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Towards an explanation of the developmental strategy in leptocephalous larvae of marine teleost fishes

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Synopsis

Various observations on the morphology, physiology and biochemistry of leptocephalous larvae of different groups of marine teleost fishes have been brought together in order to arrive at a model which attempts to explain the 'leptocephalous strategy' of larval development. The observation that basic similarities are found in the developmental pattern of all groups of fishes with a leptocephalus (Superorder: Elopomorpha) forms the basis for proposing a common strategy within the superorder. Circumstantial evidence suggesting that premetamorphic (Phase I) larvae obtain a significant fraction of their nutritional needs by absorbing dissolved organic matter across surface epithelia has been reviewed. It is suggested that this might occur via a Na^+-mediated transport system similar to that seen in various marine invertebrates. Breakdown of the gelatinous matrix formed during Phase I is assumed to provide the nutrients required for the metamorphic larvae (Phase II). This strategy is then contrasted with the more 'typical' form of larval development in marine teleosts and shown to differ in several basic respects.

Introduction

The developmental strategy utilized by marine teleost fishes which pass through the larval period as a leptocephalus appears to be unique among the fishes as a whole. Accordingly, these fishes, belonging to the orders Anguilliformes, Elopiformes and Notacanthiformes, have been grouped into a common evolutionary lineage (Superorder: Elopomorpha), considered to comprise the most primitive of the teleosts (Greenwood et al. 1966). In this essay I will review basic similarities of leptocephali of these groups and, using recent biochemical and physiological data from the developing bonefish (Elopiformes: Albulidae: *Albula* sp.) leptocephalus, attempt to define a common developmental pattern within the Elopomorpha. This pattern will then be contrasted with, and shown to differ markedly from, the more 'typical' form of development in other groups of marine teleost fishes.

An extensive amount of transparent gelatinous material is a feature of all leptocephali. Most of the body is composed of this substance, which later disappears as the larva transforms into a juvenile fish. Why does the larva form a vast amount of material which must then be removed before development can continue? This would seem an apparent waste of energy during a critical period in the life history of the fish. Here I will argue that both the synthesis and degradation of the gelatinous matrix play a central role in providing for the nutritional needs of the developing leptocephalus. I will also argue that (1) there is now strong circum-

stantial evidence to support the hypothesis that developing leptocephali obtain at least some of their nutritional requirements by epithelial uptake of dissolved organic matter (DOM) from the surrounding medium and (2) that surface to volume relations appropriate for efficient epithelial uptake of DOM might have played a role in selecting for what has been referred to as 'bizarre' (Hulet 1978) shapes in the leptocephalus.

In attempting to present a common pattern of development within the Elopomorpha I have had to rely on empirical data from only a few different species. I will begin by reviewing the support for the assumption that these observations can be extended to include the Elopomorpha as a whole.

Common characteristics of leptocephalous larvae

Although the morphology of the leptocephalus can vary widely among different species, certain characteristics appear to be common to all groups. The description given here has been condensed from Smith (1979). The most distinctive feature of all known leptocephali is the presence of a nearly transparent, laterally compressed body which, as mentioned previously, is composed primarily of gelatinous material. The head is small with respect to the elongated, ribbon-shaped body. In some species the body is also expanded dorso-ventrally, sometimes extremely so, producing strange-looking, leaf-shaped larvae. However, in all forms the body remains very thin, resulting in a high surface to volume ratio. A thin epidermis covers the body.

The pattern of development in the leptocephalus appears to follow that shown in Figure 1 for the bonefish, at least with respect to the major points. After hatching, the larva undergoes a period of growth which, although variable, is usually of relatively long duration (Castle 1984). For example, in the tarpon, *Megalops atlantica,* this period is estimated to last about three months (Smith 1980) whereas it continues for up to three years in the eel *Anguilla anguilla* (Schmidt 1925 cited in Smith 1979). This growth period is referred to as the premetamorphic interval (Phase or Stage I) (Hardy 1978, Jones et al. 1978).

Several points are worth emphasizing here. Firstly, a significant increase in size occurs during Phase I, although the maximum length attained can be quite variable [e.g. from as little as 28 mm in *M. atlantica* (Mercado & Ciardelli 1972) to at least 1.8 m in notacanthiform leptocephali (Smith 1979)]. Maximum standard length in the bonefish larvae is about 70 mm (Pfeiler 1984a), which falls within the range of 50–100 mm reported to be common in leptocephali (Smith 1979). Secondly, most of Phase I growth occurs in the apparent absence of an endogenous nutrient supply (see Fig. 1). Any yolk reserves are resorbed within a relatively short time after hatching since very young Phase I larvae, only a few millimeters in length, show little or no signs of the yolksac (Hardy 1978, Jones et al. 1978, Smith 1979, 1980). For example, in the eel, *Anguilla japonica,* the yolksac is absorbed about 1–2 weeks after hatching when the larva is only about 7 mm in length (Yamamoto & Yamauchi 1974, Yamauchi et al. 1976). Thirdly, no evidence for identifiable food material has ever been reported in Phase I leptocephali although these larvae have been studied for years by many different workers (Alexander 1961, Hulet 1978, Kracht & Tesch 1981). Thus, the means of obtaining nutrients during the premetamorphic growth interval is unknown but clearly it cannot arise from breakdown of stored yolk material.

Phase I is followed by the metamorphic interval (Phase or Stage II) (Hardy 1978, Jones et al. 1978). A reduction in size appears to be a common characteristic of metamorphosing larvae (Smith 1970, 1984, also see Fig. 1). Phase II larvae gradually resorb the gelatinous matrix and at the end of metamorphosis the body is no longer laterally compressed. Compared with Phase I, the metamorphic interval is shorter (Castle 1984), lasting for only 8–12 days in the bonefish (Hollister 1936, Rasquin 1955, Pfeiler 1984b) and 20–25 days in the tarpon *M. atlantica* (Mercado & Ciardelli 1972).

Although a second growth period between Phase II and the juvenile period (Phase or Stage III) has been applied to elopiform leptocephali (Jones et al. 1978), by the end of Phase II the leptocephalus has completely lost its characteristic form and has begun feeding orally (Rasquin 1955,

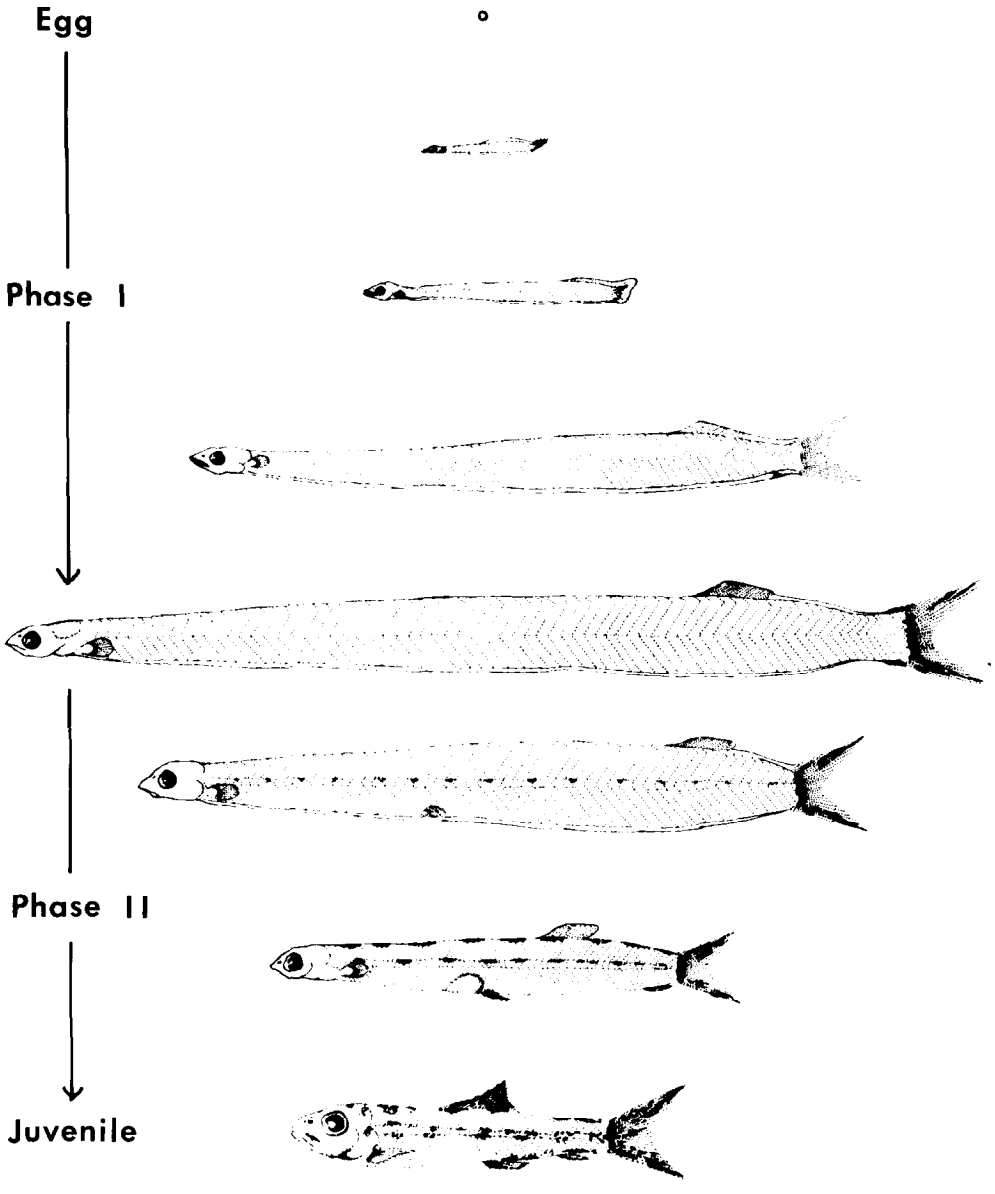

Fig. 1. Phases of larval development in the bonefish (*Albula*). All stages are drawn approximately to scale. Diameter of the unfertilized egg is about 0.5 mm (Pfeiler, unpublished observation). The three Phase I leptocephali (7.8, 17.8, and 43.5 mm SL) were redrawn from Alexander (1961). The three Phase II metamorphosing larvae (63, 47, and 30 mm SL) and the juvenile (25 mm SL) are original drawings made from photographs of specimens collected in the Gulf of California (Guaymas, Sonora, Mexico). Duration of Phase I is unknown; Phase II is completed in 8–12 days (Hollister 1936, Rasquin 1955, Pfeiler 1984b). SL = standard length.

Mercado & Ciardelli 1972). Bonefish at the end of Phase II, and before any growth has occurred, have replaced the gelatinous supporting material with an ossified vertebral column and have the adult number of fin rays (Pfeiler, unpublished observations). Therefore, both on anatomical and physiological grounds, the existence of a so-called Phase III leptocephalus in the bonefish seems questionable and is not considered in the arguments developed below.

Salt loading and unloading during development

Hulet et al. (1972) have shown that Phase I leptocephali accumulate NaCl as they grow (Fig. 2). Their experiments were performed on a mixed group of 43 anguilliform larvae, about half of which could be identified to the family level. Individuals of the Congridae were the most common, with those of Xenocongridae, Ophichthidae, Muraenidae and Anguillidae also present. These data clearly show that, even in a group of different species, total body NaCl content is directly related to larval wet weight. The average sodium concentration of these leptocephali was almost 10-fold higher than the average potassium concentration. In comparison, sodium content of early Phase II bonefish leptocephali is about 7-fold higher than potassium (Pfeiler 1984b). Since it is highly unlikely that sodium accumulates within cells at this ratio, it can be assumed that it is localized predominately in the extracellular matrix.

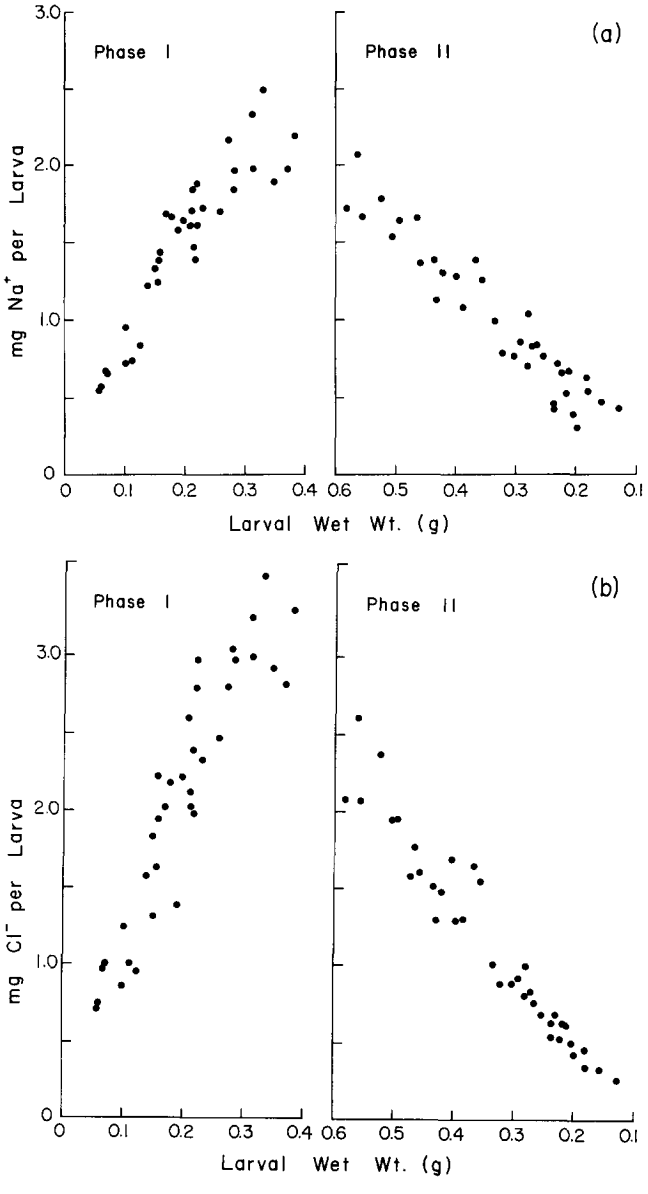

Fig. 2. Sequential loading and unloading of Na^+ (a) and Cl^- (b) during Phases I and II of development in leptocephalous larvae. The data for Phase I were taken from Hulet et al. (1972) and represent various species of anguilliform leptocephali. The data for Phase II were taken from Pfeiler (1984b, c) and represent a single species (*Albula* sp.) of elopiform leptocephali.

My experiments with bonefish leptocephali (Pfeiler 1984b, c) have shown that salt unloading occurs during Phase II (Fig. 2). Metamorphosing larvae lose about 80–90% of their whole-body NaCl content during this period.

Although salt loading has not yet been demonstrated in Phase I bonefish leptocephali (nor has salt unloading been demonstrated in Phase II eel leptocephali) it can be assumed that the NaCl that is lost during Phase II in the bonefish accumulates during Phase I in a manner similar to that shown for eels (Fig. 2). The converse hypothesis would require that the recently hatched embryo contain a salt load equivalent to a fully developed Phase I larva, which is highly unlikely. Circumstantial evidence presented below also suggests that all leptocephali, including eels, will be found to unload NaCl during Phase II, as well as load NaCl during Phase I.

The questions that arise out of these considerations are: (1) What are the factors responsible for controlling NaCl flux during development? and (2) Does this NaCl flux have any physiological role in the developing leptocephalus? These questions will be addressed in the following sections.

Glycosaminoglycans, hydration changes and salt fluxes

Early Phase II bonefish leptocephali contain relatively high amounts (equivalent to 5–7% of the total larval dry weight) of sulfated glycosamino-

glycans (GAG), composed principally of a keratan sulfate-like compound (Rasquin 1955, Pfeiler 1984d). Sulfated GAG chains are normally formed of repeating disaccharide units of either neutral sugar or hexuronic acid and sulfated hexosamine (Comper & Laurent 1978). Intact polysaccharide chains therefore contain a repeating sequence of carboxylate and/or sulfate groups resulting in a high anionic charge density. Consequently, GAGs confer a high water retaining capability to tissues (due to mutual charge repulsion resulting in high hydrodynamic volumes) and affect the distribution of microions such as Na^+ (reviewed by Comper & Laurent 1978, Hascall & Hascall 1981, Toole 1981).

Water content in both Phase I eel leptocephali (Callamand 1943, Hulet et al. 1972) and early Phase II bonefish leptocephali (Pfeiler 1984b) is over 90% of the total wet weight. During the Phase I growth period in eels there is little change in this high larval water content (Hulet et al. 1972). However, in Phase II bonefish leptocephali, water content decreases during metamorphosis (Pfeiler 1984b). This loss corresponds to the period when the gelatinous matrix is being degraded and muscle tissue is being formed. Water loss is substantial, accounting for almost 80% of the total body water of early Phase II larvae. A similar water loss is probably also occurring in eel leptocephali since metamorphosed eels have a total body water content of 80–85% (Tarr & Hill 1978, Otwell & Rickards 1981), identical to that of recently metamorphosed bonefish (Pfeiler 1984b).

Since Hulet et al. (1972) found that percent body water in eels remains constant during Phase I, these larvae must accumulate water as they grow and increase wet weight. By analogy, it can be argued that Phase I bonefish leptocephali do the same. To argue otherwise would require that the recently hatched leptocephalus contain an amount of water equal to that of a fully developed Phase I leptocephalus, or about 0.5 g (Pfeiler 1984b). Since this amount is estimated to be at least 10-fold greater than total wet weight at hatching, this explanation can be eliminated. We are left with the conclusion that Phase I leptocephali load water and Phase II leptocephali unload water, a pattern identical to that seen for NaCl (Fig. 2).

Total GAG content in Phase II bonefish leptocephali decreases by about 87% during metamorphosis (Pfeiler 1984d). Since GAGs are known to affect tissue water content and microion distribution, I argued that GAG loss during metamorphosis was responsible for water and NaCl loss. This conclusion is supported by the observation that a direct relationship exists between larval GAG and water content and that the percent losses in these substances, as well as NaCl, are very similar during metamorphosis (Pfeiler 1984d). Figure 3 shows that a direct relationship also exists between larval GAG and Na^+ content.

Although GAG synthesis has yet to be reported for Phase I leptocephali, it seems almost certain that it will be found to occur. Again, to argue otherwise would require a high GAG content in recently hatched embryos which remains constant during the time when larvae form an extensive amount of gelatinous matrix.

Therefore, I propose the following pattern of development in the leptocephalus. After hatching, Phase I larvae form a large amount of gelatinous material, in the absence of any yolk reserves, while the body remains laterally compressed. This increase in gelatinous material is presumably due to GAG synthesis. Increased GAG content causes the developing larva to load water, although the percent water with respect to total wet weight remains constant. Because of the increase in anionic charge in the matrix, Na^+ will be accumulated (Fig. 3). Chloride also enters, although the factors influ-

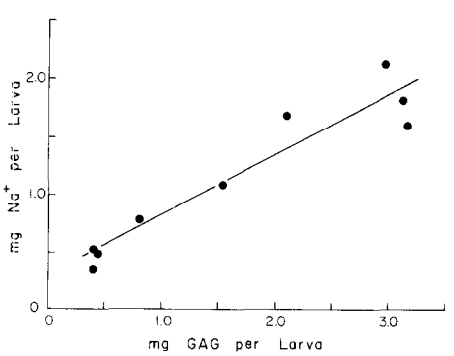

Fig. 3. Relationship between whole-body Na^+ and glycosaminoglycan (GAG) contents of Phase II bonefish leptocephali. Data taken from Pfeiler (1984d). Line fitted by linear regression analysis ($y = 0.308 + 0.519x$; $r = 0.95$; $N = 9$).

encing its distribution may be more complex. The net effect is that GAG synthesis results in both water and salt loading during Phase I. At the onset of metamorphosis, GAG begins to be catabolized and the matrix is no longer able to maintain its water and salt load. These substances are then lost to the external medium.

This model predicts that water and salt loading and unloading are a direct result of GAG synthesis and breakdown, a point which has recently received some support. Phase II bonefish leptocephali are euryhaline (Pfeiler 1981). If larvae are placed in dilute (8‰) or concentrated (48‰) sea water the metamorphic process is not affected. Larvae develop normally and unload NaCl and water at the same rate in both salinity extremes (Pfeiler 1984c). This result was unexpected since a priori it would seem that hypertonic media would favor and accelerate water loss while impeding NaCl loss and hypotonic media would favor NaCl loss but impede water loss. Since water and salt loss could be independent of external salinity if they were being regulated primarily by internal GAG content, these results are consistent with the model.

Evidence for uptake of dissolved organic matter in the Phase I leptocephalus

The feeding mechanism(s) utilized by premetamorphic leptocephali remains unknown. In this section I will review some of the more important observations that have been made on the digestive system and then discuss the circumstantial evidence that supports the hypothesis that Phase I leptocephali may obtain at least part of their nutritional requirements by absorption of DOM from the medium.

Probably the most enigmatic structures of the premetamorphic leptocephalus are the well-developed, forwardly-directed teeth, which are lost, or possibly absorbed, during metamorphosis (Hulet 1978, Smith 1979, Castle 1984). It seems that these larvae would be readily able to commence active feeding. However, and quite interestingly, many other observations suggest that this may not be occurring to any large extent. Active feeding would require a functional digestive system. The gut of the leptocephalus, located along the ventral margin, is usually described as a simple and narrow straight tube, which in some forms contains swellings and loops that can sometimes be useful taxonomic characters (Smith 1979, 1984, Castle 1984). Histological studies on the bonefish and eel, *Ariosoma balearicum,* have shown that the digestive system, including associated organs such as the pancreas, are not yet fully developed in the premetamorphic leptocephalus (Hulet 1978) and remain in this condition until near the end of metamorphosis when ingested material first appears in the gut (Rasquin 1955). In *A. balearicum* the midgut sometimes is without a lumen (Hulet 1978) and in the bonefish it is filled with a 'coagulate' which lacks identifiable food material (Alexander 1961). The anterior portion of the gut in the bonefish leptocephalus was found to be empty. The results of Alexander (1961) are particularly impressive since gut contents of more than five hundred Phase I and II leptocephali were examined. As mentioned previously, recognizable food material has never been reported in Phase I leptocephali. While it is conceivable that larvae are actively feeding, as suggested by Rasquin (1955), and that gut evacuations occur when larvae are collected, it seems highly unlikely that this would occur in all larvae. Experimental studies on other larval teleosts have shown that handling and collecting procedures can cause evacuation of food material from the gut, but this never occurs in 100% of the larvae tested (reviewed by Blaxter & Hunter 1982).

If Phase I leptocephali are not actively feeding, or doing so at a reduced level, we are still left with the problem of explaining the function of the well-developed larval teeth and also how larvae supply their nutritional needs. Hulet (1978) suggests that larval teeth could be used to grasp and puncture prey, or possibly even represent a mechanism to keep material out of the digestive system. Alexander (1961) also mentions that the teeth might be involved in filtering small food particles. Other functions, including defense, are also a possibility but none of these has been proven.

The absorption of DOM from the external me-

dium, as an alternate means of supplying nutritional needs in the premetamorphic leptocephalus, has been suggested by previous workers (Alexander 1961, Hulet 1978). Several lines of circumstantial evidence support this hypothesis. The thin surface-epithelial layer of the leptocephalus seems ideally suited for such a function. In the eel, *A. balearicum,* the surface epithelium is only 2–3 cell layers thick, with the outer layer of cells possessing numerous filamentous projections, very similar in appearance to intestinal microvilli (Hulet 1978). Such structures are customarily thought of as being involved in absorption since they provide a large surface area which favors surface-related processes.

Surface to volume relations also suggest a possible explanation for the strange, expanded shapes seen in many leptocephali (see Smith 1979, 1984, Castle 1984). In these forms the body always remains laterally compressed. The most obvious explanation for this phenomenon is that it is an adaptive mechanism employed by the leptocephalus to further increase the surface to volume ratio. This would favor nutrient absorption from the external medium, as well as other surface processes such as cutaneous respiration. Although a functional circulatory system is present in Phase I larvae (Hulet 1978), undeveloped gill filaments, lack of erythrocytes, and lack of hemoglobin (Rasquin 1955, Hulet 1978, Castle 1984) suggest that gas exchange across thin surface epithelia could play a significant role in larval respiratory physiology.

The evidence presented to this point for uptake of DOM is admittedly more provocative than compelling. However results of recent biochemical experiments with bonefish leptocephali lend support to the argument. Early Phase II larvae contain relatively high levels of free amino acids, equivalent to, or exceeding, those found in muscle tissue of adult marine teleosts (Pfeiler, unpublished observations). The essential amino acids (Mertz 1972) leucine, isoleucine, phenylalanine, histidine, valine, methionine, lysine and arginine account for about half of the total. The presence of a high percentage of essential amino acids, which the larva is presumably unable to synthesize, together with the absence of an obvious nutrient supply, is certainly consistent with the hypothesis that the leptocephalus obtains these compounds by epithelial uptake.

A comparison of the developing leptocephalus with those marine invertebrates that are known to take up DOM from the medium, suggests a possible role for the high quantities of NaCl that are loaded and then unloaded during development. Surface epithelia of these marine invertebrates contain cells which have microvilli exposed to the external medium (Preston & Stevens 1982), analogous to the situation in the leptocephalus of the eel *A. balearicum* (Hulet 1978). In many invertebrate species, uptake of DOM occurs via a Na^+ (or salinity)-dependent, carrier-mediated process (reviewed by Preston & Stevens 1982). If putative uptake of DOM were also Na^+-dependent in the leptocephalus, NaCl loading which occurs during the prolonged growth phase may have a physiological function. In this scenario of Phase I development, GAG synthesis would increase polyanionic charge content, resulting in NaCl (and water) loading, with Na^+ entering via a Na^+-mediated co-transport system which drives the uphill transport of amino acids and possibly other organic compounds as well. Although highly speculative, the hypothesis is testable and is presented here in order to form a framework for possible future research.

Sources of nutrition for the metamorphosing (Phase II) leptocephalus

The only information to date on possible sources of energy during Phase II comes from experiments on the bonefish leptocephalus (Rasquin 1955, Pfeiler 1984d, Pfeiler & Luna 1984). Since the metamorphic period is relatively short in the bonefish, as is probably true in other species of elopomorphs as well, and since large decreases in endogenous biochemical components occur during this time, it is assumed that the larva derives most of its nutritional requirements from the catabolism of these endogenous food stores formed during Phase I and stored within the gelatinous matrix. If the model presented in the previous section is correct, meta-

morphosing larvae would not be obtaining substantial nutrients by a Na^+-linked uptake of DOM since NaCl unloading is occurring. Also, both in the bonefish (Rasquin 1955) and in the tarpon (Mercado & Ciardelli 1972), the leptocephalus does not begin exogenous feeding until near the end of metamorphosis.

Endogenous carbohydrate (mainly GAG) and lipid appear to be the main nutritional sources during Phase II in the bonefish (Pfeiler 1984d, Pfeiler & Luna 1984). Total soluble protein in the larva remains relatively constant during this time (Pfeiler & Luna 1984). This is in contrast to energy use in marine teleosts such as the winter flounder *Pseudopleuronectes americanus* that rely on yolk reserves before exogenous feeding begins, where lipid and protein content of the yolk provide most of the nutritional requirements while carbohydrate is of little importance (Cetta & Capuzzo 1982).

Besides providing a nutritional source during metamorphosis, the gelatinous matrix of Phase I larvae might also be involved in maintaining neutral buoyancy. The premetamorphic leptocephalus lacks a functional swim bladder (Hulet 1978). In the bonefish, this structure first becomes apparent to the unaided eye during metamorphosis (Rasquin 1955). When early Phase II bonefish leptocephali, in which the swim bladder is still underdeveloped (Fig. 4A), are placed in dilute (8‰) or concentrated (48‰) sea water they are unable to maintain

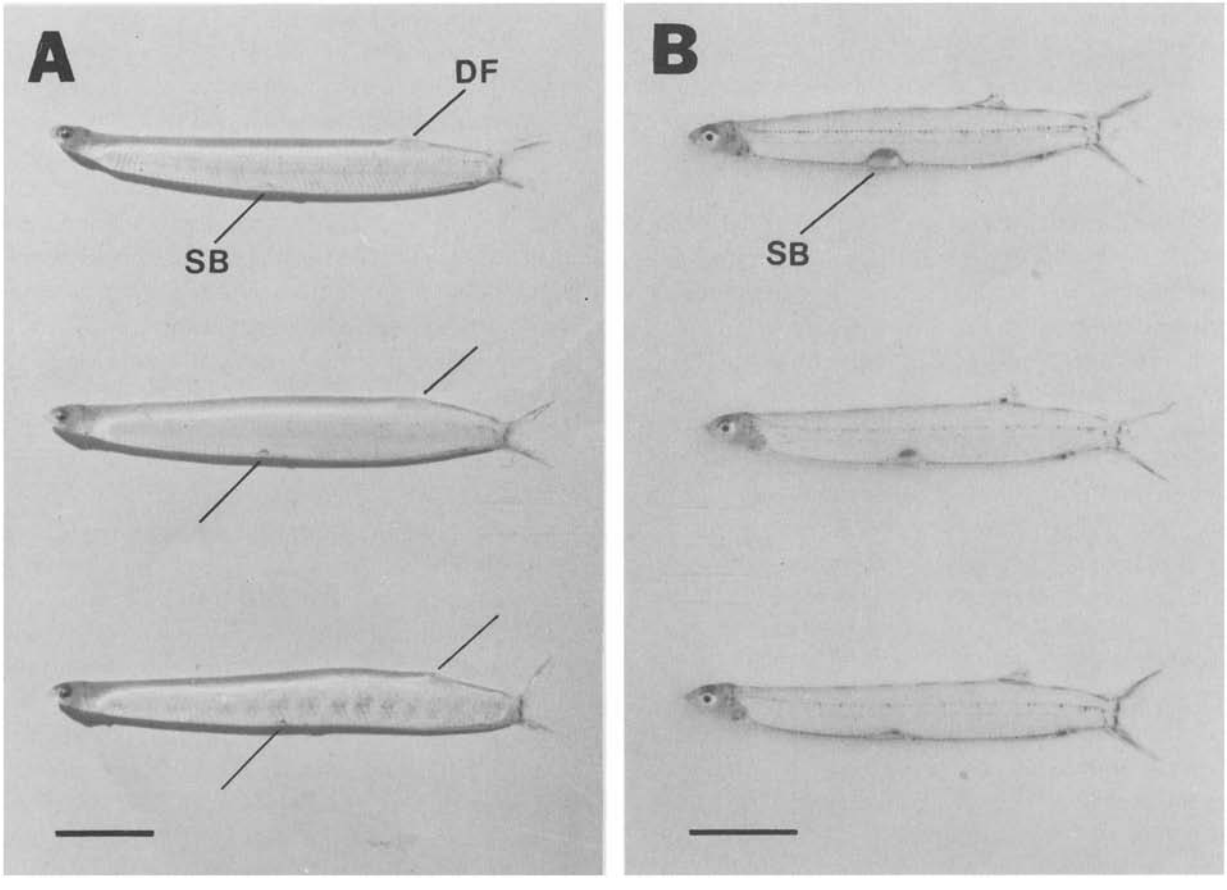

Fig. 4. Phase II bonefish leptocephali from the Gulf of California (Pfeiler 1984c) after 16 hours (A) and 64 hours (B) in salinities of 8‰ (upper), 35‰ (middle) and 48‰ (lower). Water temperature was 19–20° C. Note the posterior location of dorsal fin (DF) and similar sizes of developing swimbladder (SB) in (A). Larvae in (A) are 46–49 mm SL and already several days into the metamorphic interval. In (B) note the increased development of the swimbladder in 35‰ sea water and the difference in swim bladder size as a function of salinity. Larvae in (B) are 38–40 mm SL. Dorsal and caudal fins were lightly marked with a pencil for better contrast. Bar = 10 mm.

their position in the water column and either sink to the bottom (8‰) or float to the surface (48‰) while actively attempting to regain their original position (Pfeiler 1984c). In more advanced Phase II larvae, the swim bladder becomes functional and larvae begin to compensate for the different salinities by showing an apparent increase in swim bladder volume in dilute sea water and an apparent decrease in volume in concentrated sea water (Fig. 4B).

Developmental strategy in the Elopomorpha compared with other teleosts

Because the 'leptocephalous strategy' of development outlined in the preceding sections is quite different from that employed by most fish larvae, it would be worthwhile at this point to summarize these differences. A 'typical' pattern of development in marine teleost fishes, that do not have a leptocephalus, could be generalized as follows. After hatching, the yolk-sac larva or eleutheroembryo (Balon 1981) receives nourishment from the attached yolk-sac. Yolk reserves are usually depleted within a relatively short period (sometimes in as few as 1–7 days) after which time exogenous feeding, characteristic of the larval period, begins. During yolk depletion, the embryo shows relatively little increase in length. After exogenous feeding begins, the larva increases in size and continues to develop into a juvenile fish.

In the Elopomorpha, the developmental interval immediately following hatching and terminating with yolk absorption is probably analogous to that of other fishes. However, at this point the two developmental strategies begin to diverge. Whereas most teleost larvae begin exogenous feeding and subsequently develop into juveniles, elopomorph larvae show no sign of external feeding yet increase dramatically in size (Phase I). Then, at the end of Phase I, the gelatinous larva must be radically transformed (Fig. 1) before the juvenile period is reached, again in the absence of exogenous feeding. Thus, a basic difference between most teleosts and the elopomorphs during larval development appears to be related to the source of nutrients. In the former, nutrients are provided by the yolk and subsequently by exogenous feeding. In the latter, they are evidently provided by a yolk for a short period. Afterwards, and for most of the larval growth period, at least part of the energy supply is postulated to arise from uptake of DOM. The macromolecular components synthesized during this period, mainly GAG and lipid, are then viewed as providing an energy source as the larva metamorphoses into an orally-feeding juvenile fish. Whether other teleost embryos are also able to take up DOM, and thereby supplement yolk reserves, is not known.

The basic differences in developmental strategy, outlined above, lead to questions concerning the evolutionary implications of these observations: (1) What were the important factors that originally favored the leptocephalous form of development in some primitive groups of teleosts?; (2) Today, why do we find only a very few groups of marine teleosts that employ the 'leptocephalous strategy'?; and (3) Did certain fundamental characteristics of this strategy tend to reduce overall fitness during evolution of the fishes and, if so, what were these characteristics? Of course, precise answers to these questions cannot be given at this time, but the arguments developed in this paper may provide a clue as where to begin. I have suggested that the manner of supplying energetic needs during development is a basic difference between elopomorphs and other teleost fishes. Assuming that this model is correct provides a point of departure and suggests that we look at larval nutritional needs in attempting to explain developmental strategies. For example, absorption of DOM across surface epithelia, if it were the primary means of obtaining nutrients, would certainly lessen competition for available food reserves. Since the larva would be, in essence, living and developing in a nutrient 'bath', it would theoretically be able to survive for long periods if other ecological factors such as predation, etc., were not taken into account. Thus, it is easy to visualize how the prolonged developmental period in the leptocephalus, lasting for several years in *A. anguilla,* could be more easily sustained. However, increasing the length of a relatively weak period in the life history of the fish may

have also been a contributing factor in selecting against the leptocephalous form of development in the more advanced teleosts.

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