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Recovery of ghost crabs metapopulations on urban beaches during the Covid-19 “anthropause”

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1. Introduction

Sandy beaches are social-ecological systems, where physical, ecological, social and economic dimensions interact, providing several services for human well-being (Defeo et al., 2021). Overuse of beaches as recreational assets to society has pervasive effects on animal assemblages and ecosystem services (Defeo et al., 2021). While some sandy beaches experience chronic stressors that rarely cease, others are exposed to acute events causing sudden short-term changes such as tourism activities, including trampling, vehicle traffic and cleaning services (Defeo et al., 2009; Costa et al., 2020a). Many indicator species respond negatively to human disturbances, including seasonal decreasing in abundance during tourist season or lower abundance when comparing beaches with tourism infrastructure with pristine beaches (reviewed by Costa et al., 2020a). Although this pattern is well-known, evidences that biodiversity benefits from removal of anthropogenic stressors at different temporal scales is scanty, making the assessment of the recovery capacity of the system challenging.

The majority of government authorities initially responded to COVID-19 pandemic by declaring lockdown to facilitate social distancing and minimize virus spreading. This period termed “anthropause” provided a unique opportunity to evaluate the recovery of wildlife in the absence of stressors on urban ecosystems. We assessed whether the anthropause associated with beach closures during the COVID-19 pandemic resulted in repopulation of the Atlantic ghost crab Ocypode quadrata (Fabricius, 1787) on urban beaches. For this purpose, we compiled a historic dataset (2013–2019) of the ghost crab density and performed biweekly burrow measurements from June/2020 to May/2021. Recovery of ghost crab metapopulation during the lockdown occurred even in more human-modified beaches. Burrow abundance significantly increased in urban sectors, but not in control site along with the time of pandemic. The reduction in the mean burrow opening diameter during this period evidenced that young metapopulation have thrived on urban beaches when recreational activities ceased. Our results show that urban beaches should not be exclusively managed for recreational purposes. Initiatives with a focus on wildlife conservation including spatial-temporal controlled beach closures may increase the biodiversity resilience.
2021; Thiel et al., 2021) and spreading of illegal activities such as vehicle traffic due to reduction in law enforcement (Manenti et al., 2020).

Commonly abundant, ghost crabs are relatively large semi-terrestrial and scavenger species that inhabit sandy beaches worldwide (Lucrezi and Schlacher, 2014). They are widespread ecological-disturbance indicator species from tropical to temperate sandy beaches and the most studied macroinvertebrate of this ecosystem, responding negatively to vehicle traffic, nourishment and coastal modification at multiple spatial scales (Schlacher et al., 2016; Costa et al., 2020a). The construction of burrows visible on the sand surface provides a unique opportunity to apply non-destructive and low-cost estimates of ghost crabs’ population sizes for monitoring purposes of beach condition. Burrow counts have offered an optimal benefit-cost in beach impact assessments for decades, mainly because the protection of habitat requirements of ghost crabs might favour the conservation of co-occurring species (Barboza et al., 2021; Costa and Zalmon, 2021).

Although ghost crabs are semi-terrestrial crustacean closely associated with dry beach zones, they have an oceanic larvae phase. Their larvae are free swimming in the plankton, and this is the main dispersal stage (Lucrezi and Schlacher, 2014). Despite their low densities on high-disturbed beaches (Barboza et al., 2021), ghost crabs are not commonly extinct from these areas. That is because they are probably maintained as metapopulations by a source-sink dynamics, in which adjacent low-impacted beach populations are sources for larvae due to higher breeding success (Veas et al., 2013). If human disturbances exert major influences on post-recruitment processes of ghost crabs on high-disturbed beaches, we expect that reduced human activities during the lockdown would allow a higher settlement rate and increased population size. Thus, ghost crabs are interesting models for assessing the recovery potential of beach populations during the “anthropause” related to COVID-19 pandemic.

The objective of the present study was to assess whether the effect of different human disturbance levels on the Atlantic ghost crab Ocypode quadrata (Fabricius, 1787) was minimized during the COVID-19 pandemic lockdown in southeastern Brazil sandy beaches (Costa and Zalmon, 2019; Costa et al., 2021), resulting in population increment. We tested the hypothesis that crab’s burrow density increased on urban beaches along with the pandemic because of an expected reducing of recreational activities, especially during lockdown periods. For this purpose, we compiled a temporal dataset (2013–2019) of the ghost crab density and compared the results to biweekly field samplings during the pandemic from June/2020 to May/2021 in the same sandy beach arc.

2. Methods

2.1. Study site

An extensive beach arc in Southeastern Brazil (21°S, 41°W) was chosen to monitor the Atlantic ghost crab populations before and during the COVID-19 pandemic lockdown period (Fig. 1). The Grussaí Beach Arc, northern coast of Rio de Janeiro, Brazil, has a set of microtidal beach sectors with intermediate morphodynamics and areas with distinct human disturbance levels. The municipality of São João da Barra receives 150,000 tourists during the summer, mostly on Grussaí Beach Arc, which has a regional touristic value and offers leisure activities, food, inns, and shows (Suciu et al., 2017).

Three disturbance levels were categorized in the region in previous studies: high-impact, moderate-impact and low-impact (Costa and Zalmon, 2019). Previous data revealed lower burrow densities (~4 occupied burrows/100 m²) on high-impact sites, where high vehicle traffic (~2 vehicles/hour/100 m in the intertidal zone), litter pollution (~4 items/m²) and coastal development occur, when compared to low-impact sectors (~16 occupied burrows/100 m²). The low-impact

Fig. 1. Map of the study area showing the beach sectors with distinct impact levels (LI = low-impact, MI = moderate-impact and HI = high-impact) on Grussaí Beach Arc, southeastern Brazil. The moderate- and high-impact areas have walkways accesses to the beach (right picture) and were sampled during the COVID-19 pandemic along with the control beach sector (LI).
sector are located approximately 4 km far from the main urban settlements (Fig. 1), and have received low human presence (<1 person per m²) before and during the “anthropause” (Costa and Zalmon, 2019; Suciu et al., 2017). Moderate-impact sectors also receive recreational activities and have some urban infrastructure, but the shore is less developed than high-impact beaches and sand vegetation is still present (Costa and Zalmon, 2019; Suciu et al., 2017). In addition, the visitors are mainly members of the local population throughout the year, and vehicle traffic, trampling, and marine litter are lower compared with the high-impact sectors (Arueteira et al., 2022). Beach cleaning occurs in high-impact and moderate-impact sectors at the same frequency (daily during the high tourist season) and intensity (use of rakes to collect litter and one tractor to transport it), but this activity also paused during lockdown periods.

2.2. Sampling design

A total of 17 sampling campaigns were carried out before the COVID-19 pandemic between 2013 and 2019. Burrow counts were performed in the most impacted area (one high-impact sector) and in the low-impact sector. Opened burrows were counted and measured with a calliper rule (burrow opening diameter) along five transects (3 m width) with random distance from each other and arranged perpendicularly to the waterline from the upper swash limit to the beginning of supralittoral vegetation. The surveys were always performed in the morning (6:00 to 10:00 h) and during tide height low enough (<0.5 m) to avoid covering the main distribution area of ghost crab burrows (Costa and Zalmon, 2019).

From June 2020 to May 2021 (during pandemic), the same approach was applied biweekly up to December and weekly from January (n = 16 sampling days). To assess whether changes in ghost crab abundance and size structure on urban sectors during the pandemic is related to the interruption of recreational activities, we sampled two high-impact sectors and two moderate-impact sectors, where human activities paused during lockdown, along with the low-impact sector (control). As the control beach sector is neither urbanized nor impacted by recreational activities (before and during the pandemic), our sampling design fits to the before-after-control-impact approach (BACI) (Underwood, 1992).

2.3. Data analysis

The magnitude of the effects of human disturbances on ghost crab population between 2013 and 2021 was assessed using log-response ratios (RR), which is a common statistic of ecological effect sizes in population biology (Underwood, 1997). Regression analysis was also performed to evaluate the relationship between RR and time of pandemic (12 months of monitoring). Burrow abundance was transformed by square root and ln x + 10, respectively, to ensure linearity, homoscedasticity and normality of the ANCOVA model. We used graphical inspection of residuals to validate linear models (Zuur et al., 2010). Statistical analyses were carried out with the R software (R Core Team, 2019). ANCOVA was also applied to test whether the maximum abundance values of the ghost crab burrows have changed between 2013 and 2021 in the low- and high-impact beach sectors.

3. Results

Since 2013, the Atlantic ghost crab has been more abundant in low-impact sector than in the most impacted one in almost all sampling months on Grussai Beach Arc (Fig. 2). Temporal cycles have been observed in low- and high-impact beach sectors; however, in the lowest impacted sector, the peaks of burrow abundance have slightly decreased between 2013 and 2021 (R² = 0.40, p = 0.077) (Fig. 2, Appendix 1).

The responses ratios (RR) of burrow abundance evidenced a more negative impact before than during the COVID-19 pandemic (F = 8.269, p = 0.008) (Fig. 2). Specifically, during the COVID-19 pandemic, the human-induced impact on burrow abundance (RR) decreased monthly (R² = 0.32, p = 0.015) (Fig. 2).

During the COVID-19 pandemic, the burrows abundance increased in all the four beach sectors affected by recreational activities before the anthropause (F = 9.085; p = 0.003) (Fig. 3A, C, 3B, 3G). The ANCOVA model did not evidenced statistical support for the interaction between “beach sector” and “time of pandemic” factors (F = 1.035; p = 0.396), evidencing that the positive effect of the former did not depend on the level of human disturbance (high- or moderate-impact). Differently, the number of burrows in the low impact sector showed similar values before and after the pandemic sampling (Fig. 3I).

The mean burrow opening size decreased linearly in all sectors during the COVID-19 pandemic (F = 10.112; p = 0.002), except in one moderate-impact one (Fig. 3). The interaction between “beach sector” and “time of pandemic” factors was not significant according to ANCOVA (F = 1.063; p = 0.382). Thus, in general burrow opening size decreased during the pandemic regardless of the disturbance level.

4. Discussion

Since 2013, the lower ghost crab abundance in high-impact beach sector compared to low-impact one on Grussai Beach Arc has been attributed to urbanization and recreational activities (Suciu et al., 2018; Machado et al., 2019; Costa and Zalmon, 2019). Even though ghost crab larvae potentially settle in the most impacted beach sectors, pulse and press disturbances have hindered metapopulation establishment in urban areas (Costa and Zalmon, 2019; Costa et al., 2020b; Machado et al., 2019). It is widely documented that trampling, vehicle traffic and beach cleaning alter the natural substrate stability and prevents the establishment and growth of macroinvertebrates worldwide, similar to ghost crabs in the region (Machado et al., 2019; Suciu et al., 2018; Costa et al., 2020b).

At a continental scale, burrow density is clearly negatively related to natural habitat modification (Barboza et al., 2021). Physical modification of sandy beaches, mainly the suppression of the dry upper zones associated with coastal urbanization, impacts ghost crabs due to habitat loss; these crabs depend directly on intertidal and supralittoral to feed and construct their semi-permanent burrows (Lucrezi and Schlacher, 2014). However, at local scale, we showed that recreational activities exert the main negative effects, since a recovery of ghost crab metapopulation, from the beginning of the lockdown period, occurred even in the more urbanized beach sectors. Even though human trampling, vehicle traffic, beach cleaning and litter pollution reduce during low touristic season at local scale, they did not cease as during the lockdown (Machado et al., 2017; Suciu et al., 2017).

The assessment of recovery capacity of ghost crab at beaches with continuous disturbance was thitiberto virtually impossible, but the COVID-19 anthropause provided an opportunity to show that beach populations can be resilient to human disturbances (Soto et al., 2021). Herein, we confirmed the hypothesis that burrow abundance increases...
in all urban sectors during the pandemic, whilst in the control ones it remained relatively constant. Noticeably, the reduction in human activities allowed recruitment of ghost crabs on high-impact beaches in comparable levels to that occurred in areas where disturbances level did not change during lockdown period. The reduction on burrow opening diameter in all beach sectors is further evidence that the ghost crab thrived a young metapopulation even under chronically modified shores, as rarely did since 2013. Despite de oscillatory pattern in burrow abundance, our results suggest that when recruitment period does not occur simultaneously with recreational activities, ghost crab can establish successful metapopulations in urban areas, when overuse is properly managed.

Our study reinforces how the dramatic slowdown in human activity during lockdown periods has benefited beach wildlife worldwide. Manenti et al. (2020) surveyed the breeding activity of the threatened plover Charadrius alexandrinus (Linnaeus, 1758) during the lockdown in northern Italy and found that some pairs built nests on disturbed sandy beaches, where they never settled between 2016 and 2019. Similarly, Soto et al. (2021) reported that the low frequency of beach users reduced litter, noise and unnatural odors, while dune vegetation increased in most sites; ghost crabs (Crustacea: Ocypodidae) were also more abundant during the lockdown. A study in Florida found that female loggerhead turtles lay eggs about 50% of the time that they crawl onto shore, but during beach closures, this rate increased to 61% (Stokstad, 2020). Unavailability of food scraps during COVID-19 lockdown can also contribute to displace synatropic species from urban beaches, providing more suitable habitats to more vulnerable species (Gilby et al., 2021). These convergent results show that urban beaches should not be exclusively managed for recreational purposes. Initiatives that focus on wildlife conservation including spatial-temporal controlled beach closures coupled with environmental education actions may increase the biodiversity resilience.

Therefore, our outcomes have several implications for restoration and mitigation actions, assuming that ghost crabs are surrogate species for the monitoring and conservation of sandy beaches wildlife (Barboza et al., 2021). Firstly, management of urban beaches should target recreational activities and some tourist-based management, even because these are more suitable actions than to restrict coastal development. For example, vehicle traffic and grooming, which notably impact beach populations (revised by Costa et al., 2020a), are avoidable on urban beaches. Secondly, even non-pristine beaches could be target of natural passive restoration, at least for mobile or indirect-developing species with oceanic larval stage, such as ghost crabs. The experience of re-establishment on fringing habitats have reinforced the notion that in open marine areas, the most appropriate management action is to allow passive recovery after removing or mitigating the main causes of degradation (Elliott et al., 2007). For direct-developers with limited dispersion ability, passive restoration is probably not viable, demanding specific strategies such as reintroduction and environmental enrichment (Schlacher et al., 2017; Elliott et al., 2007).

Monitoring and conservation initiatives are imperative not only for urban beaches, but also for surrounding non-urban fringes, mainly
because they are usually confined or near to high-developed landscapes (Veloso et al., 2006). This usually disrupts connectivity and weakens the efficiency of protected areas (Ortodossi et al., 2013; Vargas-Fonseca et al., 2016). Our medium-term assessment (eight years) allowed verifying that the peaks of abundance are decreasing overtime in the low-impact beach sector. Possible explanations for this pattern are: (1) increasing of climatic anomalies, including sea surface temperature, frequency and intensity of storms; this has several implication for larvae development, settling and recruitment on beaches (Ortega et al., 2016; Celentano and Defeo, 2016); and (2) spreading of human disturbances, including low-intense vehicle traffic (Davies et al., 2016); previous studies showed that the majority of the ghost crabs crushed by vehicles was found in low-urbanized beaches, where they are more abundant and surface-active (Costa et al., 2020b). Long-term monitoring depicting the role of climatic variables on sandy beach population is a pressing demand, including ghost crabs that are an important study model and ecological-disturbance indicator species on sandy beaches (Schoeman et al., 2014).

5. Conclusions

In conclusion, the COVID-19 pandemic and consequent slowdown in human activity during lockdown periods provided the recovery of ghost crab metapopulations even in the high-impact beaches, where sand vegetation has been suppressed for years. Thus, stressors associated with recreational activities, rather than urbanization and its associated modifications (i.e., artificial light, litter pollution and vegetation suppression), seem to hinder post-recruitment processes. Recreation is the primary service provided by tourist beaches to society, whilst conservation aims are secondary (Schlacher et al., 2008). Thus, to implement severe restriction to tourism and target a complete passive restoration is not feasible. However, initial recovery of indicator species during the COVID-19 anthropause is a strong argument that the sacrifice of urban beaches for touristic purposes is not always necessary.

We agree with Soto et al. (2021) that the recovery capacity observed in several beaches related to wildlife population could be an ecological criterion for setting restoration and mitigation targets on urban beaches. Initiatives with a focus on wildlife conservation including environmental education coupled with sustainable management (e.g. environmental enrichment and manual beach cleaning) and law efforts (surveillance of vehicle traffic) may be effective mitigation actions. Implementation of nature-based tourism, scientific outreach and environmental awareness projects are pivotal, providing a biocentric point of view for beachgoers and political support for beach wildlife conservation.

Ethical standards

None.

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Leonardo Lopes Costa and Carlos Alberto de Moura Barboza. The first draft of the manuscript was written by Leonardo Lopes Costa and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declaration of competing interest

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Data availability

Data will be made available on request.

Appendix 1. Maximum abundance values of the Atlantic ghost crab burrows in low-impact beach sector and in high-impact beach sector in the Grussaí Beach Arc, southeastern Brazil, between 2013 and 2021

Appendix 2. ANCOVA model showing the effect of beach sector and time of pandemic on the burrow abundance of the Atlantic ghost crab *Ocypode quadrata* in in the Grussaí Beach Arc, southeastern Brazil

| Burrow abundance | dF | SS   | MS   | F-value | p    |
|------------------|----|------|------|---------|------|
| Beach sector (BS) | 4  | 5.865| 1.466| 4.681   | 0.002|
| Time of pandemic (TP) | 1  | 2.846| 2.846| 9.085   | 0.004|
| BS x TP           | 4  | 1.296| 0.324| 1.035   | 0.396|
| Residuals    | 70 |      | 0.313|         |      |

| Burrow opening diameter | dF | SS   | MS   | F-value | p    |
|-------------------------|----|------|------|---------|------|
| Beach sector (BS)       | 4  | 0.381| 0.095| 4.438   | 0.003|
| Time of pandemic (TP)   | 1  | 0.217| 0.217| 10.112  | 0.002|
| BS x TP                 | 4  | 0.091| 0.023| 1.063   | 0.381|
| Residuals               | 70 |      | 0.021|         |      |

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