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NOTE

Aftereffects of Hurricanes Irma and Ian on queen conch *Aliger gigas* in the Florida Keys, USA

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ABSTRACT: Hurricanes can have substantial impacts on shallow-water marine habitats and species. Populations of slow-moving benthic species that are subject to depensation such as the queen conch *Aliger gigas* may be particularly vulnerable to hurricanes. The species is protected in Florida (USA), which allowed us to investigate the effects of Hurricanes Irma (2017) and Ian (2022) on the population without the confounding effects of fishing. Adult queen conch density had declined over 80% at sites resurveyed immediately after the passage of Hurricane Irma. Additionally, the sites closest to the eye of Hurricane Irma had a significant increase in the percent cover of sand. The sand mobilized by the storm likely buried numerous conch and caused mortality. Subsequent Florida Keys-wide annual monitoring did not show any substantial recovery in adult density prior to Hurricane Ian. Adult density had declined by ~45% at sites resurveyed after Hurricane Ian. Unlike after Irma, we did not detect any significant correlation in the change to the percent cover of sand with distance from Ian. This was probably because the eye of Hurricane Ian was farther away from the main portion of the Keys than that of Hurricane Irma. Nevertheless, after both hurricanes, adult density dropped below the minimum threshold for mating in the Keys, demonstrating the depensatory implications of hurricanes for conch populations. Consequently, fishery managers must consider the synergistic effects of hurricanes and harvest on exploited populations, especially since the intensity, longevity, and frequency of hurricanes are expected to increase due to climate change.

KEY WORDS: Queen conch · Hurricanes · Depensation · Allee effect · Habitat · Sedimentation

1. INTRODUCTION

Large physical disturbances, such as hurricanes, can have substantial, landscape-scale impacts on marine ecosystems (Jackson 1991, Pimm et al. 1994). The level of ecosystem impact depends on a variety of factors such as cyclonic energy, areal extent, and trajectory (Emanuel 2005, Mallin & Corbett 2006), but powerful hurricanes can shear sessile organisms from the substrate, topple massive boulder corals, bury or excavate large sections of coral reef, and eradicate seagrass beds through burial or erosion (Jackson 1991, Pimm et al. 1994, Fourqurean & Rutten 2004, Wilson et al. 2020, Jones et al. 2022). Such habitat alterations can displace or kill benthic organisms, and depending on the extent of the disturbance, population recovery could be prolonged (Fourqurean & Rutten 2004, Jones et al. 2022). In addition, many populations of slow-moving, benthic species are subject to depensation (i.e. Allee effects, Gascoigne & Lipcius 2004). A population near its depensation threshold may be driven to local extirpation by the

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exacerbating effects of hurricanes (Aalto et al. 2019, White et al. 2021), especially if there is no exogenous source of new recruits.

The queen conch *Aliger gigas* (Linnaeus, 1758), formerly known as *Strombus gigas*, is a gonochoristic marine gastropod that is found in shallow-water habitats throughout the Tropical Western Atlantic including Florida (USA). Reproduction in queen conch is density dependent; the species is vulnerable to depensation if densities fall below threshold values (Delgado & Glazer 2020, Stoner & Appeldoorn 2022, Morris et al. 2023). In Florida, the queen conch is a protected species, with all harvest banned since 1985 (Florida Administrative Code 68B-16.001) partly because of depensatory effects when aggregation densities are <200 adults ha^{-1} (Delgado & Glazer 2020) and larval supply from upstream sources is limited (Delgado et al. 2008, Vaz et al. 2022).

The absence of queen conch harvest in Florida permits the examination of the effects of hurricanes on the density of the species and the corresponding depensatory implications for the population without the confounding effects of fishing. Recently, the Florida Keys experienced the passage of 2 major hurricanes. Hurricane Irma made landfall in the Keys on 10 September 2017 as a Category 4 storm (Fig. 1) on the Saffir-Simpson Hurricane Wind Scale (Cangialosi et al. 2018), and Hurricane Ian passed directly over Dry Tortugas National Park, 113 km west of the main portion of the archipelago, on 27 September 2022 as a Category 3 storm (Fig. 1) (Bucci et al. 2023). Prior to the passage of both storms, we had quantified queen conch densities and characterized benthic habitat at randomly selected locations within queen conch aggregations as part of our annual monitoring. This provided us the opportunity to quantify the acute effects of each storm on adult queen conch density through before and after surveys as well as evaluate the long-term effects of Hurricane Irma.

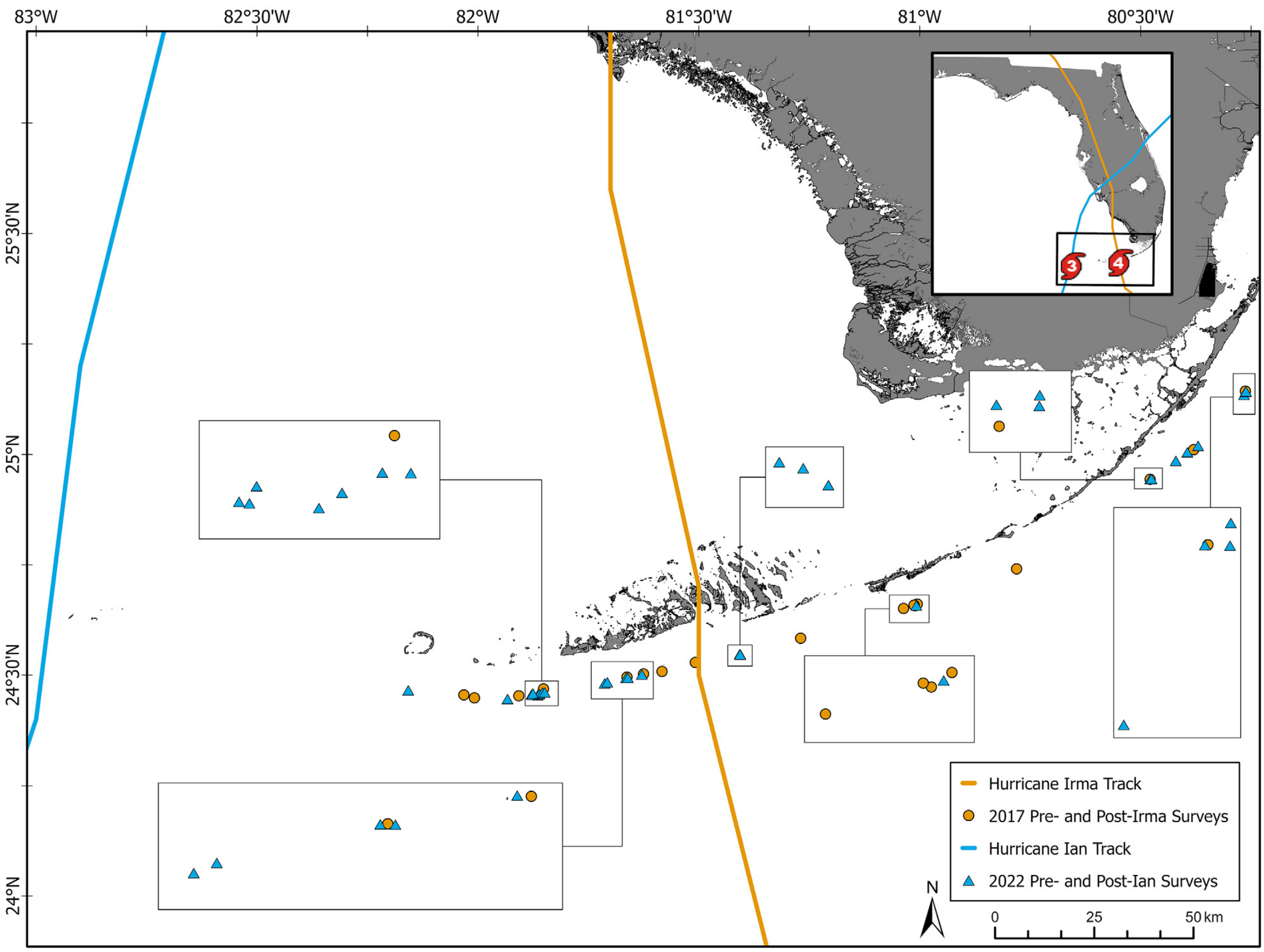

Fig. 1. Tracks of Hurricanes Irma and Ian across the Florida Keys and fixed queen conch survey sites. Cyclonic symbols in the inset map represent the hurricane's category on the Saffir-Simpson wind scale at time of landfall

2. MATERIALS AND METHODS

2.1. Queen conch and habitat surveys

Queen conch in the Florida Keys have a clumped distribution and are often found in aggregations (Delgado & Glazer 2020). As part of our annual monitoring, we divided the 139 known aggregations in the Florida Keys (Fig. 2) into 100 m × 100 m cells (n = 1071) and randomly selected a subset of these cells to survey from 2017 to 2022 (n: 2017 = 85, 2018 = 77, 2019 = 70, 2020 = no surveys due to COVID, 2021 = 160, 2022 = 108). Monitoring was conducted from March through September. In each cell, 4 nonoverlapping 25 m × 2 m transects (1 in each cardinal direction) were surveyed by SCUBA divers. All adult queen conch, defined as having a fully flared lip > 10 mm in thickness, were enumerated to calculate the density of adult queen conch within the cell. Water depth at the centroid of the cell was also recorded.

Habitat data were also recorded along the 4 transects in each cell based on 3 categories derived from Glazer & Kidney (2004): (1) sand, defined as particles visually estimated to be less than ~12 mm in size, (2) rubble, defined as particles visually estimated to be ~12 mm or larger, and (3) seagrass, either monospecific or mixed-species beds. A habitat category was denoted at the start of the transect. When the habitat changed, the new habitat was recorded along with the position (meter number along the transect) of the change. This allowed us to calculate the percent cover of each habitat category along the transects in a cell.

Post-hurricane assessments were conducted after Hurricanes Irma and Ian passed the Florida Keys. Not all cells were resurveyed due to time constraints. We resurveyed 17 cells from October to December 2017 (Hurricane Irma) and 28 cells in October 2022 (Hurricane Ian; Fig. 1). Resurveyed cells were haphazardly chosen, but an attempt was made to ensure their spa-

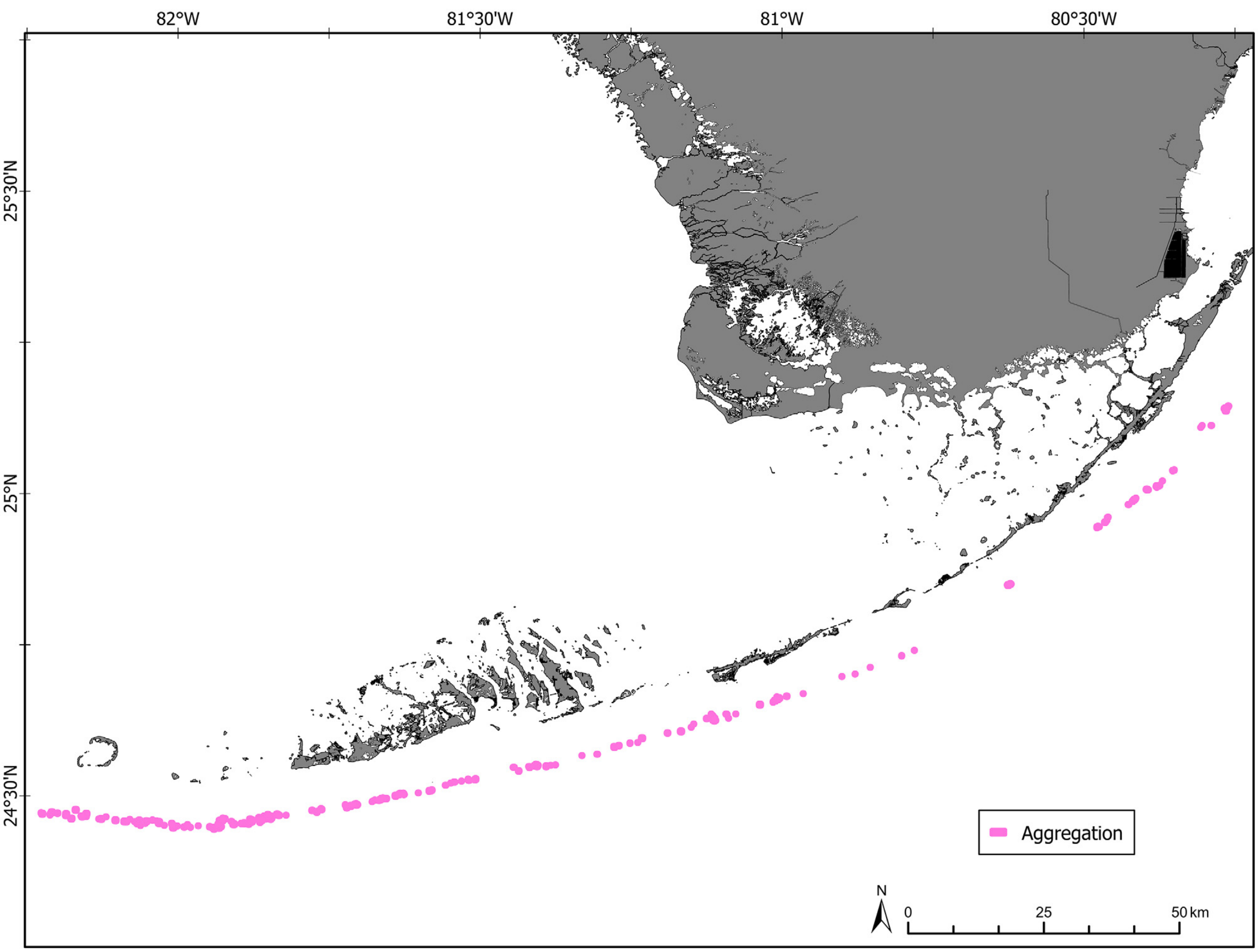

Fig. 2. Known queen conch aggregations (n = 139) in the Florida Keys (aggregation not depicted to scale)

tial distribution spanned the length of the archipelago. The resurveyed cells will be referred to as 'fixed sites' hereafter.

2.2. Statistical analyses

To evaluate the acute effect of the hurricanes, we compared pre- and post-hurricane adult queen conch density at our fixed sites using Welch's unequal variances *t*-test for Hurricane Irma and Hurricane Ian separately. We used partial correlations to determine if the distance from the storms, with water depth as a covariate, influenced adult density. The percent change in density — (post-hurricane − pre-hurricane) / pre-hurricane — was calculated at each fixed site. Distance (km) from the eye of the storm to each fixed site was calculated using ArcGIS Pro 3.1.1. Measurements were taken from the center of the hurricane eye based on the position of the storm on the morning of 10 September 2017 for Hurricane Irma and 27 September 2022 for Hurricane Ian. Separate partial correlations were run for each hurricane.

We also calculated the change in the percent cover of sand, rubble, and seagrass at each fixed site after the passage of the storms. We used partial correlations to assess if the distance from the storms, once again using water depth as a covariate, influenced habitat. Separate partial correlations were run for each hurricane.

To evaluate any longer-term effects from the passage of Hurricane Irma on adult queen conch density, we compared the mean adult density from our annual monitoring from 2017 to 2022. An aligned rank transform (ART) ANOVA was used to assess potential differences in adult density across time. Post hoc, Bonferroni-adjusted, multiple-comparison *t*-tests were used to determine which years differed. All tests were performed in R version 4.0.3 (2020-10-10), and results were considered significant at $p < 0.05$.

3. RESULTS

3.1. Hurricane Irma

The density of adult queen conch at our pre- and post-Hurricane Irma fixed sites showed a significant decline (Welch's *t*-test: $t_{23.4} = -3.98$, $p < 0.001$; Fig. 3A). Mean ± SE density decreased from 750 ± 138 to 138 ± 68 adults ha^{-1} (Fig. 3A), an immediate post-Irma decline of over 80% (Hedge's effect size =

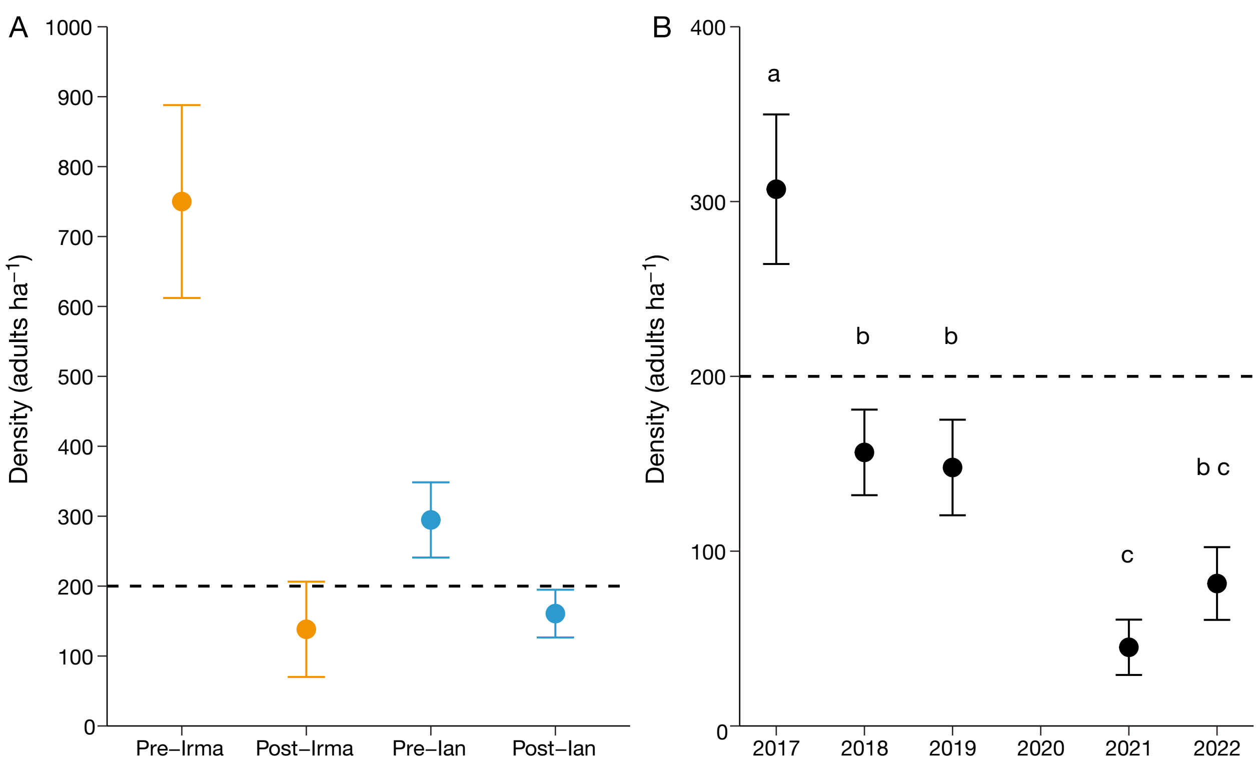

Fig. 3. Mean (±SE) density of adult queen conch at (A) pre- and post-hurricane fixed sites and (B) Florida Keys-wide annual monitoring sites (2017–2022). Non-shared letters indicate a significant difference among groups (Bonferroni-adjusted *t*-test, $p \le 0.05$). Dotted line: threshold density below which no mating is observed in the Florida Keys (Delgado & Glazer 2020)

1.33). The closest of our 17 fixed sites was 3 km from the eye of Hurricane Irma; the farthest was 144 km. Water depth ranged from 2 to 16 m. However, there was no significant correlation between the percent change in adult density and the distance from the storm with water depth as a covariate (partial correlation: $\rho_{14} = 0.329$, $p = 0.746$).

The partial correlations between the changes in the habitat categories at our fixed sites and the site's distance from the center of Hurricane Irma were contingent on the habitat type. The change in the percentage of sand showed a significant negative association with distance from Hurricane Irma, with those fixed sites closest to the eye of the storm having a higher percentage of sand post-hurricane (partial correlation: $\rho_{14} = -3.11$, $p = 0.007$; Fig. 4A). In contrast, the change in rubble showed a significant positive association with distance from Hurricane Irma (partial correlation: $\rho_{14} = 2.35$, $p = 0.033$; Fig. 4B). There was no significant association between the change in seagrass and the distance from the storm (partial correlation: $\rho_{14} = 0.661$, $p = 0.174$; Fig. 4C).

3.2. Hurricane Ian

Much like Hurricane Irma, the density of adult queen conch at our pre- and post-Hurricane Ian fixed sites showed a significant decline after the storm's passage (Welch's *t*-test: $t_{45.7} = -2.10$, $p = 0.041$; Fig. 3A) even though the fixed sites for Hurricane Ian were considerably farther away from the center of the storm compared to those for Hurricane Irma. Mean ± SE density decreased from 295 ± 54 to 161 ± 34 adults ha^{-1} (Fig. 3A), a ~45% decline (Hedge's effect size = 0.554). Distances from Hurricane Ian for our fixed

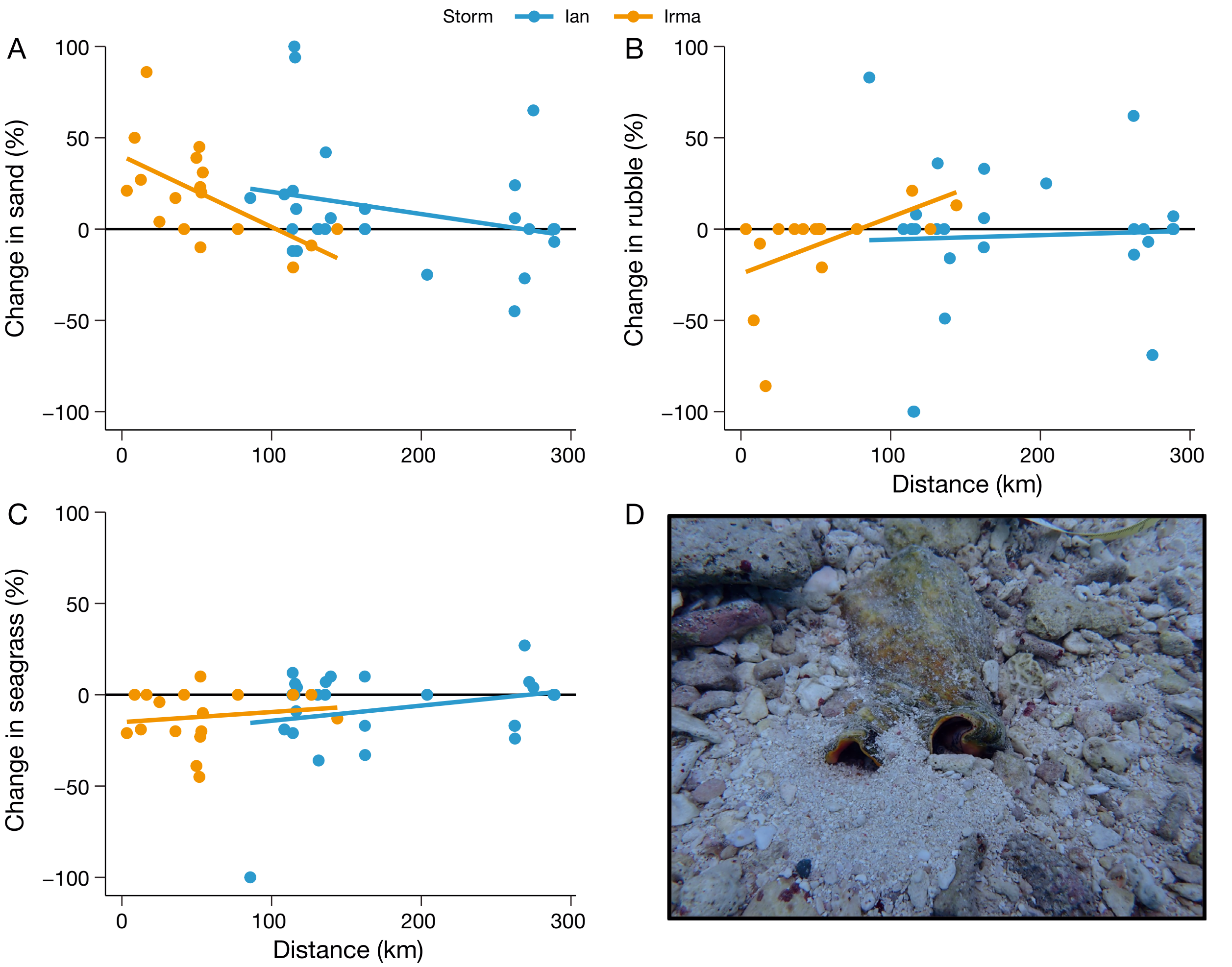

Fig. 4. Association between the % change in (A) sand, (B) rubble, and (C) seagrass at fixed sites and the distance of each site from the center of either Hurricane Irma or Hurricane Ian. (D) Partially buried queen conch at one of our fixed sites after the passage of Hurricane Ian

sites ranged from 86 to 289 km; water depth ranged from 1.5 to 10.5 m. As with Hurricane Irma, there was no significant correlation between the percent change in adult density and the distance from Hurricane Ian including water depth as a covariate (partial correlation: $\rho_{25} = -0.077$, $p = 0.938$).

The partial correlations between the changes in habitat categories at our fixed queen conch survey sites and the distance from the center of Hurricane Ian were not significant. Neither the change in the percentage of sand (partial correlation: $\rho_{25} = -1.14$, $p = 0.262$; Fig. 4A), rubble (partial correlation: $\rho_{25} = 0.041$, $p = 0.967$; Fig. 4B), nor seagrass (partial correlation: $\rho_{25} = 1.23$, $p = 0.228$; Fig. 4C) had a significant association with the distance from Hurricane Ian with water depth as a covariate.

3.3. Annual monitoring

From 2017 through 2022, we counted 1290 adult queen conch in 500 surveys. There was a significant difference in the mean density of adults across our survey period (ART ANOVA: $F_{4,495} = 35.03$, $p < 0.001$; Fig. 3B). The highest mean ± SE density was recorded in 2017 and was 307 ± 43 adults ha^{-1} (Fig. 3B). In 2018, after Hurricane Irma had passed through the Florida Keys, mean density declined to 156 ± 25 adults ha^{-1} (Fig. 3B). Mean density declined further in 2021 to 45 ± 16 adults ha^{-1} before increasing slightly in 2022 to 81 ± 21 adults ha^{-1} (Fig. 3B).

4. DISCUSSION

Hurricanes can rapidly cause major changes to marine habitats (Jackson 1991, Pimm et al. 1994, Fourqurean & Rutten 2004). After Hurricane Irma, marine habitats throughout the Florida Keys experienced sedimentation or erosion leading to a decline in many marine and coastal species (Kobelt et al. 2020, Radabaugh et al. 2020, Wilson et al. 2020). Our results similarly demonstrate the acute effects that hurricanes can have on shallow-water habitats and organisms, especially after Irma suspended and redeposited sand, burying not only other habitats (i.e. rubble) but also queen conch (Fig. 4D). The sand mobilized by Hurricanes Irma and Ian was at least partially responsible for the declines in adult density after both storms.

Mean adult queen conch density fell below the 200 adults ha^{-1} threshold for mating in the Keys (Delgado & Glazer 2020) after both hurricanes (Fig. 3A). Our long-term, annual monitoring also showed a decline in adult density below the minimum mating threshold from which the population in the Florida Keys has yet to recover 5 yr after Hurricane Irma (Fig. 3B). This lack of recovery is not unexpected given that the species has density-dependent reproduction (Delgado & Glazer 2020) and reaches sexual maturity at ~4 yr of age (Stoner & Appeldoorn 2022). A greater age at sexual maturity can extend recovery times and makes a species particularly vulnerable to both harvest (Anderson et al. 2008) and catastrophic disturbances. Furthermore, since the queen conch population in the Keys receives very little recruitment from upstream sources (Delgado et al. 2008, Vaz et al. 2022) and is therefore reliant on local retention, the depensatory mechanisms triggered by the hurricanes will probably prolong recovery. This is also a likely issue for exploited stocks; larval connectivity among queen conch populations throughout the Tropical Western Atlantic may be limited (Delgado et al. 2008, Kough et al. 2017, Vaz et al. 2022), making the conservation of local source populations critical.

The vulnerability of queen conch to hurricanes in Florida where the species is protected from harvest has profound implications to the sustainability of exploited stocks elsewhere in its range. Queen conch have probably been affected by hurricanes throughout time (Stoner & Appeldoorn 2022), but the predicted increase in the intensity, longevity, and frequency of hurricanes due to climate change (Emanuel 2005, Webster et al. 2005) will be an added challenge to fishery managers. Indeed, hurricanes can aggravate the effects of exploitation and have been linked to declines in queen conch harvest as well as slowing queen conch recovery by damaging juvenile nursery habitat (reviewed by Stoner & Appeldoorn 2022). Marine protected areas (i.e. spatial management) may provide a buffer against future hurricanes if appropriately placed and if sufficient in number (Aalto et al. 2019, White et al. 2021). Reducing fishing pressure after a hurricane may also help mitigate the impact on exploited stocks (Aalto et al. 2019). Fishery managers must be cognizant of the detrimental synergistic interaction between hurricanes and harvest to ensure the proper management and persistence of exploited queen conch populations, especially since the species is particularly susceptible to depensatory mechanisms.

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