BIOLOGY OF PARROTFISHES

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Foreword

No one questions that parrotfishes have evolved from wrasses, and we show this close relationship by grouping them in the same suborder, Labroidei (Nelson, 2006). Parrotfishes were recognized as a distinct group by Aristotle who wrote, “All fishes are saw-toothed excepting the Scarus” and “of all fishes the so-called Scarus, or parrrot, is the only one known to chew the cud like a quadruped.” He was, of course, referring to the unique pharyngeal mill of scarids that grinds limestone fragments ingested with turf algae into a fine sand, and at the same time reducing the algae to more digestible fragments. Another unique scarid character that facilitates digestion is the very long intestine and the lack of a stomach. Parrotfishes have evolved to utilize a new resource of nutrition that is denied other herbivores. Once the herbivorous acanthurids, siganids, and pomacentrids have grazed algae to a low stubble, the scarid fishes still have a food resource. Surely this, the morphological differences, and being recognized as a family for 215 years support recognition as a family. The divers and fishermen readily distinguish parrotfishes from wrasses. If we tell them a parrotfish belongs in the wrasse family, they will think we are joking.

Jack Randall
Honolulu

Preface

Parrotfish are found on almost every coral reef in the world. It is this ubiquity, coupled with their brilliant colouration and fused 'beak-like' jaws, that have long attracted the attention of those looking and working on tropical reefs. Parrotfishes also have an incredibly diverse and complex array of reproductive and mating strategies that vary both among and within species. However, it is their unique feeding action that has stimulated much scientific endeavour. The morphological innovations of the oral jaws allow parrotfishes to bite through reef carbonates, while the pharyngeal jaws allow them to grind ingested carbonates into sand particles. These innovations not only enable parrotfishes to access nutritional resources that are largely unavailable to other fishes, but make them one of the most important groups of fishes within coral reef ecosystems. No other group of fishes is so inextricably linked to the structural dynamics of their ecosystem. Despite their importance to reef ecosystems, the threats to parrotfish are numerous and severe: from the global effects of ocean warming and acidification to the local effects of overfishing, pollution and habitat degradation.

The aim of this book is to synthesise what is currently known about the biology of parrotfishes, and to consider why are parrotfishes so important to the ecology of coral reefs? The book provides a series of reviews that are intended to provide a firm grounding in the understanding of the morphology, diet, demography, distribution, functional ecology, and current threats of this group. Importantly, it provides new insights into their diet and food processing ability, their life-histories, and the influence of habitat and environment on parrotfish populations, and also identifies emerging research topics and future directions. We hope this book will appeal to students, early-career and established researchers, alike, and will stimulate further investigation into this fascinating and unique group of fishes.

Lastly, we wish to thank to all of those who contributed to this book. We invited the international authorities on various aspects of the biology of parrotfishes to contribute to the book and were overwhelmed by their positive and enthusiastic responses. We would also like to thank David Bellwood for initiating our interest in parrotfishes, sharing his extensive knowledge, and guiding our scientific development. We sincerely thank the reviewers of each chapter of this book for their constructive and insightful comments. Finally, we are extremely grateful for the ongoing support from our families (especially Jess, Kiara, Caelen, and João) for their ongoing support that has enabled us to undertake important and interesting scientific pursuits.

Andrew Hoey (Townsville, Australia)
Roberta Bonaldo (Campinas, Brazil)

Contents

CHAPTER
1

Cranial Specializations of Parrotfishes, Genus *Scarus* (Scarinae, Labridae) for Scraping Reef Surfaces

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Introduction

Parrotfishes (family Labridae) forage by excavating or scraping surfaces of rocks and carbonate substrate that are encrusted with algae, bacterial mats, and detritus (Bellwood 1994, Choat et al. 2004, Rice and Westneat 2005), often leaving scratches and scars on the rock and coral surfaces (Cousteau 1952, Newell 1956, Clements and Bellwood 1988, Bellwood and Choat 1990, Bellwood 1994, 1996b). Ingested material is then ground into a slurry by their impressive pharyngeal jaws, that have been described to be "like a cement mixer in reverse" (Bellwood 1996b). Analysis of their gut contents indicates that they consume staggering quantities of inorganic residue (Randall 1967, Clements and Bellwood 1988, Bellwood 1995a, 1995b, Choat et al. 2002), accounting for over 70% of the gut volume in some cases (Gobalet 1980), and recent work has shown this residue is a major contributor to island-building sediments (Perry et al. 2015). The unique morphology of parrotfish feeding apparatus has facilitated the functional decoupling of the mandibular and pharyngeal jaws, with the mandibular jaws collecting the materials that are pulverized by the pharyngeal jaws.

Parrotfishes have distinctive modifications of their skulls associated with feeding on massive quantities of abrasive material that is scraped from resistant surfaces. Several early studies describing the anatomical features of parrotfishes largely focused on the mandibular, or oral, jaws (Cuvier and Valenciennes 1839, Boas 1879, Lubosch 1923, Gregory 1933, Monod 1951, Board 1956). In the last few decades there have been several more extensive studies of the mandibular and pharyngeal jaws, as well as the associated musculature (Tedman 1980a, b, Clements and Bellwood 1988, Bellwood 1994, Monod et al. 1994, Bullock and Monod 1997, Wainwright et al. 2004, Price et al. 2010). However, the connective tissue elements of the jaws of labroid fishes have been minimally addressed (for exceptions see van Hasselt 1978, Tedman 1980b, Bellwood and Choat 1990, Bellwood 1994). In this chapter the specializations of the bones, joints and ligaments of the mandibular jaws of parrotfishes, that allow them to withstand the stress generated during frequent contact with hard surfaces, are described and interpreted along with other elements of the head. The investigators cited above have also noted many of the features described here, but what makes this study noteworthy is the detail of the study and the elaboration of the connective tissue features. In particular, I provide detailed anatomical descriptions of five parrotfish species that reside in the southern Gulf of California (Thomson et al. 1979): the azure parrotfish *Scarus compressus,* bluechin parrotfish *Sc. ghobban*, bumphead parrotfish *Sc. perrico*, bicolor parrotfish *Sc. rubroviolaceus,* and loosetooth parrotfish *Nicholsina denticulata.*

The study of these species complement Clements and Bellwood (1988) and Bellwood (1994) who included one or more of these species in their authoritative studies. The descriptions presented here are a refinement and substantial update of Gobalet (1980). I fully agree with Clements and Bellwood (1988) that in the absence of any data from electromyography, cine radiology, or readings from force transducers, much of the interpretation made here is logical but speculative. It is hoped that this chapter stimulates additional investigations on this unique group of fishes.

Materials

The specimens examined in this study were collected while spear fishing from the coast of the Baja Peninsula, Mexico. Most of the specimens were collected near Danzante Island (just south of Loreto and east of Puerto Escondido, Baja California, Sur). Additional specimens were collected from Pulmo Reef located between La Paz and Cabo San Lucas just north of Punta Los Frailes. For the study, 19 *Sc. compressus* (Standard Length (SL) range: 206-559 mm), 25 *Sc. ghobban* (SL 206-482 mm), 18 *Sc. perrico* (SL 263-540 mm), 10 *Sc. rubroviolaceus* (SL 206-394 mm), a single *Nicholsina denticulata* (SL 291mm)**,** 17 *Mycteroperea rosacea* (Epinephelidae, SL 349-610 mm) and small numbers of several other labrids, and epinephelids were collected (see Gobalet 1980 for details)**.** Dissections were completed on fresh material and specimens preserved for later study. Skeletonized material supplemented the dissections, most of which are now housed at the Ichthyology Department, California Academy of Sciences, San Francisco. The skeletons were prepared by maceration, enzyme digestion, or with the use of dermestid beetles. Identifications follow Rosenblatt and Hobson (1969) and the nomenclature follows Page et al. (2013). The terminology for skeletal elements generally follows Rognes (1973) or Patterson (1977). The features described below are for *Scarus* except where indicated otherwise. The anatomical differences between these four *Scarus* species are subtle at best.

Results and Discussion

Detailed and technical descriptions of the hard and soft connective tissue elements of the cranium of parrotfishes are present in the appendix to this chapter, as is a table of abbreviations used in the figures. Parrotfishes are not delicate nibblers, but feed by forceful scraping or excavating chunks of algae-bearing substrate. Their feeding requires a coordinated action of the locomotor, sensory, and mandibular jaws (Rice and Westneat 2005). When their open jaws come in contact with rock surfaces, often the whole body thrashes to maintain contact with what is often an irregular substrate. Though they propel themselves toward the substrate with their pectoral fins in typical labriform motion, they break prior to contact. Rice and Westneat (2005: p 3512) provide a classic description of parrotfish feeding: "During many *Scarus* bites, it appears as though the fish is slamming its head into the rock”. Grooves may actually be left on the rocks (Cousteau 1952, Newell 1956, Bellwood and Choat 1990) depending upon whether or not the species is a browser, excavator, or a scraper (Bellwood 1994). Chunks were missing from the scraping edges of the jaws of many specimens in this study and a large *Sc. compressus* had a longitudinal fracture across the palatine-ectopterygoid suture and ventral palatine. Bonaldo et al. (2007) quantified the dental damage to three species of *Sparisoma* off the coast of northeastern Brazil, and suggested the frequency of damage was related to the harder composition of the basaltic rock substratum at this marginal reef environment. Irrespective, these injuries testify to the hazards of this feeding behavior.

There are numerous connective tissue elements that encircle and tightly interconnect the bones surrounding the comparatively small mouth of parrotfishes. Ligaments and connective tissue bands encircle the snout within the lips and attach to the mass of connective tissue between the broad posterolateral surface of the coronoid process and the maxilla. These findings are consistent with Board’s (1956) assessment that these bands collectively serve to resist distortion of the jaws during contact with the substrate and during jaw closing. They apparently help to prevent the dorsal displacement of one premaxilla (upper jaw) relative to the other during feeding and complement the interpremaxillary cruciate ligament (Fig. 1A) in this function. Further, the maxillary-dentary ligaments that attach to elements of the upper and lower jaws (Fig. 1C) are too substantial to serve only for mandibular-maxillary coupling that leads to upper jaw protrusion in actinoperygian fishes (Schaeffer and Rosen 1961). Alfaro and Westneat (1999) have documented upper jaw protrusion in *Sc. iseri* despite the inferences of Bellwood (1994) and Wainwright et al. (2004) that it is limited in parrotfishes.

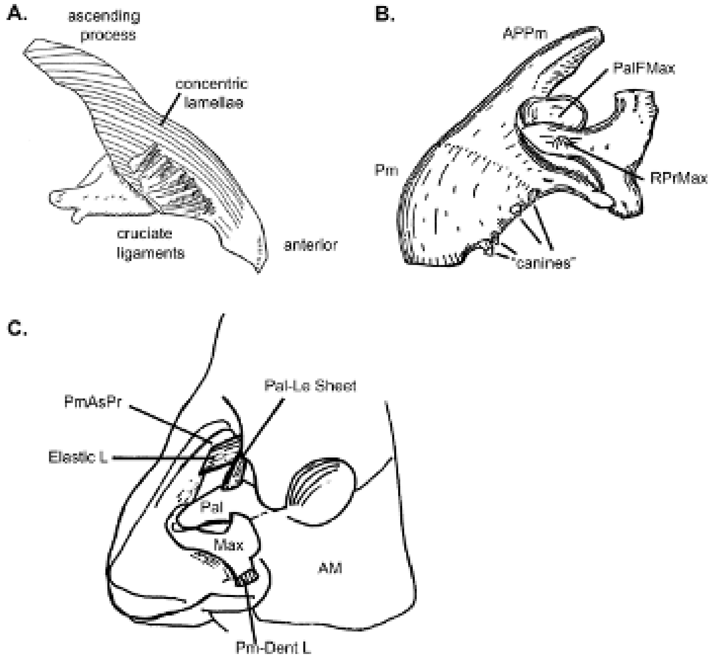


Fig. 1. Mandibular jaws and connective tissues of parrotfishes. A. *Scarus perrico* (530 mm SL): medial view of the left premaxilla. B. *Scarus ghobban* (482 mm SL): maxilla and premaxilla in lateral view. C. *Scarus ghobban*: dorsolateral view of the rostrum showing the elastic ligament and maxillary-dentary ligament (Pm-Dent L).

Trabeculae of bone are laid down along lines of stress (Murray 1936) and the concentric laminae of the medial premaxillae (Fig. 1A) look like a diagrammatic representation of the stress lines one would expect if a load were applied by the premaxillary tip (e.g. see images in Kardong 2006: p 151). The most superficial laminae arch almost the complete length of the bone and the laminae of the posterior portion of the robust ascending process are oriented almost perpendicular to the rostrum so they contact the rostral cartilage when the upper jaw is abducted with the laminae and cartilage dampening the forces. The premaxillary-frontal elastic ligament (Fig. 1C: Elastic L) apparently stretches during abduction and protrusion and could help dampen the dorsal deflection of the anterior tip of the premaxilla while the ascending process is anteroventrally positioned. It may also recoil to retract the upper jaw across the substrate.

Though many parrotfishes scrape flat or convex surfaces (Choat and Bellwood 1985, Konow and Bellwood 2005), shearing forces resulting from feeding on heterogeneous surfaces might tend to dislocate the premaxillae or dentaries (i.e., upper and lower oral jaws) relative to each other. Cruciate ligaments are positioned to resist shearing forces (Beecher 1979) and the cruciate ligaments between the premaxillae (Fig. 1A) are radially arranged and probably can resist shearing forces over a range of positions. The symphysis between the dentaries is broad and bears a series of long interdigitating ridges and grooves (for illustrations, see Bellwood 1994: p 16). The ridges are perpendicular to the radius of curvature of the outer edge of the beak, an orientation that increases the area of contact and thus the surface for transmission of forces from one bone to the other (Herring 1972). Stresses would thus be minimized through the serrate joint and the cruciate ligaments.

A forward thrust with abducted jaws against an unyielding substrate will force the premaxilla against the premaxillary condyle of the maxilla; the maxilla against the palatine; and the ascending process of the premaxilla against the rostrum. Menisci are present between maxilla and premaxilla, maxilla and vomer, and the rostral cartilage between the premaxilla and rostrum are positioned to provide cushioning. Consistent with the findings of Clements and Bellwood (1988) there is no synovial connection between the neurocranium and anterior suspensorium as exists in the less derived epinephelids. The lateral ethmoid-palatine ligament and bands (Fig. 1C: Pal-Le Sheet), and the endopterygoid-lateral ethmoid ligament restrict free motion of the anterodorsal portion of the suspensorium. These connections also would transmit forces from the palatine to the neurocranium as well as limit suspensorial abduction consistent with the reduced suction feeding (Clements and Bellwood 1988, Alfaro and Westneat 1999, Wainwright et al. 2004). Therefore, there appears to have been an evolutionary tradeoff between the selective forces encouraging reinforcement of the skull versus the generation of suction (Alfaro and Westneat 1999).

The palatine must withstand the forces transmitted to it. Longitudinal forces from the upper jaws will also be directly transmitted to the neurocranium because the posterior palatine fits in a notch on the lateral ethmoid. This is noteworthy in large specimens of *Sc. compressus* and *Sc. perrico*, which have a high posterior edge of the palatine. The maxillary condyle of the palatine is a particularly conspicuous and robust feature in large specimens (Fig. 2A: PaMax). Trabeculae within the anterior palatine generally have an orientation that reflects the application of longitudinal forces (Hildebrand and Goslow 2001). The lachrymal (Fig. 2B: La) is tightly bound to the preorbital process by the lachrymal-lateral ethmoid bands and ligaments. Anteriorly the tough lachrymal-palatine ligament connects the lachrymal with the lateral surface of the palatine. Stresses may also be dissipated along the track from the palatine to the preorbital process of the neurocranium via these bones and ligaments.

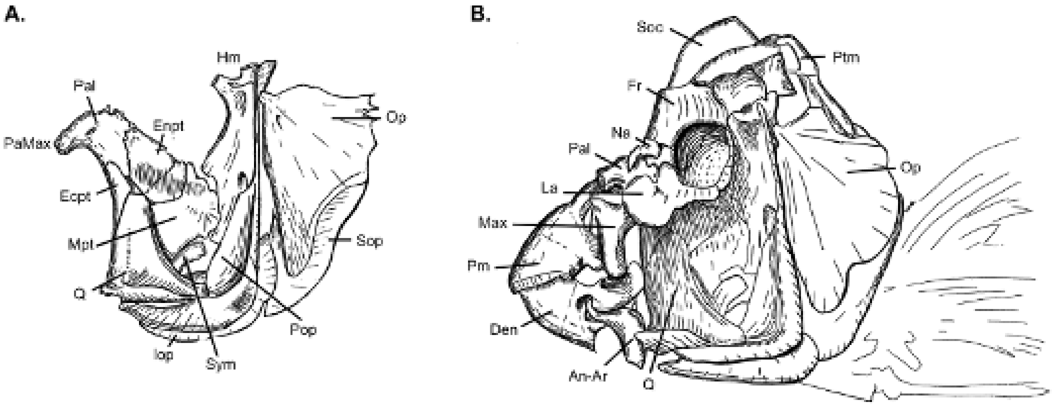
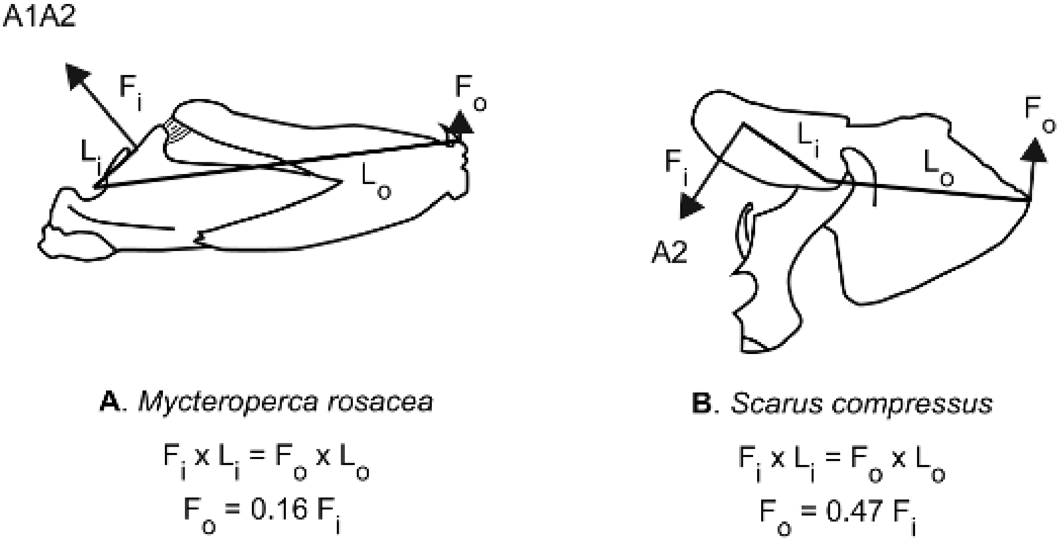


Fig. 2. A. Lateral view of left suspensorium and opercular series of *Scarus compressus* (477 mm SL); B. Lateral view of skull of *Scarus perrico* (510 mm SL).

Attention has deservedly been given to the intramandibular joint of derived percimorphs (Konow and Bellwood 2005, Konow et al. 2008, Price et al. 2010). In pomacanthids this novel joint between the dentary and anguloarticular allows 35 degrees of motion and permits gape closure when the mandibles are fully protruded (Konow et al. 2008). More derived parrotfishes (*Hipposcarus+Chlorurus+Scarus)* possess this intramandibular joint (Streelman et al. 2002) and it has been treated as a key portion of a unique four-bar linkage (Bühler 1977, Wainwright et al. 2004). Price et al. (2010) pose that the modulation of this joint may allow parrotfishes to maintain a consistent orientation with a wide gape on the surface throughout the scraping bite. The parrotfish innovations of the intramandibular joint and the pharyngeal jaws together led to rapid diversification of the oral jaws (Price et al. 2010). Parrotfishes have higher jaw-closing lever ratios than the wrasses, reflecting the greater force required to scrape hard substrata (Bellwood 2003, Wainwright et al. 2004, Westneat et al. 2005). These previous evaluations were made on the mechanics of the entire mandible with a pivot between the quadrate and mandible. I suggest that the mechanics is even more complicated because it is a double lever. Wainwright et al. (2004) hinted at this. Of particular interest are modifications of the mandible that enhance force applied at the dentary tip. A distinctive syndesmosis between the dentary and anguloarticular is present along with a shift in the insertion of the A2 of the adductor mandibulae to the coronoid process from the typical actinopterygian insertion on the ascending process of the anguloarticular (Winterbottom 1973). The consequence is a shortened out-lever of the mandible with the intramandibular joint as the pivot from that seen in generalized percimorphs like *Mycteroperca* (Fig. 3). The quadrate-mandibular articulation is the other joint. The A3 subdivision of the adductor mandibulae attaches to the medial anguloarticular (Fig. 4B, C) and is in a position to effect adduction around the quadrate-mandibular joint but it likely has only a minor role because it is quite thin. The A2 subdivision of the adductor mandibulae, on the other hand, is in a position to adduct the dentary on its pivot at the intramandibular joint. The A2 thus would be an important adductor of the dentary as previously noted by Lubosch (1923). In generalized percimorphs like *Mycteroperca* the A2 inserts on the ascending process of the anguloarticular, close to the quadratomandibular joint, which is thus the fulcrum of a third class lever and being close to the pivot is positioned to enhance speed rather than force. In *Scarus* the insertion of A2 is on the coronoid process of the dentary, and the fiber direction is almost parallel with the anterodorsal ramus of the anguloarticular (Figs. 3B, 4A). With this orientation it can generate little force that would cause mandibular rotation around the quadrate-mandibular joint and being roughly perpendicular to the coronoid process has a mechanically optimal orientation at least during limited rotation. Therefore, this is a first class lever with a shortened out-lever arm (Lo in Fig. 3B). Its in-lever of the dentary is also lengthened as a result of the elongation of the coronoid process. For a given in-force generated by the adductor mandibulae, the out-force at the tip of the dentary will be three times that of the generalist which feeds by inertial suction (Fig. 3). The Aw muscle is also in a position to abduct (Fig. 4C: Aw ab) or adduct (Fig. 4C: Aw ad) the dentary around the intramandibular joint. The muscle is delicate, however, and likely functions to modulate the position of the dentary rather than generate much force.

Considering the presence of only subtle anatomical differences among the members of the genus *Scarus* studied here, one can speculate on how these sympatric species divide the resources because it does not appear to be on the basis of their feeding. The gut content of *Scarus* spp. is composed primarily of fine particles (Hoey and Bellwood 2008, Bonaldo et al. 2014), with over 70% of the gut contents of the *Scarus* species in this study passing through a 630 µm mesh (Gobalet 1980). This small particle size makes it extremely difficult to evaluate what they are targeting, and it would take a creative, perhaps molecular, approach to discriminate what exactly has been pulverized and resides in the intestines (see Clements and Choat, Chapter 3). Considering that parrotfishes have been estimated to spend in excess of 84-91% of the daylight hours feeding (*Chlorurus* spp: Bellwood 1995a) and their impact on reefs can be bioerosion in excess of 5,000 kg per individual per year (Bellwood et al. 2003, 2012) it is logical that they are going to possess anatomical features consistent with the forceful cropping of chunks of inorganic materials. Collectively, the numerous structural adaptations in parrotfishes described above contribute to a spectacular eating machine.



A. *Mycteroperca rosacea*

$F_i \times L_i = F_o \times L_o$

$F_o = 0.16\ F_i$

B. *Scarus compressus*

$F_i \times L_i = F_o \times L_o$

$F_o = 0.47\ F_i$

Fig. 3. Comparison of the lower oral jaw of a generalized percimorph and *Scarus*. A. Lateral view of the right mandible of *Mycteroperca rosacea* (610 mm SL); B. Lateral view of the right mandible of *Scarus compressus* (457 mm SL). F_i = in-force generated by the adductor mandibulae; F_o = out-force at the tip of the dentary, L_i = in-lever (distance from fulcrum to the point of application of the in-force); L_o = out-lever (distance from the fulcrum to the point of application of the out-force). *Scarus* demonstrates three times the mechanical advantage as in the generalist, *Mycteroperca.*

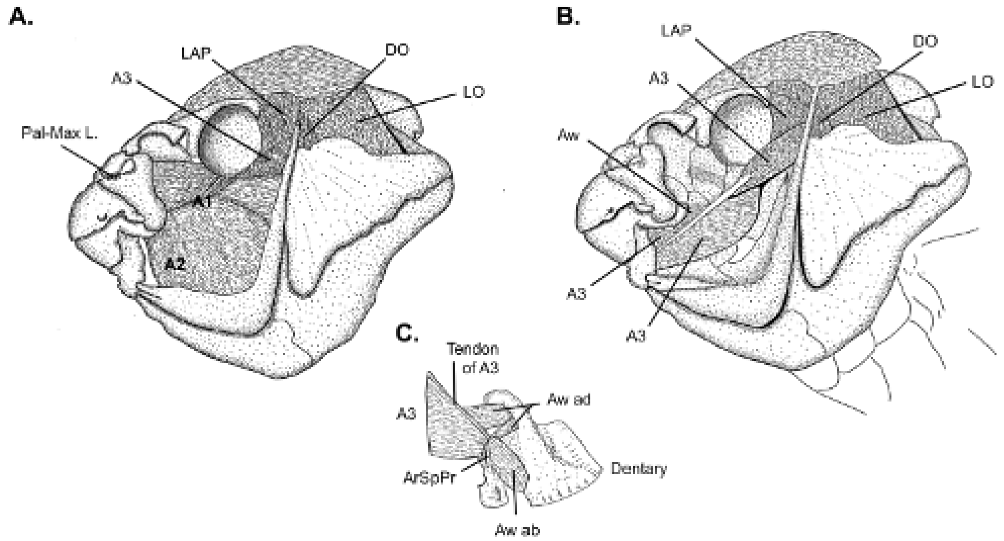


Fig. 4. Muscles of the head of *Scarus*. A. Lateral view of the muscles of the head of *Scarus ghobban* (460 mm SL). Connective tissue of the A1A2 to the premaxillary symphysis has been removed. B. Lateral muscles of the head of *Scarus ghobban* (460 mm SL) with the A1A2 complex of the adductor mandibulae removed. C. Medial complex of the left adductor mandibulae of *Scarus perrico* (540 mm SL) in medial view. Anterior is to the right.

Summary

In this chapter I have presented the details of the anatomy of parrotfishes of the genus *Scarus* that emphasize the features of the head that resist the forces applied during the scraping of rocky substrates that are encrusted with the organic materials they ingest. These descriptions and interpretations complement the growing literature on this monophyletic group of almost 100 species (Parenti and Randall 2011). The connective tissue elements (ligaments, menisci, fascia, joints) were emphasized with the following specializations being of particular interest: within the tissues surrounding the mouth, and likely deeper, are connective tissue bands and ligaments that encircle the snout; serrate joints between the dentaries and cruciate ligaments between the ascending processes of the premaxillae are positioned to resist dislocations; the intramandibular joint between the dentary and anguloarticular is a syndesmosis that likely functions to dampen forces generated during the scraping of the rigid surfaces upon which parrotfishes feed; this joint also enhances the leverage of the system powered by the A2 portion of the adductor mandibulae acting on the enlarged coronoid process; menisci are present between the premaxillae and maxillae, maxillae and vomers, and between the ascending processes of the premaxillae and the rostrum; the boney structure of the ascending processes of the premaxillae are concentrically laminar to resist compressive forces; there are unique elastic ligaments interconnecting the frontals with the ventral surfaces of the premaxillary ascending processes. Along with a highly derived pharyngeal grinding apparatus, the impressive mandibular jaws and their associated connective tissues have contributed to the parrotfishes having a substantial influence on the turnover of substrate in tropical and subtropical reefs.

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Nutritional Ecology of Parrotfishes (Scarinae, Labridae)

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Dynamic Demography: Investigations of Life-history Variation in the Parrotfishes

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Vision and Colour Diversity in Parrotfishes

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The Role of Parrotfishes in the Destruction and Construction of Coral Reefs

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The Good, the Bad, and the Ugly: Parrotfishes as Coral Predators

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Geographic Variation in the Composition and Function of Parrotfishes

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Phenological Aspects of Parrotfish Ecology on Coral Reefs

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The Ecology of Parrotfishes in Marginal Reef Systems

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The Ecology of Parrotfishes on Low Coral Cover Reefs

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No-take Marine Reserve Effects on Parrotfish and Parrotfish-benthos Interactions

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Parrotfishes, are We Still Scraping the Surface? Emerging Topics and Future Research Directions

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