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Patterns of population connectivity in marine organisms of Cuba

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ABSTRACT.—Understanding of population genetics is important for the conservation and management of species and ecosystems, providing information on population structure, connectivity, and demography. Here, we review the genetic patterns and processes that shape the natural populations of marine organisms in Cuba, including penaeid shrimps, reef fishes, marine turtles, and bottlenose dolphins. Investigations performed over the last 20 yrs indicate three general patterns of population structure across the Cuban coast: a north-south break, an east-west split in the south, and local genetic differentiation. These patterns have been shaped by factors that include the size of the island, current patterns, lack of suitable habitats for reproduction, larval recruitment, and foraging behaviors. No single trait can predict dispersal and population structure across these diverse groups, but in every case, there are key life-history features that guide connectivity. These include limited larval dispersal in damselfishes and shrimps, social structure in dolphins, and natal homing in marine turtles. Population genetic partitions can reveal the boundaries of isolated ecosystems, guiding the design of marine protected areas.

Most marine organisms have the potential to disperse across large geographic distances. In many reef fishes and most invertebrates, pelagic larval stages have a dispersal potential driven in part by oceanic currents (Cowen 2002). However, historical isolation, adult dispersal abilities, larval behavior, larval-stage duration, egg type, and temporal and local oceanographic processes can intervene, shaping this dispersal potential (Jones et al. 2005, Selkoe and Toonen 2011, Puebla et al. 2012). In other organisms, including marine mammals and turtles, reproductive and foraging behaviors play major roles in mediating dispersal (Escorza-Treviño and Dizon 2000, Bowen and Karl 2007, Andrews et al. 2010).

With the increase in the resolution of available genetic markers over the last two decades, population genetics has provided enhanced insights for the conservation and management of species (Avise 1995, Bowen et al. 2014). Population genetic studies have demonstrated that, in spite of the great dispersal potential of marine organisms,

most species have genetically structured populations (Ruzzante et al. 1996, Galarza et al. 2009, Hepburn et al. 2009, Salas et al. 2010, Wiszniewski et al. 2010, DiBattista et al. 2012, Damerau et al. 2014). Knowledge about connectivity among subdivided populations is essential to understand species evolution and demography, and to assist management programs (Cowen 2002, Frankham et al. 2010).

Different patterns of population genetic structure and connectivity have been revealed in marine organisms with similar geographic distributions in the Caribbean Sea. For instance, population genetic differentiation has been observed in corals (Fukami et al. 2004, Baums et al. 2005, Fukami and Knowlton 2005, Galindo et al. 2006, Foster et al. 2012, Porto-Hannes et al. 2015), mollusks (Mitton et al. 1989, Lee and Foighil 2004, Diaz-Ferguson et al. 2012), echinoderms (Lessios et al. 2001, 2003), crustaceans (Silberman et al. 1994, MacMillen-Jackson and Bert 2003, Maggioni et al. 2003), reef fishes (Shulman and Bermingham 1995, Rocha et al. 2002, McCartney et al. 2003, Ramon et al. 2003, Taylor and Hellberg 2006, Floeter et al. 2008, Puebla et al. 2008, Villegas-Sánchez et al. 2010, Carson et al. 2011, Jackson et al. 2014), marine turtles (Bowen and Karl 2007, Leroux et al. 2012), bottlenose dolphin (Sellas et al. 2005, Caballero et al. 2012), and West Indian manatee (Garcia-Rodriguez et al. 1998, Hunter et al. 2010). From these studies, we can conclude that the magnitude of population subdivisions and their geographic scale vary widely among species. MacMillen-Jackson and Bert (2003), for example, found different patterns of population genetic structure in two cohabitating penaeid shrimps (*Penaeus aztecus* Ives, 1891 and *Penaeus schmitti* Burkenroad, 1936) and suggested that such differences show species-specific disparities in physiological tolerances to habitat variations. Similarly, Bowen et al. (2006) compared population connectivity of different coral reef fishes, concluding that the observed patterns are more likely related to the evolutionary history of the lineages than to a single factor such as larval duration.

Over recent decades, population genetic-studies of marine organisms in Cuban waters have developed, providing valuable information about the patterns of connectivity around the archipelago and in the Caribbean region (e.g., Díaz-Fernández et al. 1999, García-Machado et al. 2001, Borrell et al. 2007, Ruiz-Urquiola et al. 2010, Castellanos-Gell et al. 2012, 2016, Hernández-Martínez et al. 2013). In these studies, efforts have been made to shed light upon population connectivity and the role of Cuban island morphology and species life-history traits on dispersal: Is the island a barrier to dispersal between southern and northern populations? Does the fragmented nature of the Cuban platform limit dispersal between subregions? Do some life history traits affect population connectivity around the island? What are the relationships between Cuban populations and the rest of the Caribbean region?

Here, we review the main results obtained to date and provide a view of the patterns of connectivity identified for penaeid shrimps, reef fishes, marine turtles, and bottlenose dolphin.

The Scene: Geography and Marine Currents

With its large size and central position between the Caribbean Sea and Gulf of Mexico, Cuba is integral to the region's biogeography. It represents a physical barrier influencing regional sea currents among the Caribbean Sea, Gulf of Mexico, and Florida peninsula. The Cuban archipelago is composed of a main island (1200 km long) surrounded by about 4000 keys and islets. The submerged shelf is the largest in
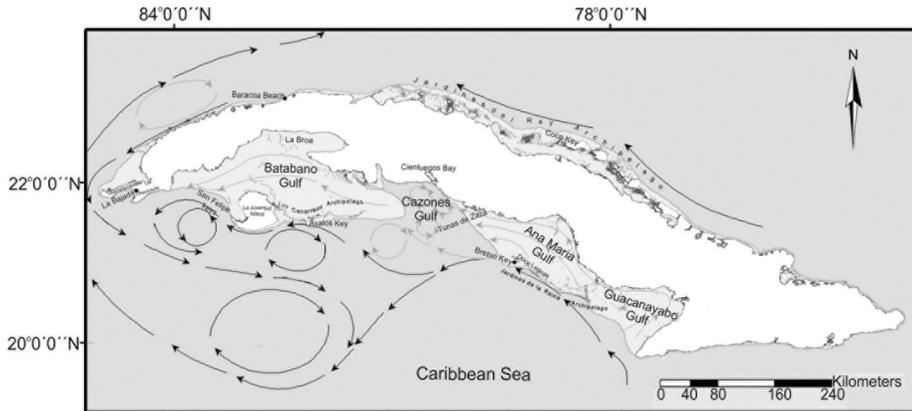
Figure 1. Cuban archipelago with lighter gray areas indicating the insular shelf. Arrows indicate major (black) and secondary (gray) oceanic and shelf circulation. Relevant geographic localities mentioned in the text are named.

the insular Caribbean region and can be divided into four relatively wide platforms separated by long stretches of narrow shelf areas (Fig. 1). The shelf is bordered, for most of its length, by extensive reefs, before it drops steeply to 400 m or greater (Claro et al. 2001). This configuration promotes divergent ecosystems providing support for a large number of species during their different life stages.

Three main marine current systems run along the Cuban coast and vicinity: a western current off southern Cuba, a northeastern current off northwestern Cuba, and a western current in northeastern Cuba (Fig. 1; Claro et al. 2001). These general circulation patterns are complex and include temporal changes, cyclonic and anticyclonic eddies, meanders, and countercurrents near the coast—products of local factors and current intensity (Paris et al. 2005, Arriaza et al. 2012). Additionally, intense meteorological events, such as hurricanes, promote strong, but ephemeral changes in marine circulation patterns, salinity, and sediment suspension (Allison et al. 2003).

Knowledge of these current patterns is essential to test hypotheses about dispersal and connectivity mediated by eggs and larvae (Cowen 2002). For example, Paris et al. (2005) suggested that a relatively high level of self-recruitment should occur in Cuban snapper populations, particularly those from the southern and north-central regions. These estimations can then be corroborated by other methodologies, including population genetics and tag/recapture studies.

Penaeid Shrimps: Small-scale Population Structure

The first population genetic study conducted on Cuban marine organisms was on penaeid shrimps, prompted by the growing problem of overfishing and the development of the shrimp aquaculture industry. Two species, the white shrimp, *P. schmitti* and the pink shrimp, *Penaeus notialis* Pérez Farfante, 1967, are prominent species on the southern Cuban platforms (Pérez-Farfante and Kensley 1997). *Penaeus schmitti* is abundant nearshore and was exploited by fisheries from 1953 until the early 1980s, when signs of overfishing were first acknowledged. At this time, the potential for shrimp aquaculture was explored in the region, and *P. schmitti* became the basis for shrimp production in the country until the early 2000s.

Penaeus notialis lives offshore, representing >95% of shrimp wild harvest. Despite regulations, it has been heavily exploited by fisheries (Giménez et al. 2012).

Biological factors and the distribution of populations suggests that these penaeid populations could be genetically differentiated at relatively small geographic scales. The two main southern platforms are separated by a stretch of deep sea, which precludes adult dispersal, and no habitat is available to support larval settlement over a stretch of approximately 350 km along the Gulf of Cazones. Larval duration is relatively short, about 15–20 d, spawning occurs inside the platforms, and the nursery grounds are distributed patchily (Guitart et al. 1985, Páez et al. 1997).

García-Machado et al. (2001) analyzed *P. notialis* collected at 11 localities along the southern platforms: 3 from the Gulf of Batabanó, 7 from the Gulf of Ana María, and 1 from the Gulf of Guacanayabo. Restriction fragment length polymorphism (RFLP) analysis, conducted on a 2027 bp fragment of mtDNA, revealed two haplotypes, one of which is shared by individuals from the gulfs of Ana María and Guacanayabos and the other exclusively observed in the Gulf of Batabanó. The authors suggested that the characteristics of the Gulf of Cazones (one of the deepest in Cuba) and the lack of nursery grounds for larval settlement and development in the area could prevent gene flow among areas separated by approximately 350 km. Allozyme loci analysis was carried out on samples of the Gulf of Ana María, and all but one pairwise comparison produced statistically significant F_{ST} values (0.033–0.350) between local populations. In addition, Nei's (1978) genetic distances grouped sampling locations according to their geographical distances, highlighting the influence of distance and the direction of marine circulation, which restricts gene flow inside the gulf area. Similar results were obtained by Espinosa et al. (1996), who detected population structure ($F_{ST} = 0.045$) at a very small geographic scale (two localities separated by 15 km inside the Gulf of Batabanó) in *P. notialis* also using allozyme loci.

Robainas-Barcia et al. (2005) did not find the genetic structure previously observed in the Gulf of Ana María (García-Machado et al. 2001) when replicating the analysis using samples collected in 2003 from the same area. Rather, they found evidence of genetic homogeneity and high gene flow. Surprisingly, highly significant differences were observed between genetic diversity estimates (or F_{ST} statistics) obtained from temporal replicates of each population (F_{ST} ranging between 0.136 and 0.191). The same results were obtained using microsatellite loci to compare annual and temporal samples collected in 1995, 1999, and 2003 (Robainas-Barcia et al. 2008). There were significant differences among populations inside the Gulf of Ana María for 1995, but not for the 1999 and 2003 samples. Such temporal instability could be the result of climatic factors, such as intense hurricanes, causing habitat loss and increasing migration inside the gulf. Interestingly, the microsatellite data were consistent with mtDNA, detecting significant and persistent differences between the gulfs of Ana María and Batabanó for the years 1995 and 2003 (Robainas-Barcia et al. 2008).

Using mtDNA and the sequences flanking two microsatellite loci, Robainas-Barcia and García-Machado (2012) found that the present Gulf of Ana María population has experienced a reduction in effective population size in the relatively recent past followed by a positive growth rate. In contrast, the Gulf of Batabanó population seems stable or decreasing. These results for *P. notialis* raise concerns about the conservation status of the species, since a reduction in the effective population size of *P. notialis* was estimated in the largest and most productive zone for the species in Cuba despite high levels of migration between the study areas.

Espinosa et al. (2003) and Borrell et al. (2004) have analyzed *P. schmitti* samples from four localities (Gulf of Batabanó, Cienfuegos Bay, Tunas de Zaza, and Gulf of Guacanayabo) covering most of its distribution in Cuba. Espinosa et al. (2003) analyzed eight polymorphic allozyme loci, and they found significant allele frequency differences between the surveyed localities. Genetic distances were small, but most noticeable between the most geographically distant populations of the gulfs of Batabanó and Guacanayabo. Using five microsatellite loci, Borrell et al. (2004) also found significant overall genetic differentiation (F_{ST} = 0.012, P < 0.001). In this case, however, the Batabanó population was genetically differentiated from Cienfuegos Bay and the Gulf of Guacanayabo, and the assignment test yielded a mean of 74.5% of individuals correctly assigned to their sampling origin, suggesting that all populations were genetically differentiated.

Borrell et al. (2007) did a more comprehensive analysis surveying geographical variation in the same area using both allozymes and microsatellite loci, with replication over time (1992 and 2003). The results indicated significant variation of allele frequencies over time, which could be the consequence of adverse environmental conditions promoting a decline in genetic diversity while maintaining strong population structure.

Compared with *P. notialis*, the smaller population sizes, nearshore vs offshore distribution, and higher habitat fragmentation in *P. schmitti* could have promoted a relatively stable local population differentiation due to a stronger effect of genetic drift and restricted gene flow.

Marine Fishes: Behavior, Egg Type, and Marine Currents

Pelagic larval duration and geographic distance have been frequently identified as factors influencing spatial genetic variation in marine fishes (Lessios and Robertson 2006, Selkoe and Toonen 2011, Riginos et al. 2014). Paris et al. (2005) simulated larval transport of five snapper species from the Cuban shelf and concluded that there is a high level of self-recruitment, particularly in the southern and north-central regions. The authors also found that the level of recruitment can vary among species because of the temporal variability of spawning and differential site utilization. Other biological factors, such as reproductive behavior (Portnoy et al. 2013), egg type (benthic or pelagic; Bradbury et al. 2008, Riginos et al. 2011), variation in reproductive success (Hedgecock 1994), and adult dispersal ability (Sponaugle et al. 2003), can also affect genetic structure of reef fish populations.

In an attempt to elucidate connectivity patterns of marine fishes around the Cuban archipelago based on predictions derived from Paris et al. (2005), Castellanos-Gell et al. (2016) used mitochondrial sequences and microsatellite loci to study the genetic structure of three coral fish species: the bicolor damselfish [*Stegastes partitus* (Poey, 1868)], the French grunt [*Haemulon flavolineatum* (Desmarest, 1823)], and the ocean surgeonfish (*Acanthurus bahianus* Castelnau, 1855). These species have contrasting life history traits, providing the opportunity to explore the possible influence of reproductive behavior, egg type, larval and adult dispersal, and marine currents on population structure and history.

Fishes were sampled at five locations around Cuba representing the four main coral reef areas and the western region of the archipelago. For all three species, mtDNA haplotype and microsatellite allele frequencies were stable over time (2007 and

2009), with differences observed in the patterns of population structure. In *S. partitus,* mtDNA sequence analyses indicated significant population differentiation in most pairwise comparisons. The Coco Key (northeast) sample differed statistically from all other sampling localities except Baracoa Beach (northwest), and differentiation was also significant between the southern localities of Breton (southeastern platform) and Avalos Keys (southwestern platform). No significant differentiation among any localities was found in *H. flavolineatum* and *A. bahianus*, indicating genetic homogeneity.

Similar results were observed when microsatellite loci were analyzed, with greater genetic variation. In *S. partitus,* population differentiation was significant between all populations (pairwise standardized F_{ST} values ranged between 0.038 and 0.198). Genetic distances showed two main population clusters: the southern localities (Breton and Avalos Keys) and the western-northern localities (La Bajada, Baracoa Beach, and Coco Key). In *H. flavolineatum,* no population structure was detected, although a subtle differentiation was observed in Breton Key population. Although the pattern of spatial connectivity identified using microsatellites, quite strong in *S. partitus* and subtler in *H. flavolineatum,* do not fit a stepping-stone model, the assignment probabilities and the distinction between southern and northern localities revealed a fairly clear change in genetic relationships around the archipelago coast.

The genetic structure observed in *S. partitus* most likely results from the combined effects of low dispersal capacity, benthic eggs, and ocean-current patterns. Planktonic eggs, reproductive migrations, and high vagility seem to enhance dispersal in *H. flavolineatum* and *A. bahianus,* producing population homogeneity at the geographic scale of Cuba.

Sea Turtles: Genetic Endemism and Foraging Aggregations

Marine turtles have been the focus of many genetic analyses because of their life cycle and threats from fishing, bycatch, and habitat loss (Avise 2007). Four species of sea turtles have been reported in Cuba, and three regularly nest there: the loggerhead turtle, *Caretta caretta* (Linnaeus, 1758); the green turtle, *Chelonia mydas* (Linnaeus, 1758); and the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus, 1766). The leatherback turtle, *Dermochelys coriacea* (Vandelli, 1761), occurs in Cuban waters, but rarely nests in Cuba. According to IUCN criteria and on the basis of current knowledge, *C. caretta* is listed as "Vulnerable," *C. mydas* as "Endangered," and *E. imbricata* as "Critically Endangered" (Seminoff 2004, Mortimer and Donnelly 2008, Casale and Tucker 2015). These species are highly migratory when young and exhibit natal homing behavior (Carr 1967), although females can switch nesting beaches in rare cases (Carr 1975). Because mtDNA is maternally inherited, this genome has been the focus of natal site philopatry studies in marine turtles (Bowen et al. 1992, FitzSimmons et al. 1997, Vargas et al. 2016).

Chelonia mydas.—Two major green turtle lineages have been identified in the Atlantic basin: (I) those found in the eastern Caribbean Sea, South Atlantic Ocean, and off western Africa; and (II) those found in the western Caribbean Sea and Mediterranean Sea (Encalada et al. 1996). In Cuba, 11 *C. mydas* samples were taken from San Felipe Keys in 1998 and 17 from Guanahacabibes Peninsula during 2000 (Ruiz-Urquiola et al. 2010). As expected, all southwestern Cuban haplotypes (seven)

belonged to lineage II. Three new haplotypes endemic to Cuba were described: CM-A48, CM-A56, and CM-A57 (following the Archie Carr Center for Sea Turtle Research nomenclature). Two other haplotypes (CM-A27 and CM-A28) previously founded in foraging areas (Bass et al. 2006, Bjorndal and Bolten 2008) also were identified as endemic to the Guanahacabibes Peninsula rookery. Haplotype CM-A27 was previously described as "Hypothetical 1" by Encalada et al. (1996). The other two haplotypes (CM-A01 and CM-A03) were shared with the remaining Greater Caribbean rookeries (Bjorndal et al. 2005, Anderson et al. 2013) and have been reported in foraging areas of Cuba, North Carolina, Florida, Barbados, and in the western Gulf of Mexico (Bass et al. 2006, Anderson et al. 2013). Only one of the endemic haplotypes (CM-A48), reported for the foraging areas of Florida (Bagley 2003), was observed in both Cuban rookeries (Ruiz-Urquiola et al. 2010). No significant genetic structure was detected between the Guanahacabibes Peninsula and San Felipe Keys, indicating that they represent a single breeding population with high genetic endemism. An analysis of molecular variance analysis considering Cuban colonies as a single unit, compared to the colonies of the remaining Greater Caribbean rookeries (Florida, Quintana Roo, and Tortuguero), indicates that the Cuban nesting turtles are a genetically distinct management unit (Ruiz-Urquiola et al. 2010).

Caretta caretta.—To study the Cuban population of the loggerhead turtle, 36 samples were taken between 1998 and 2006 from areas along the southwest of the island (6 from San Felipe Keys in 1998, 10 from Guanahacabibes Peninsula in 2000–2006, 12 from Island of Youth in 2006, and 8 from Cayo Largo del Sur in 2006; Ruiz et al. 2008). Two (CC-A1 and CC-A14) of the six haplotypes reported in southwestern Cuba rookeries were identified as belonging to the Atlantic lineage (Encalada et al. 1998; haplogroup I by Shamblin et al. 2014), which are shared with nesting aggregation colonies in the United States. These lineages have also been observed in foraging areas in the United States, the Azores, Madeira, and the Mediterranean Sea (Reis et al. 2010). Haplotype CC-A14 was proposed by Shamblin et al. (2014) as a relict Caribbean lineage. Four haplotypes (CC-A2, CC-A8, CC-A10, and CC-A12) were included into the Great Caribbean and Mediterranean lineage (Encalada et al. 1998, haplogroup II by Shamblin et al. 2014). Haplotype CC-A2 is ubiquitous in all Mediterranean rookeries and northwest Atlantic rookeries except in the northern managements units, as well as in South African rookeries (Shamblin et al. 2014). Haplotypes CC-A8, CC-A10, and CC-A12 are present in other rookeries, including Quintana Roo (Mexico), Florida (USA), and Greece (Shamblin et al. 2014). Ruiz et al. (2008) concluded that the southwestern Cuban rookeries constitute a single panmictic breeding population, genetically differentiated from the other Greater Caribbean rookeries. Later analysis indicated that the Cuban and Quintana Roo rookeries conform a single regional management unit after using a false discovery rate (FDR) method to adjust significance levels of the F_{ST} statistic under multiple comparisons (Shamblin et al. 2014). Nonetheless, Shamblin et al. (2014) concluded that both rockeries should be managed independently until new data were available from Cuban rockeries.

Eretmochelys imbricata.—An extensive sampling effort of hawksbill turtles was conducted in Cuba during the period of 1992–1997 (Díaz-Fernández et al. 1999). In total, 288 samples were collected, comprising 70 nest samples from Doce Leguas rookery and 218 samples from foraging areas on the Cuban shelf: 44 samples from

the southeast (Doce Leguas and Santa Cruz), 123 samples from the southwest, and 59 samples from the northeast (Nuevitas, Las Tunas, Cayo Romano, and offshore).

Using a 480-bp sequence of the mtDNA control region, one endemic nesting haplotype (EiA13) was identified in Cuba at a low frequency (five individuals; Díaz-Fernández et al. 1999). Haplotype EiA29 (found in one individual) has been reported in foraging aggregations in Mona Island and Cayman Islands (Velez-Zuazo et al. 2008, Blumenthal et al. 2009) and is shared with the Tortugero rookery (Costa Rica; Bowen et al. 2007). Haplotype EiA30 (reported in one individual from Cuba by Díaz-Fernández et al. 1999) was also found in one individual from Tortuguero (Troëng et al. 2005, but it was not found in Cuban foraging aggregations (Díaz-Fernández et al. 1999). Even when Bowen et al. (2007) used the data from Troëng et al. (2005), they did not consider EiA30 as a shared haplotype between Cuba and Costa Rica. This incongruence warrants verification.

Haplotype EiA11, observed at high frequencies in the Virgin Islands, Puerto Rico, Nicaragua, Barbados-Windward, and Costa Rica (Bowen et al. 2007, Leroux et al. 2012), was found in the Doce Leguas rookery (one individual; Díaz-Fernández et al. 1999). Most of the nesting specimens in Cuba (62) exhibit haplotype EiA1 (Díaz-Fernández et al. 1999), which is found at a high frequency in Antigua, Venezuela, Barbados-Leeward islands, and Brazil (Bowen et al. 2007, Leroux et al. 2012). A re-analysis of the Cuban samples with new primers as described by Leroux et al. (2012) could reveal new haplotype variants undetected by Díaz-Fernández et al. (1999). Yet Leroux et al. (2012) note that it is unlikely that the current results of interpopulation differentiation would be greatly modified, even if novel variation were found in the Cuban rookery. Cuban rookery haplotypes have been detected in all Caribbean foraging populations, including those in Cuban waters (Bowen et al. 2007, Proietti et al. 2014). Approximately 55% of foraging hawksbill turtles in Cuban waters originate from other Caribbean rookeries (Bowen et al. 2007). The three main marine turtle's species living in the Caribbean region are listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) with some level of conservation concern. In all cases, migratory behavior, complex life cycles, and the natal homing behavior of adults for reproduction are factors making turtles highly vulnerability to harvest and habitat destruction. Population genetic data has revealed the interconnection between foraging and nesting populations, which suggest that any management effort should be conducted on a regional basis (e.g., Bowen et al. 2007).

Bottlenose Dolphin: Behavior Matters

The bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), is the only cetacean that occurs year-round in Cuban waters. Like marine turtles, it has a high potential for long-distance dispersal, though studies have shown that the relationship between geographic distance and the level of genetic differentiation is unclear. Whereas in some cases gene flow is extensive over long distances (Quérouil et al. 2007, Tezanos-Pinto et al. 2009), in many others strong population subdivisions exist (Hoelzel et al. 1998, Natoli et al. 2005, Sellas et al. 2005, Parsons et al. 2006, Rosel et al. 2009, Wiszniewski et al. 2010). It is apparent that the environment, social influences, foraging and sex-related associations, and geographic barriers (Parsons et al. 2003, Möller

and Beheregaray 2004, Wiszniewski et al. 2009, 2010) are factors promoting genetic isolation at small geographic scales.

Caballero et al. (2012) included 57 samples from the north-central Cuban platform (Sabana-Camagüey archipelago) in a study of bottlenose dolphin populations of the northwest Atlantic. Three of five mtDNA control region haplotypes found in Cuban specimens were shared with samples of The Bahamas, the Gulf of Mexico, and Puerto Rico, suggesting a clear historical association between these areas. Recently, we have conducted a preliminary analysis of the mtDNA control region sequence variation in 108 *T. truncatus* specimens from four regions: Sabana-Camagüey archipelago (north-central platform, n = 95), Gulf of Guacanayabo (southeastern platform, n = 9), Gulf of Ana María (southeastern platform, n = 3), and Gulf of Batabanó (south-western platform, n = 1). The analysis revealed 17 haplotypes clustered in two highly differentiated (14 mutational changes) groups, one including the individuals sampled in the north-central platform and southwestern platforms (Gulf of Batabanó) and the second comprising those from the southeastern platform (G García-Machado, unpubl data). The analysis of the relationships between haplotypes in Cuba and from other regions of the Caribbean Sea revealed a clear partition between the northern and the southeastern Cuban populations. The population subdivision may correlate with evidence of population stability in the western north-central platform (López et al. 2013). Although preliminary, the results indicate that the position and structure of the archipelago and possibly foraging specializations can restrict dispersal of bottlenose dolphins in the area. Microsatellite loci analysis is underway to test if similar partitions are found and if gender-associated gene flow occurs along the Cuban coast.

General Remarks

As most marine organisms have potentially high dispersal capabilities, we might expect that at the relatively small geographic scale of Cuba, population homogeneity would extend throughout the archipelago for all or most species. As shown above, the data from species with different evolutionary histories and biology indicate that varying levels of connectivity exist with no universal patterns (Fig. 2). There are, however, two major patterns of population structure along the Cuban coast: a north-south break and an east-west split in the south. As described below, it is likely that several biotic and abiotic factors have shaped the patterns observed.

Cuba as a Barrier.—The Cuban archipelago holds a unique position, acting as a potential barrier between the Caribbean Sea and the Gulf of Mexico, and influencing the marine currents between these water bodies and the Florida Peninsula. The archipelago influences dispersal between both the Caribbean Sea and Gulf of Mexico, exhibiting divisions between northern and southern Cuba. Results from studies of the damselfish (Castellanos-Gell et al. 2016) and bottlenose dolphin (E García-Machado unpubl data) reveal a high level of population subdivision between south-ern and northern localities. Paris et al. (2005) found high levels of self-recruitment of snapper larvae in the Cuban shelf, which occurs in association with the larval region of origin (southern and north-central regions). Samples of the reef-building coral *Orbicella* (formerly *Montastraea*) *annularis* (Ellis and Solander, 1786) form two
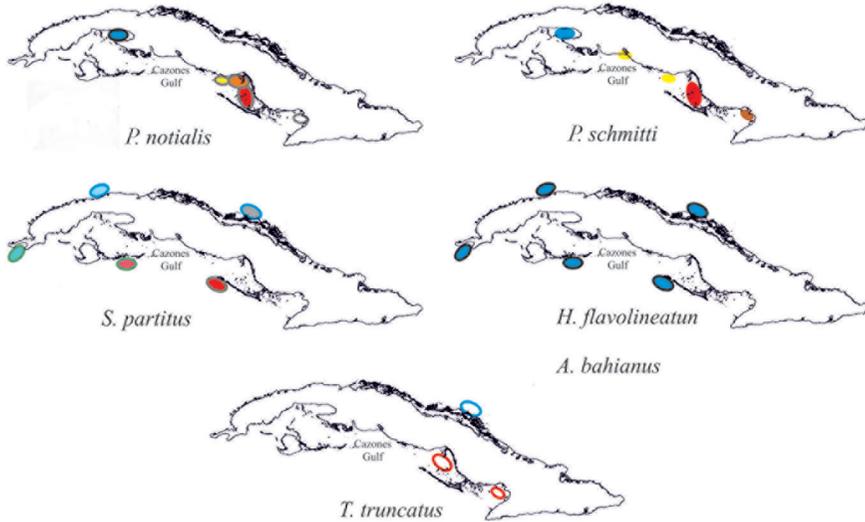
Figure 2. Schematic patterns of population structure for marine species in Cuba. Ellipses indicate approximate area of distribution of populations. Outline colors indicate genetically differentiated populations identified by mitochondrial DNA analysis. Fill colors indicate populations identified by allozyme and/or microsatellite DNA markers. Empty ellipses indicate lack of data for allozyme and microsatellite DNA markers. For *Penaeus notialis,* the pattern of population structure found in 1995 is represented using both allozyme (García-Machado et al. 2001) and microsatellite loci (Robainas-Barcia et al. 2008). In *Penaeus schmitti* the pattern of differentiation is a consensus of the patterns described by Borrell et al. (2004, 2007).

clusters in northwestern and southeastern Cuba, based on genetic projection model of larval transition probabilities (Foster et al. 2012).

Discontinuous Habitats, Discontinuous Shelf, and Marine Currents.—The occurrence of unfavorable habitats and intervening barriers can hinder dispersal for some species. The most evident is the population subdivision observed in penaeid shrimps *P. notialis* and *P. schmitti* (Fig. 2; García-Machado et al. 2001, Robainas-Barcia et al. 2008). These species develop relatively rapidly and postlarvae settle in nursery grounds scattered along the shelf (Revilla and Páez 1990). Regional self-recruitment and local current systems seem to promote population isolation at smaller geographic scales (Espinosa et al. 1996, García-Machado et al. 2001, Borrell et al. 2007). Shelf discontinuities could also influence damselfish population genetic differentiation as suggested by the significant differentiation between southwestern Avalos and southeastern Breton Keys (Castellanos-Gell et al. 2016).

Life-history Traits.—The biology and evolutionary history of marine organisms appears to play a major role in determining the connectivity patterns along the archipelago. Species such as some penaeid shrimps, with short pelagic larval stages and larval settlement occurring in inner-shelf nursery grounds (Revilla and Páez 1990) are more prone to population subdivision at smaller geographic scales (Espinosa et al. 1996, García-Machado et al. 2001, Borrell et al. 2007, Robainas-Barcia et al. 2008), and they can be sensitive to deep marine barriers, such as the Gulf of Cazones (Figs. 1, 2). In fishes, egg type, reproductive behavior, and dispersal potential can

limit dispersal. The damselfish *S. partitus* has highly territorial adults that do not disperse once they settle in the reef and produce benthic eggs (Castellanos-Gell et al. 2016). Other organisms with high dispersal potential, such as bottlenose dolphins, appear to have genetically differentiated populations in Cuba, which could be related to their social and foraging behaviors.

Future Directions

Different patterns of genetic diversity can be observed in different species of the Cuba archipelago. So what questions should be tackled in the future? The study of sessile or low-dispersal organisms will provide more clues as to the importance of marine currents on dispersal and retention patterns of larvae. Recently, Foster et al. (2012) used experimental and modelled gene flow to provide evidence of genetic differentiation between two sampling areas of the reef-building coral, *O. annularis*. The geographic position of Cuba also raises the issue of its role as a barrier between the populations of the Caribbean Sea and the Gulf of Mexico, and northwestern Atlantic Ocean. Regarding this question, we need to explore the relationships between the populations of Cuba and the rest of the Caribbean region. Although many of the studies at this geographic scale do not include samples from Cuba, studies of corals (Foster et al. 2012), reef fishes (Castellanos-Gell et al. 2012, Jackson et al. 2014), marine turtles (Bowen and Karl 2007, Ruiz et al. 2008, Proietti et al. 2014, Shamblin et al. 2014), and dolphins (Caballero et al. 2012) reveal that gene flow between Cuban populations and other in the region are species dependent. For instance, Paris et al. (2005) used hydrodynamic models to predict that snapper larval exportation from northern Cuba to Florida and The Bahamas, and from southwestern Cuba to Central Caribbean and Mesoamerica, could be important. Yet genetic analysis of the Nassau grouper [*Epinephelus striatus* (Bloch, 1792)], a species with similar spawning aggregations, only confirmed central Caribbean connections (Jackson et al. 2014). It should be noted that the Cuban samples in Jackson et al. (2014) were limited to two western localities. A study of the coral-reef-building *O. annularis* showed genetic connectivity between Cuba, Cayman Islands, Santo Domingo, part of Jamaica, and Mesoamerica (Belize and Honduras) to the exclusion of other areas in the region such as The Bahamas (Foster et al. 2012). In these two species that are dependent on larval dispersal, the predicted biogeographical discontinuity between the Caribbean Sea and The Bahamas is confirmed (Cowen et al. 2006), but the connection between Cuba, Cayman Islands, and Mesoamerican reef area may vary (Cowen et al. 2006, Salas et al. 2010). Turtle and dolphin population structure is highly influenced by life cycle and behavior. In turtles, natal homing, neonate and juvenile dispersal, and foraging area use determine complex patterns of connectivity (Bowen et al. 2007). Dolphins also show relatively complex associations associated to behavior. Differences in population structure found with mtDNA and microsatellite loci were associated with the occurrence of worldwide distributed lineages and local ecotypes in particular population units (Caballero et al. 2012). Mitochondrial DNA exhibited a Cuba, Colombia, The Bahamas, and Mexico association, whereas microsatellite loci were identified as a single unit.

The population structure and patterns of connectivity found in Cuba represent valuable information that should be used more actively for fisheries management and marine conservation programs. One example is the permanent moratorium on

fishing for marine turtles, established in 2008 and based largely on population genetic data (Lee-González et al. 2015). Population genetic data can also be used to designate isolated ecosystems, based on concordant genetic breaks across multiple species (Toonen et al. 2011). Ecosystem-based management is widely viewed as the future of wildlife conservation, as indicated by the United Nations Global Centre for Ecosystem Management (http://www.unep.org/ecosystemmanagement/) and the IUCN Commission on Ecosystem Management (https://www.iucn.org/about/union/commissions/cem/). Genetic data can reveal the boundaries of these ecosystems and help guide the placement of marine protected areas.

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