

Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs?

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Abstract With coral cover in decline on many Caribbean reefs, any process of coral mortality is of potential concern. While sparismid parrotfishes are major grazers of Caribbean reefs and help control algal blooms, the fact that they also undertake corallivory has prompted some to question the rationale for their conservation. Here the weight of evidence for beneficial effects of parrotfishes, in terms of reducing algal cover and facilitating demographic processes in corals, and the deleterious effects of parrotfishes in terms of causing coral mortality and chronic stress, are reviewed. While elevated parrotfish density will likely increase the predation rate upon juvenile corals, the net effect appears to be positive in enhancing coral recruitment through removal of macroalgal competitors. Parrotfish corallivory can cause modest partial colony mortality in the most intensively grazed species of *Montastraea* but the generation and healing of bite scars appear to be in near equilibrium, even when coral cover is low. Whole colony mortality in adult corals can lead to complete exclusion of some delicate, lagoonal species of *Porites* from forereef environments but is only reported for one reef species (*Porites astreoides*), for one habitat (backreef), and with uncertain incidence (though likely $\ll 10\%$). No deleterious effects of predation on coral growth or fecundity have been reported, though recovery of zooxanthellae after bleaching events may be retarded. The balance of evidence to date finds strong support for the herbivory role of

parrotfishes in facilitating coral recruitment, growth, and fecundity. In contrast, no net deleterious effects of corallivory have been reported for reef corals. Corallivory is unlikely to constrain overall coral cover but constraints upon dwindling populations of the *Montastraea annularis* species complex are feasible and the role of parrotfishes as a vector of coral disease requires evaluation. However, any assertion that conservation practices should guard against protecting corallivorous parrotfishes appears to be unwarranted at this stage.

Keywords Conservation · Mortality · Coral · Herbivore

Introduction

Parrotfish are some of the most abundant fish on Caribbean reefs and they usually dominate the biomass of herbivorous fishes ($>80\%$), which also includes acanthurids, kyphosids and pomacentrids. The impacts of parrotfish feeding have been studied since the 1960s (Randall 1965) and while it differs among species (Bruggemann et al. 1996; Burkepile and Hay 2008), the vast majority of feeding activity is directed towards algal substrates, including encrusting corallines, algal turfs and macroalgae (Barlow 1975; Gygi 1975; Bruggemann et al. 1994a). Not surprisingly, experimental and observational studies have found that parrotfish grazing can exert strong top-down impacts on the cover of macroalgae on reefs (Hay 1981; Carpenter 1986; Lewis 1986; Steneck 1997; Williams and Polunin 2000; Williams et al. 2001; Mumby et al. 2006; Burkepile and Hay 2008). Given concern over the deleterious consequences of phase shifts towards increased macroalgal cover (Done et al. 1996), many authors have argued that parrotfish conservation should, in principle, benefit coral reefs

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and the ecosystem services they provide (Steneck 1988; Hughes 1994; Bellwood et al. 2004; Newman et al. 2006; Hoegh-Guldberg et al. 2007; Knowlton and Jackson 2008; Mumby and Steneck 2008; Nystrom et al. 2008). The point made by these studies is that the grazing behaviour of parrotfish should benefit corals by helping to limit their algal competitors.

While parrotfishes primarily feed from algal substrates, corallivory has also been widely reported (Fig. 1), particularly from species in the genus *Sparisoma* such as *S. viride* and *S. aurofrenatum* (Barlow 1975; Frydl 1979; Bruggemann et al. 1994b; Bruckner and Bruckner 1998; Bruckner et al. 2000; Sanchez et al. 2004; Rotjan and Lewis 2006). Two forms of parrotfish corallivory have been described; ‘spot biting’ in which individual bite-sized lesions are distributed over the coral skeleton and ‘focused biting’ in which a larger, continuous patch of coral tissue is excavated by repeated, overlapping predation (Fig. 2; Bruckner et al. 2000).

With coral cover having declined in much of the Caribbean (Gardner et al. 2003), any process of corallivory has the potential to exacerbate other sources of coral mortality such as coral disease or bleaching (Kramer 2003). Indeed, the dual trophic role of parrotfishes in grazing algae and corals has led some to question the rationale for conserving corallivorous parrotfishes (Rotjan and Lewis 2008). This review aims to assess the net impact of



Fig. 1 Predation of *Montastraea annularis* by a terminal phase stoplight parrotfish, *Sparisoma viride*. Photo credit: Andrew Bruckner

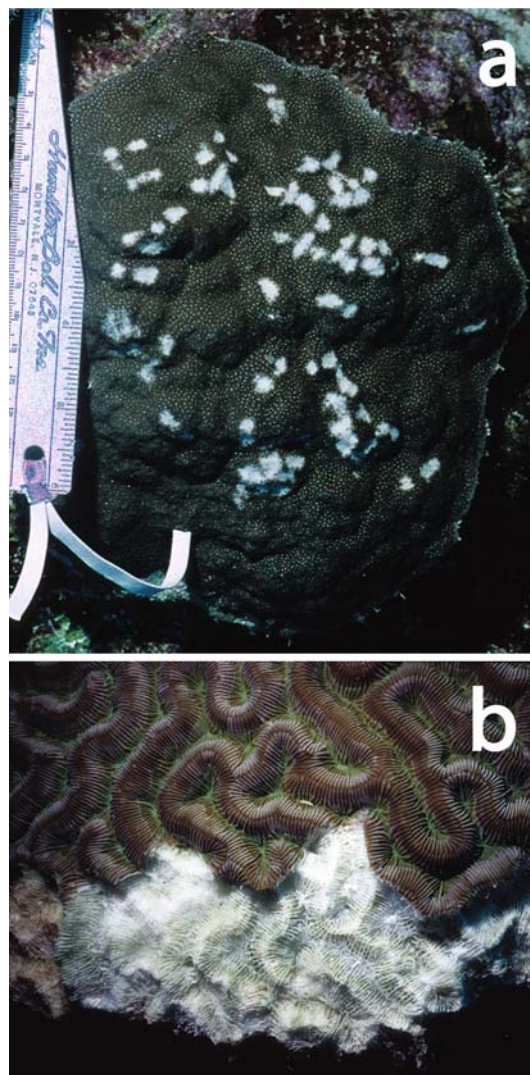


Fig. 2 Bite patterns of parrotfish corallivory showing **a** spot biting on *Porites astreoides* and **b** focused-biting on *Colpophyllia natans*. Photo credit: Andrew Bruckner

parrotfish feeding on the population dynamics of corals. Given that corals underpin ecosystem services, processes of corallivory are considered to be negative impacts whereas the consumption of algae is considered a positive effect. In short, the review attempts to weigh the evidence for negative and positive impacts of parrotfish on Caribbean reefs, and in so doing, highlights implications for reef management and future research. The impacts of parrotfish grazing are reviewed separately for each major demographic process of corals.

Coral recruitment

The degree to which parrotfishes prey directly or inadvertently on coral recruits is unknown. In a study of macroalgal impacts on recruits of the coral *Agaricia* (diameter

1 cm), Box and Mumby (2007) found that 15% of uncaged corals suddenly disappeared. They attributed this mortality to parrotfish predation rather than physical dislodgement by wave action because none of the caged treatments exhibited such sudden mortality, and it was unlikely that caging effects would have been sufficient to account for a refuge from wave disturbance in all replicates given the high flow in some microhabitats that were not potentially sheltered by adult colonies. Moreover, Bak and Engel also observed that grazing fishes could damage juvenile corals (Bak and Engel 1979). In contrast, Birkeland (1977) found no evidence of predation upon coral recruits, when examining coral settlement substrates after they had been grazed intensively by acanthurids and small parrotfishes in Panama. While it should be borne in mind that Box and Mumby (2007) did not prove that parrotfish predation was the cause of recruit mortality, the two studies may be partly reconciled by considering the parrotfish species involved. The study by Box and Mumby (2007) was carried out on a forereef in Honduras and *S. viride*, possibly the most important parrotfish corallivore (Miller and Hay 1998), dominated the parrotfish community (Box 2008). The predominant parrotfish grazers in Birkeland's (1977) study were small parrotfishes, primarily of the species *Scarus iserti*, which rarely feeds on coral (Mumby, personal observation).

Parrotfish grazing has been hypothesized to facilitate coral recruitment through at least three mechanisms. Firstly, grazing of the reef surface helps promote encrusting coralline algae and limit macroalgae, thereby increasing the settlement space available for coral planulae (Steneck 1988). Secondly, grazing helps prevent the establishment of thick algal turfs which can trap sediment and induce post-settlement mortality in coral recruits (Birkeland 1977; Birrell et al. 2005). Similarly, by reducing the cover of macroalgae, grazing may reduce the frequency and duration of competitive interactions between coral recruits and macroalgae. Contact between coral recruits (at least of the genus *Agaricia*) and common macroalgae such as *Lobophora variegata* and *Dictyota pulchella* can reduce recruit growth rates dramatically (Box and Mumby 2007), and possibly reduce their survivorship because the time spent at vulnerable, small sizes is extended.

Overall, if corallivorous species of parrotfish are common on a reef, it seems reasonable to expect a degree of parrotfish-based mortality on coral recruits. Logically, if the number of corallivorous parrotfishes increases on a reef, then the predation rate on coral recruits would be expected to increase also. So, is there any evidence that increasing the number of parrotfish actually has a net negative impact on coral recruitment? Apparently not. In a study of the impact of the Exumas Land and Sea Park which is one of the oldest and most successful marine

reserves in the Caribbean, Mumby et al. (2007a) found a strong positive correlation ($r > 0.8$, $P < 0.001$) between the grazing activity of the parrotfish community and the density of juvenile corals (diameter up to 2 cm). Corallivorous species of parrotfish dominated the community yet coral recruitment increased with grazing, largely in response to the decrease in macroalgae. The study discounted potentially confounding effects of reef rugosity, damselfish abundance and coral cover on coral recruitment, and used high-resolution models of potential larval supply to discount the likelihood that the pattern of grazing coincided with that of larval supply. In short, available evidence suggests that parrotfish grazing has a net positive impact on coral recruitment.

Partial colony mortality

Some of the most detailed studies of partial colony mortality in Caribbean corals took place before the late 1990s (Hughes and Jackson 1985; Bythell et al. 1993; Meesters et al. 1996; Meesters et al. 1997), after which coral diseases have increasingly become a major source of partial mortality (Weil et al. 2006). Parrotfish corallivory was found to be an important source of chronic partial colony mortality in studies from the US Virgin Islands (Bythell et al. 1993) and Curaçao (Meesters et al. 1996; Meesters et al. 1997). Not surprisingly, the number of bite scars on corals has been found to increase with colony size (Meesters et al. 1997), though, whether this indicates a preferential selection of larger colonies by parrotfishes or merely reflects the null expectation that bite prevalence will scale positively with colony surface area is not clear.

Not all coral species are equally susceptible to parrotfish corallivory. In those reef habitats where they are present, the coral species *Montastraea faveolata* and *M. annularis* tend to have the greatest prevalence of bite scars, often exceeding 20% of colonies (Garzon-Ferreira and Reyes-Nivia 2001). Bythell et al. (1993) found that up to 10% of the tissue surface area of *M. annularis* could have been removed by parrotfish in St. Croix. In contrast, several coral species including *Montastraea cavernosa*, *Diploria strigosa* and adult encrusting corals like *Agaricia agaricites* show very low prevalences of corallivory, often less than 1% (Bythell et al. 1993; Garzon-Ferreira and Reyes-Nivia 2001; Reyes-Nivia et al. 2003). The coral *Porites astreoides* appears to experience intermediate levels of predation (Bythell et al. 1993). In Belize, Rotjan and Lewis (2005) generally found low levels of predation on this species, and while the prevalence of scarred colonies varied among reef zones, the greatest prevalence reported was only 4%, and often either 2% or absent. However, in the minority of corals that exhibited predation, the intensity of grazing could be great with nearly half (48%) of the

scarred colonies in backreef areas having lost at least half of their tissue.

Despite the relatively high predation pressure on *M. annularis*, bite scars usually heal within 1–2 months (Bythell et al. 1993; Sanchez et al. 2004). In a particularly revealing study, Sanchez et al. (2004) transplanted 23 ramets of *M. annularis* to a highly-grazed forereef at 10 m. At the beginning of the study, all ramets were free of grazing scars. For the following 13 months, a monthly census was undertaken of the extent of parrotfish-induced mortality on colonies, and used to parameterise a transition matrix of four injury states: 0% of tissue consumed, < 1% consumed, < 5% consumed, > 5% consumed. The study revealed that processes of injury (predation) and recovery are remarkably dynamic. By the end of the study all ramets had experienced injury at some stage but 50% were free of any bite scars, and only a small fraction (< 10%) of ramets had more than 5% of missing tissue. In general, the modal state of a ramet was to remain with < 1% injury (probability 0.31 per month) and the transitions between no bite scars and < 1% injury were virtually at equilibrium (probability of 0% to < 1% was 0.17 and from < 1% to 0% was 0.16).

In summary, parrotfish corallivory varies significantly among species with *M. annularis* and *M. faveolata* being among the most intensively-consumed species and *Diplora strigosa* and *A. agaricites* being among the least. However, even the most intensively-grazed species appears to have a high capacity for tissue regeneration and there is little evidence that processes of predation exceed recovery even on small ramets of coral.

Whole colony mortality (of post-recruits)

The effects of parrotfish predation in causing whole colony coral mortality appears to be restricted to a few, highly-palatable species. Working in the Florida Keys, Miller and Hay (1998) found that delicate colonies of *Porites divaracata* were completely consumed by sparismids within 48 hours of being transplanted from seagrass beds to the forereef. Similarly, intense predation by *S. viride* has excluded the highly-palatable, small branching coral *Porites porites furcata* from parts of a Belizean backreef that are deep enough to allow access for larger herbivores (Littler et al. 1989). Another species of *Porites*, *P. astreoides* has a harder skeleton (Littler et al. 1989) and, while experiencing significant predation (Rotjan and Lewis 2005), is not excluded from either forereef or backreef habitats (Littler et al. 1989; Miller and Hay 1998).

Few, if any, Caribbean cases of parrotfish-driven whole colony mortality have been described for corals that are typically found in reef habitats for which large-bodied fishes have access (i.e., all reef habitats except very

shallow areas). Rotjan and Lewis (2005) categorised 10% of *P. astreoides* colonies in a Belizean backreef system as exhibiting whole colony mortality due to parrotfish predation. While parrotfish predation may indeed have been the cause of mortality, a causal link was not verified by observation, and it remains possible that alternative processes caused the mortality and that parrotfish grazing happened to be intense on the subsequent dead substrate. Uncertainty over the actual causation notwithstanding, it appears that whole colony mortality in reef-associated coral species is—at worst—confined to a small proportion of colonies, within a single species (*P. astreoides*), and a single reef habitat (backreef). Even on these corals, the demographic significance of such mortality is unclear because dead corals can remain in an intensively grazed state for months (Rotjan and Lewis 2005), if not years. Thus, the actual mortality rate might be considerably lower than the observed prevalence of dead, yet intensively grazed, corals.

Coral growth, physiology, and reproduction

Chronic forms of stress, including coral bleaching, have been found to exert deleterious impacts on coral growth (Mascarelli and Bunkley-Williams 1999). Whether parrotfish corallivory exerts a significant deleterious influence on the physiology of the coral holobiont remains unclear. There is clearly a metabolic cost to healing bite lesions but no evidence to date that such costs extend to significant reductions in coral growth rate or fecundity. A study of zooxanthellae densities in the coral *Montastraea* spp. found that recovery rates shortly after a minor bleaching event (and hurricane) were lower in colonies that had experienced some parrotfish predation (>6 scars) than in colonies that had no grazing scars (Rotjan et al. 2006). Whether differences in the zooxanthellae communities between grazed and non-grazed colonies persist for long after the bleaching event is unclear, as are the physiological implications of such differences in symbionts for coral growth, but the study implies that bite lesions may be a contributory form of stress in *Montastraea*.

The direct effects (if any) of parrotfish predation on the fecundity of coral colonies has not yet been quantified. However, contact between common Caribbean macroalgae, including *Dictyota* and *Lobophora*, during the period of gametogenesis in the coral *M. annularis* have been shown to reduce egg size, the number of eggs per gonad and the number of gonads per polyp (Foster et al. 2008). Thus, the removal of macroalgae by grazing is likely to alleviate macroalgal impacts on coral fecundity and help maintain larval connectivity.

Discussion

The title of this article, ‘Are parrotfish good or bad for Caribbean reefs?’, is intended to be provocative rather than pose an appropriate question for discussion; few aspects of nature warrant such polarised viewpoints. The real aim of this review is to weigh the negative demographic impacts of corallivory against the positive demographic impacts on coral of reducing the cover of algal competitors.

Parrotfish corallivory has received a modest degree of research over the last two decades and the conclusions of most studies appear to be consistent. Evidence for negative influences of corallivory principally find that corallivory is able to exclude a few highly palatable species of *Porites* from reefs and that predation-based partial colony mortality can be modest (10% of tissue) in the most intensively grazed species of *Montastraea*, but its prevalence is generally low (<4%) in the community for most species. Claims that ‘parrotfish predation has a direct adverse effect on coral survival’ (Rotjan and Lewis 2005) are not borne out by data at a population scale. As a source of partial coral mortality, bite scars on the most intensively grazed corals can heal within weeks, generating a potentially equilibrium dynamic between injury and recovery (Sanchez et al. 2004). Corallivory may constitute a source of acute mortality in coral recruits, but the available evidence implies that any negative impacts are outweighed by positive effects in removing algal competitors (Mumby et al. 2007a). With the exception of a few (<1%) intensively grazed coral colonies, there is little evidence that parrotfish corallivory contributes to whole colony mortality in adult corals. One possible exception is *P. astreoides* in backreef habitats, but even here where whole colony mortality has been attributed to corallivory (Rotjan and Lewis 2005), the demographic significance of such mortality is likely to be limited. For example, if we assume that heavily grazed corals can remain in that state for 2 years (after which they become colonised by fleshy algae), then the observed prevalence of 10% of *P. astreoides* colonies found in a wholly grazed state (Rotjan and Lewis 2005) could, in principle, reflect an underlying parrotfish-driven coral mortality rate of only 5% or less (assuming that the system is in steady state). Such low levels of mortality are predicted to have limited demographic consequences for this rapidly recruiting species (Mumby 2006).

From a coral perspective, the positive effects of grazing in reducing the cover of thick algal turfs and macroalgae have been reviewed elsewhere (Burkepile and Hay 2006; Mumby and Steneck 2008). In summary, thick algal turfs and macroalgae can kill juvenile corals (Birkeland 1977), cause partial colony mortality of some adult corals (Lewis 1986; Lirman 2001; Nugues and Bak 2006), cause a cessation of growth in juvenile *A. agaricites* (Box and Mumby

2007), reduce the growth rate of adult *P. astreoides* (Chasqui-Velasco et al. 2007) and *P. porites* (Miller and Hay 1998) and reduce the fecundity of *M. annularis* (Foster et al. 2008). Comparable results have also been found in the Pacific (Tanner 1995; Jompa and McCook 2002; Hughes et al. 2007). Clearly, the positive impacts of grazing are unequivocal, although the full demographic implications for corals after sustained reductions in macroalgal cover have not yet been measured in the field.

Balancing the positive effects of grazing and negative impacts of corallivory on coral population dynamics is challenging and warrants continued study. One study that explored this question directly for *Porites porites* concluded that the negative impact of greater corallivory on coral growth was balanced by the positive impact of grazers removing algal competitors (Miller and Hay 1998). However, even here, while corallivory reduced coral growth rate, coral growth remained positive. To date, no study has demonstrated net negative impacts of corallivory on coral population dynamics. Of course, the critical question is whether this scenario might change in future.

From the perspective of total coral cover which supports many ecosystem services (Done et al. 1996) and has the desirable property of enhancing grazing intensity and reducing macroalgal cover (Williams et al. 2001), it is difficult to conceive that corallivory will cause a net negative impact. The reason for this is that many of the coral species that recruit and grow rapidly on Caribbean reefs, such as *Agaricia* spp, are relatively lightly affected by parrotfish predation. Indeed, some of these ‘weedy’ species, such as *Agaricia*, are particularly vulnerable to macroalgal overgrowth (Nugues and Bak 2006) and are therefore poised to benefit significantly from a reduction in macroalgal cover in response to elevated parrotfish biomass.

While corallivory might not be expected to affect total coral cover significantly, the story could be different for the major framework-builders *M. faveolata*, *M. franksi*, and *M. annularis*. Natural processes of recruitment appear to be highly sporadic in these species (Edmunds and Elahi 2007), and asexual reproduction appears to be a significant mode of reproduction in at least *M. annularis* (Foster et al. 2007). It is unknown whether rates of corallivory on juveniles of *Montastraea* are exceptionally high, but some species in this genus are susceptible to a recruitment bottleneck (Edmunds 2002; Mumby 2006). With the continued rise in disease incidence on these species (Weil et al. 2006), the future persistence of *Montastraea* is questionable in many locations. Of particular concern is whether the incidence of corallivory will increase as coral cover declines and whether this might lead to demographic consequences for these long-lived corals that appear to have limited potential for recovery. The evidence to date is limited but does not

imply a problem. For example, the study of corallivory on *M. annularis* by Sanchez et al. (2004) implicitly created a scenario of low coral cover in a high grazing environment by placing corals within a zone of dead *Acropora*. The authors found no evidence for net deleterious impacts on corals.

Further insight into the effects of corallivory at low coral cover can be obtained from ecological models of coral and algal dynamics and empirical studies of reef recovery. The question can be stated explicitly as, ‘does corallivory prevent coral recovery once total coral cover becomes low?’ An initial ecological model of Caribbean coral population dynamics used a parameterisation for partial colony mortality from the study by Bythell et al. (1993), in which parrotfish grazing was a major component of the observed mortality (Mumby 2006). Despite such corallivory, coral recovery was found to occur from low cover providing that grazing levels were high enough to remove an adequate amount of algae. The model parameterisation for corallivory was extended in a follow-up study by adding an explicit parrotfish predation rate on coral recruits (from Box and Mumby 2007) and observed relationships from Curaçao (Meesters et al. 1997) for the incidence of parrotfish lesions with colony size and extent of partial mortality on such colonies (Mumby et al. 2007b). While this model did not increase the rate of corallivory above that observed in situ, coral recovery was found to be feasible despite what are likely to be relatively high levels of corallivory, given the density of large herbivores in the sites used to parameterise the model.

While models predict that corallivory should not retard coral recovery if grazing levels are high, there are few (if any) tests of this prediction. Few monitoring studies have observed low coral cover during a period of high grazing. In St. Croix, Bythell et al. (2000) found no recovery over a decadal period at a site whose coral cover had been low (<5%) since white band disease removed *Acropora* in the 1970s. The lack of recovery was attributed to a failure of coral recruitment, though macroalgae were not implicated and other processes such as recruitment limitation or unsuitable substrata could be responsible rather than corallivory. Coral recovery has been associated with the recovery of functionally significant densities of *Diadema* (Idjadi et al. 2006) but few data exist on trends of coral cover once levels become low.

In conclusion, the balance of evidence from Caribbean systems does not imply that parrotfish corallivory has a net negative impact on coral populations. Whether such conclusions extend to the Indo-Pacific is likely to be doubtful because of the greater number of corallivorous species in this region. Several aspects of parrotfish corallivory remain unclear and should be clarified in future studies. The nutritional importance of corallivory to *Sparisoma* is not

fully understood (Bruggemann et al. 1994a) and while parrotfishes prefer to feed from lower density coral substrates (Bruggemann et al. 1996), the reasons for favouring particular coral species or even individuals are unclear. Indeed, the underlying reasons for corallivory remain speculative and include the marking of territorial boundaries. The response of parrotfishes to fluctuating availability of coral is also uncertain; for example, how does the rate of coral predation scale with parrotfish density and the availability of prey? At low coral cover, will predation tend to be intensive on individual coral colonies—tending to cause whole colony mortality—or extensive, tending to cause chronic partial colony mortality on a larger number of colonies? Similarly, will parrotfishes feed on a greater diversity of coral prey as the abundance of preferred species declines? Importantly, future research might discover whether corallivory can exert an additive or synergistic affect on coral growth with other stressors, such as algal competition or reduced aragonite saturation state. The role of parrotfishes as vectors of coral disease also needs to be investigated given that other corallivores have been associated with the transmission of some coral diseases (Williams and Miller 2005). With many uncertainties notwithstanding, any assertion that conservation practices should guard against protecting corallivorous parrotfishes (Rotjan and Lewis 2008) appears to be unwarranted at this stage.

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