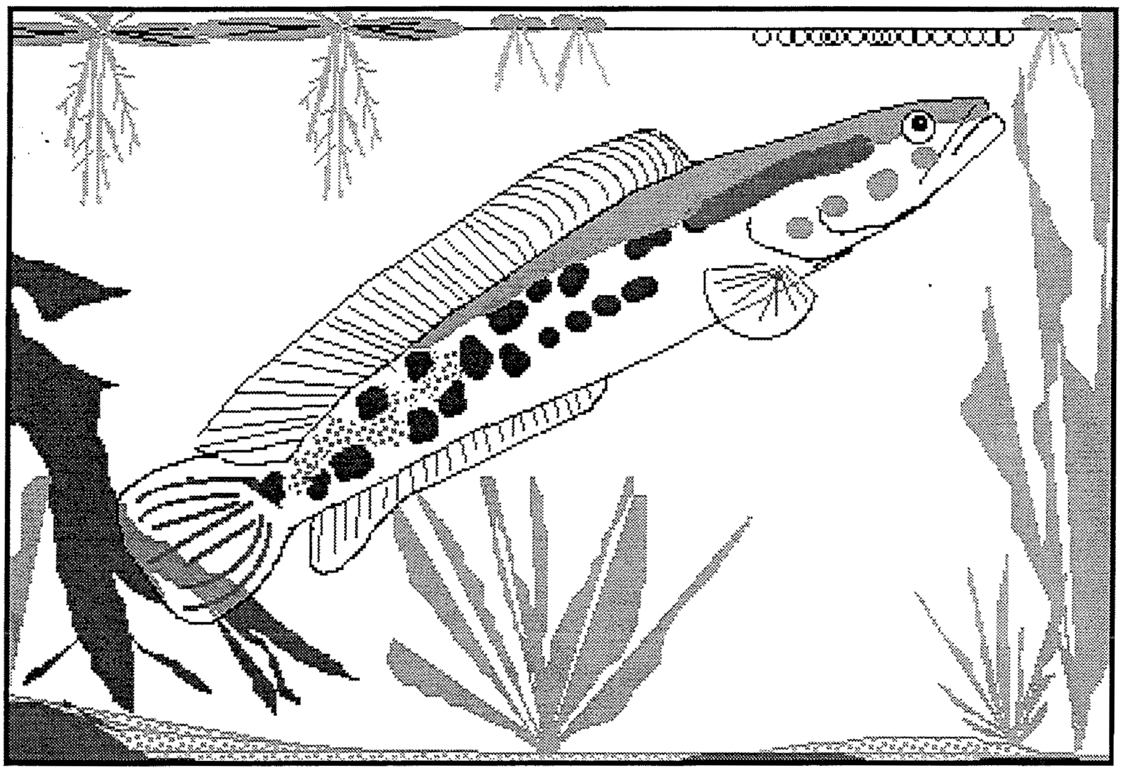


Fig. 13. A guarding substrate choosing pelagic spawner.

(Et eksempel på fisk som gyter pelagisk men som vokter eggene sine)

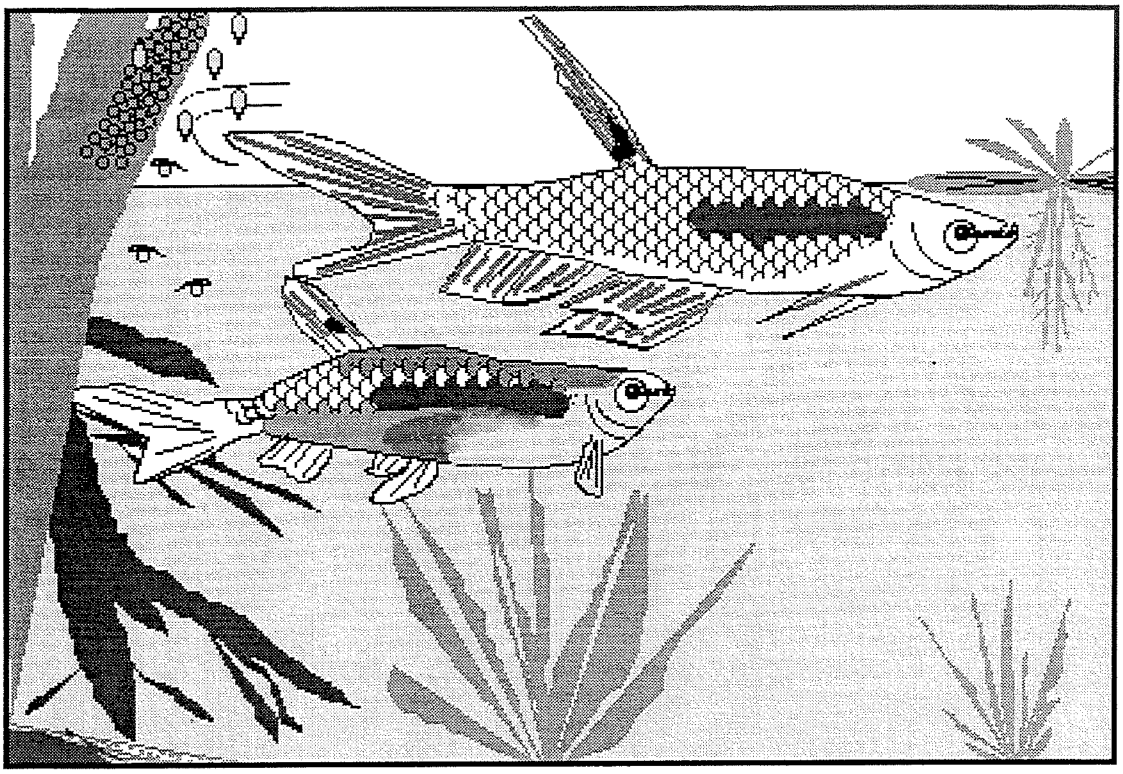


Fig. 14. A guarding, substrate choosing above water spawner.
(Eksempel på fisk som vokter eggene sine som er avsatt på en vannplante over vannflaten)

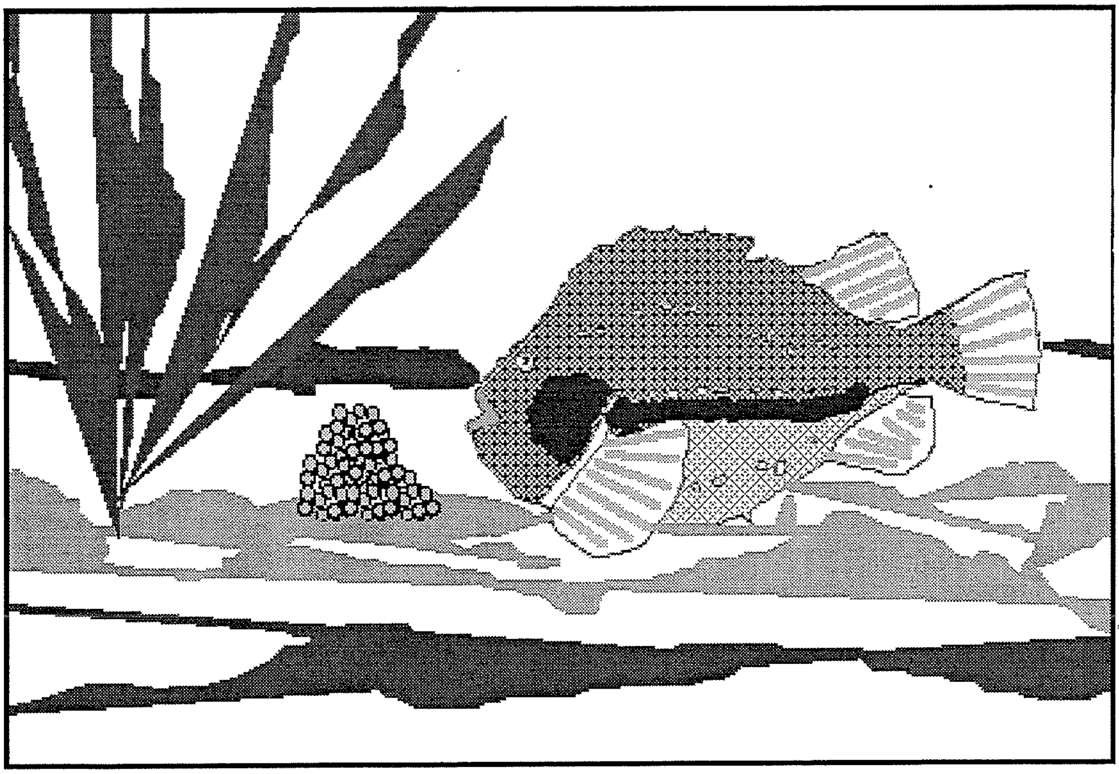


Fig. 15. A guarding substrate choosing rock spawner.
(Eksempel på fisk som vokter en eggansampling på en stein)

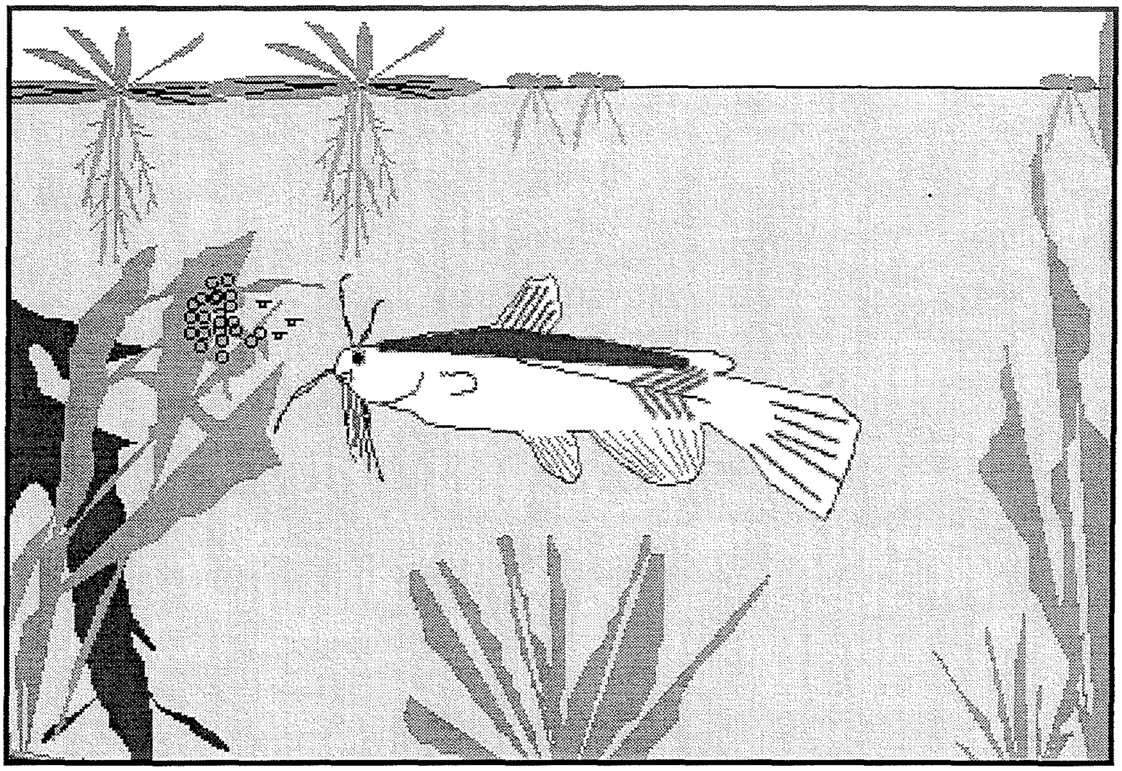


Fig. 16. A guarding substrate choosing plant spawner.
(Eksempel på fisk som vokter egg avsatt på en vannplante)

Plant spawners (Fig. 16) scatter their eggs or attach them to submerged plants. The male guard and fan them.

Nest spawners

The last ecological group of the guarders is the nest spawners (Tab. 5). They build more or less elaborate structures for egg deposition, or for guarding and herding of the hatched offspring. The first guild is the froth-nesters (Fig. 17). Mucus-covered bubbles are blown up against the surface forming a froth-nest into where the eggs are blown. The eggs and larvae develops in the froth where they are protected against predators, direct sunlight and where they can feed on microorganisms which are attracted to the froth. The nest also serve as an anchor for the eggs amid plants.

The nest guild is miscellaneous substrate and material nesters (Fig. 18). They are not particular in the selection of nest building material, some attach their eggs to any cleaned surface, other makes nests of gravel, plant and algal material. In some species the young feeds directly on mucus produced on their parents body.

Table 5. The different guilds of nest spawning guarders (after Balon 1981). *(De forskjellige «laugene» av fisk som vokter eggene sine i reirlignende strukturer)*

GUILDS	EXAMPLES
Froth nesters	*Betta splendens*(kampfisk)
Miscellaneous substrate and material nesters	*Crenilabrus quinquemaculatus*, *Symphysodon discus*(diskusfisk)
Rock and gravel nesters	*Cottidae*(ulker), *Sparidae*(hav-karusser), *Cichlidae*, *Labridae*(gylter)
Plant material nesters	Pike-perch(gjørs), cichlids
Gluemaking nesters	Pipefishes(nålefisk), Sticklebacks(stingsild)
Sand nesters	*Cichlasoma nicaraguense*, *Abbottina rivularis*
Hole nesters	Butterfish(tangsprell), *Gobidae*(kuttlinger), *Cottidae*(ulker)
Anemone nesters	26 species of the genus *Amphiprion*(klovnefisk)

Rock and gravel spawners (Fig. 18) deposits their eggs on cleaned areas of rocks or in pits dug in the gravel. They guard the eggs and in cichlids the 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. When the larvae begin swimming, both sexes guard them. There is evidence of inclination towards polygyny but this is counteracted by selective pressure from predation, requiring both parents for protection of the progeny.

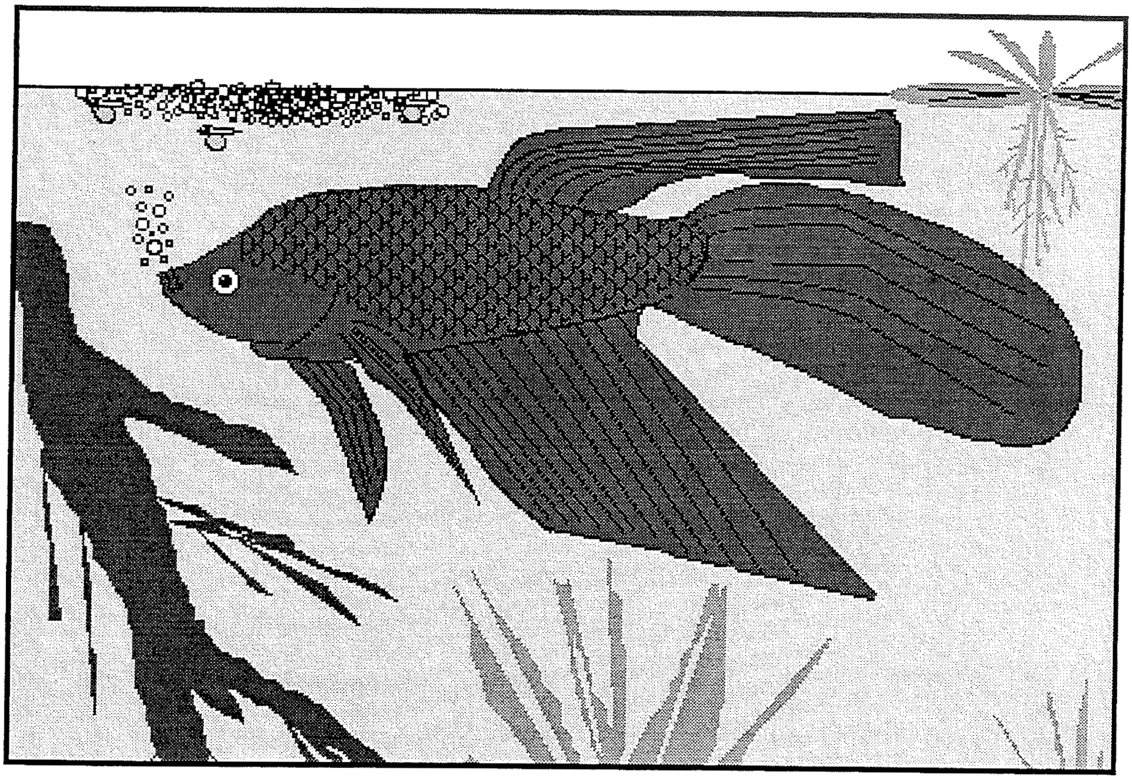


Fig. 17. A guarder who builds a froth nest.

(Eksempel på en art som vokter sitt avkom i et skumrede)

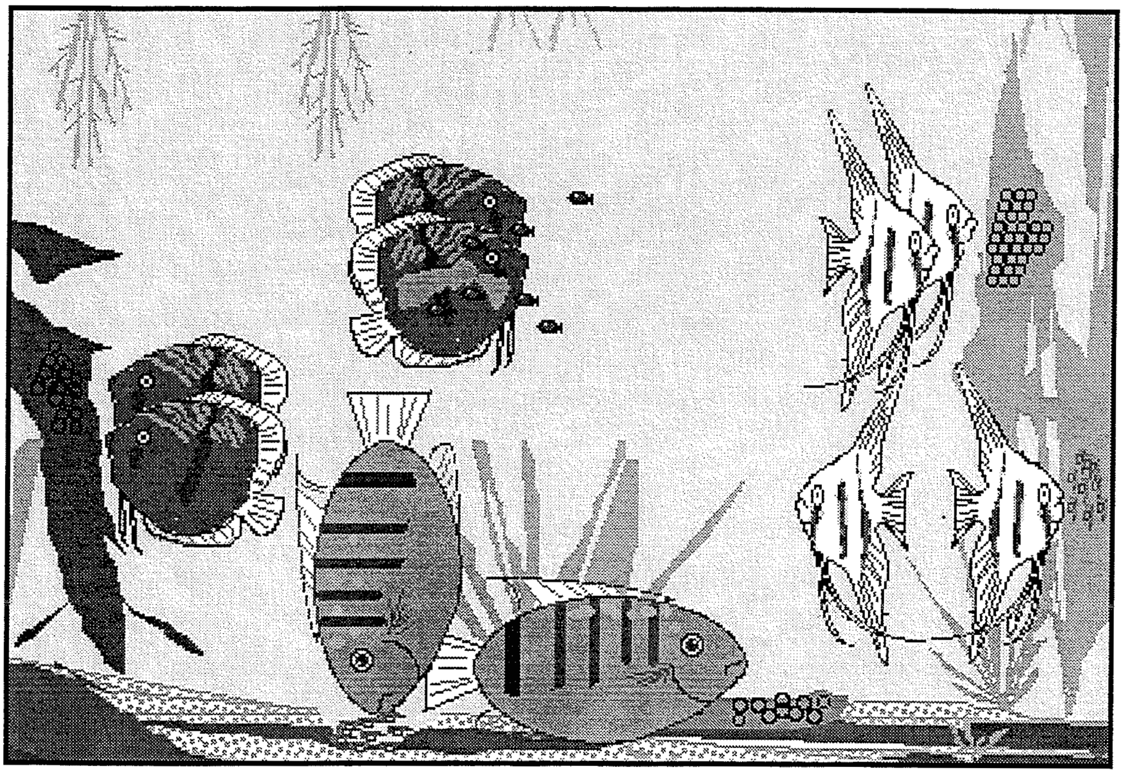


Fig. 18. Nest building guarders using different types of substrate.

(Eksempler på redebygging på forskjellige substrattyper)

Plant spawners (Fig. 18) are much like the previous guild, they build nests of plant material or clean the surface of a broad leaf. The newly hatched eleutheroembryos are in the species with parental care moved to another cleaned leaf. If the embryos get detached, each is picked up and returned by the mouth of their parents to the plant where they hang by means of cement glands.

Gluemaking nesters (Fig. 19) have remarkable skill in nest building and parental care. The nestbuilding 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 lay eggs in the nest of one male but only the male remains to guard. The eggs are constantly ventilated by the guarding male and he guard the young until he can no longer orally return the wandering offspring back in the nest. This makes the male of the stickleback "about the busiest thing among fishes that can be imagined".

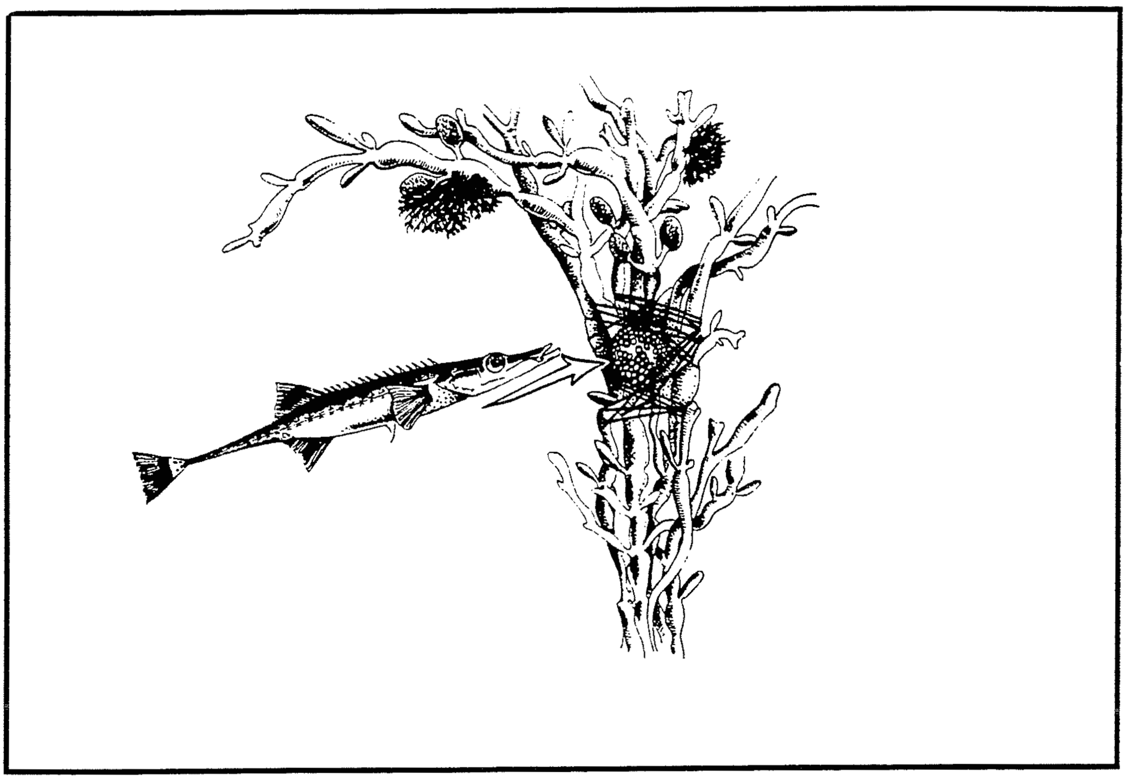


Fig. 19. One of the gluemaking nesters.

(Noen arter bygger reder av plantedeler som de syr sammen med et sekret som de skiller ut fra nyrene)

Sand nesters bury nests in the sand in where they guard the eggs and embryos.

Hole nesters (Fig. 20) guard their spawn in natural holes, in cavities or in specially constructed burrows. The majority simply deposit their eggs on a cleaned area of the undersurface of flat stones and the males guards the eggs. Butterfish females often can be found coiled around the eggs. In some species complex burrows are built. African lung fish males dig a long tunnels and oval-shaped chambers. 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 after 50 days when they still return to the nest.

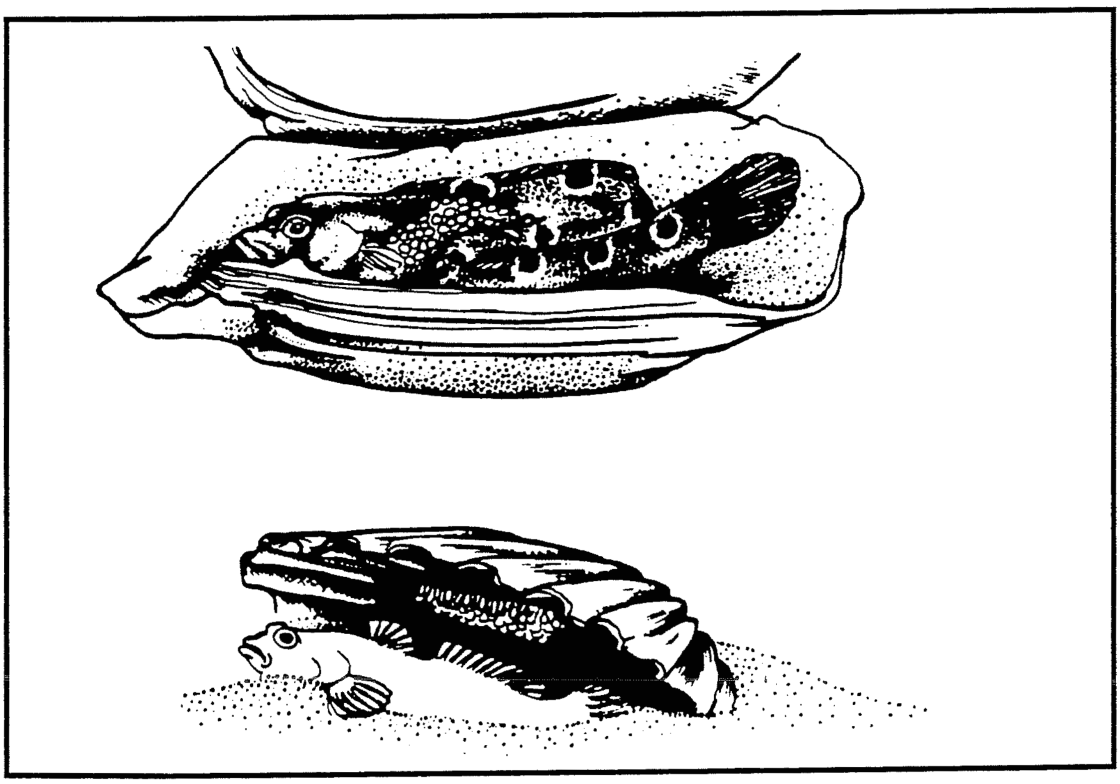


Fig. 20. The guarding hole nesters .

(Eksempler på arter som vokter eggene sine i huler eller hulrom)

The last guild of this ecological group is the anemone nesters (Fig. 21). They nest under the active protection of the tentacles of sea anemones. An area next to the pedal disc of an actinarian is cleaned and the eggs are attached to it. The eggs are guarded and fanned and covered with mucus for protection. Larvae have a short pelagic phase then they acclimate to their host anemone. After 24 hours they are able to enter the oral disc of the anemone without harm.

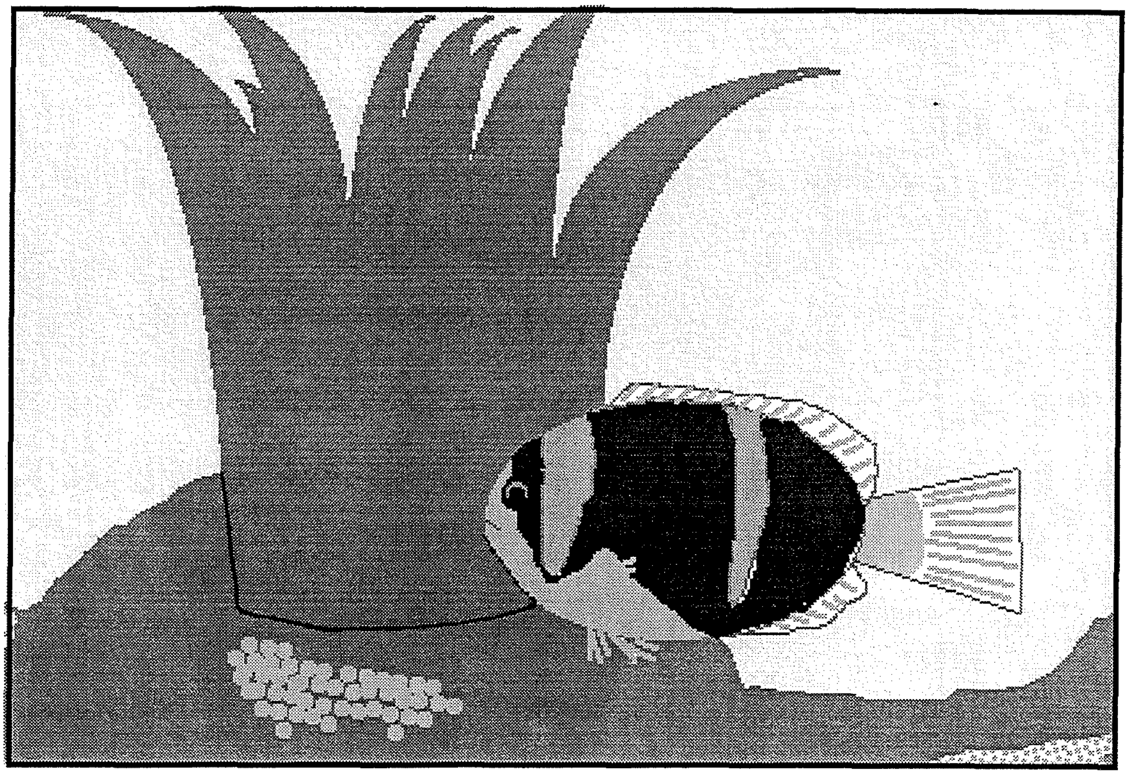


Fig. 21. One of the anemone nesters.
(Eksempel på en art som benytter anemoner til beskyttelse)

BEARERS

Bearers are divided into external and internal bearers.

External bearers

External bearers (Tab. 6) carry their developing eggs on the surface of their bodies or in externally filled body cavities or special organs. There are five guild of external bearers; transfer brooders, auxiliary brooders, pouch brooders, mouth brooders, and gill chamber brooders.

Table 6. The different guilds of external bearers.

(De forskjellige "laugene" som bærer med seg egg og ev. larver)

GUILDS	EXAMPLES
Transfer brooders	*Corydoras sp., Curtus gulliveri*
Auxiliary brooders	Group of S. American catfishes, Some Pipefishes(nålefisker)
Mouth brooders	*Tilapia sp.,* Malawi og Tanganika-cichlider(afrikanske cichlider)
Gill chamber brooders	North american cavefishes
Pouch brooders	Pipefishes and seahorses(nålefisker og sjøhester)

In transfer brooders eggs are carried for some time in cupped pelvic fins or in a cluster hanging from genital pore. The eggs are carried during a prolonged search for a suitable place to hide them.

Auxiliary brooders (Fig. 22) carry the eggs attached to the body as clusters, on the spongy skin or on a hook in the superoccipital region. Some develop a special spongy skin on their ventrum. They 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 and perform some kind of gas and nutrient exchange.

Pouch brooders (Fig. 22) encompass the same phyletic lines as skin brooders. The eggs, similarly incubated on modified skin are enveloped by specially transformed structures, or covered of membranes or plates. In pipefishes and seahorses a special marsupium is formed on the ventrum of the males. The eggs are deposited in the pouch during mating when both partners embrace face to face. The protruding oviduct of the female is "trust into the buttonhole-shaped opening at the anterior end of the marsupium", the 150 eggs are fertilized as they pass into the pouch.The offspring leave the pouch late, as juveniles.

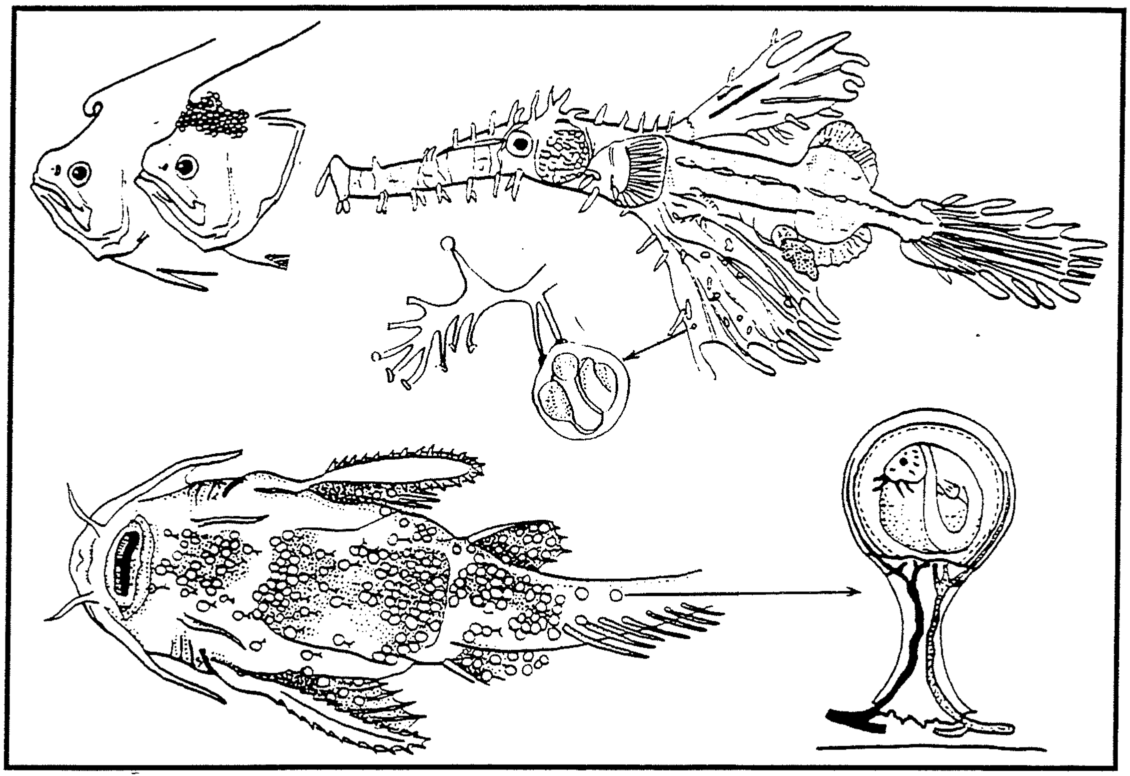


Fig. 22. Examples transfer brooders, auxiliary brooders and pouch brooders.

(Eksempler på fisk som bærer eggene og eventuelt larvene sine med seg)

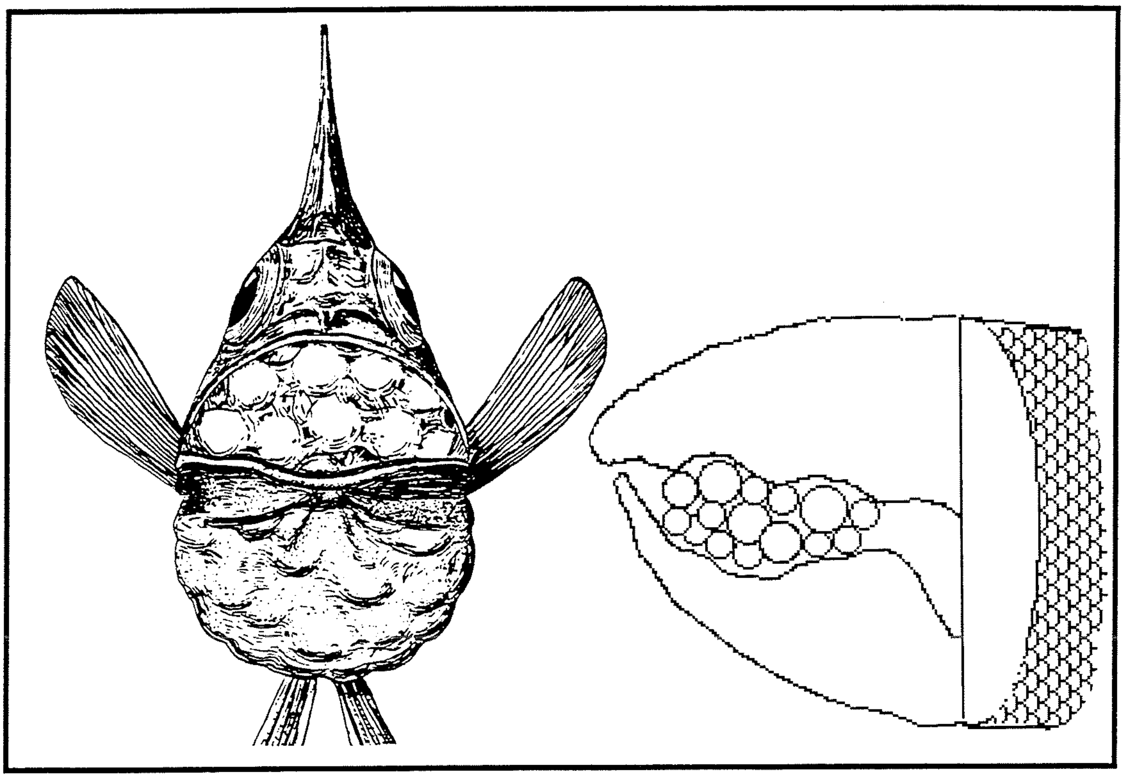


Fig. 23. Mouth brooding an advanced form of bearing and guarding.

(Munnruging en avansert form for yngelpleie)

Mouth brooders (Fig. 23) incubate their eggs in the buccal cavity. Mouth brooding evolved from the substrate guarders practice of cleaning and taking eggs into the mouth during hatching and of transferring brood orally from incubation substrate to nursery pits. Some construct beautiful nests where the eggs are deposited and fertilized before they are picked up. Others more advanced mouth brooders have egg-dummies on the anal fin, which stimulates the female to pick them and thereby inhale sperm into the buccal cavity where the eggs are picked up immediately after egg laying. The eggs are few but large and that the most advanced ones can not brood more than 20 eggs. The yolk content is high and the larvae are brooded to the end of the larval period and released from the mouth as juveniles. The young periodically seek refuge in their parents mouth, and they are herded for some time. Gill chamber brooders carry about 70 eggs in the gill chamber until some time after hatching.

Internal bearers

Internal bearers form the following three guilds (Tab. 7); ovoviviparous, viviparous oophages and viviparous trophoderms.

Table 7. The different guilds of internal bearers.
(De forskjellige "laugene" med innvendig befruktning og utvikling av egg og larver)

GUILDS	EXAMPLES
Ovoviviparous	Live Bearing Tooth Carps(levende-fødende tannkarper, Red Fish(uer), *Latimeria chalumna, Rivulus marmoratus*
Viviparous oophages	Sharks e.g. Sand Tiger Shark
Viviparous trophoderms	Eel-pout(ålekone), sharks and rays

Retention of internally fertilized eggs for some time after activation in most cases until hatching, when the individual embryo is dependent on its own yolk reserves is classified as ovoviviparity. The embryo decrease in weight during the development. Ovoviviparity is probably the initial step in the evolution of true bearers from guarders.

In true livebearing fishes, however, endogenous and oxidative metabolism from the yolk is supplemented or replaced before parturition by nutrients and gaseous exchange from the mother. Those elasmobranchiomorphs that produce a free embryo and/ or juvenile which feeds on other ova and siblings within the uterus, are classified as viviparous oophages.

More specialized livebearers produce embryos whose partial or entire nutrition comes from the female by uterine milk secretion, also the gaseous exchange is supplied by the female. The embryo develop special adsorptive organs, e.g. trophonemata, trophotaenia, yolksac placenta (Fig. 24). These fish are placed into a separate guild- viviparous trophoderms.

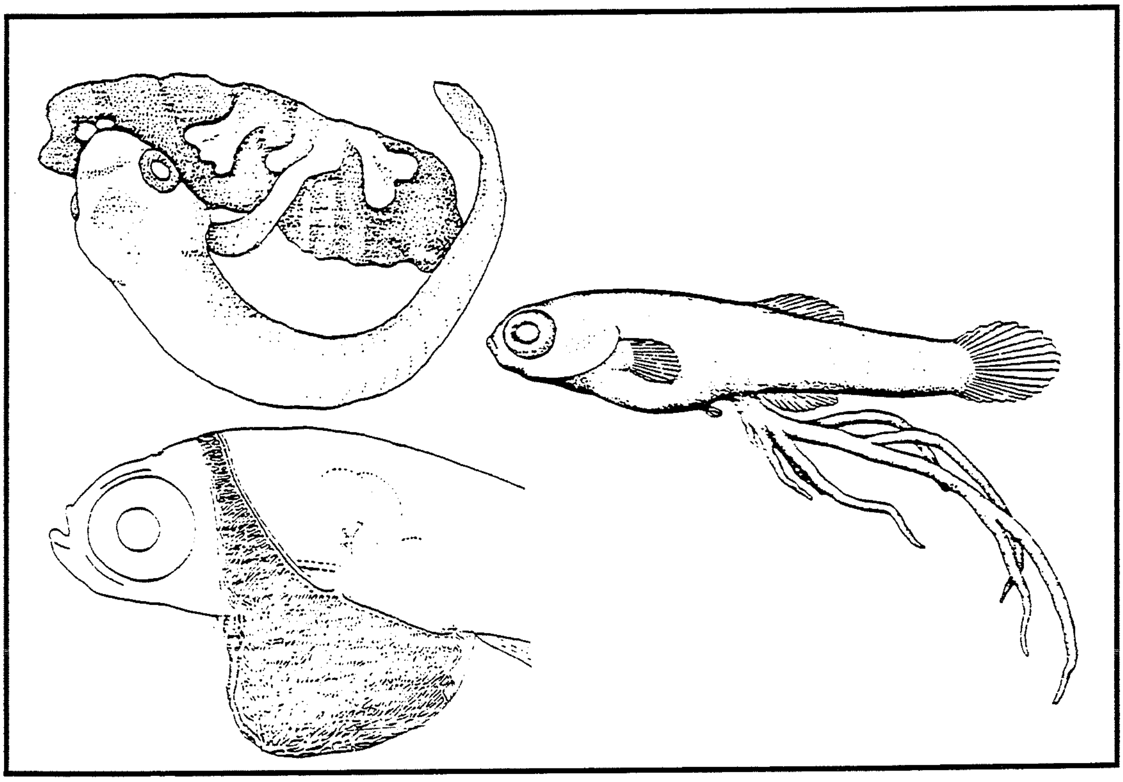


Fig. 24. Special adsorptive organs used by viviparous trophoderms

(Spesielle organer som larvene benytter seg av for å oppta næring inne i moren)

INTERVALS IN FISH DEVELOPMENT, SALTATORY ONTOGENY AND A HIERARCHICAL LIFE HISTORY MODEL

As we saw in the first part of this talk, reproduction in fish is indeed a complex process. Therefore is it important to define what stage one are talking about and terms utilizing the prefixed pre- and post- lack elementary logic.

The developmental periods in the life of a fish are the embryonic, larval, juvenile, adult and the senescent period, and they are more distinct than those that separate the shorter intervals of ontogeny. One can separate the development into periods (Tab. 8), the longest interval, divided into phases, and each phase subsequently into several steps. Stages refers explicit to a just observed immediate moment of development like the 8 cell stage in the first step of the cleavage phase. The relationship of periods, phases, steps and stages can be compared to the relationship existing between measurable units of time like days, hours, minutes, seconds.

The embryonic period last from fertilization or activation until exogenic feeding (Tab. 8). The embryo is completely endogenic fed in this period, which is divided into; a cleavage phase lasting from activation to the start of the organogenesis an embryonic phase which lasts until hatching and eleutheroembryonic phase lasting until the start of exogenic feeding. The larval period last from the start of exogenous nutrition or mixed feeding till ossification of main organ are completed and larval finfold is resorbed. The larval period is divided into ; a protopterygiolarval phase lasting from the start of exogenic nutrition until the start of differentiation of the embryonic median finfold, and a pterygiolarval phase that lasts until the finfold is completely differentiated and the axial skeleton is ossificated.

Examples on steps are jerky swimming, substrate change, phototropic reaction etc.

Table 8. Periods and phases in the ontogeny of fish eggs and larvae.
(Perioder og faser i egg og larvestadiet)

PERIOD		PHASE	
Embryonic	From activation to exogenic feeding	Cleavage	Activation-organogenesis
		Embryonic	Organogenesis-hatching
		Eleuthero-embryonic	Hatching-exogenic feeding
Larval	From exogenic feeding to completion of larval finfold differentiation	Protopterygiolarval	Exogenic feeding-Start of diffrent. of larval finfold
		Pterygio-larval	Start of diffrent. of larval finfold Differentiation completed

Fish like salmonids and mouth breeding cichlids have direct development and jump over the larval stage. They have large eggs with high yolk-content. Examples of fishes with indirect and a more direct development are shown in Fig. 25.

Ontogeny is the development of an individual from activation to death and can occur by two possible processes; by developmental gradualism or with saltatory changes.

According to Balon the development is a sequence of longer steady states called steps and rapid changes in form and function called thresholds. Structures that together form a system align their rates of development to become functional

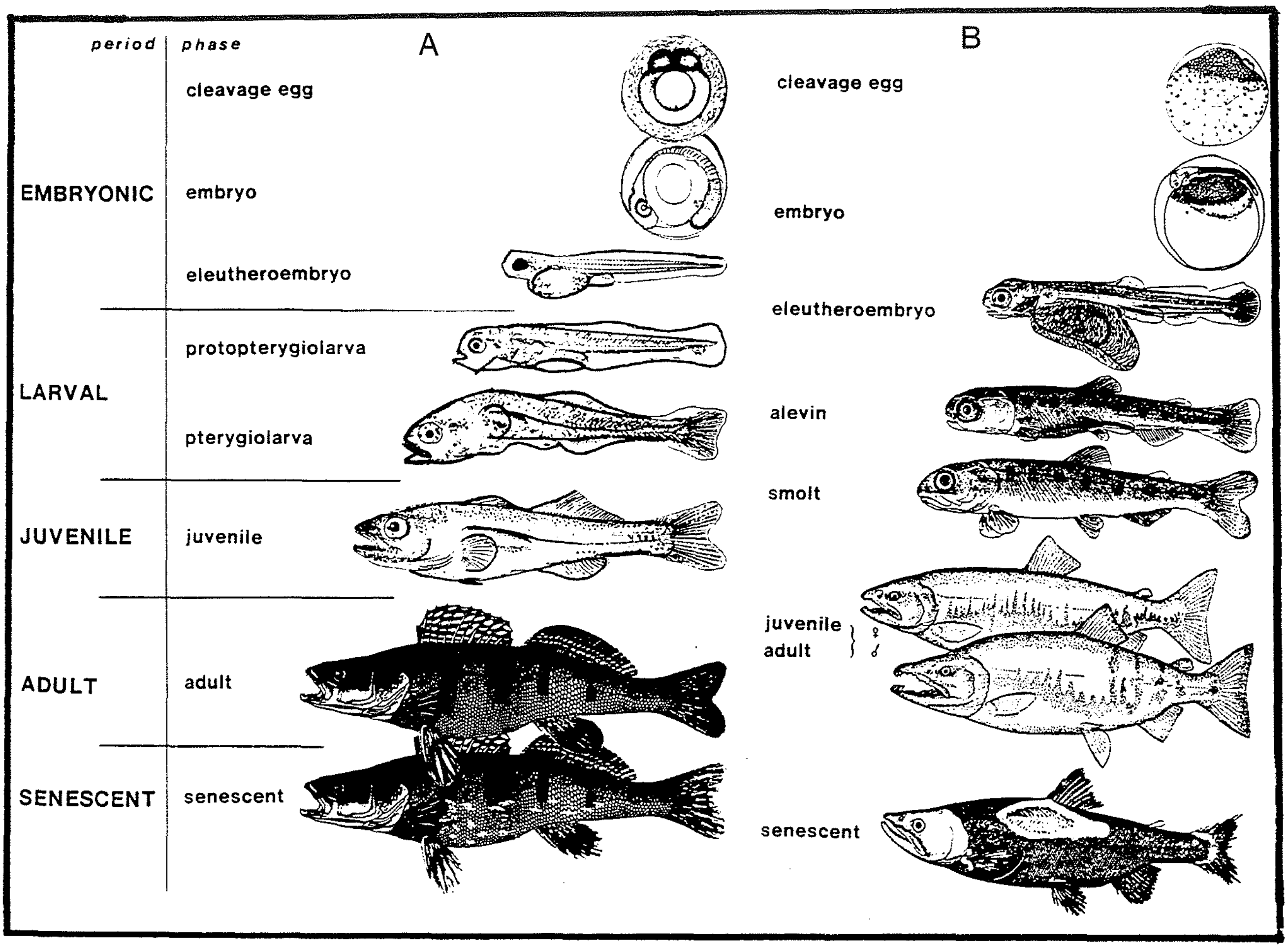


Fig. 25. Successive intervals of ontogeny of a Percidae with indirect development (A) and a Salmonidae with a more direct development (B), from Balon (1975). *(Eksempel på indirekte utvikling (gjørs), (A) og en mer direkte utvikling (stillehavslaks), (B))*

simultaneously and initiate a new vital function like photoresponse, change of substratum, exogenic nutrition at an accelerated rate.

This "switch" is called a threshold; a rapid transition from one steady state to another.The strength of the thresholds will vary, as will the preceding and following life-history intervals (Fig. 26).

If we accept that life processes in organisms function best at homeostatic states, we can no longer view ontogeny as gradual but as a sequence of steady states interrupted by less steady tresholds, through which the organism passes at accelerated rates in order to achieve the relative comfort of the next steady state.

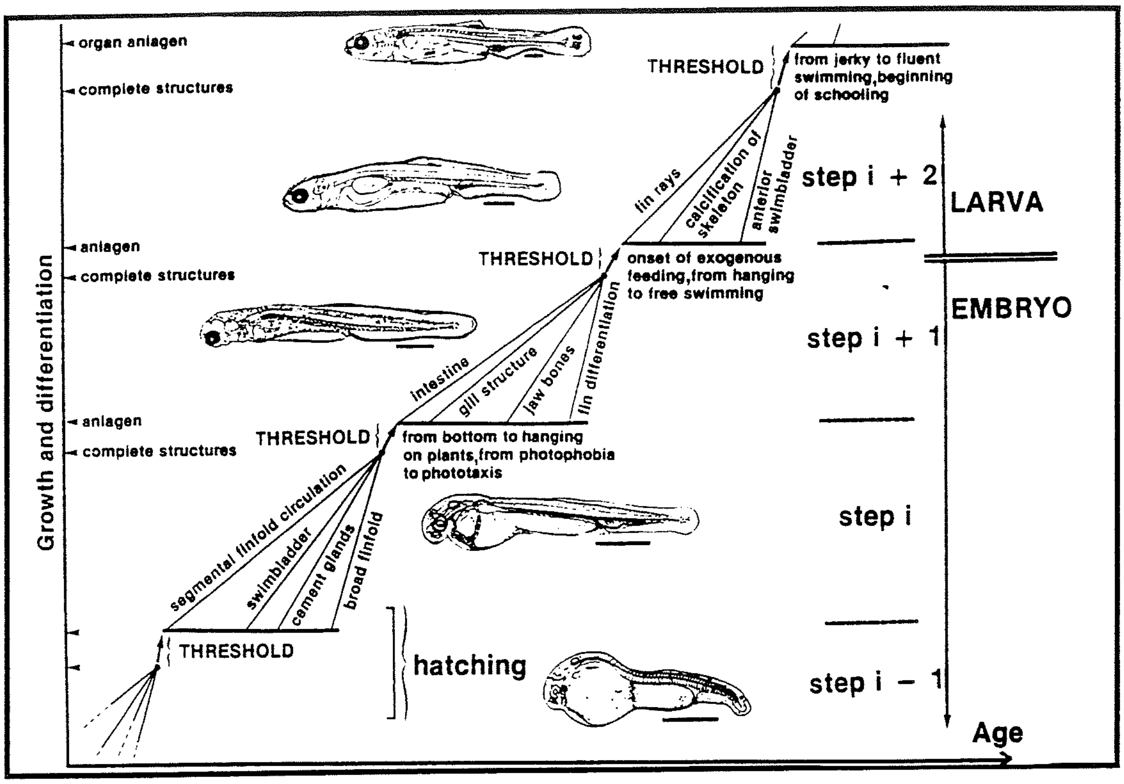


Fig. 26. Three consecutive steps in the ontogeny of a Danubian cyprinid *Abramis ballerus* demonstrating saltatory development. During one step various structures grow and differentiate at different rates but so that they complete and become functional at the same time- at the end of a step- thereby enabling the individual to undergo a rapid change in relation to the internal or external environment in a threshold fashion. Hatching is not an instantaneous event but occurs in different individuals at different times during step i-1 and the beginning of step i. At the end of step i, the completion of a broad finfold, a posterior part of the swimbladder and cement glands combined with a switch from photophobia to phototaxis enable and induce the embryo to leave the bottom, swim up to the surface and attach itself to plants. In step i+1 that follows, embryos build additional structures from the endogenous food supply while hanging motionless on plants above the hypoxic bottom and camouflaged from predators. One of the most decisive thresholds, the transition from embryo to the larva period is shown here between steps i+1 and i+2. As essential for the uptake of exogenous food the intestinal epithelium and jaw bones are completed and free but jerky swimming is possible because of some fin differentiation (from Balon 1985). *(Tre påfølgende step i embryonalutviklingen til en karpe som viser hvordan utviklingen går i "rykk og napp" med raske forandringer etterfulgt av lange perioder der utviklingen tilsynelatende står stille)*

A natural consequence of the theory of saltatory ontogeny is the hierarchical life-history model of embryo-larva-juvenile-adult and senescence periods each separated by a threshold and each consisting of a sequence of saltatory

The decisive events and processes during the ontogeny of fishes seem to be activation, onset of oral feeding, metamorphosis in taxa with indirect ontogeny, maturation of gametes leading to reproduction and death.

Inadequate provision for embryonic nutrition is the primary factor governing the occurrence of a larval stage, and Fig. (27) shows this in a comparison between egg size and development in lampreys and hagfish.

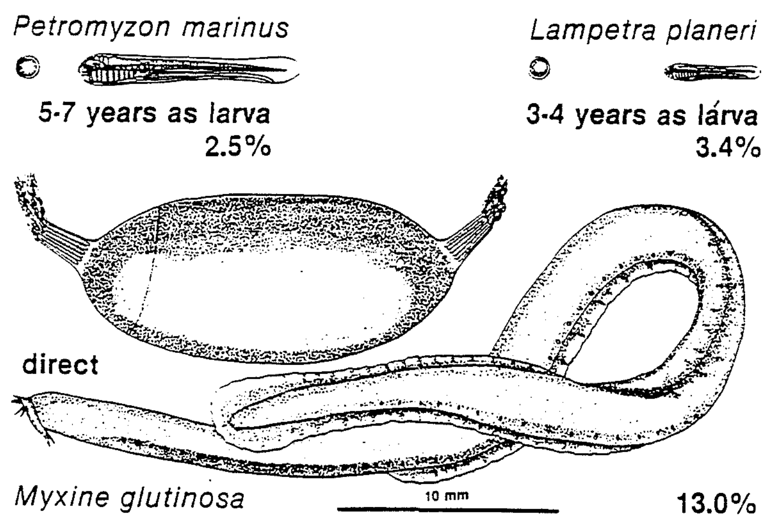


Fig. 27. The sea lamprey, *Petromyzon marinus,* develops from an egg of 1.0mm in diameter to hatch at 4 mm and to first feed orally at 10mm, i.e. 2.5% of an average adult female size, living as larvae from 5-7 years, the nonparasitic brook lamprey,*Lampetra planeri* , with an egg diameter of 1.1 mm only slightly improves on its indirect ontogeny by growing into an adult, definitive phenotype much smaller ≈1/3 of sea lamprey, hatching when 2.3mm and first feeding at 4.4mm (3.4% of the average female adult size), living as a larva 3-4 years and dying after reproduction. The hagfish,*Myxine sp.*, on the other hand, produces a few large eggs 17mm long, hatching at 65mm as a fully formed definite phenotype 13% of an average female's size, feeding immediately like an adult; the large yolk volume made the elimination of a larva and a direct development from embryo to juvenile possible (from Balon 1986).*(Om utviklingen skal gå direkte (uten en larveperiode) eller indirekte, er til en stor grad bestemt av eggets energiinnhold, dette er her vist i en sammenligning mellom utviklingen hos niøye og slimål)*

Low amount of yolk is insufficient to build the definite phenotype and a temporary larva needs to become part of the life history as an highly effective feeding machine, until there is enough building material to proceed with the formation of the definitive phenotype. A larva is, therefore, the transitory vegetative form, often inhabiting an entirely different niche and habitat than the definite form and equipped with numerous temporary organs like respiratory vessels, spines, flaps and filamentous appendages and different body shape. The larva period can be extremely long in some species and conspicuous because of bizarre transient features, essential for the specific purposes of larval existence - acquisition of energy from external sources, dispersal (Barlow 1981), and escape from adult competition or from predation.

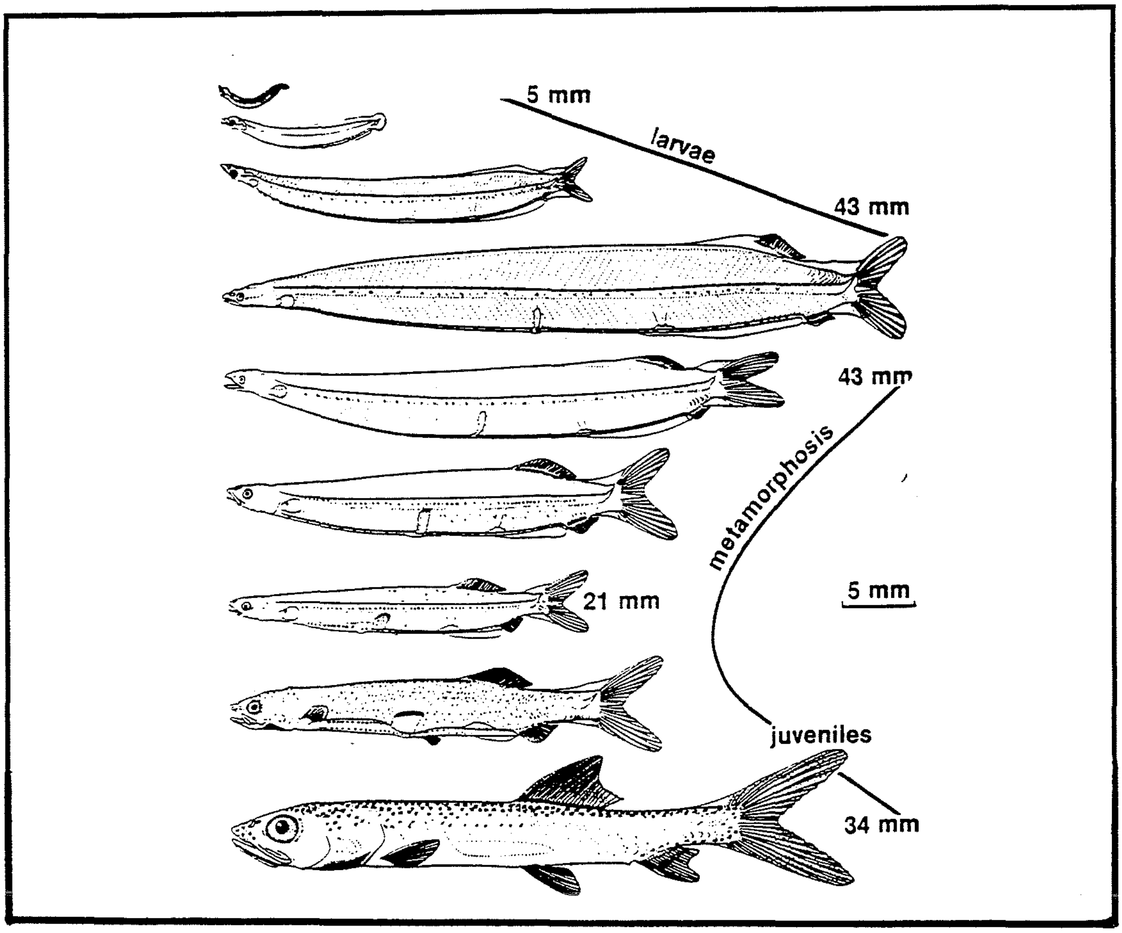
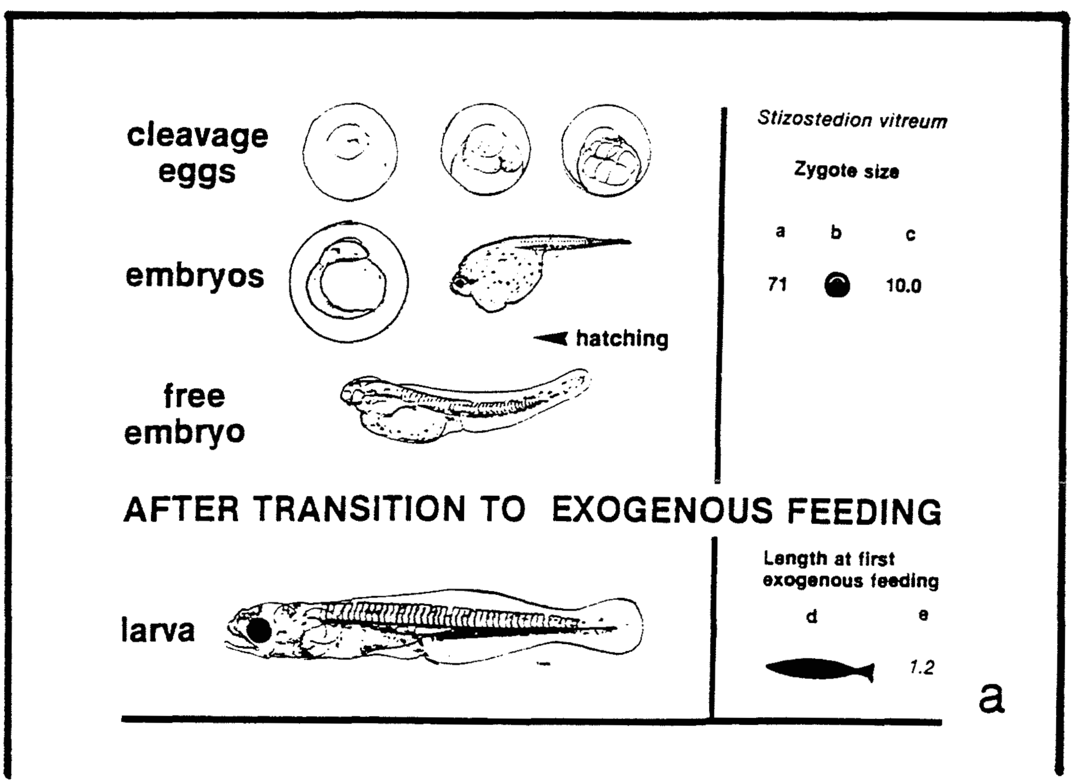


Fig. 28. The cost of metamorphosis is demonstrated for the ladyfish Elops saurus that shrinks from 43 to 21 mm due to this remodelling (from Balon 1986). *(Metamorfose kan føre til at endel av størrelsen oppnådd i larvefasen går tapt på grunn av de store forandringene som skjer i denne fasen)*

"The Metamorphosis" by Franz Kafka begins "As Gregor Samsa awoke one morning from uneasy dreams he found himself transformed in his bed into a gigantic insect". More precisely, the process of metamorphosis includes a complete remodelling "from a highly adapted transitory vegetative feeding machine, to a highly adapted sexual form in order to breed. Much of the size gained during the larva period can be sacrificed for the remodelling during metamorphosis (Fig. 28).

With further specialization of reproductive styles towards increased supply of endogenous energy source in the ovum and parental care the larva period becomes truncated and finally eliminated and the next figure (Fig. 29) show fish with indirect, transitory and direct ontogeny. In fish with large yolk supply the permanent organs are produced directly without remodelling. This occurs in most animal classes including amphibians, and the common belief that larvae occur in all fishes is a bias caused by studies concentrating on marine ichthyoplankton. The planktonic habitat is the very reason that fish do have distinct larvae. It presents a "soup" rich in small food particles as well as space for dispersal.



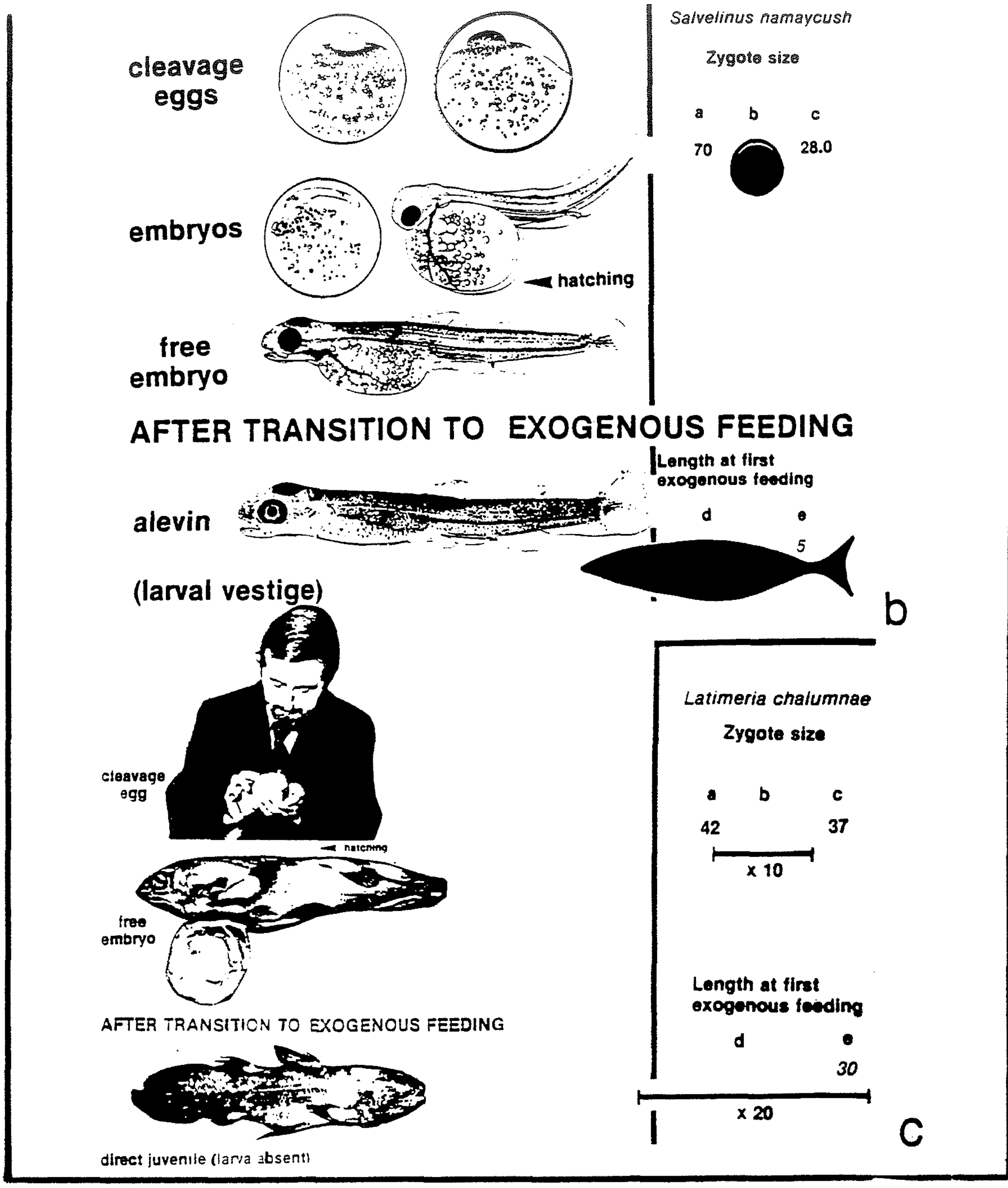


Fig. 29. Comparison of egg sizes, embryos, larvae or juvenile, in fishes with indirect, transitory, and direct ontogenesis in a (a) nonguarding open substratum rock and gravel spawner, with pelagic eggs and larvae, the walleye, (b) a nonguarding broodhiding rock and gravel spawner, the lake charr and (c) the internal bearing ovoviviparous coelacanth *Latimeria chalumnae* a-represent a low energy supplied ovum supplemented with a vegetative larvae remodelled into a definite phenotype via metamorphosis; b-larger, energy rich and less numerous ova which develop in hiding and emerge as feeding alevins, large larval vestiges in possession of most of the permanent adult structures ; c-represent an extreme case, a specialized fish bearing largest ova, a few in number, and developing internally into a fully grown young 30% of its mothers size at parturition. Zygote size right column : a=moisture content, b=relative size of yolk and envelopes, c=%lipid content, d=length at first exogenic feeding and e=in % of average adult size at first exogenic feeding (from Balon 1985). *(Sammenligning mellom fisk som har indirekte (a), en mellomting (b) og direkte utvikling (c))*

SUMMING UP

"The specialized multicellular organism is reduced by each act of reproduction into a large number of nonspecialized single cells, available for natural selection to act upon. Epigenesis creates new phenotypes under the "instruction" given by the genome. The latter results from selection by the past environments, but the phenotype is formed by an interaction with the present environment". To create each time a new phenotype from a single unspecialized cell requires not only the "instructions" passed with the germ material, but also "building material" in form of nutrients (Calow 1977).

Within a more unpredicted perturbed environment the slowly differentiating generalist- with its larvae ready to scatter through large areas and feed on any peaks in density of food organisms - has better changes to survive than a specialist, finely tuned into an unperturbed (or predictably perturbed) and therefore highly competitive environment. Definition of three manistyles of recruitment:

1. Some fishes platy a low cost and high number game described by Sale (1978) as a lottery for living space.

2. An intermediate group of taxa adapted a style of risk distribution based on extreme flexibility of zygotes called by Wourms (1971) a "multiplier effect" and compared "to a roulette game in which the player bets on all numbers. Some portion of his capital will be retained even most of it is lost".

3. Finally many taxa play a high cost and low number game "not adapted to gamble in the lottery", investing instead in real estate- a few zygotes loaded with nutrients and metabolites and intensely guarded (Balon 1978).

Direct ontogeny, therefore, seems to be more specialized type of development, and the evolutionary trends should proceed in this direction in an attempt to shorten the most vulnerable period and even more important to improve competitiveness when the community structure eventually becomes more diverse and complex through speciation and invasion (Balon 1983,1985).

I hope I have managed to explain what a diverse and fascinating period the egg and larval period is, and this is the time in the ontogeny when the individual answers to the environments through epigenesis. Perhaps it has some significance for human beings too for if according to a little rewriting of Samuel Butlers aphorism, "a female and a male fish is only an eggs way of making another egg, then a woman or a man is only an embryos way of making another embryo".

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