The Nature of Turf and Boring Algae and Their Interactions on Reefs

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ABSTRACT. A major goal of this short review is to familiarize the scientific diving community with the importance, seasonality, and high diversity of juvenile and microalgal turf assemblages and rock-boring cyanobacteria on coral reefs to stimulate further interest in research on these groups. Boring endolith activity not only negatively inflicts damage to living carbonate coral reef hosts, but also positively benefits primary productivity and provides the nutritional base for excavating grazers in otherwise dead substrates. Algal turfs, like all subtidal assemblages on reefs, are best studied by scuba techniques, which have greatly facilitated observation, collection, photographic sampling, and manipulative studies. Prior to scuba, studies in the shallow intertidal and by dredging dominated, which focused by necessity primarily on taxonomy and distributional records. Scuba has enabled studies on ecology, physiology, interactions, etc., that were impossible before its development.

TURF ALGAE INTERACTIONS

Turf algae are multispecies assemblages of diminutive, mostly filamentous algae that attain a vertical height of only 1 mm to 2 cm (Figure 1). Turf algae often exist as assemblages (algal turfs), are ubiquitous in reef systems and are composed of the small, juvenile stages of macroalgae (e.g., *Gelidium* spp., *Gelidiella* spp., *Digenia simplex*) along with faster-growing filamentous species (usually red algae such as *Polysiphonia* spp., *Herposiphonia* spp., and *Ceramium* spp.; blue-green algae (cyanobacteria); diatoms; brown algae; green algae; and coralline algae) and detritus and sediments. The assemblages of juvenile and microalgal species have a high diversity, exceeding 100 species in some western Atlantic turfs, although 30–50 species co-occurring is more common (Steneck, 1988). Within the turf assemblage, there is often a high turnover of individual turf algal species seasonally, and only a few taxa are able to persist or remain abundant throughout the year. However, the assemblages, when viewed as a functional indicator group, remain relatively stable year round. They are often able to recover rapidly after being partially removed by physical disturbance.

Algal turfs characteristically trap ambient sediments and smother corals and other competitors for space by gradual encroachment. These algal forms become predominant under minimal inhibitory top-down (e.g., herbivory) and stimulatory bottom-up (e.g., nutrient supply) controls (Littler et al., 2006). Algal turfs have been shown to form extensive horizontal mats under reduced nutrient-loading rates (Fong et al., 1987) or infrequent nutrient inputs (Fujita et al., 1988). Domination of horizontal reef space by turf algae suggests desirably low nutrient levels but an inadequate herbivory component required for healthy coral-dominated reefs. Their relatively small size and rapid regeneration from basal remnants (perennation) result in only moderate losses to herbivory at low grazing pressures.

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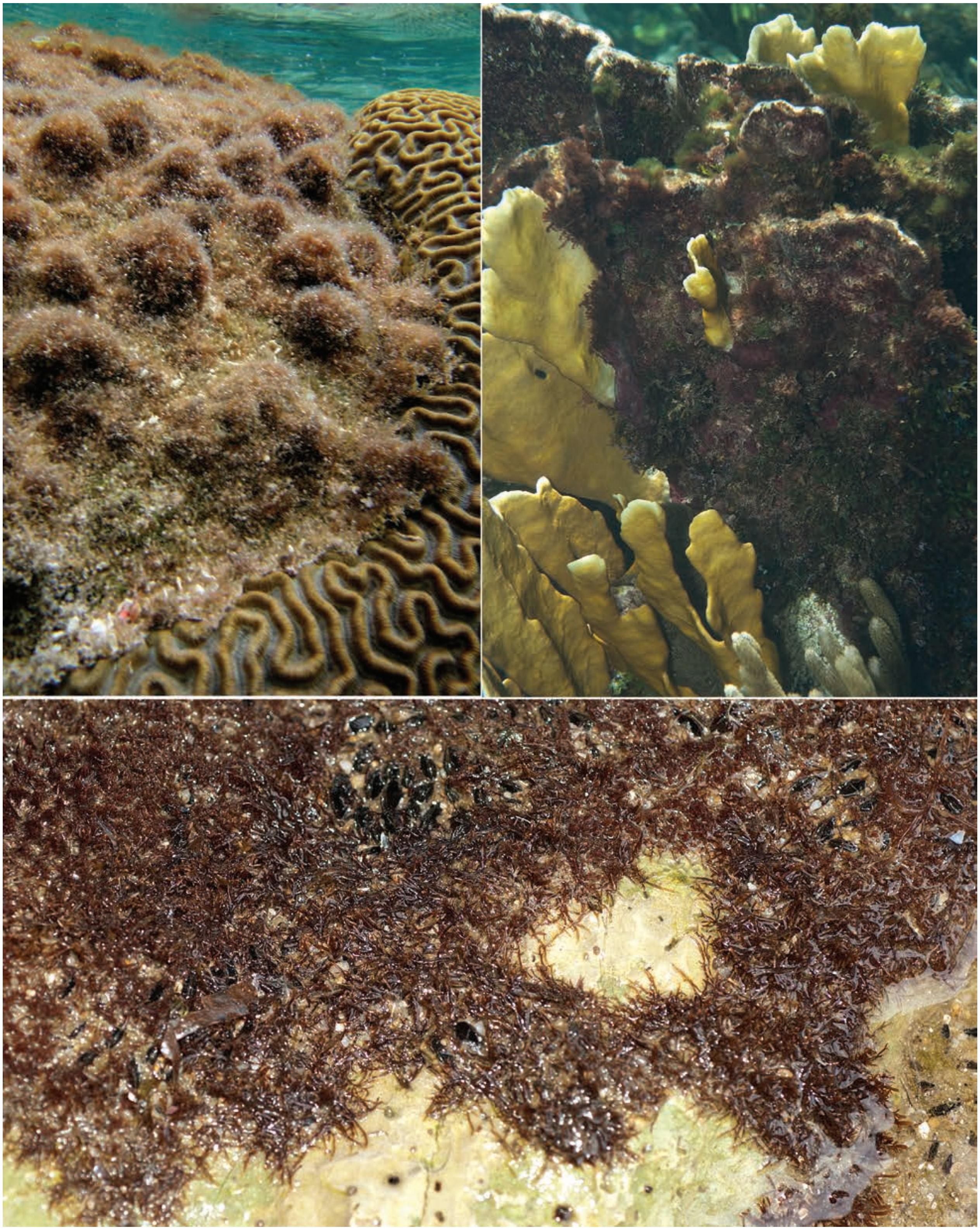

FIGURE 1. Naturally occurring algal turf communities. Top left: *Polysiphonia* sp. Top right: *Laurencia obtusa*. Bottom: *Gelidium pusillum.* (Photos by D. Littler.)

Turf algal assemblages are very much affected by the behavior of territorial damselfish that chase off any larger herbivores that may come into their areas. Because of their preferential grazing and protection, damselfish cultivate more diverse alga turfs with higher biomass within their territories.

Turf algae have opportunistic ("weedy") life-history characteristics, including high surface area to volume ratios and the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus, 1984). Turfs also contain populations of nitrogen-fixing cyanobacteria (Adey, 1998) that can enrich the other low-growing members within the dense turf assemblage in oligotrophic waters. Turf algae have been utilized effectively as a functional group in the burgeoning saltwater aquarium trade, where they are grown in brightly lit, circulating flumes (i.e., patented scrubbers; Adey et al., 2011) to remove excessive nutrient pollutants.

BORING CYANOBACTERIA INTERACTIONS

Boring cyanobacteria are filamentous, prokaryotic, mostly photosynthetic organisms that chemically bore into calcareous rock and limestone. Penetrating or boring algae play important roles in the bioerosion of coral reefs; these filamentous microorganisms result in the breakdown of carbonate structure both directly and indirectly (reviewed by Tribollet, 2008). The most common are blue-green algae (Cyanophyta, cyanobacteria) that attack calcareous substrates differentially; the aragonite skeletons of corals are most easily penetrated and the denser calcite deposits of coralline algae are most resistant. However, the mechanism of carbonate dissolution remains largely unknown and actually contradicts geochemical models that predict the precipitation of carbonates by photosynthetically induced pH increases. As a consequence of variable processes such as selective settling, competition, persistence, and subsequent grazing of euendolithic (true endoliths) cyanobacteria, coastal rocks are biodegraded differentially, resulting in grotesque, sharp-edged features called karsts (Figure 2). These processes act as feedback mechanisms by producing diverse microbial habitats with patchy water-retention pockets, which further enhance bioerosion and endolithic community diversity.

Boring endoliths colonize all carbonate substrates on coral reefs and are distributed throughout the world's tropical seas. Intertidal carbonate coasts are most intensively bioeroded (Figure 3). However, although endolithic activity inflicts damage to living hosts, it also can provide positive overall benefits to reefs, including important primary productivity yields in otherwise

FIGURE 2. Irregular and sharp karsts formed from habitats colonized by boring cyanobacteria and their deeply rasping predators. Inset: rasping organisms such as chitons and other mollusks. (Photos by D. Littler.)

FIGURE 3. Extreme undercut formed by boring intertidal blue-green algae grazed by deep-rasping chitons. (Photo by D. Littler.)

dead substrates. Endoliths attract excavating grazers, and this contributes to massive biodestruction processes and sediment formation. In other words, the bioerosional effect of boring cyanobacteria themselves is secondary; their primary significance is in providing the nutritional base for excavating grazers.

Boring cyanobacteria have been important in the destruction of carbonate throughout geological time. They occur from the upper intertidal to abyssal depths (Golubic et al., 1984), but in general show a decrease with depth. Marine limestone can be infested by more than half a million endolithic filaments per square centimeter. The oldest recorded endolithic blue-green—and the earliest known occurrence of bioerosion—was found in 1.5 billion-year-old stromatolite rocks in China (Zhang and Golubic, 1987).

The diversity of boring microflora is thought to be large, comprising not only undiscovered blue-green algae, but also other algae (chlorophytes, rhodophytes) and fungi. Although their taxonomy has been studied for decades, new species are still being discovered, especially with the advent of molecular techniques (Gutner-Hoch and Fine, 2011). However, the taxonomy and diversity of boring blue-green algae remain relatively unknown and there is still much to be learned regarding this important group.

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