

Macroalgal palatability and the flux of ciguatera toxins through marine food webs

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Abstract

The benthic dinoflagellate *Gambierdiscus toxicus* produces polyether toxins that cause ciguatera fish poisoning in humans. The toxins initially enter food webs when fish forage on macroalgae, or other substrates, hosting this epiphytic dinoflagellate. Population studies of *G. toxicus* and risk assessments in ciguatera-prone regions often rely on quantifying dinoflagellates on macroalgae. Underlying these studies is the assumption that the algae sampled represent a readily consumable resource equally available for benthic grazers. However, many algal hosts of *G. toxicus* possess a variety of defenses against grazing, and host–dinoflagellate associations may act as toxin sources or sinks depending on their palatability. Marine macroalgae may tolerate or avoid herbivory by exhibiting fast growth, by having poor nutritional quality, by utilizing spatial or temporal escapes or by using chemical or structural defenses. Thus, rapidly consumed algae that cope with herbivores by growing fast, such as many filamentous turfs, could be responsible for a high toxin flux even at low dinoflagellate densities. In contrast, ubiquitous unpalatable algae with much higher dinoflagellate densities might contribute little to toxin flux, and effectively act as refuges for *G. toxicus*. To date, *G. toxicus* has been reported from 56 algal genera, two cyanobacteria, one diatom, and one seagrass; 63% of these contain species that are defended from fish grazing and other grazers via chemical, morphological or structural defenses, by low nutritional quality, or by a combination of defensive strategies. High dinoflagellate densities on unpalatable macroalgae could indicate passive accumulation of cells on undisturbed hosts, rather than population explosions or active toxin sources for food webs. Understanding the flow of ciguatoxins in nature requires consideration of the ecology of both *G. toxicus* and its algal hosts. The complexity of marine algal–herbivore interactions also has consequences for other benthic dinoflagellates that produce toxins, which accumulate in consumers.

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1. Introduction

Ciguatera is the most common disease associated with fish consumption in tropical and subtropical regions (Lehane, 1999; Lehane and Lewis, 2000). Although typically considered a disease of the tropics, export of reef fish for human consumption has resulted in a wider distribution of outbreaks. The disease is caused by the

transformation and bioaccumulation of toxins produced by particular strains of the benthic dinoflagellate *Gambierdiscus toxicus*, as well as other species of *Gambierdiscus* (Chinain et al., 1999a; Yasumoto, 2005). Lipophilic gambiertoxins (GTX) produced by the dinoflagellates are ingested by herbivorous fishes that, in turn, are preyed upon by larger carnivorous fishes. As the toxins are passed between trophic levels, they are both oxidized into ciguatoxins and accumulated in muscle tissues. While the exact pathways are unknown, it seems likely that mixed-function oxidases that serve as detoxifying enzymes in the fish are responsible for the biotransformation of gambiertoxins into ciguatoxins

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(Lewis and Holmes, 1993). Over 400 fish have been noted to be ciguatera toxic at some time (Halstead, 1978).

Other dinoflagellates have been implicated as causal agents of ciguatera poisoning, but only the toxins from *Gambierdiscus* produce the symptomology corresponding to this illness. While *Gambierdiscus toxicus* has received the most attention in the literature, *G. australes*, *G. pacificus* and *G. polynesiensis* also produce ciguatoxins (Chinain et al., 1999a). *G. yasumotoi* produces an intoxication in mice more consistent with the production of maitotoxin (Holmes et al., 1998) and the toxicity of *G. belizeanus* (Faust, 1995) remains to be studied. Identifying *Gambierdiscus* species without the use of electron microscopy or molecular tools is a difficult task (Adachi and Fukuyo, 1979; Chinain et al., 1999a; Holmes and Teo, 2002; Hernández-Becerril and Almazán Becerril, 2004). Under lower magnification, diagnostic traits such as thecal plate morphology cannot be observed accurately. Some caution should be exercised when interpreting survey data collected from microscopic observation of preserved field samples as it is possible that other dorsoventrally flattened species of *Gambierdiscus* may have been misidentified as *G. toxicus* (Holmes and Teo, 2002). Because of these limitations, we discuss studies on *G. toxicus* as they have been reported, but readers should be aware that this taxon is likely a species complex.

Gambierdiscus toxicus is a benthic dinoflagellate that can be found on sandy bottoms, detrital aggregates, seagrasses, algae and cyanobacteria (Ballantine et al., 1985; Bourdeau and Durand-Clement, 1991; Faust, 1995). However, most works have focused on the distribution and persistence of this dinoflagellate on macroalgae. The same applies to other toxin producing benthic dinoflagellates that could play a role on ciguatera-like poisonings. Although using dinoflagellate abundance on host macroalgae has value for understanding the dinoflagellate's autecology, the utility for understanding ciguatera relies on the assumption that the macroalgae in question are equally palatable to fish and readily consumed by herbivores. However, this is unrealistic. In coral reefs, the strong selective pressure that herbivores exert on food resources has led to the evolution of complex strategies and defenses that allow algae to persist in areas where herbivory is intense (Hay and Steinberg, 1992; Hay, 1997; Paul et al., 2001). If algae that act as hosts for toxic dinoflagellates are protected from herbivory, then they effectively serve as refugia or "enemy-free space" for *Gambierdiscus*, rather than as a source of toxins to enter trophic webs. This has important consequences for our understanding of ciguatera flux pathways and for

the monitoring of risk areas as it has been classically done.

Anderson and Lobel (1987) were the first to note that some algal hosts of *G. toxicus* had structural or chemical defenses against fishes and that these were often the algae sampled in field assessments of ciguatera risk. However, they did not explore how diverse macroalgal strategies that allow them to cope with herbivores might directly and indirectly alter flux of ciguatoxins into complex marine food webs. In this review, we bring attention to the ecology of marine plant-herbivore interactions and how traits of host algae may indirectly influence the uptake of gambiertoxins and other compounds produced by benthic dinoflagellates. Our purpose is to underscore the need for a more comprehensive approach that considers the characteristics of dinoflagellate host algae when monitoring and managing marine areas where ciguatera risk is high. Although we focus on *Gambierdiscus toxicus* and ciguatera, our considerations apply to other dinoflagellates that associate with algae and whose toxins enter marine food webs, potentially becoming a health risk to marine life as well as humans.

2. Distribution patterns of *Gambierdiscus toxicus* on macroalgae

The study of ciguatera has a long history, with reports of the disease dating as far back as 1550s (Halstead, 1978). Although the disease was clearly associated with "poisonous fishes", a causal agent was not found until 1979 (Yasumoto et al., 1979; Yasumoto, 1979; Bagnis et al., 1980; Yasumoto, 2005). Evidence pointed to a benthic dinoflagellate, eventually named *Gambierdiscus toxicus* because it was originally isolated from benthic seaweeds in the Gambier Islands. The isolation of various toxins from this organism coupled with studies on the physiological effects of the compounds established *G. toxicus* as the toxin source of ciguatera poisoning (Anderson and Lobel, 1987; Lehane, 1999; Lehane and Lewis, 2000; Yasumoto, 2005).

Following its discovery, a number of studies have focused on describing the patterns of distribution, population dynamics and habitat preferences of *G. toxicus*, particularly in regions where ciguatera poisoning appears prevalent. Because the dinoflagellate was originally found on macroalgae, surveys have been predominantly aimed at collecting obvious or abundant seaweeds. The most commonly used methodology entails shaking collected macroalgae in seawater to dislodge epiphytic microorganisms, filtering the water to concentrate the sample, and counting *G. toxicus* cells

found (following the original surveys by Yasumoto et al., 1979; Yasumoto, 1979). Population densities are then approximated to the number of cells per mass of algae. Alternatively, the number of cells per area has been used to quantify the occurrence of *G. toxicus* on the surface of corals, zooanthids and rubble (Ballantine et al., 1985) and on patches of turf algae (Lewis et al., 1994b). This last study differs from the rest because sampling of dinoflagellates was conducted using an air-lift vacuum apparatus. Although *G. toxicus* has been found on sessile invertebrates and sand as well (Ballantine et al., 1985; Bourdeau and Durand-Clement, 1991; Faust, 1995), most data available are from studies focusing on dinoflagellate-macroalgal assemblages.

Such studies have provided valuable insights on the diversity of habitats and algal hosts where *Gambierdiscus toxicus* can be found, with more than 50 algal genera yielding *G. toxicus* cells, and attaining densities ranging from 0.01 to >75,000 cells/g alga (Carlson et al., 1984; Inoue and Raj, 1985, Table 1). Population fluctuations of this dinoflagellate on algae can be large and have been documented both spatially and temporally. For example, the number of *G. toxicus* cells on the surface of a specific algal host can vary by an order of

magnitude between individuals of the alga only 5–10 cm apart (Taylor and Gustavson, 1985). Similarly, long-term monitoring efforts have often quantified population explosions of a few orders of magnitude (Carlson, 1984; Carlson and Tindall, 1985; Thomassin et al., 1992; Turquet et al., 1998, 2001), and have related such differences to seasonal cycles in rainfall (Carlson and Tindall, 1985; Thomassin et al., 1992), temperature (Chateau-Degat et al., 2005) or to environmental disturbances that clear substrates which can be colonized by algae, thus creating readily available substrate for the dinoflagellate (Inoue and Gawel, 1986; Kohler and Kohler, 1992; Kaly and Jones, 1994; Chinain et al., 1999b; Turquet et al., 2001, but see McCaffrey et al., 1992).

However, seasonality is sometimes, but not always observed (Ballantine et al., 1985; Gillespie et al., 1985a; Bomber et al., 1988a; Hokama et al., 1996; Chinain et al., 1999b; Chineah et al., 2000; Hurbungs et al., 2002), and the underlying parameters that ultimately control population increases of this dinoflagellate remain unknown. While some monitoring efforts have complemented their field surveys with culture experiments or measurements of nutrients, temperature, irradiance,

Table 1

Cell densities of *Gambierdiscus toxicus* per algal gram for the highest 20 densities ever recorded, along with the relative palatability of these algae (No assessment was attempted for “turfs” as seldom have their genera been reported in the literature. Cell densities are not always averages from several algal conspecifics. See “Refs.” for full citations.)

Algal host genus	<i>G. toxicus</i> maximum density	Palatability
<i>Chaetomorpha</i>	75793 (Carlson et al., 1984)	Palatable
Turfs	60463 (Turquet et al., 2001)	Variable
<i>Dictyota</i>	45532 (Carlson et al., 1984)	Chemically defended but consumed by particular herbivores
<i>Jania</i>	41820 (Yasumoto et al., 1979; Yasumoto, 1979)	Calcified
<i>Heterosiphonia</i>	6844 (Bomber et al., 1989)	No defenses known, no data on palatability
<i>Acanthophora</i>	6095 (Carlson, 1984)	Palatable
<i>Penicillus</i>	5131 (Bomber et al., 1989)	Calcified and chemically defended
<i>Halimeda</i>	4774 (Bomber et al., 1988a)	Calcified and chemically defended
<i>Laurencia</i>	2901 (Carlson, 1984)	Both chemically-defended, and highly palatable, species
<i>Digenia</i>	2180 (Gillespie et al., 1985a)	Little available data; of low or high preference depending on fish species
<i>Turbinaria</i>	1617 (Carlson et al., 1984)	Leathery consistency suggests some structural defense, but often found in low herbivory areas such as reef lagoons
<i>Thalassia</i>	1463 (Ballantine et al., 1985)	Palatable to particular fishes and urchins
<i>Spyridia</i>	1036 (Taylor and Gustavson, 1985)	Palatable
<i>Bryopsis</i>	680 (Asuncion et al., 1995)	Some species are chemically defended
<i>Asparagopsis</i>	660 (Gillespie et al., 1985a)	Produces halogenated compounds and causes reduced growth in some herbivores
<i>Dictyopteris</i>	589 (Popowski et al., 2001)	Chemically defended species occur in this genus
<i>Bryothamnion</i>	531 (Popowski et al., 2001)	Field and laboratory assays show low palatability and suggest toxicity in some species
<i>Udotea</i>	514 (Bomber et al., 1989)	Calcified and chemically defended
<i>Galaxaura</i>	395 (Popowski et al., 2001)	Calcified and some cytotoxins have been isolated
<i>Delisea</i>	305 (Gillespie et al., 1985a)	Chemically defended

salinity or dissolved oxygen (Withers, 1981; Carlson, 1984; Carlson and Tindall, 1985; Chineah et al., 2000; Hurbungs et al., 2002), correlations between environmental variables and *G. toxicus* population densities are not always consistent. Laboratory studies have defined optimal growth parameters for *G. toxicus*, but have also shown that this organism can grow, or at least survive, within a relatively broad range of values for temperature, salinity and light intensity (Yasumoto et al., 1980; Bomber et al., 1988a; Morton et al., 1992). Furthermore, the association of *G. toxicus* with algal hosts might buffer some potentially harmful fluctuations on environmental parameters. For example, Villareal and Morton (2002) provided evidence that shading by macroalgae might allow *G. toxicus* to thrive on shallow-water tropical environments without suffering photoinhibition. Correlating growth rate or cell densities to surface irradiance might be misleading in this case.

Similarly, arguments regarding the distribution of *G. toxicus* as a function of turbulence are often contradictory. While some studies conclude that this species prefers areas of high wave action such as barrier reefs, other studies suggest a preference for protected environments (Carlson, 1984; Carlson and Tindall, 1985; Tindall and Morton, 1998; Popowski et al., 2001). Tindall and Morton (1998) proposed four types of environments (Systems I–IV) to describe particular community types as a function of various physico-chemical parameters. They argue that in higher energy environments (system I), such as barrier reefs and fore reefs, standing crop estimations of benthic dinoflagellates do not reflect real production due to the low carrying capacity of the system. This has important consequences for the interpretation of monitoring data and toxin flux into food webs, particularly when assessments are made in order to forecast the propensity of ciguatera in a particular region. If wave turbulence causes dinoflagellate cells to be dislodged and carried away, then surveys performed with conventional methodologies would underestimate actual dinoflagellate productivity. Conversely, *Gambierdiscus* behavior in laboratory cultures suggests that turbulence may increase attachment (Nakahara et al., 1996).

Although the role of invertebrates as ciguatera vectors in pelagic and benthic food webs has been discussed (Kelly et al., 1992; Lewis et al., 1994a), it is universally accepted that ciguatoxins generally enter food webs via the consumption of dinoflagellate-laden algae by herbivorous fishes (Anderson and Lobel, 1987; Lewis and Holmes, 1993). However, the dynamics of toxin flux are poorly understood. Studies do not always observe correlations between the incidence of ciguatera

and the prevalence of *G. toxicus* in a region (Bagnis et al., 1985, 1988; Taylor and Gustavson, 1985; Turquet et al., 2001). Similarly, changes in the levels of ciguatoxin in fish tissues may or may not follow the dynamics of *G. toxicus* blooms (Bagnis et al., 1985, 1988). These observations argue for a higher degree of complexity in the routes by which ciguatoxins enter food webs. The majority of population studies on toxic benthic dinoflagellates use visually obvious macroalgae as their sampling unit because it is assumed that these algae represent a readily available source of toxins for fish to ingest (e.g., Carlson et al., 1984). Studies on marine herbivory, particularly from the tropics, argue strongly against this simplified view. We propose that conceptual models explaining the development of ciguatera need to consider both the ecology of dinoflagellate host algae and the complexities of marine plant–herbivore interactions in order to elucidate the flow of ciguatoxins through marine food webs.

3. Marine herbivory and algal palatability

Algae have evolved a variety of strategies and adaptations to cope with grazing pressure. Marine systems experience the highest rates of herbivory on earth, and this particularly true for tropical environments (Hay, 1991). Coral reef herbivores can remove more than 90% of the biomass produced daily by palatable marine macroalgae and measurements of grazing intensity have demonstrated rates of 20,000–156,000 bites/m²/day by herbivorous fishes alone (Carpenter, 1986). Thus, marine herbivory constitutes a primary determinant of algal distribution and population dynamics. In contrast with terrestrial plants that produce subterranean structures such as roots, bulbs and tubers, which are generally protected from grazing, the vast majority of marine algae do not produce equivalent underground parts; virtually all algal biomass in the ocean is potentially exposed to consumers.

Marine herbivores are more phylogenetically diverse than terrestrial herbivores, including vertebrates and an array of invertebrates spanning at least four different phyla. Because of their size and mobility, marine grazers are often grouped in three general categories (Hay, 1992; Hay and Steinberg, 1992; Paul et al., 2001). Macrograzers such as fishes, urchins and large gastropods have relatively higher mobility due to their size, feed on foods generally smaller than themselves and sample a variety of individual algae through their life. Smaller consumers such as amphipods, isopods, sacoglossans, and small herbivorous crabs, shrimps, sea hares, snails and polychaetes feed on algal hosts larger

than themselves, are generally more limited in mobility than macrograzers due to their size, and likely sample fewer hosts through their lifetime. For these animals, termed mesograzers, food and shelter can be tightly coupled. Micrograzers such as copepods and cladocerans are better studied for pelagic systems, but some copepods can inhabit or feed on, macroalgae (Paul et al., 2001). Because meso- and micro-grazers feed on a smaller scale than fishes, they may consume either macroalgae or algal epiphytes (such as dinoflagellates) selectively, or both. This is a potentially important aspect of ciguatoxin flux that has received little attention. The potential of some invertebrates to act as links in the ciguatera food web has been suggested (Kelly et al., 1992; Lewis et al., 1994a) but more studies are needed to adequately assess their importance as vectors of ciguatoxins.

The intensity of herbivory on marine systems, along with the natural physiological and nutritional constraints on the evolution and maintenance of herbivory as a *modus vivendi* (Mattson, 1980; Cruz-Rivera and Hay, 2003), place a strong selective pressure on marine algae. As a result, seaweeds have evolved numerous adaptations to tolerate or avoid herbivory. Seaweeds that are otherwise excluded from areas of high grazing find spatial or temporal refuges by growing at times of the year when herbivores are rare, in sheltered places that are less accessible to grazers or by associating with unpalatable organisms that might provide some protection (Hay, 1986; Kerr and Paul, 1995). For example, palatable algae can decrease herbivory on their thalli by as much as 80% by growing intertwined with unpalatable seaweeds. Such algae turn “competitors into accomplices” (Hay, 1986) by trading off reductions in average growth (due to competition for light and nutrients) for the ability to survive in areas where herbivores could potentially drive them to local extinction. Palatable seaweeds may also tolerate herbivory by exhibiting high growth rates and, essentially, growing faster than they are consumed. This strategy is commonly seen on turf algae (Carpenter, 1986).

The nutritional quality of seaweeds has important consequences for algal susceptibility to grazing and, thus, indirectly may affect consumption of epiphytic dinoflagellates. Because herbivores make a living by consuming foods that are lower in nutrients and higher in structural materials than their own bodies, they need to ingest larger amounts of material than carnivores (Mattson, 1980; White, 1993). For example, coral reef fishes may eat many times their required energetic needs in order to gain enough nitrogen from seaweeds (Hatcher, 1981). Similarly, some invertebrates will

increase their consumption of algae (compensatory feeding) as a function of their organic content (Cruz-Rivera and Hay, 2000a, 2001, 2003; Stachowicz and Hay, 1999; Sotka and Hay, 2002). Because algal nutrient content is highly variable (Cruz-Rivera and Hay, 2003) and can influence the amount of a particular alga that is ingested by consumers, the nutritional quality of an alga may indirectly influence ingestion of ciguatoxic dinoflagellates by consumers. Low nutritional quality can also act as a defensive mechanism. Seaweeds with a very low nutritional value might be too costly to consume because herbivores might spend more nutrients by processing the food than they are assimilating. Below a certain threshold, even herbivores capable of compensatory feeding might suffer poor long-term performance and decreased fitness if confined with low quality algae (Cruz-Rivera and Hay, 2000a, 2000b, 2001, 2003). In mixed algal communities, the net result would almost certainly be to shift feeding preferences to more nutritious species. In other words, more palatable neighbors will draw herbivores away from less nutritious algal species (Atsatt and O’Dowd, 1976).

Many seaweeds deter herbivores by using morphological, structural, and chemical defenses either individually or in combination (Hay and Fenical, 1988; Hay and Steinberg, 1992; Hay, 1997; Paul et al., 2001). Structural defenses such as calcification (incorporation of calcium carbonate into algal tissues) and toughness (which offers mechanical resistance to biting and chewing herbivores) are common in certain groups of seaweeds and can strongly influence the foraging choices of vertebrate and invertebrate consumers (Pennings and Paul, 1992; Kennish and Williams, 1997). Particular green algae such as *Halimeda*, *Udotea* and *Penicillus*, some of which contain more than 90% calcium carbonate per dry mass of tissue are well studied examples of this (Hay et al., 1994). Calcium carbonate not only can increase the toughness of algae, but it also increases the amount of structural, non-digestive material, thus decreasing the overall organic content of seaweeds and lowering their overall nutritional value (Hay et al., 1994). Calcium carbonate may also interfere with digestion, particularly in herbivores with acid guts such as some herbivorous fishes (Horn, 1989) and, therefore, act also as a chemical defense. While toughness and calcification are simple to understand as structural defenses, a less intuitive mechanism of protection is provided by the shape of algal thalli. Morphology of an alga itself may influence consumer choice because it can mechanically reduce the ability of an herbivore to manipulate the alga.

For example, it was shown that the herbivorous crab *Grapsus albolineatus* selects algae based on the shape of the thallus rather than the nutritional content of algae (Kennish and Williams, 1997).

Perhaps one of the best studied defensive strategies in marine macroalgae is the production of noxious secondary metabolites that deter herbivore feeding (Hay and Fenical, 1988; Hay and Steinberg, 1992; Paul et al., 2001). More than 2400 natural products have been isolated from marine red, brown and green algae, and the majority of these have come from tropical species (Paul et al., 2001). Although the ecological function of many marine algal secondary metabolites remains untested, some of the most thorough and ecologically realistic studies on the use of chemical defenses in consumer prey interactions come from the realm of marine–algal–herbivore interactions (Hay and Fenical, 1988; Hay and Steinberg, 1992; Paul et al., 2001). The chemical identity of defensive secondary metabolites is diverse, encompassing terpenes, acetogenins, epoxydes, peptides and lipopeptides, phenolic acids, phlorotannins, and a variety of halogenated compounds (Paul et al., 2001). Some algae such as *Desmarestia* spp. will accumulate sulfuric acid up to 18% of dry mass which serves as a feeding deterrent (Sasaki et al., 2004). Many of the compounds tested against consumers thus far, show strong deterrence against larger consumers such as fishes and urchins, while smaller invertebrate grazer often prefer, and sometimes specialize, on chemically defended algae. These small consumers that live in areas where pressure from predation is high may sequester compounds from their host algae and incorporate them in their own tissues as defense, or may hide in, or cover themselves with, noxious algae and find “enemy-free” space from their natural enemies (Stachowicz and Hay, 1999; Cruz-Rivera, 2001; Hay, 1992). If macroorganisms such as small crustaceans, gastropods and polychaetes can find refuge from consumers by associating with noxious algae, it is then reasonable to assume that less visible organisms such as dinoflagellates could benefit the same way by finding refuge in chemically defended algae that are less susceptible to large grazers.

A particular alga can combine different defensive mechanisms and the importance of multiple defenses may be very significant in herbivore-rich tropical waters. The common co-occurrence of CaCO_3 and defensive secondary metabolites in tropical seaweeds has been suggested to be adaptive because the high diversity of tropical herbivores limits the effectiveness of any single defense (Schupp and Paul, 1994; Hay, 1997; Paul et al., 2001). Multiple defenses can also act additively or

synergistically to decrease palatability of an alga. For example, combinations of CaCO_3 and secondary metabolites have been tested as feeding deterrents and both additive and synergistic effects of these combined defenses have been observed (Pennings and Paul, 1992; Hay et al., 1994). Similarly, low nutritional quality of prey may enhance the negative effects of defensive secondary metabolites resulting in lower prey palatability (Duffy and Paul, 1992; Pennings et al., 1994), decreased per capita consumption of that prey and potentially on lower fitness of herbivores confined with such diets (Cruz-Rivera and Hay, 2003).

Given the array of defensive strategies displayed by marine macroalgae, it is clear that seaweeds cannot be regarded as a homogeneous “ready to eat” group. In fact, algae that seem conspicuous in reefs are often those that are unpalatable to grazers. Their deterrent capabilities, in turn, are often exploited by small macrofauna that find refuge on such algal species. Dinoflagellates living on defended algae would find similar refuge. Thus, large, abundant, conspicuous macroalgae may, in fact, represent sinks for ciguatera toxins rather than pools of available dinoflagellates to enter the food web. It is important to note that many unpalatable species have congeners that are palatable (e.g., *Bryopsis*, *Laurencia*, etc., Appendix A). Thus, it is important that surveys of *G. toxicus* report the species of algae from which dinoflagellates were collected. Generic assessments of algal hosts, might lead to erroneous estimations of ciguatoxin sources and flux.

3.1. Associational defenses, protective coatings and shared doom

Because unpalatable algae avoid or decrease consumption, they represent available substrates for epifauna and epiphytes, and potential safe sites for smaller organisms from larger consumers. This interaction has led to the evolution of complex associations between unpalatable algae (e.g., chemically defended) and a diverse array of mesograzers (Hay, 1992; Paul et al., 2001). If unpalatable seaweeds represent a refuge for mesograzers from macroconsumers, it is likely that epiphytic dinoflagellates can exploit this refuge in a similar fashion. This has important implications for our understanding of ciguatoxin fluxes through food webs and the interpretation of field surveys, particularly those aimed at identifying ciguatera-prone areas. Traditionally, high densities of *Gambierdiscus toxicus* on algae have been interpreted through bottom–up controls such as nutrient inputs into the environment or reef degradation caused by eutrophication or coral bleaching

(Anderson and Lobel, 1987; Lehane and Lewis, 2000). However, if dinoflagellates associate with algae that are not consumed by herbivores, then the importance of top-down control in toxin fluxes becomes more evident. Low preference macroalgae may passively accumulate dinoflagellates because they are not disturbed as often by grazers and, thus, act as sinks for ciguatera toxins (see also Anderson and Lobel, 1987). Such reservoirs of *G. toxicus* might even serve as “seed banks” that help repopulate nearby areas when conditions are favorable.

One of the basic mechanisms by which unpalatable algae can serve as refugia is by creating “enemy-free space.” Because fish can recognize and learn to avoid distasteful prey (Lindquist and Hay, 1995; Thacker et al., 1997), they visit unpalatable seaweeds less often. This, in turn, lowers potential encounters between fishes and prey dwelling in low preference seaweeds. For example the brown alga *Dictyota menstrualis* (previously *D. dichotoma* in Hay et al., 1987a,b; Duffy and Hay, 1994) produces two terpene alcohols (pachydictyol A and dictyol E; Cronin et al., 1995) that are unpalatable to omnivorous fishes and urchins, but the alga is also a preferred food of the amphipod *Ampithoe longimana* which is generally not deterred by natural concentrations of the chemicals (Hay et al., 1987a; Duffy and Hay, 1994; Cronin and Hay, 1996; Cruz-Rivera and Hay, 2003). The amphipod does not sequester compounds from the alga, but by living in a chemically defended host, is able to maintain its populations during times when other amphipods that do not associate with *Dictyota* are driven to local extinction by omnivorous fishes (Hay et al., 1987a; Duffy and Hay, 1994; Cronin and Hay, 1996).

This example is particularly relevant because *Dictyota* spp. have been used as sources of *Gambierdiscus toxicus* for physiological studies (Villareal and Morton, 2002) and are commonly sampled in population studies of this dinoflagellate (Withers, 1981; Carlson, 1984; Carlson et al., 1984; Ballantine et al., 1985; Taylor, 1985; Taylor and Gustavson, 1985; Inoue and Gawel, 1986; Bomber et al., 1989; Bourdeau and Durand-Clement, 1991; Kohler and Kohler, 1992; Popowski et al., 2001). Populations of more than 45,000 cells of *G. toxicus* per gram of *Dictyota* have been recorded (Carlson et al., 1984; Table 1). Most, if not all, species in the genus *Dictyota* produce dictyols (Faulkner, 1994) and species that occur widely in the tropics such as *Dictyota acutiloba*, *D. bartayresiana* (= *D. bartayresii*), *D. ciliolata*, *D. menstrualis*, and *D. pfaffi* have been shown to be chemically defended (Hay et al., 1987a, 1990b; Hay and Steinberg, 1992; Faulkner, 1994; Cronin and Hay, 1996; Cronin et al., 1997;

Barbosa et al., 2004). Given the widespread deterrence of this algal genus, it is possible that large populations of *G. toxicus* accumulate as a result of lower grazing disturbance on these algae.

The fact that many defended marine algae serve as refugia to a wide variety of mesograzers (Hay, 1992; Paul et al., 2001) carries also other consequences. The potential for marine mesograzers as ciguatoxin vectors remains unexplored. However, if indeed mesograzers are a link in the ciguatera food web, those finding refuge in defended algae might act as ciguatoxin sinks. In such cases, even if the animal can accumulate or vector toxins, its protected status (within its algal refuge) may reduce transfer to higher trophic levels.

A wide variety of macroalgae containing deterrent or bioactive secondary metabolites are known to host intermediate to dense (hundreds to thousands of cells per gram of algae) populations of *Gambierdiscus toxicus* and other benthic dinoflagellates (summarized in Appendix A). These include species of red algae such as *Asparagopsis* (*Fankenbergia*), *Portieria* and *Laurencia* which produce halogenated compounds, various brown algae like *Sargassum*, *Lobophora* and *Zonaria* species, which contain phlorotannins, *Dictyopteris* spp. some of which produce potent feeding deterrents, *Styopodium zonale*, which contains the deterrent styopodial and syphonous green algae like *Avrainvillea*, *Bryopsis* and *Caulerpa* species, which produce terpenes that are deterrent to fishes and sequestered by certain gastropods for their own defense (Paul et al., 2001). *Gambierdiscus toxicus* has also been found on cyanobacteria such as *Lyngbya* and *Calothrix* spp. which produce an array of cytotoxic and deterrent compounds (over 400 different secondary metabolites isolated from *Lyngbya* spp., Paul et al., 2001), and seagrasses such as *Thalassia testudinum* which contain phenolic acids (Zapata and McMillan, 1979), although their role in palatability is unknown (Valentine and Heck, 1999, Appendix A).

Just as the use of noxious algae as enemy-free space by invertebrates has been well documented, associational defenses between palatable and unpalatable seaweeds (e.g., *Hypnea* or *Spyridia* growing with *Sargassum*) have been studied (Hay, 1986) and provide analogs for *Gambierdiscus* and host macroalgae. In this case, algae that would otherwise suffer large losses in biomass due to herbivory, are able to survive by growing near, or intertwined with, less palatable algae. In some cases, these palatable algae trade reduced growth rates due to competition for light and nutrients with the host, for survival (lower mortality) by growing on defended hosts. Although there are no equivalent studies on

associational defenses between benthic dinoflagellates and their algal hosts, similar mechanisms could, and likely do, operate in such interactions. Whether *G. toxicus* significantly competes for nutrients or light with their algal hosts is unknown. However, it is known that this dinoflagellate benefits from the shade provided by algae, thus reducing the potential for photoinhibition (Villareal and Morton, 2002).

It is likely that *G. toxicus* also finds benefits by associating with algae that are structurally defended (Schupp and Paul, 1994; Hay, 1997). Some calcified algae and tough leathery algae experience reduced herbivory because they are less susceptible to grazing from herbivores with weak mouthparts. Calcification is widespread in some green and red algae and genera such as *Halimeda* can contain >90% CaCO₃ per mass (Hay et al., 1994). Calcified macroalgae known to host populations of *Gambierdiscus toxicus* include species of *Acetabularia*, *Amphiroa*, *Galaxaura*, *Halimeda*, *Jania*, *Padina*, *Penicillus*, *Lithothamnion* and *Udotea* (Table 1). In fact, some of the highest densities known for this dinoflagellate come from collections of the widespread algal genus *Jania* from the Gambier Islands (Yasumoto et al., 1979; Table 1).

The importance of toughness as a structural defense has received less attention than chemical defense in general. However, tests have shown calcification to be important for the preferences of large herbivorous gastropods and some fishes (Pennings and Paul, 1992; Schupp and Paul, 1994). The morphology of an alga itself can influence susceptibility to herbivores as it is the case with crabs that select food algae based on algal form, rather than nutritional value (Kennish and Williams, 1997). While tests clearly demonstrating toughness as a defensive mechanism in non-calcified algae are few, it is likely that this strategy is used by a wider variety of algae than currently appreciated. As such, *G. toxicus* likely finds some protection by living on tough or crisp algae such as *Turbinaria*, *Colpomenia* and some species of *Sargassum* (but see Lewis, 1985, Appendix A). Some of these algae have thick, leathery thalli and probably find some escape from grazers through toughness.

In addition to calcification, some green siphonous algae such as *Acetabularia*, *Halimeda*, *Udotea* and *Penicillus* produce chemical defenses. Multiple defenses can act additively or synergistically, thus enhancing the survival of some macroalgae in heavily grazed tropical reefs (Hay et al., 1994). Siphonous algal hosts of *G. toxicus* have evolved some of the most sophisticated defensive systems in the ocean, including activated chemical defenses, differential allocation of

noxious compounds into softer newer growths, and the ability of producing new, more susceptible shoots at night when herbivores are less active (Hay et al., 1988b).

Epiphytism can enhance or decrease the palatability of a host alga. Wahl and Hay (1995) used the term “shared doom” to designate associations in which a more palatable epiphyte enhances the susceptibility of a less palatable host by growing on it. Without the epiphyte, the host loses less biomass due to its own defensive mechanisms, but these are “masked” by the attractiveness of the palatable epiphyte. On the contrary, palatable hosts might be protected by unpalatable epiphytes that are avoided by grazers. It is not known whether similar interactions develop between microbial epiphytes and macroalgae, however, the potential for microbial metabolites to alter the palatability of a host has been shown for some marine sponges (Unson and Faulkner, 1993; Unson et al., 1994; Bewley et al., 1996). Just as palatable and unpalatable hosts may influence the intake of *G. toxicus* by herbivores, the compounds produced by the dinoflagellate could potentially alter the palatability of the host.

These examples emphasize the complexities of marine plant–herbivore interactions. Current understanding of ciguatoxin fluxes largely overlooks the role of different host algae as sources or sinks of ciguatoxins (but see Anderson and Lobel, 1987), although some authors have argued that specific groups of algae, particularly filamentous turfs, are mainly responsible for the intake of toxins by fishes (Anderson and Lobel, 1987; Lewis and Holmes, 1993; Abbott, 1995; Lehané and Lewis, 2000). Turf algae can contain large numbers of *Gambierdiscus* (Table 1), but turfs themselves may be comprised of palatable or unpalatable species. Until now the underlying mechanisms leading to such differences in algal palatability have not been addressed comprehensively as important factors regulating ciguatoxin flux.

3.2. Spatial variation in herbivory, herbivore selectivity and algal abundance

In addition to the role that chemical and/or structural defenses play in modifying grazing rates at a single site, grazing may be affected by spatial location within the reef complex. Herbivory decreases with depth and with distance from the shore, being lower in lagoons and high energy areas such as reef crests and higher in the upper reef slope (Hay, 1981a, 1981b, 1984; Hay et al., 1983; Lewis, 1985). Herbivory is also lower in mangrove channels and shallow reef flats. Thus, all other things

being equal, ciguatoxin influx to food webs could be potentially faster in these environments than in low energy areas such as lagoons and mangroves.

Because of these variations, palatable seaweeds can find spatial escapes by growing where herbivory is low. Species in genera such as *Turbinaria* and *Sargassum*, both of which have often been sampled for *Gambierdiscus toxicus*, often form dense bands in shallow flats or lagoons. High densities of dinoflagellates in these algae might reflect accumulation on hosts that are disturbed less often by herbivore feeding, and in fact represent food sources that are spatially protected from where most herbivores forage. While both these genera contain species that are chemically or structurally defended (Appendix A), some evidence has shown that these genera will be consumed in areas where herbivory is high (Lewis, 1985; Cruz-Rivera and Paul, 2002).

While many defensive mechanisms have been shown in seaweeds, it is important to note that susceptibility to herbivores is relative. Starvation, for example, can cause consumers to be less selective and more likely to eat defended hosts (Cronin and Hay, 1996). In Guam, seasonal recruitment of juvenile rabbitfishes (*Siganus* spp.) can sometimes be so high that both palatable and normally unpalatable or lower preference algae are completely consumed (E. Cruz-Rivera, personal observation). More importantly, the same algal host is often differentially palatable to different fishes and invertebrates.

Herbivore selectivity has not been included in current models of ciguatoxin flux, but it is very likely that incidental consumption of *Gambierdiscus* is heterogeneous depending on the fish species involved. Behavioral traits such as feeding preference interact with evolutionary adaptations such as biomechanical properties of mouthparts to influence foraging. For example, certain fishes like the surgeonfish *Ctenochaetus striatus* that forage on macroalgae, actually target epiphytes and detritus accumulated on the surface of larger seaweeds (Polunin et al., 1995; Choat et al., 2004). In this sense, these fishes are omnivores and might depend less on chemical or nutritional traits of macroalgae than strictly herbivorous fishes. Yet these fish can be important links on the transfer of ciguatoxins between trophic levels (Campbell et al., 1987; Hokama et al., 1988; Lewis et al., 1994b and references therein). Similarly, some small invertebrate consumers that feed at microscopic scales and pick cells directly from the surface of host algae could depend less on macroalgal traits and still be important links on the ciguatera food web. Such an alternative food web has been described for floating communities in pelagic *Sargassum* (Kelly et al., 1992).

Just as herbivory varies spatially overall, the dominant herbivores in a region determine algal community structure. For example, Cruz-Rivera and Paul (2002) exposed similar arrays of macroalgae and cyanobacteria suspended in ropes at two different reefs in Guam and found strikingly different results. At Cocos Lagoon, five algae (but not the cyanobacteria) were eaten significantly by the natural fish assemblage, whereas in Western Shoals, only two macroalgal species were consumed significantly. Observations during the experiments noted that at Western Shoals one herbivore was dominant (the unicornfish *Naso hexacanthus*) while Cocos Lagoon had a more diverse fish community. Even herbivorous fishes that occur sympatrically could forage on very different resources and the degree at which *G. toxicus* occurs on different host algae might affect toxin flux by biasing certain fish species as vectors and not others.

Because different herbivores show different preferences, the degree by which an alga can be a source of ciguatoxins or a refuge for *Gambierdiscus* is variable. In particular, little is known of invertebrates as vectors of ciguatoxins. This is important, because mesograzers often show preference or specialize on algae that are unpalatable to macrograzers (Hay, 1992; Hay and Steinberg, 1992; Paul et al., 2001). If these smaller invertebrate herbivores incidentally consume *G. toxicus*, they could represent an underappreciated link in the ciguatera food web. Kelly et al. (1992) have noted such a food web where crustaceans appear to play an important role.

4. Ciguatoxin fluxes and more realistic food webs

The complexities of marine plant-herbivore interactions require that a broader view of how ciguatoxin enters marine food webs be developed. In particular, the importance of top-down processes (i.e., herbivory) should be evaluated in the context of algal host defenses and palatability. In Fig. 1, we expand on the current model of ciguatera food webs to include differences in algal traits that lead to variability in algal susceptibility to herbivores. Once these traits are considered, the potential for different algae to serve as sources or sinks of ciguatoxins becomes more evident. Algae with diverse traits essentially represent various stages of a continuum. At the extremes are seaweeds with no known defenses and that tolerate herbivory by having high productivity. This is the case of many turf-forming algae (Carpenter, 1986). The other extreme is represented by algae having multiple defensive mechanisms such as calcification

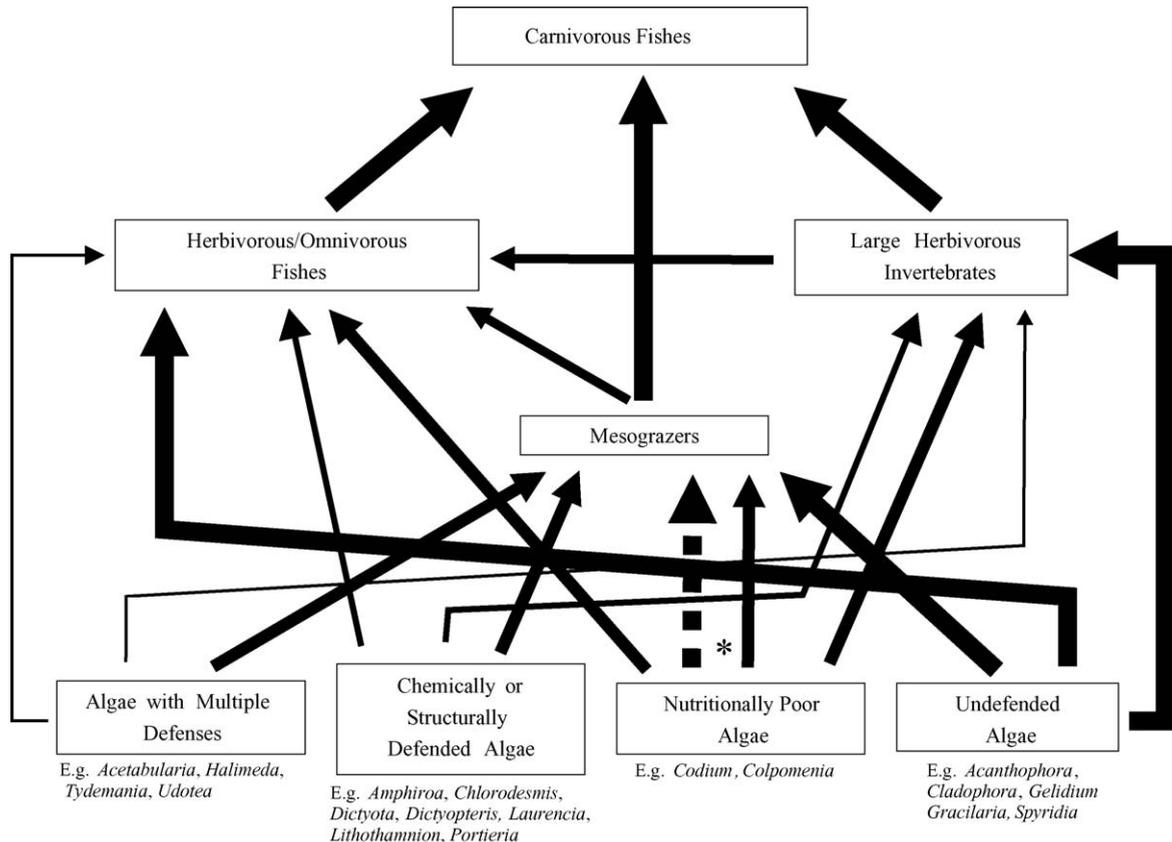


Fig. 1. A conceptual model illustrating potential pathways and intensity of fluxes from different algal sources. The asterisk indicates two potential types of flux from the same source: seaweeds of low nutritional quality may be generally avoided by herbivores. However, certain mesograzers (e.g. some amphipods and crabs) will increase consumption as a response to low nutrient level in their food (compensatory feeding). Thus, for these algae, different mesograzers might respond by eating less, or by accelerating consumption.

(structural defense) and noxious secondary metabolites (chemical defense). It is not difficult to see how the same amount of *G. toxicus* on each of these algal hosts might be consumed differently by the same herbivore community. The former might represent an available source of ciguatoxins that enters the food web, while the latter would decelerate toxin flux and act as a sink. Furthermore, because they are a quickly-renewing consumable resource, palatable and fast-growing algae might contribute more to toxin flux even with low densities of *G. toxicus* than unpalatable algae with higher dinoflagellate burdens.

This model also includes the potential role of mesograzers as ciguatoxin vectors. Predatory fishes are a key determinant of population densities and dynamics for small marine invertebrates. The potential of mesograzers as ciguatoxin vectors is unexplored, but could be particularly important when dealing with species that consume defended seaweeds. These mesograzers, in essence, would serve as a link between

algae that would ordinarily act as sinks of ciguatoxins and higher trophic levels.

An interesting aspect of marine–plant herbivore interactions pertains to algae with low nutritional quality. While this can benefit the alga by causing an herbivore to consume other resources, but it can also elicit a compensatory response in some mesograzers (Cruz-Rivera and Hay, 2000a, 2001, 2003). Thus, when faced with an alga of low nutrient content, some herbivores will respond by increasing consumption on that alga to gain enough nutrition. Thus an alga with low nutrient content laden with *Gambierdiscus toxicus* could potentially act as a sink for herbivores that reject it, or enhance toxin flux via consumers capable of compensatory feeding. A similar argument can be made for herbivores that feed on complementary resources to balance their nutritional requirements (Pennings et al., 1993; Cruz-Rivera and Hay, 2000b). If complementary resources are rare, they will be consumed disproportionately compared to more abundant seaweeds (Pennings

et al., 1993). In summary, the underlying assumption that all algae carrying *G. toxicus* represent equivalent sources of ciguatoxins to enter food webs is more context-dependent than currently appreciated.

5. Other dinoflagellates

While this review focuses on *Gambierdiscus toxicus*, the diversity of symptoms in ciguatera-related cases suggests that other dinoflagellate toxins also bioaccumulate on fish tissues and that these toxins might have a benthic origin. Species in the genera *Amphidinium*, *Coolia*, *Gonyaulax*, *Ostreopsis*, *Prorocentrum* and *Scropsiella*, are confirmed toxin producers and dwell on macroalgae (e.g., Yasumoto et al., 1980; Tindall et al., 1984; Carlson and Tindall, 1985; Bomber et al., 1989; Tindall and Morton, 1998; Holmes et al., 1998; Pocsidio and Dimaano, 2004). It is likely their compounds enter fish food webs in a similar fashion as those of *Gambierdiscus*, although biomagnification to the level required to affect human health has not been documented. Thus, the processes described above can be applied to understand fluxes of other microbial toxins of benthic origin.

It is important to note that, while we present a theoretical framework based on studies of marine plant–herbivore interactions, our purpose is not to present our model as complete. Rather, we highlight areas in which future research can be directed to elucidate actual spatial and temporal variations in ciguatoxin flux, thus contributing to a more complete understanding of the ciguatera food web. At the base of our arguments is a simple testable hypothesis: algal host traits affect strongly the flux of ciguatera because different seaweeds are differentially palatable to herbivores.

6. Conclusions

Some strong patterns do emerge from considering available studies in marine algal–herbivore interactions. Algae as sources of *Gambierdiscus* cannot be considered homogeneous or equally available to fishes

(Appendix A). The diversity of defensive strategies and adaptations in seaweeds against herbivory demonstrates a need for considering the ecology of host algae as a determining factor in the routes and fluxes of ciguatoxins. While defenses might not completely eliminate grazing of well defended algae (e.g., against mesograzers), they can strongly influence ciguatoxin fluxes by diverting consumers to other sources or reducing the per capita amount of the resource consumed. Furthermore, because congeneric algae can have dramatically different susceptibilities to herbivores, surveys would benefit from identifying algae at the species level. Also, the diversity of herbivores in marine systems argues for the potential role of invertebrates as vectors or even sinks (for herbivores that are themselves defended) of ciguatoxins. Such pathways remain unexplored.

Assessments of ciguatera outbreaks and endemicity can no longer be performed solely by sampling algae that are conspicuous and readily collected because these potentially represent species that are not consumed in great quantities by herbivores (Anderson and Lobel, 1987). Measured in this way, the standing stock of *Gambierdiscus toxicus* in a reef may not adequately approximate toxin flux because large, slower growing algae carrying dense dinoflagellate populations might contribute little toxin for consumption. In contrast, small pools of fast growing algae (e.g., palatable turfs) could be responsible for most of the toxin flux, even at much lower dinoflagellate densities, due to the rapid turnover of the resource.

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Appendix A

This table includes all algal genera from which *Gambierdiscus toxicus* has been recorded. When available, densities on different sources are also included. Because only genera are recorded, highest and lowest *G. toxicus* cell densities might correspond to different congeneric seaweeds. Remarks on macroalgal relative palatability were evaluated by reviewing >200 articles on algal–herbivore interactions. See “Refs.” for full citations.

Algal genus	Remarks	<i>Gambierdiscus toxicus</i> densities (cells/gwm alga)	References
<i>Acanthophora</i>	Branching red algae either epiphytic or on primary substrate (Gacia et al., 1999; Littler and Littler, 2000). Palatable to fishes, urchins, crabs and sea turtles (Hay, 1981a, 1984; Hay et al., 1989, 1990b; Lewis, 1985; Paul and Hay, 1986; Paul, 1987; Russell and Balazs, 1994; Stimson et al., 2001; Cruz-Rivera and Paul, 2002; Pillans et al., 2004)	15–6095	Withers (1981), Shimizu et al. (1982), Carlson (1984), Taylor (1985), Ballantine et al. (1985), Bourdeau and Durand-Clement (1991), Morton and Faust (1997), Tindall and Morton (1998) Bomber et al. (1989)
<i>Acetabularia</i>	Calcified algae (Kingsley et al., 2003; Kerkar, 1994). Secondary metabolites have also been observed in some species and chemical defenses have been suggested (Cetrulo and Hay, 2000). However, urchins and fishes can readily consume some species (Hay, 1984; Bulleri et al., 2002)	19	
<i>Acrochaetium</i>	Filamentous, epiphytic red alga (Wear et al., 1999; Sanson et al., 2002; N’Yeurt and Payri, 2004). This genus has been revised repeatedly with different species now belonging to different genera such as <i>Audouinella</i> (Harper and Saunders, 2002; Woelkerling, 1983). No data on palatability is available for this genus, although some data exist for related or revised genera (e.g., Wahl and Hay, 1995)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Actinotrichia</i>	Calcified red algae (Kerkar, 1994). No studies available on palatability	2 in Koike et al. (1991), 0–7 cells/cm ² in Abuso et al. (2000)	Koike et al. (1991), Abuso et al. (2000)
<i>Amphiroa</i>	Heavily calcified red algae (Kerkar, 1994; Payri, 1995), which likely offers some structural defense. Field experiments showed some species to be unpalatable to tropical fishes (Hay, 1981a; Hay et al., 1989; Paul and Hay, 1986), although some gastropods and urchins will consume these algae (Klump et al., 1993; Tahil and Junio-Menez, 1999). Palatability in this genus is variable with some tropical species being less palatable than their temperate counterparts (Bolser and Hay, 1996)	21–34	Gillespie et al. (1985a), Chinain et al. (1999a)
<i>Asparagopsis</i> (<i>Falkenbergia</i>)	Produces halogenated compounds (McConnell and Fenical, 1977; Bruneau et al., 1978; Combaut et al., 1978; Marshall et al., 1999) although their function as feeding deterrents has not been explicitly tested. Urchins show decreased consumption, growth and fitness when confined with some species of <i>Asparagopsis</i> (Frantzis et al., 1992; Frantzis and Gremare, 1993). While <i>Asparagopsis</i> and <i>Falkenbergia</i> were originally placed in different genera, and have been sampled for dinoflagellates as such, it is now known that these are the gametophyte and sporophyte stages (respectively) of the same alga (Guiry and Dawes, 1992)	17–660 Densities not explicitly stated in Bourdeau and Durand-Clement (1991)	Gillespie et al. (1985a), Bourdeau and Durand-Clement (1991)
<i>Avrainvillea</i>	Some species known to be of low preference to fishes (Hay, 1984; Paul and Hay, 1986; Paul et al., 1987a) and chemically defended by producing the feeding deterrent avrainvilleol (Sun et al., 1983; Hay et al., 1990b, Meyer et al., 1994). Certain mesograzers exploit this genus as food and refuge (Gavagnin et al., 2000; Hay et al., 1990b, E. Cruz-Rivera, unpublished). Other bioactive secondary metabolites have been isolated from <i>Avrainvillea</i> spp. but their role in plant-herbivore interactions is unknown (Colon et al., 1987; Chen et al., 1994)	31	Gillespie et al. (1985a)

<i>Boodlea</i>	Green filamentous turf alga with a spongy thallus (Littler and Littler, 2000). Little data available on palatability although it is consumed to some extent by certain crabs (Sato and Wada, 2000)	10–78	Kaly and Jones (1994)
<i>Bryopsis</i>	Chemically defended species are unpalatable to some fishes and serve as food and sources of sequestered chemicals for certain gastropods (Meyer et al., 1994; Hamann et al., 1996; Horgen et al., 2000; Becerro et al., 2001). Some fishes, including territorial damselfishes, however, may prefer <i>Bryopsis</i> as food (Paul and Hay, 1986; Hixon and Brostoff, 1996; Ferreira et al., 1998). Certain compounds from this algal genus induce ecdysis in <i>G. toxicus</i> (Sakamoto et al., 2000)	2–680	Shimizu et al. (1982), Asuncion et al. (1995)
<i>Bryothamnion</i>	Toxicity towards fish has been suggested, but not rigorously tested (De Lara-Isassi et al., 2000). Transplant experiments, however, showed one species to be unpalatable (Hay, 1981a)	1–531	Taylor and Gustavson (1985), Popowski et al. (2001)
<i>Calothrix</i>	Cyanobacterium. A number of toxic and bioactive secondary metabolites have been isolated mostly from freshwater species. (Rickards et al., 1999; Hockelmann and Juttner, 2004). Less is known about marine species	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Caulerpa</i>	Chemical defenses against fishes and gastropods are known in this genus (Paul and Fenical, 1982, 1986; Paul and Hay, 1986; Paul et al., 1987b; Pennings and Paul, 1992). However, the palatability of the same species, and of species containing the same secondary metabolites varies strongly among herbivores (e.g., Hay, 1981a; Hay, 1984; Lewis, 1985; Paul and Fenical, 1985; Paul and Hay, 1986; Morrison, 1988; Meyer and Paul, 1992; Cruz-Rivera and Paul, 2002; McClanahan et al., 2002; Andre et al., 2005)	0.03–209	Ballantine et al. (1985), Gillespie et al. (1985a), Inoue and Gawel (1986), Bomber et al. (1989), Bourdeau and Durand-Clement (1991), Kaly et al. (1991), Kaly and Jones (1994)
<i>Centroceras</i>	Filamentous turf on primary substrate or epiphytic (Littler and Littler, 2000). Palatable to surgeonfishes, parrot fishes, and kypnosids (in higher latitudes) (Barry and Ehret, 1993; Hixon and Brostoff, 1996). However, it can be of low or high preference to different species of “gardening” damselfishes (Hixon and Brostoff, 1996; Ferreira et al., 1998). As an epiphyte on seagrasses it is readily consumed by gastropods (Klump et al., 1992)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Ceramium</i>	Filamentous turf on primary substrate or epiphytic (Littler and Littler, 2000; Kamer et al., 2001; Anderson et al., 1998; Jagtap, 1998). Some species are known to be fast growing (Pedersen and Borum, 1997) and can form large blooms under eutrophic conditions (Kamer et al., 2001). Species can be very low to high preference foods for fishes, including tropical “gardening” damselfishes (Paul and Hay, 1986; Hixon and Brostoff, 1996; Ferreira et al., 1998) and temperate species are known to be consumed by some mesograzers (Anderson et al., 1998)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Chaetomorpha</i>	Filamentous, mat forming algae (Littler and Littler, 2000). No defenses are known against larger grazers, although some species can be unpalatable to some mesograzers (Cruz-Rivera and Hay, 2001). It is a common food item for green turtles (Seminoff et al., 2002).	75793	Withers (1981), Carlson et al. (1984), Carlson and Tindall (1985), Bourdeau and Durand-Clement (1991)
<i>Chlorodesmis</i>	Chemically defended algae (Paul, 1987) that serves as host for specialist crabs and gastropods that use this alga as refuge (Hay et al., 1989). Some rabbitfish will consume <i>Chlorodesmis</i> (Tsuda and Bryan, 1973; Paul et al., 1990)	26	Yasumoto et al. (1979), Hahn (1991 as cited in Lehane, 1999)
<i>Chnoospora</i>	Branching wiry brown alga (Littler and Littler, 2000). No data available on palatability. Some species can enhance productivity quickly after nutrient pulses (Schaffelke, 1999), suggesting fast growth rate	240	Heil et al. (1998)

Appendix A (Continued)

Algal genus	Remarks	<i>Gambierdiscus toxicus</i> densities (cells/gwm alga)	References
<i>Cladophora</i>	Green filamentous turf algae growing on primary substrate or epiphytic (Gacia et al., 1999). This is a ubiquitous marine and freshwater genus often associated with eutrophication and considered an important food source for a diverse array of organisms (Littler and Arnold, 1982; Dodds and Gudder, 1992; Ferreira et al., 1998). Some marine species are fast growing and can form large accumulations under eutrophic conditions (Littler and Arnold, 1982; Dodds and Gudder, 1992; Peckol and Rivers, 1995; Pedersen and Borum, 1997; Hauxwell et al., 1998). This genus is preferred by diverse temperate (Friedlander et al., 1996) and tropical fishes such as “gardening” damselfishes (Hixon and Brostoff, 1996; Lison de Loma and Ballesteros, 2002) and rabbitfishes (Elsayed, 1994), although some species are of low preference to Caribbean fishes (Paul and Hay, 1986). Also consumed by crustaceans (Hauxwell et al., 1998)	1.8–8.1	Carlson and Tindall (1985), Taylor (1985), Bourdeau and Durand-Clement (1991), Hahn (1991 as cited in Lehane, 1999)
<i>Codium</i>	Spongy green alga. Studies on temperate (Hay et al., 1988c, but see Hay et al., 1986) and tropical (Paul and Hay, 1986) species have shown low palatability to fish or invertebrates. Suggested defensive mechanisms range from low nutritional quality (Cruz-Rivera and Hay, 2001), and structural defenses (Cruz-Rivera, 2001) to activated chemical defenses (Van Alstyne et al., 2001). Some species are food items for sea turtles and urchins (Seminoff et al., 2002)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991), Koike et al. (1991)
<i>Colpomenia</i>	Brown alga with a smooth, hollow, rigid, irregularly globular thallus; almost with a plastic-like appearance and consistency (Littler and Littler, 2000; E. Cruz-Rivera, personal observation). Palatability for larger herbivores is unknown, although it is possible that the crisp thallus could provide some protection against certain grazers. Studies on temperate amphipods found this alga unpalatable and suggest low nutritional quality as the reason for avoidance (Poore and Steinberg, 1999)	68–250	Yasumoto et al. (1979), Heil et al. (1998)
<i>Delisea</i>	Chemically defended red algae (de Nys et al., 1996; Williamson et al., 2004; Wright et al., 2004). Furanones from this alga deter feeding in invertebrates and inhibit biofouling by bacteria and other epiphytes	305	Gillespie et al. (1985a)
<i>Dictyota</i>	Diterpenoid chemical defenses are widespread in this genus of brown algae and many studies have shown <i>Dictyota</i> spp. to be low preference or unpalatable to a variety of vertebrate and invertebrate grazers (Hay, 1981a, 1984; Paul and Hay, 1986; Paul, 1987; Hay et al., 1987a, 1987b, 1990a,b; Hay and Steinberg, 1992; Duffy and Hay, 1994; Faulkner, 1994; Cronin and Hay, 1996; Cronin et al., 1997; Cruz-Rivera and Hay, 2003; Barbosa et al., 2004; Pillans et al., 2004). However, particular fishes and urchins will consume certain <i>Dictyota</i> species (Paul et al., 1987a; Morrison, 1988; Thacker et al., 2001; Tuya et al., 2001; McClanahan et al., 2002), and some mesograzers exploit certain species as food and chemically defended shelter or cover (Hay et al., 1987a, 1988c, 1990a; Duffy and Hay, 1991, 1994; Stachowicz and Hay, 1996, 1999; Cruz-Rivera, 2001). More than 230 compounds have been isolated from <i>Dictyota</i> spp. (Paul et al., 2001)	2–45532	Withers (1981), Ballantine et al. (1985), Carlson et al. (1984), Carlson and Tindall (1985), Gillespie et al. (1985a), Taylor (1985), Taylor and Gustavson (1985), Inoue and Gawel (1986), Bomber et al. (1989), Bourdeau and Durand-Clement (1991), Kohler and Kohler (1992), Morton and Faust (1997), Tindall and Morton (1998), Popowski et al. (2001), Villareal and Morton (2002)
<i>Dictyopteris</i>	Some tropical species are low preference foods for fishes (Paul and Hay, 1986) and a variety of feeding deterrents against macro- and mesograzers have been studied in tropical and temperate species of this genus (Hay et al., 1988a; Taniguchi et al., 1993; Bolser and Hay, 1996; Poore and Steinberg, 1999; Schnitzler et al., 2001), although some species are highly palatable to tropical fishes (Paul et al., 1987a)	12–589	Koike et al. (1991), Popowski et al. (2001)

<i>Digenia</i>	Finely branched, wiry red alga (Littler and Littler, 2000). Field experiments suggest it is of intermediate to low palatability to some fishes (Hay, 1984; Paul and Hay, 1986; Hay et al., 1989; Lapointe et al., 2004), but preferred by some species of surgeonfishes (Lewis, 1985)	158–2180 Densities not explicitly stated in Bourdeau and Durand-Clement (1991)	Gillespie et al. (1985a, 1985b), Bourdeau and Durand-Clement (1991)
<i>Enantiocladia</i>	Branching red algae. No data available on palatability	114	Gillespie et al. (1985a)
<i>Enteromorpha</i>	Palatable algae that can occur as short turfs or longer tubular thalli, either epiphytic or on primary substrate (Gacia et al., 1999; Littler and Littler, 2000; McClanahan et al., 2002). They are consumed by a variety of tropical and temperate herbivores including fishes (Littler and Arnold, 1982; Hay, 1986; Paul, 1987; Barry and Ehret, 1993; Friedlander et al., 1996; Hixon and Brostoff, 1996; Ferreira et al., 1998; Cruz-Rivera and Hay, 2000b, 2001; Cruz-Rivera and Paul, 2002; Lison de Loma and Ballesteros, 2002); often used as basic diet in studies testing chemical defenses of other algae due to its lack of structural or chemical defenses (Hay et al., 1998). The existence of activated chemical defenses against invertebrates has been recently shown for two temperate species (Van Alstyne and Houser, 2003; Van Alstyne et al., 2001), but no tropical species have been tested. Some species are fast growing and can form blooms under eutrophic conditions (Littler and Arnold, 1982; Cohen and Fong, 2004; Bintz et al., 2003; McClanahan et al., 2002; Nelson et al., 2003). The genus <i>Enteromorpha</i> has recently been changed to <i>Ulva</i> (Hayden et al., 2003)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Galaxaura</i>	Calcified red algae (Kerker, 1994) that also produce unusual, and sometimes cytotoxic, secondary metabolites (Paul and Hay, 1986; Sheu et al., 1996, 1997a) although their function as feeding deterrents has not been rigorously tested. Some species are abundant in areas of high fish herbivory (Cruz-Rivera personal observation) and field experiments have shown intermediate to low palatability of various tropical species (Paul and Hay, 1986). Some <i>Galaxaura</i> spp. will be consumed by tropical urchins (Solandt and Campbell, 2001)	0.05–395	Inoue and Raj (1985), Taylor (1985), Inoue and Gawel (1986), Bourdeau and Durand-Clement (1991), Koike et al. (1991), Ichinotsubo et al. (1994), Tindall and Morton (1998), Popowski et al. (2001)
<i>Gelidiella</i>	Finely branched red turfs (Littler and Littler, 2000). Field experiments suggest moderate to low palatability depending on the species (Hay, 1984; Hixon and Brostoff, 1996). Species are sometimes found within damselfish territories (Hixon and Brostoff, 1996)	Data from mixed algal collections (Gillespie et al., 1985a); 7 cells/cm ² (Abuso et al., 2000)	Gillespie et al. (1985a), Abuso et al. (2000)
<i>Gelidiopsis</i>	Finely branched red turfs (Littler and Littler, 2000). Some species are a preferred food for territorial damselfishes (Lison de Loma and Ballesteros, 2002)	Data from mixed algal collections	Gillespie et al. (1985a)
<i>Gelidium</i>	Finely branched red turfs (Littler and Littler, 2000). Field experiments suggest this is a palatable genus to fishes, often found within damselfish territories (Hixon and Brostoff, 1996; Ferreira et al., 1998; Ojeda and Munoz, 1999), and consumed also by marine reptiles, crabs and gastropods (Kyomo, 1999; Lopez et al., 2003; Rubenstein and Wikelski, 2003)	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Gracilaria</i>	Some toxins have been isolated from this red algal genus and consumption has led to human fatalities (Higa and Kuniyoshi, 2000; Yotsu-Yamashita et al., 2004; Yasumoto, 2005), but the compounds are likely produced by cyanobacterial epiphytes, not the host alga (Yasumoto, 2005). This genus is consumed by fishes, sea turtles, urchins, gastropods and crustaceans (Nelson and Tsutsui, 1980; Hay, 1981a, 1986; Hay et al., 1986; Paul and Hay, 1986; Friedlander et al., 1996; Upatham et al., 1998; Brand-Gardner et al., 1999; Cruz-Rivera and Hay, 2001; Elfving and Tedengren, 2002; Seminoff et al., 2002; Pillans et al., 2004, but see Hay, 1984; Hay et al., 1989). This genus is capable of fast growth under eutrophic conditions (Peckol and Rivers, 1995), likely an advantage for aquaculture of this agarophyte	Data from mixed algal collections	Hurbungs et al. (2002)

Appendix A (Continued)

Algal genus	Remarks	<i>Gambierdiscus toxicus</i> densities (cells/gwm alga)	References
<i>Halimeda</i>	Chemically and structurally (calcified- Wefer, 1980; Payri, 1995) defended green algae (Hay, 1984; Paul and Hay, 1986). This group contains some of the most sophisticated defensive systems known including differential allocation of defensive metabolites to softer tissues, nocturnal growth (when herbivores are mostly inactive), activated chemical defenses, and heavy calcification which interacts with chemistry to decrease palatability (Hay, 1981a, 1984; Paul and Fenical, 1983; Lewis, 1985; Paul and Hay, 1986; Hay et al., 1988b, 1990b, 1994; Paul and Van Alstyne, 1988, 1992; Pennings and Paul, 1992; Meyer et al., 1994; Schupp and Paul, 1994). Some parrotfishes, sea urchins, and specialized mesograzers represent the few consumers that will eat <i>Halimeda</i> (Paul and Van Alstyne, 1992; Stachowicz and Hay, 1996; Overholtzer and Motta, 1999; Munoz and Motta, 2000; Solandt and Campbell, 2001)	0.01–4774	Yasumoto et al. (1979), Bergmann and Alam (1981), Withers (1981), Ballantine et al. (1985), Gillespie et al. (1985a), Inoue and Raj (1985), Inoue and Gawel (1986), Bomber et al. (1988a, 1989), Bourdeau and Durand-Clement (1991), Kaly and Jones (1994), Hahn (1991 as cited in Lehane, 1999), Morton and Faust (1997), Tindall and Morton (1998) Grzebyk et al., 1994
<i>Halymenia</i>	Flattened branching red alga. Some large and conspicuous species are common in areas of high herbivory (Cruz-Rivera, personal observation). Some studies have shown grazing on this genus (Hay, 1981a, 1984; Paul and Hay, 1986), while other field assays have shown this genus to be of very low preference to fishes (Paul et al., 1987a; Hay et al., 1988a, 1989). Some work suggests some species are chemically defended (V.J. Paul personal communication)	<1	
<i>Herposiphonia</i>	Filamentous red turf algae. No chemical or structural defenses known. No experimental data available on palatability	Densities not explicitly stated	Bourdeau and Durand-Clement (1991)
<i>Heterosiphonia</i>	Red turf algae either epiphytic or on primary substrate. No chemical or structural defenses known. No experimental data on palatability	6844	Bomber et al. (1988a, 1989), Morton et al. (1992)
<i>Hypnea</i>	Palatable fast growing red algae, either growing as epiphytes or on primary substrate (Gacia et al., 1999; Littler and Littler, 2000). It is consumed by fishes, sea turtles, crustaceans and gastropods (Hay, 1986; Paul and Hay, 1986; Hay et al., 1988c; Duffy and Hay, 1991; Russell and Balazs, 1994; Wood and Buxton, 1996; Tahil and Juinio-Menez, 1999; Andre et al., 2005). Some halogenated terpenes have been isolated from one species, but their role as feeding deterrents is unknown (Afaqhusain et al., 1991)	18–48	Shimizu et al. (1982), Gillespie et al. (1985a), Bourdeau and Durand-Clement (1991), Kaly and Jones (1994), Heil et al. (1998), Hurbungs et al. (2002)

<i>Jania</i>	Calcified red turf algae. Brominated diterpenes have also been isolated from this genus, but their ecological function is unknown (Awad, 2004). Palatability varies among species, with some <i>Jania</i> spp. being palatable to some herbivores (Barry and Ehret, 1993; McClanahan et al., 2002), but not others (Cruz-Rivera, 2001). Some damselfish will consume considerable amounts of <i>Jania</i> as part of their gardening activities, despite it being a low preference food (Ferreira et al., 1998)	0.01–41820	Yasumoto et al. (1979), Yasumoto (1979), Yasumoto et al. (1980), Bagnis et al. (1985), Bagnis et al. (1990), Gillespie et al. (1985a), Inoue and Raj (1985), Inoue and Gawel (1986), Bourdeau and Durand-Clement (1991), Kaly et al. (1991), Shirai et al. (1991 as cited in Lehane, 1999), Hokama et al., 1993, Ichinotsubo et al. (1994), Kaly and Jones (1994), Tindall and Morton (1998), Chinain et al., 1999a, Hurbungs et al. (2001)
<i>Laurencia</i>	Over 570 secondary metabolites have been isolated from this genus (Faulkner, 1994; Paul et al., 2001), some of which are potent chemical defenses against tropical fish, urchins and gastropods (Hay et al., 1987b; Morrison, 1988; Granado and Caballero, 1995, 2001; Kurata et al., 1998; Biggs, 2000). Palatability to generalist grazers varies from lower preference (Paul and Hay, 1986; Paul et al., 1987a; Hay et al., 1989) to highly palatable species (Hay, 1981a, 1984; Paul and Hay, 1986; Hay et al., 1990b; Lewis, 1985; Tahil and Juinio-Menez, 1999; Boaventura et al., 2002; Lapointe et al., 2004; Andre et al., 2005). There is also considerable variance in the tolerance of marine herbivores towards <i>Laurencia</i> secondary metabolites (Paul et al., 2001) Some chemically defended species are grazed by more specialized invertebrate herbivores (Stachowicz and Hay, 1996; Rogers et al., 2000, 2002; Jongaramruong et al., 2002)	229–2901	Withers (1981), Carlson (1984), Gillespie et al. (1985a), Bomber et al. (1989), Bourdeau and Durand-Clement (1991), Shirai et al. (1991 as cited in Lehane, 1999), Abbott (1995), Tindall and Morton (1998)
<i>Lithothamnion</i>	Heavily calcified red algal crusts. Some species form rodoliths in deep waters (Littler and Littler, 2000). In general, crustose corallines are the most resistant algae to grazers (Littler and Littler, 1984)	Densities not explicitly stated	Gillespie et al. (1985a)

Appendix A (Continued)

Algal genus	Remarks	<i>Gambierdiscus toxicus</i> densities (cells/gwm alga)	References
<i>Lobophora</i>	Produces polyphenolics (phlorotannins) that can deter fish grazers (Targett et al., 1995; Bolser and Hay, 1996; Arnold and Targett, 1998, 2000). Toxicity of extracts towards fish has been suggested, but not rigorously tested (De Lara-Isassi et al., 2000). Field experiments have shown very low to moderately high palatability of <i>Lobophora variegata</i> to fishes (Hay, 1981a, 1984; Lewis, 1985; Paul and Hay, 1986; Kennelly, 1991; Jompa and McCook, 2002; McClanahan et al., 2002; Diaz-Pulido and McCook, 2003) depending on grazers and geographic region. Laboratory assays have shown this species to be avoided by rabbitfish (Pillans et al., 2004). Data using the common tropical sea urchin <i>Diadema antillarum</i> are contradictory with <i>L. variegata</i> being a high or low preference item depending on geographic location (De Ruyter van Steveninck and Breeman, 1987; Morrison, 1988; Solandt and Campbell, 2001; Tuya et al., 2001). Tropical populations of this alga can be considerably less palatable than temperate ones (Bolser and Hay, 1996). As an additional defense, this alga also produces a different, more herbivore-resistant, morphotype in areas of high herbivory (Coen and Tanner, 1989)	Densities not explicitly stated	Gillespie et al. (1985a)
<i>Lophosiphonia</i>	Red algal finely branched turfs (Littler and Littler, 2000). No data on palatability	Densities not explicitly stated	Bourdeau and Durand-Clement (1991) Gillespie et al. (1985a), Bourdeau and Durand-Clement (1991)
<i>Lynghya</i>	Hundreds of bioactive secondary metabolites have been isolated from this cyanobacterial genus (Paul et al., 2001) Various studies have shown strong deterrence and toxicity of these metabolites against vertebrate and invertebrate consumers (Nagle et al., 1996; Thacker et al., 1997; Nagle and Paul, 1999; Cruz-Rivera and Paul, 2002), however, some specialized gastropods prefer to feed on this genus (Paul and Pennings, 1991; Pennings et al., 1996; Nagle et al., 1998; Cruz-Rivera and Paul, 2002)		
<i>Martensia</i>	Epiphytic, flattened fan-like red algae Some species produce indole alkaloids (Kirkup and Moore, 1983; Murakami et al., 1994; Takahashi et al., 1998), suggesting a potential chemical defense, but no data are available on palatability	Densities not explicitly stated	Withers (1981)
<i>Melosira</i>	Colonial diatom. No chemical or structural defenses known from benthic species. This genus is a common item in the diet of some estuarine fishes (Almeida, 2003), but it is likely grazed upon more commonly by smaller invertebrates such as crustaceans and snails (Aurioles-Gamboa and PerezFlores, 1997; Jensen and Asplen, 1998; Sommer, 1999; Aikins and Kikuchi, 2002)	2	Shimizu et al. (1982)
<i>Microdictyon</i>	Finely branched “cushion-like” green algae with a crisp and fragile thallus (Littler and Littler, 2000). No data are available on palatability	9	Shimizu et al. (1982), Gillespie et al. (1985a)
<i>Padina</i>	Lightly to moderately calcified (Wefer, 1980; Okazaki et al., 1986; Kerkar, 1994; Payri, 1995) fan-shaped brown algal genus, with some species also producing halogenated terpenes (Parameswaran et al., 1994) and polyphenolics (Karez and Pereira, 1995). Some species are unpalatable to local fishes and invertebrates (Hay, 1986; Hay et al., 1988c), are low preference items for sea urchins and crustaceans (Tuya et al., 2001; Poore and Steinberg, 1999) or support poor growth on gastropods (Upatham et al., 1998), while others are preferred foods for urchins and fish (Hay, 1981a, 1984; Paul and Hay, 1986; Paul et al., 1987a; Thacker et al., 2001; Bulleri et al., 2002; McClanahan et al., 2002; Lapointe et al., 2004). There can be marked geographic differences in relative palatability to fishes for a given species (Cruz-Rivera and Paul, 2002), and tropical species can be significantly less palatable than temperate counterparts (Bolser and Hay, 1996). These algae may also produce morphological phenotypes that are less susceptible to herbivory, depending on grazing intensity (Lewis et al., 1987)	0.01–42	Gillespie et al. (1985a), Inoue and Raj (1985), Bomber et al. (1989), McCaffrey et al. (1992), Tindall and Morton (1998)
<i>Penicillus</i>	Calcified and chemically defended (Wefer, 1980; Hay, 1984; Paul and Fenical, 1984; Paul and Hay, 1986) green algal genus. Although some consumption has been observed (Hay et al., 1990b), palatability of different species in this genus appears very low to tropical fishes (Hay, 1984; Paul and Hay, 1986)	17–5131	Ballantine et al. (1985), Bomber et al. (1989), Tindall and Morton (1998)

<i>Polysiphonia</i>	Variably palatable red turf algae, either epiphytic or on primary substrate (Littler and Littler, 2000). Some toxic halogenated compounds have been isolated (De Rosa et al., 2001; Shoeib et al., 2004), but their function as feeding deterrents is unknown. At least one species might contain an activated chemical defense against grazers (Van Alstyne et al., 2001). Some experiments have shown variable palatability to, and poor performance of, mesograzers feeding on this algal genus (Cruz-Rivera and Hay, 2000b; Duffy and Harvilicz, 2001; Norderhaug, 2004). However, some damselfishes consume, and even maintain monocultures of, <i>Polysiphonia</i> in their territories (Ferreira et al., 1998; Hata and Kato, 2003). It is a main food for some temperate fish and invertebrates (Barry and Ehret, 1993; Ito et al., 1996; Sturm and Horn, 1998). Some species are early successional species (Agatsuma et al., 1997; Diaz-Pulido and McCook, 2002), and have fast growth rates (Campbell, 2001)	Observations based on mixed algal collections (Gillespie et al., 1985a) or densities not explicitly stated (Bourdeau and Durand-Clement, 1991)	Bourdeau and Durand-Clement (1991)
<i>Portieria</i>	Foliose red algae chemically defended by halogenated monoterpenes. (Paul et al., 1990, 1992; Meyer et al., 1994; Ginsburg and Paul, 2001). Some specialized gastropods sequester chemicals from these algae and use them as acquired defenses (Ginsburg and Paul, 2001)	120	Grzebyk et al. (1994)
<i>Pterocladia</i>	Branching, red algae. Low preference to snails and crabs (Kennish and Williams, 1987; Wakefield and Murray, 1998). It has been argued that morphology influences preference for some crabs, despite the high caloric content of the alga, making some species of <i>Pterocladia</i> less preferred (Kennish and Williams, 1987). No data on palatability to tropical consumers	270 Densities not explicitly stated in Bourdeau and Durand-Clement (1991)	Gillespie et al. (1985a), Bourdeau and Durand-Clement (1991), Ichinotsubo et al. (1994)
<i>Rhizoclonium</i>	Freshwater and marine green filamentous algae. No data available on palatability	28	Shimizu et al. (1982)
<i>Sargassum</i>	Conspicuous brown algae, occurring either attached to substrate or as free floating communities. Some species are low preference items for fishes (Hay, 1981a, 1984, 1986; Paul et al., 1987a; Paul and Hay, 1986; Hay et al., 1988c), and palatability can vary strongly among populations of the same species (Taylor et al., 2003) or when species are compared (Bolser and Hay, 1996). Some species have a coarse consistency and are likely structurally defended (although this remains untested), while other species are palatable (Lewis, 1985; Paul and Hay, 1986; Paul, 1987; Cruz-Rivera and Paul, 2002). This genus produces phlorotannins (Ragan and Glombitza, 1986), but the amount of these chemical deterrents is highly variable among species (Targett et al., 1995; Arnold and Targett, 2000). Defenses can be induced by grazing in some species (Sotka et al., 2002; Taylor et al., 2002)	29	Withers (1981), Gillespie et al. (1985a), Inoue and Raj (1985), Ballantine et al. (1985), Bomber et al., 1988b, Bourdeau and Durand-Clement (1991), Hahn (1991 as cited in Lehane, 1999), Holmes et al. (1998), Tindall and Morton (1998)
<i>Spyridia</i>	Branching red alga either growing as epiphyte or on primary substrate. Generally palatable to grazers including gastropods (Wood and Buxton, 1996), and fish (Hay, 1981a, 1986; Paul and Hay, 1986; Hay et al., 1989). It is a lower preference food for some urchins (Hay, 1984)	31–1036	Withers (1981), Shimizu et al. (1982), Carlson and Tindall (1985), Ballantine et al. (1985), Taylor and Gustavson (1985), McCaffrey et al. (1992), Bourdeau and Durand-Clement (1991), Shirai et al. (1991 as cited in Lehane, 1999), Tindall and Morton (1998)
<i>Styopodium</i>	Chemically defended brown algae of intermediate to very low preference to fishes (Hay, 1981a, 1984; Paul and Hay, 1986; Paul et al., 1987a). They produce a variety of compounds, depending on species, location and ontogenetic stage (Gerwick and Fenical, 1981; Gerwick et al., 1985; Hay et al., 1987b, 1988a, Wessels et al., 1999; Soares et al., 2003; Pereira et al., 2004)	27–250	Popowski et al. (2001)

Appendix A (Continued)

Algal genus	Remarks	<i>Gambierdiscus toxicus</i> densities (cells/gwm alga)	References
<i>Thalassia</i>	Marine angiosperm. Although they produce phenolic acids (Zapata and McMillan, 1979), it is palatable to urchins, parrotfishes, sea turtles and dugongs (Lewis, 1985; Paul and Hay, 1986; Hay et al., 1990b; Cebrian and Duarte, 1998; Rose et al., 1999; Valentine and Heck, 1999; Valentine et al., 2000; Macia, 2000; Sluka and Miller, 2001; Kirsch et al., 2002; Andre and Lawler, 2003; Andre et al., 2005, but see Hay et al., 1989)	8–1463	Ballantine et al. (1985), Morton and Faust (1997)
<i>Tolypocladia</i>	Hokama et al. (1993) referred to a <i>Tolycarpidia glomurata</i> . We believe this is a misspelling of <i>Toyipocladia glomerulata</i> as <i>Tolycarpidia</i> is not a valid algal genus. <i>Tolypocladia</i> is a branching turf-forming red alga either epiphytic or on primary substrate. Palatable to fishes and invertebrates although it can rank lower in herbivore preference than other sympatric algae (Thacker et al., 2001; E. Cruz-Rivera, unpublished)	291	Hokama et al. (1993), Ichinotsubo et al. (1994),
<i>Turbinaria</i>	Brown algae, which produce polyphenolics (Hay, 1984; Norris and Fenical, 1982; Targett et al., 1995), feeding deterrents against gastropods (Sawai et al., 1994), and some cytotoxic compounds (Asari et al., 1989; Sheu et al., 1997b; Sheu et al., 1999). It is often found in backreefs, lagoons, and protected areas, which are places of low herbivory (Lewis, 1985). It has a tough leathery consistency, which suggests some structural defense, however, this has yet to be tested. Field assays have shown intermediate to low palatability of some species to fish (Hay, 1984; Lewis, 1985; Hay et al., 1989); but herbivores with strong jaws such as parrotfishes and sea urchins can readily consume these algae (Lewis, 1985; Lison de Loma et al., 2002)	0.01–1617	Yasumoto et al. (1979, 1980), Yasumoto (1979), Withers (1981), Carlson et al. (1984), Bagnis et al. (1985), Gillespie et al. (1985a), Inoue and Raj (1985), Inoue and Gawel (1986), Bourdeau and Durand-Clement (1991), Hahn (1991 as cited in Lehane, 1999), Koike et al. (1991), Shirai et al. (1991 as cited in Lehane, 1999), Hokama et al. (1993), Grzebyk et al. (1994), Ichinotsubo et al. (1994), Abbott (1995), Tindall and Morton (1998) Grzebyk et al., 1994
<i>Tydemania</i>	Calcified and possibly chemically defended. Various secondary metabolites, including triterpenes, have been isolated from this genus (Paul et al., 1982a, 1982b; Govindan et al., 1994). I often occurs in areas of high herbivory (Cruz-Rivera, personal observation), although no experimental data on palatability are available	>235	Grzebyk et al., 1994
<i>Udotea</i>	Calcified and chemically defended algae (Hay, 1984; Paul and Hay, 1986; Kerkar, 1994), unpalatable to both vertebrate and invertebrate consumers (Paul and Fenical, 1984; Paul and Hay, 1986; Paul, 1987; Hay et al., 1994; Pillans et al., 2004)	16–514	Ballantine et al. (1985), Bomber et al. (1989)
<i>Zonaria</i>	Leathery brown foliose algae. This genus produces phlorotannins and their role as feeding deterrents has been suggested by various authors (Blackman et al., 1988; Targett et al., 1995; Bolser and Hay, 1996; Poore and Steinberg, 1999; Wisespongpan and Kuniyoshi, 2003). Some species are a preferred food for certain mesograzers (Poore, 1994)	62–112	Gillespie et al. (1985a)

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