CHAPTER 2

Functional Morphology of Butterflyfishes

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INTRODUCTION

Butterflyfishes (family Chaetodontidae) have historically been grouped with several deep-bodied reef fish families into the squamipinnes, or *'scaly-finned'* fishes (Mok and Shen, 1982; Gosline, 1985; Blum, 1988; Tyler et al., 1989). However, it is presently uncertain whether this grouping is monophyletic (Konow et al., 2008). Apart from butterflyfishes (128 species worldwide; Fig. 2.1), and their purported sister-family (Burgess, 1974), the angelfish, family Pomacanthidae (86 species), the squamipinnes are comprised of acanthuroid surgeonfishes (Acanthuridae), rabbitfishes (Siganidae) and the Moorish Idol (Zanclidae), the Kyphosidae (incl. microcanthids and girellids) and the fairly species-depauperate Ephippidae, Drepanidae and Scatophagidae (Tyler et al., 1989; Froese and Pauly, 2012).
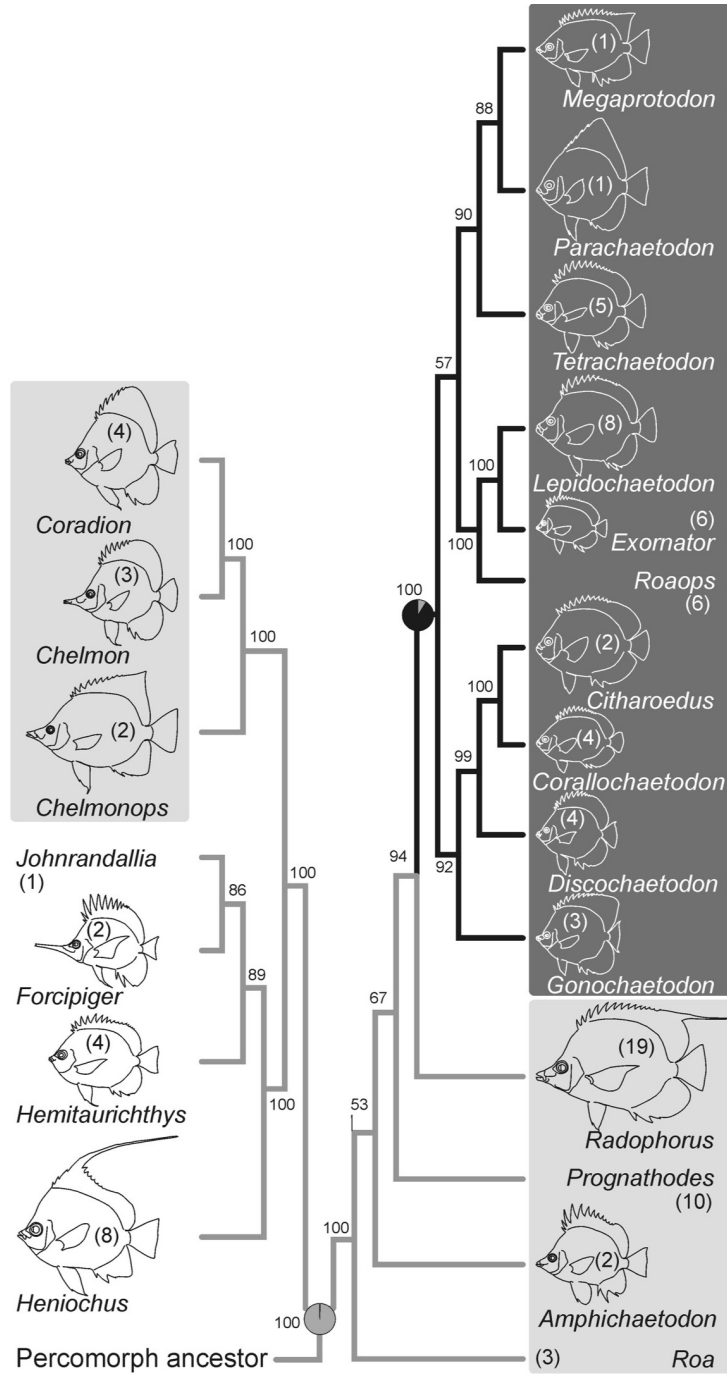
Butterflyfish morphology has, in the past decades, primarily been investigated for the purpose of systematic classification (Mok and Shen, 1982; Smith et al., 2003; Blum, 1988) (Fig. 2.1). Until very recently (Littlewood et al., 2004; Hsu et al., 2007; Fessler and Westneat, 2007), phylogenetic

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research on the family based on molecular data also lagged behind most of the other squamipinnes families (c.f. Tang et al., 1999; Clements et al., 2003; Bellwood et al., 2004). The basic lack of information regarding morphology and its evolution is puzzling, considering that this family has attained iconic status as coral reef fishes and marine ornamentals. This status has been assigned primarily based upon the key role of butterflyfishes as predators on stony (scleractinian) corals. While ecological studies of this derived feeding guild exist (for example Irons, 1989; Tricas, 1989; Alwany et al., 2003; Pratchett, 2005; Berumen and Pratchett, 2007), these tended to focus on regional patterns, and only very recently attempted to understand how butterflyfish accomplish such evolutionarily novel foraging-related tasks (Motta, 1985, 1989; Ferry-Graham et al., 2001a, b; Konow et al., 2008). Currently, the information relating morphology to ecology concerns a highly specialised pelagic *Thorlichthyes* larval morphology, the derived laterophysic canal structures involved in balance-maintenance and sound production (i.e., a joint locomotory and behavioural specialisation), the functional morphology of the locomotory fin apparatus itself, and a range of feeding specialisations based on novel origins of joints within the feeding apparatus.

Fig. 2.1 Interrelationships of the Chaetodontidae, reconstructed using data from Blum (1988), Ferry-Graham et al. (2001b), and Smith et al. (2003), which was modified using the super-tree technique Matrix-recombination with Parsimony (MRP). Fish icons are scaled to the mean of reported maximum body-sizes for those particular subgenera, the species number of which is given in brackets on the fish body. Branch-lengths are chosen for clarity of presentation only and numbers at branch nodes are bootstrap-values from the MRP analysis. Note how butterflyfishes naturally divide into two groups of banner and forceps fishes (left), and butterflyfishes (right). The following ecomechanic traits were mapped and optimised onto the tree in the Mesquite phylogenetics package module under maximum parsimony: Character-states for intramandibular joint (IMJ) possession are optimised to branches using black for presence and grey for absence of the joint. For the IMJ, the likelihood of the ancestral state (presumably the lack of an IMJ) was reconstructed as posterior probabilities and is reported using pie-charts at relevant nodes leading to the cladogenesis of the genus *Chaetodon.* Pie-chart shading corresponds with the branch optimising colour-scheme, and the second most probable state is indicated when its probability is greater than 0.05. Feeding mode is mapped onto the major clades using shaded boxes to delineate obligate and facultative coral-biting taxa (black), those utilising both invertebrate-picking and ram-suction feeding guilds (light grey) and pure ram-suction feeders (white). Note that the combination of obligate biting strategies and possession of an IMJ coincides in the genus *Chaetodon* only. Moreover, butterflyfish jaw-lengths are typically intermediary to long in taxa that prioritise the ram-feeding end of the feeding mode continuum (see text). The exception to this rule is members of the bannerfish clade (i.e., *Heniochus* and *Hemitaurichthys*), which commonly engage in suction-feeding planktivory. The biting *Chaetodon* butterflyfishes are, apart from their IMJ, characterised by having relatively short jaws that are mechanically efficient for biting. However, standing out are the forcepsfishes (*Chelmon* and *Chelmonops*) in their possession of ram-suction feeder traits (long jaws, suspensorial flexion; Fig. 2.4), while almost exclusively feeding using biting. For details on tree-construction, see Konow et al. (2008), after which this figure was modified.

Given the authors' primary research specialisations and the prevalent emphasis on trophic ecology and dietary specialisations of these fishes in the present volume, this chapter will treat the three latter areas of hearing and sound production, locomotion, and feeding specialisations. In this chapter, we will take a functional morphological approach, specifically to summarise our present understanding of butterflyfish ecomechanics. We define ecomechanics as the link between organismal functional morphology (i.e., a biomechanical apparatus such as the fins or the jaws), and ecological performance, being the relative capacity and capability of the organism to use said apparatus to complete vital everyday tasks (in these cases, swimming and feeding).

Most of the recent studies of swimming and feeding have involved strong experimental components and have used a comparative approach, and these studies can therefore be used to evaluate the relative advantage of certain structures over others in performing ecological tasks. Earlier swimming functional morphology studies (Webb, 1982; Gerstner, 1999a, b; Blake, 2004) proposed that species group into guilds depending on their swimming mode. More recently, Fulton (2007) measured the swimming performance of fishes empirically, in a flow tank, and conducted habitat-based validations of swimming performance. This approach served to identify characteristics of the fin apparatus that potentially explained prominent interspecific differences in swimming capability, which was then verified on the coral reef (Fulton, 2007). Similarly, in early analyses of feeding functional morphology, Motta (1982–1989) identified morphological characters within the feeding apparatus that differed across taxa and appeared to characterise different feeding guilds. Kinematics of the jaw apparatus were only measured more recently, using motion analyses of high speed video, which served to validate some functional hypotheses but refute others (Ferry-Graham et al., 2001a, b; Konow et al., 2008; but see Motta, 1985). Thus, while the earlier swimming and feeding work provided important morphological knowledge as a baseline, none of them were particularly informative in terms of identifying a link between morphology and ecology (i.e., eco-morphology; Motta, 1988; Wainwright, 1991). A major reason for this lack of early success could be that several salient ecomorphological relationships were only identified in later analyses, when a more integrative experimental approach could be incorporated.

Where comparative studies are lacking, we cannot place too much weight on inferred performance consequences. However, we can look to extensive personal observations, including video documentation, from reefs and aquaria in order to make inference about organismal function. In the following, we are careful to place those inferences within an appropriate cautionary framework, adhering to the adage that one cannot infer function without directly measuring it (Motta, 1988; Wainwright, 1991).

THE MECHANOSENSORY SYSTEM

Butterflyfish have been well studied in the context of mating systems and the associated behavioural ecology of mating (e.g., Yabuta and Berumen, Chapter 8). Recently, we have begun to understand the unique functional morphological underpinnings of these behaviours. This work falls into two general areas: the study of chaetodontid hearing and the associated laterophysic canal system, and the concomitant study of chaetodontid sound production.

The Laterophysic System

The laterophysic system is unique to chaetodontids and consists of a pair of projections, on the right and left sides of the body, extending from the swim bladder to the posterior region of the neurocranium. These projections facilitate a connection with the lateral line canal located within the supracleithrum (Fig. 2.2A), although the specifics of the structure varies among species (Webb and Smith, 2000; Smith et al., 2003; Webb et al., 2006). This connection was named the laterophysic connection due to its morphological similarly to otophysic connections (Webb, 1998a; Webb and Smith, 2000); which are connections found in other fishes (i.e., otophysans) that have specialised hearing (reviewed in Webb et al., 2006).

It is hypothesised that the function of the laterophysic connection is to increase the sensitivity of the accoustico-lateralis system, the inner ear plus the lateral line, to sound pressures. Receiving sound is typically the role of the pars inferior, or the ventral portion of the inner ear. The inner ear is composed of three semi-circular canals projecting in the three dimensions. The ventral portions of the inner ear contain three chambers that each house a dense crystalline structure; these are collectively called otoliths. These otoliths rest on a bed of sensory hair cells that have an afferent connection directly to the nervous system. As a fish is nearly the same density as water, sound waves tend to pass through the fish. The dense otoliths, however, vibrate when sound waves impact them. These vibrations set the hair cells in motion and thus the sound information is transferred to the brain for processing. The lateral line also contains sensory hair cells, also referred to as lateral line neuromasts, which are similar in structure and function to the inner ear hair cells (although there are both afferent and efferent neuronal connections). The lateral line is typically used for receiving far field sound; low pressure waves that transmit at lower frequencies and over longer distances (Kalmijn, 1989).

The swim bladder contains air and is therefore also of a different density than the fish, and the surrounding medium. It, therefore, can also act as a receiver of sound waves being transmitted through the water. By extending
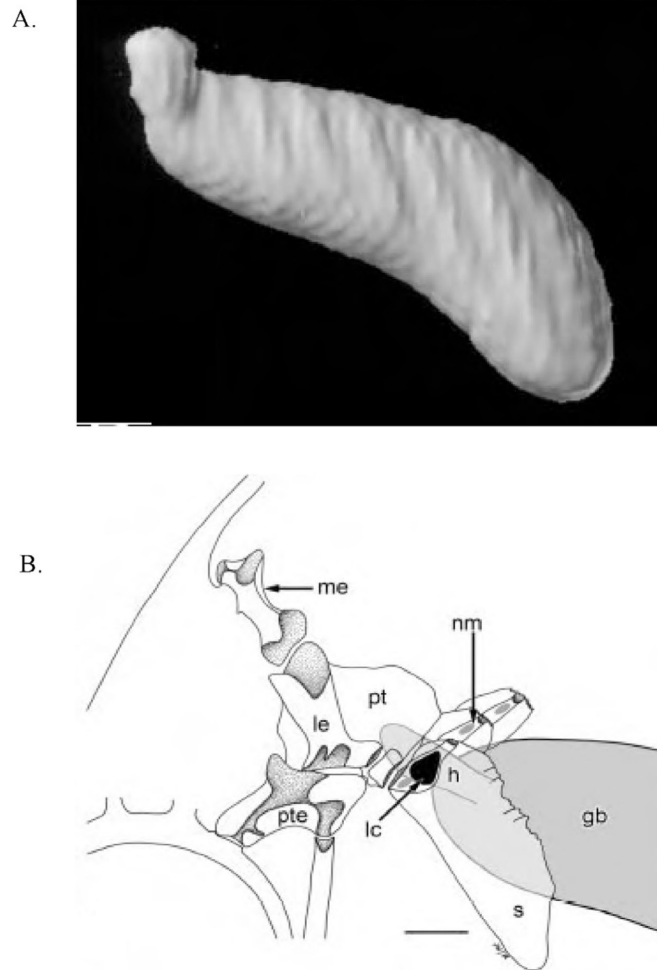
A.

B.

Fig. 2.2 Laterophysic plate (= schmoo CT and cranial anatomy). 3D CT reconstruction of the volume of the swim bladder and swim bladder horns in *Chaetodon punctofasciatus* **(A)** periodic indentations in lateral surface correspond to ribs, and **(B)** camera lucida drawing of skeletal elements posterior to the orbit at the posterior margin of the skull in *Chaetodon octofasciatus*. gb, swim bladder; h, horn; le, lateral extrascapular; me, medial extrascapular; nm, neuromast; pt, posttemporal; pte, pterotic; s, supracleithrum. Scale bars 1 mm. Modified after Webb et al. (2006) with permission of author.

projections towards the sensory apparatus of the accoustico-lateralis system, the sound waves intercepted by the swim bladder are transmitted to the nervous system for processing (Schellart and Popper, 1992). Variants on the nature of the connection between the swim bladder horns and the lateral line in species of *Chaetodon* are thought to be directly related to the degree of enhancement of sound reception.

The variations range from a direct to an indirect connection between the projections of the swim bladder and the lateral line (Fig. 2.2B). A direct connection consists of layers of tissue that act as a tympanic membrane resting between the fluid filled lateral line and the air-filled swim bladder. Thus, sound waves received by the swim-bladder are putatively converted to fluid flow in the lateral line system, where they can be processed by the nervous system (Webb et al., 2006). This tympanum may be well developed, consisting of up to 4 layers of mucoid tissue, or less strongly developed and formed of only two layers of non-mucoid tissue. Generally, if the tympanic connection is less developed, the swim bladder is subdivided into two sections anteriorly and posteriorly. The projections of the swim bladder tend to be relatively long to facilitate this connection, though they vary in width. Indirect laterophysic connections contain a physical space between the swim bladder projections and the lateral line, ranging from 0.2 mm to 1 mm. Mucoid tissue may or may not be present, and the projections of the swim bladder may be long or short.

Sound Production

The presence of such elaborations for sound reception led researchers to speculate that sound production might also be present in species of *Chaetodon*. Indeed, a single series of field experiments verified that sounds were produced in a variety of social contexts, including territorial displays and alert calls (Tricas et al., 2006), and this study is summarised here. Sounds were evoked by placing a single fish within the territory of a pair of *Chaetodonmulticinctus.* This species is monogamous, has strong site fidelity, and is aggressive. It is also known that visual signals are fundamentally important in this species as a means of communication on the reef. From a functional morphological perspective, the production of these sounds is interesting because they assign a function to a particular mechanical movement.

The sounds recorded from this species can be grouped into motor-based and acoustic-based sounds (Tricas et al., 2006). Four motor-based sounds were recorded that were associated with actual movement of portions of the body; the tail-slap, the jump, the pelvic-fin flip, and the dorsal-anal fin erect (Fig. 2.3). Each of these movements, produced by resident fishes in this context, presumably sends a visual signal to conspecifics. However, the motion of the body also produced a recordable sound within the hearing range of chaetodontid fishes. These were low frequency, hydrodynamic sounds associated largely with the flow of water induced by the fin movement. The sounds were typically between 50 and 200 Hz peak frequency, and most lasted from 20–150 milliseconds in duration. The jump, in particular, was associated with a pulse train of four to eight pulses,
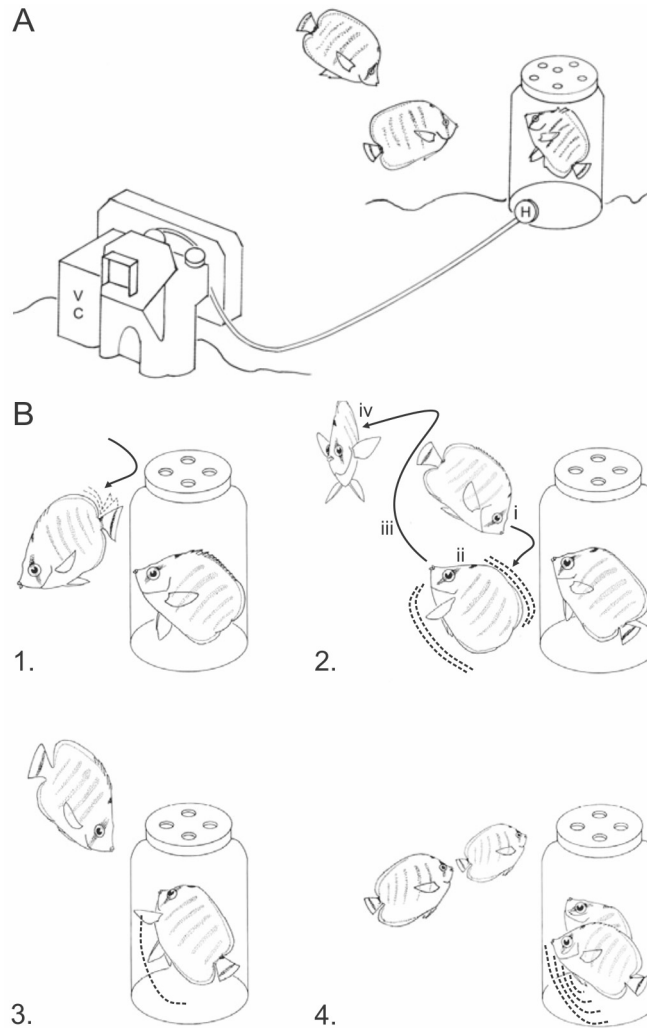
Fig. 2.3 Sound production plate. Diagram of experimental trials to elicit sound production **(A)**, and **(B)** behaviours associated with recorded sounds in the multi-banded butterflyfish, *Chaetodon multicinctus*. Broken lines indicate sound production. (1) The tail slap behaviour, exhibited after escalated displays and aggression by territorial residents towards bottled intruders, produces both a low frequency hydrodynamic pulse and a brief broadband acoustic click. (2) The jump behaviour is displayed by resident fish and involves four parts: 1) the approach and face, 2) and rapid turn (produces a low frequency hydrodynamic pulse followed by several rapid acoustic pulses), 3) short swimming ascent, and 4) intense lateral display. (3) The pelvic fin flick behaviour, produced by both residents and bottled intruders, involves the extension of the pelvic fins and a single acoustic pulse. (4) The grunt train sound, produced only by bottled fish when approached by territory residents; no body movements were observed during the production of this sound. After Tricas et al. (2006) with permission of author.

and was of slightly higher peak frequency (400 Hz). The individual pulse lasted only about 20 ms, but a train could take up to about 350 ms.

An acoustic "click" sound was recorded from resident fish during tail slaps (Tricas et al., 2006). This was a high-frequency sound, over 3000 Hz, of short duration, 10 ms. A lower frequency grunt train was also recorded from intruder fish when fish were approached, during direct confrontations, and during displays. The peak frequency of grunt trains was about 150 Hz, and these consisted of about 20 pulses per train, lasting over 5 s. Each individual pulse was fairly long, lasting about 40 ms.

The actual mechanism of sound production remains unknown, but Tricas et al. (2006) offer some hypotheses. The grunts, for example, were produced when no visible external movement was recorded, thusly they may be produced by structures inside the body, such as the swim bladder and modifications thereof. The high-frequency of the click suggests stridulation, but cavitation of water, as is seen in many shrimp species (e.g., Patek et al., 2007), cannot be eliminated. The pulse-trains associated with jumps were probably generated by the visible vibrations of the entire body during the sequence of behaviours associated with the jump. The pelvic and dorsal-anal fin behaviours are likely the result of skeletal anatomy and contact between bony structures in some fashion. All of these hypotheses, however, have yet to be tested.

BUTTERFLYFISH LOCOMOTORY MORPHOLOGY

The emergence of benthic feeding habits among coral reef fishes led to a need for navigating in close proximity with a complex, potentially noxious and abrasive reefal substratum. Therefore, fine-scale maneuverability and rapid braking became a priority. Butterflyfishes appear to be exceptional swimming performers in this capacity in that they can hover in abnormal postures close to the substratum and perform precise and repetitive feeding strikes within a microhabitat—area restricted to the circumference of a single scleractinian zooid or polyp. Below, we review the surprisingly limited existing evidence that either directly or indirectly investigated this type of scenario in an ecomechanical context.

Girdle Rotation and Fine-scale Maneuverability

Among spiny-rayed fishes (the acanthopterygians), the pelvic fin-bearing girdle has, over the course of evolution, gradually been rotated anteriorly (Fig. 2.4A) and moved into a position immediately ventral to the pectoral fin-bearing girdle (Webb, 1982; Blake, 2004). This rotation is pronounced among both labroid and squamipinnes taxa and appears to reach its extreme
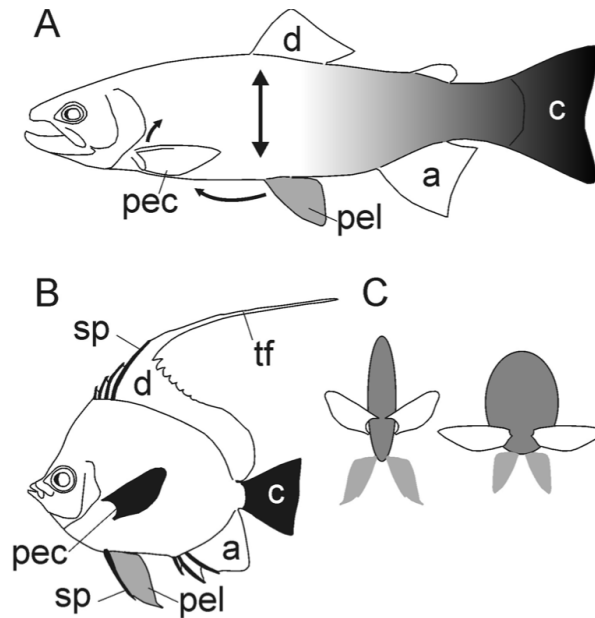
Fig. 2.4 Fin placement and fin use during swimming in **(A)** basal teleost fishes, exemplified by a protacanthopterygian trout (*Salmo*), and **(B)** in derived acanthomorph reef fishes, exemplified by a bannerfish (*Heniochus*). Abbreviations: a, anal fin; c, caudal (tail) fin; d, dorsal fin; pec, pectoral fin; pel, pelvic fin; sp, spine; tf, training filament. **(A)** The trout is a characteristic BCF (body-caudal fin) swimmer, involving undulations of the entire caudal body region in addition to the caudal fin itself, as illustrated by the shaded body-area. **(B)** In contrast, the bannerfish uses a combination of lift-based pectoral fin and undulatory caudal fin propulsion, as illustrated by the fins in black. Users of this Chaetodontiform swimming mode also have several modifications of the fin apparatus, including rotation of the pectoral and pelvic girdles (see curved arrows in **A**) to a constellation where the pelvic girdle is positioned directly ventral to the pectoral girdle **(B)**. Additional specialisations include trailing fin edge filaments and leading edge reinforcements by spiny rays. The typical deepening of the body in Chaetodontiform swimmers relative to BCF swimmers, as seen in the cross-sections in **(C)** is considered an adaptation towards a more stable body (keel-effect) and a paired-fin constellation that is more efficient for braking [Figure generated de-novo].

within chaetodontoid fishes, encompassing butterflyfishes and angelfishes (Fig. 2.4B). In these taxa, the pelvic fins are positioned directly ventral to, and even sometimes immediately anterior to the pectoral fins.

As a result, these two fin pairs, with an ancestral ventral placement, are brought into a novel constellation among bony fishes, yielding a combined fin surface area that permits efficient braking (Gerstner, 1999a). Furthermore, when this fin constellation is combined with a deepened body shape, as seen in the squamipinnes (Fig. 2.4C), fine-scale maneuverability is strongly enhanced (Gerstner, 1999b). A stiff body, as seen in chaetodontoids and most other squamipinnes, is a trait that theoretically adds to the optimisation of maneuverability during 'unsteady' swimming, *sensu* Webb (1982, 1984).

However, most predictions presented by early authors either lacked empirical evidence or were not supported by experimental data (Blake, 2004). Nevertheless, the work of Fulton (2007) supports this notion, as elaborated upon in the following section.

The Chaetodontiform Swimming Mode

Fish swimming modes are generally divided into undulatory and oscillatory mechanisms, of which typically only the undulatory modes are seen among reef fishes (Webb, 1998b; Blake, 2004). Undulatory modes can be classified along a gradient of fin-use modes ranging from drag-based and caudal-fin dominated, or sub-carangiform propulsion (Fig. 2.4A), named after trevallies and other carangid fishes, and anguilliform or eel-like propulsion relying on an elongated tail section (Webb, 1984). Meanwhile, at the opposite end of the fin-use continuum is lift-based, or labriform propulsion, named after wrasses and parrotfishes (f. Labridae), which typically use their pectoral fins almost exclusively in a "flapping" manner analogous to aerial flight to provide the means of steady swimming.

The general locomotory-mode among butterflyfishes is characterised by use of both the median and paired finds, and thus is often termed medial-paired fin locomotion (MPF) (Webb, 1984; Gerstner, 1999a, b; Blake, 2004). A series of characteristic body morphologies in animals using MPF propulsion were initially identified by Webb (1984). These included the pectoral fins being placed mid-lateral, the pelvic fins being placed ventrolateral, symmetrical and soft-rayed dorsal and anal fins, spine-reinforcements of fin leading edges and a short, deep (i.e., saucer-shaped), and laterally compressed body (Webb, 1984). All these traits in combination are almost exclusively observed among chaetodontoid fishes (Fig. 2.4B), thus making it appropriate to coin the associated swimming mode *chaetodontiform locomotion* (Webb, 1984; Webb and Weihs, 1986).

However, experimental evidence remained unavailable to determine whether chaetodontoid taxa equipped with these traits, indeed, used their fins differently than fishes swimming using alternative propulsive modes. It was only recently demonstrated empirically that chaetodontoids, and a very few other taxa, including some pomacenthrids (damselfishes) and nemipterids (threadfin breams), use a novel pairing of body and caudal fin (BCF) and MPF propulsion (Fulton, 2007). When examined empirically, the swimming speeds achieved by a range of butterflyfish species came close to matching those achieved by highly efficient labriform swimmers (Fulton, 2007). Also, butterflyfish field cruising speeds were maintained at a very high percentage of the maximum prolonged speeds achieved in flow-tank trials. By utilising drag-based caudal fin undulation in combination with lift-based pectoral fin rowing, chaetodontoid swimmers arrive at an effective

means of negotiating high-energy, wave-swept habitats while maintaining the maneuverability and braking capability required for effective close range negotiation of complex habitat topographies. The energetically and physically efficient propulsion-mode, paired with a fin constellation ideal for fine-scale maneuvering and braking, yield predators with intimately specialised locomotory capabilities for taking advantage of the novel and complex resource opportunities on the reef.

BUTTERFLYFISH FEEDING MECHANICS AND FUNCTIONAL MORPHOLOGY

It is difficult to think of a fish group with as diverse and varied feeding related morphology as the butterflyfishes (Fig. 2.5). Yet, there are only three major mechanisms of prey capture that are used by fishes (e.g., Liem, 1980), and chaetodontids are no exception to this rule: (1) "suction feeding" in which they expand the oral cavity, thus generating a pressure gradient that draws water and prey into the mouth, (2) "ram feeding" in which the prey remains stationary and the predator overtakes and engulfs the prey in the oral cavity, and (3) "dislodging" or "manipulation" in which the fish directly applies its jaws to the prey, removing it from the substratum with a scraping or biting action. As far as is known, all teleost fish prey capture events can be described by one, or a combination of these three behaviours (Motta, 1982; Ferry-Graham et al., 2001a, b; Konow et al., 2008).

Butterflyfishes typically have short, robust jaws (Fig. 2.1) that are used for biting corals and other attached prey, and even parasites off the bodies of marine macrofauna (Fig. 2.5B-E), as this is the most common feeding mode in the family (Harmelin-Vivien and Bouchon-Navaro, 1983; Sano, 1989). The jaw mechanics associated with this feeding mode have been described (Motta, 1985, 1989); as have the associated foraging behaviours (e.g., Harmelin-Vivien and Bouchon-Navaro, 1983; Tricas, 1989; Cox, 1994). Planktivory is also common across the family (Fig. 2.5A), and several short-jawed species have been studied in the context of how their jaws function to capture mid-water prey (Table 2.1; Motta, 1982, 1984b). While corallivorous species presumably have retained a robust jaw, and typically also strong teeth, from a biting ancestor (Motta, 1989), planktivorous species may secondarily have lost some of these features, while many species use modified behaviours to engage novel feeding guilds, such as cleaning behaviours (Table 2.1; Motta, 1988, 1989).

In all cases, the butterflyfish feeding mechanism by and large resembles the generalised perciform (perch-like fish) condition in terms of mechanical movements. And, there is a basic series of movements of the cranial region that characterises prey capture: 1) the ventral head region,
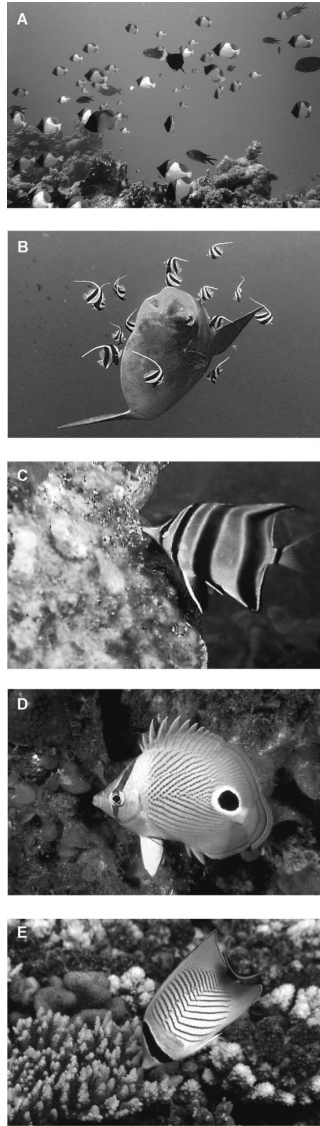
Fig. 2.5 Prey-capture diversity in the Chaetodontidae. **(A)** Facultative cleaning: *Heniochus acuminatus* cleaning Giant Sunfish at Nusa Lembogan, Indonesia; **(B)** Facultative planktivory: *Hemitaurichthys polylepis* plankton-feeding off Osprey Reef, Australia; **(C)** Invertivory: *Chelmonops curiosus* feeding on attached invertebrates at Rapid Bay Jetty, South Australia; **(D)** Soft-coral feeders: *Chaetodon capistratus* feeding on soft coral in the Caribbean. **(E)** Obligate hard-coral feeders: *Chaetodon trifascialis* feeding on scleractinian coral polyps (*Acropora hyacinthus*) in Moorea, French Polynesia [All photos have been released from copyright by the authors and editors].

Colour image of this figure appears in the colour plate section at the end of the book.

Table 2.1 Non-reefal feeding guilds in Chaetodontidae.

Species	Plankton feeding	Cleaning activity	Source
Chaetodonstriatus	+	+	Sazima and Sazima (2001)
Chaetodonlitus	+	+	Allen et al. (1989)
Chaetodonsmithi	+		Allen (1985)
Chaetodonkleinii	+		Hobson (1974)
Chaetodonmilliaris	+	+	Hobson (1991); Motta (1982); Ralston (1981)
Chaetodonsanctahelenae	+		Hourigan (1989)
Chaetodonsedentarius	+		Sazima and Sazima (2001)
Heniochusdipreutes	+	+	Konow et al. (2006)
Hemitaurichthyspolylepis	+		Allen et al. (1989)
Hemitaurichthys zoster	+		Allen et al. (1989)
Hemitaurichthysmultispinnis	+		Allen et al. (1989)
Hemitaurichthysthompsoni	+		Allen et al. (1989)
Johnrandallianigrirostris		+	Allen et al. (1989)
Forcipigerflavissimus		+	Ludwig (1984)

or hyoid (essentially the fish 'tongue'), is rapidly lowered concomitantly with elevation of the cranium. This causes expansion of the mouth and gill chambers, causing a negative pressure gradient between the inside and outside of the fish; 2) The lower jaw is then depressed to open the mouth, typically with the additional contribution of the upper jaw being pushed out, or protruded. This facilitates a release of the pressure gradient, pulling water and prey into the mouth (these traits may be less fully developed in primarily biting taxa); 3) the opercular region is expanded to move the water through the head and out the gill openings; while 4) the mouth is closed onto or around the prey.

However, there appear to be several examples within this clade of rather extreme modifications to the basic teleostean feeding mechanism for prey capture (Fig. 2.6). Below, we treat two major axes of variation in feeding specialisations, which appear to have evolved in separate major branches of the butterflyfish phylogeny, i.e., in two distinct butterflyfish lineages (Blum, 1988; Ferry-Graham et al., 2001b; Smith et al., 2003; Fessler and Westneat, 2007; Konow et al., 2008). Our first case-study concerns the evolution of suspensorial flexion and associated lower jaw protrusion in banner (*Heniochus*) and forcepsfishes (*Chelmon*, *Forcipiger*). These taxa catch their prey using ram-suction feeding, which is the basal predacious feeding mode among jawed fishes. The second case-study concerns the iconic corallivorous *Chaetodon* butterflyfishes. These fishes have abandoned ram-suction feeding in the water column, engaged the complex reef-matrix and adopted biting strategies, an entirely novel bony fish feeding mode, in
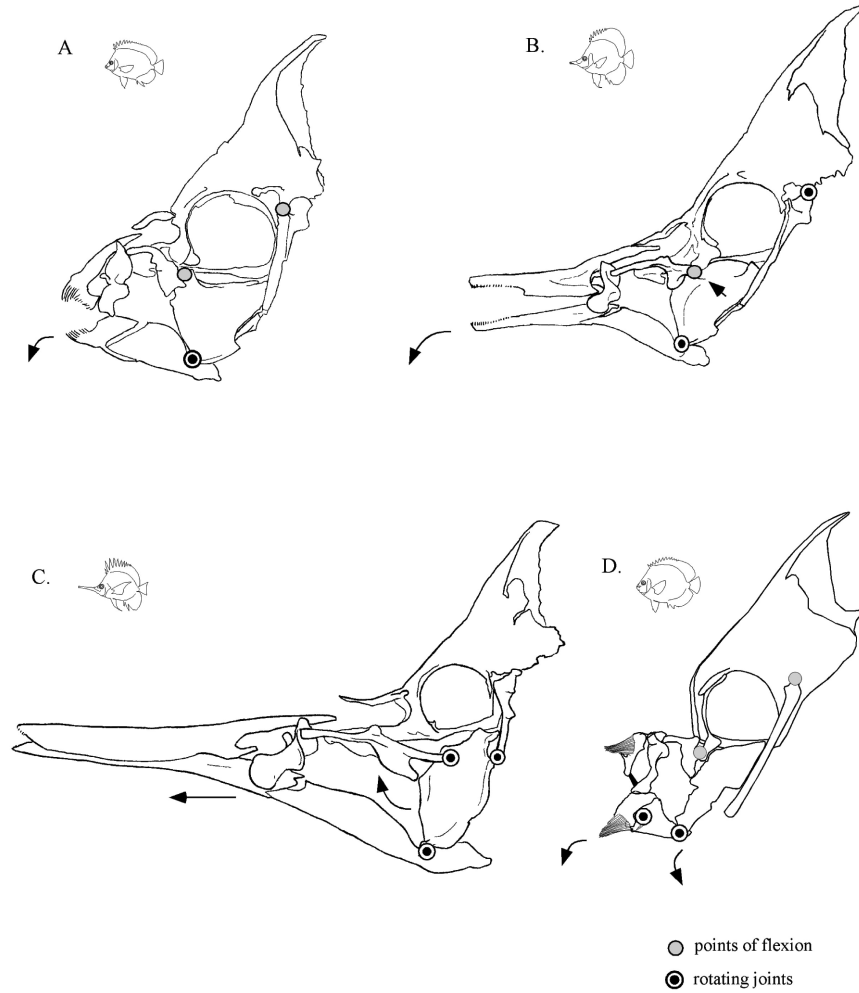
Fig. 2.6 Skull morphology in the Chaetodontidae. Specific aspects of the cranial anatomy of **(A)** *Chaetodon xanthurus* illustrating lower jaw motion with one joint at the quadrate, **(B)** *Chelmon rostratus* illustrating jaw motion when two joints are present, one within the suspensorium (note that the joint between the palatine and the quadrate complex is a sliding joint), and **(C)** *Forcipiger longirostris* illustrating jaw motion when three joints are present, two within the suspensorium. Points of flexion are indicated by grey points, rotating joints are indicated by bulls-eyes and the direction of movement is indicated by arrows. Scale bars are 1.0 cm. After Ferry-Graham et al. (2001a). **(D)** *Chaetodon ornatissimus* the position of joints and flexion resembles *C. xanthurus* **(A)**, yet, this and other members of the subgenera *Citharoedus* and *Corallochaetodon* have an extra, intramandibular joint in the position marked by the anterior-most bulls-eye, at the junction between the distal-most dentary and proximal-most articular bones forming the lower jaw [Fig. 2.6D was generated de novo].

order to feed on coral tissue. In the process, the biting butterflyfishes have also evolved novel joints in their feeding apparatus. We summarise how joints in novel regions of the skull promote different themes in butterflyfish ecomechanics.

Elongate Jaws, Jointed Heads

Several lineages of butterflyfishes have an exceptionally elongate upper jaw (premaxilla) and lower jaw (mandible), compared to their sibling species and to other fishes (see Figs. 2.1 and 2.6). In fact, elongate jaws are fairly widespread in the family Chaetodontidae, occurring in all members of the genera *Forcipiger, Chelmon*, and *Chelmonops*. Slightly elongate jaws are also found in some members of *Prognathodes* and even some *Chaetodon (Radophorus)*. Common names assigned within the general literature, such as "forceps fish" (e.g., Allen et al., 1998; Kuiter, 2002), suggest a function of the elongate jaws that is similar to how biting short jaws might work, except that the jaws are longer. Motta (1988) however noted that there is rotation of the suspensorium during feeding in *Forcipiger* species. The result of this rotation is that, during feeding, both the upper and lower jaws are protruded anteriorly. Indeed, detailed studies of the anatomy, and high-speed video analysis of several species capturing live prey, confirmed that the protrusion of the upper and lower jaws is achieved through rotation of the suspensorial elements via the addition of joints to the existing range of flexion-points within this mechanical unit (Ferry-Graham et al., 2001a, b).

Up to three distinct joints may be involved in lower jaw motion; two of which are novel and derived within the Chaetodontidae. Depending on the number of joints present, there are different consequences for the path of motion of the lower jaw. The cranial anatomy of *Chaetodonxanthurus* is drawn here (Fig. 2.6A) to demonstrate the condition found in short-jawed butterflyfishes, including genera such as *Prognathodes, Heniochus,* and *Johnrandallia.* This condition is analogous to that found in generalised perciforms. The suspensorial bones are fixed such that there is no rotation during jaw depression, and no movement of the jaw joint. The lower jaw rotates on the fixed quadrate and the jaw rotates ventrally through an arc (arrow).

Chelmonrostratus is drawn illustrating the intermediate modifications found in this species (Fig. 2.6B). The hyomandible moves with the quadrate complex, thus a posterior point of limited rotation is at the articulation of the hyomandible with the skull. The quadrate complex slides under the palatine due to the loose articulation between the two. The palatine itself is largely fixed, but slight movement of the quadrate relative to the palatine provides the freedom necessary for the quadrate to rotate a small amount on the lower jaw during depression, thus the lower jaw moves both anteriorly and ventrally.

Forcipiger longirostris is shown to illustrate the condition in both *Forcipiger* sp. There is a total of three joints; two novel joints in the suspensorium and one at the quadrate-articular jaw joint. Two suspensorial joints facilitate rotation relative to the fixed neurocranium (Fig. 2.6C). The rotating quadrate complex is shown pivoting on the hyomandible and the palatine. Anterior rotation of the quadrate facilitates anterior motion of the jaw joint, and therefore protrusion of the lower jaw. If rotation occurs simultaneously at the hyomandibular-metapterygoid joint and the quadrate-lower jaw joint, the lower jaw will follow an anterior course, with little dorsal or ventral motion. *F. flavissimus* exhibits a less mobile version of this model than *F. longirostris* due to the constraints outlined in the previous section.

The result of these changes in feeding apparatus functional morphology is that species with elongate jaws are afforded a feeding advantage in terms of absolute protrusion (Fig. 2.7). The addition of extra joints within the suspensorium provides for increased mobility and therefore increased
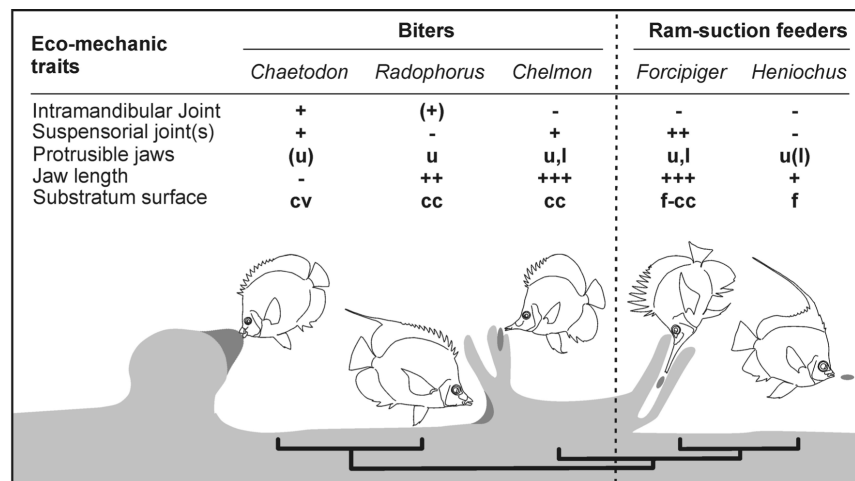

Eco-mechanic traits	Biters			Ram-suction feeders	
	Chaetodon	*Radophorus*	*Chelmon*	*Forcipiger*	*Heniochus*
Intramandibular Joint	+	(+)	-	-	-
Suspensorial joint(s)	+	-	+	++	-
Protrusible jaws	(u)	u	u,l	u,l	u(l)
Jaw length	-	++	+++	+++	+
Substratum surface	cv	cc	cc	f-cc	f

Fig. 2.7 Ecomechanic feeding guilds and functional specialisations in the Chaetodontidae. Diagram depicting previously studied feeding guilds and the functional specialisations that are thought to be underpinning these diverse guilds. Note that the diagram is segregated into exemplification of biters (L) and ram-suction feeders (R) with the phylogenetic interrelationships outlined at the bottom of the diagram for comparison (for phylogenetic interrelationships of the butterflyfishes, see also Fig. 2.1 and Bellwood and Pratchett–Chapter 1). The eco-mechanical traits listed over the fish images are important functional attributes that are treated in this chapter. These include the intramandibular joint (+, joint presence; (+), flexion presence; –, joint absence), which allows for increased gape expansion; (number of) novel joints in the suspensorium that enables protrusion of the lower jaw (l), in addition to the upper (u); variation in oral jaw length (–, minute; +, short; ++, intermediary; +++, long) and the prevalent shape of the microhabitat-types, being either concave (cc), convex (cv), utilisation of free-living prey (f) or combinations of the three. For each of the treated taxa, the unique combinations of traits characterise drastically differing feeding guilds that butterflyfishes utilise on reefs. Dark shading = prey [Figure generated de novo].

anteriorly-directed protrusion of the upper and lower jaws (Ferry-Graham et al., 2001a). The most modified of the long-jawed species, *F. longirostris*, has the advantage that it can initiate a strike significantly farther from the prey than any other species (Ferry-Graham et al., 2001b). This species covers the distance between predator and prey using protrusion of the jaws, or a *jaw-ram* based attack, as opposed to a body-ram based attack, where the predator "over-swims" the prey, or strong inertial suction, where the predator draws the prey into the mouth. The capacity for generation of suction in this species is no better, but interestingly, not less pronounced either, than in any other butterflyfish that has been studied to date (Ferry-Graham et al., 2001b). The long distance that the prey has to travel between the oral aperture and the esophagus certainly puts a premium on suction generation in order to prevent elusive prey-escape. Considering that the natural diet of *F. longirostris* almost exclusively consists of highly elusive calaenoid copepods (Ludwig, 1984; Motta, 1988; Ferry-Graham et al., 2001a), it is however highly interesting that the strike in this species is significantly slower than in the other *Forciper, Chelmon, Heniochus*, and planktivorous *Chaetodon* species studied (Ferry-Graham et al., 2001b).

Protrusion of the lower jaw is unusual, both among butterflyfishes and among teleosts in general. Most fishes protrude only the upper jaw (premaxilla) when they feed, and not nearly to the extent seen in *Forcipiger* (Motta, 1984a). The only other quantitative descriptions of anteriorly directed protrusion of the lower jaw, thus accomplishing 'whole-mouth' protrusion, are for the sling-jaw wrasse *Epibulus insidiator*, the cichlid *Petenia splendida* and pomacanthid angelfishes. *Epibulus* also possesses a novel joint within the suspensorium that facilitates anterior translation of the jaw joint and hence extensive jaw protrusion (Westneat and Wainwright, 1989; Westneat, 1990). *Petenia,* and to some degree the closely related *Caquetaia* species, have similarly evolved two joints within the suspensorium to facilitate rotation of the unit and anteriorly-directed protrusion of the lower jaw (Walzek and Wainwright, 2003). Finally, among angelfishes (f. Pomacanthidae), the purported sister group to the butterflyfishes (Burgess, 1974), a mechanism involving suspensorial rotation that facilitates lower jaw protrusion has also evolved (Konow and Bellwood, 2005).

Suspensorial Flexion at the Palatoethmoid Junction

Among the key-characters in previous morphology-based taxonomical analyses was palatoethmoid flexion or anterior loosening of the jaw apparatus (mandibular and palatine arch) bones from the suspensorium, with accompanying separation of the ligaments holding the palatine bone in place on the vomerine/ethmoid bones of the neurocranium. This trait was among the principal diagnostics that led to separation of the butterflyfishes

from the angelfishes (Burgess, 1974), and later to separate the coral-feeding *Chaetodon* butterflyfishes, which have palatoethmoid flexion, from their non-*Chaetodon* sister taxa (Blum, 1988; Ferry-Graham et al., 2001b; Smith et al., 2003; Littlewood et al., 2004). Separation and reduction of the otherwise tight and stout ligaments connecting the jaw apparatus with the skull in non-*Chaetodon* butterflyfishes enabled the jaws in *Chaetodon* butterflyfishes to move more freely during feeding and thus may be a key-trait in augmenting the capabilities of coral-feeding butterflyfishes, allowing them to move their jaws over an intricately shaped substratum (Figs. 2.7 and 2.8). Loosening of the suspensorium, however, would theoretically lead to a functional compromising of the rapid and precise jaw-protrusion movements involved with ram-suction feeding among banner and forcepsfishes (Ferry-Graham et al., 2001a, b; Konow et al., 2008).
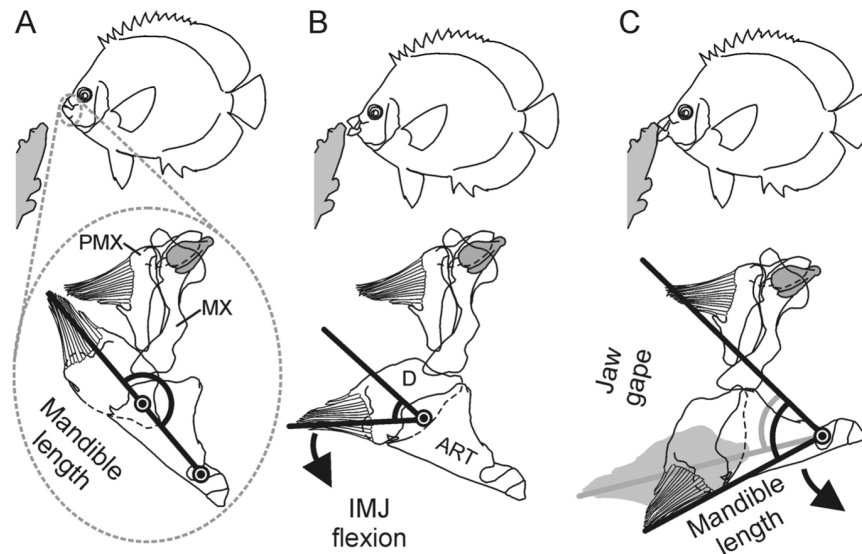

Fig. 2.8 Biomechanical function of the intramandibular joint in *Chaetodon*. Sequential illustrations of IMJ function during substratum scraping in *C. ornatissimus.* Diagrams were created by superimposing outlines of jaw structures onto video frames recorded at the time of bite onset **(A)**, maximum IMJ rotation (bulls-eye in **B)** and maximum lower jaw joint rotation (bulls-eye in **C)**, coinciding with prey-contact **(C** then returns to **A** in a scraping lunge, *sensu* Motta, 1988). The shaded outline of the dentary bone **(C)** indicates the hypothetical position of this bone in a lower jaw where intramandibular flexion is absent. By comparing the rotation angle in black with the hypothetical angle corresponding with a non-jointed lower jaw in grey, the augmented jaw-gape in an IMJ-bearing mandible is made evident. By comparing the lower leg lengths of the black and grey angles, the shortening of the mandible out-lever caused by rotation around the IMJ is illustrated. Abbreviations: PMX, premaxilla; MX, maxilla; D, dentary; ART, articular [Figure generated de novo].

Intramandibular Flexion and Biting Mechanics

When a fish adopts biting strategies, entirely novel challenges are placed on the feeding apparatus. Whereas suction feeding activity clearly benefits from an expansive skull, a biting, or prey-dislodging feeding mode, requires highly articulate jaws to excavate, scrape, or nip prey off its attachment. This gradient of highly robust excavators to relatively gracile nippers is found in its entirety among *Chaetodon* butterflyfishes.

Biologists commonly use engineering principles to obtain a more sophisticated understanding of how a muscle-skeleton system operates and moves to accomplish an ecological task (e.g., Westneat, 1990). From a biomechanical perspective, the function of a fish lower jaw system is described by a third-order lever mechanism in which velocity of opening and closing trades off with the ability to generate a forceful action. It is a reasonable assumption that when the feeding target is prey attached to the substratum, speed is typically not a priority. However, given the sturdiness of substratum attachment common to reef-dwelling invertebrates, a forceful jaw closure certainly could be important. In terms of speed-force relationships in a lower jaw system, a shorter lower jaw out-lever will, every thing else being equal, provide the fish with a greater force transmission advantage (Konow et al., 2008). This mechanical theorem provides at least a hypothetical explanation for the apparent evolutionary selection against the long jaws of many ram-suction feeding butterflyfishes in favour of the short, stout jaws that characterise *Chaetodon* butterflyfishes (Blum, 1988; Motta, 1988, 1989; Ferry-Graham et al., 2001a, b; Konow et al., 2008).

However, an alternative mechanism exists that is capable of dynamically altering the lower jaw out-lever length at a critical point in time when the upper and lower jaw tooth-bearing surfaces engage the substratum, and jaw muscles contract to retract the jaws, with the prey (Fig. 2.6D). This mechanism has only recently been comprehensively described and quantified (Konow et al., 2008), although its presence in a wide variety of coral reef fishes that bite their prey of the substratum has been anecdotally mentioned in publications spanning the past century (angelfishes, Gregory, 1933; sea-chubs, Vial and Ojeda, 1990; parrotfishes, Bellwood, 1994; surgeonfishes, Purcell and Bellwood, 1993). A novel intramandibular lower jaw joint (IMJ), placed between the dentary and articular of the mandible (lower jaw), allows the dentary tooth surfaces to rotate, or move dorso-ventrally relative to the articular bone (Konow and Bellwood, 2005). This extra joint doubles the degree-of-freedom in the lower jaw system, which means that the dentary toothed area can move in radically different ways compared to a generalised single-hinged mandible (Fig. 2.8).

One of the few known biting reef fish groups where the IMJ had not previously been identified was among the corallivorous butterflyfishes.

Using manipulations of dissected specimens and analyses of feeding movements in the lower jaw obtained from high-speed video recordings, it was observed that flexion at the junction between the distal dentary and proximal articular bones of the mandible (lower jaw) is a basal trait for *Chaetodon*. This flexion increases gradually from subgenus to subgenus towards *Corallochaetodon* and *Citharoedus* (Fig. 2.9), the *Chaetodon* crown taxa (Fig. 2.1). In these obligate corallivorous taxa; more pronounced flexion at the IMJ is seen than among any other known IMJ-bearing coral reef fish.

Via rotation of the IMJ, in concert with rotation in the generalised lower jaw articulation, coral-feeding *Chaetodon* butterflyfishes can not only shorten the lower jaw instantaneously (Fig. 2.8B-C), but also displace the lower jaw tooth rows further away from the upper jaw tooth rows than if the IMJ had not been present (Fig. 2.8C). This function, analogous to how
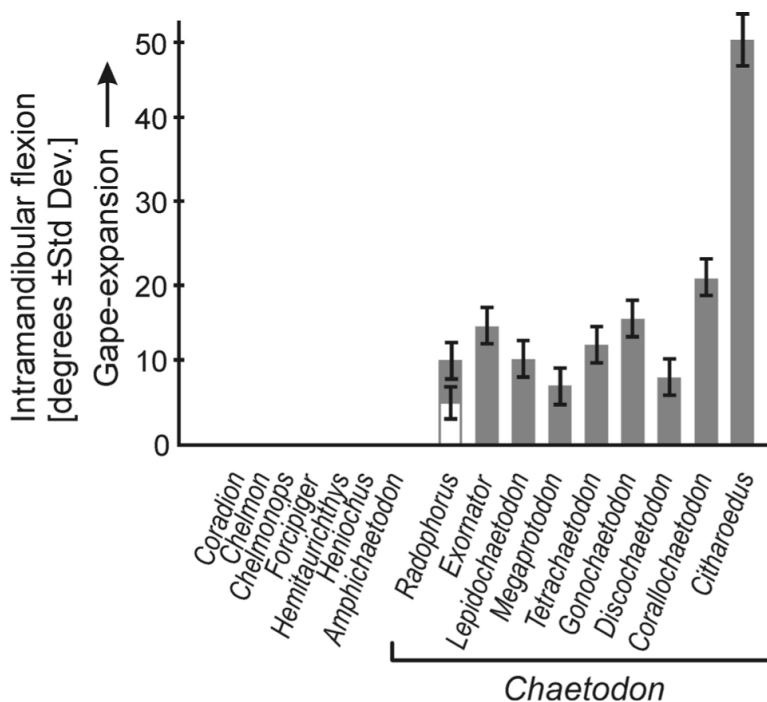

Fig. 2.9 Flexion in the Intramandibular joint during feeding in *Chaetodon*. The histogram depicts maximum rotation in the intramandibular joint (IMJ) for each nominal subgenus in the genus Chaetodon (*sensu* Blum, 1988; Ferry-Graham et al., 2001b; Smith et al., 2003; Konow et al., 2008). The measurements were obtained via motion analyses of high-speed video, measuring the angle in Fig. 2.8A, of live fish feeding in aquaria or in the wild, or of direct manipulations of the IMJ in sacrificed or anaesthetised specimens. For *Chaetodon* [*Radophorus*], the grey column represents *Chaetodon* [*Radophorus*] *melannotus*, an obligate corallivore, while the white column represents the mean IMJ rotation in other [*Radophorus*] taxa. Modified from Konow et al. (2008).

the IMJ functions in most acanthuroid taxa, allows the fish to produce a wider gape and thus contact a larger area of substratum per bite (Motta, 1989) while the lower jaw is shortened for maximised mechanical efficiency (Konow et al., 2008).

Interestingly, intramandibular flexion does not appear to be a basal trait for the butterflyfishes, as it is in both acanthuroid surgeonfishes and chaetodontoid angelfishes. Instead, the IMJ in butterflyfishes has evolved through a gradual increase in flexion (Fig. 2.9), seemingly in concert with the adoption of biting prey capture modes and corallivory (Fig. 2.1). Documentation of such a close evolutionary correlation between IMJ flexion and biting prey capture only existed for the labroid parrotfishes. During parrotfish evolution, an IMJ has evolved at least on two separate occasions (Bellwood, 1994; Streelman et al., 2002).

So far, the exact sequential relationship between the origin of specialised and obligate corallivory, and acquisition of the IMJ, remains unresolved. Because flexion within the lower jaw is not present in all butterflyfishes, and a true IMJ in fact only is found in a few *Chaetodon* crown taxa (Fig. 2.9), it is a reasonable assumption that the IMJ is a fairly recent functional innovation within the Chaetodontidae (Fig. 2.1). Confident determination of the time since cladogenesis of such traits requires analyses of morphological evolution that are ancestry-corrected. Such analyses can only be carried out when a chronogram has been acquired by time-calibration of existing phylogenetic data (e.g., Fessler and Westneat, 2007) with available fossil (Carnevale, 2006) and biogeographical evidence (Bellwood and Pratchett –Chapter 1). Such an approach would be an important first step towards answering several ecomorphology questions in butterflyfish evolutionary biology.

Teeth and Guts—Food Procurement and Throughput

In a series of publications, Motta (1984b, 1987, 1989) and co-workers (Sparks et al., 1990) documented butterflyfish oral jaw dentition and associated gross morphological and ultrastructural traits. These studies focused on the evolution of dentition and tooth types among butterflyfish species utilising divergent feeding guilds. In an evolutionary context, butterflyfish dentition is generally conservative, with all species studied to date having retained a tooth shape resembling the hooked component of Velcro™. However, a change in the attachment angle of the tooth to the jaw, and a significant reduction in tooth diameter (Fig. 2.10A), was observed when comparing ram-suction feeding omnivores with biting corallivores (Motta, 1984b, 1989). Moreover, the highest levels of iron-reinforced enamel were measured from the most obligate corallivores (Motta, 1987; Sparks et al., 1990). This result
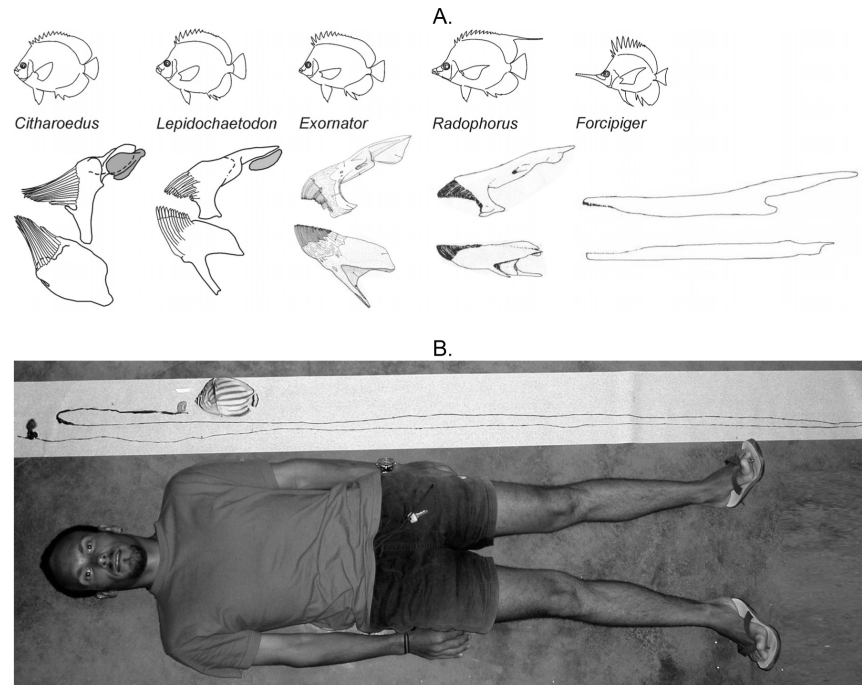
Fig. 2.10 (A) Tooth morphology and dentition diversity in the Chaetodontidae. Both tooth-bearing bony elements of the upper and lower jaws are relatively conserved within genus *Chaetodon* while dentition morphology ranges from slender villiform teeth in *Citharoedus ornatissimus*, via robust spatulate teeth in *Lepidochaetodon unimaculatus*, to diminutive brush-like teeth in *Exornator milliaris.* Basal to the genus *Chaetodon*, the length of upper and lower jaw bony elements increase, as seen in both *C. Radophorus*; in the clade comprised by *Chelmon* and *Chelmonops*, and in *Forcipiger.* Tooth morphology in the latter taxa ranges from the robust hook-like teeth in *Radophorus* to diminutive dentition in *Forcipiger*. While the teeth in *Chaetodon* taxa generally are arranged in multiple-tiered arrays in parallel with the tooth-bearing surface of the bony jaw elements, the teeth in intermediary and long-jawed taxa generally insert at a steeper angle. **(B)** Gut length in *Chaetodon* [*Citharoedus*] *ornatissimus*. Example of dramatic regional intraspecific differences in feeding-related morphology. This obligate corallivorous *C. ornatissimus* from Kaneohe Bay, Hawaii has a 4500 mm long alimentary tract, and the gut-body index averages 28 in Hawaii. On the outer Great Barrier Reef, Australia (Northern section) the same species has a much more modest 11 body lengths of alimentary tract. One author (N. K., TL= 176 cm) is depicted for scale.

matched similar findings from perciform lineages that encompass obligate substratum-biting taxa, namely acanthurids, balistoids and cichlids (Suga et al., 1992), and the obligately corallivorous tetraodontid boxfishes (Suga et al., 1989). Planktivorous taxa (Table 2.1) appear to trade-off prominent dentition in terms of distribution and tooth size with increased suction-feeding efficiency. In other words, oral jaws adorned with too many, or too prominent, teeth could potentially hinder the passage of prey into the oral

cavity during inertial suction feeding (Motta, 1982). However, even among obligate planktivores the Velcro™ hook-like dentition, which appears to be highly useful for efficient prey-handling, is still retained (Motta, 1984b, 1989).

Tight links between tooth morphology and diet of butterflyfishes, however, still remain largely obscure and this may to some extent be caused by intraspecific regional variation in variables associated with feeding guild specialisation. One of several characteristic examples is that of the tear drop butterflyfish *C. unimaculatus.* This butterflyfish species possesses the singularly most robust set of jaws found within all butterflyfishes. According to field census data collected by Motta (1988), this species typically uses its sturdy jaws for scraping scleractinian hard corals (*Montipora*) in Hawaii (Motta, 1988; Cox, 1994), and in Moorea (Pratchett, Chapter 6). However, at Lizard Island on the Northern Great Barrier Reef (GBR), this species utilisesan entirely different prey type, browsing on alcyonean soft corals (Wylie and Paul, 1989; Pratchett, 2005).

Similar intraspecific discrepancies are also encountered at the level of alimentary tract morphology (Fig. 2.10B). It has been suggested that *C. ornatissimus* (along with closely related species, *C. meyeri*) feed on coral mucous, rather than live coral tissues (Hobson, 1974; Reese, 1977). In the Hawaiian Islands, the obligate hard-coral feeder *C. ornatissimus* has an alimentary tract that averages 28 times the standard body length (Fig. 2.9; see also Motta, 1988). The gut contents of *C. ornatissimus* from Hawaii have also been shown to include a high proportion of calcium carbonate (coral skeleton). Meanwhile, guts from specimens off the Central GBR, Australia are almost 3-fold shorter (e.g., Berumen et al., 2011) and do not contain calcium carbonate. The extent to which these fishes actually feed on coral mucous versus coral tissue may vary geographically, and this in turn may be reflected in their gut morphology.

Alimentary tract morphology in butterflyfishes has primarily been investigated for systematic purposes (see Mok and Chen, 1982). However, recent studies (Elliot and Bellwood, 2003; Berumen et al., 2011) have established a strong relationship between gut length and trophic guild (i.e., corallivores, herbivores, carnivores) in butterflyfishes, and demonstrated that gut lengths of corallivorous butterflyfish exceed those seen in both pomacentrid and labrid corallivores (Elliott and Bellwood, 2003). The fact that corallivores often have even longer guts than herbivores has puzzled researchers, including Motta (1988), who found *C. trifascialis*, an obligate stony coral polyp picker with restricted flexion between the lower jaw bones, to have a short gut, analogous with carnivores. In contrast, *C. ornatissimus* (above) uses its scraping lunges of the IMJ-bearing lower jaw to browse on corals and has an extremely long gut. It has been postulated that this trend is related in some way to a distinct distribution of zooxanthellae and

symbiotic algae in separate regions of the coral tissue (i.e., mantle vs. zooids; see Motta, 1988). However, such trends in butterflyfish ecomechanics and trophic physiology have not been investigated.

FUTURE ECOMORPHOLOGY WORK

Intraspecific regional discrepancies like those described in the previous section can have the potential to strongly bias the results of future biogeographical region-spanning quantitative analyses. On the other hand, such tantalising, albeit sporadic, patterns of variation illustrate that a considerable wealth of evidence stands to be obtained via exhaustive functional morphological studies of butterflyfishes, analogous to the work of Motta (1982–1989), but expanded to a larger regional scale. Such undertakings will be required in order to confidently link morphology, function, behaviour and resource-use via ecomorphological analyses (e.g., Motta, 1988; Wainwright, 1991).

Similarly, jaw morphology data should be explored to test an ecomorphological hypothesis remaining after Motta's (1988) work; namely that key feeding morphological traits are linked to the feeding guild of butterflyfishes. In lieu of recently discovered functional novelties in the feeding apparatus of corallivorous butterflyfishes, post-dating his work, we should revisit Motta's (1988) hypothesis, by testing whether acquisition of novel joints in their feeding apparatus has resulted in eco-mechanically predictable changes to the associated jaw bones in butterflyfishes.

Given the relative ease with which a broad species-range of butterflyfishes with relatively large body-size can be obtained from the aquarium trade, it would be a worthy avenue of research to use electromyography for quantification of the shift in feeding muscle activity that may have accompanied the transition from ram-suction feeding to biting in butterflyfishes, especially in conjunction with IMJ acquisition. Given the prevalence of hypotheses from other fish groups that motor patterns are largely conserved (e.g., Wainwright, 1991), it would be interesting to know if a motor pattern shift accompanies the trophic shifts within the butterflyfish family, and if said changes to motor pattern are at all consistent with changes recorded from other fish families.

ACKNOWLEDGEMENTS

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