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Range expansion of the lady crab *Ovalipes ocellatus* Herbst, 1799 (Decapoda: Brachyura: Portunidae) due to ocean warming

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ABSTRACT

Ocean warming caused by global climate change is driving range expansions and shifts in marine species. The lady crab *Ovalipes ocellatus* (Herbst, 1799) is generally found south of Cape Cod, Massachusetts, USA with a disjunct population in the southern Gulf of St. Lawrence, Canada, but absent in the Gulf of Maine and Bay of Fundy. Here we present trawl survey data, recent crowd-sourced observations, and temperature data that suggest a range expansion of *O. ocellatus* north of Cape Cod into the Gulf of Maine and Bay of Fundy after a marine heat wave in 2012. Crowd-sourced observations of lady crabs increased in the Gulf of Maine at the same time that abundances surged after 2000. In the Gulf of Maine, *O. ocellatus* was found as far north as Freeport, Maine (43°48'17.136"N, 70°6'30.9594"W) and in the Bay of Fundy as far north as Alma, New Brunswick, Canada (45°36' 13.6794"N, 64°56'29.184"W). We also extend the southern limit of *O. ocellatus* to St. Augustine, Florida, USA (29°42'9.432"N, 81°13'56.028"W). The recent observations of *O. ocellatus* in the northwestern Atlantic and higher abundances combined with continued warming in this area may signal a permanent expansion of this species. If so, a key goal for ecologists and managers will be to understand the effects of *O. ocellatus* on food webs and fisheries in the Gulf of Maine and Bay of Fundy.

KEYWORDS: calico crab, Crustacea, climate change, climate migrants

INTRODUCTION

In response to climate change, species can shift, contract, or expand their ranges. Many marine species are expanding or shifting their ranges poleward, largely due to ocean warming (Johnson 2014, 2015; McBride, 2018; Rosenberg, 2018, Lenoir *et al.*, 2020; Silliman *et al.*, 2025). Cape Cod, Massachusetts, USA is an important zoogeographic break between the Acadian and Virginian provinces (Allee, 1923; Sanford *et al.*, 2006). It is the northern limit for many marine species in the western Atlantic. The Gulf of Maine, which is north of Cape Cod, is one of the fastest-warming areas in the world due to global climate change (Pershing *et al.*, 2021), warming faster than 99.9% of the global ocean between 2004–2013 (Pershing *et al.*, 2015). The Gulf of Maine experienced a severe marine heatwave in 2012, which constituted one of the largest and most persistent sea-surface temperature anomalies on record in the region (Scattergood, 1960; Pershing *et al.*, 2013). As a consequence, several species expanded their range north into the Gulf of Maine, likely as a result of this warming, including a fiddler crab *Minuca pugnax* (Smith, 1870), the blue crab *Callinectes sapidus* (Rathbun, 1896), and the black sea bass *Centropristis striata* (Linnaeus, 1758) (Johnson, 2014, 2015; McBride, 2018). Given the continued warming in the Gulf of Maine, it is likely that other range expansions are occurring in this region.

The lady, or calico, crab *Ovalipes ocellatus* (Herbst, 1799) is a swimming crab (family Portunidae) with a distinctive calico-patterned carapace. The historical limit of the species in the United States is generally accepted as Cape Cod and Georges Bank, with an isolated, disjunct population in the southern Gulf of St. Lawrence, Canada (Stehlik *et al.*, 1991; Burchsted & Burchsted, 2006; Voutier & Hanson, 2008). Williams (1984) and Nizinski (2003) gave the range as Prince Edward Island, Canada to Georgia, USA; however, these authors omit the apparent gap in the Gulf of Maine and the Bay of Fundy. Burchsted & Burchsted (2006) noted a local population in northeastern Massachusetts in the 1990s, but it did not persist. Recent observations since the 2012 marine heatwave in the Gulf of Maine, however, suggest that *O. ocellatus* has returned. Here we document the potential range expansion of *O. ocellatus* into the Gulf of Maine and the Bay of Fundy.

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MATERIALS AND METHODS

We conducted a search of occurrence records from the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.3hrdru) within the polygon 41°42'–45°51'N, 76°–61°W from 1852 to 2024. GBIF occurrence records include observations from a variety of sources, including museum specimens and research-grade observations on iNaturalist.org (Supplementary material Tables S1, S2, Fig. S4). We also included observations from the Plum Island Ecosystem Long Term Ecological Research site in northeastern Massachusetts from 1993 to 2015 (Deegan, 2015a, b, c, d; Deegan & Buchsbaum, 2015a, b; Deegan & Nelson, 2016; Mather & Taylor, 2016), our own personal observations, and a newspaper report (Goethel, 2024).

To determine if a recent range expansion has occurred since the 2012 marine heatwave in the Gulf of Maine, we focused on personal observations and those from iNaturalist.org. We verified online observations via photographs from the website and focused on observations that met the following criteria: they carried the research-grade tag, the crab pictured appeared alive or recently dead, and was mostly intact (i.e. possessed the majority of its legs and at least one claw). Observations of legs, claws, or carapaces alone were not counted. Observations were also rejected if the crab pictured was visibly a molt, judged by looking for transparent paddles and eyes.

To determine if abundances of lady crabs changed over time in the Gulf of Maine, we plotted fall trawl survey data taken by the Massachusetts Division of Marine Fisheries that have been taken annually since 1978 (except 2020 during the COVID-19 pandemic). We selected the 12 strata in the Massachusetts portion of the Gulf of Maine (Cape Cod Bay to southern New Hampshire border). These trawl depths ranged 4–80 m. For more detailed methods see King *et al.* (2010).

To document a potential change in the southern limit of *O. ocellatus*, we again examined iNaturalist observations. Following the criteria above, we looked for individuals of this species south of Georgia, USA, which is the accepted southern limit of *O. ocellatus* (Williams, 1984; Nizinski, 2003).

To determine if water temperature may be a driver of an *O. ocellatus* range expansion, we examined sea surface temperature data from 2001 to 2024 in Massachusetts Bay at the NERACOOS Buoy A01 (1 m and 50 m depths), data from the Northeast Regional Association of Coastal and Ocean Observing Systems (https://www.neracoos.org).

RESULTS

GBIF records showed 651 total occurrences of *O. ocellatus* in the Gulf of Maine including Cape Cod Bay and the Bay of Fundy during 1852–2024. iNaturalist had 491 recorded occurrences in the same area from 2004 to 2024, 165 of which fit our criteria, beginning in 2015 (Supplementary material Table S1). Of the records in GBIF, 11 occurrences were given prior to 1950 and 40 before 2000. A spike in observations occurred after 2000 (Supplementary material Fig. S4). From 2000 to 2010, 5% of observations were from iNaturalist and during 2010–2020, 98% of observations were from iNaturalist (Supplementary material Table S2, Fig. S4).

After the 2012 marine heatwave in the Gulf of Maine, lady crabs were found as far north as Freeport, Maine (43°48'17.136"N, 70°6'30.9594"W) (Figs. 1, 2, Supplementary material Table S1), 238 km north of Cape Cod, Massachusetts. Within the Bay of Fundy, crabs were found on the New Brunswick and Nova Scotia, Canada sides of the Bay with the farthest located at Alma, New Brunswick (45°36'13.6794"N, 64°56'29.184"W) (Figs. 1, 2, Supplementary material Table S1), 614 km north of Cape Cod, Massachusetts. A zoea was collected in the Plum Island estuary (northeastern Massachusetts) in 2021, and two ovigerous females were documented in the Bay of Fundy (Supplementary material Table S1). Two occurrences of male and female crabs in mating embraces were also recorded, with one in Rockport, Massachusetts and the second in Provincetown, Massachusetts, USA (Supplementary material Table S1).

Lady crabs were observed in trawl surveys by the Massachusetts Division of Marine Fisheries in the Gulf of Maine (Cape Cod Bay north to the New Hampshire border) throughout their timeseries beginning in 1978. The stratified mean abundance was low (30 year mean: 1.3 crabs per tow; mean range: 0–3.6 crabs per tow) from 1978 to 2007. Abundances surged during 2008–2019, followed by a decline to lower levels in recent years (2008–2024 annual mean: 21.5 crabs per tow; annual mean range: 1.3–21.5 crabs per tow) (Fig. 3). Catches in the Massachusetts portion of Gulf of Maine have mostly occurred in Cape Cod Bay in the shallow strata near Billingsgate Shoal and in the shallow stratum of Ipswich Bay (Steve Wilcox, personal communication).

Based on iNaturalist observations and personal communication with Nikki Dix, research director at the Guana Tolomato Matanzas National Estuarine Research Reserve, a long-term monitoring site in northern Florida, the southern limit of lady crabs appears to be approximately St. Augustine, Florida (Supplementary material Table S3).

Sea-surface temperature data show consistent rapid warming in the Gulf of Maine (Belkin 2009; Pershing *et al.*, 2013, 2015, 2021). Monthly means in 2023 were of 1.2°C higher than the 2001–2024 mean at 1 m and 1.4°C higher at 50 m

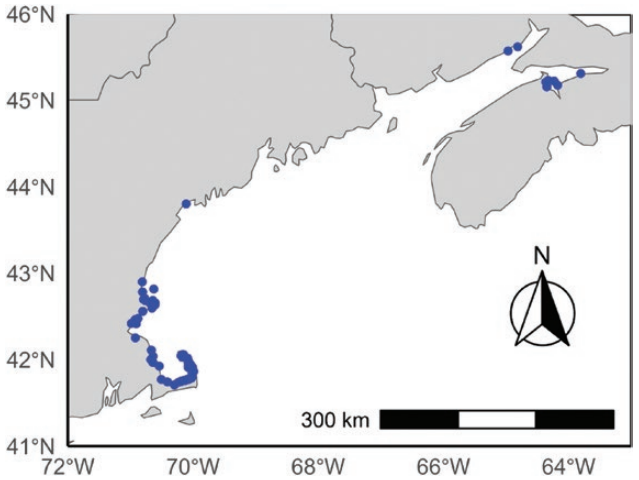

Figure 1. A map of observations of *Ovalipes ocellatus* in the Gulf of Maine and Bay of Fundy since 2012 based on Supplementary material Table S1.

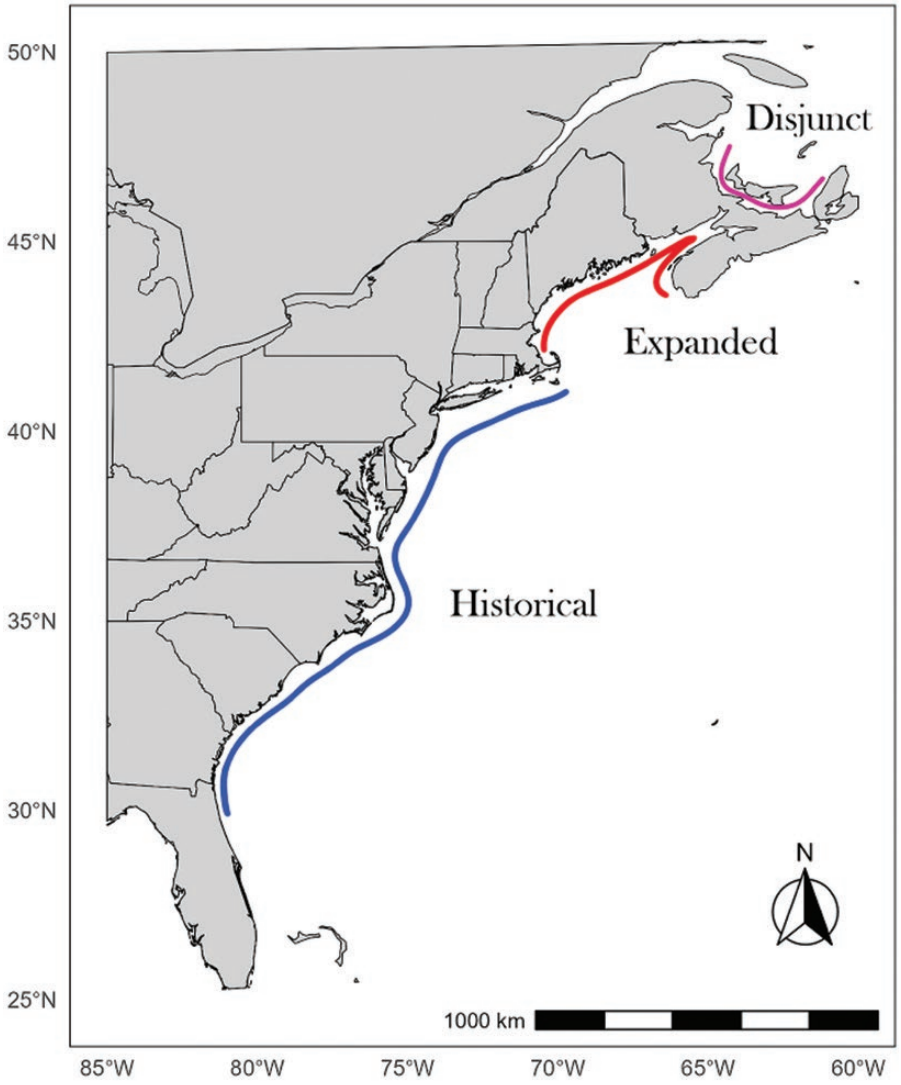

Figure 2. A map of historical range, disjunct Gulf of St. Lawrence population, and expanded Gulf of Maine range of *Ovalipes ocellatus*.

(NERACOOS monthly climatology; Figs. 4, 5). Sea-surface temperature at 1 m in the Gulf of Maine was higher than the mean for every month but August 2023, and water temperature at 50 m was higher than the mean throughout the year. Maximum mean monthly temperature in 2023 peaked at 1 m in July at 19.8°C, and at 50 m in November at 10.9°C. For comparison, the Gulf of St. Lawrence is also warming but has later summer peaks in temperature (August) that are lower than the Gulf of Maine. Mean monthly sea surface temperature in 2021 peaked in the Gulf of St. Lawrence at approximately 18°C in August (Galbraith *et al.*, 2022).

DISCUSSION

Based on observations since the 2012 marine heatwave, lady crabs are likely now residents of the Gulf of Maine and the Bay of Fundy. These are among the first reports of lady crabs in the Bay of Fundy according to historical data going back to 1852. The number of observations of lady crabs north of Cape Cod spiked after 2000 based on GBIF occurrence records. At the same time, abundances in the Massachusetts part of the Gulf of Maine also surged. Combined, these data strongly suggest a lady-crab range expansion into the Gulf of Maine and Bay of Fundy.

Ocean temperature data show that warming continues in the Gulf of Maine for 2023, consistent with previously reported warming trends (Belkin, 2009; Pershing *et al.*, 2013, 2015, 2021). This warming pattern has allowed other warmer-water taxa to overcome the zoogeographic barrier formed by Cape Cod (Johnson, 2014, 2015; McBride, 2018). We believe the reported observations represent the front of a new range expansion for *O. ocellatus* into the Gulf of Maine and Bay of Fundy as a result of ocean warming.

It is important to note that observations since the 2012 marine heatwave are not the first observations of lady crabs in the Gulf of Maine. GBIF records include museum specimens dating as far back as 1852; however, only 11 occurrences exist prior to 1950. Dexter (1985) reported *O. ocellatus*, as well as other range expanders including the brachyuran crabs *Minuca pugnax* (Smith, 1870) and *C. sapidus*, and the fish *Centropristis striata* (Linnaeus, 1758) (Johnson, 2014, 2015; McBride, 2018) in the Gulf of Maine around Cape Ann during 1952–1964, though the number of observations was not provided. These observations

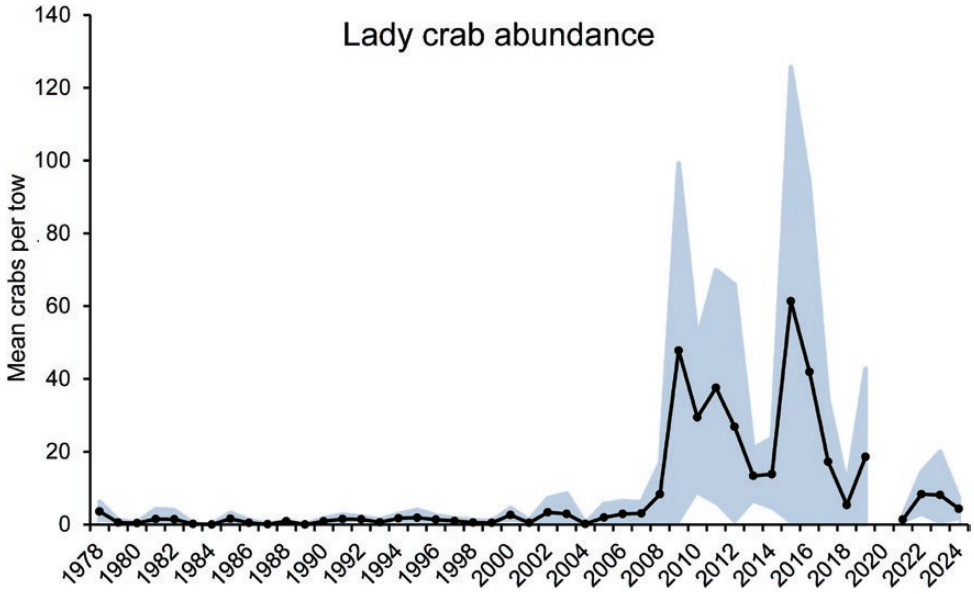

Figure 3. Stratified means ($N = 12$ strata) with 95% confidence intervals of trawl survey data of lady crab abundances during 1978–2024 taken in the Massachusetts portion of the Gulf of Maine (Cape Cod Bay to New Hampshire border). Data collected by and courtesy of the Massachusetts Division of Marine Fisheries. Data not collected in 2020.

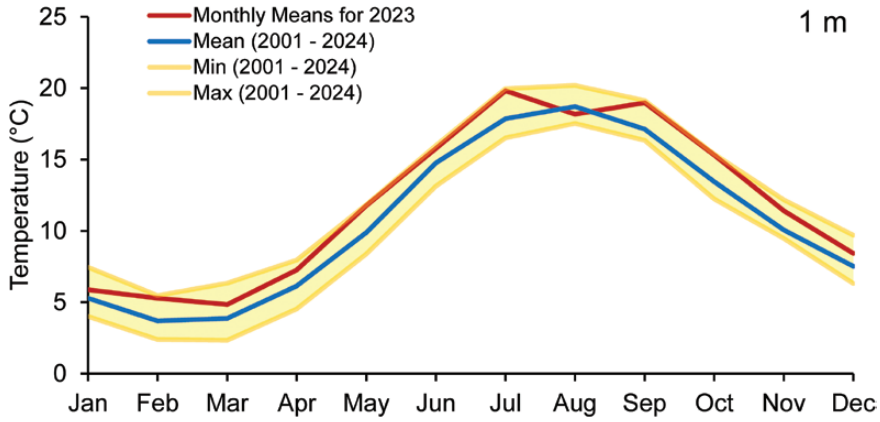

Figure 4. NERACOOS (Northeastern Regional Association of Coastal Ocean Observing; https://neracoos.org/) data at 1 m for 2001–2024.

coincide with a cyclic warm water regime and 1952 marine heat wave (Scattergood, 1960; Pershing *et al.*, 2013), but lady crabs disappeared in the colder periods that followed (Burchsted & Burchsted, 2006). For instance, no lady crabs were observed in a 10-year trawl survey in the Gulf of Maine conducted during 1978–1987 (Stehlik *et al.*, 1991) and they were rare during the Massachusetts Division of Marine Fisheries surveys until the 2000s (Fig. 3). A local population of *O. ocellatus* was observed near Salem, Massachusetts in the 1990s, but disappeared within a decade (Burchsted & Burchsted, 2006; Deegan, 2015a, b, c, d; Deegan & Buchsbaum, 2015a, b; Deegan & Nelson, 2016; Mather & Taylor, 2016). Given that water temperatures are predicted to continue to rise (Pershing *et al.*, 2021) and over a decade of lady crab observations exist in the region, we suggest that this is the beginning of a permanent range expansion.We also examined the southern limit of *O. ocellatus* to determine whether their range had expanded or shifted. The southern limit appears to be near St. Augustine, Florida (iNaturalist.org; Nikki Dix, personal communication 2024). This southern limit is only about 90 km farther south than the previously described southern limit, so it is unlikely that the southern limit is expanding.

Although lady crabs appear to have expanded their range into the Gulf of Maine and the Bay of Fundy, it is not yet known if this expansion represents an established local population or spillover from adjacent populations (i.e., south of Cape Cod/Gulf of St. Lawrence) or both. Future studies to determine whether or not the population is established should include determining whether *O. ocellatus* overwinter in the Gulf of Maine, examining larval dispersal patterns via in currents in the Gulf of Maine, comparing genetic markers of range-expanding lady crabs to those south of Cape Cod and in the disjunct Gulf of St. Lawrence population, and determining whether temperatures are warm enough for long enough to allow full brooding and larval maturation to occur. As with many portunids, lady crabs may hibernate during winter when water temperatures are low by burying (Musick & McEachran, 1972, Stehlik *et al.*, 1991)

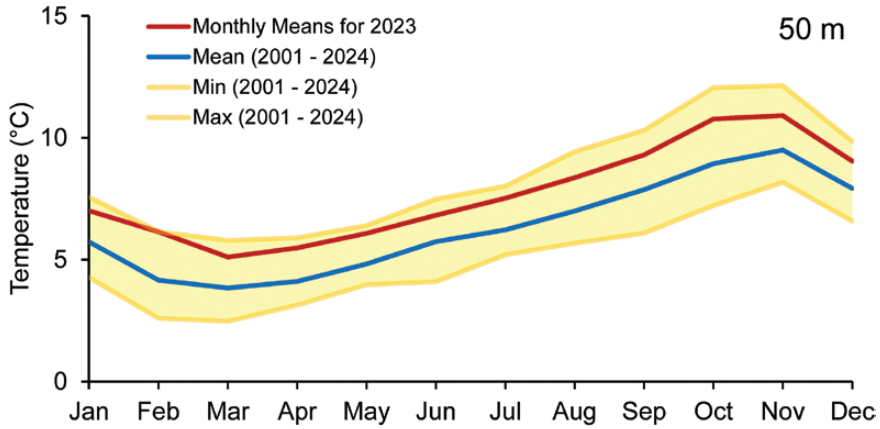

Figure 5. NERACOOS (Northeastern Regional Association of Coastal Ocean Observing; https://neracoos.org/) data at 50 m for 2001–2024.

and seem to prefer sand or sandy gravel substrate both south of Cape Cod and in the southern Gulf of St. Lawrence (Stehlik *et al.*, 1991, Voutier & Hanson, 2008). The distribution of lady crabs south of Cape Cod is largely along the coast. Individuals were found most commonly in trawl and dredge surveys of the middle-Atlantic shelf and Georges Bank at depths of less than 27 m (Stehlik *et al.*, 1991). Almost all (> 99%) lady crabs caught in the trawl surveys conducted by the Massachusetts Division of Marine Fisheries during 1978–2024 in the Massachusetts portion of the Gulf of Maine were caught in water < 30 m deep. In trawl surveys conducted in the Gulf of St. Lawrence, 95% of lady crabs were caught at depths of less than 15 m and 50% at depths of less than 10 m (Voutier & Hanson, 2008). Crowd-sourced (iNaturalist) observations are largely along beaches or shallow sandy bottoms.

Adult lady crabs are most commonly found at temperatures ranging 11–24°C (Stehlik *et al.*, 1991). Larval development takes 27 d at 20°C in salinities of 25–35 ppt (Costlow & Bookhout, 1966) in their historical range (i.e. south of Cape Cod). The Gulf of Maine is rarely warmer than 20°C for more than a few days at a time; however, larvae may be able to develop at lower temperatures, albeit more slowly. Burchsted & Burchsted (2006) suggested a short-term local population of lady crabs in northern Massachusetts in the 1990s when summer temperatures were rarely above 16°C. We also have evidence that the species may be reproducing in the Gulf of Maine. A lady crab zoea was collected in the Plum Island estuary, northern Massachusetts in 2021 and pairs in a mating embrace have been observed in Rockport and Provincetown, Massachusetts, USA. Ovigerous females have been documented twice in the Bay of Fundy since 2018.

Because lady crabs are predators of benthic invertebrates and serve as prey for fishes, they may impact food webs in the Gulf of Maine and the Bay of Fundy. Bivalves are important fishery species in the northwestern Atlantic Ocean (Timbs *et al.*, 2018), and lady crabs are predators of several of these including the Atlantic surf clam *Spisula solidissima* (Dillwyn, 1817) and blue mussel *Mytilus edulis* (Linnaeus, 1758) (Ropes, 1988; Stehlik, 1993; Voutier & Hanson, 2008). Predation by green crabs *Carcinus maenas* (Linnaeus, 1758) can threaten commercial bivalve fisheries (Ropes, 1988), but it is not known whether lady crabs can reach densities high enough to have a similar impact. Lady crabs are also predators of polychaetes, particularly *Pherusa affinis* (Leidy, 1855) (Stehlik 1993). Lady crabs are important prey items of several fish species including tautog *Tautoga onitis* (Linnaeus, 1758) and smooth dogfish *Mustelus canis* (Mitchill, 1815) (Rountree & Able, 1996; Clark *et al.*, 2006). Consequences of a permanent range expansion could include trophic shifts due to changes in predation and competition and changes to ecosystem processes such as energy flow and primary production; however, these may depend on their abundance and the degree of novelty of *O. ocellatus* in any given context (Essl *et al.*, 2019; Martínez-Soto & Johnson, 2024). Future studies should include examining lady crab abundance in the Gulf of Maine and the Bay of Fundy and investigating their potential ecological impacts.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Observations of *Ovalipes ocellatus* in the Gulf of Maine and Bay of Fundy recorded in iNaturalist as well as our observations, beginning with the first observation reported in 2015.

S2 Table. GBIF occurrence record sources.

S3 Table. Observations of *Ovalipes ocellatus* in southern Georgia and northern Florida recorded in iNaturalist.

S4 Figure. Number of Global Biodiversity Information Facility (GBIF) records per decade, including *iNaturalist* research-grade observations, occurrences from trawl surveys and museum specimens.

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