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Body Form, Locomotion and Foraging in Aquatic Vertebrates[1]

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SYNOPSIS. Four functional categories are defined to embrace the range of locomotor diversity of aquatic vertebrates; (1) body/caudal fin (BCF) periodic propulsion where locomotor movements repeat, as occurs in cruising and sprint swimming; (2) BCF transient propulsion where kinematics are brief and non-cylic, as occurs in fast-starts and powered turns; (3) median and paired fin (MPF) propulsion, with very diverse fin kinematics, used in slow swimming and precise maneuver; (4) occasional propulsion or "non-swimming." Specialization in any one of these categories compromises performance in one or more of the others, thereby reducing locomotor diversity and hence behavioral options. Food characteristics influencing the role of locomotion in search and capture are; (1) distribution in space and/or time and (2) evasive capabilities. BCF periodic swimmers take food that is widely dispersed in space/time; BCF transient swimmers consume locally abundant evasive items and MPF swimmers consume non-evasive food in structurally complex habitats. Locomotor specialists under-utilize smaller food items in exposed habitats. This resource is exploited by smaller fish, which are locomotor generalists because of predation pressures. For such locomotor generalists, locomotor adaptations for food capture are of diminished importance and other adaptations such as suction and protrusible jaws in fish are common.

INTRODUCTION

Biomechanical studies typically determine the mechanical properties of structures or suites of structures. As such, they also define performance boundaries which in turn must constrain options for behaviors using a given structure. As a result, biomechanics is increasingly seen as an essential component in understanding the complex relationships between structure and function of an organism. In addition, as more structures are scrutinised, generalizations begin to emerge. These can be used to focus new hypotheses on "design" tradeoffs, to identify unexpected morphological adaptations, and to develop ideas on the evolution and ecological roles of various composite animal designs.

Analyses interrelating morphology, physiology and foraging behavior have been particularly productive in placing biomechanical studies in ecological and evolutionary context. This emphasis on foraging functions has probably been effective because successful feeding is necessary for growth and reproduction, hence contributing meaningfully to fitness (Bennett and Licht, 1973; Ruben, 1976; Vitt and Congdon, 1978; Ruben and Battalia, 1979; Bennett, 1980; Bennett *et al.*, 1981; Huey and Pianka, 1981; Toft, 1981). In particular, theoretical and experimental studies on amphibians, reptiles and birds have established a dichotomy in morphological, physiological and ecological characters for two foraging patterns; (a) more active, cruising, wide ranging foragers and (b) more sedentary, sit-and-wait foragers (Pianka, 1966; Schoener, 1971; Eckhardt, 1979; Huey and Pianka, 1981; Taigen *et al.*, 1982). Among aquatic vertebrates there are clear physiological parallels (compare tuna and pike). In addition, the rigors of moving in the dense, viscous medium that is water suggest that morphological correlates should also be particularly clear. However, there has been little attempt to examine foraging patterns in terms of modern mechanical principles on aquatic animal locomotion.

My objective here, therefore, is to explore morphological-ecological relationships for foraging by aquatic vertebrates. This extends ideas developed for other vertebrates and ecosystems to the aquatic biosphere utilizing principles derived from hydrodynamic theory and experiments over the last decade and a half. I first define classes of locomotor mechanisms independent of any foraging considerations. Sec-

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ond, broad characteristics of food are described and discussed in terms of locomotor correlates for effective search and capture of food items. Non-locomotor search and capture mechanisms are also discussed so that the role of locomotion can be seen within the context of suites of complimentary adaptations. Adaptations significant in post-capture food treatment are not discussed.

LOCOMOTOR PRINCIPLES

The functions of diverse locomotor mechanisms can be placed into one of four categories: (1) "Periodic" propulsion is characterized by cyclically repeating kinematic patterns using the body and caudal fin, *i.e., BCF periodic propulsion.* It is used in activities sustained for periods from a second (chases; Major, 1978) to several weeks (migrations) and hence includes constant speed cruising, prolonged and sprint swimming, and two-phase locomotor patterns (Weihs, 1973*b*; Hoar and Randall, 1978; Weihs and Webb, 1983). (2) Transient propulsion is characterized by brief, non-cyclic kinematics, as in fast-starts and powered turns (Weihs, 1972, 1973*a*; Webb, 1978*a*; Weihs and Webb, 1983) using the body/caudal fin; *i.e., BCF transient propulsion.* Such performance is crucial to survival as the ability to accelerate rapidly and to quickly execute turns is used to escape predators (Howland, 1974; Eaton and Hackett, 1983; Webb, 1981, 1982*c*; Weihs and Webb, 1983). (3) The use of median and paired fins for swimming, typical in low speed, fine maneuver activities, *i.e., MPF propulsion* (Alexander, 1967; Gosline, 1971). (4) Fish that rarely swim, *i.e., non-swimmers.* Table 1 summarizes the optimal morphological characteristics attributable to each category.

The four functional categories are based on various observations suggesting that specialization for locomotor performance in any one area is associated with reduced performance in one or more of the others. This evidence is discussed below.

Body/caudal fin (BCF) propulsion

The definition of two functionally distinct categories of BCF propulsion, (1) BCF periodic and (2) BCF transient propulsion with mutually exclusive optimal forms is based on numerous theoretical (see Lighthill, 1975; Weihs, 1972, 1973*a*) and experimental studies (Weihs, 1973*a*; Webb, 1973, 1977). Detailed arguments are summarized by Webb (1977, 1982*a*) and Weihs and Webb (1983). Optimal morphologies are defined as those maximizing thrust while minimizing drag (Fig. 1). For BCF periodic propulsion, thrust is maximized by a lunate tail of large span, but relatively small chord (high aspect ratio), joining the body by a narrow caudal peduncle to provide for locally large amplitude displacements and control of the angle of attack. A large anterior body depth and mass reduce recoil energy losses. Drag is minimized by the same type of morphology that maximizes thrust, *i.e.,* a relatively rigid streamlined body, with minimal area between the shoulder and the caudal fin trailing edge where frictional drag is greatly increased by swimming movements (Lighthill, 1975; Wu *et al.,* 1975; Pedley, 1977; Weihs and Webb, 1983). There are many convergent forms among diverse vertebrate phylogenetic groups; cetaceans, certain sharks (Cladoselachidae, Lamnidae), extinct reptilian ichthyosaurs, and tunas (Thunnidae), the latter providing the type-name of thunniform swimmers (Lindsey, 1978). Endothermy is common, presumably increasing muscle power.

The thunniform design represents the optimal morphology of BCF periodic swimmers, but there are different *levels* of specialization and different *types* of specialization for sustained periodic propulsion. The morphology of non-endothermic cruising carangiform swimmers approaches but is less specialized than thunniform animals. Sharks are also usually specialized cruisers, *e.g.,* Carcharhinidae and Sphyrnidae (Thomson and Simanek, 1977), but have different kinematics and body form (Fig. 1). They retain eel-like body movements and exploit interactions between the sidewash from an anterior median fin with the next posterior fin, increasing the effective angle of attack of the latter, and hence thrust (Lighthill, 1975; Sparenberg and Wiersma, 1975;

TABLE 1. *A functional classification of aquatic locomotor propulsion mechanisms.*

Characteristics	Optimal design features	Functions
A) *Body/caudal fin (BCF) periodic propulsion*		
Cyclically repeating kinematics. Relatively high power. Small linear and angular accelerations.	High aspect ratio lunate tail. Narrow caudal peduncle. Relatively stiff, streamlined anterior body. Large anterior depth/mass. Endothermy?	Swimming sustained for several seconds to several weeks in cruising, prolonged and sprint swimming (steady and two-phase patterns), during chases, patrolling, station holding, searching, migration, etc.
B) *Body/caudal fin (BCF) transient propulsion*		
Brief non-cyclic kinematics. High power. Linear and/or angular acceleration, usually large.	Large body depth and area, especially caudally. Flexible body. Large muscle mass relative to body mass.	Fast-starts and powered turns lasting tens of milliseconds and used in prey capture, predator evasion, etc.
C) *Median and paired fin (MPF) propulsion*		
Variable kinematics involving discrete fins. Low power. Low speed, low acceleration rates.	Lateral insertion pectoral fins. Anterior ventro-lateral insertion of pelvic fins. Extended anal and dorsal fins. Deep, laterally flattened body.	Slow swimming and precise maneuver in searching, stalking, feeding, hiding, etc.
D) *Occasional and non-swimmers*		
Whole body movements relatively unimportant.	—	—

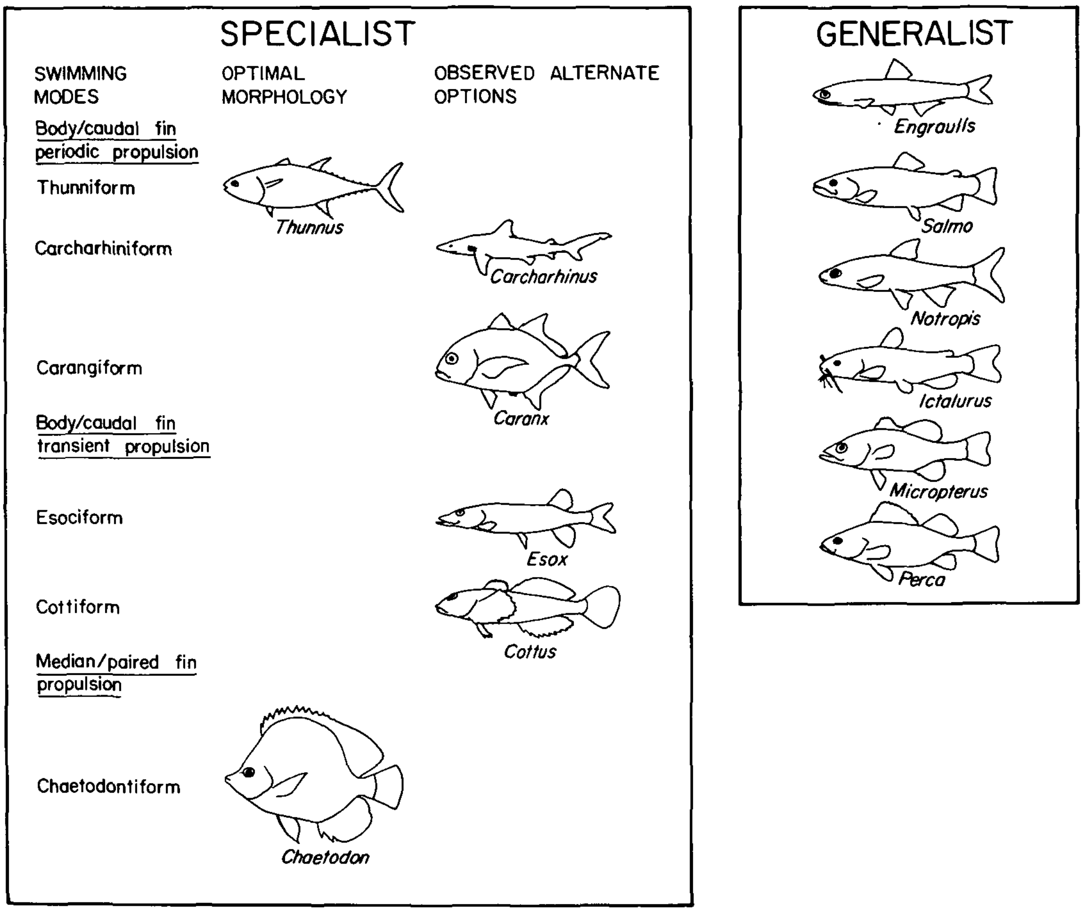

Fig. 1. Examples of external morphologies of locomotor specialists and generalists among fish.

Webb and Keyes, 1982). Following the established practice among fish locomotor morphologists, I will call this the carcharhiniform mode, as sharks such as *Carcharhinus* have representative body forms and kinematics.

For BCF transient propulsion, the optimal morphology maximizing thrust is one with a large body depth along the body length (especially caudally) and a flexible body allowing large amplitude propulsive movements. Optimal designs for minimizing resistance have a small "dead-weight," *i.e.*, a small non-muscle mass to be accelerated (Webb, 1982*b*; Weihs and Webb, 1983) and hence differ from that to maximize thrust. This contrasts with BCF periodic adaptations where thrust maximizing, drag minimizing forms are largely congruent. For BCF transient propulsion, the body forms of different species utilize various combinations of improved thrust or reduced resistance such that overall performance converges among species. Extremes in design can be considered thrust maximizing or resistance minimizing. For example, the cottid form (Fig. 1) exemplifies thrust maximizing morphology for transient swimming as the body dorsoventral depth is extended along the whole length by fins. In contrast, the esocoid form illustrates resistance minimization as the large percentage of myotomal muscle reduces non-essential mass (Webb, 1978*b*; Webb and Skadsen, 1979).

Optimal forms for BCF periodic and

transient performance are clearly exclusive; for one, body flexibility is reduced, in the other enhanced; BCF periodic propulsion performance is optimized by a small body/fin area, transient performance by large area, etc. (see Table 1). It follows that a shape specialized for one activity pattern will reduce performance in the other (see Webb, 1977, 1982*a*; Webb and Smith, 1980; Webb and Keyes, 1981), although this can be mitigated to a certain extent by collapsible fins in ray-finned fishes (Webb, 1977).

Specialization for BCF periodic propulsion also reduces or eliminates MPF performance options. The paired fins are usually reduced to relatively stiff hydroplanes because hydrodynamic lift is more economical than other methods for controlling buoyancy in faster, continuously swimming animals (Alexander, 1977; Gee, 1983). The median fins are also stiff, when present, and may act as keels (Aleyev, 1977).

Median and paired fin (MPF) propulsion

MPF propulsion is characteristic of actinopterygian and batoidimorph fish and is distinct from BCF propulsion in terms of efficiency and the range of thrust vectors that may be generated.

Froude (propellor) efficiency of propulsion systems declines with decreasing speed. However, at low speeds, the efficiency of BCF propulsors declines faster than MPF propulsors. At low speeds median and paired fins work at higher efficiency (Fig. 2). The muscles for each propulsion system will also have their own analogous speed-dependent performance curves (Goldspink, 1977). Thus, muscle efficiency for MPF systems is likely higher at low speeds than muscles of the BCF system. MPF propulsion is, therefore, an adaptation for efficient low speed swimming (Blake, 1983*b*).

There are some apparent exceptions. The non-caudal fins of Molidae, Labridae and Embiotocidae propel fish at cruising speeds with aerobic performance capabilities comparable to BCF swimmers (Webb, 1973*b*; Dorn *et al.*, 1979). However, where present, BCF mechanisms are recruited to swim at sprint speeds (Wardle, 1975), and since power requirements increase roughly with (speed)^3, the maximum power of these MPF mechanisms is still relatively small. Thus, the generalization that MPF mechanisms are used for low speed, low acceleration activities remaines appropriate.

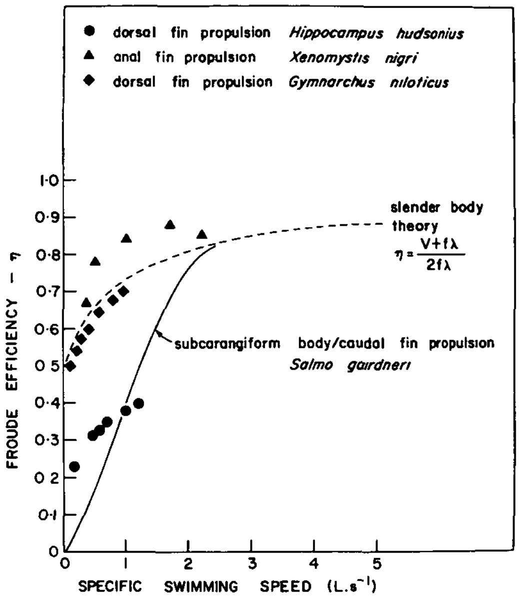

FIG. 2. Relationship between swimming speed and Froude efficiency for some propulsion systems in fish to show the higher efficiency of MPF systems at low swimming speeds. Note that slender body theory that is usually used to interpret BCF propulsors is least appropriate at low speeds. It assumes lateral speeds of body displacements are small compared to forward speeds (Lighthill, 1975; Yates, 1983), which is increasingly violated as speed declines. As a result the theory (dotted line) overestimates efficiency compared to observations (solid line) at low speeds. Nevertheless, because the theory is such a common method of calculating efficiency for BCF systems, it is included for comparison. The curve shown (dotted line) is based on Bainbridge's equation relating speed and tail-beat frequency, and a propulsive wavelength of 0.8 × body length: calculations are based on a length of 20 cm. Note the relatively low efficiency of *Hippocampus* may be associated with crypsis (Blake, 1980). Remaining data are from Blake (1979, 1980, 1983*a*).

In MPF swimming, individual fins are typically arranged in pairs (pectorals, pelvics and dorsal/anal) and can usually function independently. As a result, the fins precisely orient thrust in any direction about the center of mass (Harris, 1937, 1953; Gosline, 1971), facilitating precise maneuver. MPF swimming fish can turn about the vertical axis near the center of mass, without the body translocation necessary in BCF turns (Blake, 1976, 1977, 1978).

An optimal design for MPF propulsion has not been experimentally proven, except for the role of paired fins used as brakes (Harris, 1937, 1953). Nevertheless, there is circumstantial evidence (summarized by Webb, 1982*a*) for expecting the optimal form to include; (1) mid-lateral pectoral fin insertion; (2) ventrolateral insertion of the pelvic fins somewhat beneath the pectorals; (3) soft-rayed, dorso-ventrally symmetrical dorsal and anal fins, extending caudally; (4) leading edge reinforcement of fins; (5) short, deep, laterally compressed body. This form combines many individual mechanisms, each of which has been named (Breder, 1926; Lindsey, 1978). I suggest the integrative aspect of these be recognized by the term chaetodontiform (Fig. 1), after *Chaetodon.*

Actinopterygian fin distributions are variable, and Rosen (1982) has argued that the chaetodontiform (acanthopterygian) pattern may "just represent an alternative solution to the problems of swimming and feeding" compared to more primitive fish. Fins of primitive fish are used for slow swimming and maneuver, but in competition situations, the more chaetodontiform species are usually found in more structurally complex habitats requiring greatest control of maneuver (*e.g.*, Keast and D. Webb, 1966; Gosline, 1971; Hobson, 1974; Hobson and Chess, 1976, 1978). In addition, Werner (1977) observed that maneuverability of the somewhat chaetodontiform bluegill (Centrarchidae; *Lepomis macrochirus*) leads to niche separation along the food axis from fusiform juvenile largemouth bass (Centrarchidae; *Micropterus salmoides*). Consistent habitat segregations clearly suggests advantages of the chaetodontoid form for slow swimming and maneuver.

Specialization for MPF propulsion appears to reduce performance in other areas. Many skates and rays among the elasmobranchs, and many knife-fishes (Notopteridae and Rhamphichthyidae), knife-eels (Gymnotidae) and ocean sunfish (Molidae) lack a caudal expansion essential to BCF propulsion. In others, the very large surface areas of chaetodontiform fish will carry a large drag penalty in BCF periodic swimming especially because body movements increase drag up to 10 times (Webb, 1973*a*, 1975; Videler, 1981). Therefore, BCF periodic performance should be impaired.

Definitive evidence is lacking, but some observations suggest support indirectly. Hobson and Chess (1978) found that planktivores feeding away from shelter on a reef usually had body forms designed to sprint to distant cover while chaetodontiform fish tended to remain close to shelter. The degree of development of the paired-fin muscle is inversely related to the amount of myotomal slow muscle, so that only one of the systems can be effectively utilized for routine swimming (Greer-Walker and Pull, 1975; Johnson, 1983).

Non-swimming

Many post-larval benthic fish live in nutrient poor habitats where food is rare or episodic carcass falls provide unpredictable inputs (Sullivan and Smith, 1982; Gee, 1983). Such fish often have reduced axial skeletal and muscle systems (Childress and Hygaard, 1973; Torres *et al.*, 1979) inhibiting locomotion and probably metabolic expenditures between feeding (Smith and Hessler, 1974; Smith, 1978; Somero and Childress, 1979).

Foraging and Locomotion

Virtually all aquatic vertebrates move to locate and/or consume food. The relative importance of location *versus* consumption of food depends on food distribution and item-specific characteristics. Distribution ranges along a continuum from food widely dispersed in space and time to food-abundant patches where a consumer's life-cycle can be largely completed without exhausting local supplies. Item-specific characteristics of primary concern here are size and mobility, and to a lesser extent defense capabilities. These characteristics also vary along continua.

Similarly, the locomotor abilities of aquatic vertebrates should determine their effectiveness in cropping widely dispersed *versus* locally abundant food. Locomotor performance should also influence the ability to take food items when located. However, at the same time other demands, especially predator avoidance, will modify the importance of locomotion in feeding. Then, not only must behavior be modified, but so will optimal morphologies. In addition, optimization criteria must be recognized that are influenced by locomotor capabilities; animals should behave to maximize net rates of return of limiting nutrients, usually energy. This applies equally to energy maximizers and to feeding periods of time minimizers (Schoerer, 1971; Krebs, 1978; Pianka, 1978).

Accordingly, locomotor repertoires and foraging behavior should be inter-related. Furthermore, these correlations should be most clearly seen for the locomotor specialists since their locomotor *options* are most constrained by specialization. Therefore, these are discussed first.

LOCOMOTOR SPECIALISTS

Widely dispersed food

The general requirement to exploit food widely dispersed in space/time is to move at speeds that sample the greatest volume (travel the greatest non-overlapping distance) for the least expenditure of energy (Weihs and Webb, 1983). This applies equally to macrophages and filter feeders. Weihs (1973*c*), Ware (1975) and Weihs *et al.* (1981) have shown that optimality is achieved by BCF periodic propulsion at relatively low speeds (*i.e.*, cruising speeds) where the ratio M/P of the standard metabolic energy expenditure, M, to the component of power required for swimming, P, is 0.7 to 1.3. Further gains in range may be achieved by two-phase beat-and-coast and beat-and-glide propulsion (Weihs, 1973*b*, 1974). Therefore, the specialist with thunniform morphology and associated BCF periodic swimming behaviors are typical of fish and mammals taking widely distributed food (Fig. 3).

Thunniform animals are not scavengers or detritivores, yet exploiting both resources could be facilitated by efficient cruising. The occurrence of food for scavengers is episodic in space/time (Sullivan and Smith, 1982). Detritus is often abundant, but of such low quality (Bowen, 1979) that relatively large quantities distributed over relatively large areas are necessary to satisfy energy needs. These resources *are* exploited by BCF periodic propulsion specialists, but by the non-thunniform elasmobranchs, using carcharhiniform principles. Additional non-locomotor adaptations appear important for these fish to reduce energy costs and which are not available to thunniform animals. Thus elasmobranchs tend to be benthopelagic so that the high cost of non-stop swimming seen in thunniform animals is avoided. Elasmobranch metabolic rates are low compared to other fish (Brett and Blackburn, 1978) whereas those of the usually endothermic thunniform vertebrates are very high (Gooding *et al.*, 1981). Thus the rate of utilization of resources by elasmobranchs is reduced in periods between food becoming available. Finally, elasmobranchs have electroreception and a well developed sense of smell, more appropriate distance senses for carrion and detritus.

An alternative scavenging/detritivore locomotor correlation is found among elasmobranchs in the rajiform mode. Batoidimorphs presumably share the other non-locomotor adaptations of elasmobranchs, but we do not yet know enough about their propulsion to understand what design principles or compromises might be involved in their evolution.

Locally abundant food

When food is locally abundant and persistent, so that life cycles can be completed largely in its vicinity, then specialization in locomotor functional morphology is expected to be among the adaptations related to specific food characteristics, particularly size and evasive ability (Weihs and Webb, 1983). For predators, feeding behavior must be predicated on the assumption that prey will try to escape. Then, the objective of a predator is to minimize the duration of an interaction (see Isaacs, 1975) to catch prey before they can maneuver and/or reach shelter. Ideally,

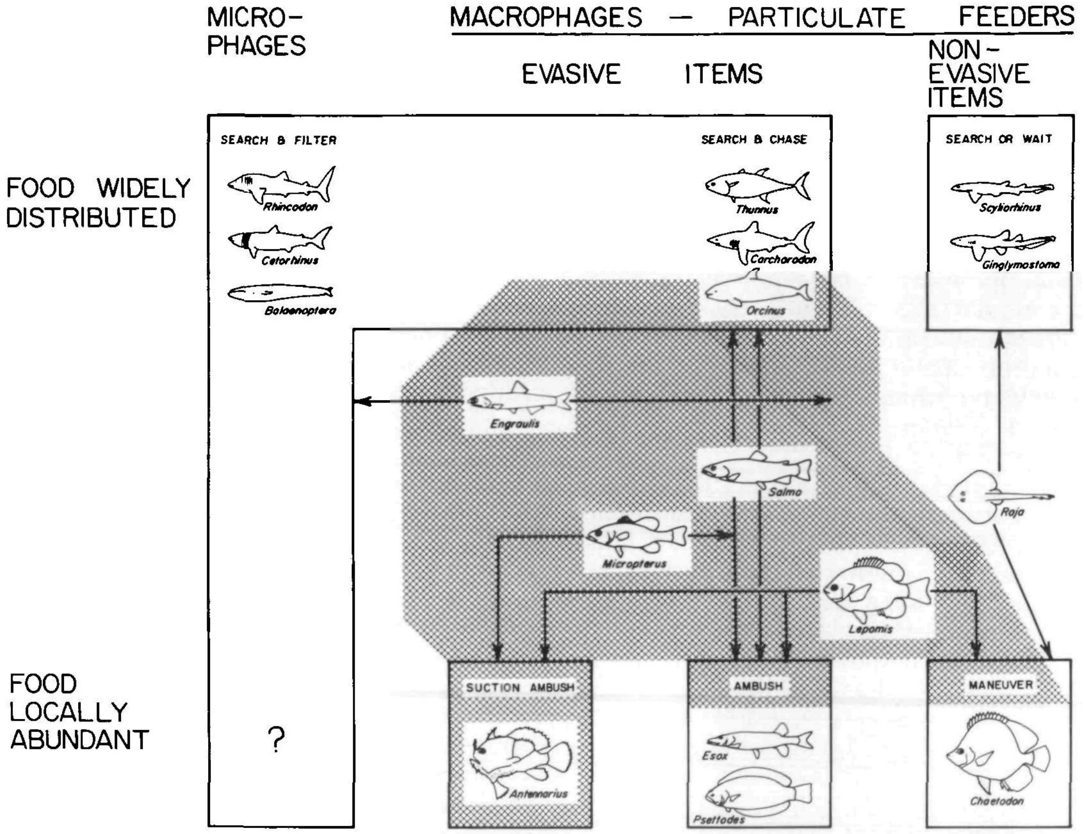

FIG. 3. Summary of postulated functional relationships between aquatic locomotor forms and food properties. The cross-hatching shows the area where suction is a major feeding adaptation.

predators of evasive prey require maximal acceleration (Webb and Skadsen, 1980; Rand and Lauder, 1981; Vinyard, 1982) and hence BCF transient propulsion, as characterized by the Esocidae or Cottidae (Fig. 3). Ideal ambush sites are frequently structurally complex so that predatory BCF transient propulsion specialists retain MPF propulsion as an important component of their locomotor repertoire.

Specialists for BCF periodic propulsion also take evasive prey (Drenner *et al.*, 1978; Major, 1977, 1978), yet they appear to lack locomotor adaptations to facilitate prey capture. For filter feeders this should be of little concern since, by definition, individual particles are not sense. However, thunniform fish and mammals chase prey, and are clearly less effective in actually capturing prey than specialists in BCF transient propulsion. For example, catch success of scombrids predating on fish is of the order of 15% compared to >60% for esocids (Neill and Cullen, 1974; Major, 1977, 1978: Webb and Skadsen, 1980; Rand and Lauder, 1981). Thus, non-locomotor complimentary adaptations should be expected. Thunniform predators tend to break up schools (presumably to force disorientation and straggling) and/or use pack hunting (Major, 1977, 1978; Partridge, 1982).

Non-evasive food. Animal, vegetable and detrital food may be concentrated in a bewildering diversity of locations, ranging from suspended in the water column, through lying on surfaces to hidden in holes etc. Habitat complexity is usual due to other living organisms (*e.g.*, macrophytes, corals) contributing to both productivity and topographic variability. The essential feature of utilizing such resources is the ability to take food in any plane, and to move through restricted spaces. Thus, utilization of non-evasive items will tend to select for specialization in MPF propulsion, characteristic of chaetodontiform tropical reef fish or freshwater centrarchid sunfishes (Fig. 3).

THE LOCOMOTOR GENERALISTS

The locomotor specialists represent a small portion of the total number of species of aquatic vertebrates. Species unspecialized for locomotion are more numerous. These generalists overlap all the locomotor/feeding modes of the specialists where it would seem they should be less competitive. Yet generalists occur and recur throughout fish evolution and they are successful. The basic reason appears to be that the locomotor specialists exploit only part of the food resource base.

Consider first BCF periodic propulsion specialists. Extinct (*e.g., Cladoselache*, ichthyosaurs) and modern thunniform animals (whales, dolphins, porpoises, tunas, lamnid sharks, etc.) are large. Less specialized carangiform and carcharhiniform cruisers are also large compared to most aquatic vertebrates (Marshall, 1966; Nelson, 1976). Forager size is important because the theoretical minimum size of an item that may be included in the diet is approximately that which just returns zero net calories when consumed (Mittelbach, 1981*a*; Werner and Mittelbach, 1982). Therefore, the large BCF specialists, with high energy demands, must concentrate on food items that have a large absolute size, as well as utilizing energy dense areas. However, it is well known that the size-frequency distribution of food item sizes tends to be log-normal (Schoener and Janzen, 1968; Hemmingsen, 1970; Mittelbach, 1981b; Werner and Mittelbach, 1982) so that if large BCF periodic specialists are consuming items of large absolute size, they omit from their diet the energy resources in abundant small particles/patches (Fig. 4).

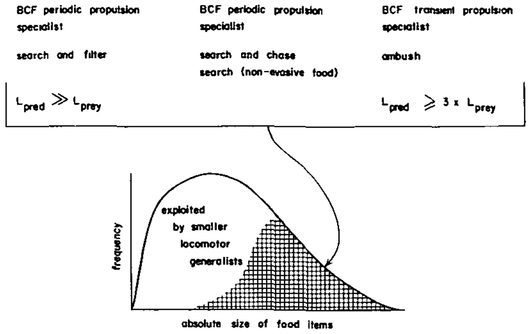

FIG. 4. Diagrammatic illustration of the distribution of food items in a habitat, showing probable resource exploitation by BCF propulsion specialists (hatched area) and generalists (unhatched area).

Similarly, BCF transient specialists, usually sit-and-wait predators, tend to harvest items of large absolute and relative size (Werner, 1977; Popova, 1978). Many small and intermediate sized items/patches are too widely distributed to exploit economically without cruising capabilities.

The small and intermediate sized items, underutilized by BCF specialists, can be eaten by MFP specialists. These, however, harvest food near cover and hence they too omit a large part of the resource base from their diets, in this case due to food distribution, not food item size.

Thus, the various locomotor specialists underutilize a food base of small and intermediate sized food items, usually in exposed habitats. These resources are exploited by small fish. However, because food is often exposed and the fish are small, these fish are a major food base for many locomotor specialists. Thus aquatic vertebrates exploiting smaller food items must retain predator-evasion capabilities, and locomotor specialization in any given direction must be limited. For example, excessive specialization in BCF periodic propulsion to harvest food would increase vulnerability to predators of these small fish, while excessive specialization in BCF transient propulsion to reduce vulnerability would decrease ability to find sufficient food.

These arguments only limit the extent of permissible specialization. It is clear that some specialization related to feeding habits occurs among these generalists, paralleling that seen among specialists. Minnows, for example, tend to have slender caudal peduncles and deeply forked tails and small total area tending towards BCF periodic swimming morphologies. These fish tend to forage widely on suspended food or drift. Perch, on the other hand, have thicker caudal peduncles, more rounded fins, and caudal area is enhanced by dorsal and anal fins. This is reminiscent of BCF transient specialists morphology, and accordingly, perch tend to consume more evasive prey (Keast and D. Webb, 1966; Scott and Crossman, 1973; Webb, 1978*b*). Nevertheless, the essential feature remains that variation is relatively small, and fast-start capabilities for predator evasion are protected (Webb, 1978*a*). Somewhat greater specialization is seen only associated with passive defenses such as spines, cryptic coloration, toxins, etc.

Food-specific locomotor adaptations may be of diminished importance, due to predation, for locomotor generalists exploiting smaller-sized food items. Generalist locomotor forms will be adequate when densities of small items are high because filter feeding remains effective (Leong and O'Connor, 1969; Ware, 1978) as illustrated by many Clupeiformes. However, locomotion must be diminished in importance for food collection by particulate feeders. This is not only because of predation but also because small items must be cropped at a high rate. The energy return on each item is small and particles are taken at rates of the order of tens per second (Mittelbach, 1981*a*). Then, feeding events approach the same duration as minimum response times for locomotor events (Webb, 1980*b*; Eaton *et al.*, 1983). Whole body movements over prey at the rates required would probably be impossible. In addition, the costs of such movements are particularly high (Vinyard, 1982; Webb, 1982*b*) which would reduce net energy gains. Clearly, non-locomotor adaptations are essential for particulate feeding locomotor generalists.

The critical adaptations are suction and protrusible jaws, features central to the evolution of actinopterygian fishes (Lauder, 1982; Rosen, 1982), and vital to food selection and the extension of diet breadth to include small and evasive food particles (Werner and Hall, 1974; Stein and Magnuson, 1976; Drenner *et al.*, 1978; O'Brien, 1979; Gillen *et al.*, 1981; Mittelbach, 1981; McComas and Drenner, 1982; Werner and Mittelbach, 1982). In many situations whole body movements are only used to supplement suction when attacking certain evasive prey (O'Brien, 1979; Vinyard, 1981). Then speed extends the suction zone (Weihs, 1980). Suction may be less expensive than lunging, when it would improve the energy gain per unit of small prey and permit extension of the diet to increasingly small items. Thus suction and jaw protrusion appear necessary correlates to exploiting small-item resources that are too dispersed to filter, by permitting rapid and economical cropping (Fig. 3).

No special fin/body plan is necessary for suction feeders (Rosen, 1982). Among actinopterygian fish, improvements in suction and jaw protrusion (Lauder, 1982) probably led to broader utilization of smaller and/or evasive food particles, and, in addition, facilitated radiation into structurally complex habitats by later MPF specialists (acanthopterygians). Indeed, the success of the actinopterygians might be attributed to solving the problems of necessary accessory structures to mitigate the locomotor boundaries imposed on generalists by predation.

NON-SWIMMERS

Non-swimmers would seem to be excluded from a discussion of locomotor adaptations. However, suction feeding is advantageous in the capture of any food, especially when evasive. Thus, with suction, generalists can again encroach on the resource base of the locomotor specialists; bass (Serranidae, Centrarchidae) are excellent examples. Eventually, costly lunging (Vinyard, 1982) can be eliminated entirely providing for new specialized ambush possibilities. This has occurred among anglerfish (Grobecker and Pietsch, 1979) and in reducing ambush costs, may be an adaptation to the energy poor habitats occupied by such fish (Marshall, 1971). Thus problems of locomotor generalists may underlie the specialized suction mechanisms of fish such as ceratoid anglerfish, essentially nonswimmers or at most occasional swimmers.

CONCLUSION

My objective is to seek correlations between locomotor morphology and the feeding niche of aquatic animals. Although information is incomplete, and no definitive exposition is possible, several general trends are indicated. A continuum of forms is recognized that at the extremes clearly parallels the dichotomy between wide foragers and sit-and-wait predators shown for terrestrial animals. The continuum arises in aquatic animals because the locomotor specialists omit a large part of the food base from their diet. This is exploited by smaller fish which, because of predation, are essentially generalists. Nevertheless, among the generalists, trends paralleling the specialists persist within the limits set by predation. Thus a dichotomy is again approached, but it is more subtle.

Amongst the generalists, locomotor adaptations specific to food types are of diminished importance in foraging and instead other adaptations (*i.e.*, suction) are required to overtake prey. Hence the actinopterygian fishes in particular exploit the smaller food-item resource base omitted by specialists.

Adaptations and tradeoffs complementing locomotion are found in the functional design of locomotor specialists. The differences in locomotor, metabolic and sensory profiles of thunniform and carcharhiniform fish are postulated to relate to levels of uncertainty and energy density of various widely dispersed food types. Esociform and cottiform BCF transient propulsion specialists are drag minimizers and thrust maximizers respectively. These different strategies probably relate to competing demands for other essential aspects of foraging. For example, *Cottus* has a large heavy head for feeding. *Esox* may lack anterior fins to reduce its effective "visibility" to prey (Webb, 1982*c*). Thunniform animals appear to use behavioral mechanisms to disorient prey to facilitate final capture. Therefore, in spite of the obvious adaptations in body form and function, and the clarity with which they can be seen in locomotor specialists, locomotion is always only one of a suite of characters used in feeding and other life activities.

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