# The Functional Morphology, Systematics and Behavioural Ecology of Parrotfishes (Family Scaridae).

Volume 1

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## ABSTRACT

The functional morphology and behavioural ecology of the parrotfishes (family Scaridae) were investigated to assess the degree of correlation between them.

Twenty-two species of parrotfishes from the subfamily Scarinae were examined mainly from reefs around Lizard Island, Great Barrier Reef, Australia.

Morphological studies of the osteology and myology of the heads of adult parrotfishes revealed two morphological groups within the genus *Scarus*, *viz.* the 'sordidus' and 'frenatus' groups. Species in the 'sordidus' group are characterized by: uneven cutting edges on the jaws, an entopterygoid lateral process, a tightly bound interdigitating maxilla and premaxilla, three rows of teeth on the upper pharyngeal bones, well developed adductor mandibulae sections A1, A2 and A3 and an additional unique muscle, the Awy. Species in the 'frenatus' group are characterized by: even cutting edges on the jaws, a slightly protrusible premaxilla, two rows of teeth on the upper pharyngeal bones, fusion of the abductor muscle section A1α and A2 in some species and a thin strap-like A3 section which inserts only on the articular. The morphology of the heads of species in other genera, namely, *Cetoscarus bicolor*, *Bolbometopon muricatum* and *Hipposcarus longiceps* was marked by their possession of a quadrato mandibularis internus muscle and the non-articulatory articular-dentary joint in *C. bicolor* and *B. muricatum*.

Analyses of the two morphological groups indicated a marked difference in the functional abilities of species in the two groups. The morphological characteristics of 'sordidus' group species enable them to bite the substratum with a large powerful cracking bite. Species in this group are therefore described as 'biters'. The morphological characteristics of 'frenatus' group species are consistent with the requirements necessary for scraping the substratum with small, weak bites. Species in this group are therefore described as 'scrapers'.

Of the species examined in this study, the following species are functional 'biters': *S. bleekeri*, *S. gibbus* and *S. sordidus*, whereas the following are functional 'scrapers': *S. brevifilis*, *S. dimidiatus*, *S. flavipectoralis*, *S. frenatus*, *S. ghobban*, *S. globiceps*, *S. longipinnis*, *S. niger*, *S. oviceps*, *S. psittacus*, *S. rivulatus*, *S. rubroviolaceus*, *S. schlegeli*, *S. spinus*, *S. tricolor* and *Scarus* sp. (*cf. lunula*). Because they lack some specialized morphological features associated with the biting or scraping strategies of species in the genus *Scarus*, *Cetoscarus bicolor* and *Bolbometopon muricatum* are considered 'proto-biters', whilst *Hipposcarus longiceps* is considered a 'proto-scraper'.

These differences are not apparent in juvenile specimens less than 50 mm standard length. Specimens of *Scarus* smaller than this are extremely similar. Small specimens (< 14 mm S.L.), in particular, differ markedly from the adults in the possession of caniform teeth and a simple, non-sacculated intestine.

Functional interpretations of the anatomy of the head and intestine of juvenile scarids suggest that they progress from an initial carnivorous phase to a selective grazing stage before becoming functional 'scrapers' at about 50 mm S.L. 'Biting' species only possess the full complement of biting characteristics above 90 mm S.L.

Field observations of adults revealed two feeding guilds within the genus *Scarus* which correspond with the two functional groups. (1) 'Biting' *i.e.* 'sordidus' group species are characterized by: i) infrequent, large bites which scar the substratum, ii) a propensity to feed upon convex substrata, and iii) aggressive interspecific interactions, when displayed, predominantly directed towards other 'sordidus' group species. (2) 'Scraping' *i.e.* 'frenatus' group species are characterized by: i) numerous small bites which rarely scar the substratum, ii) a tendency to feed on a range of substrata, and iii) aggressive interspecific interactions, when displayed, predominantly directed towards other 'frenatus' group species. These feeding strategies strongly influence the roles played by parrotfishes as coral predators and bioeroding agents. The major coral predator is *Bolbometopon muricatum*. Bioerosion is primarily the result of feeding by 'sordidus' group species, *Cetoscarus bicolor* and *B. muricatum*. It is therefore proposed that the distribution of these species within and between reefs may influence the extent and rates of bioerosion, the topography of the substratum and the distribution of various coral morphs.

Field observations of juvenile scarids revealed a wide range of behavioural traits, although these did not correspond with the 'sordidus' and 'frenatus' groupings. *S. frenatus* in particular, differed from other juvenile 'frenatus' group species in its feeding behaviour. An analysis of the gut contents of the juveniles of several species showed marked changes in the diet, from being initially predominantly carnivorous to herbivorous. These changes were strongly correlated with changes in morphology and behaviour.

In addition to functional considerations, the morphological analyses in this study were used to examine the systematic relationships between genera in the subfamily Scarinae. The present generic status of *Cetoscarus*, *Bolbometopon* and *Hipposcarus* is supported. The genus *Scarus* contains two distinct groups which may be recognized at the generic level.

A descriptive account of the ontogeny of the colour patterns of the juvenile phase of 22 species is presented to facilitate the study of juvenile scarids in the field. The colour patterns of juvenile scarids are interpreted in terms of concealment colouration, including crypticism, camouflage and mimicry. In the species examined, there is a strong correlation between schooling behaviour, the range of patterns displayed, and the speed with which the patterns may be changed.

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## DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

D.R. Bellwood

December, 1985

# GENERAL INTRODUCTION

The Scaridae† is a distinctive group of perciform teleosts, characterized by the possession of a pharyngeal mill and fused teeth, which form dental plates. Scarid species have a tropical and sub-tropical distribution and are typically associated with coral reefs. They are predominantly herbivorous and form a conspicuous part of the herbivorous reef fish community. At present, there are 69 recognised species in 12 genera (Schultz, 1969 and Randall & Bruce, 1983).

Members of the Scaridae are predominantly protogynous hermaphrodites, with two main colour phases, a drab initial phase (IP) and a colourful terminal phase (TP) (Robertson & Warner, 1978). Initial phase individuals may be either male or female, whilst terminal phase individuals are invariably male. Some individuals are male throughout their life, during both initial and terminal phases; these are referred to as primary males. Most males, however, are secondary males and, as such, spend the initial phase period as females before developing testes and exhibiting the terminal phase colouration (Choat, 1966, Choat and Robertson, 1975, Robertson and Warner, 1978 and Bruce, 1979). The common name for the family, the parrotfishes, has arisen from the striking colours of the terminal phase and the close resemblance of the dental plates to a parrot's beak.

† The conventional nomenclature is utilized. The recently proposed familial synonomies are discussed in Chapter 3.

Parrotfishes have many unusual characteristics. These include the secretion of a mucous cocoon at night (Winn, 1955, Winn & Bardach, 1959, 1960 and Casimir, 1971), a diet that includes live coral (Hiatt & Strasburg, 1960, Glynn *et al.*, 1972 and Randall & Bruce, 1983), a grinding pharyngeal mill (Al Hussaini, 1945 and Board, 1956), an additional articulation point in the lower jaw (Lubosch, 1923 and Gregory, 1933), an unusual sacculated intestine (Al Hussaini, 1945, 1947 and Gohar & Latif, 1959) and a range of physiological adaptations to the exceptionally high carbonate content of the diet (Fontaine *et al.*, 1973 and Smith & Paulson, 1975). Parrotfishes have been implicated as important agents in bioerosion (Gygi, 1975 and Frydl & Stearn, 1978), sediment transport (Bardach, 1961) and in the regulation of benthic invertebrates (Glynn *et al.*, 1972, Kaufman, 1977, Brock, 1979 and Wellington, 1982), as well as being an important component of the grazing reef fish community (Stephenson & Searles, 1960, Randall, 1965, Day, 1977, Ogden & Lobel, 1978, Bouchon-Navaro & Harmelin-Vivien, 1981, Hatcher, 1981, Miller, 1982 and Russ, 1984 a, b). The parrotfishes form a significant proportion of the food fishes caught in many tropical regions and include at least one highly prized species (Alcala & Luchavez, 1981 and Johannes, 1981).

Despite the recent increase in the number of studies on coral reef fishes (Ehrlich, 1975), parrotfishes have received relatively little attention, particularly in the Indo-Pacific region. One aspect that appears to have deterred many prospective investigators is that of identification. The identification of scarids in the field and in preserved collections is difficult owing to the lack of diagnostic morphological characters. Because of this, species descriptions are frequently based on colour patterns. This has resulted in considerable confusion as colour patterns change with size, sex, reproductive status and a variety of environmental and behavioural factors. The colours also change during fixation. On the Great Barrier Reef, there are about 26 scarid species with a total of approximately 125 colour phases or patterns. Of these, seven are shared by at least two species.

Recent studies (including Randall & Ormond, 1978, Randall & Choat, 1980, Randall, 1983, Randall & Bruce, 1983 and Choat & Randall, pers. comm.) are contributing greatly to a more stable scarid nomenclature. Detailed morphological analyses have revealed useful characters that were previously overlooked. The initial and terminal phase colour patterns of most species have now been linked and the problems of synonomy, as a result of colour phases being identified as different species, have been largely resolved.

The aim of this study was to investigate the relationship between the functional morphology and behavioural ecology of parrotfishes. Parrotfishes are ideally suited for such comparative studies as they have highly specialized morphological characters and distinctive behavioural traits. Parrotfishes are also suitable study species in that they are diurnally active, strongly reef associated and numerous, and have a limited mobility.

This study includes analyses of both adults and juveniles. The biology of adults and juveniles are clearly not independent, although often different, and an investigation of the biology of a species must therefore include both stages, if a broad understanding of it is to be obtained. The biology of larval and juvenile tropical marine fishes have received increasing attention in recent years (*eg*. Sale *et al*., 1980, Williams, 1980, Williams & Sale, 1981, Leis, 1982, Brothers *et al*., 1983, Doherty, 1983 and Shulman, 1984) but integrated studies of several life history stages are limited.

This thesis is presented in three main parts: morphology (Chapters 1 & 2), systematics (Chapters 3 & 4) and behavioural ecology (Chapters 5 & 6). Each part is further subdivided into adult and juvenile chapters. The descriptions in Chapters 1 and 2 are detailed, but unavoidably so, as they form a prerequisite for: a) the systematic considerations in Chapter 3 and b) the functional analyses in Chapters 1 and 2, which form the basis for designing and interpreting the ecological studies described in Chapters 5 and 6. The lack of published information on the taxonomy of juvenile scarids made the systematic analyses in Chapter 4 necessary, prior to the studies of juvenile scarids in Chapters 2 and 6.