INTEGRATION OF VERSATILE FUNCTIONAL DESIGN, POPULATION ECOLOGY, ONTOGENY AND PHYLOGENY

by

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ABSTRACT

The study of the functional morphology of fishes has been greatly influenced by interactions with related fields. We give examples of some possible confounding factors when trying to assess the functional repertoire of fishes, including the effect of prey availability and the effect of captivity. A narrow range of prey items and an extended period in captivity both decrease the scope of the functional repertoire. Specialists and generalists have not been able to coexist in conventional competition based models of optimal foraging. A recent extension of this model does succeed in modeling the communities which are typical of the African Rift Lakes. This warrants a re-evaluation of the importance of competition in structuring fish communities. Ontogenetic shifts in the functional morphology of the feeding apparatus of teleostean fishes may explain why a synapomorphy of the group is not always important functionally in the adult. The levator operculi-opercular rotation mode of mouth opening is vital for larval fishes but in some cases becomes unimportant in adults. We emphasize that examination of early life history stages holds important information about the adaptive significance of diverse structures.

KEY WORDS: specialist, generalist, optimal foraging, function, design.

INTRODUCTION

Professor J.W.M Osse has advanced the field of functional morphology to new heights, making it possible to attempt the new integration in this paper.

The technological and methodological innovations of the past 30 years have revolutionized our approach to form and function in fishes. Diverse anatomical details and the mechanics of musculoskeletal systems in relation to prey capture in teleosts have become common knowledge in vertebrate biology. This growing body of experimentally obtained data has enabled us to formulate models that predict the nature and efficiency of the prey capture apparatus (*e.g.*, MULLER, 1987; WESTNEAT, 1990; NORTON & BRAINERD, 1993). A precise biomechanical knowledge has, in turn enabled us to recognize certain types of constraint, in the form of

couplings, that explain a lack of diversification in some lineages; while decouplings may trigger morphological and functional radiations in other lineages (*e.g.*, LAUDER, 1981). Correlations between functional design and ecological specializations have been made, especially in relation to cichlid evolution in the Great Lakes of East Africa (BAREL, 1983). OSSE (1990), OTTEN (1983) and GALIS (1983) discovered extensive transformations in the functional design of the feeding and locomotory apparatus during the ontogeny of fishes. Each of the developmental intervals possesses precise features adapted to cope with characteristic environmental challenges encountered by the particular stage of the organism.

In this paper we will not attempt to synthesize the state of the art in functional morphology, but instead identify new areas of inquiry, and highlight some particularly fruitful intersections between functional morphology and other disciplines. First, we review various understudied aspects of the elusive problem of versatility. Second, we try to put versatile functional design in an ecological context using an explanatory theoretical model rather than the customary correlations. Third, the developmentally profound transformations of biomechanical systems are identified and discussed as precisely defined adaptations. Finally, we demonstrate that the largest group of vertebrates, the Teleostei share a defining character that has great survival value during a brief ontogenetic interval, though the functional role may diminish or even disappear in adult life.

EFFECTS OF CAPTIVITY AND PREY SELECTION ON VERSATILITY

ELSHOUD-OLDENHAVE & OSSE (1976) were the first to discover experimentally that some teleosts modulate their prey capture mechanism and behavior according to the behavior, site and nature of the prey. All other studies emphasized the optimal fixed conserved prey capture action, until LIEM (1978; 1980) found extensive repertoires which he called "modulatory multiplicity". These findings were at variance with virtually all other studies. In recent studies, on a wide taxonomic array of fishes, functional versatility has been confirmed as a common feature of feeding behavior (COUGHLIN & STRICKLER, 1990; WAINWRIGHT & TURINGAN, 1993; NEMETH, 1997a, b; FROST & SANFORD, 1999). Comparing versatility between lineages (LIEM, 1980) and within ontogenetic stages is emerging as an important methodological tool (FREIL & WAINWRIGHT, 1999; WAINWRIGHT & RICHARDS, 1995). Unfortunately in-depth comparisons of the feeding anatomy, function and performance during the entire development of a fish is lacking. Thus the possible existence of major

transitions and the full spectrum of versatility and their interactions with environmental factors remain as future challenges. Within very few cichlid fishes a preliminary understanding is emerging. We point out several factors that may confound the determination of the naturally occurring ability to modulate prey capture.

The effect of captivity

In experiments on the motor patterns of jaw muscles during prey capture by the cichlid fish *Petrotilapia tridentiger*, LIEM (1980) revealed a repertoire of 8 distinct patterns depending on the nature of the food and its location in the water column. This broad repertoire is seen only shortly after capture from the wild when the fish is offered multiple foods (fig. 1). The longer the fish is kept in captivity, the narrower the repertoire becomes, culminating in just two patterns (fig. 1) identified as slow suction and biting by LIEM (1980). When the fish is offered a single food, live juvenile *Poecilia reticulata*, the fish employs only 2 patterns irrespective of the duration of captivity (fig. 1). These findings seem to indicate a profound influence of the duration of captivity and choice of foods on the feeding strategies and behavior of cichlid fishes, because similar effects have been found in *Lobotes chilotes*, *Petrochromis polyodon*, *Simochromis diagramma* and *Limnotilapia dardenni*. Unfortunately in none of the experiments was it possible to collect a statistically sufficient number of profiles especially shortly after capture on multiple foods. However, the decrease in repertoire width with the increasing length of captivity is sufficiently striking and consistent (fig. 1) to caution future investigators about the effects of captivity, conditioning and diversity of prey items.

The effect of prey type and availability

When four species of cichlids are offered four different prey items, 7-10 days after being captured in the wild, their prey consumption is influenced both by food abundance and the functional design of their feeding apparatus (fig. 2). The four species differ functionally in

Fig. 1. Summary of motor patterns of key jaw muscles (epaxial, levator operculi, dilator operculi, sternohyoideus, geniohyoideus anterior and posterior, adductor mandibulae pars A_1 and pars $A_{2,3}$, levator hymandibulae, adductor operculi) during prey capture by *Petrotilapia tridentiger* under varying conditions. Center panel shows the electromyographical patterns of fishes 7 days after capture when multiple foods are offered. On the left the fish is offered a single food after varying days of post-capture showing consistently 2 patterns. On the right the fish is offered multiple foods and show a decrease in its repertoire the longer the fish is in captivity.
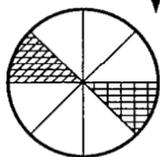
Motor patterns of *Petrotilapia tridentiger* in captivity
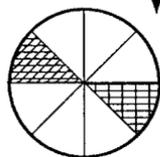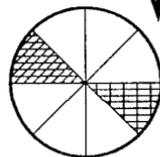

Fed a single food
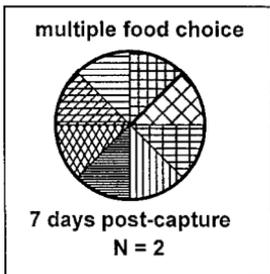
Juvenile *Poecilia*
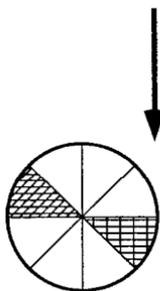
21 days post-capture
N = 1

42 days post-capture
N = 5

56 days post-capture
N = 5

300 days post-capture
N = 4

multiple food choice

7 days post-capture
N = 2

EMG Legend
slow suction
up suction
down suction
fast suction
biting
horiz. scrape
vert. scrape
manipulating

Fed multiple foods

Callothrix
Tetramin flakes
Tubifex
Artemia
Drosophila
Cockroach (legs)
Juvenile *Poecilia*

21 days post-capture
N = 1

42 days post-capture
N = 5
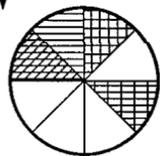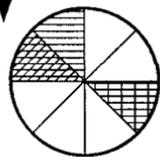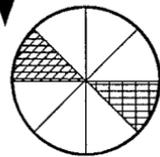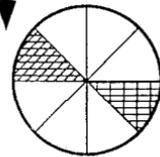
56 days post-capture
N = 4

300 days post-capture
N = 4
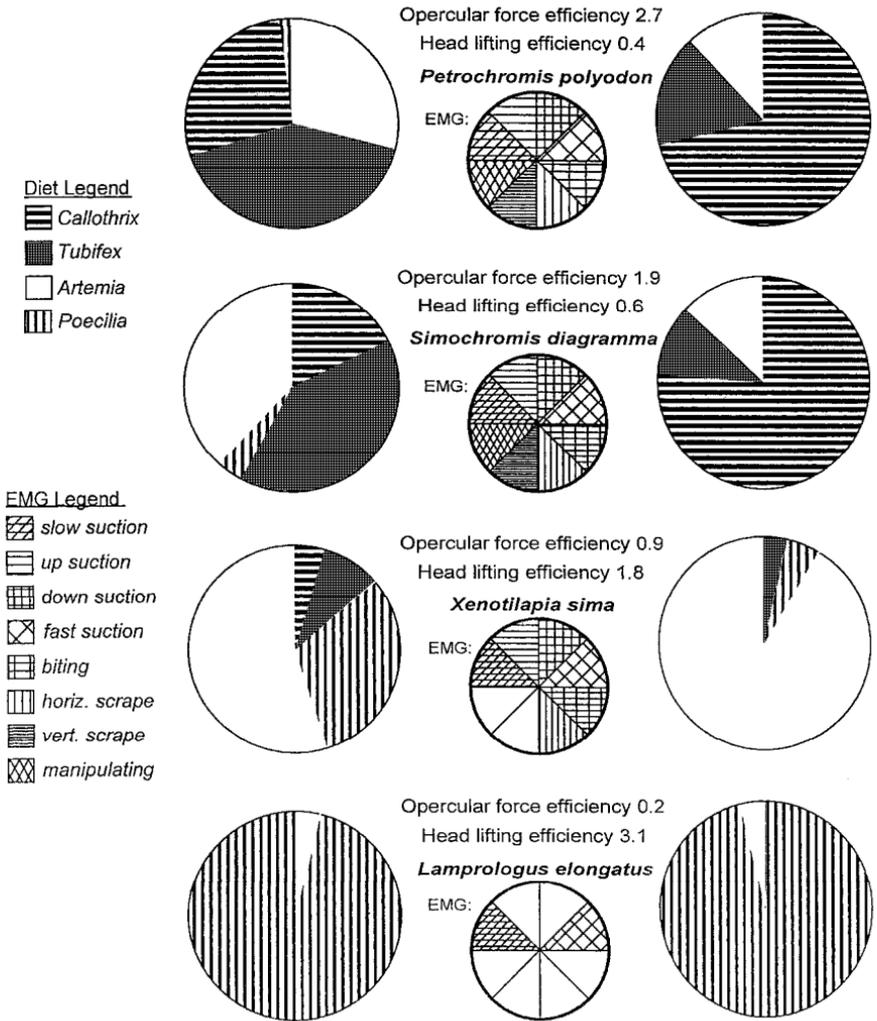
Fig. 2.   Summary of diet selectivity motor patterns and food abundance in individual cichlid fishes 7-11 days postcapture. For each taxon, opercular force and head-lifting efficiencies and pattern repertoires are indicated in the center, while the feeding selectivity during high (on left) and low (right) food abundance are expressed in pie diagrams. For *P. polyodon* and *L. elongatus* N = 5; *S. diagramma* N = 2; *X sima* N = 3.

opercular force efficiency and head-lifting efficiency, parameters that have been shown to be important biomechanically (BAREL *et al.*, 1977; MULLER, 1987; WESTNEAT, 1990). *P. polyodon* and *S. diagramma*

are generally regarded as algae scrapers (YAMAOKA, 1982) and have a relatively high opercular force efficiency while the piscivore *L. elongatus* (HORI, 1991; LIEM, 1980) has a low opercular force efficiency and a high head-lifting efficiency (fig. 2). High head-lifting efficiency is accompanied by a very restricted repertoire. Thus, in *L. elongatus* the repertoire is limited to slow and fast suction and food abundance has no effect on the food taken. *L. elongatus* feeds primarily on *Poecilia* and some *Artemia* ignoring other prey items regardless of abundance. In *P. polyodon* and *S. diagramma* the full complement of electromyographic patterns is expressed showing a well-developed capacity to modulate. When these two fishes are feeding under high food abundance they feed on all four prey items, while under low food abundance both fishes fail to capture the juvenile *Poecilia reticulata*. It is only during low food abundance that *Callothrix*, for which both species have special adaptations (YAMAOKA, 1991), becomes the dominant food. During high food abundance, food preference switches to *Tubifex* and *Artemia* for which no special adaptations are present. The adaptation in both *P. polyodon* and *S. simochromis* is for the refugium food and not for the preferred food. This principle is also demonstrated by the molariform morph of *Cichlasoma minckleyi* that uses snails as a refugium food (LIEM & KAUFMAN, 1984). The morphological "generalist" *Xenotilapia sima* has a reduced repertoire of motor patterns (fig. 2) and modulates its prey capture when food abundance is high by including *Callothrix* and a significant percentage of *Poecilia reticulata* in its diet of *Artemia* and *Tubifex*. When food abundance is low, *X. sima* switches primarily to *Artemia* (fig. 2). *Xenotilapia sima* is a morphological generalist with a broad diet but a narrow functional repertoire. We can conclude that food abundance has a profound influence on feeding selectivity in fishes with a broader range of motor patterns.

GENERALISTS, SPECIALISTS, AND OPTIMAL FORAGING MODELS

Morphological and functional specializations have been closely correlated with narrow specialized niches (*e.g.*, BAREL, 1983; YAMAOKA, 1991). These allegedly very faithful correlations between functional design and niche width were thought to be the result of competition (HORI, 1991). In contrast, generalists were regarded as possessing no particular specializations for prey capture and a broad diet. These notions were undermined by the description of morphological specialists with a wide array of prey capture techniques and motor patterns (*e.g.*, LIEM, 1978; 1979). These

"jack-of-all-trade" specialists require recognition of more than one type of specialist and have directly led to the proposal of an important extension to competition based models of optimal foraging.

Petrochromis polyodon and *Simochromis diagramma* are considered specialists designed for algae scraping with the highly specialized dentition and high opercular force efficiencies (YAMAOKA, 1991). However, these species are capable of exploiting other foods especially when food is abundant (fig. 2), moreover they possess a full range of motor patterns shortly after they have been captured from the field. These are "jack-of-all-trade" fishes that can feed on specialized prey not ordinarily exploited by others or "eurytopic specialists". This is in sharp contrast to the piscivorous *Lamprologus elongatus*, a "stenotopic specialist", which feeds mostly on other fishes in low as well as high food abundance (fig. 2). We propose that specialists fall into two categories: **stenotopic specialists** are morphologically and functionally specialized with a narrow dietary breadth and very little modulatory multiplicity; and **eurytopic specialists** are morphologically specialized and, under certain conditions, exhibit a broad array of prey capture motor patterns and behaviors, as well as, a broad diet when examined over a wide geographical or temporal area. Fishes such as *Xenotilapia sima*, which prefer a particular prey item regardless of food abundance but always include a variety of other prey items (fig. 2), we call **generalists**. Classification of fishes into eurytopic specialists, stenotopic specialists, and generalists should only be made after a careful analysis of functional design and feeding behavior on multiple foods at high as well as low food abundance in recently captured wild-caught fishes.

In the absence of a theoretical framework combining competitive foraging with functional design, LIEM (1980) embraced the concept of flexibility, opportunism, and prey switching to explain communities that include eurytopic specialists in favor of competitive exclusion and optimal foraging principles. The proposal that competition was an unimportant factor in fish communities was radical and generated several specific ecological examples to the contrary. However, without a competition-based model for the role of eurytopic specialists it is difficult to argue that competition is the rule rather than the exception. An important extension to optimal foraging models proposed by ROBINSON & WILSON (1998) seems to have resolved the issue of specialists that easily access a wide variety of prey items. Using matrices of prey availability, prey value and ease of capture they have devised a model in which eurytopic specialists co-exist with generalists.

As an example, let us examine the new ecological model as it relates to three Lake Tanganyika cichlids: the generalist *Lobochilotes labiatus*, the

stenotopic (HORI, 1991) *Perissodus paradoxus*, and the eurytopic spe-
cialist *Petrochromis polyodon* (fig. 3). The dynamic relationships between
the generalist and eurytopic specialist are expressed in the graph adopted
from Robinson and Wilson. At first the generalist (*L. labiatus*) dominates
the community until the eurytopic specialist (*P. polyodon*) is added. Soon
after this addition, the eurytopic specialist undergoes a significant popula-
tion growth at the expense of the generalist whose population declines sig-
nificantly. However, the populations of both the generalist and eurytopic
specialist reach an equilibrium at which both ecotypes co-exist. Thus, the
two functional designs and their dynamic interactions are predicted to co-
exist competitively. ROBINSON & WILSON (1998) argue that it is the
very nature of the eurytopic specialist that ensures its co-existence with
the generalist.

The model accounts for the functional and behavioral capacity of fish to
exploit resources that are energy rich and collectible without special adap-
tive mechanisms (*i.e.*, insect larvae, shrimp, *Artemia*) and resources that
contain less energy and require extraordinary devices for exploitation (fig.
3). These resources are differentiated as "easy" and "hard" resources re-
spectively in the graph of figure 3. In the lower area fishes consuming the
easy resource (a) dominate since their design limits the exploitation of re-
sources for which they are not significantly equipped. In the right top part
of the graph eurytopic specialists (c) prevail because their behavioral and
functional abilities allow them to exploit the "easy" resource while readily
switching to the "hard" food thereby displacing the generalist. However,
in the center area (b) both the eurytopic specialists and the generalists
co-occur, exploiting both types of food effectively, but without displacing
each other. It is in this area that eurytopic specialists play a unique role,
adding significantly to diversity of the community as encountered in the
cichlid assemblages of Lakes Tanganyika, Malawi and Victoria.

ROBINSON & WILSON (1998) identified Liem's inability to explain
the wide spread existence of specialists that are simultaneously jack-of-
all-trades as "Liem's Paradox". The problem remained a paradox because
functional design was viewed separately as a dynamic entity and morpho-
logical correlates with ecology were limited to static analysis. The para-
dox has been resolved by ROBINSON & WILSON (1998) with a modifica-
tion of optimal foraging theory inspired by concepts put forth in papers on
modular multiplicity (LIEM, 1978, 1979, 1980). This integration of func-
tional anatomy and population ecology, makes a reassessment of the role
of competition a priority. Further extensions of optimal foraging theory
may provide further insight into the adaptive radiation of the Cichlidae in
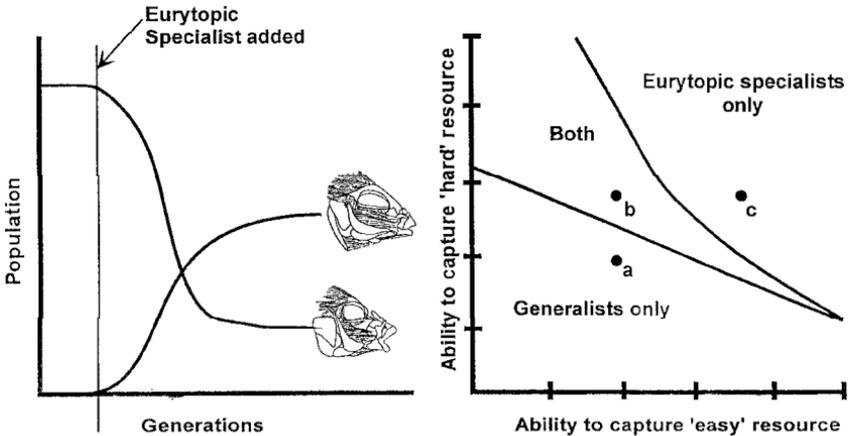the Great Lakes of East Africa.
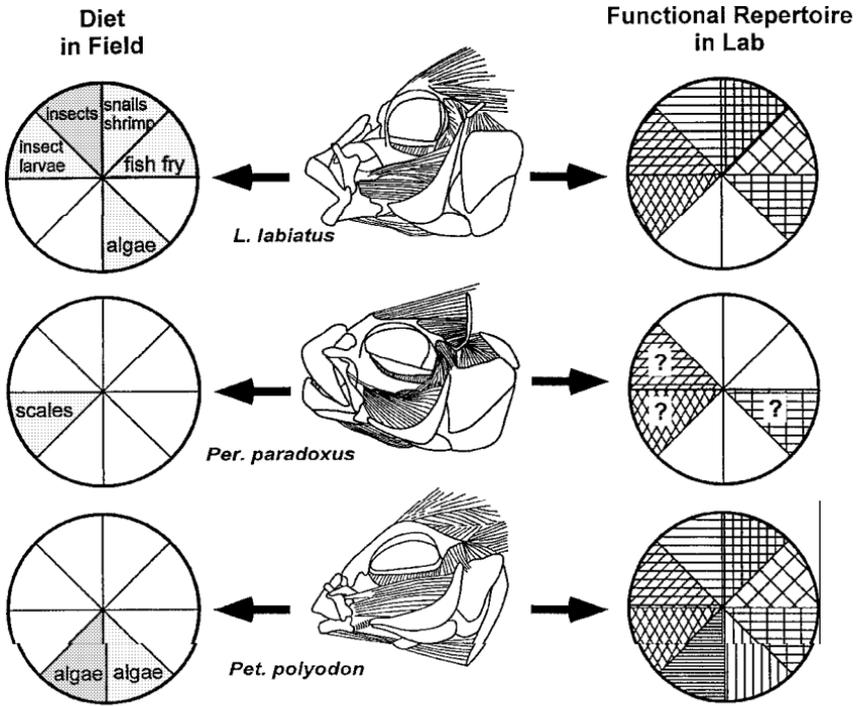
Fig. 3. Top three rows summarizes diet as observed in the field (YAMAOKA, 1991) and the range of motor patterns obtained in the laboratory 8 days after capture except in *Perissodus paradoxus* which did not feed *L. labiatus* N = 3; *P. polyodon* N = 5. Shading equivalent to figures 1 and 2. Graphs summarized the theory of ROBINSON & WILSON (1998) as applied to the generalist *L. labiatus* and the eurytopic specialist *P. polyodon*.

EARLY ONTOGENETIC STAGES AND ADAPTIVE SIGNIFICANCE

OSSE & VAN DEN BOOGAART (1997) pioneered the integration of func-
tional anatomical approaches with ontogeny, exploring the effects of the
drastically changing environmental parameters during the development of
fishes. Osse's studies on feeding and locomotion during the ontogeny of
fishes explain not only the adaptive nature of canalized pathways but also
the prevalent constraints that have a moulding influence on adult func-
tional design (OSSE, 1990). In this tradition of analyzing function in var-
ious life history stages we believe that the functional morphology of the
early life history stages of teleostean fishes holds the key to understand-
ing one of the uniting characters of the group. The character in question
is a functional complex consisting of the levator operculi muscle insert-
ing on an interconnected opercular series (operculum, subopeculum and
interoperculum) which transmits force to the mandible via an interoper-
culomandibular ligament.

This apomorphy was considered a functional innovation giving the
teleosts an alternative mode of opening the mouth allowing more options
for prey capture. WESTNEAT (1990) challenged this notion when he
showed that in many labrid fishes the mouth opening system does not
rely on the levator operculi coupling but on head-lifting triggered by
the epaxial and sternohyoideus muscle as shown in the head-lifting
interval (MULLER, 1987) (fig. 4). There are also fishes which, as adults,
possess only a rudimentary, and therefore probably functionless, levator
operculi. Indeed, the adult king-of-the-salmon, *Trachipterus altivela* has
the opercular series fused to the suspensorium, completely preventing the
levator operculi from assisting in mouth opening (LIEM & SUMMERS,
1997). It would seem that in many fishes a phylogenetically important
functional innovation lies unused.

OTTEN (1983) has shown that the developing cichlid *Astatotilapia el-
egans* begins mouth opening by the action of the geniohyoideus on the
lower jaw with the large, relatively stationary hyoid as the origin (fig. 4).
This functional stage is referred to as the hyoid interval. Subsequently,
this system is taken over by the morphologically and functionally dif-
ferentiated levator operculi, which rotates the entire opercular apparatus
thereby pulling on the posteroventral articular process of the mandible
via the interoperculomandibular ligament (fig. 4). This is the opercular
interval. Much later in ontogeny, and in many adult fishes, the epaxial
muscles play the dominant role in jaw opening by lifting the head. This
third and last mechanism leads to the head-lifting interval (fig. 4). LIEM
(1991; 1997) verified this ontogenetic sequence for other cichlid species
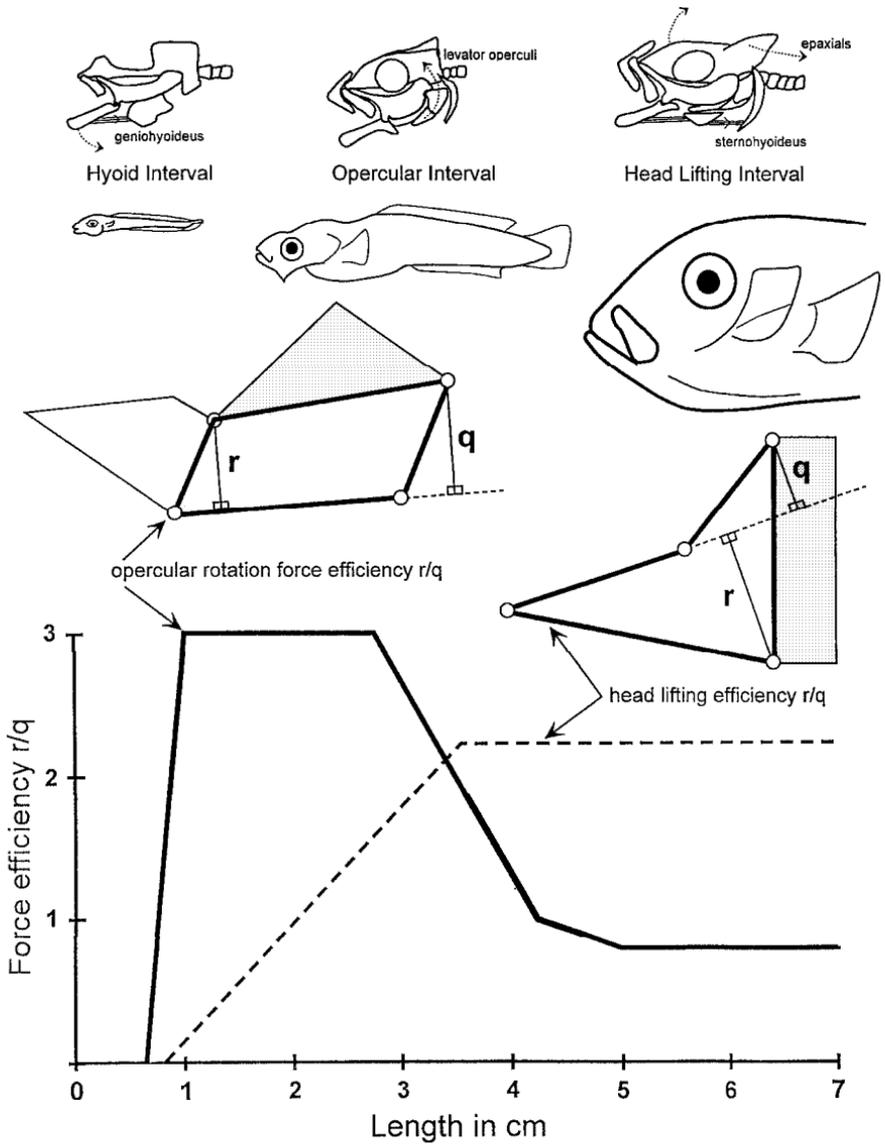and pomacentrids.

Fig. 4. Ontogenetic transformations in functional design in fish development. In the top and second row, note the pronounced retroarticular process on the posteroventral corner of the mandible during the opercular interval (see text for further explanation).

Biomechanically, major changes occur during the switch from the opercular to the head-lifting interval. During the opercular interval the op-

ercular rotation force efficiency (fig. 4) is very large, reflecting the functional effectiveness of the levator operculi muscle (BAREL *et al.*, 1977; WESTNEAT, 1990). The large force efficiency is in large part due to the exceptional length of the retroarticular process of the mandible (fig. 4). Every larval teleost we have examined possesses a pronounced retroarticular process during the opercular interval, giving the developing fish a characteristic "larval profile". As development proceeds the opercular rotation force efficiency declines rather steeply while the head-lifting efficiency (MULLER, 1987; WESTNEAT, 1996) increases until it reaches a higher value than the opercular rotation efficiency (fig. 4, graph). It is at this juncture that the opercular interval is replaced by the head-lifting interval (fig. 4).

In many adult teleosts a balance between the opercular and head-lifting mechanism is maintained giving both systems a shared role in jaw opening. Some algae scraping cichlids have a dominant opercular mechanism (LIEM, 1980), but in many teleosts the opercular mechanism diminishes or loses its original function as mouth opener and is replaced by the head-lifting mechanism (WESTNEAT, 1990). Unfortunately, experimentally based data on the trophic differences between primarily opercular rotation and mainly head-lifting taxa are not available. It appears that pure ram feeders are head-lifters while pure suction feeders use a dual strategy of opercular rotation and head-lifting. This duality may be explained by the work of MULLER & OSSE (1984). They have broken the feeding event down into two expansive phases (1) a carefully controlled suction phase, in which water is drawn into the mouth to counteract the tendency of the forward motion of the fish to push the prey away; and (2) a fast un-modulated opening phase in which the prey is drawn towards the predator. The ecological meaning of the ontogenetic transformation from the opercular rotation to head-lifting based mouth opening mechanism is still unknown.

By examining early life history stages of fishes we have discovered functional aspects of developmental intervals. It is clear that while the levator operculi driven jaw opening mechanism is not important for all adult teleosts, it is absolutely vital for making a transition from the hyoid stage to the head-lifting stage. Thus, the synapomorphy for the largest assemblage of fishes is functionally critical during a developmental interval, even if it can no longer be recognized in the adult.

CONCLUDING REMARKS

In the last 30 years we have moved from purely descriptive studies, based primarily on dissection and observation, to rigorous, experimentally based

examinations of function. Of far greater importance than the technological advances have been the diverse applications of the form/function relationship. From investigations of evolutionary transitions to developmental canalization, there has been an explosion of interesting well-founded studies of function in fishes. It is clear that the greatest leaps forward come from the juxtaposition of disparate fields, and functional morphology is no exception. The perspective that we as functional morphologists can offer facts and concepts to theoretical ecologists, and *vice versa* is a model of reciprocal illumination. Developmental and evolutionary biology are other examples of fields that benefit from a functional viewpoint. Reciprocal illumination of functional anatomy, population ecology, ontogeny and phylogeny constitutes a powerful, pragmatic integration and promises explanations and major advances, which are not likely if each discipline is executed in isolation.

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