The Abstract must have five subtitles: Introduction; Objective; Methods (include **study period and sample size**); Results and Conclusions (see examples in recent articles).

Include 5-7 key words that **do not appear** in the title or in the abstract (if you have doubts see a recent article).

Introduction summarizes recent findings in chronological order and ends with the **objective** of the study.

ABSTRACT

Introduction: Punta Descartes, a little peninsula in the northern pacific coast of Costa Rica, hosts all over the year three of the seven species of sea turtles that exist worldwide, listed as Vulnerable (*Lepidochelys olivacea*), Endangered (*Chelonia mydas*) and Critically Endangered (*Eretmochelys imbricate*) by the IUCN. Moreover, this region is highly influenced by seasonal events of deep, cold water upwellings that occur during the dry season (from January to April).

Objective: In order to shed light on the non-reproductive ecology of sea turtles in the Eastern Pacific, the main goal of this study is to clearly define the habitats that these species use in these stages of their life cycles around Punta Descartes.

Methods: For this purpose, the seafloor coverage composition of 5 different points along the peninsula were weekly to monthly monitored during 6 months: from October of 2018 to March of 2019, using photographic quadrants that comprised a total sampled area of $2.5m^2$. In parallel, thermal water conditions were also recorded for each study site. Moreover, data from previous capture and reacapture research on sea turtle species in the region were used in order to relate the seafloor composition of each site with the habitat use of sea turtle species.

Results: It was observed that on both seasons the phytobenthos was the predominant category of the seafloor for four of the study sites (average of 83% and 50% on the rocky and sandy substrates, respectively), the remaining one (Matapalito Bay) was mostly composed of coral coverage (70%). This feature, added to the high ratio of juvenile individuals of *E. imbricata* and *C. mydas* (100% and 90% of all captures, respectively), suggests that Matapalito Bay is a development ground. In all sites, the main effect of the upwellings was reflected in an increase of macroalgae and cyanobacteria coverage (except from Salinas Bay, where cyanobacteria coverage did not show any seasonal pattern), leading to the spatial dominance of these groups during the dry season (up to 40% of growth in some sites). However, Salinas Bay shown high, constant percentage of macroalgae potentially eatable by sea turtles along both seasons (38% in the rainy season and 35% in the dry season) which, together with the abundance of adult individuals of *C. mydas* in this site (67% of all captures) hints that it could be a foraging ground for this species.

Conclusions: In spite of the proximity of the 5 sites surveyed and the general trend to the overgrowth of the photosynthetic organisms along the dry months, seasonal dynamics of the 5 sites showed differences and were described, in addition to the localization and characterization of a foraging ground and a development ground in the region. This project attempts to motivate a research path towards the spatial and temporal analysis of the sites that sea turtles use in their non-reproductive phases in order to protect them all along their complex life cycle.

Key words: Benthos, Reef, Algae, Conservation, Guanacaste

INTRODUCTION

Each of the seven sea turtle species that exist worldwide are listed under the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List of Threatened Species™, 1948) and have likewise been added to the Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2013).

Despite being protected through/by several treaties, sea turtle populations all over the world are currently decreasing due to natural and anthropogenic threats that they face during each stage of their life cycle (IUCN, 2012; National Marine Fisheries Service and US Fish and Wildlife service [NMFS/USFWS], 1998). These threats include exploitation for the trade of its shell in jewellery and decoration, of its eggs and even of its meat for human consumption; accidental capture by inadequate fishing methods; and the destruction of its habitat due to coastal development, pollution and climate change (Bräutigam & Eckert, 2006; Chacón, 2002; Fleming, 2001; Sheppard, 2006; TRAFFIC Southeast Asia, 2004; van Dijk and Shepherd, 2004; Wallace et al. 2011).

This problematic context is stressed by the complexity of the life cycles performed by all sea turtle species, which, on the one hand, lends them huge vulnerability and, on the other hand, greatly hinder their study. Sea turtles' life histories are coupled to large migratory events, encompassing a wide range of geographically distant habitats throughout their different stages (Alvarado and Figueroa, 1998; Hirth, 1997; Limpus & Miller, 2000; Limpus et al., 1997; Musick and Limpus, 1997; Plotkin, 2003; Witzell, 1983). Apart from complicating their study, the management of the protected areas where these species live is legislatively complex since their migratory nature leads to a geographic segregation of their habitats, usually implying territories regulated by dissimilar jurisdictions (Mortimer et al., 2007 y Plotkin, 2003, citados por Gaos et al., 2012). Roughly, when an egg hatch on the nesting beach it was laid, neonates undertake a big journey including an early nursery stage, followed by a development stage. Afterwards, individuals carry out huge migrations towards the foraging grounds, where juveniles and adults inhabit during their non-reproductive periods. In most sea turtles populations, breeding grounds are different from the foraging grounds. In these cases, adult males and females perform periodic migrations between their reproductive and non-reproductive stages. Females come back to the same beach they were born to lay their eggs (nesting beach), according to a phenomenon called philopatry (Plotkin, 2002).

Foraging grounds of sea turtles are characterized by being neritic environments, where juvenile and adult individuals reside during their non-reproductive periods. Despite the fact that the feeding ecology of these species, especially in the Eastern Pacific, is very little studied, it has been deduced from various reports that it is closely related to the marine benthos, mainly with seaweed or seagrass beds (for the Black turtle; Arthur et al., 2008) and rocky and coral reefs (for the Hawksbill turtle; Carrión-Cortez et al., 2013) where they feed on benthic organisms such as algae, sponges and tunicates. This theoretical description of the foraging grounds matches to the constitution of some different bays that surround Punta Descartes and the Santa Rosa National Park, although these environments have not been properly characterized yet.

For the recent few years, big research and conservation efforts have been allocated around the reproductive biology of sea turtles, increasing the ecotourism addressed to the protection of nesting beaches. Although this is a big step forward, focusing the conservation efforts in a single phase of such a complex life cycle is not enough. There is still a large information gap in the ecology of the foraging and development habitats of sea turtles in the Eastern Pacific, especially for the hawksbill turtle (E. imbricata), not only about the state of the populations and the connections between the different stages of their life cycles, but also about their diet (Carrión-Cortez et al., 2013). It has already been reported the occurrence of hawksbill turtles (E. imbricata) and green turtles (C. mydas) feeding along the coast of the Baja California peninsula in Mexico (Seminoff et al., 2003a; Seminoff et al. , 2003b). Likewise, it has recently been certified the presence of foraging grounds around Punta Descartes, on the north-pacific coast of Costa Rica, in an region that is not fully protected by any type of legislation (Heidemeyer et al. , 2014). The species that inhabit this area are the Hawksbill turtle (E. imbricata; Fig 5a), categorized as Critically Endangered according to the IUCN (Mortimer & Donnelly, 2008) and the Black and Indopacific turtle (C. mydas agassizii; Fig 5c and 5b, respectively), Endangered (Seminoff, 2004). Although the Indopacific turtle is actually the same species as the Black turtle, it is a population that comes from the Indo-Pacific Ocean and presents enough morphological and ecological differences to be traditionally known as different species by the fishing communities in the area. Furthermore, adult females of Black and Olive Ridley turtles (*Lepidochelys olivacea*, listed as Vulnerable according to the IUCN; Abreu-Grobois & Plotkin, 2008), use the area to nest in many beaches along the peninsula (source: data base from the NGO Equipo Tora Carey).

Thus, this work is located in Punta Descartes, the northernmost peninsula of the Costa Rican Pacific. This area is also under the influence of important annual deep-water upwelling events, responding to two factors: the Costa Rica Thermic Dome (a), which consists of a marine upwelling led by the circulation of the North Equatorial Countercurrent, the Costa Rican Coastal Current and the North Equatorial Current; and which is intensified by the circulation of the Trade Winds (b) that cross the Lake of Nicaragua depression and the plains of northern Costa Rica (Fiedler, 2002; Umatani & Yamagata, 1991). This wind flow (commonly known as "Chorro del Papagayo") strengthens during December, displacing the surface layer of the water column in the area and thus causing an upwelling of deep water; and ceases after April. So, during the dry season (from January to April), this vertical movement of deep water displaces the thermocline towards the surface, produces a great decrease in water temperature (from 30ºC it reaches 14ºC) and promote the rise of nutrients, which become available in the photic zone (Fielder, 2002). This results in an increase of the primary production; which in turn causes a growth of certain fish populations, including species of great commercial interest, such as snapper or tuna (Cortés et al., 2016); and it has a substantial impact on all trophic levels subsequent to primary production.

The characteristics of the area provide a an scenario with a great deal of interest to study how certain physical (oceanographic) forces can influence food availability and habitat characteristics for sea turtles. Thus, it has been reported an increase in the growth rate of the algae *Sargassum sp.* directly related to the increase in nutrients, which causes their seasonal dominance along the Punta Descartes coast during upwelling periods (Cortés et al. 2014). Although the work of Cortés et al. represents, to date, the only prolonged survey of a benthic species in the region, the results suggest that the benthic community of these ecosystems has such a high degree of dynamism that has a key role in defining and describing these sites as habitats of other species such as sea turtles.

The lack of environmental protection of Punta Descartes and its exceptional biodiversity richness are additional arguments that emphasize the need to increase ecological and biological knowledge about the area (Alvarado et al., 2011; Heidemeyer et al., 2014). Moreover, Punta Descartes is currently under high pressure due to coastal development, as well as to the tourism and fishing sector, since local populations have traditionally depend on fishing, which has often included methods not allowed in the country, such as trammel nets or bottom lines. An example of these threats is the building, in 2014, of Dreams Las Mareas All Inclusive Resort, on El Jobo beach, which is one of the nesting beaches for sea turtles in the area (specifically C. mydas agassizii and L. olivacea). This hotel was opened in December, the month in which the nesting of the black turtle (C. mydas agassizii) is at its peak in the area (source: Equipo Tora Carey database).

Only when the dynamics of sea turtle non-reproductive habitats and their connection with nesting areas are clearly studied, will it be possible to design effective conservation strategies that provide them solid protection throughout their life cycle, all including the legislative and scientific sectors, local communities and tourism. The critical degree of vulnerability stalking all sea turtle species and their global threats magnify the necessity to understand these animals at every stage of their life cycle in order to create effective conservation plans, which indirectly mean the conservation of whole ecosystems with great value, not only ecological, but also economic (Bulte & Van Kooten, 1999).

Thence, the main goal of this research is to broaden the knowledge in the ecology of sea turtles of the Northeast Pacific during their non-reproductive stages by studying their foraging and development grounds, as well as evaluating the role in these ecosystems of seasonal variations in nutrient concentration caused by the upwelling events. More specifically, the objectives can be summarized in two sections: one the one hand, the characterization of the non-reproductive habitats of sea turtles around Punta Descartes in terms of the seafloor composition by an evaluating the relative coverage of the main categories of organisms (eg algae, tunicates, porifers) or abiotic groups (eg sand, sediment, rock), delimiting and describing these categories previously. And, on the other hand, the analysis of the seasonal dynamics of this seafloor composition derived from the rise of deep, nutrient-rich water, using the water temperature as a proxy for these upwelling events.

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Study sites

Research was carried out in 5 different sites around Punta Descartes, a little northernmost peninsula pacific coast of Costa Rica, where it has been identified the aggregation of sea turtles in non-reproductive adult and juvenile stages and one of which has not, although its characteristics make it necessary to include it in the study for a complete analysis of the benthic communities' response to oceanographic events in the area (Heidemeyer et al., 2014).

Salinas Bay (BS; 11°02'57"N 85°41'40"W) is a large bay with muddy and shallow seafloor. It is surrounded by numerous mangroves and field areas, which often form wetlands in the rainy season. In addition, all along the coast there are several cattle fields and a coastal town, Puerto Soley. In this area it has been reported the presence of the Black turtle individuals (Chelonia mydas agassizii) throughout the year (source: NGO Equipo Tora Carey database).

El Jobo Beach (EJ; 11°02'02"N 85°44'05"W) is a sandy bottom bay, surrounded by shallow rocky reefs. In 2014, large patches of *Halophila baillonis* were identified on the sandy substrate, whose growth showed a high dynamism and growth rate, being able reaching clear dominance and disappearance throughout the year (Samper-Villarreal et al., 2014). Despite being an important nesting area, this beach has never reported the presence of aggregations or resident populations of sea turtles during its non-reproductive stages. On the other hand, the tourist and coastal development derived from the construction, six years ago, of the Dreams Las Mareas Resort could be generating an impact on the marine ecosystem that has not yet been adequately evaluated.

Cornuda Island (IC; 11°00'37"N 85°45'01"W) is a small rocky outcrop, at about 700m from the coast, surrounded by rocky lows that reach depths of up to 12m. Named for the ancient presence of hammerhead sharks (Sphyrna lewini, commonly known as horned sharks, referring to their large lateral head expansions), this site is exposed, unlike the others, to a channel of ocean currents due to its remoteness from the coast.

Puerto Manzanillo (Mz; 11°00'28"N 85°43'58"W), a small pebble beach, with rocky reefs around, is actually a small port where the local artisanal fishing fleet (El Jobo Fishermen's Association) moore, with around 15 boats. The fishermen carry out the entire process of fish cleaning there, discarding those catches or parts of them not suitable for sale. This generates an impact due to the contribution of organic waste to the ecosystem, in addition to influencing the eating habits of turtles, especially the black turtle, considered fully herbivorous in its adult life (Arthur et al., 2008; Reich et al., 2007). In the last third of the year, this area is exposed to southwest currents (Sierra et al., 1997).

Matapalito Bay (Mp; 10°56’06”N, 85°47’42"W), on the Santa Elena Peninsula, is a small and remote bay, quite sheltered by the profile of its coast. This area hosts a unique coral reef made up of different Pocillopora species, generally *P. damicornis* and *P. elegans* (this one categorized as Vulnerable; Cortés, 1997; Hoeksema et al., 2014), in addition to patches of seagrass *Haliophila baillonis*. Despite being one of the richest resource areas along the eastern Pacific coast, the composition of this habitat has yet to be characterized. Matapalito Bay is part of the Bahía Santa Elena Marine

Management Area, created in June 2018. This protection framework implies restrictions towards some fishing methods, although not its prohibition (Área de Conservación Guanacaste, 2018).

Sampling photoquadrants

Surveys of the seafloor coverage were performed using ten non-fixed gridded photographic quadrants of polyvinyl chloride (PVC) and 50 x 50cm (n=10) for each type of substrate (rocky and sandy) at each of the five study sites, meaning the total sampled area was $2.5m^2$ for each site and substrate. PVC quadrants were positioned every one meter along a random linear transect at low tide using snorkel equipment and photographs were taken with an Olympus Tough tg-5 digital camera. For each sampling event, environmental data on water temperature was recorded by the thermal sensor of the photographic camera (previously calibrated). It was used as a proxy of upwelling conditions, since they are directly correlated with a decrease in this parameter: in the water column, the temperature decreases with depth, for what the upwelling of deep waters unavoidably implies the cooling of surface water. In parallel, samples of each unidentified benthic species were taken during the monitoring events in order to properly classify them. This process was carried out weekly (for Manzanillo and El Jobo), biweekly or monthly (for Cornuda, Salinas Bay and Matapalito Bay, since the samplings are subject to the availability of the boat by which these most remote areas are reached). Monitoring began in October 2018 and ended in March 2019, so the study included three months in the rainy season (from October to December) and three in the dry season (from January to March).

Seafloor coverage data analysis

Images taken in each sampling were analysed or edited (in cases where it was necessary to scale them or improve their visualization) using computer software for visualization and image processing: ImageJ and Microsoft Picture Manager. The percentage of coverage corresponding to the different defined categories (detailed below) was determined by means of a visual estimation in such a way that, for a quadrant, the sum of percentages corresponding to each category is always 100.
The categorization of seabed groups distinguished between (1) biotic coverage, including (1.a) phytobenthos (photosynthetic sessile benthic organisms, i. e. crustose algae; turf (macroscopic benthic algae with a stem less than 5cm); erect algae (benthic macroalgae with a stem greater than 5 cm); and cyanobacteria); (1.b) tunicates; (1.c) porifera; (1.d) cnidarians (mainly corals of the order Scleractinia); and (1.e) seagrasses. And, on the other hand, (2) abiotic coverage, considering (2.a) sand; (2.b) sediment (composed non-organic materials such as calcium carbonate compounds); (2.c) gravel; and (2.d) rock.

Since the data presented a distribution that deviated from normality, a Permutational Analysis of Variance (PERMANOVA) was performed using the R software (R Development Core Team, Vegan statistical package; Oskenen et al., 2019) in order to (i) compare each five sites in terms of average benthic coverage composition for each site and substrate and (ii) compare the seafloor composition of each site throughout the six months (from October to March). In order to evaluate the correlation between the temporal variations of each coverage category for each site and substrate and the temperature, correlation tests were performed through R software (R Development Core Team, Stats statistical package; R Core Team, 2019). For the purpose of simplify the results presentation, the percentage coverage data obtained during the six months of study (October, November, December, January, February, and March) were grouped into the two seasons (rainy, from October to December; and dry, from January to March) for each site and substrate.

RESULTS

Seafloor coverage

The phytobenthos is the dominant category (67.4%±31.9) for all the sites and in both substrates studied except for the hard substrate of Bahía Matapalito, where they are the cnidarians, specifically the corals of the order Scleractinia (73.6%±12.4). The biotic coverage is higher in the rock substrate than in the sandy one, where the only biotic category that was registered was the algal type (in addition to the sea grass in Matapalito). The rocky substrate, in turn, shows a greater diversity of phyla, which is more noticeable during the rainy season.

As for seasonal differences, the general trend is an increase in the cyanobacteria coverage in the dry season (from a 2% of increase in Cornuda Island up to a 51% in Puerto Manzanillo), although it decreases (11%) and remains constant in the rocky and sandy substrates of Salinas Bay, respectively. Erect macroalgae coverage also performed an increase in the dry season, especially notable in the rocky substrates of El Jobo Beach (30% increase) and Puerto Manzanillo (10%), and in the sandy substrates of Bahía Salinas (19%) and Isla Cornuda (8%). It is remarkable that Bahía Salinas is the only place that, in the rainy season, shows a dominant proportion of erect macroalgae and cyanobacteria compared to the other benthic coverage categories (these two groups represent 50% of the total coverage in rocky bottoms and 40 % in sandy ones). Finally, sea grasses were observed only during dry months, specifically small patches of Halophila baillonis in the sandy substrate of Matapalito Bay (5% coverage).

Temperature related coverage variations

The phytobenthos subcategories crustose algae, erect macroalgae (>5 cm) and cyanobacteria were the ones that showed, on the one hand, significant seasonal variations and, on the other hand, a common coverage variation pattern generalizable to all five study sites. For this reason, these three seafloor categories were the ones considered when the analysis of their correlation with water temperature evolution (Fig. 3).

Crustose algae coverage showed a positive correlation with temperature variations ($r = 0.648$; $p < 0.05$), this is especially evident in El Jobo Beach, Puerto Manzanillo and Cornuda Island. In other words, the extension of this type of algae decreases as the temperature of the water does. Contrarily, erect macroalgae (> 5cm) and cyanobacteria showed a negative correlation with temperature ($r = -0.847$; $p < 0.05$ and $r = -0.824$; $p < 0.05$, respectively).

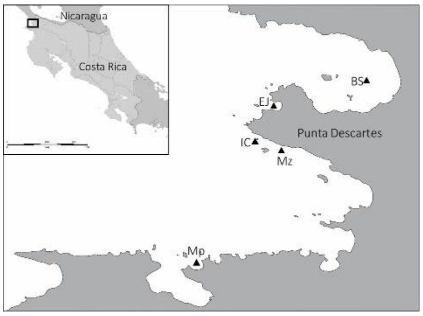


Fig. 1: Location of the study sites around Punta Descartes, the northernmost peninsula of Costa Rican pacific coast. BS: Salinas Bay, EJ: El Jobo Beach, IC: Cornuda Island, Mz: Puerto Manzanillo, Mp: Matapalito Bay.

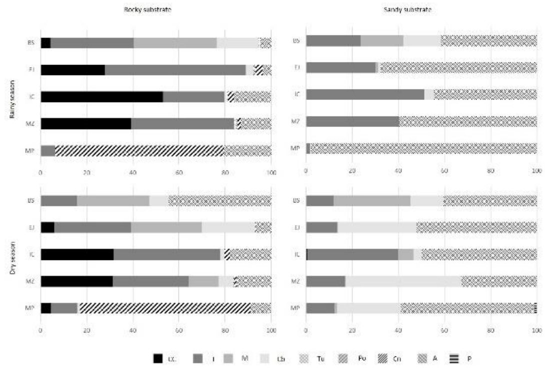


Fig. 2: Benthic coverage composition (in % of each seafloor category, see Materials and Methods) of the 5 sites surveyed for each of its substrates (rocky and sandy) in the rainy season (samples from October to December) and in the dry season (samples from January to March). CC = crustose algae; T = turf algae; M = erect macroalgae; Cb = cyanobacteria; Tu = tunicates; Po = porifera; Cn = cnidarians; A = abiotic coverage; P = sea grass.

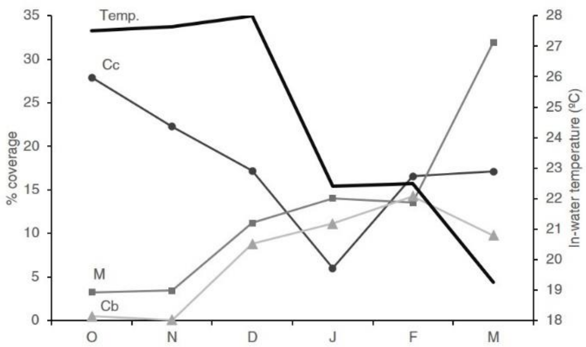


Fig. 3: Monthly evolution of crustose algae, erect macroalgae and cyanobacteria coverage proportion (primary axis) and in-water temperature (secondary axis) during the six months of survey (rainy season, from October to December; dry season, from January to March) .

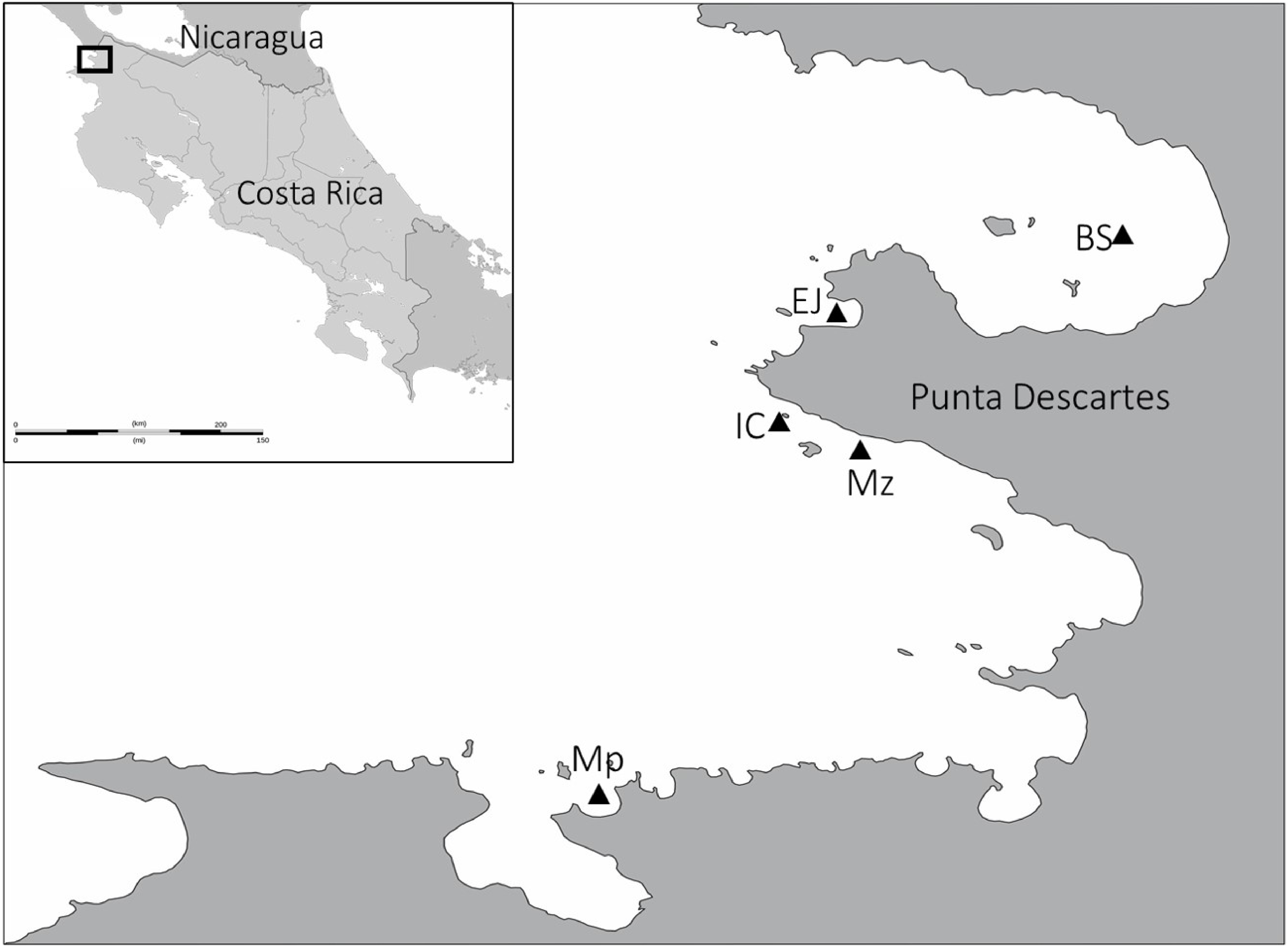
DISCUSSION

The upwelling of deep waters in the region during the dry season and the subsequent entry of nutrients through resuspension seem to provide photosynthetic organisms with the optimal conditions for their proliferation, especially cyanobacteria (reaching their dominance mainly in sandy bottoms), as well as for the growth of erect macroalgae species which, except for Salinas Bay, were not registered during the rainy months, such as *Ulva sp* and *Sargassum sp*, as it was previously reported by Cortés et al. (2014). This nutrient increase also boosts the appearance of *Halophila baillonis* patches in Matapalito Bay in the dry months, which was already observed by Samper-Villarreal et al. in Jobo Beach (Samper-Villarreal et al., 2014).

In spite of this general trend, if we delve deeper into the five sites surveyed, they show such a different seafloor composition and respond in a likewise different way to oceanographic events, which, considering their geographical proximity, could only be explained when regarding the topography of the study sites and their exposure to anthropic impacts. A small bay like Matapalito, dominated by coral reefs and under government protection, shows a much lower range of response to upwelling events than other more exposed sites such as El Jobo Beach, which is also subjected to coastal development, or Puerto Manzanillo, where the contributions of nutrients during the dry season results in an overgrowth of erect macroalgae and cyanobacteria. This occurs to a lesser extent on Cornuda Island, a completely open area where local ocean currents may be dampening the effects of the upwelling. Finally, the anthropic-origin nutrients may flow into Salinas Bay during the rainy season promoted by its hydrographic topography which, together with the oceanic-origin nutrients resuspension in the dry months, ensure nutritional income during both seasons, which probably supports a notable abundance of erect macroalgae and cyanobacteria throughout the year.

The presence of sea turtles all over the year around the entire peninsula suggests that the region meets the characteristics for the survival and feeding of these species even with the seasonal changes of the oceanographic conditions. More specifically, the great extension of the coral reefs of *Pocillopora spp*. in Matapalito Bay lend it a degree of ecosystem structuration which, together with the geographical conditions of the small bay and the protection conferred by being under the Santa Elena Bay Marine Management Area, suggest a protective context that may potentially allow threatened species of sea turtles to reside there safely in a juvenile state. In fact, Hawksbill and Indopacific turtles are found mainly in juvenile age classes with a high rate of recapture, which translates as fidelity to the habitat and juvenile individuals of this species can be observed resting among the coral formations at about 6 meters depth or swimming peacefully in the waters of this bay (pers. obs.). So Matapalito Bay is, most likely, a very important development area for Hawksbill and Indopacific turtles in the East Pacific. Besides, the dominance of macroalgae throughout the year in Salinas Bay results in potential feeding opportunities for sea turtles during the whole year, which, in addition to the population distribution of C. mydas agassizii in this site, clearly dominated by adult individuals and the idiosyncrasy of the bay itself (neritic and shallow), suggest Salinas Bay might be a feeding ground for the Black turtle in the East Pacific. Indeed, it has been reported the presence of adult Black turtles near the coast and feeding on algae in this bay.

Punta Descartes is, without a doubt, a place of great importance for the ecology of sea turtles. Such an small area as Punta Descartes supports populations, aggregations and non-aggregated individuals of 3 different species of sea turtles (Heidemeyer et al., 2014) at different crucial stages of their life cycle, both reproductive and non-reproductive, throughout the year, and therefore deserves adequate management that guarantees the survival of these species and the whole ecosystem this peninsula harbours.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BS
EJ
Punta Descartes
IC
Mz
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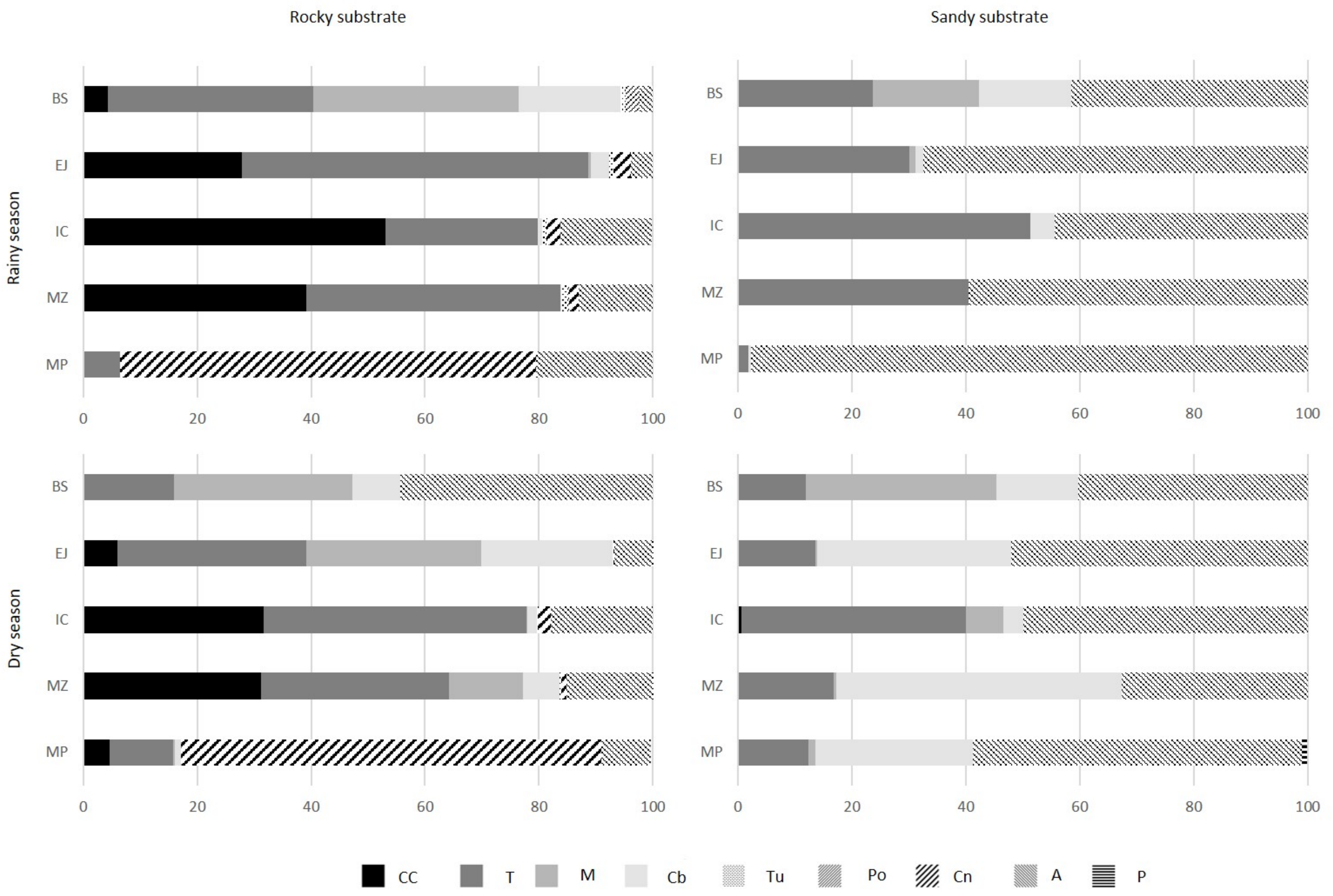

Rocky substrate
Sandy substrate
Rainy season
Dry season
BS
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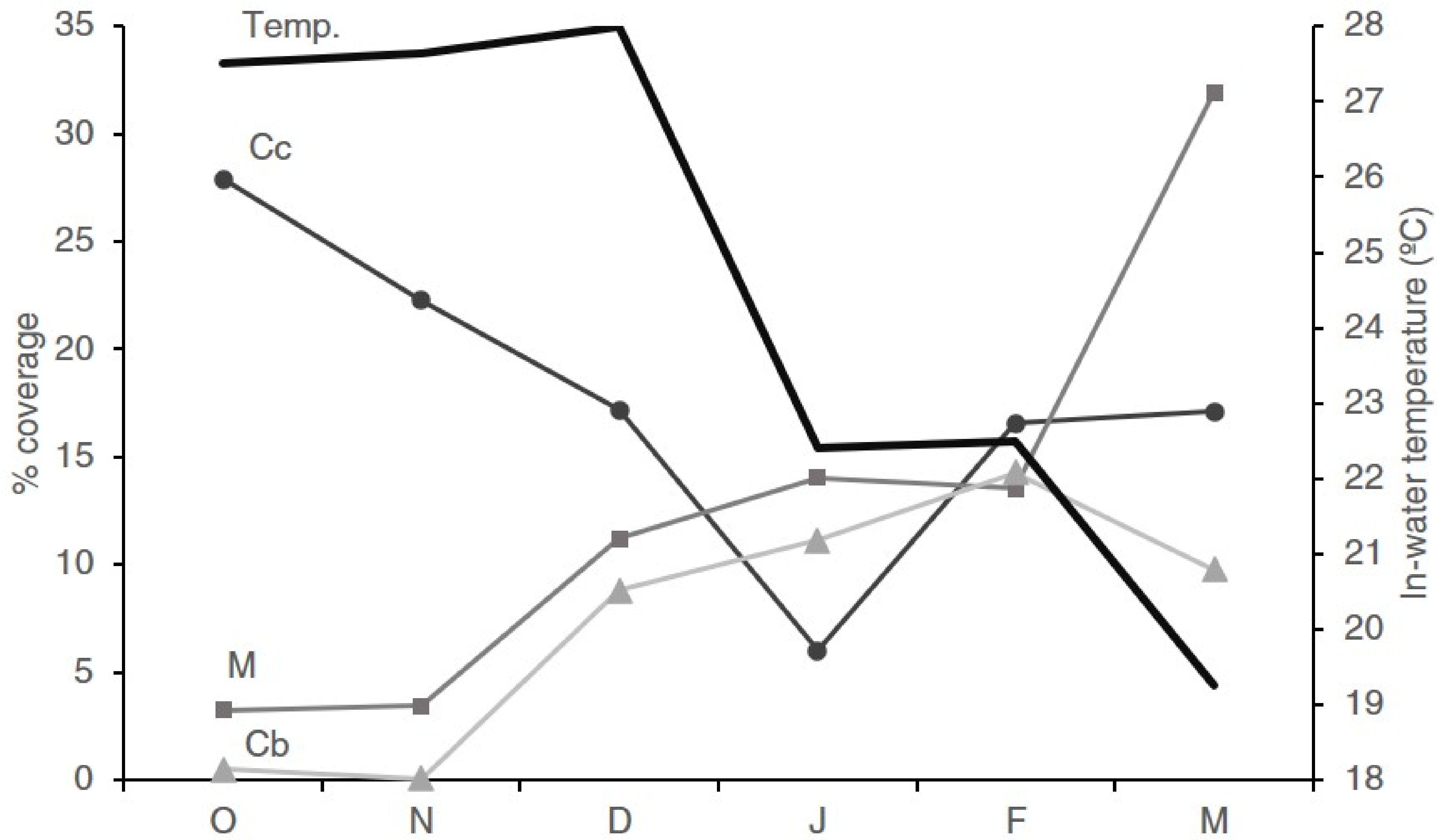

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