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ITS EXPANDED RANGE

**The density of the Atlantic marsh fiddler crab (*Minuca pugnax*,
Smith, 1870) (Decapoda: Brachyura: Ocypodidae) in its expanded
range in the Gulf of Maine, USA**

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ABSTRACT

The Atlantic marsh fiddler crab, *Minuca pugnax* (Smith, 1870), is a climate migrant that recently expanded its range northward into the Gulf of Maine. We tracked the *M. pugnax* population within the Great Marsh, in northeastern Massachusetts, USA, since it was first detected in 2014

using burrow counts. Because burrow counts can overestimate fiddler-crab density, we used camera traps to determine the relationship between burrow densities and fiddler-crab densities in 2019. The burrow count surveys show a six-fold increase in the density of *M. pugnax* in the Great Marsh from 2014 to 2019. Results indicates that the fiddler-crab population in the expanded range is established and growing. Based on burrow counts, however, the density of *M. pugnax* in the expanded range (6 burrows m⁻²) remains much lower than those found in the historical range (up to 300 burrows m⁻²). Based on the camera traps, we determined that burrow counts overestimated fiddler-crab densities by 47% in 2019. There was, on average, one crab detected for every two burrows observed. This result suggests that estimates of densities of *M. pugnax* based on burrow counts should be reduced by half. *Minuca pugnax* is an ecosystem engineer that can influence saltmarsh functioning and the magnitude of that influence is related to its density. Our results imply that the populations of *M. pugnax* in the expanded range are currently having minor impacts on marshes relative to larger populations in the historical range, but their impact will increase as the populations grow.

Key Words: climate migrant, ecosystem engineer, ocean warming, range expansion, range shift, *Uca pugnax*

INTRODUCTION

The Atlantic marsh fiddler crab, *Minuca* (= *Uca*) *pugnax*, Smith 1870, is a small burrowing crab that lives in intertidal salt marshes found along the east coast of the United States (Williams, 1984; Johnson, 2014; Johnson *et al.*, 2019). As an ecosystem engineer (*sensu* Jones *et al.*, 1994), *M. pugnax* has a strong influence on saltmarsh functioning, physical structure, food webs, and biodiversity (Katz, 1980; DePatra & Levin, 1989; Thomas & Blum, 2010). For instance, fiddler

crab bioturbation can turnover approximately 18% of the surface sediments within a salt marsh annually (Katz, 1980). *Minuca pugnax* burrows oxygenate the sediments, increasing both redox potential and soil drainage (Michaels & Zieman, 2013), which can accelerate belowground decomposition (Holdredge *et al.*, 2010). Crabs can enhance the aboveground biomass (Gittman & Keller, 2013), but decrease the belowground biomass (Thomas & Blum, 2010) of the smooth cordgrass, *Spartina alterniflora* Loisel., a foundational halophyte in Atlantic salt marshes that controls the physical structure of the marsh and fuels the food web (Bertness, 1985).

Minuca pugnax recently expanded its range into the Gulf of Maine as a result of ocean warming (Sanford *et al.*, 2006; Johnson, 2014), which makes it a climate migrant (Johnson *et al.*, 2020). The historical northern limit for *M. pugnax* was Cape Cod, Massachusetts, USA (Williams, 1984). Their northern limit is set by the thermal tolerance of its planktonic larvae (Sanford *et al.*, 2006), and the Gulf of Maine (i.e., north of Cape Cod) was historically too cold for the larvae to complete their life cycle. The Gulf of Maine is one of the fastest warming water bodies on the planet (Pershing *et al.*, 2015), and as a result of recent warming, has allowed *M. pugnax* to spread and establish as far north as New Hampshire and southern Maine (Johnson, 2014; DSJ, unpublished data). *Minuca pugnax* is currently the only burrowing crab that inhabits salt marshes in the Gulf of Maine. Because *M. pugnax* can influence saltmarsh functioning and the strength of that influence is likely related to their densities (Parker *et al.*, 1999), it is critical to track changes in densities in its expanded range in the Gulf of Maine.

Four methods are commonly used to estimate densities of fiddler crabs: pitfall traps, burrow excavations, visual surveys, and burrow counts with quadrats. These methods have advantages and disadvantages. Pitfall traps are inexpensive to make and easy to deploy, which are ideal for surveys across multiple ecosystems (Wasson *et al.*, 2019). Traps, however, provide

relative abundances, not density estimates (e.g., number m⁻²) (Skov *et al.*, 2002). They also require predator exclusion since the traps are flush with the marsh surface and leave the crabs vulnerable. Excavating burrows within a known area is the most accurate method used to estimate the density of fiddler crabs, as it can provide a direct estimate of densities (Jordão & Oliveira, 2003). Manually excavating burrows, however, is destructive as some fiddler-crab species have unbranched burrows as deep as 100 cm (Chen *et al.*, 2017). Due to the global distribution of fiddler crabs, excavation may not be viable in areas where the sediment is hard to penetrate, such as in mangroves, or in sensitive or government-protected habitats. Visual surveys can be conducted using observers equipped with binoculars or through camera trapping. Unlike burrow excavation and pitfall traps, visual surveys are non-destructive. They rely on surface activities of crabs, however, which can vary spatially and between reproductive seasons, which can lead to underestimates of fiddler-crab densities (Skov & Hartnoll, 2001). Counting burrows within a quadrat is the most common practice in surveying fiddler-crab densities since it is quick, inexpensive, and non-destructive. Burrow counts, however, may overestimate fiddler crab densities since burrows are periodically abandoned (Macia *et al.*, 2001). Furthermore, density estimates from counting burrows could be unreliable in areas with multiple species of fiddler crabs since the occupant of the burrow cannot be identified (Skov *et al.*, 2002). Each method has limitations, but when combined they can improve density estimates.

We had two objectives for this study. Our first objective was to quantify the densities of *M. pugnax* within the Great Marsh in northeast Massachusetts, which is in its expanded range. We used burrow counts to track the density of *M. pugnax* since its detection in the Great Marsh in 2014. In the historical range it is difficult to determine the species occupying the burrows since *M. pugnax* co-occurs with other burrowing crabs such as the red-jointed fiddler crab,

Minuca minax (Le Conte, 1855), the sand fiddler crab, *Leptuca pugilator* (Bosc, 1802), and the purple marsh crab, *Sesarma reticulatum* (Say, 1817). These species, to our knowledge, are not present in the expanded range. Our second objective was to measure the relationship between burrow counts and fiddler-crab densities. To do so we combined burrow counts with camera trapping. Although excavation is the most accurate method used to estimate the density of fiddler crabs (Jordão & Oliveira, 2003), excavation could not be used in the Great Marsh because crabs are exclusively found on the marsh edge, which easily erodes when disturbed (Deegan *et al.*, 2012). We used camera traps because they do not destroy the marsh and allow us to improve our estimate of fiddler-crab densities.

MATERIALS AND METHODS

Site description

Our study was conducted at a Long-Term Ecological Research Site (LTER) in the salt marshes of the Plum Island Estuary (PIE) in northeastern Massachusetts, which is near the current northern limit of the expanded range of *M. pugnax* (Johnson, 2014). It is part of the Great Marsh, the largest expanse of intertidal marsh found in the northeastern United States. The mean tide of the Plum Island Sound Estuary is 2.6 m with mean annual salinity ranging from 22–27 ppt (Johnson *et al.*, 2007). These salt marshes exhibit plant zonation common to east-coast salt marshes with tall form *Spartina alterniflora* forming a narrow (2–3 m) band in the frequently flooded intertidal nearest the marsh edge and extensive mixed meadows of salt hay, *Spartina patens* (Aiton) Muhl, and spike grass, *Distichlis spicata* (L.) Greene, in the high marsh above mean high tide (Johnson *et al.*, 2016). In the historical range (i.e., south of Cape Cod), *M. pugnax* can be found in the *S. patens* and *D. spicata* habitats (e.g., Luk & Zajac, 2013; Raposa *et*

al. 2018). In the Great Marsh, however, *M. pugnax* is found exclusively in the marsh edge, in the narrow *S. alterniflora* habitat (Johnson, 2014).

Burrow densities in the Great Marsh

To quantify changes in the density of fiddler crabs over time, we conducted annual burrow-count surveys in six marshes in May since 2014, when *M. pugnax* was first observed in these marshes (Fig. 1). At each marsh, we established a 200 m transect parallel to a tidal creek and selected 10–20 points along that transect using a random number generator. In 2014, 10 points were selected per marsh, 20 per marsh starting in 2015. We were unable to collect data for one marsh in 2017 (see Figure 2 for *N* per creek). At each point along the transect, a 0.0625 m² quadrat was placed at the meter point, 25 cm inland from the marsh edge to capture the preferred habitat of *M. pugnax*. We counted and recorded the number of fiddler crab burrows in each quadrat, any fiddler crabs seen walking on the sediment surface within the quadrat or within a burrow in the quadrat, number of live and dead *S. alterniflora* stems and any other invertebrates. Activity of any burrows in the quadrat was noted and determined by the presence of fecal pellets in front of the burrow opening. Only burrows greater than 1 cm in diameter were counted.

The burrows of *M. pugnax* cannot be confused with the burrows of other crabs because it is the only burrowing crab in this marsh. Other burrowing crabs found in the marshes in the historical range (such as the red-jointed fiddler crab *M. minax*, the sand fiddler crab *L. pugilator*, the purple marsh crab *Sesarma reticulatum*) are absent from these marshes. Other burrowing species present in the tall-form *S. alterniflora* zone in the Great Marsh include infaunal polychaetes and amphipods, whose burrows are ≤ 1 mm in diameter (Johnson *et al.*, 2007). The

ribbed mussel, *Geukensia demissa* (Dillwyn, 1817), is also present but their shells are either near or above the sediment surface.

Camera trapping

To examine the relationship between burrow density and crab density, we deployed 29 cameras (2 camera brands: SJCAM SJ4000 (SJCAM, Shenzhen, China) and Campark ACT74 (Campark Electronics, Shenzhen, Guangdong, China)) in combination with burrow counts in August 2019 at low tide. Quadrats were approximately one meter from the marsh edge in monotypic stands of *S. alterniflora*. The four corners of the 0.0625 m² quadrats were marked using wooden stakes. We clipped all vegetation within the quadrat flush with the sediment for a clear field of view for the camera. Fiddler-crab burrows that were counted by the observer were marked with toothpicks placed horizontally on the sediment surface. The toothpicks marked which burrows were counted. Mounts were constructed of PVC in an upside down “L” configuration to give the camera an unobstructed overhead view of the quadrat. The camera mounts were placed adjacent to the quadrat with the camera’s field of view looking down at the marked quadrat. The camera was placed 30 cm above of the sediment surface. The batteries of the cameras last approximately 120 min, but battery life varied, so we standardized recording time to 90 min.

Video footage was reviewed using VLC Media software (VideoLAN, Paris, France). Each video was viewed initially for 90 min at 1× speed and then a second time at 10× speed. Crabs were counted as present if they emerged from burrows that were previously marked with toothpicks. Emergence was defined as viewing, at minimum, their legs emerging from the burrow. Crabs that wandered in from outside of the plots were not counted. In two instances, juvenile crabs emerged from burrows that were not marked with toothpicks. These crabs were

not counted because their burrows were < 1 cm and burrows of that size are not counted in the annual surveys.

Statistical analysis

We fitted a generalized linear model to determine the statistical relationship between the observed number of crabs on video (response variable) and burrow counts (predictor variable). The data did not follow the assumptions of normality or homogeneity. A Quasi-Poisson model was used to determine under- or overdispersion of the data. This model indicated that the data were not zero-inflated yet were underdispersed (i.e., more uniform). A generalized linear model assuming negative binomial distribution was used to determine the statistical relationship. Analyses were conducted using R statistical software (R Core Team, 2019).

RESULTS

Burrow densities in the Great Marsh

The mean burrow density for *M. pugnax* increased six-fold from 2,014 (1 m⁻²) to 2,019 (6 m⁻²) (Fig. 2).

Camera trapping

Based on camera traps, we observed 49 crabs and 92 burrows. We did not observe more than one crab emerging from a single burrow. Fiddler crabs were observed in 53% of the burrows.

Observed crab densities increased with burrow densities, but this trend is not driven by burrow counts ($P = 0.471$) (Fig. 3). The time it took for the first fiddler crab to emerge from their burrow

on video ranged between 1 min and 27 s to 23 min and 13 s with an average emergence time of 9 min and 21 s.

Other observations

The camera traps allowed us to make additional observations that highlight another benefit of using camera traps. For instance, we observed fighting between male *M. pugnax*; and a green crab, *Carcinus maenas* (Linnaeus, 1758), walked across one plot. Although typically found in the subtidal, *C. maenas*, do come onto the marsh at high tide to feed (Deegan *et al.*, 2007). We observed a saltmarsh sparrow, *Ammodramus caudacutus* (Gmelin, 1788), walking through another plot. At that time, the male *M. pugnax* on the surface did not escaped into its burrow until 3 s after the bird entered the plot. Saltmarsh sparrows are not known predators of *M. pugnax*.

DISCUSSION

Burrow densities of *M. pugnax* in the Great Marsh have increased, on average, by six-fold over five years. Despite this, the burrow densities found in the Great Marsh (mean 6 burrows m⁻² in 2019) are low when compared to burrow densities found within the historical range (13–308 burrows m⁻²; Teal, 1958; Wolf *et al.*, 1975; Aspey, 1978; McCraith *et al.*, 2003; Smith & Tyrrell, 2012; Luk & Zajac, 2013; Smith, 2015; Raposa *et al.*, 2020). Because the impact a species has on its environment is a function, in part, of its density (Parker *et al.*, 1999), the impacts *M. pugnax* has on saltmarsh functioning in the Great Marsh may be small now but increasing as the population grows.

Our camera-trap data indicate that our burrow counts overestimated fiddler-crab densities by 47%. If our estimates are correct, then there is, on average, one crab for every two burrows. Similarly, burrow counts of the mangrove fiddler crab, *Austruca annulipes* (Milne Edwards, 1837) overestimated crab density from 25% to 46% due to the presence of unoccupied burrows (Macia *et al.*, 2001; Skov *et al.*, 2002). Burrow counts commonly overestimate the true densities of other burrowing animals such as other crustaceans, small mammals, and birds (Butler & Bird, 2007; Sardà & Aguzzi, 2012; Sutherland & Dann, 2012) due to abandoned burrows. Burrow counts are widely used to estimate the density of fiddler crabs (Macia *et al.*, 2001; McCraith *et al.*, 2003; Luk & Zajac, 2013; Smith, 2015; Raposa *et al.*, 2020). If our estimates are accurate, our results suggest that estimates of the density of *M. pugnax* based on burrow counts should be cut in half.

We acknowledge the limitations of our camera trapping. The camera traps may have underestimated crab densities by not recording ovigerous females since they tend to have long incubation periods in their burrows and emerge less often than males (Skov *et al.*, 2002). Although crabs emerged, on average, after 9 min, some crabs may have taken longer than 90 min to emerge. Thus, our estimate of one crab for every two burrows for *M. pugnax* may be conservative. The quantification of excavations is one of the most accurate methods for estimating the density of fiddler-crab populations (Jordão & Oliveira, 2003). The burrows of *M. pugnax* in the Great Marsh are found exclusively on the marsh edges that are easily eroded (Deegan *et al.*, 2012). The burrows can be as deep as 60 cm so excavating over half a meter for 29 plots to estimate crab density would have sacrificed marsh habitat for the sake of accuracy. We instead sacrificed an unknown degree of accuracy for the sake of protecting the marsh. Although camera trapping may not be perfect, it does provide a better estimate of crab densities

than burrow counts alone. We suggest that camera trapping can improve estimates of burrow counts for estimating the density of burrowing animals in sensitive habitats.

Marine ecosystems are severely understudied when it comes to climate migrants and their potential impacts on their recipient habitats (Lejeusne *et al.*, 2010). Future studies are needed to measure their potential impacts on ecosystem functioning in their expanded range. *Minuca pugnax* can affect decomposition, above- and belowground plant biomass, biogeochemistry, and animal communities in salt marshes (Bertness, 1985; DePatra & Levin, 1989; Thomas & Blum, 2010; Michaels & Zieman, 2013). Our results indicate that *M. pugnax* has an established and growing population in their expanded range into the Great Marsh. Their densities are currently low, and their impacts on marsh functioning are likely minor. We predict that as the density of *M. pugnax* in these marshes grows, so too will their impacts on the functioning of the salt marsh.

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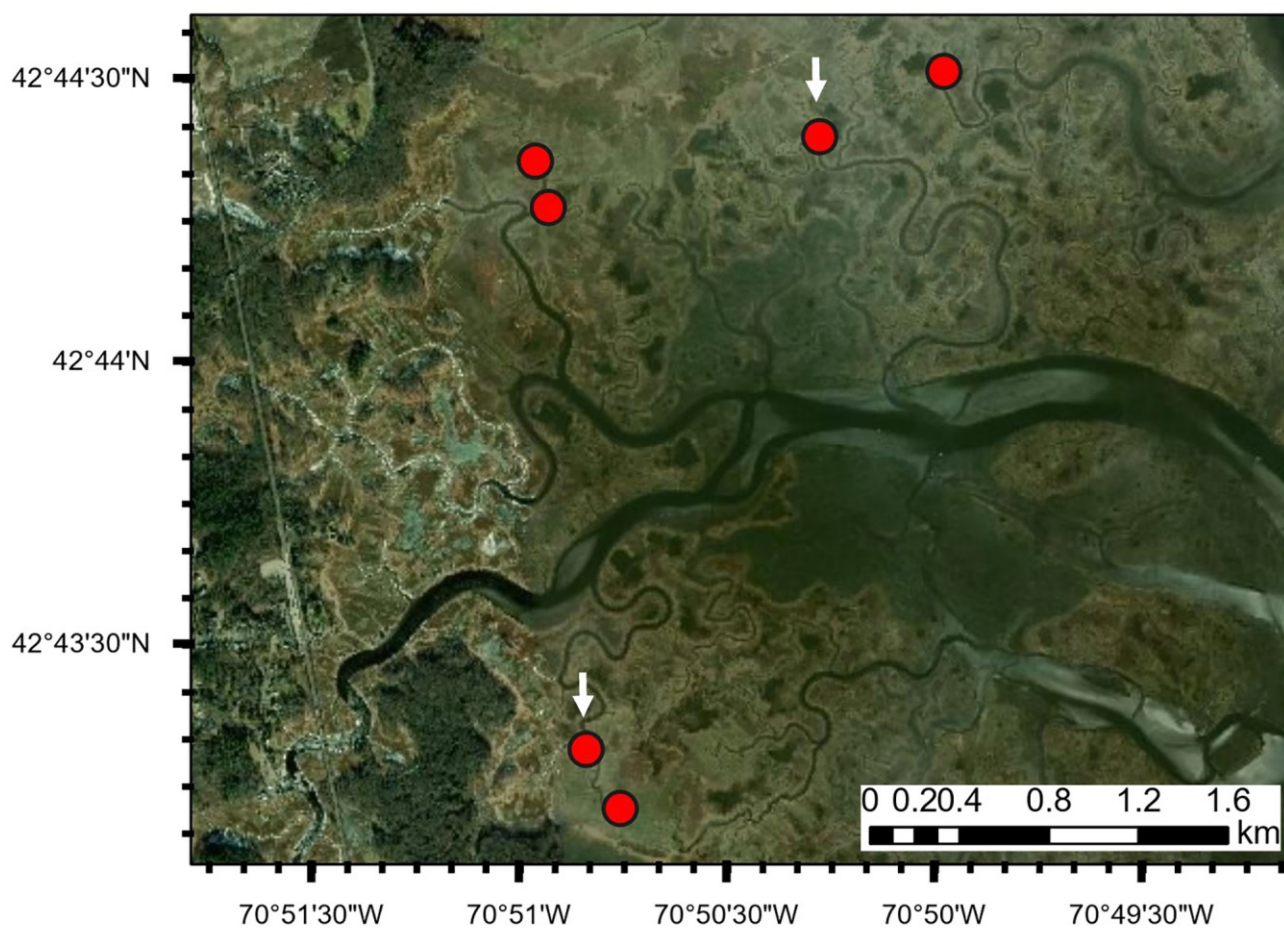
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FIGURE CAPTIONS

Figure 1. Map of the Great Marsh, Massachusetts, USA indicating locations for burrow-count surveys (red circles). White arrows point to locations where cameras were deployed in 2019.

Figure 2. Mean number of *Minuca pugnax* burrows m^{-2} for years 2014–2019. Error bars represent standard error of the mean. $N = 60$ for 2014, $N = 120$ for 2015–2019 except for 2017 ($N = 100$).

Figure 3. The relationship between the number of observed individuals of *Minuca pugnax* and the number of burrows in quadrats, 0.0625 m^{-2} ($N = 29$). Each data point represents a whole number for each variable. Because many data points were the same, they have been jittered to reveal them all.



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384 Figure 1

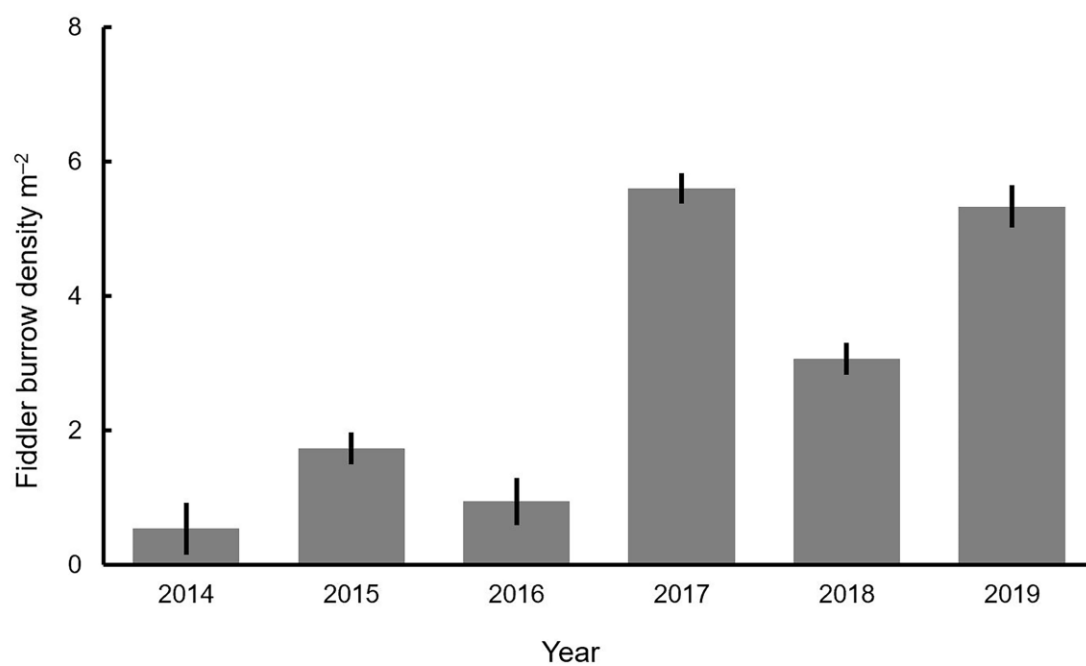


Figure 2

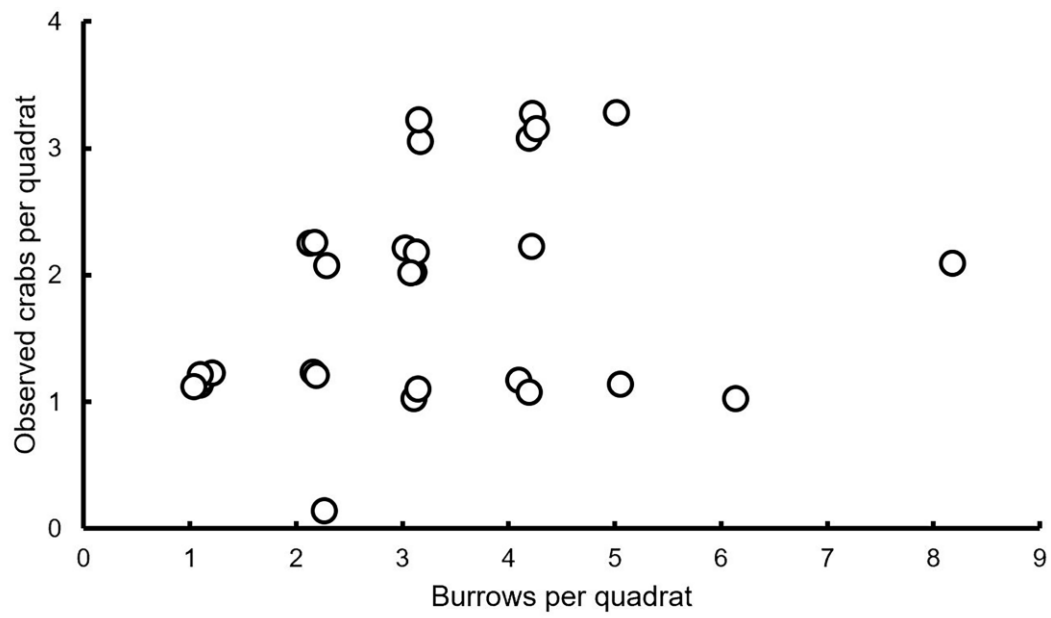


Figure 3