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Biogeography, Biodiversity and Connectivity of Bermuda's Coral Reefs

Jan M. Locke, Kathryn A. Coates, Jaret P. Bilewitch, Lyndsey P. Holland, Joanna M. Pitt, Struan R. Smith, and Henry G. Trapido-Rosenthal

Biogeographical Region and Environmental Factors

Biogeographic provinces are "Large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames. Provinces will hold some level of endemism, principally at the level of species…[and] … In ecological terms, provinces are cohesive units likely, for example, to encompass the broader life history of many constituent taxa, including mobile and dispersive species." Spalding et al. (2007). They are also "areas of relatively homogeneous species composition, clearly distinct… [but] endemism is not a key determinant in ecoregion identification." Herein, we explore the composition and genetics of the fauna of the coral reefs in Bermuda and discuss overall and taxon-specific diversity patterns, particularly as they relate to conservation and management of marine resources.

Bermuda is one of nine ecoregions in the Tropical Northwestern Atlantic (TNA) (Spalding et al. 2007), differentiated from adjacent regions by differences in sea surface temperature minima. Bermuda's marine biota is a reduced set of the biota of the TNA. Due to its northerly location, Bermuda has a distinct seasonality in temperature, incident light regimes, and ocean chemistry, which are all important factors in determining the distribution of corals and other marine species (Kleypas et al. 1999; S.A. Manuel and K.A. Coates, unpubl. data).

The Sargasso Sea is an important contributor to the biological diversity of Bermuda. *Sargassum* mats provide homes to many co-adapted species, and spawning grounds to many others that range more widely. Humpback whales (*Megaptera novaeaeangliae*) annually migrate through the Sea and congregate outside Bermuda's shallow rim reef (Stone et al. 1987). *Sargassum* and associated biota are frequently stranded on the shores of Bermuda (Butler et al. 1983) creating a diverse strandline community (Healy and Coates 2003), and other temporary residents of the Sea move into the shallow waters around Bermuda for some stages of their lives.

Ecoregion Forcing Agents for Bermuda

Of the dominant geographic and physical forcing agents on the biological diversity of Bermuda, those of most significance include isolation, temperature, currents, sediments, bathymetric or coastal complexity, and environmental seasonality, both now and in the past.

Isolation: Distance, Depth and Size

The nearest source populations for Bermuda's marine species are over 1,000 km away in the Caribbean and Florida. The Gulf Stream is recognized as the primary conduit in the recent era for the introduction of species and individuals

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J.M. Locke (✉) • K.A. Coates
Marine Ecology Section, Department of Conservation Services,
17 North Shore Road, Hamilton Parish FL 04, Bermuda
e-mail: jml100@gmail.com; kathryn.coates@dilke.com

J.P. Bilewitch
School of Biological Sciences, University of Queensland,
Brisbane, Queensland, 4072, Australia
e-mail: jbilewitch@gmail.com

L.P. Holland
Biosciences, College of Life and Environmental Sciences,
University of Exeter, Stocker Road, Exeter EX4 4QD, UK
e-mail: lynzholland@yahoo.co.uk

J.M. Pitt
Marine Resources Section, Department of Environmental Protection,
3 Coney Island Road, St. Georges CR04, Bermuda
e-mail: jpitt@gov.bm

S.R. Smith
Natural History Museum, Bermuda Aquarium, Museum and Zoo,
Department of Conservation Services,
40 North Shore Road, Hamilton Parish FL04, Bermuda
e-mail: srsmith@gov.bm

H.G. Trapido-Rosenthal
Department of Biology, Division of Natural Sciences and
Mathematics, Chaminade University of Honolulu,
Honolulu, HI 96816, USA
email: henry.trapido-rosenthal@chaminade.edu

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Table 12.1 Number of species of different groups with different coastline lengths in the Greater Caribbean region (Data adapted from Miloslavich et al. 2010)

Location	Coastline length (km)	Numbers of species Corals[a]	Sponges	Molluscs	Echinoderms
Guatemala	148	25	–	–	23
Cayman Islands	160	50	82	477	–
Costa Rica	212	37	64	638	23
Aruba, Bonaire, Curaçao	360	53	113	239	–
Trinidad, Tobago	362	29	–	–	55
Belize	386	40	193	580	134
Nicaragua	493	39	–	129	65
Puerto Rico	501	53	40	1,078	121
Honduras	644	55	–	580	95
Mexico (Yucatán)	911	47	118	733	182
Jamaica	1,022	52	169	824	86
Panama	1,295	55	146	587	155
Lesser Antilles	1,322	54	126	1,119	79
Colombia	1,880	52	142	1,168	180
Venezuela	2,722	58	144	664	124
Hispaniola	3,059	53	71	572	117
Cuba	3,735	54	255	1,300	145
Bermuda – low resolution	103	26	99	942	98
Bermuda – high resolution	296	26	99	942	98

[a] Has been changed based on review of original data

from these source populations to the marine communities of Bermuda. It is likely that species get carried into waters that encounter Bermuda's shallow platform via meso-scale eddies from the Gulf Stream. Genetic connectivity of various Bermuda populations with Caribbean, Bahamian and Floridian populations are evidence of ongoing and regular recruitment.

The Bermuda Platform is a very small area of shallow "habitable benthic environment" (see Kleypas 1997 and Pandolfi 1999), in a vast region of very deep water. The coastline is about 296 km (Meyer 2012) surrounded by a shallow marine area of about 620 km^2 (to 20 m depth). Similar length coastlines in the TNA can harbour very different numbers of species (Table 12.1) and only for corals does there seem to be a positive correlation between numbers of species and coastline length; for sponges, echinoderms and molluscs for example, there seems to be much less or no relationship (Miloslavich et al. 2010). Although Bermuda has a comparatively short coastline, that may not be a primary limitation to species diversity on the platform. Coastline length, area and configuration of shallow waters have changed many times during the development of coral reefs in Bermuda. Both extreme highstands (up to 22 m above present day sea level) and lowstands (to perhaps 140 m below present day sea level) occurring in the Pleistocene would have decreased the total area of shallow water on the platform (Hearty and Olson 2010). The most extreme recent sea level highstand, corresponding to an interglacial period, about 120 kya may have reached 9–10 m above present sea level (Hearty et al. 2007), probably drowning many areas of shallow reef. The last Pleistocene glaciation maximum and a corresponding extreme sea level lowstand about 120 m below present occurred about 18 kya. This would have limited shallow-water habitat to a narrow band on the sloping sides of the Bermuda Platform and nearby seamounts (Iliffe et al. 2011) (Fig. 12.1).

Climate Changes and Temperature

Environmental shifts during the Pleistocene glaciations could have resulted in other factors than simple loss of habitat constraining the diversity of reef communities; sea surface temperature shifts, for example, are correlated to periods of glacial minima and maxima. There are Bermudian fossils of two extant Caribbean coral taxa no longer found in Bermuda, *Cladocora* (Moore and Moore 1946) and *Colpophyllia* (Muhs et al. 2002). They are both now found in locations with higher average minimum sea surface temperatures than seen in Bermuda, and the known Bermudian fossils of *Colpophyllia* are dated to interglacial periods (Muhs et al. 2002) when sea surface temperatures may have been higher. However, species of *Acropora*, which are common in the Caribbean, never have occurred in Bermuda and this has also been interpreted as a temperature-related distribution even though acroporids occur in Florida where seawater temperature

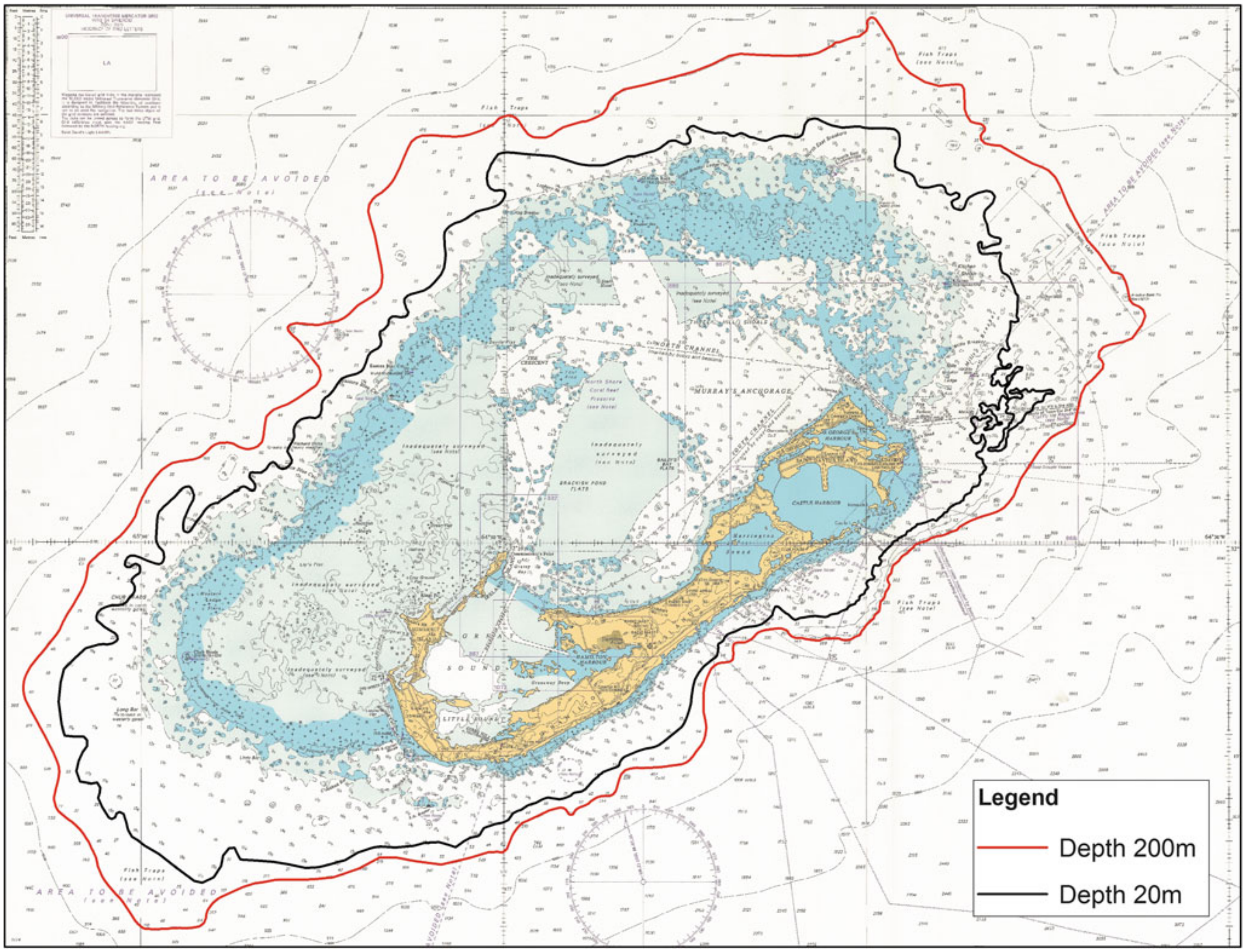

Fig. 12.1 Bathymetric contours at 20 m and 200 m that might represent Pleistocene shorelines at glacial maxima of about 80-90 kya and 18 or 424 kya, respectively. Based on Bermuda Admiralty Chart #334, reproduced by permission of the Controller of her Majesty's Stationary Office and the UK Hydrographic Office (www.ukho.gov.uk)

extremes are even greater (Precht and Miller 2007) than in Bermuda. Again, a number of factors may combine, that are related to Bermuda's northern latitude, to exclude some tropical species and not others, including duration of cooler temperatures, aragonite saturation levels (Kleypas et al. 1999; Bates et al. 2010), and low light during periods of cooler temperatures (S.A. Manuel and K.A. Coates, unpubl. data).

Habitat Complexity

There are no significant surface freshwater outflows in Bermuda, and no regular or high volume sources of terrigenous sediments, which is generally considered beneficial to coral growth. However, some highly productive and diverse tropical marine coastal communities, including mangroves and seagrasses, thrive in the finer organic sediments characteristic of terrigenous sources and estuaries. Significant and even sustaining connections exist between the communities of these habitats and of coral reefs (Nagelkerken et al. 2008) so that their reduction in relative size may decrease the success of some segments of the average coral reef community.

Seasonality in Incident Light

The low angle of the sun, combined with increased cloud cover, during the winter months limits total incident light at the sea surface, and there is a significant seasonal difference in light regime of southern versus northern exposed faces of the reefs (e.g., Murdoch 2007). This high seasonality may be a primary limiting factor to much marine life, including the depth distribution of seagrass (S.A. Manuel and K.A. Coates, unpubl. data). Neither Kleypas et al. (1999) nor Bates et al. (2010) found a strong correlation between coral growth and light for Bermuda but, they could only consider corals that were present and which must be tolerant of low light conditions. Corals that do not occur in Bermuda may well have different behaviours and physiologies, and light conditions may restrict them to lower latitudes.

Biological Diversity

A distinctive characteristic of the marine fauna and flora of Bermuda is the absence of species that are otherwise ubiquitous in the Tropical Northwestern Atlantic province. Bermuda does not show an increased diversity due to the mixing of species that survive at the boundaries of biogeographic realms, in this case the Tropical Atlantic and the Temperate Northern Atlantic. For fish, the Bermuda coastal marine fauna includes some eurythermic tropical species (Smith-Vaniz et al. 1999), which have geographic ranges crossing the tropical-temperate "boundary", but which are not restricted to the boundary region. Nonetheless, Bermuda's fish species diversity is reduced relative to both higher and lower latitude neighboring regions.

Bermuda's isolation suggests the possibility of a relatively high local level of endemism, and although Sterrer (1998) suggests Bermuda exhibits low marine endemism of about 3%, recent reviews of a number of taxa indicate much higher endemism among some major taxa that are common in coral communities, including sponges and polychaetes. Lists of species for these taxa can be accessed on the Bermuda Government, Department of Conservation Services, website www.conservation.bm.

Fig. 12.2 Bermuda's coral reef biodiversity as illustrated by the scleractinian and octocorallian species commonly found on the fore-reef terrace at Hog Breaker (Photo: JM Locke)

Scleractinia

Bermuda's reef building coral diversity fits a general idea that lower diversity characterizes areas located at the range limits of coral distribution. This is clearly visible on Bermuda's reefs, where the favids *Diploria* and *Montastraea* are the dominant scleractinian genera together with *Porites astreoides* (Fig. 12.2), and a total of 12 shallow-water genera commonly found in the Caribbean and USA are notably absent. However, a "fit" is not explanatory of this lower diversity and as noted earlier, Bermuda has similar numbers of coral species to equally small coastal areas that are much further south in the TNA – numerous factors control the species diversity of Bermuda's corals. To date, 20 species of zooxanthellate corals, in nine families and 13 genera, and six azooxanthellate corals, in four families and six genera, are known to inhabit shallow waters, including Bermuda's only endemic coral *Rhizopsammia bermudensis* (Locke 2009; Locke et al. 2013, and at www.conservation.bm/corals).

Given the similarity in diversity between Bermuda and its more northerly tropical con-provincial ecoregions in the Caribbean, it is notable that the Acroporidae, common on many Greater Caribbean reefs, is absent both from recent and fossil reefs. Ecological factors are presumed to have prevented the establishment of acroporids in Bermuda. This may also be true of other genera common to the Caribbean but not currently known from Bermuda. The species *Cladocora arbuscula* and *Colpophyllia natans* have, however, been documented from the fossil record (Moore and Moore 1946; Muhs et al. 2002). We can only speculate what led to their demise though, as noted earlier, fossil specimens of *C. natans* have been dated to the last interglacial maximum.

Limited study of the deep benthic habitats have provided brief insight into corals at and beyond the mesophotic zone. Investigations have documented 13 zooxanthellate species from 30 to 78 m with the genera *Agaricia, Scolymia* and *Montastraea* inhabiting depths greater than 60 m (the deepest is 78 m for *Montastraea cavernosa*) (Fricke and Meischner 1985; Venn et al. 2009).

Beyond the mesophotic zone, our knowledge of deep-water corals consists solely of records of species occurance. Collectively, expeditions have acquired azooxanthellate specimens at depths from 55 m to 1966 m. Bermuda's known deep-water azooxanthellate Scleractinia number 23 species from 10 families, many species being known only from single collections (Locke et al. 2013). Within the deep waters (>183 m) of the western Atlantic, 102 species of azooxanthellate corals are currently recorded (Cairns 2000). Considering this, it is difficult to interpret Bermuda as being a low diversity location; instead the number of species reported for Bermuda is likely a reflection largely of the limited sampling.

The 48 valid scleractinian species is a significant fraction, nearly 25%, of the 197 scleractinian species currently known from the western Atlantic (adapted from Cairns 2000); the majority reported from shallow-water.

Genetic Variation and Population Connectivity

Cairns and Chapman's (2001) analysis of deep-water azooxanthellate corals in Bermuda revealed components of both a warm temperate and a tropical fauna; with increasing depth, the western Atlantic cnidarian fauna becomes increasingly cosmopolitan (Cairns 1979), and deeper subhabitats of the Bermuda EEZ may be biogeographically more inclusive than those of shallow depths.

Genetic studies, utilizing various molecular markers, have produced plausible hypotheses concerning the genetic diversity and connectedness of a few scleractinian species found in Bermuda. These concern shallow-water zooxanthellate brooding species, *Favia fragum* and *Madracis auretenra*, and a single broadcast spawning species, *Montastraea cavernosa*. Gene flow was investigated at recent (Shearer 2004; Locke 2009; Nunes et al. 2009; Goodbody-Gringley et al. 2010, 2011) and historical scales (Locke 2009).

Studies reveal high levels of intraspecific genetic diversity of *M. cavernosa* and *M. auretenra*, and in some cases this diversity (i.e., numbers of haplotypes in a population from a single geographical site) exceeded that of conspecifics within other regions. Both species harbour unique (=private) and shared haplotypes for the molecular markers among the locations investigated (Locke 2009; Nunes et al. 2009; Goodbody-Gringley et al. 2010, 2011). In fact, more unique haplotypes were observed in Bermuda than in conspecific populations of any other geographic location (Locke 2009; Goodbody-Gringley et al. 2011).

In contrast, Bermuda's *F. fragum* population showed no intraspecific variation, with only one haplotype determined for each of two markers analyzed (*ITS* and *β-tubulin)*; although the single *ITS* haplotype was unique to Bermuda (Goodbody-Gringley et al. 2010). The extremely different levels of intraspecific variability reported for the two brooding species *F. fragum* and *M. auretenra* (*SRP54)* may simply be due to the different markers used in the two studies or other intrinsic, biological, factors. Studies documenting high levels of variation in *M. cavernosa* analyzed the same *β-tubulin* region as the *F. fragum* study (Nunes et al. 2009; Goodbody-Gringley et al. 2010, 2011); further evidence that these two species are experiencing gene flow regimes that may be attributed to their differing life histories and, perhaps, to their different histories in Bermuda. This does not however explain the high diversity seen in *M. auretenra.*

The greater level of genetic diversity in Bermuda coral populations contradicts predictions that oceanographically isolated reefs may be associated with lowered genetic diversity (Ayer and Hughes 2004; Miller and Ayre 2004, 2008; Nunes et al. 2009; Goodbody-Gringley et al. 2010). The unique haplotypes found in three studied Bermuda coral species may be relicts of early colonizers that were once present in US and Caribbean regions but have since been extirpated, or may be the result of post colonization diversification.

The genetic connectivity of *M. cavernosa* populations within Bermuda and to USA and Caribbean populations has been investigated on three accounts. Shearer (2004) determined, from four and five microsatellites, that Bermuda populations were differentiated from populations in the Flower Garden Banks, Florida Keys, and the Bahamas. Conversely, when compared across the Atlantic, using two nDNA *β-tubulin* regions and mtDNA *cox1-trnM*, Bermuda's *M. cavernosa* population was not significantly differentiated from populations in Puerto Rico, Belize and Panama (Nunes et al. 2009). The connection of Bermuda *M. cavernosa* populations with those in the USA and Caribbean was corroborated by Goodbody-Gringley et al. (2011) for populations in the Flower Garden Banks, Jamaica, Panama and Barbados using mtDNA *cox1-trnM*. However, based on *ITS* and a *β-tubulin* region, the same study revealed F_{st} values that indicated Bermuda populations were differentiated from Barbados and Jamaica respectively (Goodbody-Gringley et al. 2011).

Bermuda's shallow-water coral species are mostly brooding species. Studies of *F. fragum* and *M. auretenra*, showed that these species were genetically structured from USA and Caribbean conspecifics (Locke 2009; Goodbody-Gringley et al. 2010). More specifically, analyses of Bermudian *F. fragum* using nuclear regions *ITS* and *β-tubulin*, determined that gene flow was restricted between Bermuda and Jamaica, Panama and Barbados (Goodbody-Gringley et al. 2010). Likewise, analyses of a region of the nuclear gene encoding *SRP54* in *M. auretenra* populations determined that Bermuda corals were genetically structured from populations in the Florida Keys and Puerto Rico (Locke 2009).

Bermuda's connections at an evolutionary scale are investigated by Locke (2009). Shared ancestral haplotypes among the Bermuda, Puerto Rico and Florida Keys populations indicate that these regions might have shared an historic connection, but a distinctly Bermudian clade reveals that this connection may not be as prevalent as it was in the past. A recent division of Bermuda and Puerto Rico populations was proposed based on distinct haplotypes and phylogenetic clades for these regions. Shared phylogenetic clades for some Bermuda and Florida haplotypes demonstrate that the isolation of Bermuda's genetically differentiated populations may be broken in rare events.

The current theories of Bermuda coral connectivity, based on limited study only, indicate there is free exchange of genetic information among the reefs in Bermuda (Shearer 2004; Locke 2009; Goodbody-Gringley et al. 2010, 2011) (but see Shearer 2004 and Goodbody-Gringley et al. 2011 for exceptions). Brooding species appear to be self seeding with gene flow from other regions restricted to rare events, if at all, whereas, broadcast spawning coral species connectivity is at best contradictory with inferred connections between some but not all sampled Caribbean and USA populations. Opposing results for the same species and sampled locations provide an indication that these ambiguous outcomes may be related to marker resolution.

Octocorallia

Studies of deep-water diversity are deficient and existing reports rely heavily on anecdotal records and haphazard, accidentally-collected specimens (Cairns et al. 1986; Bilewitch 2008). A number of shallow-water studies exist (e.g. Chester 1913; Grode et al. 1983), but a wide-ranging field survey of octocoral diversity and abundance has only recently been attempted (L.P. Holland, unpubl. data), and thus any cumulative list of species may only represent the most obvious, non-cryptic representatives and a handful of circumstantial and anecdotal samples from the deep-seas.

We still know little of the vertical, bathymetric limits of any given species, and most zooxanthellate octocoral specimens have been obtained from less than 20 m depth, although anecdotal records indicate that certain species (e.g. *Plexaurella nutans* and *Antillogorgia acerosa*) may also be found at depths exceeding 50 m on the Challenger and Plantagenet seamounts. Study of the mesophotic zone will undoubtedly provide insights on environmental controls on octocoral distributions and phenotypic variation (e.g., Fricke and Meischner 1985; Venn et al. 2009) and overall species diversity may be high (Bridge et al. 2011). Most studies to date have been on either shallow-water or deep-water zones, and not this transition region.

With one exception, all shallow-water Bermudian octocorals are contained within the suborder Holaxonia Studer 1887, most being in the family Plexauridae Gray 1859 (Locke et al. 2013). Of the 24 shallow-water species, 18 are plexaurids, while five are Gorgoniidae. *Briareum asbestinum* represents the only known member of the Scleraxonia in Bermuda; the encrusting species *Erythropodium caribaeorum*, which is common in the Caribbean, is notably absent.

Most deep-sea species have been observed only once in Bermuda so that the lack of corroborating evidence for a species' presence and distribution from a number of records presents a serious impediment to the characterization of Bermuda's deep-sea octocoral community. Below 30 m depth we do not know whether sole specimens or observations represent one of a few or one of many such colonies in the deep-seas surrounding Bermuda, but new records of primnoids, isidids and paramuriceids, based largely on haphazard and accidental collections, suggest that many more octocorals await discovery (Locke et al. 2013).

Genetic Variation and Population Connectivity

The intraspecific genetic diversity of octocorals in Bermuda has been studied only twice (Bilewitch 2006; Bilewitch et al. 2010) and only one of these studies examined population-level differences in some depth. Bilewitch (2006) examined species-level (and above) octocoral molecular systematics but also provided indirect evidence of intraspecific genetic variation in the four shallow-water species *Plexaura flexuosa*, *Pseudoplexaura porosa*, *Gorgonia ventalina* and *Briareum asbestinum*. Of these, all except *P. flexuosa* contained some genotypes that were unique to Bermuda (Bilewitch 2006). Bilewitch et al. (2010) further examined the population variation of *B. asbestinum* and found both unique and shared genotypes in the Bermudian population. The star-like genetic diversification of *B. asbestinum*, where the wide-ranging genotypes are central to the region-specific genotypes is consistent with a pattern of Caribbean ancestry with subsequent limited allopatric diversification in Bermuda. The Bermudian population thus appears to be semi-isolated to the extent that allows some endemic genotypes to develop, but either the age of the population is too young or the influx of genotypes from the Caribbean is too frequent to have resulted in enough genetic drift to lead to speciation (Bilewitch et al. 2010). Although *B. asbestinum* may have been introduced into Bermuda through anthropogenic means, the population likely exceeds a century in age and remains genetically and morphologically similar to conspecifics in the Caribbean.

Zooxanthellae

Many reef-associated marine invertebrates including hard and soft corals, hydrozoans, sponges, and molluscs, have symbiotic associations with *Symbiodinium*; a diverse dinoflagellate assemblage comprising nine distinct lineages, or 'clades' (Clade A to Clade I). As these clades vary in physiological response to fluctuating environmental parameters, assessing diversity of *Symbiodinium* can be used as a proxy for predicting coral resilience to detrimental events such as bleaching and climate change.

In Bermuda, early research suggested that local symbiont diversity was low. Boschma (1925) concluded that symbionts within the corals *Isophyllia dipsacea* (=*Isophyllia sinuosa*) and *Siderastraea radians*, the zoanthid *Zoanthus sociatus* and the anemone *Condylactis passiflora* (=*Condylactis gigantea*) were probably the same species, an assertion based upon morphological uniformity. However, following the development of DNA-based methods such as PCR-RFLP in the 1990s, it was demonstrated that *Symbiodinium* was, in fact, extremely diverse (Rowan and Powers 1991), and one host could harbour mixed molecular variants. Generally, in Metazoa, clades A, B and C predominate on Caribbean reefs, whereas C and D are more prevalent in Pacific reefs (Baker 2003), and some clades are associated predominantly with certain host taxa (e.g., F, H and I in soritid foraminifera, Pochon and Gates 2010).

Using PCR-RFLP, the diversity of zooxanthellae has been examined in anthozoan hosts in Bermuda over a depth gradient (Billinghurst et al. 1997), at latitudinal limits (Savage et al. 2002), in Bermudian and Caribbean conspecifics (e.g., Holland 2006), and at varying temporal and spatial scales (Loram et al. 2007a, b; Venn et al. 2008). Additional data from Bermudian hosts stems from a few samples included in larger studies of *Symbiodinium* diversity in the Greater Caribbean. At cladal level, the diversity of symbionts in Bermuda is similar to the Caribbean, with most zooxanthellae belonging to clades A, B and C. Clade D has not yet been found in Bermuda. Most symbiont assemblages examined in Bermudian Anthozoa are characterised by the occurrence of a single clade, although mixed infections are also characteristic of symbioses in certain host taxa; presence of mixed infections may vary spatially or temporally (e.g., Loram et al. 2007b; Venn et al. 2008), and may differ between Bermuda and the Caribbean (e.g., Savage et al. 2002). For example, between conspecifics, a reduced diversity is observed in Bermuda corals; *Diploria labyrithiformis* contains B in Bermuda, not B and C as in the Caribbean, *Montastraea franksi* harbours A and B, as opposed to A, B, C and E, and *Porites astreoides* contains A, and not A and C (Savage et al. 2002). Several octocoral species exhibit a similar pattern; *Plexaurella dichotoma* and *Briareum asbestinum* contain clade B or C in the Caribbean (Goulet and Coffroth 2004), yet only clade B in Bermuda (Holland 2006, unpublished data).

In all octocorals sampled in Bermuda, only clade B has been found (Holland 2006; Goulet et al. 2008), with the exception of one report of clade A in the sea fan *Gorgonia ventalina* ($n=1$, LaJeunesse 2001).

The anemone *Condylactis gigantea* harbours Clades A and B *Symbiodinium*. In offshore sites, where water is cooler and less variable, it may harbour Clade B alone, while at more thermally variable inshore sites it contains either solely Clade A, or mixed Clades A and B. As water temperatures rise and fall with seasonal changes, *C. gigantea* with mixed infections can alter the proportions of Clade A and B symbionts, with populations of Clade A increasing with increasing water temperature, and Clade B increasing with declining temperature (Loram et al. 2007b; Venn et al. 2008). These variations have physiological correlates in that more photosynthate is incorporated into the host's lipid and amino acid pools when their symbiont population is dominated by the thermally-tolerant Clade A algae, than when dominated by thermally-sensitive Clade B algae (Loram et al. 2007b).

ITS-Level Symbiodinium Diversity in Bermuda

At present, symbiont diversity is not adequately represented by the denotation as clades A, B, C, etc. in phylogenies based on small or large subunits of rDNA genes. There is substantial intra-cladal variation revealed by sequence variation of spacer (ITS) regions that evolve significantly faster than rDNA sub-units. Therefore, the past decade has seen an increase in the use of rDNA spacer regions (i.e., ITS1 or ITS2) to delineate symbiont genotypes and to assess the correlation of resultant haplotypes (typically described as 'types', e.g., type B1 *sensu* LaJeunesse 2001) to ecological characteristics.

Although ITS markers have revealed finer divergence within each clade, caution must be exercised when using them. Ribosomal DNA (including both spacer regions) is multicopy, therefore several variants may co-exist within an individual *Symbiodinium* cell (see Stat and Gates 2011). Selective use of one ITS spacer may present a flawed strategy resulting in underrepresentation of isolated haplotypes (see Holland 2006). Nevertheless, the ITS region (ITS1-5.8s-ITS2) has been sequenced to identify symbionts in various anthozoan hosts in Bermuda (LaJeunesse 2001; Savage et al. 2002; Holland 2006). A proliferation of subsequent research focusing solely on ITS2 haplotypes has made it difficult to directly compare known Bermuda symbiont types to those found within the Caribbean, primarily due to incomparable datasets (see Holland 2006), although where possible the corresponding symbiont 'types' identified are listed in Table 12.2.

There is little evidence for endemism in Bermuda. There are several generalist symbiont types, exemplified by the prevalence of redundant haplotypes obtained from taxonomically and geographically disparate hosts and a lack of Bermuda-specific symbiont clusters in phylogenetic analyses (Holland 2006). Based solely upon ITS2 data, it appears that type B1 (*sensu* LaJeunesse 2001) may be the predominant symbiont in octocorals in Bermuda (Goulet et al. 2008); this warrants further investigation.

Microsatellite markers have recently been employed to assess symbiont diversity within the sea fan *Gorgonia ventalina* across the Greater Caribbean (Andras et al. 2011). Haplotypic diversity within the *Symbiodinium* B1/B184

Table 12.2 List of all host species with characterized *Symbiodinium* in Bermuda. *Type/Strain***:** Letters refer to cladal designation, whereas alphanumeric identities refer to ITS genotype designation (where available e.g., B2.1). '+' = mixed infections, e.g., A + B. N: number of host colonies sampled. *Methods:* LSU = large sub unit rDNA sequence data, ssuRFLP = small sub unit restriction fragment length polymorphism, ITS1-ITS2 = entire ITS array rDNA sequence data including 5.8S region. Numbers in superscript refer to relevant reference and those in parentheses refer to number of individual colonies with the preceding *Symbiodinium* genotype (where available)

Host species	Type/Strain	N	Method	Reference
Order Alcyonacea	–	–	–	–
Family Plexauridae	–	–	–	–
Plexaura homomalla	B	5	LSU, ITS1-ITS2	1
Plexaura flexuosa	B	6	LSU,ITS1-ITS2	1
Pseudoplexaura porosa	B	17[1], 1[2]	ssRFLP[2],LSU, ITS1-ITS2[1]	1,2
Pseudoplexaura flagellosa	B	1	ssRFLP	2
Eunicea sp.	B	8	LSU, ITS1-ITS2	1
Eunicea tourneforti	B	1	ssRFLP	3
Plexaurella dichotoma	B, B1	1	LSU,ITS1-ITS2	1
Muricea laxa	B	1	ssRFLP	3
Family Gorgoniidae	–	–	–	–
Antillogorgia americana	B	3	LSU,ITS1-ITS2	1
Gorgonia ventalina	B & B1[1], B1/B184 & A[a, 4],A2[5]	11[1],116[4],1[5]	LSU, ITS-ITS2[1,5], Microsatellites[4]	1,4,5
Family Briareidae	–	–	–	–
Briareum asbestinum	B	<10	LSU,ITS1-ITS2	1
Order Scleractinia	–	–	–	–
Family Astrocoeniidae	–	–	–	–
Stephanocoenia intersepta	B (3), C (2)	5	LSU	6
Family Oculinidae	–	–	–	–
Oculina diffusa	B2.1[5], B[6]	1[5], 11[6]	LSU, ITS1-ITS2	5,6
Family Faviidae	–	–	–	–
Favia fragum	A + B (1), B (7)[6], B (1)[1]	9	LSU,ITS1-ITS2	6,1
Diploria labyrinthiformis	B	10	LSU	6
Diploria strigosa	B	4	LSU	6
Montastraea cavernosa	C	16[6],62[7]	LSU[6], ssRFLP, allozymes[7]	6,7
Montastraea franksi	B (44), A (2)	46	LSU, ITS1-ITS2	6
Family Mussidae	–	–	–	–
Isophyllia sinuosa	B	2	LSU	6
Scolymia sp.	C	2	LSU	6
Family Siderastreidae	–	–	–	–
Siderastrea radians	B	12	LSU	6
Family Poritidae	–	–	–	–
Porites astreoides	A	11	LSU	6
Porites porites	A	11	LSU	6
Family Pocilloporidae	–	–	–	–
Madracis auretenra[a]	B[6], B[1], B7[1]	4	LSU, ITS1-ITS2	6
Madracis decactis	B[1], B[6], B + C[8]	1[1], 3[6],n/a[8]	LSU	1,6,8
Family Agariciidae	–	–	–	–
Agaricia sp.	C	18	LSU	6
Family Meandrinidae	–	–	–	–
Dichocoenia stokesi	B[6], B + C[8]	1 [6],n/a[8]	SSU	6,8
Meandrina meandrites	B[6], B + C[8]	1 [6],n/a[8]	SSU	6,8
Order Actinaria	–	–	–	–
Family Aiptasiidae	–	–	–	–
Aiptasia pallida	B, B2	32	LSU, ITS1-ITS2	6
Aiptasia tagetes	B1	1	ITS1-ITS2	5
Bartholomea annulata	A	25	LSU	6

(continued)

Table 12.2 (continued)

Host species	Type/Strain	N	Method	Reference
Family Actiniidae	–	–	–	–
Condylactis gigantea	A (8), B (7), A+B (2)[6], A, B, A+B[9]	17[6], 179[9]	LSU[6], qPCR based on LSU & AFLP[9]	6,9
Family Aliciidae	–	–	–	–
Lebrunia danae	C	8	LSU, ITS1-ITS2	6
Order Rhizostomeae	–	–	–	–
Family Cassiopeidae	–	–	–	–
Cassiopeia xamachana	A, A1	12	LSU, ITS1-ITS2	6
Order Coronatae	–	–	–	–
Family Linuchidae	–	–	–	–
Linuche unguiculata	A4	1	ITS1-ITS2	5

[a] This species was referred to as *Madracis mirabilis* in Holland (2006) and Savage et al. (2002) (See Locke et al. 2007)

References: [1]Holland (2006), [2]Goulet et al. (2008), [3]Goulet and Coffroth (2004), [4]Andras et al. (2011), [5]LaJeunesse (2001), [6]Savage et al. (2002), [7]Billinghurst et al. (1997), [8]Venn et al. (2009), [9]Venn et al. (2008)

lineage is extremely high in symbionts in *G. ventalina* which again highlights the concept that *Symbiodinium* diversity and functionality are best explained by use of faster evolving and more informative markers.

Overall, most clades found in the Caribbean are also found in Bermuda, but mixed assemblages occur less frequently in Bermuda. At present, there is no evidence of a single lineage of symbionts evolving in Bermuda. Apparently holobionts that colonized Bermuda are taxonomically indistinguishable from their (likely) source pool to the south. This is in contrast to the data for the hosts themselves, which have unique Bermudian haplotypes for more than one genetic marker.

Fish

The ichthyofauna of Bermuda is less diverse, at both the species and genus level, than at other locations in the Tropical Northwestern Atlantic (Smith-Vaniz et al. 1999). Most fishes have a western Atlantic distribution, including 62% of the nearshore fishes, but amphi-Atlantic and more widely distributed species are also common (Smith-Vaniz et al. 1999, reprinted here as Table 12.3).

Regional Faunal Similarities

A coefficient of faunal similarity (CFS) following the Sorensen index (Magurran 1988) was calculated by Smith-Vaniz et al. (1999) to compare Bermuda's ichthyofauna to other localities with closely related faunas. Included in the comparison were the Carolinian Bight, which approximates the area of the US east coast included in the Warm Temperate Northwest Atlantic (WTNA) province which represents the northerly extent of many tropical fish species in the western Atlantic; the Florida Keys and the Bahamas. Smith et al. (2002), in their analyses of the fish fauna of the Tropical Western Central Atlantic, determined that the southern coastal area of Florida harboured the most species (442–552 fish species) per cell of 0.5° lat by 0.5° long, making it a potential source for most Bermudian fish species.

The 58 families of fishes used by Smith-Vaniz et al. (1999) for estimating CFS were represented in Bermuda by 283 species, in the Carolinian Bight by 598, in the Florida Keys by 566 and in the Bahamas by 523 species. The CFS was 0.54 between Bermuda and the Carolinian Bight (238 shared species), 0.58 between Bermuda and the Florida Keys (245 shared species), and 0.63 between Bermuda and the Bahamas (253 shared species) (Smith-Vaniz et al. 1999). Bermuda is about equally similar to all these sites, although appearing slightly more similar to the Bahamas but only because the Bahamas had the fewest total species. The ichthyofauna of Bermuda is dominated by eurythermic tropical species that are distributed in the Caribbean and along the southeastern coast of the United States and shared among all the locations considered.

Many Caribbean species are strongly associated with continental shelves and are generally absent from island platforms isolated by deep water (Smith et al. 2002). Smith-Vaniz et al. (1999) remark on a few notable occurrences of some such species in Bermuda, including *Orthopristis chyrsoptera* (pigfish), *Pareques umbrosus* (cubbyu), *Holacanthus bermudensis* (blue angelfish), *Gymnothorax saxicola* (honeycomb moray) and *Mycteroperca microlepis* (gag).

Reef Fish Diversity

Smith-Vaniz et al. (1999) report 430 described plus two presumptive species of fishes native to Bermuda, with 362 species from 79 families being significantly associated with coral reefs and adjacent platform habitats, to depths of 200 m. Of

Table 12.3 Biogeographic analysis of the native ichthyofauna of Bermuda based on adult occurrences. (Updated from Table 7 in Smith-Vaniz et al. 1999, reproduced with the kind permission of the American Society of Ichthyologists and Herpetologists)

Distribution	No. of species	of total species	No. of established nearshore species	of total established nearshore species
Western Atlantic only	232	53.6	210	61.6
Amphi-Atlantic	77	17.8	56	16.4
Cosmopolitan	67	15.5	26	7.6
Atlantic and Indo-Pacific	24	5.5	19	5.6
Western and Central Atlantic	18	4.2	16	4.7
Atlantic and Eastern Pacific	4	0.9	3	0.9
Bermuda endemic	9+2	2.5	9+2	3.2
Total	433	–	341	–
Oceanic species	67	15.5	–	–
Nearshore species	366	84.5	–	–
Established nearshore species	341	78.7	–	–

these, 25 species are considered waifs or vagrants (Smith-Vaniz et al. 1999), leaving 337 species from 72 families as established components of the local nearshore ichthyofauna (Smith-Vaniz et al. 1999). Important amendments to this list include the recently described endemic halfbeak, *Hyporhamphus collettei* Banford 2010, formerly considered *Hyporhamphus unifasciatus*, and a new record of the spotted spoon-nose eel, *Echiophis intertinctus* (Richardson, 1848) (Smith 2010).

An additional 13 species of fishes are known locally only from juveniles (Smith-Vaniz et al. 1999). These are considered waifs and they do not appear to survive to maturity, either because adult habitat or dietary requirements are not met or because the numbers of larvae or juveniles never reach the critical mass required for a population to develop. During the twentieth century, there were a number of attempts to introduce fishery species from the Caribbean (Smith-Vaniz et al. 1999), however it appears that none of these species became established.

The Pacific lionfish, *Pterois volitans* has been present in Bermuda since 2000 (Whitfield et al. 2002). This brings the number of fish species known from shallow marine habitats to 339, and the total number described from Bermuda to 432. This introduced invasive is excluded from any calculations of endemism rates and biogeographic indices, as is the introduced freshwater species *Gambusia holbrooki*.

Families of fishes with no or poor representation in Bermuda, but which are found in potential source locations along the US east coast and in the Caribbean, are often small-bodied (Blennioidei, Engraulidae, Opisthognathidae) or odd-shaped, poor swimmers (Achiridae, Pleuronectidae, Batrachoididae, Uranoscopidae, Ogcocephalidae, Tetraodontiformes) (Fig. 12.3). However, filefishes (Monacanthidae) and triggerfishes (Balistidae), which fall into the latter category, are well represented.

Hermaphroditism could be considered an advantage for establishing and maintaining a population derived from small and rare initial recruitments. Families such as the protogynous Scaridae, Labridae and, to some degree, the Serranidae are well represented in Bermuda.

Endemics and Endemism

There are nine fish species endemic to Bermuda (Table 12.4) (Smith-Vaniz et al. 1999; Smith 2010; Banford 2010). A number are small to medium-sized and a study of larval distributions (Glasspool 1994) found larvae of these families only within the lagoon, indicating strong retention of larvae in these taxa, and also no evidence of regular off platform/long distance recruits. Larval retention may be significant to local speciation within these families.

An endemism rate of 2.7% for Bermuda is at the low end of the 3–25% endemism seen for shallow-water fish faunas of other isolated oceanic islands in the Atlantic and Eastern Pacific (Smith-Vaniz et al. 1999; Robertson 2001). When only reef fishes are included, rates of endemism for these types of locations range from 1 to 13% (Floeter et al. 2008), suggesting that reef-dwelling fishes have high connectivity among sites even though their habitat is discontinuous. These low levels of endemism are consistent with suggestions that shallow water marine communities were largely extirpated during Pleistocene glacial maxima (Floeter et al. 2008). Subsequent allopatric speciation would require both a change in the recruitment patterns that allowed the initial recolonization and very rapid speciation. Although time is clearly an important factor, it remains likely that dispersal is significant to the lack of endemism seen in the reef ichthyofauna of Bermuda.

Other Notable Fish Taxa in Bermuda

A number of diversification events exist. Bermuda is one of three locations where intergeneric hybrids of the coney,

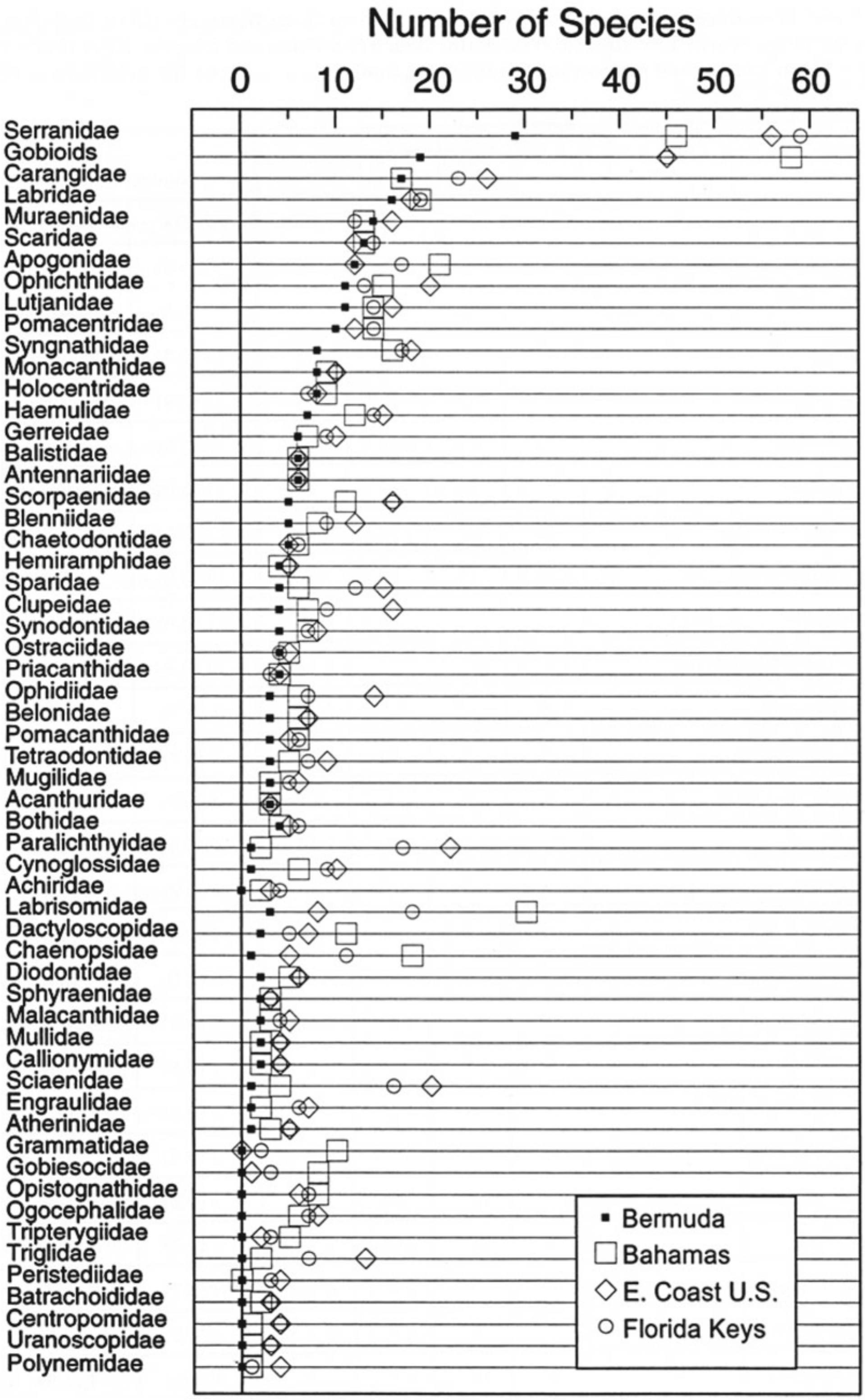

Fig. 12.3 Comparison of total number of species in selected families present in Bermuda, Bahamas, Carolinian Bight and the Florida Keys. (Figure 86 from Smith-Vaniz et al. 1999, reproduced with the kind permission of the American Society of Ichthyologists and Herpetologists)

Table 12.4 Described fish species endemic to Bermuda including key characteristics and museum catalogue numbers for collections held within the Bermuda Natural History Museum (BAMZ) and the Smithsonian National Museum of Natural History (USNM)

Species	Key characteristics	Catalogue number
Family Fundulidae	–	–
Fundulus bermudae Günther, 1874	Small; occurs in saltwater ponds, formerly inshore	BAMZ 1998.170.005
Fundulus relictus Able and Felley, 1988	Small; occurs in saltwater ponds, formerly inshore	BAMZ 1998.171.009
Family Hemiramphidae	–	–
Hemiramphus bermudensis Collette, 1962	Medium size; occurs offshore and inshore	BAMZ 1998.170.014
Hyporhamphus collettei Banford, 2010	Medium size; occurs inshore	USNM 391198 Holotype
Family Engraulidae	–	–
Anchoa choerostoma (Goode, 1874)	Small; occurs inshore	BAMZ 1990.083.012
Family Sparidae		
Diplodus bermudensis Caldwell, 1965	Medium size; occurs inshore	BAMZ 1995.124.013
Family Gobiidae		
Lythrypnus mowbrayi Bean, 1906	Small; occurs inshore, lagoon and banks	BAMZ 1998.171.004
Family Malacanthidae		
Caulolatilus bermudensis Dooley, 1981	Moderate size; occurs rim reef	BAMZ 1989.047.005
Family Serranidae		
Parasphyraenops atrimanus Bean, 1912	Moderate size, occurs on deep reefs	USNM 74085

Cephalopholis fulva, and the barber or creole-fish, *Paranthias furcifer*, have been reported (Bostrom et al. 2002). Hybrid specimens from Bermuda were first described by Poey (1860, 1875) as two species of a new serranid genus but later meristic and morphometric analyses suggested the individuals were intergeneric hybrids (Smith 1966, in Bostrom et al. 2002). The most recent analysis of 15 new specimens collected from Bermuda reported morphological characters intermediate between the two parent species and genetic patterns indicating hybridization between a female *C. fulva* and a male *P. furcifer* (Bostrom et al. 2002).

Another hybrid, the Townsend angelfish – a hybrid of *Holacanthus bermudensis* and *H. ciliaris* – is very common (Smith-Vaniz et al. 1999), and possibly the entire Bermuda population may be hybrids (Pyle et al. 2010). Small populations, concurrent restricted spawning seasons, and spatially limited spawning habitat could play a role in the frequency of hybridization; however, if the most recent supposition about the angelfish proves correct, it may be that for this species only the hybrid has been able to colonize Bermuda, perhaps an example of superior performance by a hybrid.

Mitochondrial DNA studies of the slippery dick, *Halichoeres bivittatus*, have revealed a 'subtropical' genotype occurring in Bermuda, Florida and the Gulf of Mexico. It is found in close proximity to a 'tropical' genotype, but in habitats exposed to cooler water temperatures (Rocha et al. 2005a). In Bermuda, all *H. bivittatus* collected inshore where greater temperature extremes occur, were of the 'subtropical' type, whereas half of the specimens collected on offshore reefs were of the 'tropical' type. No significant morphological differences have been recognized between the 'tropical' and 'subtropical' types. Thus the full, documented, diversity of this species, from across its geographical range, is present in Bermuda.

Finally, and uniquely, Bermuda is home to a strikingly different colour morph of the yellowhead wrasse, *Halichoeres garnoti* (Smith-Vaniz et al. 1999; Rocha 2004) (Fig. 12.4) which dominates the local population. An analysis of mtDNA cytochrome b showed variation correlated with colour differences in other *Halichoeres* species, but no similar differences in the Bermuda colour morph of *H. garnoti* (Rocha 2004).

Factors Influencing Fish Diversity in Bermuda

The absence of certain groups of reef fishes has been ascribed to their physiological, biological and ecological characteristics – narrower temperature tolerances, limited dispersal capabilities (e.g., brooders and sedentary, demersal spawners with short larval durations, poor swimming capabilities, absence of rafting behaviours), the absence of symbiotic or commensal partners (e.g., massive sponges are not available for sponge-dwelling gobies) (Smith-Vaniz et al. 1999) – and to lower overall habitat diversity in Bermuda. The absence of many common Caribbean coral species such as branching acroporids may limit the diversity of niches (see Smith-Vaniz et al. 1999). Similarly, the Sparidae, a family of medium-sized fish that are strong swimmers with moderately long larval durations and known to exhibit a range of hermaphroditic strategies – all of which are characteristics that would support their success in Bermuda – are not well represented, presumably because of the reduced availability of the inshore, reef-associated, habitat types.

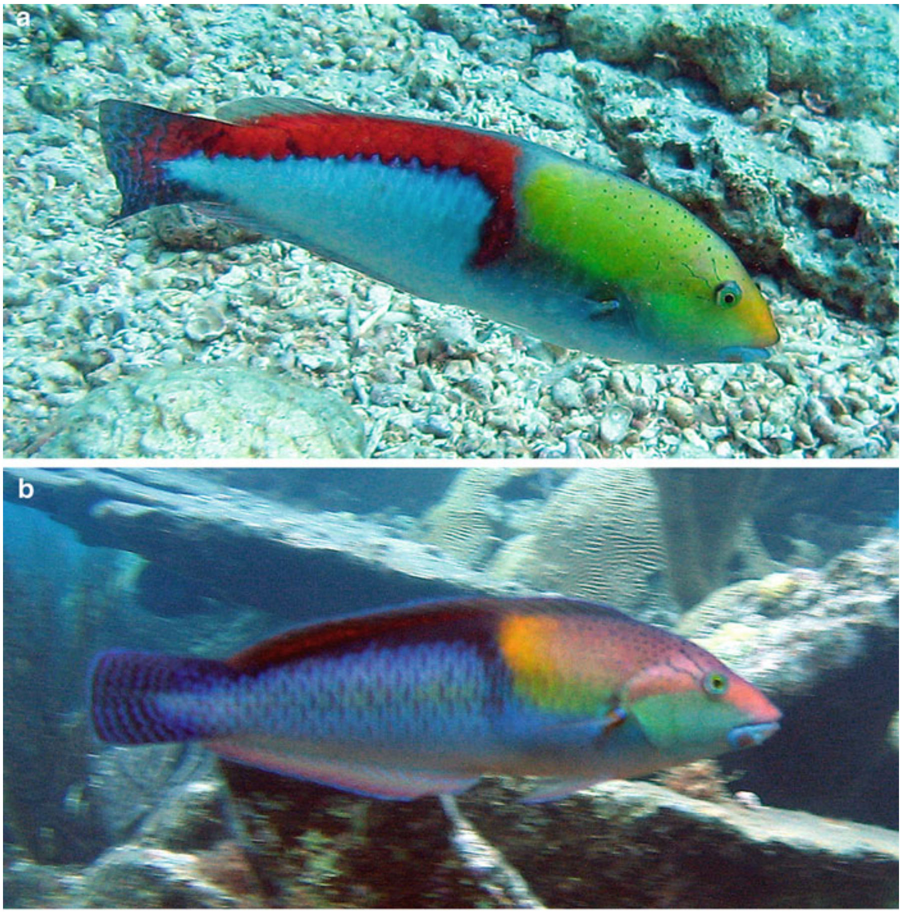

Fig. 12.4 Colour morphs of *Halichoeres garnoti*. (**a**) Bermuda colour morph and (**b**) a typical Caribbean colour morph, photographed in Bermuda (Photo: TJT Murdoch)

Conversely, the strong representation in Bermuda of some unexpected taxa, such as poor swimmers, is attributed to interactions of behavior and the environment. Such taxa include triggerfishes and filefishes, whose larvae and juveniles are well known for their rafting behaviours.

Genetic Variation and Population Connectivity

Among biological factors that control connectivity, pelagic larval duration (PLD) has an obvious significance, and species with longer PLDs are generally widely distributed and well mixed; isolated locations, such as Bermuda, are more commonly inhabited by fish species with PLDs longer than 45 days (Brothers and Thresher 1985) while species with shorter PLDs (<15 days) often have genetically structured sub-populations (Thresher et al. 1989). Indeed, PLD is often used as a proxy for dispersal and colonizing capacity.

For families with PLD data (in Victor 1986; Wellington and Victor 1989; Sponaugle and Cowen 1994; Bergenius et al. 2002), Bermudian species have similar larval duration to their Caribbean congenerics, however, species known to have long larval periods all occur in Bermuda, and Bermuda lacks a number of shorter PLD species. A classic example is the Goldspot goby, *Gnatholepis thompsoni*, which has a very long larval duration (~89 days) (Sponaugle and Cowen 1994). The Bermuda population of the species, along with St. Croix and Brazil, falls into a genetically uniform, very widespread, western Atlantic grouping, established ~115,000–139,000 years ago (Rocha et al. 2005b), indicating consistent gene flow between western Atlantic populations over geological time and implying regular larval dispersal to Bermuda.

Earlier studies, in which electromorph variation at several loci for a variety of fish species was examined among Bermudian and Caribbean populations (Glasspool 1994), showed that genetic differentiation generally covaried with distance between populations but that the relationship to PLD was more variable. The Caribbean population of the French grunt, *Haemulon flavolineatum*, with a PLD of 2 weeks did not appear to be panmictic. In individuals from Bermuda, a rare allele was present at one electromorph loci and a common allele was absent (Glasspool 1994). In contrast, the pomacentrid *Abudefduf saxatilis,* with a slightly longer PLD of 3 weeks (as well as demersal eggs), was panmictic. Species of *Abudefduf* generally have broad distributions but short PLDs, and there is evidence for pelagic rafting by pre-juveniles. These remain planktonic by associating with floating objects such as *Sargassum* (Jokiel 1990; Wellington and Victor 1989; Glasspool 1994; Casazza and Ross 2008). The bluehead wrasse, *Thalassoma bifasciatum*, which had the longest PLD also appeared to be panmictic in Bermuda, Miami and the Bahamas, but with somewhat more overall genetic separation than seen in *A. saxatilis*. Thus behavioral differences are plausible explanations for the different connectivities of these species.

Levels of genetic differentiation among populations allowed the calculation of probable migration rates among populations (Glasspool 1994). These were 4–10 migrants per generation for *H. flavolineatum*, 28–250 (mean of 41) for *A. saxatilis* and between these two for *T. bifasciatum*. Various studies suggest that even a very low migration rate, on the order of only one individual per generation, is enough to prevent speciation (Wright 1951; Slatkin 1985), and rare individuals dispersing long distances are thought to reduce the genetic differences between geographically separated populations (Palumbi 1995; Shanks 2009); thus we see genetic differences in Bermudian populations, but not distinct species.

Based on microsatellites, black grouper, *Mycteroperca bonaci*, from Bermuda are significantly different from those in southeastern United States, Gulf of Mexico and the western Caribbean, while there are no differences among those locations (Chapman et al. 2002). For this species, synchronized, aggregative spawning, large-size, and a long life span may be significant traits promoting self-recruitment, and genetic discontinuities (Swearer et al. 2002).

Even within species, there is little evidence of the direct significance of PLD to the establishment of successful populations. Schultz and Cowen (1994) found no indication that Bermuda populations were recruited from individuals with a propensity for a longer than average pelagic phase. Rather, the Bermuda individuals had a significantly shorter pelagic larval duration (PLD) in two cases, a significantly longer PLD in two cases, and a typical PLD in the remaining two cases, when compared to populations in South Florida and the Caribbean.

Genetic Variation and Population Connectivity of Other Reef Associated Fauna

Mollusca

The genetic variation and connectivity of Bermuda's molluscan populations has been investigated only briefly. Allozyme studies have shown that populations of the queen conch, *Lobatus gigas*, were reproductively isolated from a comparatively panmictic Caribbean gene pool (Mitton et al. 1989). Likewise, Bermuda's populations of the direct developing bivalve *Lasaea adansoni* sensu latu was determined to be genetically similar to, but still distinct from, Florida populations based on sequences of mitochondrial DNA. For both these taxa, overall genetic diversity was higher in the Bermudian populations than in those to which Bermuda was compared (Mitton et al. 1989; Foighil and Jozefowicz 1999; Park and Foighil 2000). However, studies based on sequences of *COI*, 28S and ITS1 of *Brachidontes exustus* (scorched mussel), which has been recognized as a species complex, indicate no significant genetic differentiation among populations of a Bahamas clade, found in Florida Keys, Bahamas and Bermuda (Lee and Foighil 2005).

Arthropoda

These studies are limited to the spiny lobster, *Panulirus argus*. Studies of allozymes and mitochondrial DNA (mtDNA) indicate high levels of gene flow between Bermudian populations and those of Florida and the Caribbean, as far south as Venezuela (Hatley and Sleeter 1993; Silberman et al. 1994). Laboratory rearing studies indicate larval durations of 5–7 months (Goldstein et al. 2008) and estimates from earlier studies fit with the higher end of this range (Silberman et al. 1994; references in Naro-Maciel et al. 2011). Studies of speciation patterns of Pacific species of *Panulirus* (Pollock 1992) suggested that individuals might remain planktonic for up to 4 years, settling and metamorphosing only when appropriate environmental cues are detected. Thus, for this taxon, with its unusually long planktonic period, the lack of genetic structure between Bermudian and Caribbean populations is easy to comprehend in the context of general assumptions about pelagic phase duration and dispersal. Recent studies (Naro-Maciel et al. 2011) of mitochondrial DNA sequence variation among spiny lobsters of Florida, the Bahamas, the Caribbean and Brazil, but excluding Bermuda, which also did not detect significant levels of genetic structure, did identify two divergent COI lineages, which overlapped geographically. The possibility that these lineages might represent cryptic species was acknowledged (Naro-Maciel et al. 2011).

Echinodermata

Bermuda is home to two genetically (mtDNA [*COI*]) distinct lineages of the very widely distributed ophiuroid *Ophiactis savignyi*, one of which is very widely distributed and seems most likely to be present in the Atlantic due to anthropogenically influenced introduction (Roy and Sponer 2002). The other lineage has a western Atlantic distribution– it is reported only from Bermuda, Florida, the Caribbean and Brazil. The Bermuda individuals of the western Atlantic lineage display one numerically common, shared, haplotype and one unique Bermudian haplotype. Interestingly, one Bermudian individual also displayed a unique haplotype in the widespread (Pacific and Atlantic) lineage. Molecular studies of the echinoid *Lytechinus variegatus* (Zigler and Lessios 2004, mtDNA [*COI*], protein [bindin], isozyme) indicated there was no significant genetic structure among populations from Brazil, Florida, other locations in the Caribbean and Bermuda.

Conservation and Management of Biodiversity in Bermuda

The success of future efforts in marine resource management and conservation in Bermuda depends on valid information on the biogeography and population connectivity of the island's marine species. At this time, we have data from a few molecular studies on population structures of even fewer species that can be applied to conservation and management. Bermuda's marine species are shared with the other ecoregions within and bordering its biogeographical province, allowing theories of population connectivity to be applied to management efforts. However, uncertainty about life histories, dispersal capabilities and behaviours, basic population statistics and ecology, of many marine species preclude formulation of an effective and responsive coral reef management plan.

Gene Flow

Studies agree that within Bermuda marine populations are panmictic and self-seeding. Due to the major currents, gene flow is one-way – into Bermuda only. On an ecological time scale, Bermudian populations of certain octocorallian and scleractinian species, molluscs and reef fish appear to be somewhat isolated from neighbouring USA and Caribbean conspecifics. Other studies of species of scleractinian, crustacean, bivalves, and echinoderms and of reef fishes concluded that Bermuda populations were panmictic with populations in the USA and Caribbean. Even rare dispersal into Bermuda for some of these species is likely sufficient to maintain genetic similarities. For certain species, the strength of connections with neighboring reef ecosystems appear to be related to reproductive mode, pelagic larval duration or specific reproductive behaviours (i.e., brooding with no pelagic larval stage but with rafting). However, reproductive pattern or history in itself is not a reliable predictor of genetic connectivity (Weersing and Toonen 2009) and any correlations may be purely coincidental.

Given the limitations of current species-level information, a best practice from the conservation point of view would be to assume characteristics for each species that would dictate the most conservative management measures and to adjust conservation plans on a species by species basis, as information is acquired. However, an argument has recently been presented that overly protected habitats lose their abilities to adjust to normal and natural events and become increasingly susceptible to these natural perturbations (Côté and Darling 2010).

Endemics, by their nature, have to be managed on a local scale, but even if carefully protected locally they may still be subject to events that are widespread and not species specific, for example diseases.

Population Maintenance

Studies of the scleractinian, *M. auretenra*, and the octocoral, *B. asbestinum*, suggest genetic divergence in the largely self-seeding Bermudian populations could be constrained by the periodic breakdown of allopatric boundaries (Locke 2009; Bilewitch et al. 2010). These species brood larvae until they are competent to settle, then release planulae that in *B. asbestinum* are known to have low-dispersal potential and typically settle in a philopatric pattern (Brazeau and Lasker 1990). It would seem nearly impossible for these species even to initially colonize Bermuda from the nearest populations in the Bahamas – over 1,300 km away. However, recent evidence of rafting in a brooding coral (Hoeksema et al. 2012) indicates there is true potential for regular, although probably infrequent, genetic exchange even among what would generally be considered poor dispersers. The transport of *Sargassum* spp. from the Gulf of Mexico to the Sargasso Sea (Gower and King 2011) provides a mobile habitat that could bridge the larval and demersal stages of a wide range of fish species (Jokiel 1990; Coston-Clements et al. 1991; Casazza and Ross 2008).

An ecological connection between the Caribbean and Bermuda, as inferred from certain population genetic studies, is directly apparent in the presence in Bermuda of recent episodic diseases shortly after they appeared in the Caribbean (e.g., diseases affecting sponges, *Diadema*, and corals). The recent colonization of Bermuda by the invasive Pacific lionfish (Whitfield et al. 2002) also seems incontrovertible evidence of immigration/recruitment on an ecological time scale. Establishment of the lionfish in Bermuda was only a few years after their invasion of the east coast of the United States (Whitfield et al. 2002; Ahrenholz and Morris 2010).

In some regards, being well-connected may not be beneficial. Thus, it is necessary to have strategies that protect local individuals and to collaborate to manage distant populations whose health can impact Bermudian populations.

Resilience

The high levels of genetic variability are suggestive of genetic resilience, and Bermuda's populations may possess an increased probability of survival during environmental or biological changes. For example the widespread and severe bleaching event of 2005, which drastically impacted the Caribbean reefs of Puerto Rico and Florida, had minimal impact in Bermuda (Wilkinson and Souter 2008, J.M. Locke, pers. obs.). Similarly, Bermudian individuals of *Diploria labyrinthiformis* are resistant to black band disease (Jones et al. 2012). Haplotypes unique to Bermudian coral and molluscan populations may be evidence of local adaptation or they could be relicts that have been lost in other regions.

The unique biological diversity of Bermuda is important to conservation strategies for the entire TNA. However, until more information and Caribbean-wide integrated management is in place, conservative, local management measures are an imperative. Currently protection is afforded to some reef species through the dedication of marine reserves and marine protected areas/no take zones, and seasonally protected areas. All corals are individually protected from the general public but habitat destruction is not as easily governed. Current legislation for these protections include the Fisheries Act 1972, (Protected Species) Order, 1978, the Fisheries (Protected Areas) Order, 1990 and 2005, the Coral Reef Preserves Act, 1966, and the Protected Species Act 2003 (www.bermudalaws.bm).

Special Concerns for Local Management

Fishery Species

Even for Bermudian marine species with high genetic connectivities, investigation into the relative importance of locally produced larvae versus immigrant recruits is warranted, particularly for species that are exploited by commercial and recreational fisheries.

Briareum asbestinum – an invader or a Native

If the Bermudian population represents a natural, rare, recruitment event from Caribbean source populations, then the endemic genetic diversity of the population, as documented by Bilewitch et al. (2010), warrants protection. Although currently not under threat, its restricted distribution and small population size in the northeastern islands of Bermuda would make it highly susceptible to loss of significant genetic diversity. On the other hand, the species may have been introduced sometime in the nineteenth century. The centre of *B. asbestinum* distribution in Bermuda lies along St. George's Channel, between Smith's and Paget Islands. This channel was the primary northeastern shipping route into St. George's Harbour throughout the nineteenth century until the opening of the 'town cut' channel to the north in 1917 (Stranack 1990). If the *B. asbestinum* population does represent a centuries-old introduction, its conservation as a naturally occurring species would obviously be unwarranted. However, the population's apparent inability to expand beyond its current distribution over at least the past decade (J.P. Bilewitch, pers. obs.), and probably more than three decades (see Cairns et al. 1986) indicate it is not highly invasive and, combined with its historical interest, it merits maintenance.

Reef Fish

It has been suggested that the black grouper, *Mycteroperca bonaci*, is predominantly self-recruiting, although the population is not genetically distinct from Caribbean populations. Thus, current management measures are conservative, based on size, distribution and behavior of the Bermuda populations (Pitt and Shailer 2010). Likewise, management measures for the two endemic species of Hemiramphidae, which are used as bait, may be warranted.

Symbiodinium

In Bermuda, symbiont clades are identical to those found in the Caribbean and not to those of the eastern Atlantic (Savage et al. 2002), with little divergence of haplotypes or endemic *Symbiodinium* types (Holland 2006). Furthermore, population-level markers suggest that shared alleles and clustering between Bermuda and Florida *Symbiodinium* in the octocoral *Gorgonia ventalina* are the result of connectivity between the two (Andras et al. 2011). It remains impossible to determine the extent and frequency of dispersal of *Symbiodinium* to Bermuda, and if this occurs via host larvae or during free-living phases. Given that up to 85% of cnidarian species acquire symbionts exogenously from the surrounding environment (Schwarz et al. 2002), it is likely that a

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local reservoir, coupled with host specificity, maintains the diversity of available *Symbiodinium* in Bermuda.

Diversity of cnidarian-algal symbioses is probably determined by local availability of the alga in addition to host-specificity. Physiological attributes of each clade are an important consideration in connection with changing temperature and light regimes, although how the *Symbiodinium* complement in Bermuda will protect or endanger corals in climate change scenarios remains unclear. The lack of clade D and the predominance of clade B could render Bermudian reefs vulnerable in a high temperature bleaching event (Savage 2001). Clade B symbionts have high regional abundance in the Caribbean (Santos et al. 2003) and are prevalent at higher latitudes, suggesting that they are generalists adapted to low irradiance and cooler seas (Holland 2006). In contrast, as they are restricted to shallower depths of the range of some hosts, clade B zooxanthellae have also been described as 'sun-specialists' (e.g., *Montastrea* spp., Rowan 1998) and 'narrowly-adapted specialists' (Toller et al. 2001). There is some suggestion that the colder temperature range in Bermuda may have resulted in coral communities with lower upper thermal tolerances than their tropical counterparts (Cook et al. 1990). Furthermore, offshore scleractinians may be more susceptible than those inshore, as more bleaching was recorded in them following the 1988 event (Cook et al. 1990). This was attributed to adaptation by inshore corals to increased temperatures, and/or the mitigating effects of turbidity in the lagoon.

As pre- and post-bleaching symbiont identities were not measured during past bleaching events, short to long-term changes in symbiont composition of anthozoans in Bermuda remains untested. Nevertheless, clade B should by no means predispose the hosts to increased susceptibility to environmental fluctuations; clade B itself is a diverse assemblage and each type is likely to vary in its response to bleaching (e.g., Santos et al. 2003; Holland 2006). Furthermore, hosts may acquire novel zooxanthellae from the environment as well as regulating the frequencies of their *in hospite* community, such as the octocoral *Briareum asbestinum* which has switched symbionts following experimentally induced bleaching (Lewis and Coffroth 2004).

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