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Aquatic Versus Terrestrial Feeding Modes: Possible Impacts on the Trophic Ecology of Vertebrates

Karel F. Liem
Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138

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SYNOPSIS. On the basis of experimental work, a clear dichotomy in design of the feeding mechanism between aquatic and terrestrial vertebrates has been found. The aquatic medium combined with suction and the hydrodynamic tongue offer an unparalleled array of prey capture opportunities for aquatic vertebrates. In the terrestrial feeding model, prey capture and prey processing require a precise functional design to match the nature of the prey. It is proposed that this dichotomy in basic design would result in fundamental differences in the aquatic and terrestrial paradigms in vertebrate ecology. Four hypotheses and their respective supporting evidence are presented: (1) Increased opportunism, more extensive prey switching and food overlap are prevalent in aquatic systems; (2) Convergent evolution which is so pervasive in terrestrial feeding systems is uncommon among aquatic vertebrate feeding systems; (3) Competition is relaxed and character displacement is absent in aquatic vertebrate feeding systems; and (4) Patterns of diversity in aquatic vertebrate feeding systems defy the terrestrial paradigm.

INTRODUCTION

With the emergence of powerful analytical tools, we have gained an ever-more accurate understanding of the feeding mechanisms of vertebrates. These experimentally-based studies have enabled us to formulate general models for both the aquatic (*e.g.*, Lauder, 1983; Muller *et al*., 1982; Brainerd, 1985) and terrestrial vertebrates (*e.g.*, Gorniak, 1977; Smith, 1982, 1984; Zweers *et al.*, 1977; Bramble and Wake, 1985). It appears that the aquatic and terrestrial models differ from each other in many important parameters. The aquatic model is medium-dependent and possesses an unparalleled versatility (Liem, 1984) while the terrestrial model is operated by a strikingly constant pattern generator (Thexton, 1976; Hiiemae and

Crompton, 1985). Terrestrial vertebrates tend to exhibit very precise adaptive designs in their jaw apparatus even though the activity pattern of their muscles remains constant across phylogenetic lineages.

The question whether the strikingly contrasting aquatic and terrestrial designs have a major impact on the behavioral ecology and the evolutionary ecology of aquatic and terrestrial vertebrates remains unanswered. In general patterns in behavioral and evolutionary ecology of vertebrates have been interpreted without taking into consideration the dichotomy in design of the feeding apparatus of aquatic and terrestrial vertebrates. If differences were found in aquatic forms, qualifiers were introduced to explain away the exception to the general ecological paradigm which was invariably based on terrestrial systems. Often the terrestrial ecological paradigm is forged upon the aquatic system.

In this paper I will attempt to examine the possible impact that the contrasting aquatic and terrestrial designs may have on behavioral and evolutionary ecology. My major goal is to stimulate further discussion and experimental analysis, since research relating design with ecology is still in its infancy.

THE AQUATIC VERTEBRATE FEEDING MODEL

In general the fish feeding apparatus can be modeled as truncated cones or cylinders (Osse and Muller, 1980; Muller *et al*., 1982; Brainerd, 1985; Fig. 1). Suction is generated when the cone expands. Timing of mouth opening can be coincident with cone expansion or mouth opening lags behind the expanding cone. According to this model the magnitude of pressure changes within the cone and flow velocities depend on the rates of cone expansion and mouth opening. Thus this model predicts that the faster a fish is capable of expanding the cone and opening of its mouth, the greater the pressure change it can generate and the greater a velocity of water flow can be produced. A comparative analysis has verified this prediction (Brainerd, 1985). This expanding truncated cone model also predicts that fishes with differing volumes and configurations of their buccal cavities will exhibit differences in suction efficiencies. There is little doubt that buccal expansion is the primary force driving suction feeding. According to this model, important parameters governing the velocity and degree of cone expansion are the shape and size of the mouth (mandible, premaxilla and maxilla), the palatoquadrate arch and the hyoid; the architecture, topography and functional features of the sternohyoideus (Fig. 1, SH), levator operculi (LO), levator arcus palatini (LAP) and epaxial (EP) muscles. Variations in these features are thought to play a key role in the different functional patterns of feeding in cichlid fishes (Barel, 1983).

In the aquatic medium a premium is placed on effective suction and fluid-propulsion mechanisms. The expanding cone provides a highly versatile and effective suction device. Velocity, magnitude and direction of suction can be controlled by varying the parameters mentioned above. As a result any kind of prey of food floating or swimming in or on the water column can be captured. Even prey items within cracks, cavities or attached to the substratum can be effectively collected by suction generated by the expanding cone or cylinder. Even limpets are known to be collected by the pile perch *Damalichillys vacca* (Jeffrey S. Jensen, personal communication) from the substratum by high velocity suction.

The combination of the dense aquatic medium and the expanding cone suction generating device has resulted in the most versatile model of feeding known in animals. Empirical data has shown that the taxonomic and ecological diversity of prey that can be collected by suction in a single teleost species is unsurpassed by any other mode of feeding in other animal species (*e.g.*, Goulding, 1980).

The versatility of the expanding cone model is not restricted to prey capture. Pressure differences in different areas within the cone are hypothesized to be generated by modulating muscle actions that can change the shape of the cone (Liem, 1980, 1990). In this way the captured prey within the cone can be moved or turned in different directions. Thus the truncated cone can also function as a most efficient and versatile hydrodynamic tongue (Lauder, 1983; Liem, 1990).

The aquatic medium combined with suction and the hydrodynamic tongue offer an unparalleled array of prey capture opportunities for teleosts.

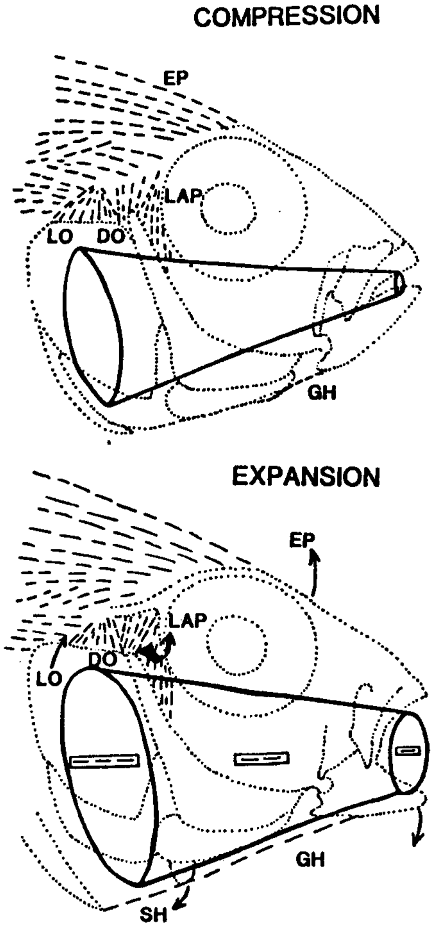

Fig. 1. Truncated cone model of a teleost fish (modified from Brainerd, 1985; Muller *et al.*, 1982; Lauder, 1983). The buccal cavity is modelled as a truncated cone which can be expanded to create progressively more negative pressures as one moves back toward the base of the cone. Principle movements are indicated with arrows. DO, dilator operculi; EP, epaxial muscles; GH, geniohyoideus; LAP, levator arcus palatini; LO, levator operculi; SH, sternohyoideus.

THE TERRESTRIAL VERTEBRATE FEEDING MODEL

Basic terrestrial vertebrate design of the feeding apparatus differs significantly from the aquatic feeding model. The terrestrial model can be briefly summarized as follows (Fig. 2). The feeding cycle begins with slow opening during which the hyolingual apparatus advances beneath the prey and the tongue is being fitted to the prey. The second phase is fast opening, when the skull and mandible move in opposite

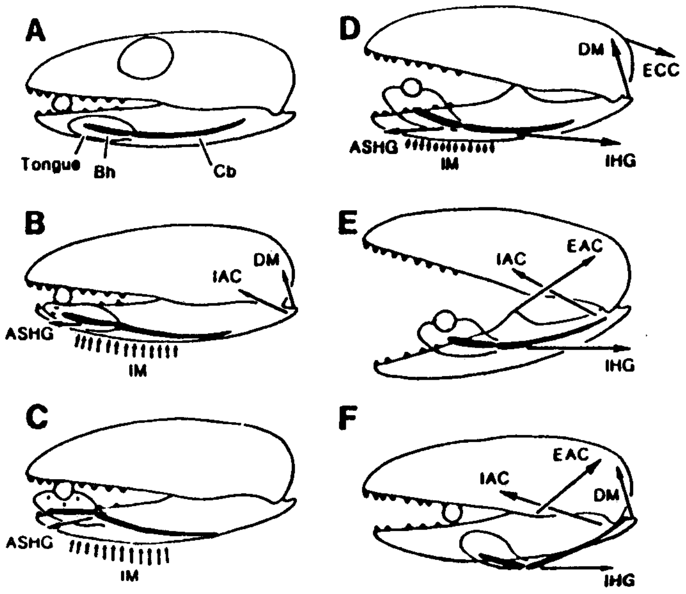

Fig. 2. Masticatory apparatus of a generalized tetrapod (from Bramble and Wake, 1985; courtesy of Harvard University Press). A: System at rest with food object (stippled) in jaws. B and C: Slow open as the hyolingual unit moves under the prey and the tongue is being fitted to the food; D: fast open with cranium and mandible moving in opposite directions; E: fast close, when cranium descends and mandible elevates and the hyoid moves backward; F: slow close or power stroke when prey is crushed. ASHG = anterior suprahyoid group; Bh, basihyal; Cb, ceratobranchial; DM, depressor mandible; EAC,external adductor group; ECC, epaxial cervical complex; IAC, internal adductor complex; IHG, infrahyoid group; IM, intermandibularis. Arrows indicate principal direction of muscle force.

directions. The prey is transported by the tongue. Fast opening is immediately followed by fast closing during which the cranium descends and the mandible is elevated while the tongue and hyoid move backward. The final phase is the slow closing or power stroke during which the prey is crushed. This pattern is pervasive among terrestrial vertebrates. It seems to involve a pattern generator to ensure the precise coordination of jaw movements with the kinematics of the hyoid apparatus and tongue.

Electromyographic analysis synchronized with cineradiography and strain gauge recordings has shown a very conserved pattern of muscle actions during the slow opening, fast opening, fast closing and slow closing (power stroke) phases (Fig. 3). Constancy of the kinematic and muscle action patterns in vertebrates is well documented (*e.g.*, Hiiemae and Crompton, 1985; Smith, 1982, 1984; Thexton, 1976; Weys, 1981).

Thus, terrestrial vertebrate feeding design can be characterized as being controlled by remarkably conserved neuromuscular outputs producing a constant kinematic pattern of jaws finely tuned with hyoid and tongue movements. The major implications of the terrestrial vertebrate feeding model are: (a) prey capture must proceed actively by special adaptations and pursuit; and (b) prey processing requires a precise design in the “hardware” of the feeding apparatus to match the nature of the prey since the underlying neuromuscular output (“software”) is constant. Moreover the

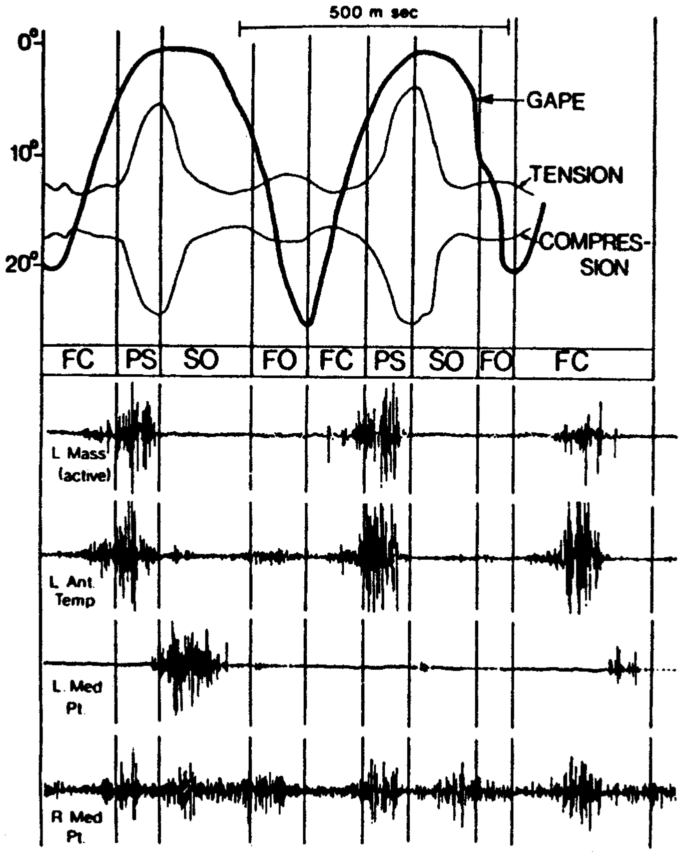

Fig. 3. Relationship among jaw movements (heavy line), strain (fine lines) and electromyograms during the chewing cycle in a macaque (from Hiiemae and Crompton, 1985; courtesy of Harvard University Press). FC, fast close; FO, fast open; L. Ant. Temp., left anterior temporalis; L. Mass., left masseter; L. Med. Pt., left medial pterygoid; PS, power stroke or slow close; R. Med. Pt., right medial pterygoid: SO, slow open.

terrestrial medium does offer numerous opportunities for defenses against predators by prey, thereby greatly limiting the potential feeding repertoires of a particular terrestrial vertebrate species.

DESIGN AND ECOLOGY

The notion that design should have a major impact on the ecological performance of organisms is widely accepted (*e.g.*), Barel, 1983; Motta, 1985; Gans, 1986; Wainwright, 1987; Yamaoka, 1982, 1983; Norton, 1989). Yet design differences seem to be assigned only a minor role, if at all, in the notions of ecological theory involving resource partitioning, optimal foraging, competition, character displacement and convergent evolution. In the search for broad generalizations most investigators have simply adopted the terrestrial paradigm when working with aquatic vertebrates. Thus the majority opinion is that what applies to terrestrial systems should also apply to aquatic systems.

I propose an alternative hypothesis that the differences in basic design between the terrestrial and aquatic feeding apparatus have a potentially major impact on the nature of ecological performance of aquatic and terrestrial vertebrates. Built-in flexibility of the expanding cone in the aquatic medium which in turn is conducive to versatility, should significantly influence the notions of competition, resource partitioning, adaptation, character displacement and convergent evolution in aquatic vertebrates. It is hypothesized that aquatic paradigms are fundamentally different from the terrestrial paradigms in vertebrate ecology.

HYPOTHESIS 1: INCREASED OPPORTUNISM AND FOOD OVERLAP PREVAIL IN AQUATIC SYSTEMS

Built-in versatility of the truncated expanding cone feeding model functioning in the aquatic medium predicts a much wider food overlap and extensive prey switching among aquatic vertebrates.

Empirical studies (*e.g.*, Goulding, 1980; Stoner, 1980; McKaye and Marsh, 1983; Ribbink *et al*., 1983) support the notion that fishes engage in extensive diet switching, opportunism, and much-reduced resource partitioning during normal food abundance. Resource partitioning in fishes has very flexible partitions or even removable partitions depending upon the species present and the prevailing resources. Goulding (1980) reported numerous examples of extensive diet switching, *e.g*., the piranha (*Serrasalmus rhombeus*) was found to feed on fish, crabs, birds, and mammals as well as porcupine spines, lizards, beetles, fruits and seeds, tree resin, flowers and leaves (Goulding, 1980, p. 159)! Cichlids also engage in diet switching with extensive diet overlap (Fig. 4) since many of them have expanding repertoires by using the same "hardware" (the expanding cone) in conjunction with a repertoire of "software" (neuromuscular outputs) (Liem, 1980).

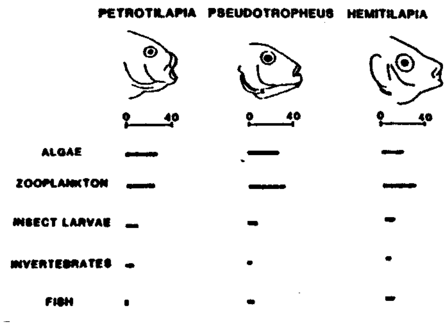

Fig. 4. Diets of three genera of "herbivorous" cichlid fishes from Lake Malawi. The length of the bars equals the percentage of food intake. Considerable food overlap occurs.

In terrestrial systems, the "hardware" (jaw apparatus) being operated by a relatively constant "software" (neuromuscular output) is more precisely matched to its biological role. The precise matching of design with biological role results in less opportunistic feeding, increased resource partitioning and limited diet switching (*e.g.*, Schoener, 1974; Morse, 1980; Vrba, 1980; Grant, 1986). Perfect matching of bill design with the nature of the preferred food and limited food overlap is well illustrated in Darwin's finches (Fig. 5). One can relate the less flexible ecological performance of terrestrial feeding systems with the design of terrestrial vertebrate feeding design. The profound effects of the differences in feeding patterns between aquatic and terrestrial vertebrates can also be seen in territorial behavior. Sale (1978) has shown that fishes have much smaller territories than terrestrial vertebrates even after correcting for size, poikilothermy and homeothermy. With the built-in versatility of the expanding cone, fishes are well poised to exploit alternative food resources within smaller areas, removing the necessity to move over larger areas in search of preferred food as is the case for terrestrial vertebrates.

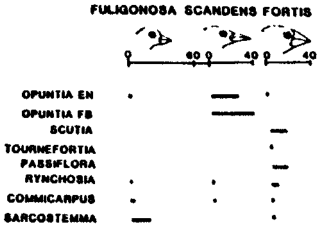

Fig. 5. Diets of three species of ground fishes from the Galapagos Islands at the end of the dry season. Overlap of food is very limited. Modified from Grant, 1986. OPUNTIA EN, *Opuntia* extrafloral nectar; OPUNTIA FB, *Opuntia* flowers and buds.

HYPOTHESIS 2: IN AQUATIC VERTEBRATE FEEDING SYSTEMS CONVERGENT EVOLUTION IS UNCOMMON

Convergence in aquatic vertebrate feeding systems is much less prevalent than in terrestrial vertebrates. Yet teleost fishes outnumber other vertebrate lineages in number and diversity. The relative rarity of convergences in feeding designs in teleosts may well be correlated with the inherent versatility and opportunism associated with the expanding cone. As a result there is a lesser selective premium for the evolution of precision in design.

The built-in versatility of the expanding cone design does not require drastic changes in its “hardware” to assume a more specialized biological role. As a result, a great diversity of forms can evolve to solve the same problem, *e.g.*, piscivory. Goulding (1980) studied pursuit hunters (Liem, 1978) in the Rio Machado and found 5 piscivores belonging to 4 families. Each of these piscivores possessed radically different jaw apparatuses (Fig. 6). Each design reflects the underlying historical factors characteristic of the lineage rather than functional convergence in response to a common environmental challenge, *i.e.*, the capture and processing of fish prey. If a precise match between design and biological role were a prerequisite for pursuit hunting piscivores, one would have predicted a convergence toward a large mouth, a cylindrical buccal cavity (rather than a conical one), increased lower jaw length, and a shallower palatoquadrate. None of these predicted convergences have emerged in the Rio Machado piscivorous fishes.

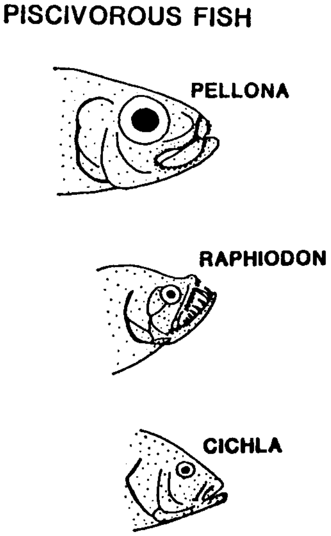

Fig. 6. Heads and jaws of three taxa of piscivorous fishes from the Rio Machado, showing great diversity in jaw structure and buccal cavity rather than convergence. Design is related to phylogenctic position.

In sharp contrast, terrestrial carnivores and herbivores exhibit very precise matching in design and biological role even if one compares these feeding specialists across phylogenetic lineages. Convergence in design has evolved in marsupial and placental carnivores in terms of their arching of the zygomatic arch, dentition, temporalis and masseter muscle architecture, shape of the temporal region of the skull and the form of the mandible (Fig. 7). Convergent evolution is very prevalent in the feeding apparatus of the terrestrial vertebrates. Common environmental challenges in feeding such as insectivory, carnivory, folivory, etc., are invariably solved by identical adaptations in the “hardware” of terrestrial vertebrates. Convergence in feeding design in terrestrial vertebrates primarily reflects the precise matching of form and function with the specialized biological role rather than the influence of historical factors.

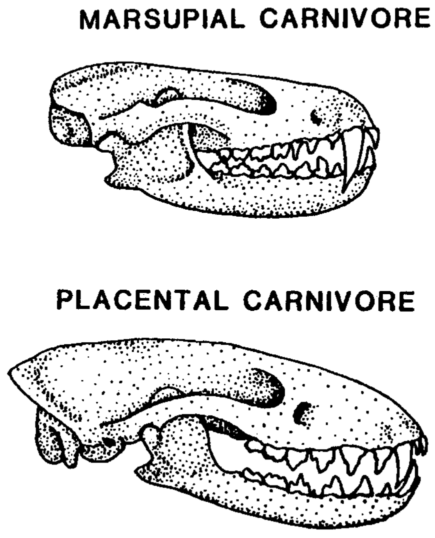

Fig. 7. Convergence in phylogenetically unrelated carnivorous mammals. Design is a reflection of adaptations to a carnivorous biological role.

HYPOTHESIS 3: AQUATIC VERTEBRATE FEEDING SYSTEMS ARE CHARACTERIZED BY RELAXED COMPETITION AND THE ABSENCE OF CHARACTER DISPLACEMENT

Not a single well-documented example of character displacement in the feeding apparatus of aquatic vertebrates has been reported! Yet, teleost fishes represent the most diverse and abundant vertebrate lineage. The apparent lack of character displacement in the most diverse vertebrate lineage can be predicted by the medium-dependent built-in versatility of the design of the feeding apparatus in fishes. Competition can be rapidly reduced or avoided by extensive food switching, which does not require a major change in the design features of the piscine feeding apparatus. In general, the matching of design with biological role is less precise in aquatic vertebrates because the truncated expanding cone is operated by a repertoire of neuromuscular outputs capable of capturing and processing a vast array of prey with sufficient efficiency to render major changes in the “hardware” unnecessary.

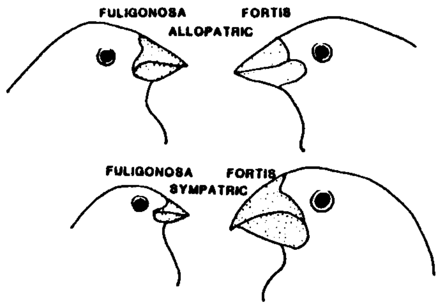

Fig. 8. Character displacement in the feeding apparatus in Darwin’s finches (redrawn from photographs in Grant, 1986). *Geospiza fuliginosa* and *G. fortis* occur allopatrically, bill size and shape are intermediate and resemble each other in two species. In sympatric situations, the two species diverge significantly in bill size and shape.

The lack or, at best, rarity of character displacement in aquatic vertebrates supports the hypothesis that the basic expanding cone design operating in the aquatic medium offers so many feeding options that competition is reduced by prey switching without a change in structure of the jaw apparatus.

In terrestrial feeding systems precise matching of design and biological role often results in very refine resource partitioning. Intense competitive interactions can produce character displacement as exhibited in Darwin's ground finches (Fig. 8). Allopatrically occurring non-competing populations of *Geospiza fuliginosa* and *G. fortis* converge in the form of the feeding apparatus since the birds feed on similar food resources for which an intermediate beak is most appropriate (Fig. 8; Grant, 1986). This convergence in interpopulations of the two species is interpreted as a result of released competition. However, the effects of competition are clearly reflected in the divergence of bill shape and size of the two species in areas where they occur sympatrically (Fig. 8). In competition with each other the two species diverge to feed on entirely different food resources. Precise matching of design with biological role results in a more slender, straight bill in *fuliginosa* and a much heavier, curved bill in *fortis*. Character displacement is one of the major results of competition among vertebrates. Character displacement has been documented only in terrestrial forms.

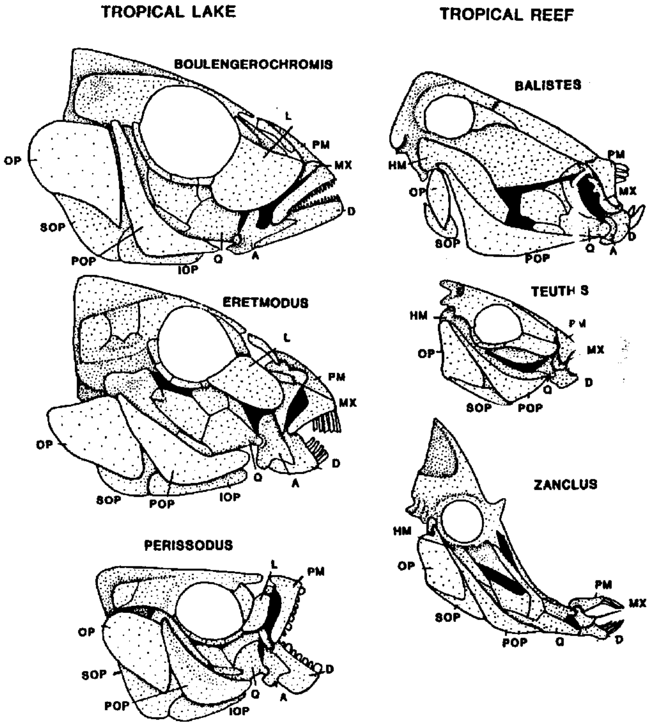

Fig.9. Diversity in jaws and palatoquadrate arches in three cichlids in Lake Tanganyika and in one balistoid and two acanthuroid fishes in coral reefs. Abbreviations: A, angulo-articular; D, dentary; HM, hyomandibula; IOP, interoperculum; L, lachrymal; MX, maxilla; OP, operculum; PM, premaxilla; POP, preoperculum; Q, quadrate; SOP, suboperculum.

HYPOTHESIS 4: PATTERNS OF DIVERSITY IN AQUATIC VERTEBRATE FEEDING DEFY THE TERRESTRIAL PARADIGM

Among terrestrial vertebrates extensive functional diversification of lineages are usually related with the presence of stable habitats that are exceptionally rich in microhabitats. Radiations in form and function of lizards on tropical islands, snakes in tropical Africa, primates in the Indomalayan Archipelago, and the birds in New Guinea represent just a few of the many well-documented examples illustrating that stable, fine-grained habitats are conducive to adaptive radiations among its occupants.

Fishes also exhibit this pattern in some environments. Among coral reefs one finds a plethora of stable microbabitats, each of which is exploited by a teleost fish even though it may not always be occupied by the same species. Microhabitats may be populated by the pelagic larvae of different species at different times resulting in the occupation of certain microhabitats of the reef by one or more species of fishes. In agreement with the terrestrial paradigm, many teleost lineages have evolved a vast array of forms (*e.g.*, Fig. 9). Likewise models explaining the diversity of terrestrial animals on oceanic islands such as the honeycreepers in Hawaii and Darwin's finches on the Galapagos Islands are generally applicable to radiations of cyprinid fishes in Lake Lanao (Kornfield, 1984), and cichlid fishes in Lake Tanganyika, Lake Malawi and Lake Victoria (Fig. 9). These important similarities in patterns of diversity in terrestrial and aquatic vertebrates seem to indicate that when competition for food resources is extraordinarily intense and prolonged, a high selective premium is put on the efficiency of feeding performance. Such a high efficiency is achieved by changes in the shape of the expanding cone, the dentition, and size and position of the mouth (Barel, 1983; Yamaoka, 1982, 1983; Liem and Kaufman, 1984).

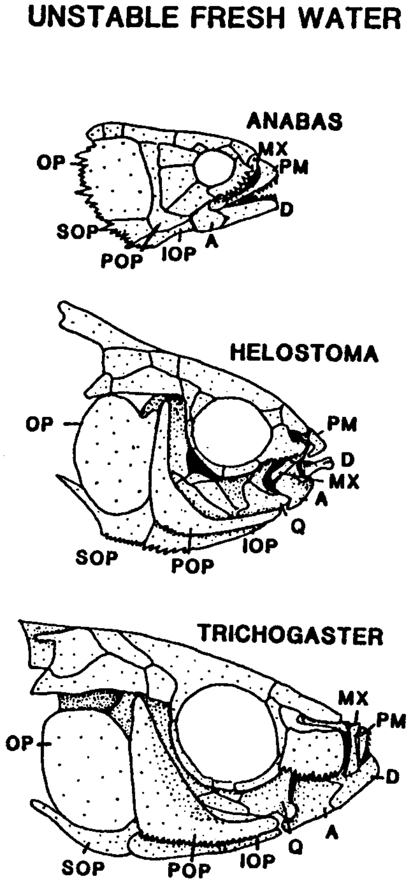

Fig.10. Diversity in the feeding apparatus in three anabantoid fishes inhabiting fluctuating habitats. Anabas is a large-mouthed ram feeder predator; Helostoma, a simultaneous suction/biting specialist; and Trichogaster, a suction/filter feeder. Abbreviations: See Figure 9.

It is generally accepted that fluctuating depauperate environments are not conducive to evolutionary radiation. Such environments are typically inhabited by terrestrial vertebrates that are not diverse in form. Aquatic vertebrates deviate from this terrestrial paradigm. In widely fluctuating tropical waters with great variations in temperature, oxygen content (which sometimes drops to zero), pH and CO2, a great diversity of fishes have evolved, even within a lineage (Fig. 10). Across lineages the diversity in feeding structures is even greater, reflecting the importance of underlying historical factors rather than the precise convergent adaptations, molded by common selective pressures.

"Hostile" environments with extreme climates are thought to limit the diversification of terrestrial vertebrates, even though a number of highly specialized forms are likely to be found in such habitats (*e.g.*, deserts [Pianka, 1967], arctic areas). The pattern of diversity in fishes inhabiting the most extreme "hostile" environments represents an exception to the rule that extreme habitats limit evolutionary diversification: Deep-sea habitats are associated with the greatest diversity in forms of fishes. The diversity of deep-sea fishes across phyletic lineages is unparalleled in vertebrate evolution (Marshall, 1954).

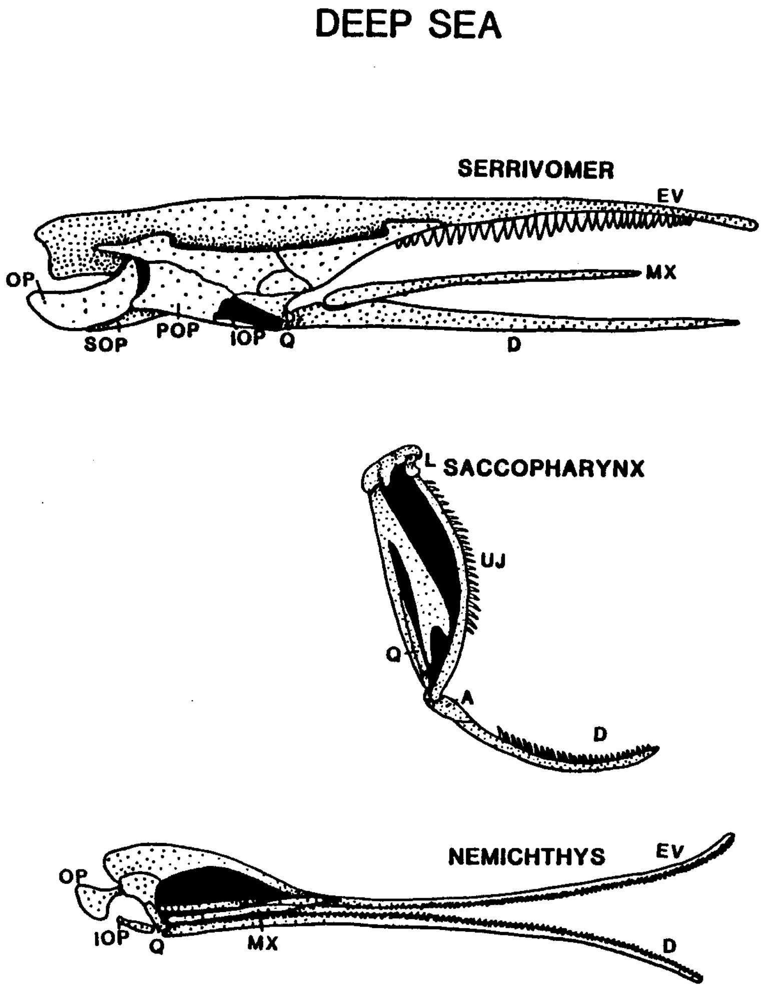

Fig. 11. Extreme diversity in jaw and skull structure in three eel-like taxa from deep seas. In these forms the expanded cone has disintegrated and entirely new feeding mechanisms have evolved. Suction in these forms is highly unlikely. Abbreviations: A, anguloarticular; D, dentary; EV, ethmovomer; IOP, interoperculum; L, lachrymal; MX, maxilla; OP, operculum; POP, preoperculum; Q, quadrate; SOP, suboperculum; UJ, upper jaw.

Even within closely-related lineages the diversity in the feeding apparatus of deep-sea fishes exceeds that of different orders inhabiting less hostile waters (Fig. 11).

Thus, rules governing patterns of diversity in terrestrial vertebrates as they relate to environments do apply in some instances to fishes, but major exceptions to that rule are very common among teleosts.

DISCUSSION

The above four hypotheses are falsifiable.

Hypothesis 1, which predicts that opportunism and diet overlap prevail in aquatic systems would be falsified, if the majority of fishes are found to engage in fine-grained resource partitioning in rich ecological communities with rigid partitions. The vast majority of empirical studies on fish feeding seem to support the notion of extensive diet overlap and highly flexible partitions in their resource partitioning. However, evidence that fishes do not feed opportunistically and do partition food resources optimally is growing (*e.g.*, Hori, 1983; Werner and Hall, 1977; van Oijen, 1982; Takamura, 1984; Yamaoka, 1982, 1983). But food partitioning in these studies may well be short-lived phenomena, which can change quickly in response to environmental changes. A demonstration that many terrestrial vertebrates living in complex ecological communities do feed opportunistically would also falsify the first hypothesis. However, such evidence against the hypothesis is lacking. If hypothesis 1 is valid, it will support a causal relationship between design and behavioral ecology with important implications in evolution.

Hypothesis 2, which predicts that convergent evolution in aquatic feeding systems is uncommon, can be falsified by finding repeated occurrences of convergent features of the feeding apparatus in unrelated lineages of fishes. “Convergences” in design of the feeding apparatus in related taxa have been found (Barel, 1983), but because of the close phylogenetic relatedness of the taxa it does not constitute a falsification of the hypothesis. If convergent evolution in the aquatic feeding apparatus is indeed uncommon, hypothesis 2 remains valid, and establishes a very important evolutionary principle: Historically molded different designs do not necessarily respond by evolving similar (convergent) solutions to a common environmental challenge (“selection pressure”). The inherent versatility of the truncated cone design is preadapted for the evolution of various designs in response to a similar selection pressure.

However, the paucity of convergence in aquatic feeding systems may be more apparent than real. The same preferred prey of various piscivores may actually be captured and processed in different ways and thus by anatomically different feeding apparatuses. In such cases one would not expect convergent evolution. For example in the Rio Machado piscivores, *Pellona* engulfs its prey, while *Raphiodon* is thought to feed on the same prey by stabbing it with the canine teeth (Goulding, 1980).

Hypothesis 3 predicts reduced competition for food and the absence of character displacement in aquatic vertebrates. If competition for food and the resulting character displacement in the feeding apparatus are demonstrated in fishes, the hypothesis is falsified. But the absence of character displacement in aquatic vertebrates seems to support hypothesis 3. Consequently diversification of a lineage in complex communities cannot be explained by the long-favored “competition for food resources in short supply” theory, which is firmly rooted in terrestrial systems.

Hypothesis 4 predicts that patterns of diversity in fishes are not only determined by environmental parameters but especially by historical factors. “Depauperate” fluctuating environments and extremely hostile habitats often contain a spectacular diversity of fishes (Fig. 11) unmatched by any other vertebrate group. The diversity of fishes in fluctuating or hostile environments reflects the presence and subsequent evolution of a multiplicity of phylogenetically independent lineages rather than an adaptive radiation of a monophyletic group into different microhabitats. Hypothesis 4 can be falsified by demonstrating that common mechanisms govern the pattern of diversity of aquatic and terrestrial vertebrates. Such a test can be made by comparing the patterns of diversity in aquatic and terrestrial vertebrates in equivalent environments of approximately the same geological ages.

If all 4 hypotheses are falsified the terrestrial paradigm would continue to prevail in ecological and evolutionary theory. But if one or more of these hypotheses are corroborated, it would require a reassessment of generally-accepted notions on functional design, behavioral ecology, competition and causation of the varying patterns of diversity of aquatic vertebrates.

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