CHAPTER 2

Ecomorphology of Feeding in Coral Reef Fishes

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I. Introduction

Once an observer gets past the stunning coloration, surely no feature inspires wonder in coral reef fishes so much as their morphological diversity. From large-mouthed groupers, to beaked parrotfish, barbeled goatfish, long-snouted trumpet fish, snaggle-toothed tusk fish, tube-mouthed planktivores, and fat-lipped sweet lips, coral reef fishes display a dazzling array of feeding structures. And, even the most casual fish watcher quickly gets a sense that this diversity means something, that fish form is related to what the animals eat. Clearly there is something to this impression, but just how are head and body morphology connected to prey choice? Are we really able to predict what a reef fish eats from studying its jaws and teeth? What are the major axes of diversification that are seen in reef fishes? Which morphological and ecological trophic types show the most common convergence? What ecological insights into reef processes have been gained from consideration of the functional design of fish feeding mechanisms?

In this chapter we explore the relationship between fish anatomy and feeding habits. Our overall goal is to show how an understanding of the functional morphology of fish feeding mechanisms can be a powerful tool when considering several ecological issues in coral reef fish biology. We have attempted to identify generalities, the major patterns that seem to cut across phylogenetic and geographic boundaries. We begin by constructing a rationale for how functional morphology can be used to enhance our insight into some long-standing ecological questions. We then review the fundamental mechanical issues associated with feeding in fishes, and the basic design features of the head that are involved in prey capture and prey processing. This sets the stage for a discussion of how the mechanical properties of fish feeding systems have been modified during reef fish diversification. With this background, we consider some of the major conclusions that have been drawn from studies of reef fish feeding ecomorphology. Because of space constraints we discuss only briefly the role of sensory modalities—vision, olfaction, electroreception, and hearing—but these are also significant and diverse elements of the feeding arsenal of coral reef fishes and entire review chapters could be written on each one.

II. How Does Morphology Influence Ecology?

There is a strong intuitive awareness of the link between the design of organisms and their natural history. We instinctively see the connection between the large mouth and sharp raptorial teeth of the coral trout, *Plectropomus leopordus,* and the observation that it preys largely on other fishes. Similarly, the massive platelike jaws and the bulky jaw muscles of the porcupine fish, *Diodon hystrix,* seem well suited to this fish's diet of hard-shelled molluscs. Why do these associations between gross morphology and feeding habits appeal to our sense of order? We see in these examples morphological attributes that we expect to enhance the ability of these fishes to perform the key tasks that are involved in feeding on their prey. Our experience with other fishes suggests that *Diodon* has unusually large jaw muscles and bones to enable an exceptionally powerful bite capable of crushing the hard shells of gastropods and bivalves. The key here is that there is a causal connection between morphology and performance, or the ability of the fish to perform key tasks. The connections between morphology and performance on the one hand, and between performance and ecological patterns on the other hand, are the focus of ecomorphology, the study of the functional and ecological consequences of organismal diversity (van der Klaauw, 1948; Barel, 1983; Motta and Kotrschal, 1992; Wainwright and Reilly, 1994; Koehl, 1996).

A. Linking Morphology and Performance

The design of physiological systems determines their performance properties. Just as the component parts of man-made machines can be modified to produce engines with differing performance qualities, so too are the elements of biological machines modified during evolution to produce diversity in performance of the overall system. So, in principle, understanding how physiological and biomechanical systems function and knowing the role of the various component parts provides the foundation for interpreting their ecological role. Research fields such as functional morphology, physiology, and biomechanics aim to learn how biological systems work, providing insights into design and thus a framework for interpreting diversity. These disciplines establish our best understanding of the causal connection between design and performance.

Biological function involves more than gross anatomy, and significant modifications to functional systems can occur at many levels of organization. Thus, one might consider the consequences of changes in the mechanical advantage of the jaw muscle as it crosses the jaw joint, the consequences of different myosin isoforms for muscle contraction speed, the spectral properties of different visual pigments, or the digestive properties of various enzymes. But, whether the problem is one of mechanics or physiology, there are two valuable consequences of accomplishing a thorough analysis of how a functional system works. First, a complete study of a system provides a rigorous framework for understanding why differences in design have the specific consequences for performance that they have. It becomes possible to interpret morphological diversity in a performance landscape. Second, if one understands how a system functions, one can make well-informed predictions about the performance of similar systems in which performance has not been measured. The significance of this point lies in the common practice of using correlations between morphological and ecological variables as a basis for generalizing to unstudied taxa. Such an approach will be strongest when thorough functional analyses underlie the selection of key morphological traits for study. Spurious correlations between morphological and ecological traits can come about for many reasons, such as underlying phylogenetic patterns, or the fact that often many morphological features are integrated so tightly that correlations will appear even when there is no causal connection. For example, the size of almost every structure in the body changes with growth in concert with overall body size, so that many structures will show a correlation with an ontogenetic change in feeding habits even if they are not related to feeding behavior.

B. The Role of Behavioral Performance in Shaping Ecological Patterns

In general, the performance capacity of individual animals is a central factor in determining patterns of resource use, such as space and prey, and ultimately their fitness. This link may be starkly direct, as in the consequences of escape locomotor performance for avoiding predation, but, direct or indirect, the ability to perform various tasks enters into the equations that determine usage of virtually all resources that an animal seeks during its life. Here we are concerned with understanding the factors that shape the feeding habits of reef fishes, in particular the connection between feeding performance and prey consumption.

The first and most obvious effect of performance on feeding habits is that limits on performance place constraints on the range of prey that potentially can be utilized. A consequence of this observation is that all individuals will be functionally incapable of successfully feeding on most of the possible prey in their environment. Many reef fishes use suction feeding to capture prey that they swallow whole. In suction-feeding predators, the size of the oral aperture directly limits the size of prey that can be eaten (Werner, 1977; Wainwright and Richard, 1995) [in some taxa it is the size of the pharynx (Lawrence, 1957)]. Given the tremendous variety of possible prey items available to a fish on a coral reef, its feeding performance places discrete boundaries on what it *can* eat. Thus, the limits of feeding performance define a potential feeding niche.

There is considerable room for further refinement of this potential niche and it is usually the case that fishes do not feed randomly on the prey that they are minimally capable of eating (Wainwright, 1988; Huckins, 1997). Here again, feeding abilities are a central factor in determining the ultimate shape of prey-use curves. Consider the forms of foraging models that estimate net energy return as a function of three primary factors: rates of encounter with the prey, the probability that the predator will attack an encountered prey, and the probability that the attack is successful (O'Brien, 1979; Greene, 1983; Osenberg and Mittelbach, 1989). For each of these factors the behavioral abilities of the predator to perform relevant tasks may play a major role in shaping the function. For example, encounter rates can be sharply limited by the sensory abilities of the predator. Visual acuity sets the minimum size of prey that planktivores can see, thus having the effect of drastically reducing encounter rates of planktivorous predators with extremely small prey (Li *et al.,* 1985).

Handling-time curves are shaped by the abilities of the predator. A typical pattern is one in which handling time, or energy expended per prey item, increases exponentially as prey size increases (Werner, 1977; Mittelbach, 1984; Stein *et al.,* 1984; Osenberg and Mittelbach, 1989; Huckins, 1997). Because the energy gained per prey item also increases with prey size, there is a prey size that maximizes net energy return for any combination of predator and prey type. The shape of the handling-time curve can differ for different predators, so that for each the prey size, or type, that maximizes net energy return will change (e.g., Werner, 1977; Huckins, 1997). Regardless of whether predators do indeed forage to optimize energy gain, the effect of behavioral performance on these components of foraging models illustrates the basis of how functional diversity can lead to specific, quantitative expectations of the differences among fish species in their feeding habits (Lavin and McPhail, 1986; Wainwright, 1988; Norton, 1991; Sanderson, 1991). Thus, there is a causal link between functional morphology of fish feeding mechanisms and the prey they eat, and the link is provided by the relationships between the phenotype and feeding performance on the one hand, and role of the latter in shaping patterns of prey use on the other hand.

The impact of diversity of feeding mechanisms reaches into other important components of fish ecology. Resource-use patterns may play a causal role in shaping patterns of abundance and habitat distributions in fishes (Mittelbach and Osenberg, 1994; Wainwright, 1996). This connection has been successfully made in some temperate, freshwater fish communities (Keast and Webb, 1966; Werner and Hall, 1974; Mittelbach, 1984), but has not been extended into coral reef fishes as yet. Competitive interactions between bluegill and pumpkinseed sunfish in North American lakes result in bluegill emerging superior in utilizing zooplankton, the preferred prey of both species (Mittelbach, 1984). However, pumpkinseed sunfish gain a competitive refuge by feeding on snails, a less preferred prey resource, but one that pumpkinseed are notably better than bluegill at utilizing (Mittelbach, 1984; Osenberg and Mittelbach, 1989). Zooplankton are abundant in open water and snails are abundant in the vegetated littoral zone, and the abundance of bluegill and pumpkinseed sunfish is proportional to the relative amount of these two habitats in different lakes (Mittelbach, 1984).

It is clear that to understand the foraging decisions that a fish makes one wants to know the shape of the handling-time curve, and other measures of feeding ability and how they impact on foraging decisions. But, what is the significance of understanding the functional basis of feeding ability? Is it not enough to measure the behavioral ability? Why should the ecologist be concerned with the details of biomechanics and musculoskeletal functional morphology that underlie prey capture and handling skills in fishes? Perhaps the major connection here is that understanding the causal basis for differences among species in feeding ability greatly enhances our ability to make predictions in new systems for which we possess limited information. If we understand why the shapes of the prey handling curves, and hence prey-use patterns, differ for two species, then we have a more solid foundation for making predictions about the shape of these curves in taxa for which few ecological data exist. As future work draws connections between prey-use patterns and the abundance and distribution of coral reef species, our understanding of the functional basis of feeding habits will enhance our ability to predict patterns of fish abundance and distribution in coral reefs altered by human fishing pressure and changes in global weather patterns. Furthermore, given that coral reef fish communities are so species rich, the potential ability to use carefully chosen morphological traits as indicators of feeding ability offers an efficient route toward gaining some understanding of the performance capacity of these exceptionally diverse fish communities.

III. The Biomechanical Basis of Feeding Performance

The past three decades have seen tremendous advances in our understanding of the functional morphology of fish feeding mechanisms and the mechanical basis of feeding performance. Several methods have figured prominently in this field, including anatomical and mechanical studies of the muscle–skeleton systems involved in feeding (Tchernavin, 1953; Alexander, 1967; Gosline, 1971; Barel, 1983; Westneat, 1990; Motta and Wilga, 1999), high-speed kinematic and video analyses (Grobecker and Pietsch, 1979; Richard and Wainwright, 1995; Wainwright and Shaw, 1999; Viladiu *et al.,* 1999), endoscopic video recording of particle motion inside the buccal cavity (reviewed in Sanderson and Wassersug, 1993), electromyography to study the use of muscles during feeding behaviors (Lauder, 1980; Sibbing *et al.,* 1986; Wainwright, 1989a; Wilga and Motta, 2000), catheter-tipped transducers to measure suction pressures (Lauder, 1983a; Grubich and Wainwright, 1997; Nemeth, 1997), and the use of particle flow velocimetry to visualize the water movement created by feeding fishes (Ferry-Graham and Lauder, 2001). In this section we describe general principles of the functional morphology of feeding in teleost fishes. We emphasize key design themes of the skull that have been shown to be particularly influential in shaping fish feeding performance and the morphological variables that can be used to estimate their mechanical properties.

A. Prey Capture

1. Methods of Prey Capture

There are generally two stages to feeding in teleost fishes, prey capture and processing; these may employ different functional systems of the skull. Fishes employ one or more of their arsenal of sensory systems to locate prey before capturing them with their oral jaw system (Fig. 1A). Capture is followed by one or more processing behaviors. The prey may be separated from unwanted material, such as sand or other debris, by winnowing behaviors, or a protective armor may be cracked to access the flesh of the prey, as in the case of a molluscivore. During these processing behaviors teleost fishes usually employ a second set of jaws, the pharyngeal jaw apparatus (Fig. 2), a musculoskeletal system formed from toothed gill arch bones and muscles that is mechanically independent of the oral jaw apparatus. Both the oral jaws and the pharyngeal jaw apparatus of coral reef fishes exhibit extensive functional diversity. This functional diversity corresponds to ecological diversity, because nearly all conceivable prey are used by one reef fish or another.

There are three broad methods of prey capture in fishes (Liem, 1980): suction feeding, ram feeding, and manipulation. When suction feeding, the fish rapidly expands the buccal cavity, creating a pressure gradient between this space and the area around the head (Figs. 3 and 4). Water comes rushing into the buccal cavity through the mouth to eliminate this pressure gradient (Muller *et al.,* 1982; Muller and Osse, 1984; Lauder, 1985). Prey that are in the region of the oral aperture are entrained in this water flow and accelerated into the mouth. Suction feeding is believed to be the primitive method of prey capture in teleost fishes (Lauder, 1985) and is seen to some degree in almost all species of coral reef fishes. It is the most common method of prey capture in predators of mobile animal prey.

Suction feeding (Muller *et al.,* 1982; Lauder, 1983a; Muller and Osse, 1984) is frequently contrasted with ram feeding (Norton and Brainerd, 1993; Van Damme and Aerts, 1997), in which the predator overtakes the prey with forward movement of the body or protruding jaws. Extreme examples of ram feeding exist on coral reefs in animals such as *Manta* and the whale shark, which sometimes capture prey in an opened mouth while they swim through dense swarms of planktonic prey (Sanderson and Wassersug, 1993; Sanderson *et al.,* 1996) [note, however, that there are also other mechanisms of suspension feeding (Goodrich *et al.,* 2000)]. However, pure ram and suction feeding appear to be relatively rare, and most feeding events employ a combination of the two (Norton, 1991, 1995; Norton and Brainerd, 1993). Ram feeding can be distinguished in practice from suction feeding based on the relative role of forward mouth movement (ram) and water flow toward the mouth (suction) in moving the prey into the oral cavity. Ram feeders face an additional challenge in having to eliminate the bow wave that may be formed if they are forcing an opened mouth through the water (Van Damme and Aerts, 1997). This problem can be relieved somewhat if the fish opens the opercular space, allowing water to flow freely through the oral cavity, but this only partly eliminates the formation of the bow wave. The solution for most predators that use considerable ram (e.g., barracuda and many serranids) is to overtake the prey with body movements, and finish the attack with an explosive strike of suction feeding (Figs. 4 and 5). At the very least, some compensatory suction is needed to eliminate the bow wave (Summers *et al.,* 1998).

Ram may be accomplished by forward motion of the entire body, or in combination with, or separately by, protrusion of the jaws, termed "jaw-ram" feeding, as seen in many zooplanktivores who use jaw protrusion to move their mouth quickly toward the prey before using a burst of suction to draw the prey into the buccal cavity (Motta, 1984a; Coughlin, 1994). This is also illustrated by the feeding method used by the sling-jaw wrasse, *Epibulus insidiator,* a predator of elusive prey that possesses the most protrusible jaws known in

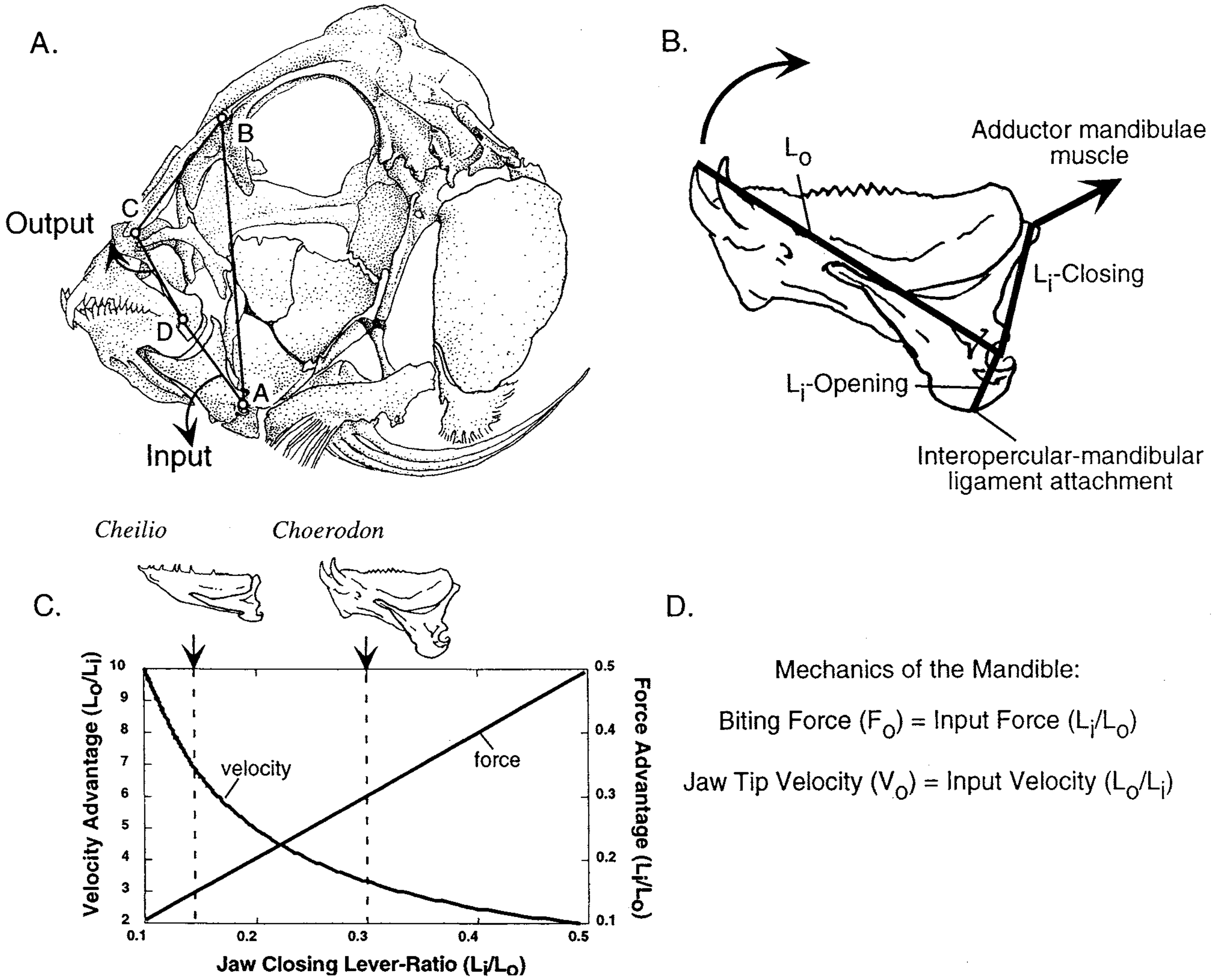

FIGURE 1 Lever mechanics of the oral jaws in fishes. (A) Illustration of the anterior jaws four-bar linkage described by Westneat (1991) for labrid fishes, based on the Caribbean wrasse *Xyrichtys martinicensis*. This planar four-bar system consists of four skeletal links connected by joints A–D. Change in any angle must be accommodated by changes in all other angles in the linkage. In this system, lower jaw depression opens the angle at joint A. This motion results in opening of the angle of joint C, an action that involves anterior rotation of the maxilla, and thus protrusion of the upper jaw. See text for additional discussion. (B) Lever system of the fish mandible. The mandible rotates about the articular-quadrate joint, and the distance of attachment of the jaw adductor muscle on the mandible from the joint is the mechanical advantage of this muscle, or the inlever for jaw closing. Similarly, the mechanical advantage of jaw depression is the distance of the interopercular-mandibular ligament from the jaw joint. (C and D) In the mechanical system of the mandible, force and velocity of jaw motion trade-off as a function of the jaw-closing lever-ratio, as given in the equations. The mandible of *Choerodon venustus* transmits adductor muscle force better than that of *Cheilio inermis*, but the *Cheilio* jaw has greater velocity advantage. *Choerodon* is a durophagous molluscivore, whereas *Cheilio* feeds on elusive prey, including other fishes.

teleost fishes (Fig. 3) (Westneat and Wainwright, 1989; Westneat, 1991). Some combination of ram and suction feeding is the dominant mode of prey capture in species of many coral reef fish families, including the Apogonidae, Anteneriidae, Aulostomidae, Carangidae, Haemulidae, Holocentridae, Lethrinidae, Lutjanidae, Nemipteridae, Pomacentridae, Scorpaenidae, and Serranidae, and many others.

The third method of prey capture is manipulation, in which the jaws are directly applied to the prey and used to remove it from the substratum (Liem, 1980; Wainwright and Turingan, 1993; Alfaro and

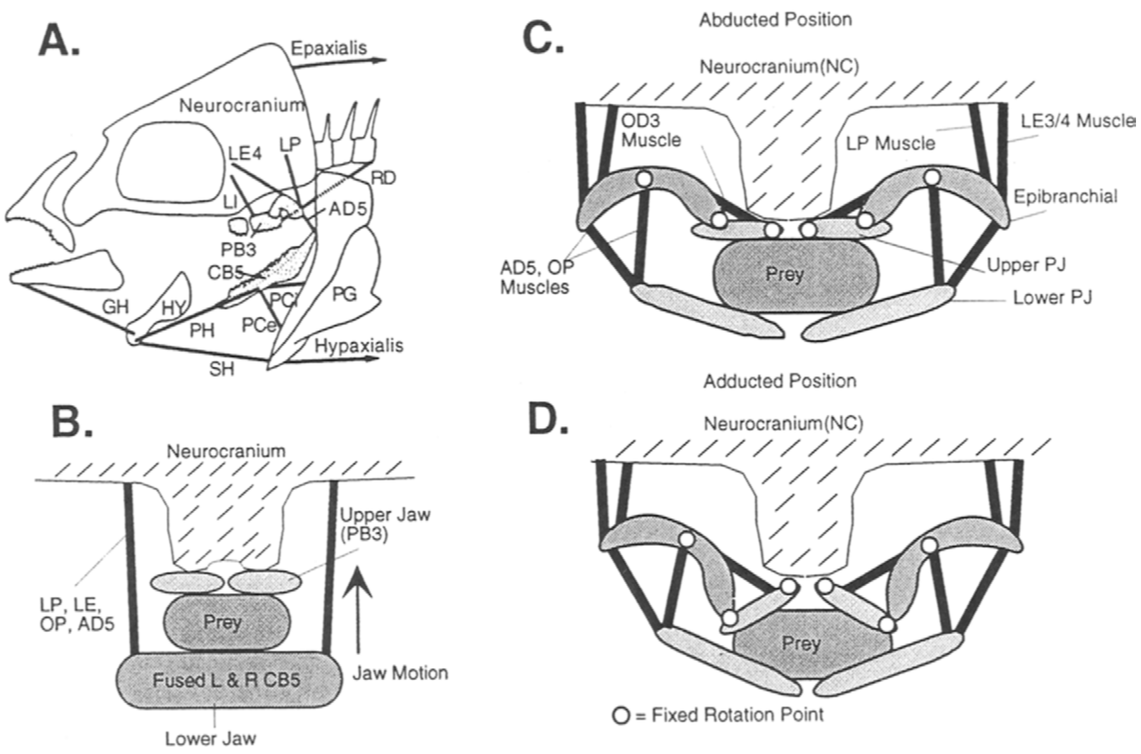

FIGURE 2 Diagram of the pharyngeal jaw (PJ) apparatus of teleost fishes. (A) Lateral view schematic showing the location of the PJ apparatus in the posterior region of the branchial chamber, with several of the major muscles indicated by thick black lines. Prey are captured by the oral jaws, and processed mostly in the PJ apparatus. (B) Diagram of the condition of the PJ apparatus in labrid fishes, in which the primitively paired lower jaw bones are fused into a single lower jaw and there is a direct muscular connection from the neurocranium to the lower jaw by the levator posterior muscle. Compare with C and D, which show the PJ apparatus of a generalized perciform (lutjanid, serranid, lethrinid, haemulid, etc.), illustrating the mechanism of biting. The epibranchial bone is rotated by action of several muscles, pressing down against the dorsal surface of the toothed upper jaw.

Westneat, 1999). Across teleosts in general this feeding method is found less frequently compared to suction and ram feeding (Liem, 1980), but this category characterizes several of the major lineages of coral reef fishes, and within this behavior there has been marked evolution in various groups of these fishes. Most reef herbivores use manipulation, including the Scaridae, Acanthuridae, Siganidae, some Ostraciidae, and the Blenniidae. Furthermore, other dominant coral reef groups use manipulation to take animal prey, including many Labridae, Chaetodontidae, Pomacanthidae, Zanclidae, Balistidae, Tetraodontidae, and Diodontidae. Perhaps no single feature characterizes the trophic nature of coral reef fish assemblages as well as the extensive use of manipulation as a dominant method of prey capture.

Suction, ram, and manipulation feeding emphasize different elements of performance. Suction and ram feeding highlight speed of motion, whereas manipulation is usually enhanced by a stronger biting action (Wainwright and Richard, 1995). Interestingly, in mechanical systems, speed and force trade off, and herein lies a dominant theme of the mechanical design of reef fish feeding systems: the contrast between systems designed for speed and those built for strength. Below we describe the functional morphology of the basic mechanism of prey capture in teleost fishes and the key design parameters that can be modified to produce jaws with greater speed or strength.

2. FUNCTIONAL MORPHOLOGY OF PREY CAPTURE IN TELEOST FISHES

Whether capturing prey by ram, suction, or manipulation all teleost fishes use a common feeding apparatus constructed of a homologous network of muscles, bones, and soft connective tissue. A dominant feature of the fish feeding mechanism that sets it apart from other vertebrate groups is the large number of moving elements. More than 20 major skeletal components are put into motion by about 40 muscles. Fortunately, it is possible to focus on a relatively small number of elements to embody the major features of feeding mechanics.

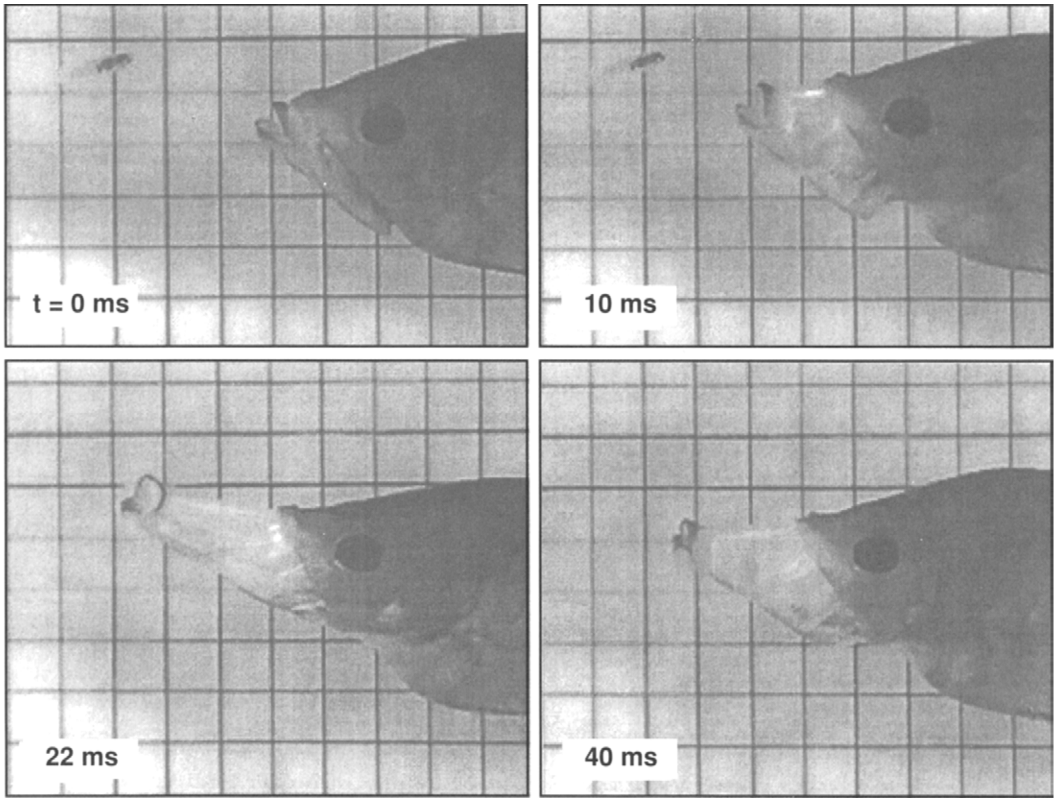

FIGURE 3 Four frames from a high-speed video recording of prey capture in the sling-jaw wrasse, *Epibulus insidiator*. This species has a highly modified jaw mechanism (Westneat and Wainwright, 1989) that permits extensive and rapid lower jaw protrusion (note the short time required for jaw extension). Associated with the origin of this mechanism, *Epibulus* also exhibits a change to feeding on elusive prey such as fishes and small prawns (Westneat, 1995). Video courtesy of L. Ferry-Graham and P. Wainwright.

Ram and suction feeding involve the rapid expansion of the buccal cavity by nearly simultaneous elevation of the neurocranium, lateral expansion of the cheek bones (suspensorium), ventral depression of the floor of the buccal cavity by depression of hyoid elements, and frequently some anterior expansion by depression of the lower jaw and protrusion of the upper jaw (Figs. 3 and 4). The major muscles that participate in these actions include the epaxialis, which dorsally rotates the neurocranium on the vertebral column; the sternohyoideus, which retracts the hyoid bar; the hypaxialis, which retracts and stabilizes the pectoral girdle; and the levator arcus palatini, which laterally rotates the suspensorium (Fig. 6) (Liem, 1970; Sanderson, 1988; Wainwright and Turingan, 1993). Muscles that produce the reverse actions (adduction of the jaws and suspensorium) include the adductor mandibulae and adductor arcus palatini muscles (Fig. 6) (Ballintijn *et al.*, 1972; Friel and Wainwright, 1999). During suction feeding buccal expansion may be coupled with strong adduction of the gill bars to prevent communication between the buccal and opercular cavities (Lauder 1980, 1983a). Adduction of the jaws during manipulation behaviors involves the actions of the adductor mandibulae complex in a variety of rasping, nipping, scraping, and forceful biting actions (Wainwright and Turingan, 1993; Ralston and Wainwright, 1997; Alfaro and Westneat, 1999).

Teeth function differently during ram/suction feeding than they do during manipulation feeding. For ram/suction feeding the teeth mainly act as a friction device, preventing captured prey from escaping back out of the mouth. Large teeth in ram/suction feeders are typically raptorial and associated with capture of particularly large and elusive prey, such as other fishes. Teeth are more diverse in manipulators, often reflecting the method used by the fish to extract prey from the substratum. In some taxa, such as many wrasses, the teeth are relatively large and recurved, though not sharp, as seen in piscivores, and are used in gripping relatively large invertebrate prey from within the reef. Manipulating predators (e.g., the Chaetodontidae) of smaller

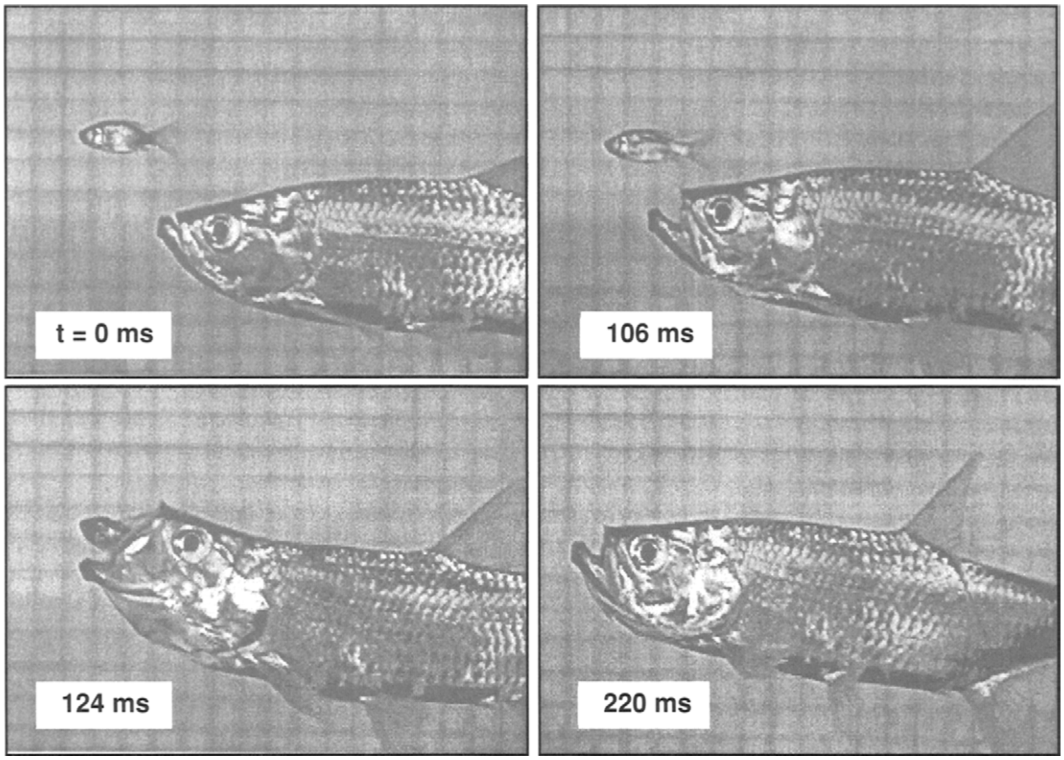

FIGURE 4 Sequence from a high-speed video of a tarpon, *Megalops atlanticus,* capturing a fish. This species illustrates the explosive expansion of the head, together with head elevation and hyoid depression, that characterizes prey capture in coral reef teleosts that use suction and ram feeding to take prey. Video courtesy of J. Grubich.

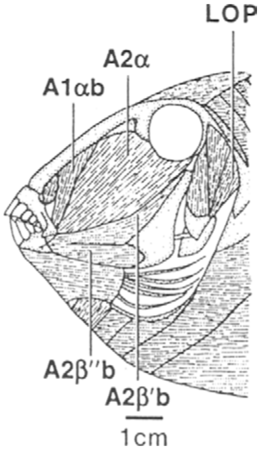

FIGURE 5 Diagram of the head of the gray triggerfish, *Balistes capriscus,* illustrating the superficial muscles of the feeding mechanism. This species feeds on infaunal invertebrates such as sand dollars, molluscs, brachyuran crabs, and polychaetes. All muscles labeled with terms beginning with an "A" are sections of the adductor mandibulae muscle; LOP, the levator operculi muscle (Wainwright and Friel, 2000; reprinted by permission of Wiley Liss, Inc., a subsidiary of John Wiley & Sons, Inc.).

invertebrate prey possess smaller teeth, sometimes arranged in pads. Herbivores show variation from the beaklike structures of the parrotfish to single rows of complex crowned teeth as seen in the surgeonfish. Teeth of manipulators frequently have significant iron deposits (Motta, 1984b, 1987; Suga *et al.,* 1989) that appear to enhance tooth strength.

Aspects of the functional morphology of feeding have been studied in representatives of many of the major coral reef groups, including the Blenniidae (Goldschmid and Kotrschal, 1985; Kotrschal, 1988, 1989a,b), the Labridae (Rognes, 1973; van Hasselt, 1978, 1979a,b, 1980; Tedman, 1980a,b; Sanderson, 1988, 1990, 1991; Wainwright, 1988; Westneat and Wainwright, 1989; Westneat, 1990, 1991, 1994, 1995; Clifton and Motta, 1998), the Scaridae (Monod, 1951; Board, 1956; Tedman, 1980a,b; Clements and Bellwood, 1988; Gobalet, 1989; Bellwood and Choat, 1990; Bellwood, 1994; Bullock and Monod, 1997; Alfaro and Westneat, 1999), the Chaetodontidae (Motta, 1982, 1984b, 1985, 1987, 1988, 1989; Sano, 1989), the Serranidae (Mullaney and Gale, 1996; Viladiu *et al.,* 1999), the Mullidae

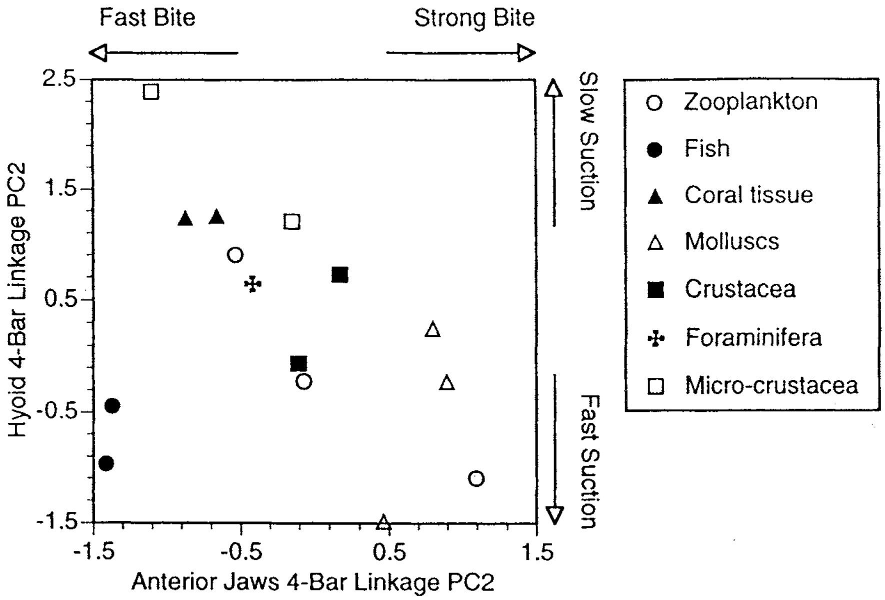

FIGURE 6 Plots of scores of 16 Great Barrier Reef labrid species in the mechanical space of the four-bar linkage systems of the oral jaws and the hyoid apparatus. Separate Principal Component Analyses were run on each linkage system from a data set of 228 specimens from 81 wrasse species of the GBR region. In each analysis the first principal component (PC) was a size factor and the second PC was the major shape axis. Mean PC2 scores were calculated for each species and examples of several major trophic types are shown. In most (but not all) cases, the species shown for each trophic group are thought to represent independent origins of that trophic habit. Note that most trophic groups tend to occupy specific regions of four-bar space. The one exception is the zooplanktivores, which are represented by considerable mechanical diversity in both four-bar systems. In order of increasing anterior jaws PC2 score, the species shown are *Cheilio inermis, Oxycheilinus digrammus, Anampses neuguinaicus, Labropsis australis, Labrichthys unilineatus, Pseudojuloides cerasinus, Macropharyngodon meleagris, Hemigymnus melapterus, Halichoeres ornatissimus, Leptojulis cyanopleura, Thalassoma jansenii, Choerodon jordani, Cheilinus fasciatus, Bodianus loxozonus,* and *Cirrhilabrus punctatus.* Data are from Wainwright, *et al.* (2002b). With permission from Wainwright and Friel, 2000, Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

(Gosline, 1984; McCormick, 1993, 1995; McCormick and Shand, 1992), the Acanthuridae (Jones, 1968; Purcell and Bellwood, 1993), Tetraodontiformes (Sarkar, 1960; Turingan and Wainwright, 1993; Wainwright and Turingan, 1993, 1997; Turingan, 1994; Turingan *et al.*, 1995; Friel and Wainwright, 1997, 1998, 1999; Ralston and Wainwright, 1997; Wainwright and Friel, 2000), the Pleuronectiforms (Gibb, 1995, 1996), and several elasmobranchs (Motta and Wilga, 1999; Wilga and Motta, 2000).

An interesting aspect of the ram/suction vs. manipulation categorization of prey capture mechanisms is that the performance attributes that are expected to enhance each feeding mode are different. In general, ram/suction feeding is expected to emphasize speed and power of jaw and head motion. Manipulation highlights forcefulness of movements, and fine motor control of the jaws in the case of taxa that pick at individual items. As we shall see in the next section, force and speed of motion trade off in the mechanical systems that underlie motion in the fish prey capture apparatus. This design trade-off reveals a major dimension of fish skull diversity, and has considerable ecological consequences.

3. LINKAGE MECHANICS OF PREY CAPTURE

The head movements associated with prey capture in fishes have been modeled in a variety of constructs that simplify the anatomy of the system and attempt to highlight the major mechanical relationships among the muscles and bones involved. The most widely discussed of these are the lever systems of the lower jaw associated with mouth opening and closing (Barel, 1983; Wainwright and Richard, 1995; Wainwright and Shaw, 1999), and several four-bar linkage systems that have been proposed to govern the mechanics of upper jaw protrusion (Westneat, 1990), hyoid depression (Muller, 1987, 1989), and lower jaw depression via opercular rotation (Aerts and Verraes, 1974; Anker, 1974). Four-bar linkages are complex lever systems and as models they provide a framework for understanding the consequences that specific morphological changes will have for skull motion during feeding behavior. A major value of these mechanical models is that they provide insight into the functional basis of major aspects of feeding performance in fishes, such as the speed and forcefulness of jaw opening and closing, the rate of oral expansion, and the rate of jaw protrusion. Studies have shown that various groups of coral reef fishes have radiated considerably within the context of these mechanical models (Wainwright and Richard, 1995; Westneat, 1995).

The four-bar linkages that have been developed reduce interconnecting networks of skull bones into a planar series of four stiff links of specific length, connected in a series (Fig. 1). At any given time the length of the diagonal will determine the conformation of the four-bar linkage. The basis of the linkage as a mechanism of skeletal motion is that a change in the joint angle between any two links results in compensatory changes in the other three angles. For example, in any four-bar linkage, the value of the angle between two links determines all other angles in the system (Fig. 1). Thus, with the linkage drawn in Fig. 1, a muscle that increases the angle at joint A will cause changes in the other angles, in particular, joint C. Notice that in this case, the linkage conformation allows the muscle to depress the lower jaw (link A–D), and simultaneously effect anterior–dorsal rotation of the maxilla (link C–D). This illustrates one of the interesting and important features of four-bar linkages: they can transform input motion into output motion in very different directions. Much like a simple lever acting across a fulcrum, four-bar linkages result in a specific mechanical advantage for the input muscle. Thus, evolutionary modifications of the relative lengths of the links result in hyoid depression, jaw protrusion, and mandible depression systems with differing mechanical properties.

The opercular linkage (Anker, 1974; Aerts and Verraes, 1974) transmits opercular rotation, via contraction of the levator operculi muscle, into posterior tension on the interopercular–mandibular ligament, resulting in jaw depression. The hyoid linkage (Muller, 1987) uses cranial elevation as the input motion, and ventral depression of the intersection point of the left and right hyoid elements is the output. The anterior jaws linkage (Westneat, 1990) uses lower jaw depression as the input to produce upper jaw protrusion by rotation of the maxilla (Fig. 1). These three linkages have been modeled only as planar systems, so their applicability to fish taxa that exhibit considerable lateral motion of the skull during feeding is unclear. However, Westneat (1990, 1991) has tested these three mechanisms with kinematic data from films of prey capture sequences in several species of wrasses from the Great Barrier Reef. He found both the hyoid and anterior jaws linkages performed quite well in accounting for skeletal motions, but that the opercular linkage was inadequate as a mechanism of lower jaw depression. The latter finding was not entirely unexpected because lower jaw depression is also known to be linked to hyoid depression by a ligament between the posterior end of the ceratohyal and the mandible (the hyomandibular ligament) that is found in virtually all fishes (Lauder, 1982; Wilga *et al.,* 2000). The levator operculi muscle that provides input to the opercular linkage is small and weak relative to the sternohyoideus muscle, which provides input to the hyoid linkage, and thus the action of the hyoid linkage in depressing the jaws may dominate any action of the opercular linkage. The opercular linkage may function during feeding in nonlabrid taxa, however, because this four-bar system has been successfully associated with respiratory movements of some other taxa (Barel *et al.,* 1977; Anker, 1974). The opercular linkage appears to function strongly in larval fishes and may represent a largely vestigial linkage in the adults of many lineages.

The mandible of the lower jaw can also be treated as a mechanical lever (Fig. 1), rotating about the joint between the quadrate and articular bones (Barel, 1983; Westneat, 1994; Wainwright and Richard, 1995). The important actions of jaw opening and closing are directly tied to levers on the mandible. The jaw-closing adductor mandibulae muscle attaches on the mandible near the coronoid process, and has a moment arm equal to the distance from the jaw joint to the insertion of the muscle. Jaw opening is effected by tension on the interopercular mandibular ligament acting on the posterior–ventral tip of the mandible, with a moment arm equal to the distance between insertion of the ligament and the jaw joint. Confirmation of the role of these two levers in determining the speed (Wainwright and Shaw, 1999; Wainwright *et al.,* 2000) and force (Hernandez and Motta, 1997) of jaw movement has met with considerable success.

B. Prey Processing

1. PHARYNGEAL JAW FUNCTIONAL MORPHOLOGY

Prey often require considerable processing before they can be swallowed and digested. For example, it may be necessary to separate the prey from a mouthful of sand or to overcome the structural defenses of a mollusc. Many of these behaviors involve the actions of the pharyngeal jaw apparatus, a set of modified gill arch muscles and bones located at the posterior end of the pharynx (Fig. 2). Many fish taxa use a variety of pharyngeal behaviors to process prey beyond simple intraoral transport, including winnowing (Drucker and Jensen, 1991), crushing (Lauder, 1983b,c; Wainwright, 1987, 1988, 1989a; Grubich, 2000), grinding/triturating (Gobalet, 1989), and chewing (Lauder, 1983b; Wainwright, 1989a; Vandewalle *et al.*, 1992). Other taxa may accomplish the same tasks with the oral jaws, including prey crushing (Ralston and Wainwright, 1997; Turingan, 1994) and winnowing.

The basic organization of the pharyngeal apparatus as seen in the majority of coral reef fish families involves paired lower pharyngeal jaw elements, paired upper jaw elements, and a number of muscles that connect these structures to the neurocranium, pectoral girdle, and other branchial bones (Fig. 2A). The mechanisms of action of this apparatus were discussed by Lauder (1983c) and Vandewalle *et al.* (1992) and a more formal model of the mechanics of biting was developed by Wainwright (1989b) and Galis and Drucker (1996). Forceful biting is produced by contraction of dorsal levator muscles that rotate the epibranchial bones, causing them to press on the dorsal surface of the upper-jaw bones (Figs. 2C and 2D). A number of reef fishes with this generalized pharyngeal apparatus are durophagous, specializing on hard prey such as bivalve and gastropod molluscs. Examples include several members of the Haemulidae (Wainwright, 1989a,b), Sciaenidae (Grubich, 2000), Gerriidae (Randall, 1967), and Carangidae (Grubich, 2000). These taxa all exhibit hypertrophication of pharyngeal jaw bones and muscles, frequently with fused or more robust teeth, and in the cases that have been studied, molluscivores exhibit a derived pattern of muscle activity when crushing prey (Lauder, 1983b; Grubich, 2000).

A derived condition of the pharyngeal apparatus is found in labrid fishes (Yamaoka, 1978; Liem and Sanderson, 1986; Stiassny and Jensen, 1987; Wainwright, 1987). Generalized labrids have a single lower pharyngeal jaw element that is suspended from the neurocranium by modified branchial muscles (Fig. 2B). The upper jaws have well-developed and buttressed joints with the underside of the neurocranium. This configuration results in a strong pharyngeal bite, because the biting action is produced more directly by muscle action than in the more generalized condition (Fig. 2B). Many species of wrasses are durophagous (Hiatt and Strasburg, 1960; Randall, 1967; Hobson, 1974; Wainwright, 1987, 1988; Clifton and Motta, 1998). Many other species of wrasses are not durophagous and the diversity of functional morphology of the pharyngeal apparatus in this group is generally poorly known.

Within the Labridae, the pharyngeal jaws are modified further in the parrotfishes, a group that uses beaklike jaws to nip, scrape, and gouge algae and associated material from hard reef substrata (Bellwood and Choat, 1990; Bellwood, 1994; Bruggemann *et al.*, 1994a,b,c, 1996). The mixture of living and dead material is ground to a fine slurry in the pharyngeal jaws, which show modifications from the generalized labrid condition and permit extensive anterior–posterior motion of the lower jaws on the upper jaws (Clements and Bellwood, 1988; Gobalet, 1989; Bellwood, 1994).

2. PERFORMANCE OF PHARYNGEAL JAW FUNCTION

Attempts to assess the morphological basis of prey processing performance of reef fishes mostly have focused on limits of crushing strength, a capacity that generally has a relatively clear basis in the size and organization of the muscles and jaw bones involved in generating and delivering a forceful bite (Wainwright, 1987, 1988; Hernandez and Motta, 1997; Ralston and Wainwright, 1997). There is some indication of a performance trade-off in the pharyngeal jaws, because a strong bite may be acquired at the cost of a large jaw gape, a trend that would limit the size of prey that can be processed by strong species (Wainwright, 1991). Estimates of crushing strength for individual fishes based on muscle morphology and the lever mechanics of the jaws have proved to be remarkably accurate in predicting actual strength of feeding in animals. In most cases this has been done by comparing estimates of biting strength in the fishes to their ability to crush molluscan prey of known resistance (Wainwright, 1987; Osenberg and Mittelbach, 1989; Hernandez and Motta, 1997; Huckins, 1997). Except in molluscivory, little attention has been paid to the performance of prey processing systems and their possible role in shaping feeding performance and patterns of prey use in reef fishes.

IV. Ecological Consequences of Functional Morphology

No habitat on Earth has been the focus of as much ecomorphological insight into fish trophic ecology as have coral reefs. The trophic biology of reef fishes is intimately intertwined with the mechanics of their feeding systems, and the inspiring morphological diversity seen in reef fishes has profound implications for their ecological diversity. In this section we identify a series of major themes that have emerged from research on reef fish trophic ecomorphology. This is not meant to be an exhaustive list of the lessons that have been learned in this area, but we hope to identify the dominant patterns.

Morphology is not a perfect predictor of prey-use patterns, of course. In part, this is because different lineages have different ancestral body forms, and so although evolutionary changes in feeding habits may generally be correlated with evolutionary changes in feeding morphology (Westneat, 1995; Ferry-Graham *et al.*, 2001b), it is not the case that lineages that converge on a common prey type would be expected to exhibit identical jaw and body form. Thus, midwater zooplanktivory has evolved numerous times in reef fishes, including members of the Labridae, Pomacentridae, Haemulidae, Lutjanidae, Serranidae, Acanthuridae, Chaetodontidae, Pomacanthidae, Balistidae, and others. In an absolute sense, zooplanktivorous members of these groups usually resemble their nonzooplankton-feeding close relatives more than they do other zooplanktivores. However, in every case, the zooplanktivores do appear to show consistent changes in their feeding functional morphology, when compared to their close relatives that do not eat zooplankton: reduced mouth size, enhanced jaw protrusion, reduced adductor mandibulae muscles and pharyngeal structures, enlarged eyes, and higher sustained swimming abilities.

A. Reef Fishes Are Models of Trophic Radiation

The exceptional species richness of reef fish communities alone makes them prime candidates for studies of trophic radiation. Several clades of teleosts have radiated primarily and extensively on coral reefs, and are represented today by large numbers of species. Although none of these families can be considered exclusively reef dwelling, among the most prominent reef radiations are the Gobiidae (>1500 species), Labridae [now defined to include both wrasses and parrotfishes (Gomon, 1997); >450 species], the Pomacentridae (>300 species), Chaetodontidae plus Pomacanthidae (>200 species combined), and the Acanthuridae (>70 species). In terms of ecology and morphology, these groups vary considerably in their diversity. Labrids are the most disparate, representing feeding habits as diverse as piscivores, zooplanktivores, ectoparasite predators, molluscivores, polychaete predators, decapod crab predators, coral predators, coral mucous feeders, herbivores, amphipod predators, and predators of various echinoderms. This diversity in patterns of prey use is matched by the morphological diversity of labrids. Species vary in body size from a few grams (e.g., *Labroides*), up to 100 kg or more (e.g., *Cheilinus undulatus*). Skull and body shape vary tremendously as well, from the elongate *Cheilio* to the deep-bodied species of *Cheilinus, Lachnolaimus,* and *Choerodon.*

Trophic diversity in labrids is strongly reflected by interspecific variation in the structures of the feeding apparatus. In an analysis of the anterior jaws and hyoid four-bar morphospace in a sample of 228 specimens from 81 wrasse species from the Great Barrier Reef, the major shape axes from Principal Component Analyses of each four-bar system reflected trade-offs between strength and speed (Fig. 6). Species that share feeding habits tend to occupy similar regions of this four-bar space. Two species representing lineages that have independently evolved piscivory, *Oxycheilinus digrammus* and *Cheilio inermis,* cluster in the lower left corner of this plot, indicating that they both possess an oral jaw apparatus modified for speed of motion and a hyoid apparatus modified for strength. Molluscivores, such as *Bodianus loxozonus, Choerodon jordani,* and *Cheilinus fasciatus,* typically have strong oral jaws (Fig. 6).

Further insights into the ecomorphology of this group of wrasses is gained from an inspection of muscle mass residuals (from regressions on body mass). Muscle mass can be used as a proxy for muscle strength (Calow and Alexander, 1973; Wainwright, 1987). The adductor mandibulae (the major jaw-closing muscle that adducts the anterior jaws four-bar linkage) and the sternohyoideus (the muscle most responsible for hyoid depression, and therefore generation of suction during the expansion of the hyoid four-bar linkage) both range in size among species by about 10-fold, after correcting for body size (Fig. 7). Even more variable is the size of the levator posterior muscle (Fig. 2B; the major pharyngeal jaw-closing muscle), which differs 500-fold in mass between the mollusc-crushing *Cheilinus fasciatus* and the coral mucous-feeding *Labrichthys unilineatus* (Fig. 7). Ecomorphological relationships are revealed by these key muscles and the size of the mouth opening. Coral mucous feeders have exceptionally small levator posterior muscles and small mouths, whereas piscivores have strong adductor mandibulae muscles (that power a linkage system built for speed), average sized levator posterior muscles, and a large mouth (Fig. 7). Molluscivores have strong pharyngeal jaws (large levator posterior muscles) and a large mouth. Zooplanktivores have the smallest adductor mandibulae muscles, weak pharyngeal jaws, smaller than average mouths, and sternohyoideus muscles.

The Pomacentridae offer a notable contrast to labrid diversity. With about two-thirds as many species,

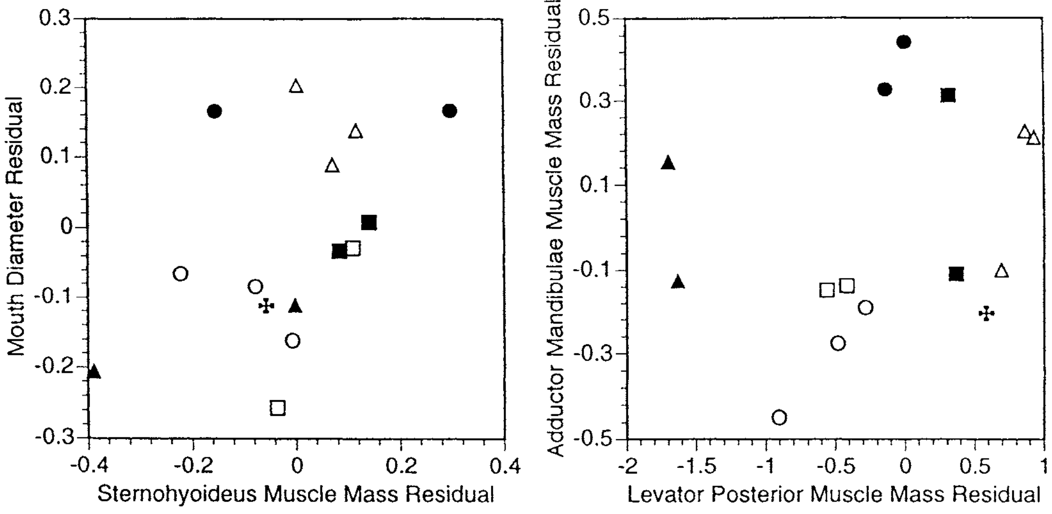

FIGURE 7 Plots of mean residuals (from regressions on Log body mass) of Log-transformed values of mouth diameter, and the masses of three feeding muscles from the heads of 16 species of wrasses from the Great Barrier Reef. Residuals are based on regressions of 228 specimens from 81 species. The sternohyoideus muscle retracts and depresses the hyoid apparatus and is believed to be the major creator of suction pressure during suction. The adductor mandibulae is the oral jaw-closing muscle, and the levator posterior muscle is the major jaw-closing muscle of the pharyngeal jaw apparatus. Species are coded by trophic category. Note how variable these muscles are in different species (e.g., there is a range of almost three orders of magnitude in size of the levator posterior muscle), and that species tend to cluster by trophic habit: molluscivores have strong pharyngeal jaws and large mouths, but average size sternohyoideus and adductor mandibulae muscles. In order of increasing sternohyoideus muscle mass residual, the species shown are *Labrichthys unilineatus, Leptojulis cyanopleura, Cheilio inermis, Cirrhilabrus punctatus, Macropharyngodon meleagris, Anampses neuguinaicus, Pseudojuloides cerasinus, Labropsis australis, Choerodon jordani, Bodianus loxozonus, Halichoeres ornatissimus, Hemigymnus melapterus, Cheilinus fasciatus, Thalassoma jansenii,* and *Oxycheilinus digrammus*. Data are from Wainwright, *et al.* (in press). ○ Zooplankton ▲ Coral tissue ■ Crustacea □ Micro-crustacea ● Fish △ Molluscs ✣ Foraminifera.

damselfishes show little of the ecological diversity found in labrids. Damselfishes are herbivorous, zooplantivorous, and some feed on small benthic invertebrates. None are known to be durophagous, specialized piscivores or many of the other specialized feeding habits seen in labrids. This relatively restricted ecological diversity is associated with what seems to be low morphological variation (Emery, 1973). Although there has never been any attempt to make such a comparison (Gluckman and Vandewalle, 1998), the general appearance is that pomacentrids are not as morphologically disparate as labrids.

The Chaetodontidae plus Pomacanthidae (butterfly fishes and angelfishes, respectively) are believed to be a monophyletic group (Blum, 1988; Ferry-Graham *et al.*, 2001b). Within these groups species can be classified as predators of benthic prey, which the fishes bite from the substratum, or open-water predators, usually of zooplankton. The former category includes predators on a range of prey taxa, including sponges, algae, zoanthids, coral, polychaetes, and other invertebrates, but in all cases the fishes directly bite the substrate to capture the prey. Within this group there is considerable diversity in jaw shape and especially in dentition (Motta, 1985, 1987, 1988, 1989). Suction and ram feeding are used by the midwater predators (Motta, 1982, 1988; Ferry-Graham *et al.*, 2001a,b). Motta (1988) analyzed the opercular four-bar linkage that contributes to jaw depression in several *Chaetodon* species and found a relationship between the form of this linkage and jaw movement times.

Several butterflyfishes have exceptionally elongate jaws, and studies of these species have mostly revealed that they are biting predators, often using their long jaws to reach invertebrates that are taking refuge inside the complex habitat of the reef substratum. However, the species with the longest jaws, *Forcipiger longirostris*, is known to feed exclusively on small, elusive caridean shrimps (Hobson, 1974; Harmelin-Vivien and Bouchon-Navarro, 1983). This species has a modified jaw apparatus that results in novel movement patterns during the strike, permitting extreme protrusion of the upper and lower jaws (Ferry-Graham *et al.*, 2001a,b). Surprisingly, this species does not appear to be an exceptional suction feeder, but rather uses rapid jaw protrusion (i.e., ram feeding) to overtake wary, elusive prey. Comparative studies of linkage mechanics in angel fishes have not been conducted, but like butterflyfishes the pomacanthids are either benthic biters or zooplankton feeders. It is therefore likely that many of the same patterns seen in butterflyfishes will apply to this group.

The acanthuroid fishes are a monophyletic group that includes surgeonfishes (Acanthuridae), rabbitfishes (Siganidae), the moorish idol (*Zanclus*), and the pelagic *Luvarus* (Winterbottom and McLennan, 1993; Tang *et al.*, 1999). Like the Chaetodontidae plus Pomacanthidae, acanthuroids mostly feed by biting attached prey, although zooplanktivory has evolved at least three times within the group (Winterbottom and McLennan, 1993). Most surgeonfishes and rabbitfishes feed on attached algae and/or detritus (Jones, 1968; Bryan, 1975; Woodland, 1990; Purcell and Bellwood, 1993), taking their food from the benthos, and a wide variety of morphological and physiological modifications of the jaws, pharyngeal apparatus, and intestines, underlie a considerable radiation within this general feeding pattern (Jones, 1968; Purcell and Bellwood, 1993). Some of these modifications include changes in the mechanics of the jaws, oral jaw dentition, variation in gill raker form and pharyngeal tooth structure, a muscular gizzard, and variation in the size and shape of the intestines (Jones, 1968; Mok, 1977; Purcell and Bellwood, 1993; Choat and Clements, 1998). In addition, some surgeonfishes harbor in their intestines specialized bacterial symbionts that appear to aid in the digestion of structural carbohydrates (Montgomery and Pollak, 1988; Clements *et al.*, 1989).

There are many other interesting and important radiations of fishes on reefs not discussed above. Among the better studied from the standpoint of the ecomorphological diversity are the Tetraodontiformes (Sarkar, 1960; Turingan, 1994; Turingan *et al.*, 1995; Ralston and Wainwright, 1997), the blennioid fishes (Kotrschal, 1988, 1989a,b), and the Serranidae (Wainwright and Richard, 1995; Mullaney and Gale, 1996; St. John, 1999; Viladiu *et al.*, 1999).

B. Feeding Mechanics Constrain Patterns of Prey Use

The ability of fishes to find, capture, and handle various prey plays a central role in shaping patterns of prey use in natural populations. These abilities have their basis in the mechanical design of the feeding apparatus, in various sensory systems, and in behavioral modifications. This link between the morphology or physiology of fishes and a major ecological feature is strongly intuitive, but it is important to ask how important these connections really are in shaping the ecology of reef fishes. Do differences among species in the construction of the feeding apparatus and in feeding abilities adequately account for diversity in patterns of prey use? What are the major functional properties of prey along which fish feeding mechanisms have radiated? In this section we first review the major ecomorphological axes seen in the feeding mechanisms of reef fishes, and then we discuss the specific evidence for how functional morphology of the feeding apparatus shapes patterns of prey use.

1. MAJOR AXES OF ECOMORPHOLOGICAL RADIATION IN REEF FISHES

The taxonomic range of prey items eaten by reef fishes is as broad as the diversity of life on coral reefs (Randall, 1967; Hiatt and Strasburg, 1960; Hobson, 1974). Virtually all organisms on reefs are prone to predation by reef fishes at some point in their life history. This fact can make the task of searching for generalities in ecomorphological associations overwhelming. One approach to summarizing the diversity of feeding habits in reef fishes is to consider the key functional properties of the prey that predators must overcome to feed on them successfully. These attributes may include elements of predator avoidance, such as elusiveness, or where the prey are located and what must be accomplished to extract the prey from the environment. Constructing "prey functional groups" makes it possible to place phylogenetically diverse prey organisms into a manageable few categories defined by some mechanical or physical variable that can then be related to the construction and performance of the feeding mechanisms used to obtain them. This approach can be used to generate predictions for the specific performance properties that are expected to be enhanced in species that take prey from a particular prey functional group. Here we identify major "prey functional groups" of reef fishes and discuss observations on the functional morphology of feeding in the various fish groups that have evolved feeding habits in these areas.

a. Hard-Shelled Prey Many prey are protected by a hard outer covering, carapace, or shell that must be cracked and disassembled if the digestive juices of the predator's intestines are to gain access to the digestible parts of the body. Examples of hard-shelled prey include gastropod and bivalve molluscs, echinoids, some decapod crustaceans, some shell-bearing anellids, foraminifera, and organisms that bore into the hard, calcareous substrate of dead coral. Hard-shelled prey are often little challenge to capture once they have been detected, but the challenge to the predator comes in handling them.

Most teleost fishes that feed largely on hard-shelled prey crush them in either the pharyngeal jaw apparatus (Labridae, some Carangidae, some Haemulidae, some Sciaenidae) or the oral jaws (Diodontidae, Tetraodontidae, Balistidae, Sparidae). The functional basis of feeding performance in these predators lies in the ability of the fish to deliver large forces to the prey. Modifications of the pharyngeal and oral jaws that facilitate the delivery of a forceful bite include enlarged biting musculature, which is often pinnate in organization, robust bones that can withstand the forces generated by the muscles, and a favorable mechanical advantage in the biting mechanism that maximizes, or amplifies, delivery of muscular tension to the protective shell of the prey (Wainwright, 1987, 1988; Turingan, 1994; Turingan *et al.*, 1995; Hernandez and Motta, 1997).

Two trade-offs have been noted in the construction of jaw systems that deliver large forces. First, because lever mechanics dictate that a high mechanical advantage must occur at the direct cost of velocity transfer, jaw systems of hard-shelled predators are expected to be slow moving (Wainwright and Richard, 1995). Second, one cost in increasing angles of pinnation in muscles is that this will limit the extensibility of the muscle compared to a similar muscle with a parallel fibered arrangement. A series of labrid fishes from the Caribbean were found to show a marked trade-off in strength of the pharyngeal jaw apparatus and the extent to which the jaws could open (Wainwright, 1991). Strong species were limited to smaller prey.

b. Large, Firmly Attached Prey Many prey gain protection by having a tenacious grip of the substrate, often combined with locating themselves in hard-to-reach interstices of the reef. Included here are many gastropod and bivalve molluscs, including some that do not have to be crushed once captured, such as limpets and chitons, echinoids, and some decapod crabs. Predators of these prey must be able to grasp them firmly in their oral jaws and to pull them out of their protective resting location. Examples of these types of predators include many Labridae (e.g., *Bodianus*, many *Thalassoma*, and *Semicossyphus*) and Balistidae (Randall, 1967; Turingan *et al.*, 1995; Westneat, 1991, 1994, 1995). Predators feeding in this category have been found to have a strong oral jaw bite, with a large adductor mandibulae muscle (Turingan, 1994; Turingan *et al.*, 1995) and a high mechanical advantage in the jaws (Westneat, 1994; Wainwright and Richard, 1995). These trends are most apparent when the fishes are compared to close relatives that feed on other prey (Turingan *et al.*, 1995; Westneat, 1995).

c. Small, Firmly Attached Prey Many other firmly attached prey are much smaller relative to the predator and are collected in groups by predatory fishes that scrape them from the substratum. These prey include epilithic algae, many sponges, and scleractinian coral polyps. Fishes that feed on these prey include many species in the Pomacanthidae, Chaetodontidae, Ostraciidae, Monacanthidae, Scaridae, Pomacentridae, Blenniidae, Acanthuridae, and Siganidae. These fishes often have small mouths with high mechanical advantage of the adductor muscles (Wainwright and Richard, 1995). The teeth either form a single cutting edge, as in scarids, acanthurids, kyphosids, ostraciids, monacanthids, and some pomacentrids, or they form a broad pad, many tooth rows deep, as seen in pomacanthids, chaetodontids, and some pomacentrids. Tooth form is often a key factor associated with trophic diversity within this "small-attached" category (Jones, 1968; Motta, 1984b, 1987, 1989). Scarids that gouge deep troughs in the calcareous substratum have larger adductor muscles than do species that graze the surface of similar substrata (Bellwood and Choat, 1990), but data on adductor muscle design in most taxa in this category have not yet been collected.

d. Zooplankton Many reef fishes feed individually on the small organisms of the plankton that are carried onto the reef by currents. Included in this prey category are copepods, siphonophores, pteropods, and the eggs and larvae of fishes, crustaceans, and other invertebrates. Predators of the zooplankton are often seen in schools hovering over the upstream end of the reef, feeding on individual plankters. The primary challenge for these fishes appears to be in seeing the prey items, many of which are protected by being partially translucent. Zooplanktivorous fishes typically have smaller mouths compared to their close relatives, and some have moderately protrusible jaws that form a distinctly circular aperture when opened. A zooplanktivorous habit has evolved independently in many groups of reef fishes, often repeatedly. Among the families that have given rise to zooplanktivorous taxa are the Pomacentridae (Emery, 1973), Labridae, Pomacanthidae (*Genicanthus*; Randall *et al.*, 1997), Chaetodontidae (Motta, 1982; Harmelin-Vivien and Bouchon-Navarro, 1983), Lutjanidae (Carpenter, 1987), Serranidae, Inermiidae, Congridae, Balistidae (Turingan, 1994), and Acanthuridae (Winterbottom and McLennan, 1993) [see Randall (1967) for diet data on planktivores of all of these families except Pomacanthidae]. Prey-type-related diversity in the feeding mechanism within this trophic group has not been described, although on any given reef there are clearly differences in body size, mouth size, and finer detail of branchial and jaw anatomy among species of zooplanktivores. Foraging location in the water column has been proposed to be related to swimming ability, in that it may be related to escape ability of these fish in the face of their own predators. Hobson and Chess (1978) observed that fish species with body forms that appear to confer greater swimming abilities feed in locations farthest from the reef. To date, no comprehensive study of the relationship between body form and swimming ability in these fishes has been conducted. It also appears that zooplanktivores as a group are faster swimmers than are their close relatives.

e. Large, Elusive Prey Other fishes, cephalopods, and several types of crustaceans present predatory fishes with a special challenge. These prey are relatively large and alert and possess well-developed escape responses. Fishes that specialize in this prey functional category typically have larger mouths compared to their close relatives, raptorial teeth, and large adductor mandibulae (jaw-closing) muscles, and the mouth-opening and -closing mechanical systems are modified toward a high-velocity transfer (Wainwright and Richard, 1995; Westneat, 1995). These fishes typically employ a stealth tactic to approach their prey, striking with an explosive lunge that involves considerable ram and suction (Fig. 4). The large mouth allows them to take large prey, the large adductor muscles enhance the strength and power of the jaw grip, and the mechanical system of the jaw translates muscular contractions into rapid motion. Included in this category are representatives of the Serranidae (Wainwright and Richard, 1995; Viladiu *et al.,* 1999), Labridae (Westneat, 1991, 1994, 1995), Antennariidae (Grobecker and Pietsch, 1979, 1987), Scorpaenidae (Grobecker, 1983), Lutjanidae, Aulostomidae, Scorpaenidae, Muraenidae, Carangidae, Sphyraenidae, and a number of other groups. Some of these families are exclusively in this category (e.g., Sphyraenidae and Antennariidae), but in other groups this mode has evolved as part of a trophic radiation within the family (e.g., Serranidae, Labridae, and Lutjanidae).

The families of fishes that are characterized by predation on the "firmly attached prey" category often give rise to zooplanktivores (e.g., Acanthuridae, Chaetodontidae, Pomacentridae, and Balistidae). However, only one group, the Labridae, includes several lineages of predators of "firmly attached prey" that have given rise to predators of "large, elusive prey." It is possible that the functional morphology of a predator of firmly attached prey is simpler to modify into an effective zooplanktivore than into a predator of large, elusive prey. Several groups that are primarily made up of predators of large, elusive prey have given rise to highly successful lineages of zooplanktivores. Examples include the Serranidae, which includes the zooplanktivorous Anthiinae; the Lutjanidae, which gave rise (perhaps separately) to the caesionids (Carpenter, 1987, 1990, 1993), *Pinjalo* (Randall *et al.,* 1997), and *Ocyurus* (Randall, 1967); and the Haemulidae, which apparently gave rise to the Inermiidae (Johnson, 1981). Thus, based on the weight of evidence from modern reef fish assemblages, zooplanktivory has evolved frequently from both benthic biting predators and predators of large, elusive prey.

f. Mobile Benthic Prey Many reef fishes feed on relatively small invertebrate and fish prey that live in very close association with the substratum. These elusive prey are usually found within the matrix of the reef. Common microhabitats that are exploited include the interstices of the reef: coral, dead coral, algal turf, and sand. Here the predators apparently use suction feeding, and sometimes employ biting with the strike. Included in this category of predators are many members of the Labridae, Lutjanidae, Haemulidae, Lethrinids, Mullidae, Nemipteridae, Serranidae, Gobiidae, Chaetodontidae, and several other groups. The morphology of these predators is often very similar to that of species that feed on large, elusive prey, except that body size or the structures of the feeding apparatus are scaled down to a smaller size.

A subset of this group includes fishes that are familiar components of the coral reef, but which actually do not feed on the reef, instead only using it as a refuge during the day when they are inactive. Most Haemulidae, Lutjanidae, Lethrinidae, Sciaenidae, and Nemipteridae actually feed in nearby seagrass beds or in sandy areas that lie adjacent to reefs (Randall, 1967; Hiatt and Strasburg, 1960). These fishes feed mostly at night on mobile benthic prey and sometimes on zooplankton.

g. Sand-Dwelling Prey Prey that live buried in sand present two types of challenges to predatory fishes. They can be both difficult to locate and difficult to separate from the mouthful of sand that accompanies them when captured. A variety of behaviors are used to locate infaunal prey that live in sand. Jets of water blown out of the mouth are used to excavate buried prey in numerous species of the Balistidae (Fricke, 1971, 1975; Frazer *et al.,* 1991; Wainwright and Turingan, 1997), Monacanthidae, Ostraciidae, Labridae, and Haemulidae. Some haemulids and sciaenids appear to locate buried prey through the use of mechanosensory pits located in the lower jaw and other structures of the skull. Goatfishes protrude their snout into the sand and use a pair of mobile barbels mounted on the end of the hyoid apparatus to locate buried prey mechanically (Gosline, 1984).

Labrids use a particularly diverse battery of behaviors to locate buried prey. Several species will grip and move large rocks or coral with their oral jaws in order to search the space under the rock (e.g., *Novaculichthys,* some *Choerodon,* and some *Halichoeres*). Buried prey will be located by probing the substrate with the snout, digging with the snout, blowing jets of water, and even fanning the sand with the pectoral fin (P. C. Wainwright and D. R. Bellwood, unpublished observations on *Choerodon schoenlinii*). These behaviors are generally poorly documented and their phylogenetic distribution within the Labridae has not been explored.

Infaunal prey are typically captured with a mouthful of sand and a winnowing behavior is typically then used to separate the prey and sand. Recorded in some haemulids, labrids, mullids, and gobies, among others, the morphological basis of winnowing is not well understood, but it appears usually to involve a combination of water motion inside the buccal cavity and fine manipulation by the pharyngeal jaw apparatus (Liem, 1986; Drucker and Jensen, 1991).

h. Nocturnal vs. Diurnal Feeding The basis for resource partitioning along the 24-hour temporal axis is based largely on visual and other sensory modalities. These systems are beyond the scope of this review, but we mention this major axis of ecological radiation in reef fishes, in part because the implications of feeding in low light at night, with respect to the functional morphology of the prey capture apparatus, have not been explored. We note that nocturnal reef fish tend to be either predators of large, elusive prey, mobile benthic prey, or zooplankton. Very few nocturnal fish predators feed on hard-shelled prey (e.g., *Diodon*) or firmly attached prey.

2. THE MECHANICAL BASIS OF FEEDING PATTERNS IN FISHES

In the previous section we described a context for organizing the bewildering diversity of reef fish feeding habits. The identification of functional groups of prey allows one to organize trophic diversity along lines that may be more readily viewed from the standpoint of functional morphology of the feeding mechanism. What are the chief performance features that we expect to be important for the predators in each category, and how might the feeding mechanism be modified to enhance these features? Although very general correlations can be described between key morphological features and patterns of prey use in reef fishes, in the vast majority of cases there is a lack of strong experimental data that would address thoroughly the causal basis of feeding performance.

One focus of work on the ecomorphology of reef fishes has been on the relative importance of, and functional basis of strength and speed in, the feeding mechanism. Recall from Section III, A, 3 that the mechanics of linkage systems and muscles create a trade-off between force transmission and velocity transfer. The mechanical advantage of the adductor mandibulae (jaw-closing muscle) on the mandible can be modified to enhance the forcefulness of the bite, or to enhance the speed of jaw-closing, but both cannot be enhanced simultaneously. Indeed, interspecific analyses of fishes have shown that speed of motion of the mandible during jaw closing has a strong negative correlation with the mechanical advantage of the adductor mandibulae muscle (Wainwright and Shaw, 1999; Wainwright *et al.,* 2000).

An analogous situation exists in the four-bar linkage mechanics that have been described to govern hyoid depression, and upper and lower jaw motion in the fish skull (Westneat, 1991; Muller, 1996). Westneat (1994, 1995), in elegant and thorough analyses that corrected for phylogenetic relatedness among taxa, has shown that the evolution of mechanical properties in the skull linkage systems is strongly correlated with changes in feeding habits in cheiline wrasses. Historical changes to taxa that feed more heavily on elusive prey are significantly correlated with changes in skull linkage mechanics that enhance velocity transfer. Similarly, changes to feeding on prey that require a forceful bite are associated with linkage changes that enhance force transmission in the jaws.

Attempts to identify the morphological features that are good indicators of the ability to feed on hard-shelled prey have met with considerable success. Mollusc crushing performance appears to be directly related to biting force, a parameter that has a direct morphological basis in the size of biting muscles. Working with the pharyngeal jaw apparatus of labrid fishes in the Caribbean, Wainwright (1987, 1988) showed that the physiological cross-sectional area of one dominant muscle (the levator posterior muscle) accurately reflected the crushing strength of individual fishes feeding on gastropods. Maximal crushing strength of fishes was shown to be an active constraint on the ranges of prey that were eaten. Because labrid species differed in their crushing strength, among species this led to differences in feeding habits that could be accounted for by difference in crushing ability (Wainwright, 1988).

Performance in oral jaw crushing has also been found to be predicted accurately by jaw adductor muscle morphology and lever mechanics of the lower jaw (Hernandez and Motta, 1997).

C. Scaling of Feeding Mechanics Results in Strong Ontogenetic Effects

One of the most striking generalities about reef fishes, and fishes in general, is that patterns of prey use change ontogenetically in virtually every species. These changes are typically drastic, usually taking species from being zooplanktivores when they are larvae and newly metamorphosed, through a series of distinct stages in which one or another prey type dominates the diet. Well-documented examples of ontogenetic diet changes in reef fishes include members of the Serranidae (Randall, 1965; Mullaney and Gale, 1996; St John, 1999), Labridae (Wainwright, 1988; Kanashiro, 1998), parrotfishes (Bellwood, 1988b), Mullidae (Lukosek and McCormick, 2002), and others. Ontogenetic diet shifts reflect the influence of life stage and body size on habitat use and feeding capabilities. Almost all reef fishes begin as planktonic larvae (when they feed mostly on small planktonic animals) and most move through substantial or subtle habitat shifts after they settle onto the reef, then grow and mature. To some extent, feeding habits must be constrained by what is available in the habitat.

As fishes grow the mechanical properties of their feeding mechanism change. Even in the simplest scaling case, wherein shape is maintained during growth, the larger feeding apparatus will exhibit its most effective feeding performance on larger prey (Werner, 1977; Wainwright, 1987). Changes in optimal or preferred prey size often result in changes in the taxonomic composition of the diet.

An example of this phenomenon is provided in an analysis of feeding habits of several Caribbean species of the Serranidae (Wainwright and Richard, 1995). Serranids make an interesting case because there are relatively few shape differences between species, and ontogeny produces large animals that are similar in shape to small animals. The major morphological axis of the serranid radiation is body size. Several small species may be only a few centimeters long when fully grown, but the large species of *Epinephalus* may exceed 2 m and weigh over 250 kg (Randall, 1983). However, the shape of those species that vary so much in size is strikingly similar. In the 18 species analyzed from the Caribbean there was a strong match between body size and the dominant prey in the diet (Fig. 8). The smallest species feed on copepods and similar small crustaceans; somewhat larger species feed on various free-moving prawns and at about 200 mm body size the dominant prey is decapod crabs, and above that most species feed on fishes and cephalopod molluscs. Detailed ontogenetic data for one species from the Western Atlantic, *Mycteroperca microlepis,* reveal that this species matches this body size/diet pattern during its ontogeny. Some exceptions to this trend exist, most notably in taxa that diverge significantly from the generalized serranid body plan and show distinct trophic specializations. For example, *Paranthias furcifer* is a midwater species with a relatively small mouth and gracile feeding structures. At 200 mm this species is a zooplanktivore, rather than a crab or fish predator like most groupers of this size (Fig. 8).

Studies of the scaling of feeding mechanisms in other reef fish groups indicate that strength often scales more rapidly than expected under models of isometry (Wainwright, 1988; Westneat, 1994, 1995; Hernandez and Motta, 1997). In Caribbean labrids, diet breadth increased during ontogeny, as fishes are increasingly strong-jawed, but once a biting strength of 5 Newtons was achieved, individuals became increasingly specialized on a taxonomically narrow diet of molluscs (Wainwright, 1987, 1988; Clifton and Motta, 1998). An interesting area for future work will be to develop mechanical models of the scaling of suction feeding performance, and to explore the consequences of this relationship on prey-use patterns in suction-feeding predators.

D. Behavioral Differences between Species Can Affect Prey Use

Feeding functional morphology provides one level at which the interaction between predator and prey can be modified during evolution to produce differences in patterns of prey use. However, mechanics of the feeding apparatus are brought to bear on prey through the filter of animal behavior. Species with quite similar feeding morphology may have different patterns of prey use because they feed in different habitats, or they may feed in exactly the same habitat but use subtle variations of feeding kinematics or strategies to obtain prey. Particularly striking examples of both are found within the Acanthuridae and the Scaridae.

The surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus* of the Great Barrier Reef are morphologically similar species that appear to be completely sympatric, even to the point of feeding on the same turf-algae-covered rock (Purcell and Bellwood,

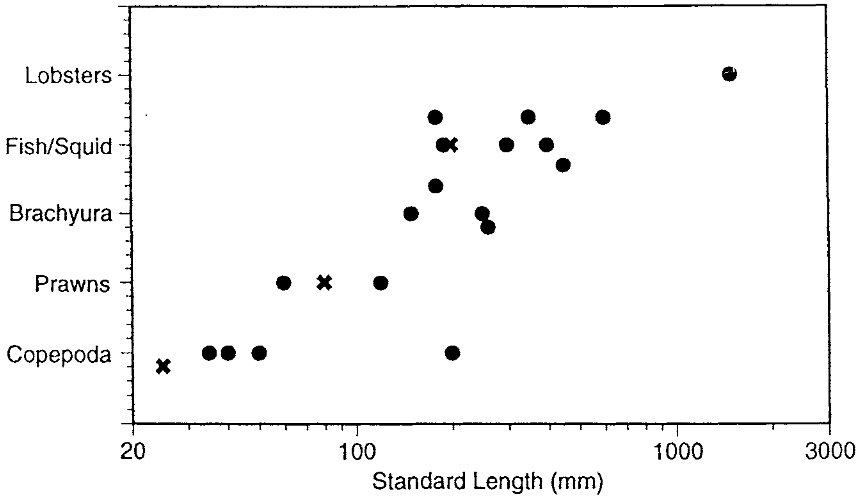

FIGURE 8 Plots of major prey eaten vs. body size for 18 species of groupers (Serranidae) from the Caribbean. The effects of body size are seen in this fish group, which varies mostly in size rather than shape. The three "x" symbols represent data from three size classes of *Mycteroperca microlepis* (Mullaney and Gale, 1996). Data are from Randall (1967); plot redrawn from Wainwright and Richard (1995), with kind permission from Kluwer Academic Publishers.

1993). However, they use different prey: *A. nigrofuscus* grazes on turf algae, whereas *C. striatus* feeds on the particulate and epiphytic material that occurs on the surface of the turf-algae blades. Subtle differences in jaw morphology and the kinematics of biting behavior reveal the basis of these different feeding habits. The teeth of *C. striatus* are finer and form a brushlike surface, but the major factor that accounts for the difference in prey use is biting behavior. Algae are sheared or torn by the teeth of *A. nigrofuscus* while the jaws are simultaneously adducted and the head is quickly rotated laterally. The mouth of C. *striatus* is opened wider and the surface of the turf algae is brushed by the fine teeth during a quick adduction of the lower jaw (Purcell and Bellwood, 1993). Similar subtleties in biting behavior have been used to account for interspecific differences in prey-use patterns of chaetodontids (Motta, 1988, 1989).

Other species of surgeonfishes appear to share similar jaw morphology and patterns of prey use, and yet segregate spatially. *Acanthurus nigrofuscus* and *Acanthurus lineatus* have very similar tooth form and feeding behavior, and both nip and tear turf algae from hard substrata (Choat 1991). However, *A. lineatus* is territorial and excludes other species, including *A. nigrofuscus,* from its shallow-water feeding areas (Choat and Bellwood, 1985; Robertson and Gaines, 1986). Here, niche separation occurs along a spatial axis due to behavioral interference in two species that feed on similar prey with similar feeding methods and morphology.

Parrotfishes provide a second example of how behavioral differences can underlie marked ecological variation among close relatives. Two functional groups of parrotfishes were identified by Bellwood and Choat (1990), who found Great Barrier Reef scarids either excavated deep bites into rocky substratum or scraped the surface of the same hard surfaces. In this case, substantial morphological differences were subsequently discovered in the two groups; representative excavating species had heavier jaw musculature, heavier jaw bones, and stronger ligamentous connections in the jaws compared to the scraping species (Bellwood and Choat, 1990). In this example, the differences produced by these patterns of feeding kinematics result in profound consequences for the impact of the two groups on coral reef ecology, in that the excavating species probably account for the majority of reef bioerosion by fishes (Kiene, 1988; Bellwood, 1995a,b).

As in the acanthurids, however, parrotfishes can also show habitat segregation within an ecomorph. On the Great Barrier Reef, *Scarus frenatus* and *Scarus niger* both exhibit the scraping morphology and behavior (Bellwood and Choat, 1990). However, these species segregate spatially, with *S. frenatus* usually being found in shallower locations (Russ, 1984). *Scarus frenatus* may defend the shallower feeding sites in behavioral interactions with *S. niger* (D. R. Bellwood, unpublished data).

There is a lesson in the behavioral differences between species: although analyzing the functional design of a feeding mechanism allows the researcher to identify potential feeding niches and make inferences about relative feeding abilities in different species, a number of other factors interact with the inherent abilities of a predator, all of which ultimately determine usage patterns of prey and other resources. Interactions between species on the reef are one factor that can further shape resource-use patterns, as do the distribution and value of the prey resource. Being able to infer relative feeding performance from morphological observations does not necessarily also provide direct insight into patterns of resource use.

E. Feeding Mechanics and Prey Use Can Vary among Populations

One understudied aspect of reef fish feeding ecomorphology that is relevant to the process of diversification is variation within species. Freshwater fishes, particularly lake-dwelling taxa, have provided numerous cases of intraspecific polymorphisms associated with divergent forms within species that make use of different prey resources (Robinson and Wilson, 1994). These systems are often characterized by being relatively species poor, so that trophic niches are unfilled by existing species (Robinson and Wilson, 1994; Schluter, 1996; Smith and Skulason, 1996; Bell and Andrews, 1997; Robinson and Schluter, 1999). Similar patterns of polymorphism or descriptions of potentially adaptive intraspecific variation in general are lacking for marine systems. Although the prevailing views of the existence of polymorphisms in lakes very much focus on the isolated and depauperate nature of these faunas, there are very few empirical data on marine taxa. Thus, it is unclear to what extent marine forms exhibit polymorphisms or extensive trophic variation within species.

Several studies have examined patterns of prey use and trophic morphology within species of reef fishes (Turingan *et al.,* 1995; Cutwa and Turingan, 2000; Durie and Turingan, 2001). In each of these analyses, fish populations were found to differ markedly in feeding habits and in trophic morphology. Examples include several triggerfishes (Turingan *et al.,* 1995; Durie and Turingan, 2001), a sparid (Cutwa and Turingan, 2000), and a haemulid (Turingan and Roth, 2001). In some cases, different populations appear to emphasize the use of different prey capture modes, as in the case of *Xanthichtys ringens,* which feeds predominantly on zooplankton at Mona Island, but grazes on benthic sponges in Puerto Rico (Turingan *et al.,* 1995). Among populations variation in trophic morphology can be extensive, but in none of these cases is it clear whether the differences observed are the result of developmental plasticity or genetic variation among the populations. We should note that although genetic polymorphisms are thought to be common in the temperate lake systems, an exclusive role of phenotypic plasticity has only been experimentally refuted in a few cases (Schluter and McPhail, 1993; Smith and Skulason, 1996). Adaptive developmental plasticity may be expected in reef fishes, and in marine fishes in general, because offspring may typically recruit away from their natal reefs, to locations where prey availability and community structure can differ considerably from the habitat of their parents. This uncertainty in the environment of the offspring may lead to some adaptive flexibility in the development of the phenotype.

Other issues concerning intraspecific variation in reef fishes remain unexplored. Are trophically generalized species sometimes composed of populations of specialized individuals? Do the complex life histories of labrids, serranids, and other lineages result in sex-specific patterns of prey use? What are the patterns of natural selection on reef fish feeding mechanisms, and how do they vary across broad biogeographic ranges? These and other questions await future researchers of reef fish ecomorphology.

F. Other Areas of Progress in Reef Fish Ecomorphology

In this chapter we have focused on the functional morphology of prey capture and prey processing in juvenile and adult reef fishes, but there are a number of related areas in which an ecomorphological framework has also proved insightful. Here, we briefly mention several and indicate some potential areas of future research.

Work on the ecomorphology of locomotion has shown patterns of association between habitat use and functional design of the swimming apparatus in reef fishes. Like most dominant reef fish groups, labrids swim predominantly by use of their pectoral fins. However, within the family there is diversity in the mechanical mechanisms that are used by labrids to generate thrust with their fins, with extremes being represented by either a paddling mechanism or a general flapping behavior (Westneat, 1996; Walker and Westneat, 2000). Theoretical results suggest that a paddling mechanism is best suited to a rounded fin morphology, whereas effectiveness in the flapping behavior is maximized by an elongate, high-aspect-ratio fin (Walker and Westneat, 2000). Furthermore, the paddling behavior is thought to be most efficient at slow swimming speeds, and the flapping behavior to be most efficient at high swimming speeds (Vogel, 1994; Walker and Westneat, 2000). Laboratory observations in flow tank swimming trials with four wrasse species indicate that swimming speed is positively correlated with pectoral fin aspect ratio. Field data on 41 labrid species on the Great Barrier Reef further support this pattern, because swimming speeds of undisturbed fishes on the reef were positively correlated with pectoral fin aspect ratio (Wainwright *et al.,* in press). Fin shape, and hence swimming mechanism and performance, are also correlated with patterns of habitat use in labrids. A strong pattern was seen within reef locations, and across the shelf of the Great Barrier Reef, in which shallow, high-energy, high-water-flow areas were dominated by labrids with high-aspect-ratio fins (Bellwood and Wainwright, 2001; Fulton *et al.,* 2001).

Gut morphology is extremely diverse in reef fishes and may be strongly correlated with diet (Motta, 1988; Horn, 1989). Ecomorphological relationships between the anatomy of the digestive tract of reef fishes and the prey type have been known since the pioneering work of Al-Hussaini (1947), who showed that fishes that depend on poor-quality diets, such as herbivores and coral predators, tend to have longer intestines than do carnivores, whose diets are nutritionally denser. Comparisons across families have supported this observation, with comparable relationships between gut length and diet in the Labridae, Pomacentridae, and Chaetodontidae (Elliott and Bellwood, 2002). Although based on soft anatomy, the digestive tract is likely to be subject to a set of constraints and trade-offs comparable to those seen in the mechanical operations of the oral and pharyngeal jaws. Initial observations, for example, suggest that particle size of the ingesta may be strongly correlated with intestinal diameter (J. K. Elliott and D. R. Bellwood, unpublished data).

Although ecomorphology has primarily been applied to the study of juvenile and adult fishes, its application to the biology of the enigmatic larval stage of reef fishes has provided some particularly useful insights. Reef fish larvae are morphologically diverse and in many cases this diversity has functional consequences. In the past decade a number of studies have examined the relationship between larval reef fish morphology, performance, and ecology. This includes studies of sensory systems (McCormick and Shand, 1992; Job and Bellwood, 1996, 2000; Shand, 1997) and locomotor systems (Stobutzki and Bellwood, 1994, 1997, 1998; Fisher *et al.,* 2000; Bellwood and Fisher, 2001), and changes during the transition at settlement (McCormick, 1993). These studies have highlighted the fact that, contrary to earlier assumptions, reef fish larvae do not drift as passive particles in ocean currents, and like their reef-based counterparts, they have a rich and varied suite of behaviors and abilities that shape their ecology. Reef fish larvae include species that are capable of swimming for short periods at over 40 body lengths a second (Fisher *et al.,* 2000), or for longer periods, covering the equivalent of over 100 km without food or rest (Stobutzki and Bellwood, 1997). Studies of the visual capabilities of larval fishes indicate remarkable sensitivity to light and, although light attenuation limits the ability of larvae to feed at depth, some species are able to feed successfully at depths of 250 m in open ocean conditions (Job and Bellwood, 1996). Species differ considerably in light sensitivity and swimming ability and this may underlie considerable variation among fishes in the depth range over which they can feed and their potential to shape dispersal by active locomotion (Job and Bellwood, 2000). Further ecomorphological analyses are likely to yield additional surprises about the early life history stages of reef fishes.

G. Reef Fish Ecomorphology in Evolutionary Biology

Our ability to understand patterns of ecomorphological diversification in coral reef fish groups depends on our ability to infer the historical sequences of these radiation events. One of the most powerful approaches to gaining historical insights involves the use of phylogenetic hypotheses of the group in question to infer a transformation series of particular functional systems and to remove phylogenetic effects from comparative analyses of trait correlations, which form the basis of many ecomorphological studies.

A phylogenetic hypothesis of tetraodontiform fishes (puffers, triggerfishes, filefishes, boxfishes, and their relatives) (Winterbottom, 1974; Tyler, 1980) was used to infer the evolutionary history of the inflation mechanism found in pufferfishes (Wainwright and Turingan, 1997). A key finding in this study was that major elements of the inflation mechanism (the pattern of muscle activation used in inflation behavior) appeared to have evolved earlier than inflation behavior in tetraodontiform phylogeny. Changes to complex functional characters may be acquired gradually in the evolution of a group until some breakthrough form is achieved that has major implications for the subsequent evolution of the clade possessing the feature. Phylogenies provide a powerful tool for investigating the sequences of changes in functional systems that lead to major functional innovations (Stiassny and Jensen, 1987; Lauder, 1990).

Phylogenetic hypotheses have also provided insights into the correlation between the evolution of functional morphological traits and ecological traits. In an analysis of the cheiline labrids from the Indo-Pacific, Westneat (1995) tested the hypothesis that evolutionary changes in the four-bar linkage mechanics of the skull were associated with evolutionary changes in prey-use patterns. The work revealed a strong association between the two, such that historical changes in skull functional morphology were predictably associated with changes in feeding habits. Patterns of historical association between morphological evolution and feeding habits were also explored by Winterbottom and McLennan (1993) in a study of acanthuroid fishes. Use of the phylogeny allowed these authors to conclude that zooplanktivory had evolved several times within this group of reef fishes, rather than just once. Phylogenies likewise suggest that an excavating bite evolved more than once in parrot fishes (Bellwood, 1994; Bernardi *et al.*, 2000). Another major roll of phylogenetic hypotheses involves their use during interpretations of historical biogeogrpahic patterns (e.g., McMillan and Palumbi, 1995). This area was explored in Chapter 1.

V. Prospectus

Coral reef fishes have taught us a tremendous amount about how the functional design of organisms relates to their ecology, and promise many exciting new areas of inquiry in the future. At least two practical features have helped propel coral reef fishes into the forefront of ecomorphological research. First, coral reefs house the most species-rich vertebrate communities on Earth, and, thus, there is a tremendous amount of diversity to attract the attention of researchers. Second, perhaps no major aquatic system on Earth lends itself so well to observational work as do coral reefs, where divers can work comfortably while submerged in clear water. This combination of spectacular diversity and unparalleled accessibility has inspired about 40 years of research on the ecological consequences of the design of the reef fish feeding apparatus and a far larger body of published research based on underwater observations than is found for any other group of fishes. In this chapter we have attempted to summarize the most prominent findings of research in reef fish ecomorphology, but where is this field headed? What major questions will become the focus of future research and where might the greatest promise lie in this field? How will further refinements in our ability to infer feeding abilities of fishes from their morphology help us gain insights into deeper ecological and evolutionary questions?

To a large extent the fish faunas of the world's reefs are now described. We expect that one of the biggest developments that will impact ecomorphological research on coral reef fishes in the next 25 years is the exponentially increasing rate at which phylogenetic hypotheses are being developed for the world's organisms (Pagel, 1997). Modern molecular sequencing methods have improved drastically and largely underlie the rapid growth rate of systematic hypotheses. With the increase in the number of phylogenies will come the ability to test many historical hypotheses with greater rigor than has been possible in the past (Martins, 2000). Do labrids actually represent a radiation of unparalleled magnitude within reef fish communities? Do pomacentrids represent a radiation of species that involved relatively minor morphological evolution? If we can calibrate the amount of time that lineages have been in existence, it will be possible to use phylogenies as the basis for comparisons of the magnitude of functional evolution within major reef fish clades. We expect that in the future such questions will be addressed with some quantitative and statistical rigor. Ecomorphological methods already give us the ability to interpret morphology quantitatively in a mechanical or functional context.

Other major questions about the history of fish feeding ecomorphology may be approached initially without explicit phylogenetic information before being integrated into formal comparative studies. Are there mechanical hotspots in skull morphospace toward which reef fishes have repeatedly evolved, or does mechanical design of the skull show a continuous distribution in morphospace? Have reef fish assemblages with different histories (i.e., the Indo-Pacific vs. the Caribbean) evolved to occupy similar ecomorphological space? Reef fish lineages, because they are diverse and accessible, will continue to be a rich system for documenting patterns of diversification and functional evolution.

By focusing attention on the causal link between functional design, performance, and patterns of resource use, ecomorphology will continue to take a prominent position in our attempts to understand not just the remarkable number of fish species on coral reefs, but also the implications of this diversity of form for ecological issues ranging from population and local community structure up to biogeographic patterns and species distributions. One key to understanding how so many species coexist on reefs is to recognize how functional design limits patterns of prey use in species, and thus permits species to partition the resource base. It remains to be seen how important this process is in structuring reef fish communities. One of the obstacles to approaching the issue is the magnitude of the diversity. It has been difficult to characterize the pairwise interactions between so many potentially interacting species and combine this information into a coherent picture of these communities. One approach to this that has yet to be developed would be to use an ecomorphological framework and assume that similarity in functional morphological traits implies similarity in feeding ability and ecological role. Such an approach obviously involves major assumptions about how morphology and patterns of resource use map onto one another, but our understanding of feeding biomechanics is such that it is possible now to infer general trends in feeding ability from anatomy. Carefully selected morphological traits could be used as surrogates for species-specific feeding abilities, and thus related to detailed habitat distribution data to address questions concerning whether taxa with similar functional abilities tend to be negatively associated with each other in microhabitat use, whether reef zones typically have communities of fishes that occupy a similar range of ecomorphs, and whether taxa with only certain trophic abilities are able to make use of certain microhabitats.

Although reef fishes have been major contributors to phylogenetically based studies of evolution, one area that has received remarkably little attention is speciation in reef fishes. Considerable insights have been gained into speciation in several freshwater fish systems, including cichlids in Central America and Africa (Markert *et al.,* 1999; Wilson *et al.,* 2000), and the low-diversity lakes of north-temperate systems (Robinson *et al.,* 2000; Rundle *et al.,* 2000). Coral reef fishes, with their planktonic larvae that offer the potential for long-distance dispersal, and their exceptionally high species richness, offer some major contrasts with these freshwater systems. The north-temperate lakes are extremely low diversity (sometimes involving only one or two species), and in general, freshwater lake systems are more prone to spatial segregation of populations, because the lakes are separated and may remain so in periods between glaciations. How does fish speciation occur on coral reefs? Are species typically generated in geographically and reproductively isolated locations before spreading out across wider geographic areas? Or, can speciation occur at the center of species richness, driven by some other means of premating isolation? The presence of endemics in peripheral, isolated areas such as Hawaii suggests that areas like this can be important generators of species. But is this the major mode of speciation in coral reef fishes? And what is the influence of trophic adaptation? It will eventually be possible to develop a clear idea about how most reef fish species are formed and specifically whether trophic specialization and the diversity of feeding ecomorphology are key players in the process or instead represent the consequences of secondary contact of species spread from distant areas of origination.

Ecomorphology is all about the integration of functional morphology and ecology. It is about understanding how organisms get to be built the way they are built, and the consequences of their design for patterns of resource use, interactions with other species, and patterns of evolution. The groundwork has been laid in coral reef fishes. Our understanding of the major design features of fish feeding systems is solid, although not entirely complete. The new generation of reef fish ecomorphologists will be able to use this foundation to examine the role of trophic biology in structuring communities, the evolution of fish feeding biomechanics, and the roll of trophic ecomorphology in reef fish speciation. These are indeed exciting times.

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