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Could marine animal conservation laws be responsible for the decline or extirpation of macroalgal populations in Bermuda over the past century?

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Abstract: Using over 10,000 archival herbarium specimens from Bermuda, we compared the presence or absence of seaweeds from a century ago with our more than 5000 collections from the last 30 years. Populations of parrotfish, important herbivores of macroalgae in the tropics, have increased since the 1993 amendment to the Bermuda 1978 Fisheries (Protected Species) Order. A fish pot ban for Bermuda was put into effect in 1990 to protect a variety of fish including parrotfish and several species of grouper, important predators of parrotfish that were rarely seen in island waters at the time. Intertidal grazing West Indian top shells were reintroduced in 1982 to Bermuda, and since then, along with the rise in parrotfish populations, inshore populations of many macroalgae have dramatically changed. We suggest that several large and abundant Bermuda macroalgal species recorded in the early 20th century appear to have been extirpated or are greatly diminished in sizes of individuals as well as population abundance, and propose that marine animal protections over the past 35 years are a possible reason for the changes we are presently observing.

Keywords: Bermuda; extirpation; macroalgae; parrotfish; West Indian top shell introduction.

Introduction

Tropical coral reefs of the world are experiencing ecosystem decline due to global climate change, overfishing, pollution and, in places, lack of conservation measures by governmental agencies (Pandolfi et al. 2005). The northernmost hermatypic coral reefs in the North Atlantic (32°14–25′N, 64°38–52′W) surround the archipelago of Bermuda (Thomas 2004), providing great ecological value to local habitats, as well as economic value to the country in the form of tourism. When its reefs began to show some of the stressors associated with ecosystem decline previously shown in the Caribbean (Aronson and Precht 2001, Smith et al. 2013), new management policies were put into effect in Bermuda during the latter part of the 20th century to maintain the health of its reefs (Glasspool 2008). These policies were created primarily to prevent the loss of marine animals, from corals to shellfish and reef fish, yet possibly posed an unintentional conservation trade-off in the environment for the organisms at the base of the rocky-bottom food web, including marine macroalgae (Estes et al. 2011). At present, however, Bermuda's coral reefs are considered "high risk" by the World Resources Institute because of the high population density and potential for coastal pollution (Burke et al. 2008). Nevertheless, although Bermuda's coral reefs are experiencing some environmental stress, they are considered one of the "healthiest" coral reef systems of the wider Caribbean region, in part due to conservation policies but also because of their northerly latitudinal advantage during global warming (Glasspool 2008, Sarkis et al. 2010, Smith et al. 2013).

Throughout the recorded history of Bermuda, there has been a long timeline of restrictions and protections for marine animal resources by the government, beginning within decades of the permanent colonization of the islands by the British in the early 1600s (Smith-Vaniz et al. 1999). The local waters were teeming with food for islanders at the outset but, even in the early days, regulations were needed to protect populations from overharvesting (Smith-Vaniz et al. 1999). In 1978, Bermuda was again compelled to protect its economically valuable marine resources by enacting the Fisheries (Protected Species) Order (BR 8/1978) setting "no harvest" protections for all marine turtles, mammals and corals, as well as several gastropod and bivalve mollusks. In 1993, the order was amended to include parrotfish "of all species" (*Scarus* spp., *Sparisoma* spp.) and in 1996 a select set of groupers (*Epinephelus* spp., *Mycteroperca* spp.) was afforded protection. Parrotfish were protected because of the important role they play in keeping seaweeds in check on rocky coasts and coral reefs (Smith-Vaniz et al. 1999), while also contributing to the formation of sand by grinding away at rocky substrates with their toothed beaks to harvest

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benthic algae (Thomas 2004). These large herbivores were not harvested for food until 1977 when other more desirable species were declining prior to forthcoming protection laws (Butler et al. 1993). At this time a shift took place from annual catches dominated by grouper and snapper to one in which herbivorous reef fishes, including parrotfish, were the bulk of the Bermuda fishery (Butler et al. 1993). From zero harvest in 1975, parrotfish catch grew to 92,000 kg in 1987, fully 36% of the total catch of miscellaneous reef fish (Butler et al. 1993).

Beginning in 1993, when local fishermen could no longer legally harvest parrotfish, Bermuda populations of this group of seaweed grazers rapidly increased, as did larger-sized individuals of these species (O'Farrell et al. 2015, 2016). In 1990, when the latest Bermuda fish pot ban (Burnett-Herkes and Barnes 1996, Smith-Vaniz et al. 1999) was put into effect to stop the by-catch of protected species, including Yellowfin (*Mycteroperca venenosa*), Gag (*Mycteroperca microlepis*), Tiger (*Mycteroperca tigris*), Nassau (*Epinephelus striatus*) and Red (*Epinephelus morio*) groupers, and Mutton hamlet (*Alphestes afer*), these predators of parrotfish were uncommon in surrounding waters. Although the fish pot ban offered some relief for these and other grouper populations, not all species in Bermuda were protected from commercial fishing. The largest species in Bermuda, the black grouper (*Mycteroperca bonaci*), known locally as rockfish, remained unprotected and showed a steady decline in reported landings between 1975 and 1981 (Burnett-Herkes and Barnes 1996, Luckhurst and Ward 1996), the assumption being a decline in its local population due to fishing pressure. Landings of black grouper remained low until 2002 when gear improvement allowed for greater success in harvesting these large predators (Luckhurst and Trott 2015). At this time, when an apex predator population was being harvested in great numbers by trawling in shallow waters (Luckhurst and Trott 2015), parrotfish were showing increased populations of larger individuals than previous years due to low predator pressure (O'Farrell et al. 2015, 2016). Other apex predators that could affect parrotfish population dynamics, Galapagos sharks (*Carcharhinus galapagensis*, called dusky or puppy sharks in Bermuda) and tiger sharks (*Galeocerdo cuvier*), faced similar fortunes due to overfishing during the same time period. From 1990 to 1991, pelagic fish harvest numbers had doubled from previous decades to 40.7% of the total fisheries catch in Bermuda (Butler et al. 1993). Although shark population data specifically for Bermuda is unavailable, pelagic and inshore shark populations in the Northwest Atlantic Ocean showed a steady decline from 1986 to 1998 due to overfishing (Baum et al. 2003), and their presence in the islands has not been robust since the 1978 Fisheries (Protected Species) Order has gone into effect (unpublished observations).

Another grazing herbivore of the intertidal and shallow subtidal, the West Indian top shell (*Cittarium pica*), was extirpated in Bermuda by human predation in the early 1800s (Olson and Hearty 2013), leaving the habitat without its largest (5–15 cm shells; Sterrer 1986) native gastropod. Several attempted Caribbean reintroductions of this species from 1901 through the 1970s failed due to a lack of government protection against renewed harvest by local Bermudians for food (Olson and Hearty 2013). The 1982 reintroduction of top shells was finally successful owing to the 1993 amendment of the 1978 Fisheries (Protected Species) Order to prevent their harvest (Bickley and Rand 1982). Along with parrotfish grazing during high tides, these top shells thereafter provided the intertidal with constant grazing pressure on macroalgae and their germlings on calcareous rock substrata (McAfee and Morgan 1996, Robertson 2003). By 2000 island-wide, top shells were estimated at 3700+ individuals mostly on windward intertidal rocks along the south shore and, by 2015 using remote sensing, the total population was estimated at over 31,000 individuals (Meyer et al. 2015).

Unlike the difficulties associated with estimating the reduction of animal size over time in marine megafauna (McClenachan 2009), early seaweed collectors left an extensive archival record of herbarium specimens from locations throughout the world useful for comparative purposes with recent collections made from the same sites today (Bates et al. 2009, Wernberg et al. 2011). Relative to all islands in the Caribbean Sea to its distant south, Bermuda is an area with a long, rich taxonomic past with archival specimens deposited in herbaria in great numbers by early workers. Based upon herbarium specimens from the late 1800s to the 1960s, the intertidal and shallow subtidal landscape in Bermuda must have looked dramatically different at the beginning of the 20th century than it does today. Presumably, where once there were abundant, diverse communities of large seaweeds on the limestone rocks at low tide, many such areas are completely devoid of macroalgae today, while other areas produce cropped turfs as intertidal species attempt regrowth under heavy herbivore grazing pressure. Some areas along the south shore have seasonal populations of macroalgae, with communities less diverse than in the past, and the species that remain are mostly protected by calcium carbonate impregnation (e.g. *Galaxaura, Titanophycus, Yamadaella*; see Steneck and Watling 1982) or chemical defenses (e.g. *Cystoseira, Dictyota, Laurencia, Liagora*; see Pereira et al. 2017).

In 1983 and 1985, Searles and Schneider (1987) initiated the latest wave of macroalgal collecting in Bermuda, and in the 1990s we began annual collections of the attached seaweed flora, visiting the islands during different seasons, including an intensive year-long collecting/molecular barcoding study in 2012. During this time period, we have cataloged nearly 5200 seaweed specimens, and many species from our collections were distinctly uncommon or rare in their habitats. In our numerous taxonomic studies, we have noted that modern individuals of some species were much smaller in size compared to their local ancestors, and many other species present in the early 1900s were no longer present in the flora. The declines seem to coincide with animal protections put in place for Bermuda from the 1970s to the 1990s. Could animal protection laws for herbivores be responsible for the declines in these formerly abundant macroalgal communities, or might the physical environment have changed significantly over a century causing the decline of many species in Bermuda?

Materials and methods

Using early 20th century seaweed biodiversity records for Bermuda from various herbaria and museums, as well as more recent collections from the islands beginning in the 1980s by C.W. Schneider (CWS) and colleagues, we compared changes in seaweed diversity over the past 100 years. The early 1900s records were compiled in an algal flora by Collins and Hervey (1917) using their own extensive collections made throughout the years from 1912 to 1917. Most of the species reported in their flora were common enough to have been collected in large numbers to make 80 pressed specimens from a single locality on the same day. These bulk collections were made for inclusion in the "published" exsiccata *Phycotheca Boreali-Americana* (*P.B.-A.*) that would be distributed to subscribers from 1895 to 1919 (Fahey and Doty 1955). The production and sale of exsiccatae were a common way to disseminate botanical specimens in the last part of the 19th and early 20th century (Sayre 1969) and they remain today as a valuable resource of the biodiversity shot in time from a number of locations worldwide. Five volumes of *P.B.-A.* were dedicated to Bermuda algae (Collins et al. 1912–1913, 1915–1917), the great majority being marine species, each fascicle containing 50 species, therefore 250 species total. Each *P.B.-A.* number is represented by a pressed archival herbarium specimen and a printed label with collection, and some environmental, data (at times depth, relative abundance, substratum etc.). A year after the Collins and Hervey flora, Howe (1918) wrote the macroalgal section for N.L. Britton's *Flora of Bermuda*, importantly mentioning that he included only the "more common and more conspicuous algae occurring in the islands …". The specimens collected by these early workers and others archived in herbaria provide evidence for the prevalence of species in Bermuda a century ago, as well as the sizes of individuals regularly collected at that time.

For comparisons, we collected data for Bermuda seaweeds from herbarium specimens and labels digitized on the (US) National Science Foundation supported online *Macroalgal Herbarium Portal* (http://macroalgae.org/portal/index.php), including hundreds of collections made by Collins, Hervey and Howe among others from the early 1900s. Of the 45 US herbaria and museums that have mounted their digital images on this portal, 25 housed archival collections from Bermuda totaling 11,776 specimens, the largest repositories being BISH, DUKE, F, MICH, MSU and UC [herbarium/museum abbreviations associated with specimens follow the online *Index Herbariorum* (http://sweetgum.nybg.org/ih/)]. We compared archival specimen sizes and presence/abundance based upon inclusion in *P.B.-A.* and notations of abundance on herbarium sheets to CWS's more recent collections, observations and field notes.

Because small microscopic algae that were poorly known to collectors at the turn of the 20th century could still be present, yet rare, in the 21st century flora of Bermuda, the species highlighted in the present paper are the larger, conspicuous seaweeds that would not be overlooked by present day collectors. Many of the microscopic algae would have been difficult to collect in large numbers and then disseminate as herbarium specimens especially in *P.B.-A.*, so using only larger seaweeds in our comparisons removes a potential source of collecting bias, as larger species usually have been collected with greater frequency. Collections in Bermuda from 1983 to the present were made by us during all seasons of the calendar year. Throughout this paper, algal species are referred to using their current nomenclature.

Results

After collecting seaweeds in Bermuda for the past 3 decades, it has become obvious to us that some of the more conspicuous and abundant species collected a century ago are no longer present in the flora (Table 1). Many species that were common in the 20th century (Collins and Hervey 1917, Howe 1918, Taylor and Bernatowicz 1969), although still found in Bermuda, have only

Table 1: Larger macroalgal species[a] recorded (X) in collections prior to the Bermuda 1978 Fisheries (Protected Species) Order.

Species	*P.B.-A.* 1912–1917	Collins and Hervey 1917	Howe 1918	Taylor 1960
Acetabularia schenckii (S)		X	X	X
Acinetospora crinita (S)	X	X	X	
Avrainvillea rawsonii (S)				X
Botryocladia occidentalis (D)	X	X	X	X
Chaetomorpha minima (S)	X	X	X	X
Dudresnaya bermudensis (D)	X	X	X	X
Ectocarpus rallsiae (S)	X	X		X
Gracilaria caudata (S)		X		X
Gracilaria cervicornis (S)	X	X	X	X
Gracilaria cornea (S)		X		X
Gracilaria crassissima (S)		X	X	X
Halymenia echinophysa (D)		X	X	X
Polysiphonia opaca (S)	X	X	X	X
Porphyropsis coccinea[b] (S)	X	X	X	X
Rhizoclonium crassipellitum (S)	X	X		X
Sargassum acinarium (S)		X	X	X
Sargassum cymosum (S)	X	X	X	X
Siphonocladus tropicus (S)		X	X	X
Trichleocarpa cylindrica (S)		X		X
Turbinaria tricostata (S)	X	X	X	X
Wrightiella tumanowiczii (S)	X	X	X	X

None of the species listed were collected from 1983 to 2015 (D, deep subtidal; S, intertidal to shallow subtidal collections).

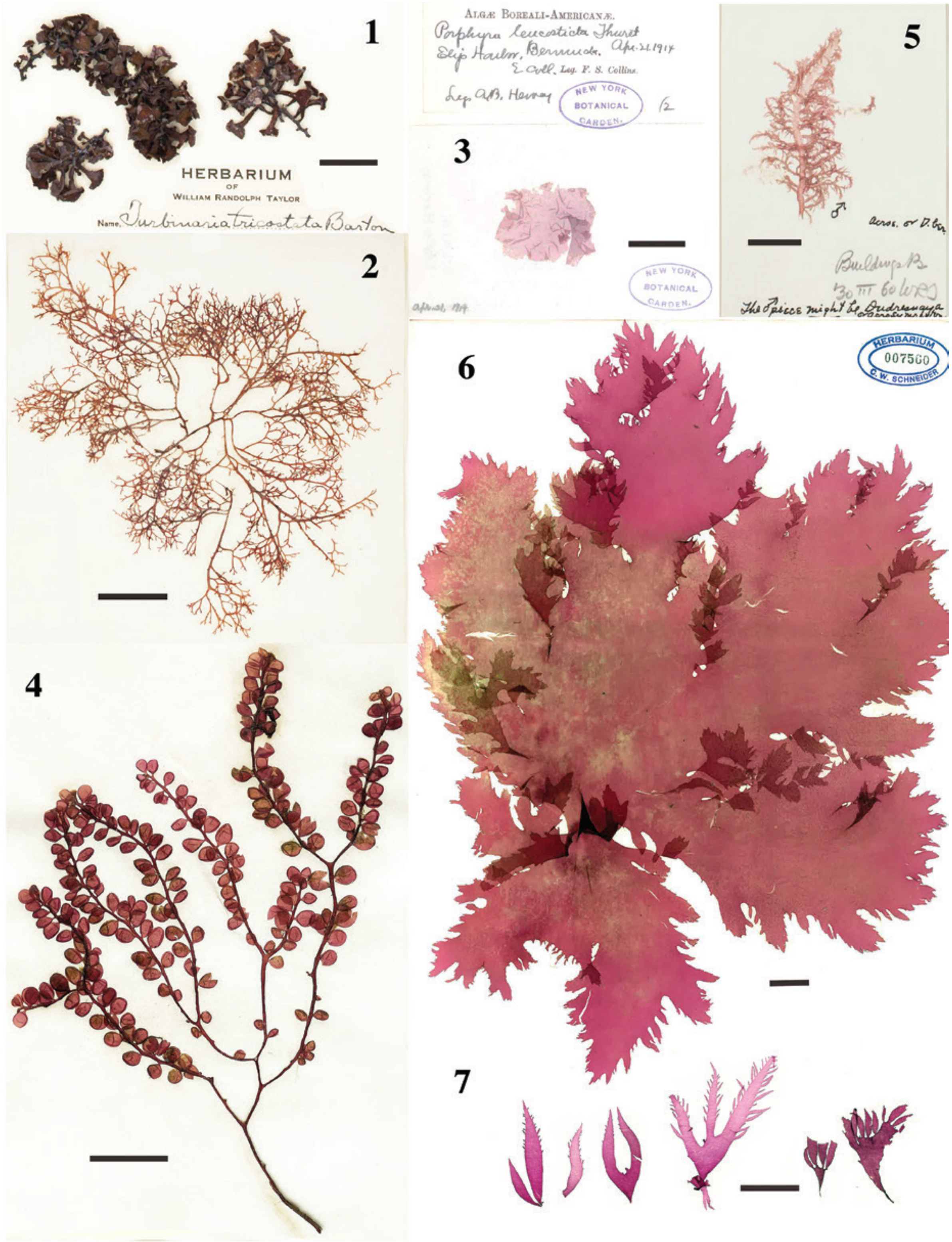
[a] Only includes species with verified observations of herbarium material. [b] Probable identification, but no specimens attributable to the same early 20th century red blades have been located since.

rarely been collected by us; for example, the red algae *Gracilaria mammillaris* (Montagne) M. Howe, *Halymenia elongata* C. Agardh, *Naccaria corymbosa* J. Agardh, *Nitophyllum wilkinsoniae* Collins *et* Hervey, *Palisada corallopsis* (Montagne) Sentíes, M.T. Fujii *et* Díaz-Larrea, the green alga *Siphonocladus rigidus* M. Howe and the brown alga *Spatoglossum schroederi* (C. Agardh) Kützing. Each of these species has been collected only once or a few times in the past 30 years, yet was distributed in large numbers in *P.B.-A*. Our comparisons also revealed that, in our collections, many species were present only as much smaller individuals in reduced populations relative to those species collected in the early 1900s. Below, we highlight some species from the 20th century in Bermuda that have not been found in the last 30+ years among over 5000 specimens we have collected, thus they can be presumed to be extremely rare or have been extirpated from these islands.

Intertidal and shallow subtidal species

The brown alga *Turbinaria tricostata* E.S. Barton (Figure 1) was reported by Agassiz (1895) as common during his visit to the islands in March, 1894. This seaweed remained abundant enough in Bermuda to be included in *P.B.-A.* (Collins et al. 1912) more than a decade later. Collections of this species from 1949 to 1950 were recorded on herbarium labels as “abundant” in tide pools and lower intertidal to shallow subtidal rocks from many locations along the south shore of Bermuda. Despite this species being reported again as abundant in the 1960s (Taylor and Bernatowicz 1969), no Bermuda collections of this species after 1950 were located in MICH, the main repository of Taylor’s collections, or any of the other seven herbaria listing it from Bermuda on the Macroalgal Portal. The specimens of *T. tricostata* from the first half of the 20th century were collected from all months of the year except December and January, yet today *Turbinaria* is no longer found in these south shore intertidal and shallow subtidal habitats or any other environment in Bermuda.

Several species of common 20th century agarophytes in the genus *Gracilaria* are likewise not found in today’s Bermuda flora. Although never commercially harvested in the islands, these species all appear to have been extirpated in the islands, with no collections made from 1983 to the present. *Gracilaria cervicornis* (Turner) J. Agardh (Figure 2) was common enough for at least 80 specimens from Horne’s Bay to be collected and distributed in *P.B.-A.* (Collins et al. 1913). Another species no longer seen,



Figures 1–5: Archival specimens of seaweed species now presumed to have been extirpated in Bermuda.
(1) *Turbinaria tricostata* [MICH]. (2) *Gracilaria cervicornis* [MICH]. (3) *Porphyropsis coccinea* [NY]. (4) *Botryocladia occidentalis* [FH].
(5) *Dudresnaya bermudensis* [MICH].
Figures 6, 7: *Halymenia pseudofloresii* [Herb. CWS].
(6) Protected salt pond specimen. (7) Smaller offshore specimens with grazed, regenerating blades at right. All scale bars = 2 cm.

Gracilaria crassissima (P. Crouan *et* H. Crouan) P. Crouan *et* H. Crouan, was common along the south shore intertidal zone in the early 1900s and described at the time as a new species, *Gracilaria horizontalis* Collins *et* Hervey (Collins and Hervey 1917). Type specimens held in NY and collections from Castle Harbor in 1881 demonstrate this species to be large and forming a robust population in Bermuda given the number of archival specimens. A further *Gracilaria* species, *Gracilaria cornea* J. Agardh, was found sparingly at mid-century (Taylor and Bernatowicz 1969), after its earlier report by Collins and Hervey (1917), but has not been collected since.

A red-bladed alga identified as *Porphyra leucosticta* Thuret (Figure 3) when collected in the early 1900s at multiple sites is almost certainly not that northern cold-water species and mostly likely represents *Porphyropsis coccinea* (Areschoug) Rosenvinge (Chris Neefus, pers. comm.). Nevertheless, no specimens comparable to the early Bermuda specimens in the family of reds where it resides have been found since.

At present, the red alga *Dichotomaria huismanii* C.W. Schneider, Popolizio *et* Spagnuolo is rare in the shallow subtidal of the south shore where it was common at the time of its issue in *P.B.-A.* [as *Dichotomaria marginata* (J. Ellis *et* Solander) J.V. Lamouroux; Collins et al. 1913]. Despite its impregnation with calcium carbonate, the tips of specimens recently collected are nearly always truncated with a regrowth of medullary filaments emerging, clear evidence of prior herbivore grazing (Schneider et al. 2016, figures 8, 9). Today's plants are half the size of mature 19th century plants (Schneider et al. 2016, figure 7), sparsely branched, and rarely found, and only then as isolated individuals.

Offshore species

Data for whether a species has been extirpated inshore are easier to ascertain than offshore, as inshore habitats can be, and have been, visited more easily many times over the year. For years we had speculated that *Botryocladia occidentalis* (Børgesen) Kylin (Figure 4), a large and charismatic seaweed, may have been extirpated from the Bermuda flora until we collected a single offshore specimen in 2016 from a depth of 60 m off the northeast coast. This species of *Botryocladia* had been found mostly in lesser depths by earlier collectors in shallow waters of Harrington Sound and Castle Harbor (Collins and Hervey 1917, Howe 1918, Taylor and Bernatowicz 1969). Scores of dives in all seasons at sites where it had been collected from the 1880s to the 1960s (Searles and Schneider 1987) had not turned up *B. occidentalis* since the early 1980s. Thus, based on our single offshore specimen after 2 weeks of intensive collecting in deep offshore Bermuda waters, this species could possibly now be restricted as scattered individuals only at great depths, no longer present in shallower habitats. We have never collected several other species known from deeper offshore waters collected prior to our work, for example *Dudresnaya bermudensis* Setchell (Figure 5), *Halymenia echinophysa* Collins *et* M. Howe, *Nemacystus howei* (W.R. Taylor) Kylin and *Schmitzia sanctae-crucis* R.T. Wilce *et* Sears (Schneider 2003).

Several species that were recorded as "abundant" offshore in the 1980s (Searles and Schneider 1987) appear to have become severely reduced in population size. *Hommersandiophycus pectinatus* (Collins *et* Hervey) Popolizio, C.W. Schneider *et* C.L. Lane (Popolizio et al. 2015) was commonly collected offshore in the 1980s (as *Liagora pectinata* Collins *et* Hervey; Searles and Schneider 1987) and now only sporadically in the 21st century. Other species that were routinely collected in the 1980s or earlier have not been collected again despite our more intensive offshore collecting starting near the turn of the millennium. Examples include the relatively small species *Antithamnionella bermudica* C.W. Schneider, *Callithamniella tingitana* (Bornet) Feldmann-Mazoyer, *Balliella pseudocorticata* (E.Y. Dawson) D.N. Young, *Discosporangium mesarthrocarpum* (Meneghini) Hauck and *Frikkiella searlesii* M.J. Wynne *et* C.W. Schneider (Wynne and Schneider 1996, Schneider and Searles 1997a,b, 1998). They have not been found in 21st century habitats where we collected them only 30 years ago despite extensive collecting and attention to the smaller species as well as the more charismatic ones.

Geologic sinkhole and artificial refugia from grazers

The red alga *Halymenia pseudofloresii* Collins *et* M. Howe (Figures 6 and 7) was originally described from Walsingham Park, Bermuda (Collins and Howe 1916). The park contains a series of limestone sinkhole ponds connected by underground caves with open connection to the sea, areas with very low herbivore pressure as compared to open coast and reef habitats (Thomas 2004). Specimens of *H. pseudofloresii* up to a meter in height can be found year round in some of the smaller sinkhole pools of the park (Figure 6; Schneider et al. 2010) where parrotfish are absent or uncommon (Thomas et al. 1992, Thomas 2004). Offshore specimens of *H. pseudofloresii* are relatively small (3–5 cm) and often truncated by herbivores (Figure 7). The ponds in Walsingham can thus be viewed as a refuge for this species and many others, where individual size and population levels are clearly the largest in the islands, for example *Corynomorpha clavata* (Harvey) J. Agardh, *Crassitegula walsinghamii* C.W. Schneider, C.E. Lane *et* G.W. Saunders, *Griffithsia aestivana* C.W. Schneider and *Meredithia crenata* C.W. Schneider, G.W. Saunders *et* C.E. Lane (Taylor and Bernatowicz 1969, Schneider et al. 2006, 2014, Schneider and Lane 2007). Although each of these species is still found occasionally on the outer reefs, often in protected crevices, their populations and individual sizes are much larger in Walsingham today. For example, Taylor and Bernatowicz (1969) mentioned that *C. clavata* was found in "considerable numbers" in several locations around the islands, but we have only sporadically collected isolated individuals, some truncated by herbivory, outside of the well-established population in Walsingham Pond.

Formerly thriving attached shallow-to-deep water communities of certain species of *Sargassum*, relatives of *Turbinaria*, are at present mostly reduced to isolated large holdfasts with short stalks and a few small blades, constantly being forced to regenerate new growth after being grazed by fish (unpublished observations). Along with *Turbinaria, Sargassum* was shown to be favored by herbivorous fish in a food preference study in the West Indies (Ogden 1976). Many species of attached *Sargassum* that were common in the 20th century are now much smaller individuals on the open coast, their tops constantly grazed by fish; however, *Sargassum bermudense* var. *stagnale* C.W. Schneider (Schneider 2003, figure 1) reaches as much as 2 m in height in the protected Walsingham Pond which is mostly free of herbivorous fish. Thomas (2004) describes Walsingham Pond as possibly the "world champion marine pond in biodiversity", and it is no coincidence that park sinkholes are the type localities for eight macroalgal species (Schneider et al. 2014) where the largest individuals of many species in Bermuda can still be found. Even though these seaweeds can occasionally be found outside their sinkhole environments, those in the park are protected from the intense grazer pressure of coastal Bermuda, growing individuals to their full potential and allowing for dense populations. As these salt ponds are connected to the ocean by subterranean caves, it is possible that they provide the "seeding" mechanism for regrowth of diminished species along the outer coast.

Walsingham Pond and the smaller sinkholes in the park can be seen as living aquaria with a low herbivore pressure on seaweed biodiversity. The Bermuda Aquarium in Flatts mimics this environment in many of its display tanks lacking herbivores, and macroalgae that grow in them are large and vigorous, as opposed to how they appear on the outer reefs. The Aquarium displays feature only local marine life, and seawater flowing through them is directly pumped in from the adjacent Harrington Sound. Three species of the palatable red seaweed *Botryocladia*, with clusters of mucilage filled bladders, can be found in display tanks at different times of the year. These artificial environments are lit with natural and supplemental lighting to give the displays the look of Bermuda's shallow subtidal. For much of the 21st century, large individuals (to 6.5 cm) of *Botryocladia bermudana* C.W. Schneider *et* C.E. Lane have been the dominant alga in one of the herbivore-free reef tanks. Molecular analysis of island *Botryocladia* species revealed that the small one- to two-bladdered plants (to 1 cm) on intertidal rock underhangs, coastal boiler reefs and deep offshore reefs were the same species as the large, multi-bladdered Bermuda Aquarium individuals (6.5 cm; Schneider and Lane 2008, figures 1–3). A similar case of protection from herbivory is found for *Botryocladia flookii* C.W. Schneider *et* C.E. Lane, with few plants found on coastal reefs, these being scattered individuals with one to a few large bladders, whereas in the Aquarium and Walsingham Pond, large populations can form seasonally due to zero or a low herbivore pressure (Schneider and Lane 2008). A third species, *Botryocladia exquisita* C.W. Schneider *et* C.E. Lane, was first collected offshore as tiny (to 2.5 mm) single-bladdered plants and thought to be the miniscule *Botryocladia monoica* Schnetter from the western Caribbean (Schneider and Lane 2008, figures 14–17). A relatively huge plant (4 cm) later turned up on the seawater input pipe of a tank lacking herbivores in the Aquarium, allowing molecular confirmation of a mature individual for the first time in this artificially protected environment (Schneider and Lane 2008). These Aquarium examples show that a lack of herbivory allows at least some macroalgal species to reach maximum growth in Bermuda, allowing for speculation that less protected individuals in the intertidal and subtidal reefs may have declined in populational and individual sizes due to intense grazing pressure.

Discussion

Specimens deposited in herbaria and museums throughout the world provide a valuable resource to reconstruct the biodiversity of selected habitats over decades and even a century, but few historical studies have examined seaweed community change. Wernberg et al. (2011) used the digitized herbarium records of more than

20,000 macroalgae collected in Australia since the 1940s to document the change in primary producer communities as well as biogeographical distributions of individual species in the Indo-Pacific during the past 5 decades of rapid ocean warming. Using archival records, Bates et al. (2009) compared which algal species were present in the past and still remain or are no longer found in the Bay of Fundy, Nova Scotia flora. Based upon archival and our own extensive collections from Bermuda, we have demonstrated that the intertidal and shallow subtidal macroalgal flora today are reduced as compared to historic biodiversity extrapolated from species data and collection abundance recorded on herbarium specimens and in published accounts from 100 years ago. The massive number of individuals of a species required for dissemination in the published exsiccata *P.B.-A*. would suggest abundant populations at their recorded collection sites from 1912 to 1917. Based upon our work, we can show that several species mounted in *P.B.-A*. from Bermuda have not been collected since the mid-20th century (Table 1), while others have seen their abundance reduced to uncommon or even rare in the habitats where they were formerly found in large enough numbers to harvest for the exsiccata.

What we observe in marine ecosystems today is clouded by the fact that prior to recorded observations by early naturalists, these environments may have looked different before human exploitation of many marine species (Jackson 2001). It is certainly possible that diminished populations of many exploited predators and herbivores created different environments in the 20th century that we are used to today (Estes et al. 2011), as each habitat may have reached a different balance of species than were present prior to recorded history. So the return of exploited species to current higher population levels may be returning these ecosystems to conditions similar to those before human exploitation. It follows then, that it is possible that the most recent marine animal protection laws and West Indian top shell reintroductions beginning in 1978 for Bermuda may have caused populations of parrotfish and top shells in Bermuda to increase to higher levels than when these herbivores were historically harvested by local Bermudians (Robertson 2003). The diminished population sizes of seaweeds, and possible extirpation of some species (Table 1), could be a causal effect of the increased populations of these efficient herbivores (Randall 1964, Robertson 2003). When analyzing the diet of West Indian top shells from the Virgin Islands and Puerto Rico, Randall (1964) found that 28–65% of their stomach contents at five different sites was made up of red, green and brown macroalgae and cyanobacteria, all but one of them species typical of the Bermuda intertidal and shallow subtidal. In a study of common herbivorous fish in tropical waters, Randall (1967) found that attached marine algae made up 94–100% of the stomach contents of three Caribbean parrotfish species. Using parrotfish and other fish representing the dominant herbivores in Hawaii, Randall (1961) also discovered that subtidal areas enclosed to prevent grazing produced luxuriant growth of attached algae not easily found outside the enclosures, confirming that these large herbivores heavily grazed reef and rocky-bottom habitats. Thus, it seems that after protections for parrotfish and the reintroduction of large gastropods to Bermuda, as well as subsequent penalties to prevent their harvest, some stands of formerly large species of seaweeds in the islands have been reduced to minute and scattered specimens showing obvious effects of grazing.

Although it appears that conservation laws and reintroductions in Bermuda have a strong association with these declining and possibly extirpated populations of several macroalgae in Bermuda, other factors could also be important in these declines, for example, climate change. During the last century there have been two significant warming events in the world’s oceans, from 1920 to 1940, then another event beginning and continuing since the 1970s (Levitus et al. 2000). Since the 1950s, sea surface temperatures in the North Atlantic have risen only slightly (estimated as +0.31°C, Levitus et al. 2000), seemingly not an increase that would negatively affect the tropical seaweed species in Bermuda (Harley et al. 2012). In fact, the macroalgal species we listed as diminished or extirpated in Bermuda (Table 1) are present in recent floras of the Caribbean and Florida (Littler and Littler 2000, Dawes and Mathieson 2008, Littler et al. 2008) without being noted in these accounts as uncommon or rare. Furthermore, at the northern extreme of the latitudinal range for tropical macroalgal species in Bermuda, slightly warmer water temperatures would only be expected to enhance conditions for these species in the islands over the past century.

After more than a quarter century of collecting, we have failed to discover some macroalgal species formerly common in their intertidal and shallow subtidal habitats in Bermuda, at least suggesting that they may have been extirpated in the flora. We can only speculate, but the evidence seems to point to the conservation laws protecting the marine fauna, in this particular case, herbivores, in Bermuda beginning in 1978. Perhaps the communities in these habitats represent a new balance of herbivore and algal diversity since these laws went into effect. Certainly top shells and parrotfish are not the only important herbivores in Bermuda that feed primarily on algae attached to rock and coral surfaces. Other herbivores that could have a role in declines of these macroalgae include chitons, sea urchins and fish such as surgeonfish, chubs and blennies (Sterrer 1986). However, because none of these herbivores are regularly harvested for human consumption, it is likely that their numbers would have risen and fallen in the past 100 years based on the environmental interactions that have shaped their populations over time. Thus, these would likely have had minimal effect on the islands' macroalgae.

The rocky intertidal became a difficult habitat for the seasonal re-establishment of large seaweeds in Bermuda, likely consequences of marine animal protections now in place. Bermuda's loss of algal diversity would not be the first case where governmental marine protections did not effectively protect all species, or the environment in which they live, when trying to manage certain species or groups of organisms (Allison et al. 1998, Heithaus et al. 2014, Wilson 2016). It is therefore not surprising that Bermuda introduced the 1978 Fisheries (Protected Species) Order to keep the coral reefs healthy and free of the overgrowth of macroalgae, as these are environments that bring a high economic value to the tourist-based economy (Sarkis et al. 2010). Fish exclusion studies in tropical intertidal rocky environments had clearly demonstrated that herbivorous fish were important in keeping the macroalgal communities at low densities (e.g. Stephenson and Searles 1960, Randall 1961, Lewis 1986), and parrotfish in Bermuda are large and colorful, obvious as part of the tourist appeal for the islands. Yet, conservation laws usually do not take into account all of the possible consequences of the intended protections (Ecke et al. 2010, Brown and Trebilco 2014). The possible extirpation of members of the macroalgal community in the rocky-bottom ecosystem of Bermuda after the protection of marine herbivores was likely not considered. Since the 1978 Fisheries (Protected Species) Order was put into effect, Fourqurean et al. (2010) speculated that green sea turtles in Bermuda may have been responsible for seagrass (*Thalassia*) bed collapse in the 1990s due to repeated and intense grazing by these large herbivores that are protected by the same law. Turtle protections and overfishing of their main shark predators (tiger sharks, Heithaus et al. 2014) may in fact have returned the seagrass beds to their lessened prehistoric state prior to the time when turtles were over harvested in the western Atlantic (Jackson 2001), but nevertheless represented an environmental change caused by the recent protection laws in Bermuda. It makes sense that Bermuda, in protecting its parrotfish and West Indian top shells, possibly may have caused the loss of seaweed species that were important members of the intertidal and shallow subtidal community a 100 years ago. Whether the present represents a balance for the ecosystem not seen since the settlement of Bermuda in the 1600s is not known (Smith-Vaniz et al. 1999). Nevertheless, archival specimens of seaweeds from 100 years ago compared with extensive recent collections suggest a change in algal biodiversity in the islands that has occurred over the past century.

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Bionotes

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