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RESEARCH ARTICLE

The Ecology of Cuba's Jardines de la Reina: A review

La Ecología de Jardines de la Reina, Cuba: Una revisión

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Abstract

It is widely recognized the importance of scientific information to advance social and economic development. Although Jardines de la Reina (JR) archipelago and its surroundings are among the most critical regions for Cuba's fisheries and marine biodiversity, comprehensive information has been collected almost only within the last 20 years. This paper summarizes the main findings from the scientific literature published about JR archipelago and its surroundings. We review the scientific contributions to conservation and management and identify research gaps. Overall, we found a steep increase in scientific publications in the last ten years due to fruitful partnerships across diverse stakeholders. Public-private partnerships in responsible ecotourism and the support of Cuban and foreign environmental institutions and conservation organizations have been instrumental in advancing research and conservation in JR. A myriad of research, mainly focused on species/groups and the effects of marine protection, has safeguard and promote sustainable use of JR biodiversity. The high abundance and biomass of large and commercially important fish such as sharks, groupers, and snappers and other conservation outcomes, result from effective enforcement and positive incentives favouring conservation, while supporting local livelihoods. Finally, we provide recommendations to guide future research and advance conservation in JR archipelago.

Keywords: Jardines de la Reina, review, marine protection, conservation outcomes, stakeholder participation

Resumen

Actualmente se reconoce la importancia de la información científica para el desarrollo económico y social. Jardines de la Reina y sus alrededores, una de las regiones más importantes desde el punto de vista pesquero y de conservación de Cuba, permaneció muy poco conocido hasta hace alrededor de 20 años. Este trabajo pretende resumir los principales resultados publicados en la literatura científica acerca de Jardines de la Reina y sus alrededores, o relacionada con ellos, su contribución a la gestión de los recursos naturales, los vacíos que existen y recomendar investigaciones científicas y medidas de gestión para avanzar aún más su conservación. Se observa un incremento de investigaciones científicas publicadas en los últimos 10 años, gracias al trabajo conjunto de los actores involucrados en la región. La empresa turística, las instituciones científicas y organizaciones de conservación cubanas y extranjeras, han trabajado de manera conjunta para apoyar y llevar a cabo investigaciones en muchos campos, principalmente en especies/grupos y efectos de la protección, para avanzar la protección y uso sostenible de la diversidad biológica en Jardines de la Reina y sus alrededores. La abundancia y biomasa de peces de gran tamaño e importancia comercial tales como tiburones, meros, pargos, son el resultado de la aplicación adecuada de las regulaciones y de incentivos que favorecen la conservación, al mismo tiempo que permiten a los seres humanos mantener su modo de vida. Se realizan varias recomendaciones para avanzar el conocimiento científico y la gestión de los recursos naturales en Jardines de la Reina y sus alrededores.

Palabras clave: Jardines de la Reina, revisión, protección marina, efectos de la conservación, participación entre actores

Introduction

Although Jardines de la Reina (JR) archipelago and its surroundings are among the most critical regions for Cuba's fisheries and marine biodiversity, comprehensive information has been collected almost only within the last 20 years. Accounts of ecological information from JR date back to Columbus' 2nd voyage to the Americas in 1494 (Jackson 1997 citing Andres Bernaldez (1988)) referring to the abundance of green turtles in southeastern Cuba). Despite anecdotal records, for many years JR and its surroundings were little explored, except for fisheries research (Carles, 1967; Báez & Álvarez-Lajonchere, 1980; Espinosa & Pozo, 1982; Valdés & Sotolongo, 1983; León & Guardiola, 1984; Páez, 1997) and biodiversity inventories (Espinosa, 1985; Espinosa & Ortea, 1998a, b, c, 1999; Abreu & del Valle, 1998; Ortea & Espinosa, 1998; Ibarzabal, *et al.*, 1999).

JR was heavily fished until 1996 (Claro, *et al.*, 2009) when around 1,000 km^2 were declared as a Marine Reserve (JRMR) (Resolution 562/1996, Former Minister of Fisheries). Since 1996, only lobster fishing and little catch and release fishing has been allowed in JRNP (Appeldorn and Lindeman 2003). In 2010 JRMR was upgraded to National Park (JRNP), covering an area of approximately 2,000 km^2 (Agreement 6803/2010, Council of the State), and becoming the largest marine protected area of the entire Caribbean (Appeldorn & Lindeman, 2003) (Fig 1). Monitoring and reporting since 2010 suggests well-enforced environmental and fisheries regulations in JRNP compared to other regions in Cuba (Pina-Amargós. *et al*., 2014b). The neighbouring Golfo de Ana María (GAM) is still a prime fishing ground contributing to about 44 % of the total national landings (Puga, *et al*., 2018) suggesting a strong spillover effect of JRNP.

Due to its strong protection (Pina – Amargós, *et al*. 2014a) JRNP has near-pristine levels of apex predators and well-preserved coral reefs (Valdivia, *et al*., 2017), making JRNP outstanding beyond the national realm. JRNP is one of the premier marine protected areas of the Caribbean region, evidenced by its effective management (Jackson, *et al*., 2014), abundance of highly valued fish species such as sharks (Perera-Valderrama, *et al*., 2018), and flowing of economic benefits (Figueredo-Martín, *et al*., 2013, 2014a, b).

It is widely recognized the importance of scientific information to advance social and economic development. Even though Cuba is recognized to base its policies for social and economic growth on science (Kritzer, *et al.,* 2014), scientific research in certain regions has been scarce up until recently. This paper summarizes the main findings from the scientific literature published about JR archipelago and its surroundings in the last two decades. We review the scientific contributions to conservation and management and identify research gaps. Finally, we provide recommendations to guide future research and advance conservation in JR archipelago (Appendix 1).

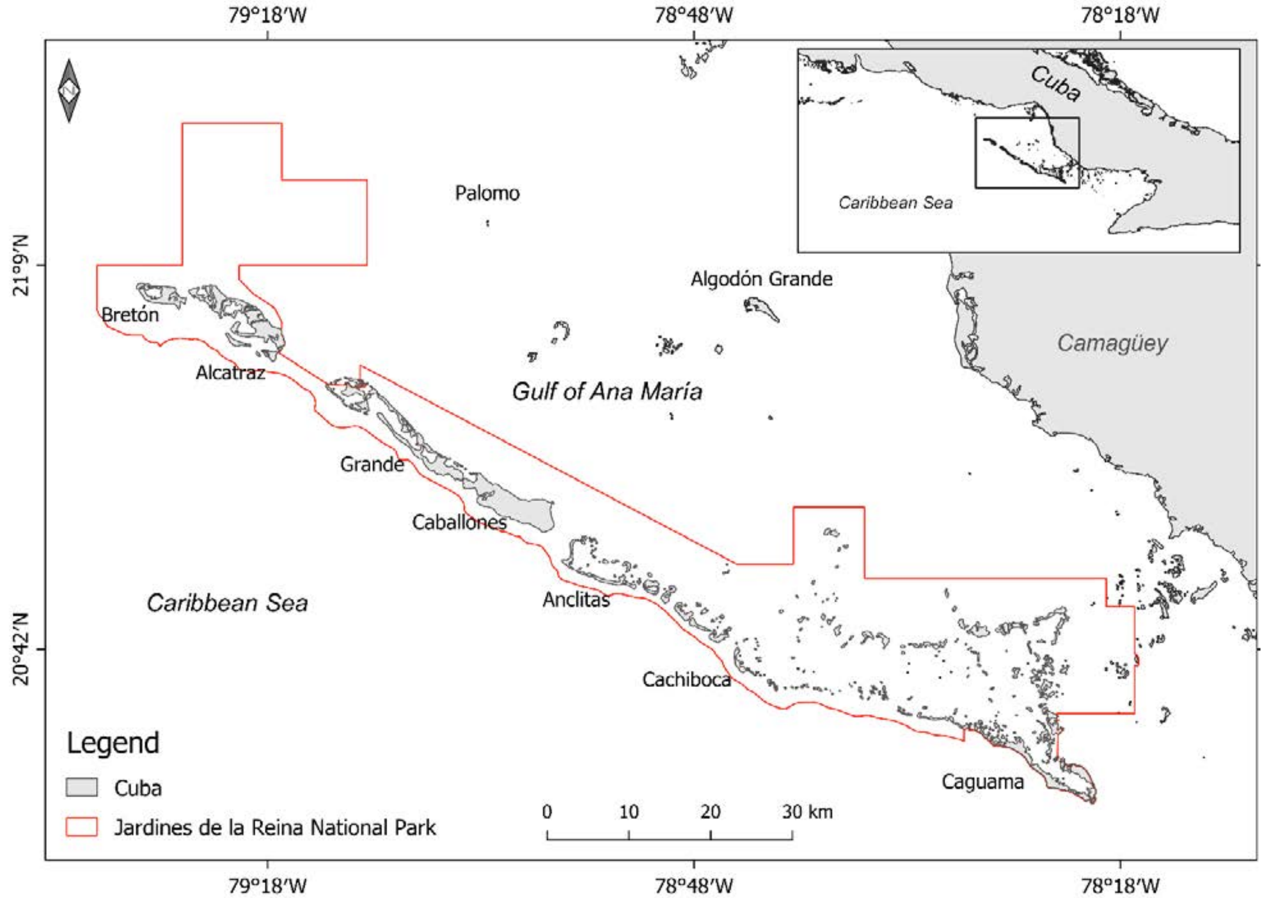

Fig. 1. Study area of Jardines de la Reina and surroundings.

Materials and methods

We conducted a systematic review of the scientific literature published about or associated with JR archipelago and its surroundings. We targeted peer-reviewed scientific journals, book chapters, and peer-reviewed reports. Peer-reviewed reports consisted of technical reports of multi-institutional projects and abstracts and manuscripts published on international conferences. We included two non-peer-reviewed reports due to their contribution to oceanography. Oceanography is generally an underrepresented research field for JRNP (González de Zayas, *et al*., 2006; Lluis Riera, 1977).

We summarised the main research findings on the results section, including their contributions to management, and existing research and information gaps. We structured the results section in several sub-sections, including I) ecosystems, II) species/groups, III) connectivity, IV) environmental good and services, V) effects of marine protection, VI) climate change, and VII) Golfo de Ana María. These sub-sections directly reflect the main themes of existing research on JR and its surroundings. We divided some sub-sections further when appropriate (i.e. the ecosystem section includes coral reefs, seagrass, and mangroves). We included cross-cutting topics across multiple sub-sections (i.e., information on corals is included on sections I, II, and IV).

Finally, we included a Discussion section summarizing the review's main findings and provided recommendations for future research and conservation of JR in Appendix 1.

Results

Overview

Our search found 171 publications about JR archipelago and its surroundings. The vast majority of publications consist of peer-reviewed scientific articles (88 %) published within the last two decades, with 20 % of articles published from 2001 to 2010, and 69 % of articles published from 2011 to 2020. More than half of the publications are about species/groups and the effects of marine protection.

I. Ecosystems

Ecosystem-level information is limited to marine ecosystems, including coral reefs, seagrass, and mangroves.

Coral reefs

Coral reefs are the most studied ecosystem in JR (see more coral studies in sections II and IV).

The microbiology of stony corals is a relatively new field of research. Weber *et al.* (2019a) first use the term *coral ecosphere* to indicate that stony corals are bathed in a "sea" of planktonic and particle-associated microorganisms. Samples taken from JR and Canarreos Archipelago revealed microbial interactions occurring within the coral ecosphere. These interactions could influence recruitment of coral-associated microorganisms and facilitate the transfer of coral metabolites into the microbial food web. Coral ecosphere processes could then foster reef biogeochemical cycling and interactions between corals and the water column.

A joint Cuba-U.S. expedition conducted in 2017 characterized for the first time the extent and health of mesophotic coral ecosystems (deeper than 30 meters) in Cuba's waters, including JR (Reed, *et al*., 2018). No specific information on JR mesophotic corals are shown.

Limited comprehensive surveys of JR coral reefs exist (Pina-Amargós, *et al*., 2008c; Caballero-Aragón & Perera-Valderrama, 2014; Hernández-Fernández, *et al*., 2018). Since these studies report coral cover change through time and explore benthonic spatial patterns in JR, we discussed them in sub-section iv. Other studies focused on fewer survey sites reported a relatively good condition of JR coral reefs when compared to other areas in Cuba and the rest of the Caribbean region (Ferrer-Rodríguez, *et al*., 2016; González-Díaz, *et al*., 2018; Caballero-Aragón *et al*., 2019; Weber, *et al*., 2019b). Their limited survey sites in JR, however, limit the reach of their conclusions. Ferrer-Rodríguez *et al*. (2016) evaluated reef health in a sector of JRNP and the Gulf of Ana María. The study set four survey stations in JRNP and two in GAM in 2015. Survey findings revealed that coral ecological and health indicators, including coral density and coral cover, show higher values in Jardines de la Reina than in other Cuban and Caribbean reefs. González-Díaz *et al*. (2018) assessed the status of Cuban coral reefs in several sites across the country, including Havana, Artemisa, Los Colorados, Punta Francés, Canarreos Archipelago (CAN), Península Ancón, and Jardines de la Reina. Authors found that offshore reefs along the south-central coast of Jardines de la Reina and Península Ancón exhibited high coral density and diversity, with a comparatively healthier condition than in any of the other survey sites. In a nationwide coral reef assessment covering 199 survey sites on 12 locations, Caballero-Aragón *et al*. (2019) reported that Jardines de la Reina had the highest coral cover values and the lowest coral mortality values (together with Cienfuegos). Authors hypothesize that coral health differences across sites result from natural and anthropogenic factors affecting Cuban reefs. Weber *et al*. (2019b) assessed the microbial signature in more than 20 coral reefs in the Florida Keys, Canarreos Archipelago and JR. The research additionally provided information of benthic components. Average live coral cover revealed to be similar in JR and the Florida Keys, and significantly higher than in Canarreos Archipelago. Conversely, average total algal cover was significantly higher in

Canarreos Archipelago than JR and similar to the total algal cover in the Florida Keys. Within JR, the offshore forereefs had average coral and algal covers of 27.4 % and 52.5 %, respectively.

One of the essential reef-building' species is the elkhorn coral, *Acropora palmata*. Hernández-Fernández *et a.l* (2019b) conducted a comprehensive survey of JR reef crests to assess spatial distribution of *A. palmata* and explore potential drivers of the species distribution patterns. Surveys revealed nearly 7,000 colonies of A. palmata. Authors found a significant increase in the number of A. palmata colonies from east to west, and a negative relationship between the number of colonies and the distance from channels. The influence of channels was greater within the first 2,000 meters of depth. The reef crests' orientation significantly influenced the abundance of *A. palmata* colonies, with more colonies found in the reef crest parallel to the latitudinal lines (0 slope). Patterns found in this research seem to be influenced by oceanographic processes acting in the hundreds-of-meters scale. Although without a solid baseline reference, authors suggested that a coral species recovery has occurred over the last 10-16 years. Results of this research informed ecotourism planning in JR, including snorkelling activities. Additional studies surveyed fewer reef crest sites (Hernández-Fernández, *et al*., 2016a; Hernández-Fernández & Bustamante-López, 2017; Caballero-Aragón, *et al*., 2020). For instance, Hernández-Fernández *et al*. (2016a) and Hernández-Fernández and Bustamante-López, (2017) compared four reef crests in two consecutive years and reported a decrease in reef health from one year to the next. However, they recognized that their sampling design could bias their overall results. Surveys did not occur in the same sites from one year to the following. Repeated surveys at the same locations are critical requirements of a before-and-after survey design of benthic organisms. Caballero-Aragón *et al*. (2020)' analysis of 41 reef crest sites surveyed from 2010 to 2012 showed an overall deteriorated health of *A. palmata* in the Cuban archipelago. However, their findings in JR are limited to only two sites, and they do not use the conclusions from Hernández-Fernández *et al*. (2019) to enrich their discussion.

On a global scale, Beyer *et al*. (2018) used Modern Portfolio Theory to identify coral reef locations globally that are likely to have an increased chance of surviving projected climate changes-in the absence of other impacts. This global analysis known as "50 Reefs" identified 50 bioclimatic units (BCU) or coral refugia worldwide, seven in the insular Caribbean, and five in Cuba. Southeastern Cuba, including JR, is one of the country's BCUs (see Figure 2 at Beyer *et al*., 2018). Moreover, JR is within the group that included the reefs with the highest condition and adaptability (23 % of the sites). The authors argue for a balanced solution approach to prioritize investment in those reefs with the highest potential of surviving climate change impacts. Thus, their balance solution scenario includes reefs in 31 of the 87 countries that have more than 500 km^2 of tropical coral reefs, with multiple reefs in countries such as Australia, Cuba, French Polynesia, Philippines, Bahamas, and Malaysia (see Figure 4 at Beyer *et al*., 2018). In their balanced scenario, JR features as part of the optimal portfolio or reefs presented in this paper (see Figure 4 Beyer *et al*., 2018). Thus, JR is one of the reef locations with highest opportunities for new and innovative conservation investments to secure resilient and well-connected coral reefs that may, in turn, help to repopulate degraded areas if climate eventually has stabilized.

Seagrass

There is insufficient knowledge of seagrasses in JR. Bustamante-López *et al*. (2018) characterized the status of four seagrass meadows at Pasa Caballones —a wide channel that divides Anclitas and Caballones cays in JR. The dominant angiosperm is *Thalassia testudinum,* and among the algae, *Halimeda* and *Penicillus* are the dominant genus. Authors reported twenty-four species of ichthyofauna in seagrass beds, with the parrotfish *Sparisoma chrysopterum* and filefish *Monacanthus spp.* the most abundant species. Juveniles of the Atlantic goliath grouper or "guasa" (Pisces: *Epinephelus itajara*) occur on Pasa Caballones seagrasses. Authors did not conduct interannual comparisons as they suspected that the same sites were not surveyed over the study years. We include additional publications about seagrasses in sub-section V.

Mangroves

Despite being one of the most extensive and essential ecosystems in JR, mangrove forests remain poorly studied. The only peer-reviewed publication about mangroves focused on stony corals associated with red mangrove roots. The dominant species in JR are *Porites astreoides* and *Porites divaricata*. One hundred per cent of the coral colonies were found associated with crustose coralline algae, mainly from the genus *Neogoniolithon* (Hernández-Fernández, 2015). Another study about fish found in or near mangroves in southern Cuba (Pina-Amargós, *et al*., 2013) reported that JR is one of the two protected areas with the highest density mangrove-associated commercial important fishes, reaching up to 40 individuals/100 m^2. The latter emphasizes the vital role of mangroves within the life cycle of valuable fish species.

Perhaps the most apparent environmental problem in JR is the patchy death of red mangroves. The causes of this mortality remain a scientific mystery, as only in a few cases it seems to be associated to the impact of hurricanes.

II. Species/Groups

We divided this sub-section into terrestrial and marine species/groups. We gathered information on plants, mollusks, reptiles, birds, and mammals for terrestrial species/groups. Besides, we gathered information on algae, plankton, corals, octocorals, sponges, long-spined sea urchin, other invertebrates, fishes, lionfish, marine turtles, and another marine-megafauna for marine species/groups.

Terrestrial species/groups

Plants

The terrestrial flora of JR encompasses 113 infrageneric taxa, 97 genera and 40 families. Of the approximately 660 cays of JR, the cays Anclitas, Grande, Caguama, Algodón Grande and Caballones possess the highest taxonomic richness (Acevedo- Rodríguez, 2013). Endemism is low in JR (4.5 %), and alien plant species represent an 8 % if the total reported flora. The flora of JR archipelago is dominated by shrubbery and herbaceous life forms, mainly of neotropical and neotropical-holarctic groups. The sandy coastal vegetation and coastal xeromorphic scrub exhibits the highest species richness. Reports of the endemic Cuban Petticoat Palm or "Guanabacoa" palm (*Copernicia macroglossa* (Arecaceae)) in Cayo Caguama at JR date to 2010 (Acevedo-Rodríguez, *et al*., 2010). A study of plant diversity's spatial distribution on sandy coastal shrubs revealed that JR's vascular flora was represented by 21 species, 21 genera and 11 families, with Cayo Caguama having the highest species richness (Acevedo-Rodríguez & González-Torres, 2013). The average species richness showed no significant differences between locations; however, the number of individuals resulted higher in Cayo Anclitas. Vegetation cover is high in Anclitas and Caguama cays, exhibiting a closed vegetation structure. Distance to the shoreline influenced vegetation richness found Anclitas and Grande cays and the number of individuals plans found Cayo Grande. Dune height and vegetation cover showed a positive association, potentially reflecting various levels of substrate stability. Despite the apparent homogeneity of coastal vegetation, there were still some differences among JR' cays (Acevedo-Rodríguez & González-Torres, 2014). Cayo Grande is structured by competition from vegetative versus seed colonization during the months with highest rains, and randomly (by resources scarcity) during the months with intermediate to low rain.

Conversely, Caguama, and Anclitas cays show the opposite pattern. This apparent contradictory trend requires further research (Acevedo-Rodríguez & González-Torres, 2015). Vegetation in cays Grande, Anclitas, and Caguama consists mainly of hemicryptophytes and chamaephytes plants. The latter possess nanophyllous leaves and display dispersal syndromes such as zoochory and anemochory. Vegetation functional groups' richness, however, varies from one cay to another. Functional diversity is similar between the rainy and dry seasons, and the interplay of a suit of abiotic factors seems to influence its spatial variation.

Mollusks

Knowledge of terrestrial mollusks in JR is poor. The most conspicuous species is *Cerion santacruzense* (Barrios-Valdés, 2016). Its density varies among JR' cays. The highest density occurs in Cayo Caguama, with an average of 24 individuals/m^2, and the lowest density is in Cayo Anclitas, with an average of 0.7 individuals/m^2. *C. santacruzense'* four studied populations have an aggregated distribution. This mollusk habitat preference is grass, particularly the species *Schizachyrium gracile*.

Reptiles

Only two peer-reviewed publications about terrestrial reptiles in JR exist. The first one reports a new species occurrence for the region (Marichal-Arbona, 2016a), and the second one describes the diet of the Cuban iguana, *Cyclura nubila nubila* Gray, 1831 (Squamata: Iguanidae) (Marichal-Arbona, 2016b). *C. nubila nubila* is an endemic subspecies of Cuba listed as Vulnerable in the IUCN Red List of Endangered Species. The diet of sampled Cuban iguanas in Cayo Caguama consisted of nine plant species, with *Cochorus hirsutus* as the most frequently consumed species. Conversely, four plant species predominated in the diet of *C. nubila nubila* in Cayo Palomo, with *Conocarpus erectus*, *Setaria parviflora* and *Thalassia testudinum* most frequently consumed. In Cayo Palomo, 45 % of faecal pellets contained corporal parts of dragonflies and 5 % of crabs. The consumption of animal matter is due, presumably, to the low floristic diversity of Cayo Palomo. In contrast, iguanas' diet in Cayo Caguam included more plant components, predominantly fruits (Marichal-Arbona, 2016b). In 2015, a specimen of Cuban boa (*Chilabothrus angulifer*) was captured on a xerophytic coastal scrub of Cayo Caballones, JR. It measured nearly 1.72 meters of length. This capture constituted *C. angulifer*' first-ever record in JR and contributed to expanding its distribution to cays on the southeastern Cuban archipelago (Marichal-Arbona, 2016a).

Birds

Inventories and ecological research of birds in Jardines de la Reina have increased significantly in the last decade.

Parada-Isada *et al*. (2012) after surveys in 2009 and 2010 added 15 new records of birds to JR, totalling 96 species. The same year, Parada-Isada and García-Quintas (2012) compiled information of bird surveys carried out since the 1980s in 44 cays of JR, Golfo de Ana María and Ana María Cays. The compilation rendered 116 species, with 10 % of those endemic to Cuba. Four bird species are listed as Near Threatened by the IUCN Red List of Endangered Species. JR's avifauna encompasses 30 permanent resident species, 18 bimodal species, 25 winter resident species, ten summer resident species, and 32 transient species. There are six most-abundant species, 17 common, 33 uncommon, 33 rare, 26 very-rare and one vagrant species. JR cays with the highest species richness was Anclitas (87 species), Caguama (71 species), and Grande (66 species).

Using information gathered in 2011, Parada-Isada *et al*. (2013) added nine new bird records to JR archipelago and its surroundings, totalling 125 species. With the information collected one year later, Barrio-Valdés and Parada-Isada (2013) added two new bird records, reaching to a new total of 127 species. An ecological study carried out in 2014 found that despite bird communities fluctuated due to migrations, their structure is considered stable (García-Quintas & Parada-Isada, 2014).

Parada-Isada, *et al*., 2015 expanded JR birds' inventory with two new additions using surveys carried out in 2012, reaching a new total of 129 species (Parada-Isada, *et al*., 2015). The authors further assessed spring and fall bird migrations between 2009 and 2012. They found no significant differences between seasons across cays, and no significant differences for the number of species captured per day (12.7 ± 3.65 in spring, and 12.8 ± 4.14 in fall). Similarly, relative bird abundance did not change significantly between seasons, with reports of 34.1 ± 13.5 birds/ 100 hours-net in spring, and 35.2 ± 16.43 birds / 100 hours-net in the fall. Female and immature individuals dominated the fall migration, and a more balanced age and sex rate made of the majority of fall migrants. Only two marked individuals were observed in two different years, constituting the first observations for Cuba's sandy coastal scrub during bird migration. The geographical location of Cuba's southern archipelagos and possibly low predation risks in JR may confer importance on the area as a stopover site for many Nearctic birds' migrants (Parada-Isada, *et al.,* 2015).

In 2012, the only survey of bird breeding colonies in JR ever carried out revealed 31 breeding colonies of six bird species, addressing the importance of this archipelago for bird reproduction and red mangroves as essential habitat for breeding birds (García-Quintas, 2016). In 2017, researchers found that habitat diversity, cay size, and cay perimeter are the most contributing factors to bird community' structure (García-Quintas & Parada-Isada, 2017). They also point out that the interaction of selective extinction and differential colonization of species are likely predictors of the observed nestedness patterns in bird assemblages, with differential species colonization having a more remarkable effect.

Latest bird surveys conducted in 2017 surveys added two more records to the bird inventory of JR, reaching a total of 131 species (Igalza-Galañena & García-Quintas, 2018). García-Quintas *et al.* (2020)' study provides evidence of the structural and functional cohesion of avifauna at JR, especially among its insect-eating taxa. Researchers recommend including this bird guild among the conservation targets of the next management plan of JRNP.

Mammals

Desmarest's hutia (*Capromys pilorides doceleguaes*) is an endemic subspecies of JR and the only native terrestrial mammal present in the archipelago. This species is very abundant, but none peer-reviewed manuscript has been published about it to the best of our knowledge.

Marine species/groups

Algae

There are several inventories for algae species of JR, including new additions featured in Algae's Cuban List. Cabrera *et al.* (2005a) added one species (*Avrainvillea nigricans* f. *floridana* Littler & Littler, 1992) to Cuba's phycoflora. Cabrera *et al.* (2005b) further included six algae species to Cuba's flora, three collected in JR. Guimarais *et al*. (2009) added three *Halimeda* species to the flora of Cuba. Clero-Alonso and Cabrera (2012) reported 112 algae species from JR. Suárez and Martínez-Daranas (2015) reported seven new records of macroalgae from JR. Additionally, algae extracts collected in JR showed high bioactivity (Valdés-Iglesias, *et al*., 2003). Besides algae-focused publications, there are several publications on coral reef, long-spined sea urchin and the effects of marine protection that include assessments of algae.

Plankton

Up until recently, little was known about plankton in JR. In a nationwide study, Lugioyo-Gallardo and

Loza-Álvarez (2018) find that the distribution of picoplanktonic and nanoplanktonic biomass in Cuba' oceanic waters did not differ significantly among years in the same season. However, there are spatial and seasonal differences in the case of JR. Picoplankton biomass is higher in the eastern half of the oceanic waters bathing JR on both seasons, and higher in summer than in winter on both portions (see Figure 2 at Lugioyo-Gallardo & Loza-Álvarez, 2018). The biomass of the heterotrophic component was much larger than that of the autotrophic component (see Figure 3 at Lugioyo-Gallardo & Loza-Álvarez, 2018). The latter stressed the role of small (<20 mm) heterotrophic organisms in the microbial loop.

Weber *et al*. (2019b) assessed microbial communities on 25 protected and unprotected Cuban and American reefs. Their study included Cuban reefs located in Canarreos Archipelago (CAN) and JR, and American reefs located in the Florida Keys (FK). This comprehensive study contributed to several thematic sections in this review (i.e., coral reefs, connectivity and oceanography). We summarized the main findings relevant to the plankton section, but we advise reviewing the original publication for detailed information. JR is an oligotrophic reef-system characterized by taxonomically diverse microbial communities with high community similarity and abundant picocyanobacterial biomass. Differently, CAN and FK reefs show greater spatial variability in reef seawater microbial community, alpha diversity, and composition. Picocyanobacterial abundances in JR were similar to abundances observed within oligotrophic open-ocean environments but were two orders of magnitude higher than abundances detected in seawater from Pacific reefs.

Furthermore, reef seawater collected from the offshore forereefs of JR had high abundances of Prochlorococcus. There was a shift to high, but variable abundances of Synechococcus in seawater collected from within the Golfo de Ana María. This negative relationship between Prochlorococcus and Synechococcus was observed previously and seemed to be associated with increased macronutrient concentrations and proximity to land. Additionally, picocyanobacteria's ratio to unpigmented cells was very similar between offshore and gulf reefs in JR, potentially indicating similar nutrient or grazing controls on both reefs. These picocyanobacteria are some of the most important primary producers in reef seawater. They are directly and indirectly grazed by single-celled eukaryotic heterotrophs, mixotrophic plankton, and reef organisms like corals and sponge. Reef seawater from JR had higher microbial alpha diversity and smaller beta diversity than seawater from CAN and FK. There was also a negative relationship between microbial alpha diversity and heterotrophic bacterial abundance between JR and FK, indicating a potential trade-off between community alpha diversity and biomass across the different reef-systems. The consistent supply of oligotrophic seawater from the Caribbean current to JR forereefs likely enhances niche partitioning within microbial communities and leads to higher alpha diversity. The hydrodynamic regime likely contributes to the increased microbial community similarity across this reef-system through mixing processes. On the opposite end of the spectrum, in more disturbed and/or nutrient-rich environments within CAN and FK, microbial alpha diversity tends to be lower, or the beta diversity is higher and more variable. The latter suggests that disturbances on these reefs favour active growth of fewer dominant microorganisms that outcompete other cells within the population for resources.

Additionally, genes indicative of photosynthesis and nitrogen metabolism were enriched in JR compared to FK, indicating the importance of photosynthesis and nitrogen acquisition in oligotrophic waters. Fewer genes were significantly enriched in JR than FK, suggesting a higher degree of functional redundancy and homogeneity across JR's more taxonomically diverse microbial communities. Authors continue to debate on the links between microbial alpha diversity and functional diversity. Findings demonstrate that alpha diversity, in the context of microbial reef communities surveyed in JR, CAN, and FK, might be a noteworthy feature of protected reefs.

Corals, octocorals and sponges

As coral reefs as an ecosystem, stony corals and related species are better studied in JR. In 2006 and 2008, two new records of octocorals were added for Cuba (Hernández-Fernández & Varela, 2006; Varela, *et al.,* 2008). More recently, Cruz-Pérez *et al*., 2020 added two additional new records of scleractinian corals for JR. The mountainous star coral, *Orbicella faveolate,* exhibited genetic differentiation across Cuba (Ulmo-Díaz, *et al*., 2018). *O. faveolate* population at JR population shares a similar genetic background with its counterparts in Baracoa beach, Cayo Coco and Canarreos Archipelago. Differentiation occurs between the latter populations and the population of *O. faveolate* in Los Colorados Archipelago, suggesting complex connectivity patterns. We present additional information of stony corals in sub-sections II and V.

Hernández-Fernández *et al*. (2019a) suggested that the presence of diverse and abundant populations of sponges in JR indicates their importance to reef communities' ecology.

Long-spined sea urchin

Data pre-die off of long-spined sea urchin in Cuba is scarce, but it seems to be as abundant as anywhere else before vanishing in 1983 in the Caribbean. Jackson (1997) citing Henderson (1914) informed the abundance of this species in an unspecified Cuban site. In his words, Henderson (1914) narrated "We were then upon the inner edge of the main reef upon which any further progress would have been difficult on account of the rapidly increasing numbers of the long black-spined sea urchins, the diademas… the usual presence of the net [dredging] of the Diadema sea-urchin… During the hours of bright sunshine the diademas seek cover under the rocks… In the late afternoon… they issue forth en masse in search of food and probably continue their slow wanderings throughout the night. In localities where hiding places are few, such as upon sandy patches in or near a reef, the *diademas* are always more or less in evidence."

Long-spined sea urchins are still scarce in most Cuban sites but seems to be recovering in JR. Martín-Blanco *et al*. (2010) studied the abundance, distribution and size structure of *Diadema antillarum* in 22 reefs sites in JR. *D. antillarum'* abundance was higher at reef crests, with mean densities of 0.08-2.18 individuals/m^2. Populations at the reef slope reached a maximum of 0.13 individuals/m^2 at only one site and showed values up to three orders of magnitude lower than those from reef crests. Highest abundance occurred at the west margin of major channels between cays where larval recruitment seems to be favoured by local oceanographic features and facilitated by the abundance of *Echinometra lucunter*. The size-frequency distribution of *D. antillarum* indicates that recruitment began to be noticeable three years before September 2005, suggesting the depletion of these populations in the past and their recovery at the time of the study. Following the previous study, Martín-Blanco *et al*. (2011) assessed *Diadema antillarum* influence on algal community structure in JR. Algal community structure at reef slopes was dominated by macroalgae, especially *Dictyota*, *Lobophora* and *Halimeda*. Conversely, the most abundant macroalgae at reef crests were *Halimeda* and *Amphiroa*. Urchin densities were negatively and positively correlated with mean coverage of macroalgae and crustose coralline algae, respectively, when analyzing data pooled across all sites. However, this trend did not hold with data from separate habitats (especially reef crest). Differences in urchin density trends suggest that, along with historical fish biomass, shallow reef community structure is being shaped by the synergistic action of other factors (e.g., fish grazing) rather than the influence of *Diadema* alone. However, the authors observed clear signs of *Diadema* grazing at reef crests and decreased macroalgal cover according to 2001 data. The latter suggest that grazing intensity at reef crests increased at the same time that *Diadema* recruitment began to be noticeable. Furthermore, the excessive abundance of macroalgae at reef slopes and the scarcity of crustose coralline algae seems to be explained by the almost complete absence of *D. antillarum* at mid-depth reefs, where local densities of this urchin were predominantly low. Caballero-Aragón and Perera-Valderrama (2014) reported densities of *Diadema* using a similar method than the studies mentioned above. Their research suggested that the recovery of *Diadema* in JR is still ongoing. Authors reported average increases in *Diadema'* density of 2.6 times in reef crests (from 0.627 to 1.62 individuals/m^2) and 5.6 times in fore reefs (from 0.014 to 0.078 individuals/m^2).

Other invertebrates

Besides the long-spined sea urchin, most of the research on marine invertebrates have focused on species inventories. The discovery of new invertebrate species, including eight endemics, is reported in the work of Espinosa (1985), Espinosa and Ortea (1998a, b, c, 1999, 2018); Espinosa *et al*. (2017a, b) and Ortea and Espinosa (1998). Abreu & del Valle (1998) reported *Lytechinus williamsi* in JR (Chesher, 1969 (Echinodermata: Echinoidea)). Ibarzabal *et al*. (1999) listed 44 species of polychaetes, 62 mollusks, and 26 echinoderms in JR, further updating polychaetes in Ibarzabal (2001). Commercially important invertebrate species such as lobster, shrimps, sea cucumber, and Queen conch are very abundant in JR. Studies of those species are summarized on sub-sections III and IV.

Fishes

Besides the effects of protection on fish and movement patterns detailed in sub-sections iii and iv, most of the research on this group focused on building species inventories. Ecological studies of fish species in JR focused only on *Lutjanus vivanus* (Pozo & Espinosa, 1982) and *Lutjanus buccanella* (Espinosa & Pozo 1982; Pozo *et al*., 1983). Claro *et al*. (2000) reported the first expedition of a USA research vessel with Cuban and American scientists in decades at that time. The joint expedition reported 34 new records of marine fishes for the Cuban shelf. Most of the reported fish species were collected or observed on the upper batial in southern Cuba. Overall, researchers reported 476 fish specimens belonging to at least 110 species on 29 dives on board the submersible Johnson-Sea-Link II along Cuba's insular slope from 15 to 620 meters of depth. Four new fish species records were found at the survey station 3050, located south of Cayo Anclitas, JR. Claro *et al*. (2001) added two new fish species records for Cuba from JR.

Two fish inventories were built for JR. The first inventory, by Pina-Amargós *et al*. (2007) found 251 fish species. The best-represented families of fishes are Serranidae, Carangidae, Haemulidae, Labridae and Scaridae. High abundance of large-size fishes of Serranidae, Lutjanidae, Sphyraenidae, Carangidae and sharks are often seen at JR. The second inventory constituted an update by Pina-Amargós *et al*. (2012a), reaching 283 fish species. In building both inventories, it was noteworthy the role of mangroves as nursery habitat for groupers. The latter was evidenced by the presence of juveniles of *Epinephelus itajara* (Lichtenstein, 1822), *Epinephelus striatus* (Bloch, 1792) and *Mycteroperca bonaci* (Poey, 1860) in mangroves. High frequency of the invasive exotic species *Pterois volitans* (Linnaeus, 1758) was also remarkable. JR hosts 25% of the Cuban ichthyofauna, including 26% of the strictly marine fish, 22% of Chondrichthyes, and 27% of the Actinopterygii.

There is only one recent publication about spawning aggregation sites in Cuba (Claro & Lindeman, 2003). This study includes one spawning aggregation site located in the fore reef of Cayo Bretón, JR, where two species of snapper (cubera and dog) and two species of grouper (yellowfin and black) spawn. Presumably there are more spawning aggregation sites in JR and around Cuba. There is a mention of spawning aggregation site of Goliath grouper in JR (Perera-Valderrama *et al.* 2018).

Fish information has been instrumental in informing the management of JRNP, including patrolling design and tourism management (SCUBA diving, snorkelling and catch and release fly fishing).

Lionfish

A few non-native species occur in JR; these include rats, mice, Australian pine (*Casuarina equisetifolia*), coconut palm (*Cocos nucifera*), and lionfish. Rats and mice are abundant but Australian pine, and coconut palm consist only in a few specimens. Of these non-native species, the lionfish is the only studied in JR. Few issues have brought more attention in the last decade or so to the western Atlantic than the lionfish invasion. A Caribbean-scale study found no relationship between lionfish density or biomass with the density or biomass of native predators (Hackerott, *et al.*, 2013). However, lionfish densities were significantly lower on windward sites, potentially because of habitat preferences. Lionfish densities were also lower in marine protected areas, most likely because of reserve managers' ongoing removal efforts. This study included JR data, showing several sites with lionfish densities of zero individuals per 100 m^2. Average lionfish density was 1.5 individuals per 100 m^2, similar to densities found in the Mesoamerican Barrier Reef. However, the authors did not survey sites representing the gradient of native predators and lionfish control efforts in JR. To date, Hackerott *et al.* (2013) study is controversial and have raised several critics. The latter made the authors re-examine their work taking into account several covariates that may affect lionfish and native fish abundance, including, among others, proxies for fishing pressure and habitat structural complexity. Valdivia *et al.* (2014) arrived to the same conclusions of Hackerott *et al.* (2013), suggesting that lionfish abundance was mainly controlled by several physical characteristics of the survey site, and possibly by lionfish culling instead of being regulated by native predator biomass. Preliminary results of the expedition on mesophotic coral ecosystems showed that lionfish were observed at most survey sites, but abundances were low compared to other Caribbean regions (Reed, *et al.*, 2018).

Marine turtles

Jackson (1997) cites Andres Bernaldez (1988) writing about Columbus' 2nd voyage to the Americas in 1494, when reaching southeastern Cuba where JR is located: "But in those twenty leagues, they saw very many more (marine turtles), for the sea was thick with them, and they were of the very largest, so numerous that it seemed that the ships would run aground on them and were as if bathing in them". Three centuries later, marine turtles and other megavertebrates were decimated in the central and northern Caribbean, and, by 1990 elsewhere (Jackson, 1997). The loss of megavertebrates had a dramatic effect on species and ecosystems. It severely reduced and qualitatively changed the grazing and excavation of seagrasses, predation on sponges, provoked productivity loss to adjacent ecosystems, and altered food chains' structure.

Moncada-Gavilán *et al.* (2011a) stated that Jardines de la Reina hosts 5 % of green turtle nests (up to 150 nests, see Fig. 2 at Gavilán, *et al.*, 2011a), 4 % of loggerhead turtle nests (up to 20 nests, see Fig. 3 at Gavilán, *et al.*, 2011a) and 69 % of hawksbill sea turtle nests (up to 250 nests, see Fig. 4 at Gavilán, *et al.*, 2011a) in Cuba. Moncada-Gavilán (2014) reported nesting of leatherback turtle in JR at Cayo Caguama, and sightings around Caguama and Cachiboca cays and the western Golfo de Ana María. The importance of JR for green turtle nesting is also stressed by Azanza-Ricardo *et al.* (2013) and Moncada-Gavilán *et al.* (2006).

Among marine turtles species nesting in JR, the hawksbill sea turtle (*Eretmochelys imbricata*) constituted the most studied marine turtle species.

Research includes *E. imbricata* reproduction studies in the Cuban archipelago by examining the gonads, and reproductive status of sampled individuals (n=8711, 1983-95) collected during the country's historical turtle fishery (Moncada-Gavilán, *et al*., 1999). The smallest female with oviductal eggs measured 51-55 cm straight-carapace-length (SCL). 50 % of females appeared mature by 76-80 cm SCL, and 100 % when reaching 80 cm SCL. The smallest female observed nesting measured 58.5 cm SCL, and the largest 83 cm SCL. Males appear to reach maturity around 68 cm. SCL. Females containing oviductal eggs were recorded in 11 months of the year (not in March) with two peaks (September and December). *E. imbricata* main nesting areas are in southeastern Cuba, particularly around JR, were most survey work has been conducted. In JR the maximum number of nests found in a single nesting season was 251 nests on 26 beaches in 1994-95. Nesting occurred almost exclusively between 20:30 and 05:00 hours, particularly on dark nights without bright moonlight. The mean distance from the high tide mark to a nest was 7.6 m (SE = 4.9, range = 1- 25 m). Mean clutch size was 135.2 ± 0.71 eggs per nest. An average of 69.2 % of eggs produced emerging hatchlings. About 85 % of nests were laid under vegetation. JR is estimated to contribute to 65 % of the annual E. imbricata nesting in Cuba. At the time of the study, 47 nesting beaches had been located on various cays. Nesting, nests, eggs and hatchlings are similar to those described elsewhere, although nest predation levels were generally lower in Cuba than in the Americas. The full extent of hawksbill nesting in Cuba is unknown, but estimations reach the range of 1700-3400 nests annually.

Moncada-Gavilán *et al*. (2010) showed monitoring of hawksbill turtle nesting at JR from 1990s to 2007, updating the study of Moncada-Gavilán *et al*. (1999). Hawksbill turtle exhibited solitary nesting behaviour. Of 84 nesting females tagged between 1997 and 2007, 29 nesting females were observed multiple times. The average internesting period reported was 17.4 days (SD = ± 4.3). Remigration occurs mainly every 2-3 years. Nest-site fidelity appears to be strong. Mean nesting frequency was 1.45 ± 0.07 nests/season, lower than that reported for other areas, most likely due to underreporting of nesting events due to staff limitations. Most nesting occurs from September to January, with a peak between October and December (similar to reports of Moncada-Gavilán *et al*., 1999). The latter is unique among hawksbills turtles in the Caribbean. Nesting females showed a mean SCL of 82.8 ± 5.8 cm (similar to reports of Moncada-Gavilán, *et al*., 1999). The smallest nesting females in JR are much smaller than those observed in other regions. The mean clutch size was 137.6 eggs (range 22-231 eggs) (similar to reports of Moncada-Gavilán. *et al*., 1999). Authors estimate that the annual average number of nest-laid per year in JR is 300.

Medina-Cruz *et al*. (2010) built upon Moncada-Gavilán *et al*. (1999) to study *E. imbricata* nest site selection and its influence on hatching success in JR. Authors found that hawksbill turtles prefer to nest in vegetation rather than areas lacking vegetation or near the high-tide line. However, hatching success on vegetated versus non-vegetated areas was statistically different only in two of the nine surveyed beaches. In those cases, the highest hatching success occurred in vegetated nesting areas.

Azanza-Ricardo *et al*. (2015) assessed sea turtle monitoring effectiveness across Cuba. Nighttime systematic monitoring only occurs in one nesting site, while sporadic monitoring with nest verification is the most used approach along nesting beaches in the country (including JR). The proportion of the nesting season covered by staff is low in most of the nesting beaches in Cuba, and for all the three nesting sea turtle species (*Chelonia mydas*, *Caretta caretta* and *Eretmochelys imbricata*). Monitoring efforts did not prove higher for the critically endangered *E. imbricata* nor in JR, where main nesting sites for this species occur. Authors found significant differences between systematic and sporadic monitoring, which has important implications for understanding sea turtle nesting behaviour, as the capacity to detect false and true crawls essentially depends on the monitoring frequency. Low detection capacity in sporadic monitoring hampered the development of efficiency assessments in all the nesting beaches. Authors argue for the need for new monitoring strategies to accurately monitor sea turtle species and build statistically robust models that estimate and follow nesting numbers across time and nesting sites, including at JR.

Sea turtle information constitutes a critical element of JRMP management plan, and all scientific information produced is used to inform management, especially the design of patrolling efforts in the park.

We further explore sea turtle information on subsection IV, and expand research into potential climate change effects on sea turtle nesting in sub-section V.

Other marine megafauna

Megafauna such as the American crocodile (*Crocodylus acutus*), the Antillean manatee (*Trichechus manatus*), and several species of dolphins and whales occur in JR. American crocodiles and dolphins are relatively abundant in JR. Baleen whales and sperm whales have been seen and photographed in JR. Antillean manatees have been reported in the Golfo de Ana María (Estrada & Ferrer 1993 unpublished, cited by Álvarez – Alemán, *et al*., 2018) and JR (no scientific evidence). To the best of our knowledge, there are no peer-reviewed publications on these species in JR.

III. Connectivity

The understanding of ecological connectivity is critical to inform conservation and management. Several ecological connectivity studies involved JR. Currently, there are three main frameworks to assess connectivity in Cuba. The first one consists of oceanography. The second one focuses on species and ecosystem modelling. The third one involves genetic analyses. This sub-section discusses existing literature on connectivity in JR based on different approaches, including discussions on nutrients, egg/larval/plankton, adult movement, and oceanography.

Nutrients

Weber *et al*. (2019b) assessed the microbial signature in 25 protected and impacted Northern Caribbean reefs, including JR. Authors discussed some of their results considering connectivity between offshore forereefs and patch reefs within the Golfo de Ana María (GAM). Differences in hydrodynamics between offshore forereefs and patch reefs within GAM likely influenced nutrient dynamics across JR. The forereefs are flushed with pelagic, oligotrophic seawater carried by the Caribbean current. In contrast, the patch reefs within GAM are influenced by productive mangrove forests and seagrass meadows that have less contact with the open ocean. However, authors missed the presumably high contribution of nutrients from the extensive area of bare muddy bottoms covering GAM. Entrainment of nutrients from these productive ecosystems within the gulf and tidal flushing of these nutrients onto the forereefs are likely essential processes that influence primary productivity, microbial diversity and metabolism, and grazing of cells by the reef community in JR. Weber *et al*. (2019b) find that most macronutrient concentrations were low or barely detectable in JR, and statistically lower than those of Canarreos and Florida Keys. Moreover, JR macronutrient concentrations were similar to concentrations measured in other oligotrophic systems, including the Sargasso Sea, the North Subtropical Pacific Gyre, the Red Sea, and other Caribbean and Pacific reefs. The latter suggests rapid turnover of macronutrient pools by microorganisms.

Organic carbon concentrations in JR were similar to concentrations reported from a reef-crest in Grand Cayman. Hernández-Fernández *et al*. (2019a) classified JR as an oligotrophic system based on nutrient and chlorophyll data assessments. Hernández-Fernández *et al*. (2019a) also discussed some of their results, taking into account connectivity at the archipelago scale. Nutrient dynamics in the JR reef system are likely influenced by several lagoons located in the adjacent cays. The three processes involved in nutrient dynamics include organic matter production by the vegetation (fundamentally mangrove trees), the regeneration of nutrient in the muddy sediments, and the tidal export of nutrients and organic matter to the open water through channels.

Egg/larval/plankton

Paris *et al*. (2005) modelled larval dispersal of snapper (Pisces: Lutjanidae) on spawning aggregation sites around Cuba (Paris *et al*., 2005). Results suggest that considerable self-recruitment levels (ca. 37 to 80% total recruitment) play a role in structuring Cuban snapper populations, particularly those from the southern and north-central regions. The spawning aggregation of JR' Cayo Bretón contributed to the recruitment of 38 % of lane snapper and 46 % of the complex cubera-grey-dog snappers of the entire country (see Fig. 3 at Paris, *et al*., 2005). Spawning aggregations in southeastern Cuba, including JR, contributed to the recruitment of 43 % of lane snapper, 14 % of mutton snapper, and 56 % of cubera-grey-dog snappers in the country. Cuba allocates amounts of the total snappers produced to satisfy local demand and exports. Lane snapper's allocation includes 5/6 within Cuba, and 1/6 export to Cayman, Hispaniola, Nicaragua, Jamaica and Bahamas. Mutton snapper allocation accounts for 3/8 within Cuba, and 5/8 export to the same regions as lane snappers. Cubera-grey-dog snappers allocation includes 3/4 within Cuba, and 1/4 export to the same regions as lane and mutton snappers (see Fig. 2, Fig. 5 and Table 2 at Paris, *et al*., 2005).

Using a similar model to Paris *et al*. (2005) but at a broader scale, Cowen *et al*. (2006) found that southeastern Cuba is one of the Caribbean's 22 subregions of coral reef fish larvae settlement (see Fig. 1 at Cowen *et al*., 2006). Southeastern Cuba showed a high self-recruitment. It exported and imported larvae to and from 12 Caribbean subregions through survival rate turned only relevant for subregions around Cuba (see Fig. 2 & 3 at Cowen *et al*. 2006), particularly southwestern Cuba (see Fig. 4 at Cowen *et al*., 2006). Subregions included Colombia, Honduras, Belize, Mexico, Florida, Bahamas, Turk and Caicos, Northwestern Cuba, Southwestern Cuba, Cayman Islands, Jamaica and west Hispaniola.

Later on, Kough *et al*. (2016) revisited Cowen *et al*. (2006) results. Biophysical simulations suggested that most larvae produced from snapper spawning aggregations are retained on-island, often within the region where they were spawned, except for an aggregation in northwestern Cuba. For southeastern Cuba, mean Cuban settlement was 52% (2 to 99%), mean Jamaican settlement was 6% (0 to 51%), and mean local retention was 50% (2 to 99%). Besides Jamaica, southeastern Cuba supplied larvae to Cayman Islands, Hispaniola (see Fig. 2 at Kough, *et al*., 2016), and The Bahamas (see Fig. 5 at Kough, *et al*., 2016). Southeastern Cuba exported and imported larvae to and from southwestern Cuba (see Fig 3 at Kough, *et al*., 2016) and northwestern/north central Cuba (see Fig. 7 at Kough, *et al*., 2016). Schill *et al*. (2015) explicitly integrated coral reef connectivity models into the design of regional-scale marine protected area networks. They found that JR has a high coral reef area (see Fig. 1 at Schill, *et al*., 2015) that is strongly connected with the broader southeastern Cuban region (see Figure 2 at Schill, *et al*., 2015). Contrarily to previous findings, JR did not seem to have a high retention rate of larvae, which is crucial to maintaining connectivity among marine protected area networks (see Figures 3 & 5 at Schill, *et al*., 2015) (see Figure 7 at Schill, *et al*., 2015). Besides, a study of lobster larvae dispersal showed that southeastern Cuba received 6 % of the larvae produced in southwestern Cuba, and 2 % of the larvae produced in Grand Cayman (Gutierrez, *et al*., 2012).

Genetic connectivity has been studied using single and multispecies assessments. Castellanos-Gell *et al*. (2012) used genetic markers to study population structure and gene flow in the surgeonfish, *Acanthurus bahianus* (currently *A. tractus*). From 149 individuals collected at five localities around Cuba, including Cayo Bretón in JR, most individuals exhibited haplotypes identical or closely related to those previously described for the Caribbean. However, south Atlantic lineage haplotypes were also found in all surveyed localities with frequencies around 5 %. This finding suggests that *A. bahianus* dispersed in recent times across the Amazon-Orinoco barrier, probably because environmental perturbations triggered their dispersal.

Castellanos-Gell *et al*. (2016) conducted a multispecies assessment in bicolour damselfish *Stegastes partitus*, french grunt *Haemulon flavolineatum* and surgeonfish *Acanthurus tractus*. Researchers collected samples at five locations around Cuba, including Bretón Cay in JR. All three species showed high genetic diversity. Mismatch distribution analyses suggested past population expansion in all species, but at different times in each species. Genetic polymorphism in *H. flavolineatum* and *A. tractus* resulted homogeneous throughout the archipelago. Conversely, *S. partitus* revealed significant genetic structuring. Castellanos-Gell *et al*. (2016) suggest that genetic differentiation among *S. partitus* populations most likely results from the combined effects of egg-type and oceanic current patterns along the Cuban coast. Differentiation of *Stegastes partitus* was also significant between the southern localities, i.e., Bretón and Avalos cays. In contrast, no statistically significant difference between any localities was found in *H. flavolineatum* and *A. tractus*, indicating genetic homogeneity.

García-Machado *et al*. (2018) described patterns of population connectivity in Cuba's marine organisms, including penaeid shrimps, reef fishes, marine turtles, and bottlenose dolphins. Investigations conducted over the last 20 years indicate three general patterns of population structure across the Cuban coast: a north-south break (dolphin), an east-west split in the south (damselfishes), and local genetic differentiation (shrimps). Researchers argue that observed patterns result from differences and interactions among geography, oceanographic features, and species' life histories. In JR-GAM, intra and inter-regional connectivity is evidenced by interactions across the above mentioned forces, resulting in different outcomes according to the individual species or species group. For instance, several shrimp populations coexist inside JR-GAM mainly due to limited larval dispersal. JR damselfish populations differ from those in other Cuban regions, primarily because of limited dispersal. However, fish species with higher dispersal abilities such as grunts and surgeonfishes, populations from around Cuba are well connected.

Moreover, JR hawksbill sea turtle population is well connected with Cuba and broader Caribbean populations likely to interconnection between foraging and nesting populations. JR-GAM bottlenose dolphin population is similar to other regions on southeastern of Cuba but differ from those on southwestern and northern Cuba due to the island's size and dolphins foraging behaviour. The reported varying levels of connectivity for different species and multispecies group are crucial for sound management and conservation.

Adult movement

Due to their mobility and importance, fish movement patterns have been studied in JR. Most studies have focused on large piscivorous fishes, leaving a knowledge gap of medium and small-sized species such as benthophagous, planktivorous and herbivorous fish. The lack of information about herbivorous fish is of particular concern due to their vital role in maintaining coral reefs, mangroves and seagrasses. Pina-Amargós et al. (2008b) described emigration of some reef fishes, focusing on their movement from JRNP to fishing areas outside via mark-recapture. Studies covered movements by the black grouper (*Mycteroperca bonaci*), Nassau grouper (*Epinephelus striatus*), and hogfish (*Lachnlaimus maximus*). For most fish species, emigration was low or nonexistent, and movement was documented in only 25 % of all recaptures. Most movement occurred within the first 200 meters off the marine reserve boundaries. Fish movement among habitats typically occurred unidirectionally from the reef crest to the reef slope for the Goliath grouper (*Epinephelus itajara*), yellow jack (*Caranx bartholomaei*), cubera snapper (*Lutjanus cyanopterus*), nurse shark (*Ginglymostoma cirratum*), and hogfish. Less movement was documented from the reef slope to the reef crest for the tiger grouper (*Mycteroperca tigris*), cubera snapper, and mutton snapper (*Lutjanus analis*). Fish movement between habitats was always greater than movement within the same habitat for all studied species. Habitat discontinuities and reduction of habitat structural complexity seem to reduce movement of fishes.

Pina-Amargós and González-Sansón (2009a) conducted a detailed study on goliath grouper movement tagging five individuals in 2001 and tracking them until 2003. The study encompassed 541 underwater resightings by SCUBA diver instructors through the summer of 2002 at the tagging sites. No goliath grouper was resighted after July 2002 at JR diving sites. In February 2002, one individual was caught 36 km northeast of the tagging site. In August 2002, a second tagged goliath grouper was caught 77 km southeast of the tagging site, while in August 2003, two individuals were captured 168 km southeast of the tagging site. All recaptures took place outside JRNP boundaries. These findings emphasized the need for synergetic management approaches to conservation of fish, including protected areas, sustainable fisheries and alternative livelihoods. This study, Perera-Valderrama *et al.* 2018 and unpublished data, lead to the complete nation-wide ban of goliath grouper in Cuban waters in 2018 (Resolucion 178/2018 MINAL).

Sharks are abundant in JR and the main attraction of SCUBA divers (Figueredo-Martín, *et al*., 2010a). Despite the benefits sharks bring to JRNP, limited research has been published for these species group. In 2004, two whale sharks (*Rhincodon typus*) encountered in JR fitted with SPOTs (position only electronic tags) moved synchronously along the coast of Cuba, most likely following the schools of tuna. Later on, one of the observed whale sharks crossed the Cayman trench to the Mexican shores within the Mesoamerican Barrier Reef. The second individual moved to the eastern coast of Florida (Graham *et al*., 2007). A whale shark study in the wider Caribbean also supported the species' region-wide connectivity, and reported movement along the south coast of JR Archipelago between October and December (Hueter, *et al*., 2013).

Three female silky sharks (*Carcharhinus falciformis*) were tracked using satellite-linked tags to characterize their movement patterns and behaviour in JR (Hueter *et al*., 2018). Results from both archival and position-only tags suggested the sharks travelled <30 km from the tagging site during the month-long deployments. Depth and temperature ranges recorded for the two silky sharks were 0-640 m and 11.5-27.5 °C, respectively. Time-at-depth and temperature data revealed preferences for the upper-mixed layer (down to 150 m) and a temperature range of 24-27 °C. A diel vertical movement pattern was observed with silky sharks, spending more time at depth during the day than at night. Plasticity of vertical habitat utilization was noted with occasional forays to depths exceeding 550 m during day and night. Daytime forays to surface waters were also observed and were most common during the morning hours between 09:00 and 11:00 AM, possibly due to bait provided to attract sharks to recreational divers. Research in silky sharks has been used to advise shark-encounter ecotourism activities in JRNP.

Moncada-Gavilán *et al.* (2006) provided information about movement patterns of green sea turtles (*Chelonia mydas*) in Cuba and adjacent Caribbean waters inferred from flipper tag recaptures. Of the 742 turtles tagged in Cuba's fishing areas, nesting beaches, and head-start facilities, 5.5 % were recaptured, mostly outside Cuban waters. Most of the tagged *C. mydas* (76.9 %) in Cuba were recaptured off Nicaragua's coast. *C. mydas* tagged elsewhere and recaptured in Cuba included head-started juveniles from Grand Cayman (45 % of the total recaptures), Mexico (2.3 %) and, Florida (1.8 %); wild juveniles from the Bahamas (14.1 %), Bermuda (5.4 %), and Florida (1.5 %); and adults from Tortuguero, Costa Rica (26 %), Florida (1.3 %), Mexico (1 %), Venezuela (1.3 %), and US Virgin Islands (0.3 %). Recapture of tags placed at sites north of Cuba (Bermuda and the Bahamas) clustered in the northeast region of Cuba. In contrast, those from the south (Grand Cayman) were recaptured in southern areas in Cuba. Tag recaptures from Tortuguero, Costa Rica, were concentrated in the southeast and westward regions of Cuba. Sea turtles from the Bahamas, Grand Cayman, and Bermuda showed the highest recapture rates in Cuban habitats, constituting 3.2%, 1.9%, and 1.0 % of the total number of tags applied, respectively. Sea turtle movement evidence for a broad range of populations and across life stages underscores the region-wide significance of Cuban sites as critical habitats (e.g., nesting) or migratory corridors. Sea turtle movement studies cited above include data gathered at JR.

Moncada-Gavilán *et al.* (1998) investigated movement patterns of hawksbill sea turtles in JR. Fifteen hawksbills tagged in JR were recaptured in the same region showing high fidelity to JR archipelago. Average movement was ≤10 to 26 km; and maximum was 132 km (See Table A8.1 and Figura A8.2 at Moncada-Gavilán, *et al.*, 1998). Stable isotopes studies suggested that hawksbill sea turtles in Cuba are less dependent on animal protein and possess a stronger link to coral reefs than elsewhere

Oceanography

The most complete oceanographical studies that include JR are around 50 years old (Emilsson & Tápanes, 1971; Lluis Riera, 1977; Siam & Hernández, 1981), and 20 years old (González-De Zayas, *et al.*, 2006 with data of 1998-1999). Studies suggested that JR's oceanographical conditions are mainly influenced by the Caribbean Sea, with limited land-based influence year around. More recently, Chollett *et al.* (2012), Hernández-Fernández *et al.* (2019a) and Weber *et al.* (2019b) provided a comprehensive picture of the physicochemical environment of JR. Chollett *et al.* (2012) classified JR into a group defined as offshore waters of the inner-Caribbean (see Table 2 at Chollett *et al.*, 2012). The group is characterized by a mixture of relatively warm waters with high salinity and high-water clarity. However, in a more detailed analysis, researchers included JR in one of the 16 physicochemical provinces of the Caribbean (see Fig. 4 and Table 1 at Chollett *et al.*, 2012). Under this classification, JR belongs to a group with lower temperature, higher water clarity and lower salinity than GAM. Besides, JR experience a medium chronic wave stress given by wave exposure with values around 5 in a scale of 9, and a medium acute wave stress given by the frequency of occurrence of hurricanes Category 1–5 in 157 yr period (1851–2008), with approximated 10 hurricanes of a maximum of 30 (see Figure 6 at Chollett, *et al.*, 2012).

IV. Environmental goods and services

This sub-section includes information on fishing, tourism and local livelihoods. Management authorities and other stakeholders have widely used information summarized in this section in JRNP management plan, and used it to guide patrolling design efforts, plan responsible tourism, and bolster community involvement.

Fishing

JR was for many years a significant fishing ground in Cuba. Before its protection, it followed a similar pattern of decrease in fish landings than most Cuban finfish fisheries (Claro, *et al*., 2009). Lane snapper spawning aggregations were intensively fished in JR, and contributed 35-40% of the national catch of yellowtail snapper (Claro, *et al*., 2009). One of the two set nets located in Pasa de Boca Grande, JR, caught 48 tons of fish in 1990, mainly spawners' snappers and mackerels (Dalmendray & Valdes, 1994-1995). Pina-Amargós *et al*. (2009b) assessed the effects of fishing effort reduction after establishing JRMR. The declaration of the marine reserve reduced fishing efforts inside JRMR by about two thirds. One-third of the original total effort was eliminated, but the other third was relocated to the reserve's surrounding zones. As a result, total landings from the archipelago area were reduced by a third. The homogeneous distribution of finfish catches through JR archipelago before the declaration of the marine reserve and the strong relationship between catch and abundance of target species after it supports the hypothesis of positive effects of the JRMR on conserving the fisheries resources.

However, fishing still takes place in the surroundings of JRNP. Puga *et al*. (2018) estimated that the majority of catch of Cuba now derives from the southeast zone, where JR is located, accounting for 44 % of the total national catch. High contemporary catch and catch-per-unit-effort in the southeast zone might be attributable to the spillover effects of JRNP. Gerhartz-Muro *et al*. (2018) evaluated the framework for national marine environmental policies in Cuba and stressed the highly valuable shrimp and lobster fisheries. Although shrimp fisheries occur in the Golfo de Ana María, northern JR encompass shrimp spawning grounds indispensable for shrimp's life cycle (Pérez *et al*., 1984; Guitart *et al*., 1985).

Southeastern Cuba, including JR, is the second-largest contributor to lobster landings in Cuba (Alzugaray & Puga, 2010). However, landings have decreased from around 3,000 tonnes in the 1980s to less than 800 tonnes in 2000s. Alzugaray & Puga (2010) showed that lobster' population size, biomass, and recruitment have significantly decreased. Even under reduced fishing effort and the expansion of the close season, the lobster fishery shows no recovery sign. The latter is likely due to environmental changes, although illegal fishing could not be ruled out.

Queen conch fishery occurs around JRNP by Casilda and Niquero fishing ports, contributing to a quarter of the total national catch (Formoso, 2013; Formoso, 2015). Sea cucumber and elasmobranch fisheries are also important in the region. The southern coast of the province of Camagüey has the highest abundances of sea cucumber in Cuban waters, accounting for 36 %-70 % of the total national landings. Such high percentage might result from spillover effects from JRNP (Hernández-Betancourt *et al*., 2015; Hernández-Betancourt *et al*., 2018). However, spillover from JRNP has been proved only experimentally on coral reef fishes (Pina-Amargós, *et al*., 2010). Between 2000-2014 fishery's zone A, where JR is located, contributed an average of 40 % of shark landings and an average of 45 % of rays' landings of the total Cuban landings (PAN-Tiburones, 2015). The intense fishing pressure in the region might be provoking ecosystem damage. Armenteros *et al*. (2018) find that macrobenthos density was lowest in GAM and attributed this trend to damaging effects of historical fisheries. Not surprisingly, due to the high abundance and large size of fishes and other highly valuable species, JRNP is susceptible to poaching. Pina-Amargós *et al*. (2009b) estimated poaching in the marine reserve at a total of 9 tonnes of fish per year. Figueredo-Martín *et al*. (2014b) reported about 50 kg/year of marine turtle meat seized, indicating that the value would most likely be an underestimation of the illegal take.

Ecotourism

About 30 % of the world's reefs are of value for the tourism sector, with a total value estimated at nearly US$36 billion, or over 9 % of all coastal tourism value in the world's coral reef countries (Spalding, *et al*., 2017). Since the 1990s, main tourism activities in JRNP have been SCUBA diving and recreational catch-and-release fly fishing (Figueredo-Martín, *et al*., 2010a, b; Perera-Valderrama, *et al*., 2018). Figueredo-Martín *et al*. (2010a) and (2010b) assessed both activities in JRNP. Divers and anglers rated JRNP from “good” to “excellent”. Reasons listed in diver and angles' surveys included enjoying their passions at JRNP and finding better environmental conditions in current than in previous visits. JRNP is regarded as one of the best SCUBA diving sites compared with 50 prime diving sites worldwide. The majority of divers and anglers are willing and eager to return. In the case of SCUBA divers, sharks and rays are among the top five attractions. This information was used in the first-ever Cuban Action Plan for the conservation of elasmobranch (PAN-Tiburones, 2015). Information from shark-ecotourism helped build the case for sharks' high value in the ecotourism industry. JR was part of an assessment looking at the global value and distribution of coral reef tourism (Spalding, *et al*., 2017). Figures showed that the economic value JR coral reef tourism ranks from “high” to “very high” ($356,000 km^{-2} yr^{-1}) (Spalding, *et al*., 2017) (see Figure 2 at Spalding, *et al*., 2017). However, poorly managed tourism could also lead to ecosystem degradation. Hernández-Fernández *et al*. (2016b) assessed SCUBA diving and carrying capacity at JRNP diving sites. The study found that, despite evidence of unwilling physical interactions of SCUBA divers with the reef, JR coral reefs showed no signs of deterioration related to SCUBA diving. They also find that carrying capacity in JRNP ranged from 15 to 35 divers/site/day, higher than the fixed legal figure in Cuba (Resolucion 48/2014 MINTUR). Graham and Pina-Amargós (2007) attributed JRNP's tourism and conservation success to the effective implementation of a public-private partnership. Under this model, patrolling and monitoring efforts are shared between management authorities and a private catch and release fly-fishing and diving company with exclusive rights to operate in JRNP. Increased patrolling guarantees high compliance with fisheries regulations in JRNP, where all commercial finfishing is illegal. Thus, tourism assists the government in fisheries enforcement and further supports research by providing the logistical support for long-term continuous monitoring in JRNP. These activities help protect the natural resources upon which tourism depends, and staff conservation ethos is concomitantly high. Several additional publications exist expanding on this conservation model and tourism design (Figueredo-Martín, *et al*., 2015a) and monitoring (Figueredo-Martín, *et al*., 2015b) for JRNP and the entire country.

Local livelihoods

Several attempts have been made to show economic benefits derived from JRNP. Figueredo-Martín *et al*. (2014b) stated that 40 % of JR tourism employees come from local communities. Figueredo-Martín *et al*. (2014a) showed that the establishment of JRNP generated better outcomes than the previous JRMR as the park' Total Economic Value and Cost-Benefit were around 4,000,000 USD yr^{-1} higher. Furthermore, Net Current Value was 33,800,000 USD yr^{-1} higher in the JRNP than in the JRMR. This study found that even when benefits derived from non-use value were higher than the use-value in both cases, direct benefits of JRNP are higher than indirect ones, meaning that more money tributes to the economy. Figueredo-Martín *et al*. (2013) showed that environmental goods and services provided by JRNP justify its management expenses. Benefits of the park to the Cuban economy ranged from 12,432,690 and 16,598,000 Cuban Pesos yr^{-1} while conservation cost only represented 8 % of those benefits. Compared to surrounding areas open to extractive uses such as GAM, Figueredo-Martín *et al*. (2014a) found that JR estimated economic value is higher in more than 13,000,000 Cuban Pesos yr^{-1} than the GAM. Thus, JRNP conservation model shows the success of sustainable economic activities that preserve ecosystems and the valuable environmental good and services they provide in JRNP.

V. Effects of protection

JRNP has been claimed as the best example of thriving marine protected area in Cuba. Most of the evidence of JR positive effects to marine conservation is compiled in this section, but additional evidence is included in other sections such as *Environmental Goods and Services*. Research on the effects of JR on marine protection mainly focused on fishes, and at a minor extent, microorganisms, stony corals, marine turtles, and another marine megafauna. This section addresses JR role in the conservation of megafauna, fishes, stony corals, and microorganisms. We include a closing remark for this section. Information on the subject supported educational and outreach activities to portray the effects of protecting nature and people.

Megafauna

Azanza-Ricardo *et al*. (2018) assessed the achievements and challenges of marine turtle conservation in Cuba and found that JR is the only region in the country where all three marine turtle species show positive nesting trends. Perera-Valderrama *et al*. (2018) reported that scientists detected the first spawning aggregation site of goliath grouper in Cuba, just outside JRNP. Goliath groupers are more abundant inside the JRNP than outside. As a result of research by Perera-Valderrama *et al*. (2018), Pina-Amargós and González-Sansón (2009) and unpublished data, fishing of goliath grouper was permanently banned in Cuba in 2018 (Resolucion 178/2018 MINAL). Perera-Valderrama *et al*. (2018) also reported that sharks being 2.5-18 times more abundant inside JRNP than outside. Consistently higher abundances of large fishes and sharks result from the effective patrolling and protection of JRNP in a cooperative and multi-stakeholder approach.

Fishes

Most studies showing the effects of protection in JR focused on reef fish assemblages (Newman, *et al*., 2006; Knowlton & Jackson, 2008; Pina-Amargós, *et al*., 2010; Hackerott, *et al*., 2013, Pina-Amargós, *et al*., 2014a, b; Jackson, *et al*., 2014, Valdivia, *et al*., 2017). We summarize density and biomass figures from several of those studies in Table 1.

Studies show that fish density and biomass seems to be increasing in JRNP. However, only Pina-Amargós *et al*. (2014a) and (2014b) used the same survey methodology to assess fish density and biomass trends. Comparisons from 2004-2005 and 2010-2013 showed that there is a 1.6 times increase on average density of large fish, 1.2-1.4 times increase on average biomass of predators/piscivore species (260/208-300/208), and 1.6 times increase on average biomass of all fish species (445/275). However, comparisons between average biomass of large fish/piscivore/predators from Pina-Amargós *et al*. (2014b) and Knowlton & Jackson (2008) showed 3.4 times decrease through time (208/61). Moreover, when compared with studies from the same period (Hackerot *et al*., 2013), a difference of up to 4.9 times (300/61) is found. These differences might be due to several factors. Observers, sampling size unit, and species sampled are different among studies but not enough to explain these big differences. Differences in sampling sites seem to be the most plausible cause for differences encountered among studies. Pina-Amargós *et al*. (2014b) surveyed the entire JR reef track and avoided SCUBA diving sites where provisioning of food to fish changes fish behaviour, whereas other research surveyed only SCUBA diving sites due to logistical constraints.

Newman *et al*. (2006) assessed Caribbean coral reef communities' structure across a large gradient of fish biomass. They found a range in fish abundances

Table 1. Density and biomass of selected species of fish in JR. All figures standardized to individuals/1000 m^2 (density) and kg/1000 m^2 (biomass). Figures rounded to the unit. For Fish species surveyed check references. Blank cells mean no data collected/available.

Source	Variable	2004-2005	2010	2011	2012	2013
Pina-Amargós *et al.* (2014a, b)	Average Density large fish	25	41	44	40	38
Pina-Amargós *et al.* (2014b)	Average Biomass large fish		57	65	59	63
Knowlton and Jackson (2008) from Newman *et al.* (2006) data	Average Biomass All fishes	275				
Knowlton and Jackson 2008 from Newman *et al.* (2006) data	Average Biomass piscivore	208				
Hackerot *et al.* (2013)	Average Biomass predators			300		
Hackerot *et al.* (2013)	Highest Biomass predators			517		
Valdivia *et al.* (2017)	Highest Biomass All fishes			445		
Valdivia *et al.* (2017)	Highest Biomass predators			260		

from 14 to 593 g/m^2, exceeding any previously reported gradient for coral reefs. Newman *et al.* (2006) (in their Figure 2) showed that three sites in JR are among the top four sites in terms of total fish biomass out of 27 sites surveyed in the Caribbean. The latter included biomass of all fishes and carnivore fishes in 15 m coral reefs. Increased fish biomass correlated with an increased proportion of apex predators, abundant only inside large marine reserves such as JRMR. Increased herbivorous fish biomass correlated with a decrease in fleshy algal biomass.

Pina-Amargós *et al.* (2010) conducted an experiment of fish spillover in JR. Density of fish was experimentally manipulated on the unprotected side of the park boundary. Before experimental manipulation, fish density was similar in experimental and control sites, and on both sides of the boundaries. After manipulation, fish density in the experimental site's unprotected side declined dramatically, and a strong gradient was established through the boundary. One month later, this forced gradient disappeared, returning to the initial condition of the study. The latter evidenced the spillover effect of JR. The mean-distance travelled by fish increased 1.5 times (mean from below 200 m to more than 300 m). The mean emigration rate doubled, and the immigration rate decreased, allowing density levels to recover after manipulation. These are important findings, but their experimental nature limits inferences about spillover effects under, more complex, natural conditions.

Hackerott *et al.* (2013) tested the hypothesis of biotic resistance between lionfish —native predators in the Caribbean. Total native predator biomass was significantly higher in the 17 marine reserves assessed and ranged widely. The highest predatory fish biomass value was found in JRNP and was comparable to some isolated reefs in the central Pacific.

Pina-Amargós *et al.* (2014a) showed evidence of protection of targeted reef fish in JRNP. Researchers gathered data in the 2004-2005 period on reef crests and fore reefs. Densities of the ten most frequent, highly targeted, and relatively large fish species showed a significant variability across the archipelago for both reef habitats, and differences depended on the month of surveys (see Table 2 at Pina-Amargós *et al*., 2014a). These ten species showed a tendency towards higher abundance inside the reserve in both reef habitats for most months during the study (see Figures 2 and 4 at Pina-Amargós, *et al*., 2014a). Moreover, average fish densities pooled by protection level showed that five out of these ten species were at least two-fold significantly higher inside than outside the reserve at one or both reef habitats (see Figures 3 at Pina-Amargós, *et al*., 2014a). Supporting evidence from previously published studies in the area indicated that habitat complexity and major benthic communities were similar inside and outside the reserve (Pina-Amargós, *et al*., 2008a), while fishing pressure appeared to be homogeneous across the archipelago before reserve establishment (Pina-Amargós, *et al*., 2009b), leaving the effective protection from fishing, as the most plausible explanation for the patterns observed.

Pina-Amargós *et al*. (2014b) showed survey results of large and commercially important fish density and biomass along the reef track of southern Cuba on reef crest and fore reef habitats from 2010 to 2013. Surveys were carried out using the same methodology, allowing meaningful spatial and temporal comparisons. Fish density and biomass in JRNP both resulted higher than those reported years before (though no statistical difference) on both habitats (see tables 4 and 5 at Pina-Amargós, *et al*., 2014b). JRNP was the region with the highest density and biomass on both habitats than ten MPAs in southern Cuba (see Figure 13 at Pina-Amargós, *et al*., 2014b). JR protected reef crests (inside the marine reserve) showed two times higher density and 1.3 times higher biomass than unprotected ones. Conversely, fish density was 1.8 times higher and biomass 1.6 times higher in the protected fore reefs than on unprotected ones (see Table 6 and Figure 13 at Pina-Amargós, *et al*., 2014b).

Valdivia *et al*. (2017) modelled predatory fish depletion and recovery potential on Caribbean reefs. Researchers found that total predatory fish biomass at sites within JRMR in Cuba and Dry Tortugas in Florida showed predatory fish biomass within the models' values. The four sites surveyed in JR included the top nine sites with the highest biomass out of 39 sites surveyed in the Caribbean (see Figure 1 at Valdivia, *et al*., 2017)). Similar patterns held when authors modelled predatory fish biomass in the absence of human activities, but several sites surpassed JR's biomass values (see Figure 3 at Valdivia, *et al*., 2017). The latter further reinforces the potential role of protection in maintaining and bolstering high biomass of predatory reef fish in JR, suggesting that high fish biomass is more a result of effective protection than due to JR ecological features.

Preliminary results of the expedition on mesophotic coral ecosystems showed that sites inside marine protected areas generally have higher reef fish abundances than fishing grounds (Reed, *et al*., 2018).

Stony corals

Effects of JR protection might also be discussed in the context of stony coral assemblages (Pina-Amargós, *et al*., 2008a; Caballero-Aragón & Perera-Valderrama, 2014; Hernández-Fernández, *et al*., 2018). We summarize coral cover from stony coral's studies in Table 2.

Change of average coral cover through time is habitat-specific. Research suggests that average coral cover increased (+4.1 %) in reef crest between 2004-2005 and 2010-2013, levelling around the same figure until 2017 (+0.7 %). Hernández-Fernández *et al*. (2019b) 's findings support these results, and suggested that *A. palmata* recovered before their fieldwork in 2017. On the other hand, the fore reef's average coral cover stayed around the same figure (-1.1%) between 2004-2005 and 2010-2013 and increased (+3 %) until 2017. Despite the relevance of these findings, since there is no scientific evidence of a direct relationship between

Table 2. Coral cover in JR (%). Blank cells mean no data collected/available

Source	Habitat	2004-2005	2010-2013	2017
Pina-Amargós *et al.* (2008a)	Reef crest	9.0		
Caballero and Perera (2014)			13.1	
Hernández-Fernández *et al.* (2018)				13.8
Pina-Amargós *et al.* (2008a)	Fore reef (drop off-spur and groove)	17.1		
Caballero and Perera (2014)			16.0	
Hernández-Fernández *et al.* (2018)				19.0

protection and coral recovery, it is impossible to establish a cause-effect relationship between protection and coral cover recovery in JR.

Pina-Amargós *et al.* (2008a) found no statistical differences among JR zones when structural complexity, density and coverage of main benthic components (stony coral, octocorals and algae) are compared. Research suggests that fore reef (40 sites) and reef crest (24 sites) seem nearly homogeneous along JR track. Hernández-Fernández *et al.* (2018) used a different survey method and did not find statistical differences among JR zones. Hernández-Fernández and Bustamante-López (2019) assessed coral recruits and supported the higher density of stony coral recruits towards the west of JR, but their results were not statistically significant. Hernández-Fernández *et al.* (2019a) explored scale variability on benthic coverage and diversity along JR, using small-sample-unit photo quadrats on terrace zones of the fore reef. They found that small-scale (10^1 m) variability characterized the coral reef community structure in JR compared with local- (10^2 m) and mesoscale (10^4-10^5 m) variability. The latter suggests that biological processes such as recruitment and competition had primacy over hydrodynamics in driving differences in reef community composition. However, the dominance of algae and low cover and diversity of scleractinian corals suggests the pervasive effects of global climate change on coral communities despite potential benefits provided by the marine protected area (e.g., oligotrophy and abundance of herbivores). However, Hernández-Fernández *et al.* (2019a) findings remain controversial, particularly the low cover and diversity of scleractinians coral reported, as they contradict several previous results. Small sample unit and habitat (terrace) might bias results. In particular, the sample size unit used did not reproduce the natural spatial scale of the benthic macroscopic components of coral reefs. The terrace was not the most appropriate habitat to explore coral reef processes due to their natural low coral cover (median of 1 % in Hernández-Fernández *et al.* (2019a) versus 9-19 % from previous studies on reef crest and drop offs-spur and grooves).

Other studies reviewed the assessments mentioned above on marine protection in JR. Examples of these include Kritzer *et al.* (2014), Navarro-Martínez and Angulo-Valdés (2015), Galford *et al.* (2018). Roman (2018) named JRNP as the “crown jewel of the Cuban MPAs” due to its near-pristine levels of apex predators, well-preserved coral reefs, vigorous enforcement, and its remoteness. Hernández-Fernández *et al.* (2019a) pointed out JR's special status globally because of its large and relatively undisturbed populations of large vertebrates (e.g., sharks, groupers and sea turtles) and its healthy reefs.

Microorganisms

Weber *et al.* (2019b) assessed the microbial signature of 25 protected and impacted northern Caribbean reefs, including JR. Overall, the authors found that seawater microbial composition and biogeochemistry were influenced by reef location and hydrogeography. Seawater from the highly protected 'crown jewel', offshore reefs of JR had low concentrations of nutrients and organic carbon, abundant Prochlorococcus, and high microbial community alpha-diversity. Seawater from the less-protected system of Los Canarreos Archipelago, Cuba, had elevated microbial community beta-diversity. Differently, waters from the most-impacted nearshore reefs in the Florida Keys contained high organic carbon and nitrogen concentrations, and potential microbial characteristic of microbialized reefs. Authors affirmed reef systems had distinct microbial signatures, and proposed that JRNP high levels of protection and its offshore nature, may preserve the oligotrophic paradigm and the community's metabolic dependence on primary production picocyanobacteria.

Section closing remark

Jackson *et al*. (2014) assessed Caribbean coral reefs' status and trends from 1970 to 2012. A portion of the data set from Cuba comes from JR. The authors summarize in their conclusions:

"Smart decisions can make an enormous difference for the wellbeing of corals reefs and the people and enterprises that depend upon them. No place is close to perfect, and everywhere is threatened. Still, the higher coral cover and comparative resilience to extreme heating events or frequent hurricanes on most reefs in Bermuda, Bonaire, Curaçao, the Venezuelan parks, the Flower Garden Banks, and the Jardines de la Reina in Cuba provide clear examples of what could begin to be achieved by strong and effective environmental regulation".

VI. Climate change

Impacts of climate change have not been extensively addressed for JR. Regional-scale studies are limited to the effects of two hurricanes: Dennis in 2005 (Pina-Amargós, *et al*., 2008c), quantitative (on coral reef), qualitative (on seagrass, mangrove, coastal vegetation and fauna)) and Paloma in 2008 (Guimarais *et al*., 2013, quantitative on seagrass). Parada-Isada *et al*. (2015) discussed to effects of hurricane Paloma on Cayo Caguama and Moncada-Gavilán *et al*. (2011b) showed some evidence of climate change-related issues on marine turtles.

None of Hurricane Dennis's effects on JR, either qualitative or quantitative, seemed to have brought substantial changes to species' abundance, composition, or behaviour (Pina-Amargós, *et al*., 2008c). Seagrass meadows were partly affected by hurricane Paloma by sediment accumulation on the shoots of *T. testudinum* and uprooting rhizomes by just 1 % of the seagrass area affected (Guimarais, *et al*., 2013). Seagrass meadows were mostly sheltered respected to the hurricane track, likely the main factor causing mild effects on this ecosystem (Guimarais, *et al*., 2013). Hurricane Paloma may have affected bird populations, as observations from September 2009 revealed a significantly higher percentage of bird juveniles and lower overall bird relative abundance on Cayo Caguama than the other two ringing sites. The latter potentially reflects temporal differences in habitat quality, as a possible result, of detrimental effects on foraging substrate and prey availability for insectivore birds following hurricane Paloma. Nearly one year after Paloma, Parada-Isada *et al*., (2015) recorded the lowest bird, relative abundance for all field seasons ever reported. Authors noted that extensive structural damage to coastal vegetation (e.g., defoliation, branch breakage, uprooting) was still visible in Cayo Caguama (Parada-Isada, *et al*., 2015).

Moncada-Gavilán *et al*. (2011b) discussed the impacts of hurricane Paloma on sea turtle reproduction and nesting habitat in JR. Authors reported significant beach erosion and vegetation damage on Anclitas and Alcatraz cays, destruction of eggs, nests and hatchlings after hurricane Paloma in 2008.

Lastly, a limited number of studies looked into coral bleaching events in JR. In 2005, high ocean temperatures in the tropical Atlantic and Caribbean resulted in the most severe bleaching event recorded in the Caribbean basin (Eakin, *et al*., 2010, Donner, *et al*., 2017). That same year, JR experienced medium thermal stress (4-7 DHW °C-weeks -maximum Degree Heating Weeks- of a maximum of 16) when in other Cuban regions thermal stress was low (1-3 DHW) (see Figure 1a at Eakin, *et al*., 2010). However, bleaching was milder in southern than in northern Cuba (see Figure 1b at Eakin, *et al*., 2010 and Figure 4 at Donner *et al*., 2017). The latter results were corroborated by in situ surveys (Hernández-Fernández, *et al*., 2011). Hernández-Fernández *et al*. (2019a) reported that JR was unaffected by bleaching in the summer of 2017. Nevertheless, follow-up surveys on specific coral colonies to assess their recovery was limited to few colonies.

VII. Golfo de Ana María

We summarized below the most recent research on the GAM, which remains connected and influenced by JR (see findings from Weber, *et al*., 2019b at connectivity section).

GAM is one of the most important fishing grounds of Cuba, especially for shrimp fisheries. For this reason, the vast majority of scientific literature produced in the last few decades focused on GAM fisheries (Pérez & Puga, 1982; Pérez *et al*., 1984; Claro, 1994; Páez, 1997; Baisre, 2004; Valdes *et al*., 2011; Giménez *et al*., 2016; Masjuan *et al*., 2017) and the biology of commercially important species (Carles, 1967; Báez & Álvarez-Lajonchere, 1980; Valdés & Sotolongo, 1983; León & Guardiola, 1984; Guitart *et al*., 1985). Shrimp species used the entire GAM throughout their life cycles, from areas close to mainland Cuba to JR (Pérez *et al*., 1984; Guitart *et al*., 1985). Shrimp fisheries showed overfishing signs since the mid-1970s (Pérez & Puga, 1982; Pérez *et al*., 1984). According to surveys carried out between 2002 and 2009, bycatch from shrimp fisheries consists primarily of fish (46 species, 82 % of the weight) and, at a lesser extent, crustaceans (12 %) (Valdés, *et al*., 2011). Four species dominated fish bycatch, including yellowfin mojarra (23 %), lane snapper (20 %), silver mojarra (12 %), and Atlantic bumper (8 %). Giménez *et al*., (2016) reported average landings (all species) from GAM of 2121,9 tonnes between 2008 and 2012. Landings came from the state fleet (61 %), fish bycatch from shrimp fishery fleet (16 %), private fleet (11 %), and self-consumption fleet (7 %) (authors' note: those figures sum 95 %, missing 5 % on the source). Few species/groups dominated the total landings, with 13 species/groups represented 79 %. The latter included rays (22 %), mojarras (11 %), seabream (9 %), sharks (7 %), lane snapper (5 %), grunts (5 %), mutton snapper (4 %), mullets (4 %), red ear sardine (4 %), mackerels (3 %), Atlantic thread herring (2 %), yellowtail snapper (2 %) and porgies (1 %). All species but rays and red ear sardine

Table 3. Species richness in the Golfo de Ana María

Group	Species richness	Reference
Corals	41	González-Díaz *et al.* (2012)
Gorgonians	23	González-Díaz *et al.* (2012)
Sponges	41	González-Díaz *et al.* (2012)
Marine mollusks	43	Rodríguez-Viera *et al.* (2012)
Echinoderms	26	Rodríguez-Viera *et al.* (2012)
Fish	170	Pina-Amargós *et al.* (2012b)
Terrestrial plants	47	Acevedo-Rodríguez (2012)
Terrestrial mollusks	4	Hernández-Álvarez (2012)
Terrestrial reptiles	8	Marichal-Arbona and López-Hernández (2012)
Insects	85	López-Rojas (2012)

showed a decline in landings likely due to overfishing between 2002 and 2009.

Whereas publications about GAM has been abundant, necessary information about its biological diversity was missing up until recently. The Journal of Marine Research ("Revista de Investigaciones Marinas") published an especial issue in 2012 about GAMs biodiversity (Table 3). The special issue included species inventories, environmental and climate information (Matos, *et al*., 2012), and a detailed habitat map (Ventura-Díaz & Rodríguez-Cueto, 2012). 78 % of GAM sea bottom was classified into four habitats: bare muddy bottom (50 %); mixed seagrass-patch coral reefs-rubble on mud-sand bottom (32 %), mixed seagrass on muddy bottom (15 %), and mixed seagrass mud-sand bottom (3 %). A previous map built with similar methods but different habitat classifications revealed that GAM's bottoms are made of mud (63 %), mud-sand (18 %), rock-coral reef (10 %), sand (5 %), and sand-mud (4 %), with seagrass distributed in 24 % of the total bottoms (Revilla & Rodríguez, 1995).

González de Zayas *et al*. (2012) described GAM's chemical oceanographic features showing conditions influenced by the Caribbean Sea and limited land-based influence, especially in the dry season (González de Zayas, *et al*., 2012). Chollett *et al*. (2012) found that GAM belongs to a group defined as offshore waters of the inner Caribbean (see Table 2 at Chollett, *et al*., 2012), consisting of a mixture of relatively warm waters with high salinity and high-water clarity. However, in a more detailed analysis, GAM is included in one of 16 physicochemical provinces (see Fig. 4 and Table 1 at Chollett, *et al*., 2012), exhibiting higher temperature, lower water clarity and higher salinity than those at the JR. GAM experienced a medium chronic stress given by wave exposure with values around 6 in a scale of 9 and a medium acute stress given by the frequency of occurrence of hurricanes Category 1-5 in 157 yr period (1851-2008), with approximated 15 hurricanes of a maximum of 30 (see Figure 6 at Chollett, *et al*., 2012).

Briones *et al*. (2017) recently estimated size, proportion of sexes, and fecundity of the ray *Hypanus americanus* in the shrimp trawl fishery of GAM, and its potential relation to designated fishing zones. The latter constitutes the first study on this topic (Briones, *et al*., 2017). Authors suggest that the proximity to JRNP might be responsible for the abundance and size ranges of the species found in GAM, suggesting the occurrence of spillover from JRNP.

Discussion

Knowledge about JR has increased in the last two decades, allowing critical assessments of ecosystem status, biological diversity, ecological function, species and ecosystem value, and vulnerabilities.

Overall, research shows that terrestrial and marine ecosystems are relatively well preserved in JR. JR coral reefs are in better condition than most in Cuban, the Caribbean, and the world. Oceanographic processes such as currents play a critical role in maintaining the health of coral reefs in JR, and marine protection seems to be also very important. Mangroves sustain nesting colonies of birds and high density and biomass of commercially and ecologically important fish species such as groupers and snappers in their juvenile and adult life phases. Coastal sandy vegetation is essential not only as vital habitats for terrestrial fauna such as mollusks, reptiles and birds, but also as preferred habitats of nesting hawksbill sea turtles.

JR and GAM's biodiversity is rich and unique. Species richness is high, particularly in the marine environment. Unique and endemic taxa occur on terrestrial and marine ecosystems. Bird communities fluctuate as they migrate, with a stable community structure in JR. JR is vital as a stopover for many Nearctic bird migrants. Keystone species such the long-spined sea urchin is recovering in JR since the early 2000s. JR is crucial for the life cycle and conservation of four sea turtles species, particularly for the critically endangered hawksbill sea turtle, as the overwhelming majority of its nesting in Cuba takes place in JR. The effective protection of JR has favoured many species/groups, including corals, sea turtles, and large fish species such as groupers, snappers and sharks.

JR possess a rich and complex interrelated group of species, habitats, and ecosystems that give rise to its incredible biodiversity. Ecological processes operate at various spatial scales at JR, and sometimes multiple, overlapping, scales such as the Caribbean, Cuba, southern Cuba, southeastern Cuba and JR/GAM. Besides oceanographic processes, larval dispersal operates at all scales. Research suggests that larval dispersal of snappers on the spawning aggregation site of JR is responsible for considerable recruitment to all Cuban regions, as well as the Caribbean region, including Cayman Islands, Hispaniola, Nicaragua, Jamaica, Colombia, Honduras, Belize, Mexico, Florida, Turk and Caicos and The Bahamas. However, the recruitment seems to be principally relevant at smaller scales, within JR, and into southeastern and southwestern Cuba. JR import snapper larvae from many of the locations listed above. Other species also disperse broadly such as grunts fishes, surgeonfishes and hawksbill sea turtles. Some species disperse at smaller scales. Damselfishes and bottlenose dolphins seem to move mainly across southeastern Cuba, and shrimp species move between JR and GAM. Connectivity patterns of larval dispersal result from the combined action of geography, oceanographic features, and species life histories. Species occurring in JR such as whale sharks and green sea turtles move between JR and the broader Caribbean. The high degree of species movement and connectivity across multiple scales makes regional coordination and cooperation imperative for the sound management and conservation of species.

JR forereefs are flushed with pelagic, oligotrophic seawater carried by the Caribbean current. Conversely, GAM patch reefs are influenced by productive mangrove forests, bare muddy bottoms and seagrass meadows that have less contact with the open ocean. Entrainment of nutrients from these productive habitats within the GAM and tidal flushing of nutrients into the JR forereefs are likely vital processes that influence primary productivity, microbial diversity and metabolism, and grazing of cells by the reef community. The majority of the macronutrient concentrations were low or barely detectable in JR, suggesting rapid turnover of nutrient pools by microorganisms. JR experiences lower temperature, higher water clarity and lower salinity than GAM. Besides, JR experiences lower chronic wave stress and acute wave stress than GAM. Invertebrates such as shrimp and bony fishes such as goliath grouper use JR, GAM and southeastern Cuba in several stages of their life cycle, contributing to the flux of energy and nutrients at the regional scale.

Nutrient dynamics in JR reefs is likely influenced by the presence of several lagoons located in JR cays. The three main processes involved in nutrient dynamics are organic matter production by the vegetation (fundamentally mangrove trees), the regeneration of nutrients in the muddy sediments, and tidal export of nutrients and organic matter to the open water through channels.

Movements of adult bony fish occur mainly at JR-scale. Movement distances are usually a few hundred meters. Large coral reef fishes such as groupers and hogfish crossed the boundaries of the JRMR, contributing to fisheries outside the park's boundaries. However, most fish species in JR move very little, even only within the same habitat or into adjacent ones. Habitat discontinuities and reduction of its structural complexity seem to reduce movement of fishes. Highly migratory species such as silky sharks and hawksbill sea turtles spend part of their life cycle in JR. In a month-long study, tagged silky sharks travelled less than 30 km. These sharks used most of the water column from 0 to more than 600 m of depth, connecting photic and aphotic environments. Hawksbill sea turtles tagged in JR did not travel out of the archipelago. The low-movement and high-locality of species revealed in these studies may allow keeping most of the energy and nutrients in JR, probably favouring the ecological systems' recovery and resilience to local and global stressors.

JR is highly valuable from the economic and social perspectives. For many years, JR was a key fishing ground for essential fisheries such as lobster, lane snapper, yellowtail snapper, mutton snapper, and cubera/gray snappers. After JR's declarations as a marine reserve in 1996 and national park in 2010, JR fishing grounds were reduced by more than 40 % and 95 %, respectively. Fishing effort in JR was reduced and relocated into other regions. The only fisheries that remain to date in JR is lobster. Lobster fisheries in JR tributes to southeastern Cuba lobster fisheries, which continues to be the second most crucial lobster fishing ground in the country. Overall, southeastern Cuba, where JR and GAM are located, is considered the country's more important fishing area. Landings from the region rank in the top two at the national level, including shrimp, sharks, rays, sea cucumber, and Queen conch. Many of these species contribute to ecotourism in JR. JR catch-and-releasee recreational fishing, SCUBA diving, and snorkelling rank very high worldwide, having a very low ecological footprint. The successful public-private partnership in JR constitutes a unique ecotourism business model in Cuba which allows to manage, protect, and conserve the park effectively. Tangible benefits from fisheries, ecotourism and conservation include employment, livelihoods, food and other environmental goods and services. These benefits are mostly going to coastal communities and reach the national level.

JR is not free from stressors such as overfishing, tourism impacts, invasive exotic species, hurricanes and storms, chronic wave exposure, and coral bleaching. Overfishing and the use of non-selective fishing gear had affected several species. Intensive historical fishing of spawning aggregations and non-selective gear such as set nets and trawls used until the 2000s constitute some examples. Decreased landings of finfish, lobster and shrimps started decades ago. Of the 13 most essential fishes in terms of landings, only two species are not declining. Despite the reduction of fishing effort within the last decades and the expansion of closed fishing season for numerous fisheries, there are no recovery signs yet. Although Cuban fisheries experts recognized that overfishing is ongoing, they attribute the decline of fisheries in Cuba (including its southeastern region) to environmental changes. We consider that fisheries management needs to be improved, and that illegal, unreported and unregulated (IUU) fisheries need to be comprehensively addressed.

Although tourism might also lead to environmental degradation, there are no signs of it in JR. However, there is some preliminary evidence on the change of silky shark behaviour that needs to be monitored. Even though JR ecosystems are in better condition than in other regions, they are not immune to exotic invasive species such as lionfish. However, lionfish density and biomass are lower in protected areas such as JR, most likely due to ongoing removal efforts and potential control by native predators.

More frequent and intense hurricanes and coral bleaching constitute climate-change driven challenges to JR's biodiversity. Limited information after the impact of hurricanes in JR suggests a level of adverse effects on sea turtle nesting, terrestrial vegetation, and birds. However, these effects do not seem to last more than a year after the hurricane struck. The latter, could be explained because the acute wave stress caused by hurricanes and storms, does not severely affect this heavily buffered area. Other regions in Cuba (southwestern Cuba, northwestern Cuba) and the Caribbean (Florida Keys, Bahamas, minor northern Antilles, Puerto Rico) experienced higher acute wave stress than JR.

Similarly, JR experienced less chronic wave stress than northern Cuba, Florida Keys, Mesoamerica and northern South America. In terms of coral bleaching, JR seems to be more resilient than other Cuban regions. Despite the fact JR had suffered higher thermal stress than northern Cuba, coral bleaching events are milder in JR.

Considering the information compiled in this review and existing research gaps, we make future research and management recommendations in Appendix 1.

In closing, we considered that the key for the effective conservation and increased scientific knowledge of JR in the last two decades has resulted from fruitful stakeholder partnerships. The ecotourism company operating in JR, Cuban and foreign environmental institutions, and conservation organizations, have worked together to support the protection, monitoring, and research in JR. The breadth of research in JR spanned from species, to connectivity, to the effects of protection in the park's status. Science-based decision making has been at the forefront of JR, and significantly contributed to advance the protection and the sustainable use of biodiversity in JR. The high abundance and biomass of large and commercially important fish such as sharks, groupers, and snappers, result from proper enforcement and incentives favouring conservation while allowing humans to make a living from it.

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Competing Interests

The authors declare there are no competing interests.

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Appendix 1. Recommendations on research and management

Considering knowledge, conservation, and sustainable use gaps emerged from this review, this section recommends future scientific research and management actions.

Any research in JR (as elsewhere) should be designed and carried out to understand spatial, temporal and intrinsic variability and features of their target subjects. When personnel, logistical or any other constraints limit these, their conclusions must take these limitations into account to prevent overestimating their findings. We recommend paying particular attention to proper replication of sites, the use of fix transects to assess changes of sessile communities on coral reefs and seagrass meadows, to tag coral colonies to evaluate recovery after impacting events such as bleaching and tropical storms, proper sample unit size, habitat choice to understand relevant ecological processes and selection of sites where human activities might influence results (confounding factors).

Red mangrove forest is suffering a patchy death in JR. Due to the ecological and economic importance of red mangrove forest in JR and elsewhere, research should be designed and carried out to elucidate the spatial and temporal patterns of red mangrove forest patchy death and its causes.

The ecological studies of JR terrestrial ecosystems are focus on species/groups. It is critical to design and carry out comprehensive studies that integrate terrestrial flora and fauna components ecologically.

The number of reproduction colonies of birds in JR is based in a single survey. A comprehensive research should be designed and carried out to fully assess JR's importance for this critical component of birds' ecology.

Jutias and iguanas are, with the birds, the largest animals on terrestrial ecosystems but they remain poorly studied. Ecological research should be designed and carried out to elucidate population size and ecology of these species.

Coral reefs ecological and conservation studies in JR has been coral and fish-centric. Research should be designed and carried out to include comprehensively algae and their relationships with the coral reef's other components and processes, particularly coral-algae interactions and grazing. The presence of diverse and abundant sponges populations suggests their importance on JR reef communities that deserve to be studied. Endangered coral species such as *Acropora cervicornis* and *Dendrogyra cylindrus* are relatively plentiful in JR and only briefly mentioned on published research. Due to their ecological importance, they require more attention. The causes underlying the recovery of long spine sea urchin *Diadema antillarum* in JR need to understand due to the relevance of this matter beyond the local realm.

Movement patterns of sharks and gamefishes (bonefish, tarpon and permit) research remain unpublished despite various efforts underway for several years. Due to their ecological and economic importance, publishing those results should be a priority.

Sharks and tourists' interaction is one of the most remarkable experiences of visiting JR. Research should be designed and carried out to understand those encounters' potential impacts to sharks biology and behaviour.

The abundance of predators in JR makes the region particularly good for studies on trophic cascades and related issues. Such research should be planned and carried out in the near future.

Although there are only two spawning aggregation site of large and commercially important fishes reported in JR, traditional knowledge reported more. This also seems to be the case for spawning aggregation sites around Cuba. This information should be updated in the near future.

Native predators control of lionfish remains a controversial issue. Studies in JR, where gradients of native predators' biomass and human control of lionfish occur, might contribute to clarify this subject.

Although marine turtles are among the best-known species groups in JR, there are still essential gaps on their ecology. Their feeding grounds are one of them, and it should be prioritized incoming efforts.

Little is known about several relatively abundant and frequent marine megafauna of JR such as American crocodile and marine mammals. Research should be designed and carried out in the near future to fill that knowledge gap.

Several studies remark the connectivity between JR and GAM, but there is a lack of quantitative scientific evidence. Research should be designed and carried out to quantitatively assess such connectivity and its implication for both areas' status.

Since there are other spawning aggregation sites in JR and spatial explicit density and biomass data on snappers available, it would be interesting to revisit the modelling studies on larval dispersal for its potential implications for conservation and fisheries management.

In the marine realm, tourism in JR is well established but almost inexistent in the islands despite its ecotourism potential. Ecotourism in the islands should be promoted, based on the legal framework, the best science available, and the fragility of JR islands and their biological diversity.

The JR successful public-private partnership of tourism and conservation business model should be replicated in other marine protected areas around Cuba.

There have been accumulating evidences of the benefits to humans of JR conservation. These results should be considered to build and implement the Bussiness Plan of JRNP and any other intervention in JR, such as natural resources, budget allocation for conservation or research, or the implementation of new mechanisms for sustainable financing.

There is also evidence of the effects of protection on nature but mostly on coral reef fishes on JR's southern side. Research on this subject should be designed, carried out and published on stony corals and other habitats such as seagrass meadows, red mangrove forest and habitats located in the northern side of JR.

Spillover effect has been assessed experimentally in JR. This subject should be evaluated on natural conditions as a critical component of accepting large and long-standing marine protected areas and its fisheries importance.

Climate change and related issues should be considered in research and monitoring design. The apparent resilience of JR coral reefs to bleaching events need to be more in-depth studied.

Oceanography of JR is better-understood thanks to the last few years' efforts. However, there is a lack of more sufficient scale oceanography studies to explore the relationship with ecological processes at a scale of hundreds of meters.