

**Marine and Tropical Sciences Research Facility (MTSRF)**  
**Preliminary Status and Trend Report: June 2007**

**Herbivory by fishes on the Great Barrier Reef:  
A review of knowledge and understanding**

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**Australian Government**  

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**Department of the Environment  
and Water Resources**

Funded through the Australian Government's  
Marine and Tropical Sciences Research Facility  
Project 2.5i.3 Resilience to Climate Change

This document should be cited as:

Cvitanovic, C., Fox, R. J. and Bellwood, D. R. (2007) *Herbivory by fishes on the Great Barrier Reef: A review of knowledge and understanding*. Unpublished Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns (33 pp.).

Published online by the Reef and Rainforest Research Centre Limited for the Australian Government's Marine and Tropical Sciences Research Facility.

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June 2007

## **Introduction**

Coral reefs exhibit a large capacity to cope with environmental change, evidence of inherent resilience (Nyström et al, 2000). Over the last two decades a decrease in the health and resilience of reefs has been reported world wide (Wilkinson 1999, Wilkinson et al 2004), with many undergoing catastrophic phase-shifts from coral to macroalgal dominance or to sea urchin barrens (Done 1992, Hughes 1994, McClanahan & Muthiga 1998). The shifts have been attributed, at least in part, to an increase in human impacts on coral reef ecosystems (Hoegh-Guldberg 1999, Jackson et al 2001, Pandolfi et al 2003, Hughes et al 2005) and have frequently proven to be persistent and difficult to reverse (Bellwood et al 2005). Although the Great Barrier Reef (GBR) has not suffered the same system-wide collapse as reefs in the Caribbean, evidence of a more subtle decline in resilience is starting to mount. (McCulloch et al 2003, Bellwood et al 2004).

In response to the increase in phase shifts seen on coral reefs, recent literature has called for the management of reef resilience (Nyström & Folke 2001, Hughes et al 2003, Bellwood et al 2004, Folke et al 2004). This has led to a reassessment of the state of our knowledge of components of reef ecosystems that play a role in supporting resilience. In many areas of the world with a history of heavy artisanal fishing, the decrease in reef resilience has been linked to the removal of herbivorous fishes (Lessios 1988, Bellwood et al 2003, Mumby et al 2006, Mumby 2007, Ledlie in press). Herbivory represents one of the key processes responsible for the persistence of coral reefs and is central to the prevention and potential reversal of phase shifts (McCook 1999, Bellwood et al 2006). Information on the distribution, abundance and ecosystem impact of individual species of herbivorous fishes will therefore be vital in the development of management plans for the GBR.

Here we review the current state of knowledge and understanding of the process of herbivory by fishes on the GBR. We (1) explore the overall status and focus of research into herbivory on the GBR, (2) examine the issue of how one actually defines a herbivorous fish, (3) summarise information currently available on distribution and abundances of herbivores across the GBR, (4) review those studies aimed at understanding the process of herbivory as it relates to the GBR, and (5) review the extent to which our current knowledge enables us to achieve the goal of active monitoring and management of reef resilience, based on the protection of functional groups that play a critical role in supporting resilience.

## **Herbivory on the Great Barrier Reef: Its overall research status and geographic focus**

Since the 1970s, published research on coral reefs globally has increased exponentially (Fig. 1a). Whilst the cumulative number of publications focussing on coral reefs of the GBR also increased from the 1970s to the current time (Fig. 1a), the GBR's proportional share of the literature on reefs has started to decline (Fig. 1b). Between 1970 and 1995, the proportion of coral reef publications focussing on the GBR jumped from 43 per cent to 73 per cent (Fig. 1b). However, since 1995, research focus has shifted away from the GBR, with its proportional share of the total publications on coral reefs falling to 56 per cent in 2005 (Fig. 1b).

Given the acknowledged importance of herbivory within coral reef ecosystems and universal calls for further understanding of the process, the total amount of published research relative to total research published on coral reefs is surprisingly low. Of the cumulative total of publications on coral reefs globally (3106), 13 per cent (411) relate to the process of herbivory (Fig. 2a). For the GBR, however, herbivory's share of the research agenda (using publications as a proxy) is even lower, never accounting for more than 2.7 per cent of total coral reef publications (Fig. 2b). This is in comparison to the rising profile of research topics such as recruitment of larval fishes and corals, which in 2005 made up 7 per cent of the cumulative total of GBR publications. The lower profile of herbivory on the GBR in relation to other research topics perhaps reflects the fact that reefs in this part of the world have not, to date, suffered the same extreme levels of herbivore-mediated degradation and shift in benthic community structure that have affected reefs in the Caribbean. However, the fact that reefs on the GBR have not suffered the same fate is no reason for complacency, nor is it a justification for the current proportion of research papers devoted to the topic.

Examining the geographic scope of existing research on herbivory conducted on the GBR reveals further limitations in our understanding. At over 2,300 km in length and consisting of more than 2,900 individual reefs, 600 continental islands and 300 coral cays, the GBR is the world's largest coral reef system. Yet nearly 60 per cent of the studies on herbivory conducted on the GBR have been based at one of two sites: Lizard Island (14° 10'S, 145° 28'E) or Orpheus Island (18° 37'S, 146° 30'E) (Fig. 3). Our knowledge of herbivory across the GBR as a whole is, therefore, extremely limited. Extending both the latitudinal and longitudinal range

of our investigations must be a priority if we are to understand herbivore populations and the process of herbivory on the GBR.

### **Defining herbivory: Who are the herbivores of the GBR?**

Perhaps nothing better illustrates the current limitations of our understanding of herbivory than the fact that the definition of a herbivorous fish is still evolving. The early characterization of herbivorous reef fishes was a relatively simple one. All fishes observed feeding on macroalgae or off the reef's epilithic algal community (EAC) (Hatcher & Larkum 1983), were defined as herbivores. It was taken for granted that the alga was the target food source and primary source of nutrition. Understanding of food selection and processing was at an early stage and only limited stomach content analyses existed. It was understood that different families processed that plant material in different ways and were accordingly classified as type I, II, III (Ogden & Lobel 1978) or type IV (Rimmer & Wiebe 1987) herbivores based on the presumed mode of digestion (Horn, 1989).

Over the last decade our understanding of the EAC has developed. Research has shown that within the matrix of algal thalli is also lodged detritus (dead organic matter), bacteria, fungi, microbes and microalgae, something which had actually been acknowledged by Lobel in 1980 and Hatcher back in 1983, but not taken to be of any wider significance. Wilson & Bellwood (1997) demonstrated that fishes could derive their primary source of nutrition from the detritus within the EAC, rather than the algae itself. They suggested that the EAC be rechristened as the epilithic algal matrix (EAM) to more accurately reflect its complex, composite nature. The EAM is more than vegetable and has multiple food groups present. Understood this way, we can begin to see the difficulties inherent in trying to categorise the trophic status of fishes feeding off such a composite resource.

The demonstration of the relative value of detritus as a food resource in comparison to algae represented a major turning point in the view of reef trophodynamics (Crossman et al 2001, Purcell & Bellwood 2001). Far from Hiatt & Strasburg's (1960) observation that comparatively few species among reef fishes are detritus feeders, detritivory has now become a trophic guild in its own right (Wilson et al. 2003) (Table 1). Many of the species previously assumed to be herbivores have turned out to be detritivores and "nominal" herbivores (sensu Choat et al 2002 - a term reflecting the current uncertainty over whether the diets of certain

fishes are dominated by algae). Table 1 summarises the published information on the trophic status of herbivorous and detritivorous species from the GBR.

There are relatively few studies aimed at identifying the diets of marine herbivores. Dietary analysis is complicated by the difficulty of algal identification, especially at the level of resolution required to distinguish between components of the EAM. There is an acknowledged lack of taxonomic resources for algal identification and little information on compositions of algal communities on the GBR (as highlighted by McCook & Price 1997 a, b). Resources need to be devoted to building up identification guides and our understanding of patterns of algal distribution across the GBR.

Ontogenetic changes in diet have been established for only a handful of species such as *Acanthurus dussumieri*, *A. olivaceus*, *Zebrasoma scopas*, *Z. veliferum*, *Siganus spinus*, *S. doliatus*, *Centropyge bicolor* and a range of parrotfishes (Bellwood 1988, Chen 2002). Other aspects of the feeding habits of herbivores have also been neglected. Seasonal shifts in composition and volume of diet may play a role in determining algal community composition, yet such shifts have rarely been acknowledged in the literature or accounted for in the documentation of changes in algal community composition (exceptions include Polunin & Klumpp 1992, Hart & Klumpp 1996). These variations in foraging behaviour, feeding rates and feeding preferences will be crucial in understanding the impact on the reef system of individual herbivores.

### **Distribution and abundance of herbivorous and nominally herbivorous fishes on the Great Barrier Reef**

The GBR exhibits considerable species richness in fishes at the herbivorous and nominally herbivorous trophic level (178 species in 9 families) (Table 1, Annex A). The reefs of the outer shelf generally display the greatest numbers of roving herbivore species, but those of the mid-shelf are similar in species composition (Russ 1984a). Inner shelf reefs tend to display a more depauperate herbivore assemblage that differs significantly in composition from the mid and outer shelf reefs (Russ 1984a).

Baseline data on herbivore populations across the GBR is crucial in order to be able to assess the natural population levels of individual functional groups. Table 2 summarises the

available data on herbivore abundance and biomass for the GBR. It is frequently assumed that a surfeit of data exists on herbivore distributions and biomass on the GBR, however Table 2 reflects the inadequacy of our understanding of populations of herbivores along the length of the GBR as a whole. Interesting cross-shelf patterns in herbivore populations and species composition have been discerned at particular latitudes (e.g. Russ 1984a, Gust et al 2001, Hoey & Bellwood, in prep), but the scope of our information needs to be extended across a wider range of latitudes, bioregions and habitats to gain a more holistic picture of herbivore populations on the GBR.

In order to provide a broader quantitative picture of herbivory on the GBR, David Bellwood and colleagues (in a collaborative ARC linkage project between JCU and The Great Barrier Reef Marine Park Authority) have collected abundance and biomass information on all major herbivorous and 'nominally' herbivorous fishes across the GBR. Fish biomass has been quantified at 12 reefs, along Northern and Central GBR transects, including many not previously surveyed. The censuses encompassed over 200 transects and over 100,000 individuals were recorded. These censuses have expanded the existing database and were supplemented by over 100 hours of direct feeding observations and 800 hours of video footage of fish feeding. These data will lay the foundation for characterising cross-shelf variation in ecosystem processes, especially herbivory. Although this work is not yet complete, some interesting, and sometimes dramatic differences in the process of herbivory between the various locations have been detected, in many cases at a scale smaller than previously reported.

### **Current state of knowledge of the process of herbivory on the GBR**

Interest in the process of herbivory on the GBR is a long-standing one. Investigations into patterns of herbivory were first undertaken by researchers intrigued by the low standing crop of algae on reefs. The hypothesis that low nutrient levels were responsible for the observed low standing crop was rejected when early exclusion experiments demonstrated that, in the absence of herbivores, algal biomass increased substantially (Stephenson & Searles 1960, Hatcher & Larkum 1983). It was concluded that algal turfs had high productivity levels and therefore the potential to achieve high standing crops, but that grazing was maintaining the turfs at low crop levels (Hatcher 1983, 1988). The Epilithic Algal Matrix (EAM) or algal turfs make up 60-80 per cent of total algal cover on reef flats and slopes and contribute most of the

net production of the reef (Klumpp & McKinnon 1992). On the GBR, it is estimated that herbivores are responsible for removing between 20-90 per cent of the net daily production of the EAC (Hatcher 1981), ensuring that its biomass turns over once every 4-12 days (Carpenter 1985, Klumpp et al 1987).

Experiments in herbivore “exclusion” and algal transplants of the 1980s and 1990s demonstrated that algal populations across a reef gradient were, indeed, subject to different grazing pressures and that herbivores were responsible for maintaining the patterns of algal zonation observed (Scott & Russ 1987, McCook 1996, 1997). At about the same time, the world began to see the effect of the unintentional geographic-scale experiment in herbivore “exclusion” when reefs in the Caribbean underwent a catastrophic phase shift from coral to macroalgal dominance (Done 1992, Hughes 1994). The focus of research on herbivory switched to exploring the relative importance of nutrients and grazing levels in contributing to the collapse of the Caribbean reefs (e.g. Lapointe 1999, Smith et al 2001, Stimson et al 2001, McClanahan et al 2003). The net result was an almost unanimous affirmation of the overall importance of herbivores, but little information as to which species were actually removing which species of algae from where (but see Lewis 1986 and Lewis & Wainwright 1985).

The one group that was singled out in many studies during this period were the territorial damselfishes (F. Pomacentridae). Klumpp et al (1987) estimated that damelfish territories covered up to 77 per cent of individual reefs. Pomacentrids were shown to affect the standing biomass of turf algae and its productivity (Wilkinson & Sammarco 1983, Klumpp et al 1987, Scott & Russ 1987, Ceccarelli et al 2005) and the structure of the surrounding coral community (Sammarco 1983, Ceccarelli et al 2001). Excluding roving herbivores from the reef was found to result in the expansion of damselfish territories and an alteration of the relative species composition levels of the benthic community (Ceccarelli et al 2006). The interaction between these territorial pomacentrids and the rest of the herbivore community is therefore likely to have consequences for reef dynamics which have yet to be fully explored.

With the exception of damselfishes, therefore, ecological studies of the 1990s tended to focus at the level of herbivores as an overall trophic grouping (highlighted by Choat 1991). However, where research did focus at the micro level of the individual species, there were interesting insights. Bellwood & Choat’s (1990) investigation of the feeding mechanisms of Indo-Pacific members of the family Labridae (Scaridae) revealed subtle differences in



myology and dentition between scarid species. They demonstrated that the family was divided along mechanistic lines into scrapers (the genus *Scarus*) and excavators (the genus *Chlororus*). It was no longer sufficient, therefore, to census the total number of scarids on a reef as a metric for the health of the herbivore population. The resilience of the reef would be dependent on having the correct balance of both functional types (scrapers and excavators) and surveys of herbivore populations would need to distinguish between individual functional groups within the overall trophic level.

The functional delineation described by Bellwood & Choat (1990) was a crucial one. It demonstrated the fact that not all herbivores are equal and that there exists limited potential for replacement of certain species. For example, the effect of removing species capable of bio-eroding (excavating) reef substratum is already being felt in parts of the Indo-Pacific, where artisanal fishing has all but removed the largest of the excavators, *Bolbometopon muricatum* (Bellwood et al 2003). Rates of reef bioerosion have declined accordingly (Bellwood et al 2003). Classification of herbivorous species down to the functional level will be key when determining the level of species redundancy within a given system and when prescribing those species that are important in terms of preserving the resilience of a particular reef.

The importance of understanding precisely where and how individual species exert their impact on the reef system was again highlighted by Purcell & Bellwood (1993) and their examination of the methods of food procurement by the two species of surgeonfish, *Acanthurus nigrofuscus* and *Ctenocheatus striatus*. The visual similarity between the two species had been noted by researchers. In fact Bouchon-Navaro & Harmelin-Vivien (1981) had admitted an inability to distinguish between the two fish and taken a deliberate decision to census them as the same species. Purcell & Bellwood (op cit) demonstrated that the two species were using the EAM resource in very different ways. *A. nigrofuscus* was tearing turf algae from the substratum, but *C. striatus* was utilizing its flexible, brush-like teeth to sweep detritus from up amongst the EAM. Functionally, therefore, the two species were very different: one was a herbivore, the other a detritivore. Censusing the two species as one and the same would not yield an accurate picture of the functional group impact at a particular reef.

Work done on the GBR during this period also revealed the importance of understanding where the critical turning points in the system lay e.g. what level of increase in algal biomass could be absorbed by existing herbivore populations? Russ & McCook (1999) used the natural effect of a cyclone event on the GBR to demonstrate that the pulse of nutrients delivered to the system resulted in greater algal production but also resulted in a higher yield to grazers, suggesting that the system did contain the potential to absorb some degree of short-term disequilibrium. However, the applicability of this result appears to be dependent on the relative palatability of the increased algal production. Hart & Klumpp (1996) looked at the response of a population of herbivorous fishes to a potentially greater food resource in the form of higher biomass of algal turfs on reefs affected by Crown-of-Thorns (COTs) starfish and found that, of the two representative species studied (*Acanthurus nigrofuscus* and *Scarus frenatus*), neither showed an increase in feeding rate when faced with a higher abundance of turf algae at the COTs-affected reefs. Further work to assess feeding responses of individual herbivores to particular levels of algal biomass of varying functional type will add to our understanding of the potential of these fishes to react to a system out of equilibrium.

### **The future of research on herbivory and implications for management**

Over the last five years, the herbivory research agenda has come to be dominated by a new perspective: one that acknowledges the role of herbivores in precipitating phase-shifts on reefs, but which also places new demands on our understanding of herbivory at the micro level. Recent literature examining the process of reef degradation has advocated a system-level approach to managing coral reefs (e.g. Nyström et al. 2000, Bellwood et al. 2004, Hughes et al. 2005). This approach sees reef dynamics in terms of a non-equilibrium environment with multiple stable states. Events such as global warming, eutrophication or over-fishing have become re-cast as disturbance factors that have the potential to dislodge the system from its initial position and shift it to a new state (Nyström et al. 2000, Bellwood et al. 2004). The resilience of the reef system reflects the size of disturbance that can be absorbed by the system without causing a shift to a new, usually undesirable state (Nyström et al. 2000). Herbivores confer resilience to the extent they exert a grazing impact that maintains a balance between corals and algae.

Herbivory from the system perspective is not just a process of energy transfer, but rather a composite function of the individual impacts that each herbivorous species has on the system.

The ability of a reef to withstand disturbance events and avoid shifts to alternate states is dependent on having the right functional composition of herbivores. Understanding the role and relative importance of herbivorous species requires a knowledge of the quantitative impact that each species and where it exerts that functional impact. As recent reviews have emphasised, the current dataset of quantitative ecosystem impacts of individual taxa is limited (McManus & Polsenberg 2004). Exceptions for the GBR include measurement of bioerosion rates and contribution to sediment production for individual species of excavating parrotfish (Bellwood 1995a, b, Bellwood et al 2003), estimation of ingestion rates of algae for individual species of scraping parrotfishes (Klumpp & Polunin 1989, Polunin et al.1995), estimation of ingestion rates of algae for one surgeonfish species (Polunin & Klumpp 1992), and for three damselfish species (Klumpp & Polunin 1989, Polunin & Klumpp 1992).

Recent research has therefore been aimed at adding to our understanding of the quantitative functional impacts of individual species of herbivores and of their trophodynamic context (e.g. see Choat et al 2002, 2004, Crossman et al 2005). Understanding what food is being eaten and assimilated by whom and at what rate will enable us to better understand reef processes. In addition, remote underwater video technology is being used in field studies of herbivores to provide an insight into the process of herbivory in the absence of divers (Bellwood et al 2006). The technique is proving to be a revealing one, showing that the removal of macroalgae from reefs cannot be assumed to be the exclusive reserve of ‘traditional’ macroalgal feeders (Bellwood et al 2006). Undoubtedly, further use can be made of this methodology to reveal an added dimension to herbivory and further our understanding of the GBR’s herbivore populations and those species which are intrinsic to the maintenance of a healthy balance between corals and algae.

## **Summary**

The GBR exhibits considerable species richness at the herbivorous and nominally herbivorous trophic level. In low diversity systems, such as the Caribbean, minor changes in biodiversity can have dramatic impacts on the ecosystem. However, it is not necessarily safe to assume that the corollary is true. High species diversity, such as that displayed by the GBR, does not necessarily confer greater resilience and high diversity systems can still display limited functional redundancy (Bellwood et al 2003, Fox & Bellwood in press). An increased

understanding of the functional role played by individual species of herbivore will be crucial if we are to make prescriptions for the prevention (and reversal) of phase shifts on coral reefs.

The focus of recent research on herbivory on the GBR has now shifted to view the process as one of a number of factors determining the resilience of coral reefs. This new focus has revealed some crucial gaps in our understanding of herbivory. We know much of what herbivores as a group do on reefs qualitatively speaking, but little about the individual functional components of the group and their quantitative effects. Viewed from the perspective of the overall reef system, however, it is precisely this quantitative understanding of ecosystem function that will provide the next insights into the process of herbivory on coral reefs.

The practical requirements of this new research agenda are considerable. It will require a fully integrated knowledge of the individual species: their ontogeny, their interactions with the substratum, their ability to consume and remove algae and their relationship to current distribution patterns of algae across the GBR. The predominant message emerging from recent studies is that the process of herbivory is a more subtle one than previously imagined and can show variation even at the scale of neighbouring reefs. Understanding herbivory on the GBR at the gross scale will not be enough to make predictions about individual systems. Estimates of existing abundances of herbivores and associated benthic algal communities should be extended to a more diverse collection of sites across the GBR and investigations of the process of herbivory should incorporate methods that allow us to witness feeding behaviour in the absence of divers.

## Literature Cited

Bellwood DR (1995a). Carbonate transport and within-reef patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 117: 127-136.

Bellwood DR (1995b). Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Mar. Biol.* 121: 419-429.

Bellwood DR (1988) Ontogenetic changes in the diet of early post-settlement *Scarus* species. *J. Fish Biol.* 33: 213-219.

Bellwood DR, Choat JH (1990). A functional analysis of grazing in parrotfishes family Scaridae the ecological implications. *Environ. Biol. Fish.* 28: 189-214.

Bellwood DR, Hoey AS, Choat JH (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6: 281-285.

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004). Confronting the coral reef crisis. *Nature* 429: 827-833.

Bellwood DR, Hughes TP, Connolly SR, Tanner J (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.* 8: 643-651.

Bellwood DR, Hughes TP, Hoey AS. (2006). Sleeping functional group drives coral reef recovery. *Curr. Biol.* 16: 2434-2439.

Bouchon-Navaro Y, Harmelin-Vivien ML (1981) Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar. Biol.* 63: 79-86.

Carpenter RC (1985). Relationships between primary production and irradiance in coral reef algal communities. *Limnol. Oceanogr.* 30: 784-793.

Ceccarelli DM, Jones GP, McCook L (2001). Territorial damselfish as determinants of benthic community structure on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.* 39: 355-389.

Ceccarelli DM, Jones GP, McCook LJ (2005a). Foragers versus farmers: contrasting effects of two behavioural groups of herbivores on coral reefs. *Oecologia* 145: 445-453.

Ceccarelli DM, Jones GP, McCook LJ (2005b). Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs* 24: 606-620.

Ceccarelli DM, Hughes, TP, McCook, LJ (2006) Impacts of simulated overfishing on the territoriality of coral reef damselfish. *Mar. Ecol. Prog. Ser.* 309: 255-262

Chen L (2002) Post-settlement diet shift of *Chlorurus sordidus* and *Scarus schlegeli* (Pisces: Scaridae). *Zool. Stud.* 41: 47-58

Choat JH (1991). The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, p120-155.

Choat JH, Clements KD, Robbins WD (2002). The trophic status of herbivorous fishes on coral reefs I: Dietary analyses. *Mar. Biol.* 140: 613-623.

Choat JH, Robbins WD, Clements, KD (2004). The trophic status of herbivorous fishes on coral reefs II: Food processing modes and trophodynamics. *Mar. Biol.* 145: 445-454.

Clements KD, Bellwood DR (1988). A comparison of the feeding mechanisms of two herbivorous labroid fishes, the temperate *Odax pullus* and the tropical *Scarus rubroviolaceus*. *Aust. J. Mar. Freshwater Res.* 39: 87-107.

Clements KD, Choat JH (1995). Fermentation in tropical marine herbivorous fishes. *Physiol. Zool.* 68: 355-378.

Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J (2001). Detritus as food for grazing fishes on coral reefs. *Limnol. Oceanogr.* 46(7): 1596-1605.

Crossman DJ, Choat JH, Clements KD (2005). Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series* 296: 129-142.

Depczynski M, Bellwood DR (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Mar. Ecol. Prog. Ser.* 256: 183-191.

Done TJ (1992). Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247: 121-132.

Folke C et al (2004). Regime shifts, resilience and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35: 557-581.

Fox RJ, Bellwood DR (in press). Quantifying herbivory across a coral reef depth gradient. *Mar. Ecol. Prog. Ser.*

Gust N (2002) Scarid biomass on the northern Great Barrier Reef: the influence of exposure, depth and substrata. *Environ. Biol. Fish* 64: 353-366

Gust N, Choat JH, McCormick MI (2001). Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Mar. Ecol. Prog. Ser.* 214: 237-251.

Hart AM, Klumpp DW (1996). Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. I. Substratum analysis and feeding ecology of *Acanthurus nigrofuscus* and *Scarus frenatus*. *Mar. Ecol. Prog. Ser.* 132: 11-19

Hart AM, Klumpp DW, Russ GR (1996). Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Mar. Ecol. Prog. Ser.* 132: 21-30.

Hatcher BG (1981). The interaction between grazing organisms and the epilithic algal community of a coral reef. *Proc. 4<sup>th</sup> Int. Coral Reef Symp.* 2: 515-524.

Hatcher BG (1983). Grazing in coral reef ecosystems. In: Barnes, D. J. (ed) *Perspectives on Coral Reefs*. Brian Clouston, Canberra. pp 164-179.





Hatcher BG, Larkum AWD (1983). An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.* 69: 61-84.

Hiatt RW, Strasburg DW (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30: 65-127.

Hoegh-Guldberg O (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw Res.* 8: 839-866.

Hoey AS, Bellwood DR (in review) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*.

Horn MH (1989) Biology of marine herbivorous fishes. *Oceanogr. Mar. Biol. Annu. Rev.* 27: 167-272

Hughes TP (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Hughes TP et al (2003). Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933.

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *TREE.* 20: 380-386.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook LJ, Molschaniwskyj N, Pratchett MS, Steneck RS and Willis B (2007). Phase shifts, herbivory and the resilience of coral reefs to climate change. *Curr. Biol.* 17: 360-365.

Jackson JBC et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-637.

Jones RS (1968). Ecological relationships in Hawaiian and Johnson Island Acanthuridae (surgeonfishes). *Micronesica* 4:309-361.

Klumpp DW, McKinnon AD (1992). Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Mar. Ecol. Prog. Ser.* 86: 77-89.

Klumpp DW, Polunin NVC (1989). Partitioning among grazers of food resources within damselfish territories on a coral reef. *J. Exp. Mar. Biol. Ecol.* 125: 145-169.

Klumpp DW, Polunin NVC (1990). Algal production, grazers and habitat partitioning on a coral reef: positive correlation between grazing rate and food availability. In: Barnes M, Gibson RN (eds) (1990) *Trophic relationships in the marine environment*. Aberdeen University Press, Aberdeen, p 372-388.

Klumpp DW, McKinnon AD, Daniel P (1987). Damselfish territories: zones of high productivity on coral reefs. *Mar. Ecol. Prog. Ser.* 40: 41-51.

Lapointe BE (1999). Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. *Limnol. Oceanogr.* 44: 1586-1592.

Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (in press) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs*

Lessios HA (1988). Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annu. Rev. Ecol. Syst.* 19: 371-393.

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56: 183-200.

Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. 87: 215-228

Lobel PS (1980). Herbivory by damselfishes and their role in coral reef community ecology. *Bull. Mar. Sci.* 30: 273-289.

Lundberg B, Lipkin Y (1979). Natural food of the herbivorous rabbitfish (*Siganus* spp.) in Northern Red Sea. *Bot. Mar.*22: 173-181.

McClanahan TR, Muthiga NA (1998). An ecological shift in a remote coral reef atoll of Belize over 25 years. *Environ. Conserv.* 25: 122-130.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones SH (2003). Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Mar. Ecol. Prog. Ser.* 261:135-147.

McCook LJ (1996). Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: Cross-shelf transplants. *Mar. Ecol. Prog. Ser.* 139: 179-192.

McCook LJ (1997). Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Mar. Biol.* 129: 713-722.

McCook LJ (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357-367.

McCook LJ, Price IR (1997a). The state of the algae of the Great Barrier Reef: what do we know? In: Wachenfeld D, Oliver J, Davis K (eds). *State of the Great Barrier Reef World Heritage Area Report*. GBRMPA, Townsville, pp 194-204.

McCook LJ, Price IR (1997b). Macroalgal distributions on the Great Barrier Reef: A review of patterns and causes. *Proc. Great Barrier Reef: science, use and management, A Nat. Conf.*, vol 2. GBRMPA, Townsville pp 37-46.

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003). Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421: 727-730.

McManus JW, Polsenberg JF (2004). Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progr.Oceanogr.*60: 263-279.

- Mumby PJ et al (2006). Fishing, trophic cascades and the process of grazing on coral reefs. *Science* 311: 98-101.
- Mumby PJ et al (2007). Trophic cascade facilitates coral recruitment in a marine reserve. *Proc. Natl. Acad. Sci.* 104: 8362-8367
- Myers RF (1989) *Micronesian reef fishes*. Coral Graphics, Guam.
- Nyström M, Folke C, Moberg F (2000). Coral reef disturbance and resilience in a human-dominated environment. *TREE*. 15: 413-417.
- Nyström M, Folke C (2001). Spatial resilience of coral reefs. *Ecosystems* 4: 406-417.
- Ogden JC, Lobel PS (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.* 3: 49-63.
- Pandolfi JM et al (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301: 955-958.
- Polunin NVC, Klumpp DW (1992). Algal food supply and grazer demand in a very productive coral-reef zone. *J. Exp. Mar. Biol. Ecol.* 164: 1-15.
- Polunin NVC, Harmelin-Vivien M, Galzin R (1995) Contrasts in algal food processing among five herbivorous coral-reef fishes. *J of Fish Biol.* 47: 455-465
- Purcell SW, Bellwood DR (1993). A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Env. Biol. Fish.* 37: 139-159.
- Purcell SW, Bellwood DR (2001). Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs* 20: 117-125.
- Randall JE, Allen GR, Steene RC (1997). *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Publishing Pty. Ltd., Australia. pp557.



Rimmer DW, Wiebe WJ (1987). Fermentative microbial digestion in herbivorous fishes. *J. Fish Biol.* 31: 229-236.

Robertson DR, Gaines SD (1986). Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67: 1372-1383.

Russ GR (1984a). Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* 20: 23-34.

Russ GR (1984b). Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II Patterns of zonation of mid-shelf and outer shelf reefs. *Mar. Ecol. Prog. Ser.* 20: 35-44.

Russ GR (2003). Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22: 63-67.

Russ GR, McCook LJ (1999). Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *J. Exp. Mar. Biol. Ecol.* 235: 237-254.

Sammarco PW (1983). Effects of fish grazing and damselfish territoriality on coral reef algae I. Algal community structure. *Mar. Ecol. Prog. Ser.* 13:1-14.

Scott FJ, Russ GR (1987). Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 39:293-304.

Smith JE, Smith CM, Hunter CL (2001). An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19: 332-342.

Stimson J, Larned ST, Conklin E (2001). Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19: 343-357.



Stephenson W, Searles RB (1960). Experimental studies on the ecology of intertidal environments at Heron Island I. Exclusion of fish from beach rock. *Austr. J. Mar. Freshwater Res.* 2: 241-267.

Wilkinson CR (1999). Global and local threats to coral reef functioning and existence: review and predictions. *Mar. Freshw. Res.* 50: 867-878.

Wilkinson CR, ed. (2004). *Status of the Coral Reefs of the World: 2004*. Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville, Queensland, Australia.

Wilkinson CR, Sammarco PW (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. *Mar. Ecol. Prog. Ser.* 13:15-19.

Wilson S, Bellwood DR (1997). Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). *Mar. Ecol. Prog. Ser.* 153: 299-310.

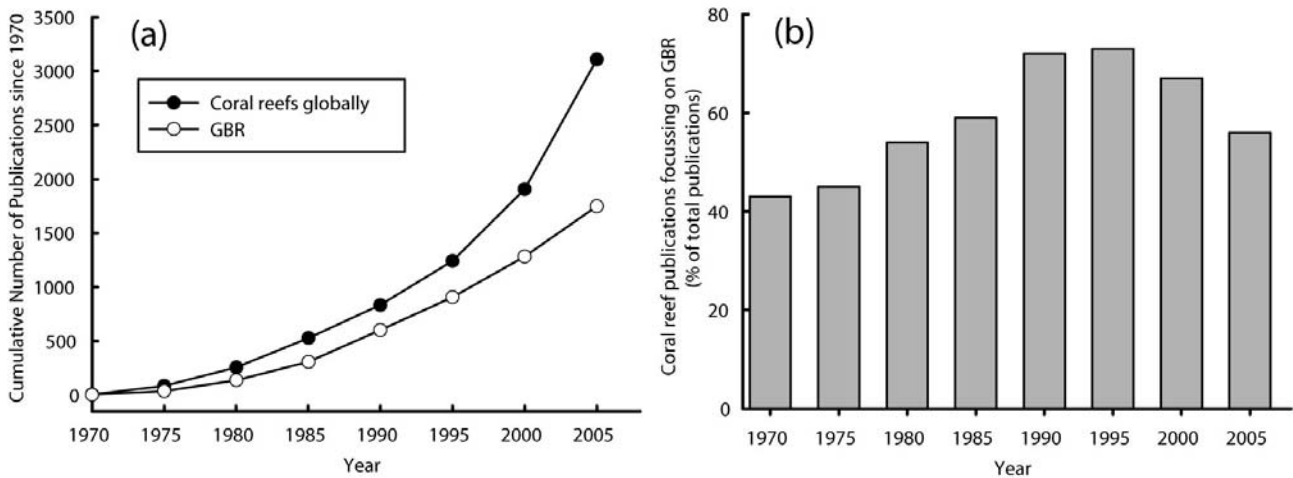
Wilson SK (2000). Trophic status and feeding selectivity of blennies (Blenniidae: Salariaiini). *Mar. Biol.* 136: 431-437.

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanogr. Mar. Biol. Ann. Rev.* 41: 279-309.

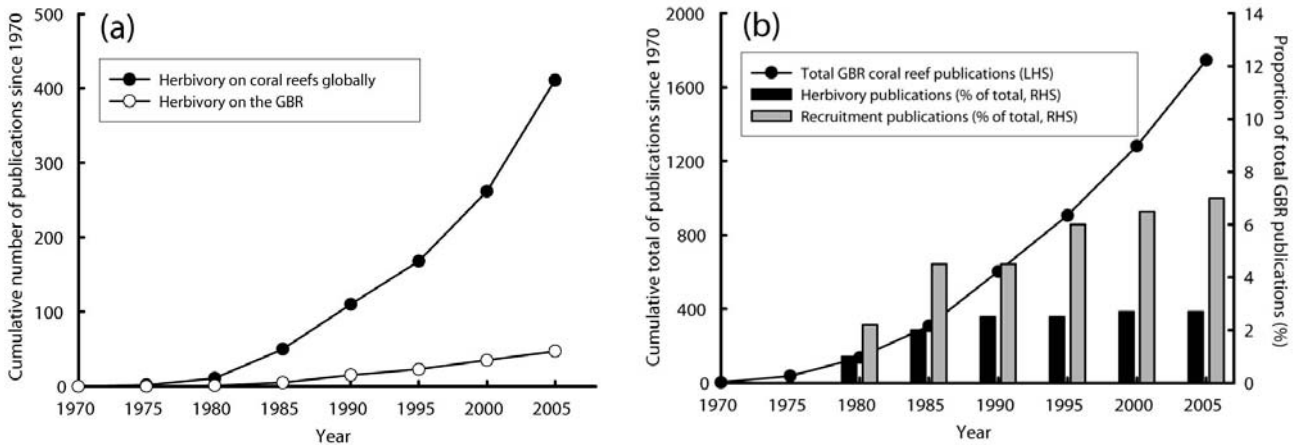
Woodland DJ (1990) Revision of the family Siganidae with descriptions of two new species and comments on the distribution and biology. *Indo-Pac. Fish.* 19: 1-136



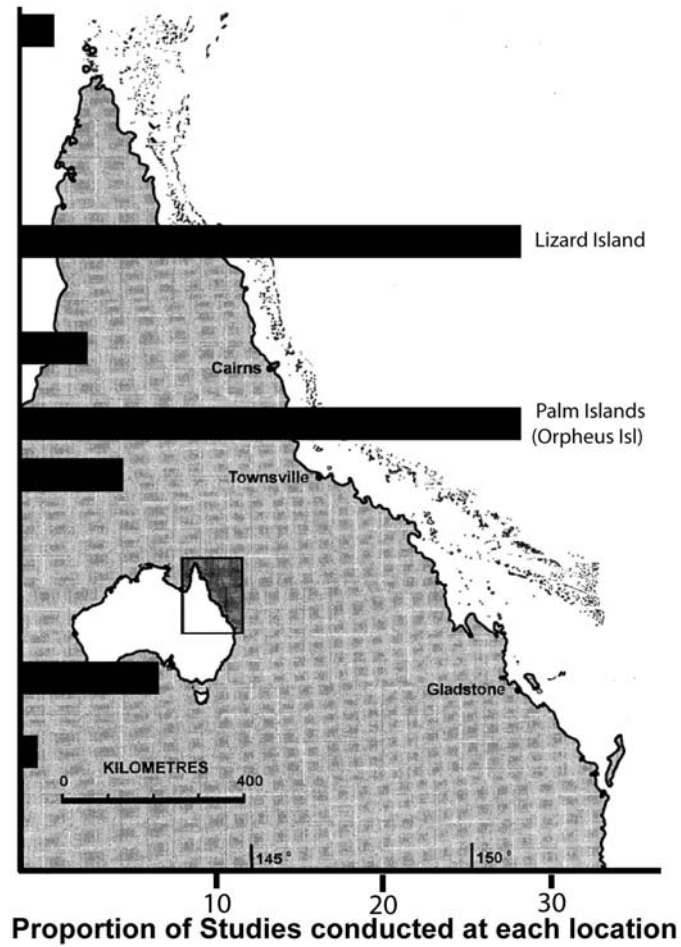
## Figures and Tables



**Fig. 1:** Share of global research on coral reefs devoted to the GBR. (a) Comparison of cumulative totals of publications in the world and the GBR region respectively (figures obtained from searches on Biological Abstracts database). (b) Research publications based on the GBR as a proportion of total publications.



**Fig. 2:** Share of research on the GBR devoted to herbivory. (a) Comparison of cumulative totals of publications since 1970 relating to herbivory on all reefs globally and on the GBR. (b) Proportion of total coral reef publications from the GBR relating specifically to herbivory compared to the proportion devoted to study of recruitment. All searches conducted on the Biological Abstracts database.



**Fig. 3:** Distribution of studies on herbivory on the GBR. The number of studies conducted at particular latitudes and locations are shown as a percentage of the total number of herbivory publications from the GBR.

**Table 1:** Summary of herbivorous, detritivorous and omnivorous species known from the GBR. Overall number of species presumed herbivores are those reported from the region (Randall et al 1997). Assumed dietary status numbers are based on published reports of feeding behaviour or diet without associated gut content analysis. Number of species confirmed as herbivores and detritivores are based on published gut content analyses – see Annex A for further detail on dietary information for individual species.

Family	Total number of herbivorous* species (GBR)	Number of species currently assumed to be within each trophic grouping (and number with published, quantitative details of predominant dietary components)		
		Herbivores	Detritivores	Omnivores
Acanthuridae	27	19 (9)	5 (3)	3 (3)
Blenniidae	47		47 (9)	
Gobiidae	1		1 (1)	
Ephippidae	1			1
Kyphosidae	2	2 (2)		
Labridae (scarids)	26		24 (3)	2 (1)
Pomacanthidae	2	2 (1)		
Pomacentridae	61	18 (0)	8 (3)	35 (0)
Siganidae	11	9 (0)		2 (1)
<b>Total</b>	<b>178</b>	<b>50 (12)</b>	<b>85 (19)</b>	<b>43 (4)</b>

\* including nominally herbivorous and detritivorous

**Table 2:** Published baseline data on the distribution, abundance and biomass (or biomass-related population impact) of herbivorous fishes on GBR.

<b>Geographic location</b>	<b>Source</b>	<b>Data</b>	<b>Reef zones</b>
Inner, mid, outer shelf and Coral Sea reefs, central GBR region	Williams 1982	Abundance categories for Pomacentridae, Acanthuridae, descriptions for Scaridae & Siganidae based on visual censuses	Reef slope from 0-13m along reef face.
Inner, mid and outer shelf reefs, central GBR region	Williams & Hatcher 1983	Abundance and biomass of families classified by trophic category based on explosive sampling	Reef slope at 5m and 9m
Inner, mid and outer shelf reefs, central GBR region	Russ 1984a	Abundance (number per census) of roving herbivores (Acanthuridae, Scaridae & Siganidae), based on visual censuses	Slope, crest, reef flat, lagoon and back reef for mid and outer shelf reefs
Mid and outer shelf reefs, central GBR region	Russ 1984b	Number of species in families Acanthuridae, Scaridae & Siganidae, based on visual censuses. Abundances of guilds and individual species across individual zones of 6 reefs.	Slope, crest, reef flat, lagoon and back reef
Lizard Isl, northern GBR	Bellwood 1995b	Total rates of bioerosion by <i>Chlorurus microrhinos</i> and <i>C. sordidus</i>	Not specified
Davies Reef, central GBR	Klumpp & Polunin 1989	Grazing rates (mg m <sup>-2</sup> day <sup>-1</sup> ) for <i>Scarus globiceps</i> , <i>Chlorurus sordidus</i> , <i>S. niger</i> , <i>S. frenatus</i> within <i>Stegastes</i> territories in winter. Grazing rate (mg C day <sup>-1</sup> ) of <i>Stegastes apicalis</i> .	Reef flat
Davies Reef, central GBR	Klumpp & Polunin 1990	Abundance and biomass estimates of <i>P. flavicauda</i> and <i>S. fasciatus</i> . Grazing rates (mg m <sup>-2</sup> day <sup>-1</sup> ) for <i>Scarus globiceps</i> , <i>Chlorurus sordidus</i> , <i>S. niger</i> , <i>S. frenatus</i> within <i>Stegastes</i> territories in April.	Reef flat

Mid and outer shelf reefs, northern GBR	Gust et al 2001	Abundance estimates for individual species of scarid and biomass estimates for scarid group as a whole, based on visual censuses	Reef crest
Mid and outer shelf reefs, northern GBR	Gust 2002	Abundance estimates for individual species of scarid and biomass estimates for scarid group as a whole, based on visual censuses	reef crest habitat, windward & leeward side
Inner, mid & outer shelf reefs, northern GBR	Bellwood et al 2003	Bioerosion rates of <i>Bolbopetopon muricatum</i> , <i>Chlorurus microrhinos</i> & <i>Scarus</i> spp.	Backreef, reef flat, reef crest, reef slope
Myrmidon Reef, central GBR	Russ 2003	Biomass of roving herbivores based on visual censuses conducted for Russ 1984a, b	Slope, crest and reef flat
Lizard Isl reefs, northern GBR	Wilson et al 2003	Density estimates of Blenniidae, Pomacentridae, Kyphosidae, Siganidae, Acanthuridae, Scaridae	Slope & crest (exposed) and shallow and slope of back reef
Magnetic Isl, central GBR	Ceccarelli et al 2005a	Abundance estimates and territory size of <i>P. tripunctatus</i> , <i>Pwardi</i> and <i>S.apicalis</i> , based on visual censuses	Slope, crest, outer reef flat, mid reef flat, inner reef flat
Orpheus Isl, central GBR	Ceccarelli et al 2006	Abundance estimates and territory size of <i>P. wardi</i> and <i>P.adelus</i> , based on visual census	Reef crest
Orpheus Isl, Central GBR	Bellwood et al 2006	Abundance and biomass estimates of roving herbivores based on visual census	Crest
Orpheus Isl, Central GBR	Fox & Bellwood (in press)	Abundance and biomass estimates of roving herbivores based on visual censuses	Slope, crest, outer reef flat, mid reef flat & inner reef flat
Inner, mid & outer shelf reefs, northern GBR	Hoey & Bellwood (in prep)	Biomass estimates of scarids based on visual censuses	Slope, crest, flat and back reef habitats

**Annex A:** Summary of species from the GBR currently presumed to be herbivores (based on Randall et al 1997). For those species where dietary status has been confirmed, the published source is listed.

H = herbivore, O = omnivore, D = detritivore, G = grazer on EAM, M = macroalgal feeder, AF = algal film on sand, T = territorial

Family	Genus	Species	Dietary Status	Source
Acanthuridae	<i>Acanthurus</i>	<i>A. auranticavus</i>	H?	
Acanthuridae	<i>Acanthurus</i>	<i>A. bariene</i>	H?	
Acanthuridae	<i>Acanthurus</i>	<i>A. blochii</i>	H?	
Acanthuridae	<i>Acanthurus</i>	<i>A. dussumieri</i>	H (G)	Jones 1968
Acanthuridae	<i>Acanthurus</i>	<i>A. grammoptilus</i>	H?	
Acanthuridae	<i>Acanthurus</i>	<i>A. guttatus</i>	H	Jones 1968
Acanthuridae	<i>Acanthurus</i>	<i>A. lineatus</i>	H (T)	Choat et al 2002
Acanthuridae	<i>Acanthurus</i>	<i>A. nigricans</i>	H	Choat et al 2002
Acanthuridae	<i>Acanthurus</i>	<i>A. nigricauda</i>	D	Choat et al 2002
Acanthuridae	<i>Acanthurus</i>	<i>A. nigrofuscus</i>	H (G)	Robertson & Gaines 1986
Acanthuridae	<i>Acanthurus</i>	<i>A. nigroris</i>	H (G)	Jones 1968
Acanthuridae	<i>Acanthurus</i>	<i>A. olivaceus</i>	D	Myers 1989
Acanthuridae	<i>Acanthurus</i>	<i>A. pyroferus</i>	H?	
Acanthuridae	<i>Acanthurus</i>	<i>A. triostegus</i>	H (G)	Robertson & Gaines 1986
Acanthuridae	<i>Acanthurus</i>	<i>A. xanthopterus</i>	H (G)	Hiatt & Strasburg 1960
Acanthuridae	<i>Ctenochaetus</i>	<i>C. binotatus</i>	D?	Choat 1991
Acanthuridae	<i>Ctenochaetus</i>	<i>C. striatus</i>	D	Choat et al 2002
Acanthuridae	<i>Ctenochaetus</i>	<i>C. strigosus</i>	D?	Choat 1991
Acanthuridae	<i>Zebrasoma</i>	<i>Z. scopas</i>	H (M)	Choat et al 2002
Acanthuridae	<i>Zebrasoma</i>	<i>Z. veliferum</i>	H (M)	Hiatt & Strasburg 1960
Acanthuridae	<i>Naso</i>	<i>N. annulatus</i>	O	Choat et al 2002
Acanthuridae	<i>Naso</i>	<i>N. brachycentron</i>	H	Clements & Choat 1995
Acanthuridae	<i>Naso</i>	<i>N. brevirostris</i>	O	Choat et al 2002
Acanthuridae	<i>Naso</i>	<i>N. lituratus</i>	H (M)	Robertson & Gaines 1986
Acanthuridae	<i>Naso</i>	<i>N. tonganus / tuberosus</i>	H (M)	Myers 1989
Acanthuridae	<i>Naso</i>	<i>N. unicornis</i>	H (M)	Robertson & Gaines 1986
Acanthuridae	<i>Naso</i>	<i>N. vlamingii</i>	O	Choat et al 2002
Blenniidae	<i>Aspidontus</i>	<i>A. dussumieri</i>	D?	
Blenniidae	<i>Atrosalarias</i>	<i>A. fuscus</i>	D	Wilson 2000
Blenniidae	<i>Blenniella</i>	<i>B. chrysoopilos</i>	D?	
Blenniidae	<i>Blenniella</i>	<i>B. paula</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. alboapicalis</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. castaneus</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. chelomatus</i>	D	Wilson 2000
Blenniidae	<i>Cirripectes</i>	<i>C. filamentosus</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. polyzona</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. quagga</i>	D?	
Blenniidae	<i>Cirripectes</i>	<i>C. stigmaticus</i>	D?	
Blenniidae	<i>Crossosalarias</i>	<i>C. macrospilus</i>	D?	
Blenniidae	<i>Ecsenius</i>	<i>E. aequalis</i>	D?	
Blenniidae	<i>Ecsenius</i>	<i>E. australianus</i>	D?	
Blenniidae	<i>Ecsenius</i>	<i>E. bicolor</i>	D	Wilson 2000
Blenniidae	<i>Ecsenius</i>	<i>E. mandibularis</i>	D	Wilson 2000
Blenniidae	<i>Ecsenius</i>	<i>E. stictus</i>	D	Wilson 2000
Blenniidae	<i>Ecsenius</i>	<i>E. tigris</i>	D?	
Blenniidae	<i>Enchelyurus</i>	<i>E. ater</i>	D?	
Blenniidae	<i>Enchelyurus</i>	<i>E. kraussi</i>	D?	
Blenniidae	<i>Entomacrodus</i>	<i>E. decussatus</i>	D?	

Blenniidae	<i>Entomacrodus</i>	<i>E. striatus</i>	D?	
Blenniidae	<i>Exallias</i>	<i>E. brevis</i>	D?	
Blenniidae	<i>Glyptoparus</i>	<i>G. delicatulus</i>	D	Wilson 2000
Blenniidae	<i>Istiblennius</i>	<i>I. dussumieri</i>	D?	
Blenniidae	<i>Istiblennius</i>	<i>I. edentulus</i>	D?	
Blenniidae	<i>Istiblennius</i>	<i>I. lineatus</i>	D?	
Blenniidae	<i>Istiblennius</i>	<i>I. meleagris</i>	D?	
Blenniidae	<i>Meiacanthus</i>	<i>M. ditrema</i>	D?	
Blenniidae	<i>Meiacanthus</i>	<i>M. grammistes</i>	D?	
Blenniidae	<i>Meiacanthus</i>	<i>M. lineatus</i>	D?	
Blenniidae	<i>Meiacanthus</i>	<i>M. luteus</i>	D?	
Blenniidae	<i>Nannosalarias</i>	<i>N. nativitatus</i>	D?	
Blenniidae	<i>Petroscirtes</i>	<i>P. fallax</i>	D?	
Blenniidae	<i>Petroscirtes</i>	<i>P. lupus</i>	D?	
Blenniidae	<i>Petroscirtes</i>	<i>P. mitratus</i>	D?	
Blenniidae	<i>Petroscirtes</i>	<i>P. variabilis</i>	D?	
Blenniidae	<i>Petroscirtes</i>	<i>P. xestus</i>	D?	
Blenniidae	<i>Plagiotremus</i>	<i>P. laudandus</i>	D?	
Blenniidae	<i>Omobranchus</i>	<i>O. anolius</i>	D?	
Blenniidae	<i>Parenchelyurus</i>	<i>P. hepburni</i>	D?	
Blenniidae	<i>Rhabdoblennius</i>	<i>R. ellipes</i>	D?	
Blenniidae	<i>Salarias</i>	<i>S. fasciatus</i>	D	Wilson 2000
Blenniidae	<i>Salarias</i>	<i>S. guttatus</i>	D	Wilson 2000
Blenniidae	<i>Salaris</i>	<i>S. patzneri</i>	D	Wilson 2000
Blenniidae	<i>Stanulus</i>	<i>S. talboti</i>	D?	
Blenniidae	<i>Xiphasia</i>	<i>X. setifer</i>	D?	
Ehippidae	<i>Platax</i>	<i>P. pinnatus</i>	O (M)	Bellwood et al 2006
Gobiidae	<i>Amblygobius</i>	<i>A. rainfordi</i>	D	Depczynski and Bellwood 2003
Kyphosidae	<i>Kyphosus</i>	<i>K. cinerascens</i>	H	Choat et al 2002
Kyphosidae	<i>Kyphosus</i>	<i>K. vaigiensis</i>	H (M)	Choat et al 2002
Labridae	<i>Bolbometapon</i>	<i>B. muricatum</i>	O	Bellwood et al 2003
Labridae	<i>Calotomus</i>	<i>C. carolinus</i>	G (D?)	
Labridae	<i>Calotomus</i>	<i>C. spinidens</i>	G (D?)	
Labridae	<i>Cetoscarus</i>	<i>C. bicolor</i>	O	Bellwood & Choat 1990
Labridae	<i>Chlorurus</i>	<i>C. bleekeri</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Chlorurus</i>	<i>C. frontalis</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Chlorurus</i>	<i>C. microrhinos</i>	D	Choat et al 2002
Labridae	<i>Chlorurus</i>	<i>C. sordidus</i>	D	Choat et al 2002
Labridae	<i>Hipposcarus</i>	<i>H. longiceps</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Leptoscarus</i>	<i>L. vaigiensis</i>	G (D?)	
Labridae	<i>Scarus</i>	<i>S. altipinnis</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. chameleon</i>	AF (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. dimidiatus</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. flavipectoralis</i>	AF (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. forsteni</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. frenatus</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. ghobban</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. globiceps</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. longipinnis</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. niger</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. oviceps</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. psittacus</i>	G (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. rivulatus</i>	O (D?)	Bellwood & Choat 1990
Labridae	<i>Scarus</i>	<i>S. rubroviolaceus</i>	G (D?)	Clements & Bellwood 1988
Labridae	<i>Scarus</i>	<i>S. schlegeli</i>	D	Choat et al 2002
Labridae	<i>Scarus</i>	<i>S. spinus</i>	G (D?)	Bellwood & Choat 1990
Pomacanthidae	<i>Centropyge</i>	<i>C. flavissimus</i>	H (G?)	
Pomacanthidae	<i>Centropyge</i>	<i>C. bicolor</i>	H (G)	Myers 1989
Pomacentridae	<i>Abudefduf</i>	<i>A. bengalensis</i>	O?	Choat 1991
Pomacentridae	<i>Abudefduf</i>	<i>A. septemfasciatus</i>	O?	Choat 1991
Pomacentridae	<i>Abudefduf</i>	<i>A. sexfasciatus</i>	O?	Choat 1991
Pomacentridae	<i>Abudefduf</i>	<i>A. sordidus</i>	O?	Choat 1991

Pomacentridae	<i>Abudefduf</i>	<i>A. vaigiensis</i>	O?	Choat 1991
Pomacentridae	<i>Abudefduf</i>	<i>A. whitleyi</i>	O?	Choat 1991
Pomacentridae	<i>Abudefduf</i>	<i>A. polyacanthus</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. biocellata</i>	H (T)?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. caeruleolineatus</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. cyanea</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. flavipinnis</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. glauca</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. brownriggii</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. rex</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. rollandi</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. starcki</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. talboti</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. taupou</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. tricineta</i>	O?	Choat 1991
Pomacentridae	<i>Chrysiptera</i>	<i>C. unimaculata</i>	O?	Choat 1991
Pomacentridae	<i>Dischistodus</i>	<i>D. melanotus</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. perspicillatus</i>	D (T)	Wilson & Bellwood 1997
Pomacentridae	<i>Dischistodus</i>	<i>D. prosopotaenia</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. pseudochrysopoecilus</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. melanotus</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. perspicillatus</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. prosopotaenia</i>	D(T)?	
Pomacentridae	<i>Dischistodus</i>	<i>D. pseudochrysopoecilus</i>	D(T)?	
Pomacentridae	<i>Hemiglyphidodon</i>	<i>H. plagiometopon</i>	D (T)	Willson & Bellwood 1997
Pomacentridae	<i>Parma</i>	<i>P. oligolepis</i>	H (T)?	Choat 1991
Pomacentridae	<i>Parma</i>	<i>P. polylepis</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. dickii</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. imparipennis</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. johnstonianus</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. lacrymatus</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. leucozonus</i>	H (T)?	Choat 1991
Pomacentridae	<i>Plectroglyphidodon</i>	<i>P. phoenixensis</i>	H (T)?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. amboinensis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. australis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. bankanensis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. brachialis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. chrysurus</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. coelestis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. grammorhynchus</i>	H (T)?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. imitator</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. lepidogenys</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. moluccensis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. nagasakiensis</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. nigromarginatus</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. pavo</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. philippinus</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. reidi</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. tripunctatus</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. vaiuli</i>	O?	Choat 1991
Pomacentridae	<i>Pomacentrus</i>	<i>P. wardi</i>	H(T)?	Choat 1991
Pomacentridae	<i>Stegastes</i>	<i>S. albifasciatus</i>	D (T)?	
Pomacentridae	<i>Stegastes</i>	<i>S. apicalis</i>	D (T)?	
Pomacentridae	<i>Stegastes</i>	<i>S. fasciolatus</i>	D (T)?	
Pomacentridae	<i>Stegastes</i>	<i>S. gascoynei</i>	D (T)?	
Pomacentridae	<i>Stegastes</i>	<i>S. lividus</i>	D (T)?	
Pomacentridae	<i>Stegastes</i>	<i>S. nigricans</i>	D (T)	Wilson & Bellwood 1997 Lundberg & Lipkin 1979, Woodland 1990
Siganidae	<i>Siganus</i>	<i>S. argenteus</i>	O	
Siganidae	<i>Siganus</i>	<i>S. canaliculatus / margaritiferus / fuscensens</i>	H (M?)	Randall et al 1997
Siganidae	<i>Siganus</i>	<i>S. corallinus</i>	H (G?)	Randall et al 1997



Siganidae	<i>Siganus</i>	<i>S. doliatus</i>	H	Woodland 1990
Siganidae	<i>Siganus</i>	<i>S. lineatus</i>	O	Woodland 1990
Siganidae	<i>Siganus</i>	<i>S. puellus</i>	H (G?)	Randall et al 1997
Siganidae	<i>Siganus</i>	<i>S. punctatissimus</i>	H (G?)	Randall et al 1997
Siganidae	<i>Siganus</i>	<i>S. punctatus</i>	H (G)	Woodland 1990
Siganidae	<i>Siganus</i>	<i>S. spinus</i>	H (M?)	Hiatt & Strasburg 1960
Siganidae	<i>Siganus</i>	<i>S. vermiculatus</i>	H (G?)	Randall et al 1997
Siganidae	<i>Siganus</i>	<i>S. vulpinus</i>	H (G?)	Randall et al 1997

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