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Regional biodiversity monitoring reveals severe population decline of the Atlantic horseshoe crab (*Limulus polyphemus*) in Long Island Sound, USA

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Horseshoe crabs are an ancient species facing modern threats. While their importance to the conservation of endangered birds has garnered them increasing protections in recent years, disparate and insufficient management strategies across regions have precluded population recovery. Six datasets spanning 22–46 years for Atlantic horseshoe crabs (*Limulus polyphemus*) in the Long Island Sound, USA region were analyzed from regional monitoring programs conducted for general biodiversity assessments that had not been previously aggregated for the evaluation of this species. In these datasets, a decline of 2–9% per year in *L. polyphemus* count per sample was observed, with significant individual declines in 5 of the 6 datasets (all datasets from bays and harbors). The central Long Island Sound dataset exhibited a significantly slower rate of decline, driven by higher counts per sample in recent years, which should be monitored to determine if an improving trend will be sustained or if the recent higher counts were anomalies. An increasing proportion of females, mean prosomal width, and mean weight of *L. polyphemus* were also observed. With management activities at the local, regional, and national level impacting the potential for population recovery in this species, it is critical for policymakers at all levels to be aware of the severe decline in observations of this species across data sources, pointing to a need for urgent action to prevent local extinction.

Keywords Arthropod, Climate change, Conservation, Endangered species, Habitat loss, Overharvest

Horseshoe crabs have existed for millions of years, an atypical constant in ever-changing marine ecosystems. Four species exist today, each facing anthropogenic threats including habitat loss and degradation, overharvest, and climate change[1]. Along the Atlantic and Gulf coasts of North America, conservation of the region's only horseshoe crab species *Limulus polyphemus* (Atlantic horseshoe crab) has been driven by the role of the species' eggs as a food source for endangered migratory birds[2–6]. As such, great attention has been paid to the population viability of *L. polyphemus* in regions that serve as important stop-over points during shorebird seasonal migration, namely Delaware Bay, USA[7]. Indeed, while the species is listed as vulnerable overall with a decreasing population trend in the most recent IUCN Red List Assessment from 2016[8], this assessment notes that in parts of its range beyond Delaware Bay, such as New England, there is a risk of endangerment and loss at the local level[8].

With the focus on *L. polyphemus* primarily as a resource in Delaware Bay, USA, areas across its range have been understudied with minimal conservation action to prevent population collapse. The 2016 IUCN Red List Assessment notes the need for quantitative analysis of the population beyond Delaware Bay and Cape Cod into other areas including in New England, which has been impeded by a lack of data. The Atlantic States Marine Fisheries Commission's most recent stock assessment for *L. polyphemus* similarly shows the depauperate nature of data available for this species in sections of its range[9]. For example, while the assessment includes five fisheries-independent datasets for Delaware Bay, it includes only one in the Connecticut waters of central Long Island Sound and no data from that state's embayments. Fisheries-independent surveys can be useful in population assessments; they do not specifically target or seek to maximize collection of the species of interest and are designed to sample systematically or randomly across a particular geographic region, enabling a more

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representative estimate of abundance. Instituting additional fishery-independent surveys is a recommendation for future work, with the New York and Northeast regions being of highest priority for additional data collection[9]. This lack of data has precluded an accurate assessment of the population health of the species at the estuary level in Long Island Sound.

There have been critical efforts to quantify population change and advocate for the protection of *L. polyphemus* in Long Island Sound, including research involving habitat modeling[10], mark-recapture[11,12], community science[13,14], reproductive behavior[15,16], and egg predation[5]. Beekey and Mattei (2015) provides a comprehensive review of the species decline in Long Island Sound in the years leading up to 2015[17]. In 2000, Sacred Heart University launched a community tagging program (www.projectlimulus.org) that also includes collecting data on adult *L. polyphemus* found on beaches during spawning[13]. None of these prior efforts have been suggestive of population recovery or even stasis.

Building off these prior efforts, and to support decision-making at a critical time for this species, here we synthesize existing data to show the current state of population change in *L. polyphemus* in Long Island Sound. Data on *L. polyphemus* counts in the greater Long Island Sound region (including Peconic Bay, which is located at the eastern end of Long Island but outside of the Sound) were aggregated from reports or individual outreach from five sources: the Connecticut Department of Energy and Environmental Protection (CT DEEP), Millstone Environmental Laboratory, New York State Department of Environmental Conservation (NYS DEC), Harbor Watch (Earthplace, Inc.), and The Maritime Aquarium at Norwalk (Fig. 1; Supplementary Tables S1-S3). These surveys used different methods and spatiotemporal regimes for collection of *L. polyphemus* count data. Because these data were collected by environmental non-profits and government agencies as part of biodiversity surveys not specifically targeting *L. polyphemus*, they provide a unique opportunity to assess population change in this important, and highly threatened, species.

Results

Analysis of the six datasets revealed a significant overall decrease in *L. polyphemus* count per sample over time (Figs. 2 and 3; Gamma generalized linear model with a log link: $t = -9.857$, $p < 0.0001$). Inspection of Q-Q plots and calculation of the overdispersion ratio (< 1) revealed no evidence of violation of assumptions. Diagnostic plots revealed some high deviance residuals; however, these observations did not have undue influence on the model results (Cook's distance < 0.12) and removal did not affect the statistical significance of the model results. The Central Sound exhibited a significantly slower rate of decline compared to the average trend across all sites (year x Central Sound interaction effect: $t = 2.324$, $p = 0.0212$). However, while the Central Sound showed a non-significant negative trend in *L. polyphemus* count per sample (slope (log scale) = -0.015, $t = -0.97$, $p = 0.33$), all other sites exhibited a significant decline over time. Specifically, Inner Norwalk Harbor had a slope (log scale) of -0.032 ($t = -2.88$, $p = 0.0045$), Manhasset Bay/Little Neck Bay had a slope (log scale) of -0.029 ($t = -3.35$, $p = 0.0010$), Niantic Bay had a slope (log scale) of -0.051 ($t = -9.09$, $p < 0.0001$), Outer Norwalk Harbor had a slope (log scale) of -0.047 ($t = -3.15$, $p = 0.0019$), and Peconic Bay exhibited the steepest decline with a slope (log scale) of -0.097 ($t = -11.24$, $p < 0.0001$). However, when excluding the two most recent years included in the analysis from the Central Sound dataset (2021 and 2022), the estimated decline in count per trawl at that site became significant (slope (log scale) = -0.041, $t = -2.343$, $p = 0.0202$), indicating a decreasing trend over time apart from those recent years. Continued monitoring of the population will be essential to determine whether these years were anomalous or representative of a change in the overall trajectory of that population. These

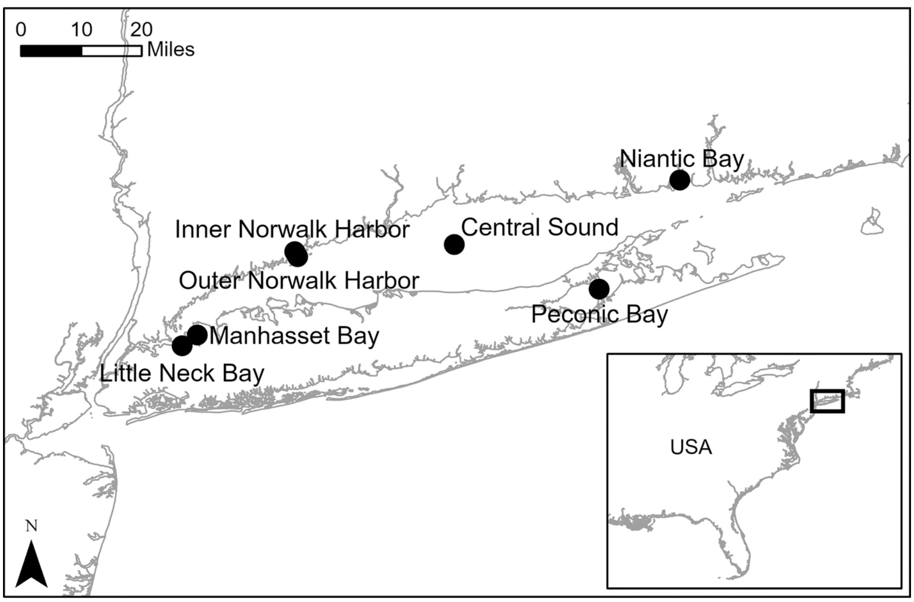

Fig. 1. Location of horseshoe crab datasets in the Long Island Sound, USA region. Basemap: NOAA shoreline. Map was created using ESRI ArcMap Version 10.8.2.

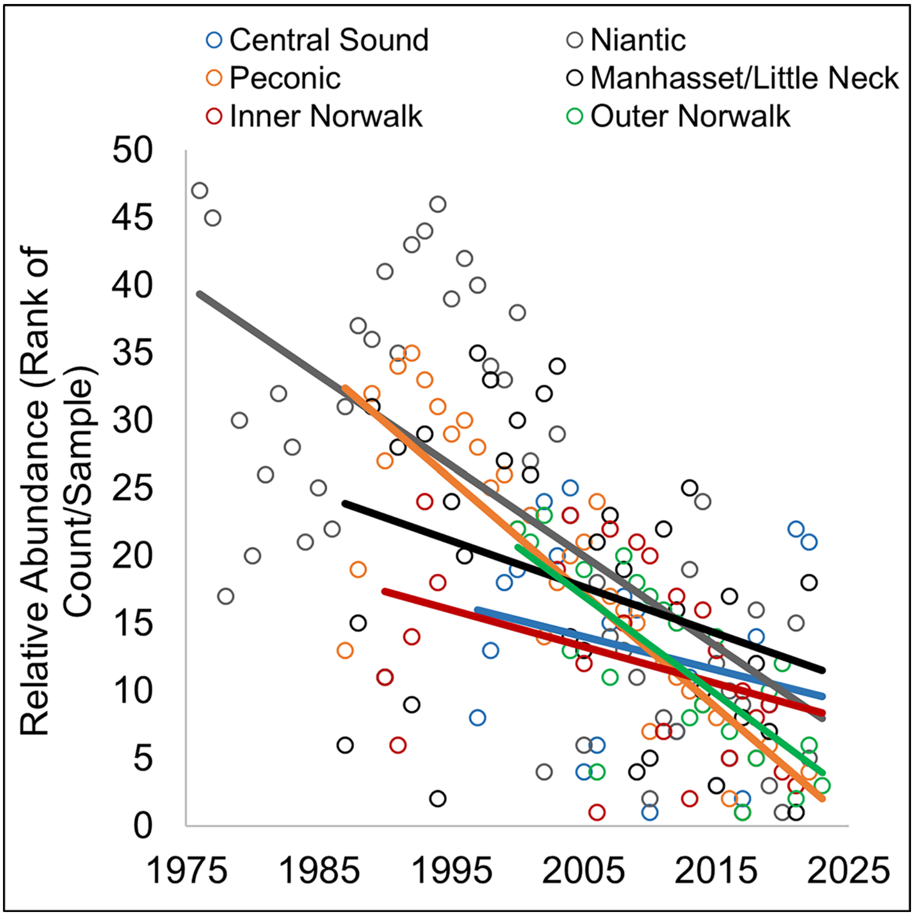

Fig. 2. Relative abundance (rank-transformed count per sample, shown with linear regression line) of *L. polyphemus* across six datasets in the Long Island Sound, USA region. There was a significant overall decrease in horseshoe crab count per sample over time (Gamma generalized linear model with a log link: $t = -9.857$, $p < 0.0001$), with significant declines individually in Inner Norwalk Harbor (slope (log scale) of –0.032, $t = -2.88$, $p = 0.0045$)), Manhasset Bay/Little Neck Bay (slope (log scale) of –0.029, $t = -3.35$, $p = 0.0010$)), Niantic Bay (slope (log scale) of –0.051, $t = -9.09$, $p < 0.0001$)), Outer Norwalk Harbor (slope (log scale) of –0.047, $t = -3.15$, $p = 0.0019$), Peconic Bay (slope (log scale) of –0.097, $t = -11.24$, $p < 0.0001$), and the Central Sound (2021—2022 excluded; slope (log scale) = –0.041, $t = -2.343$, $p = 0.0202$).

declines in observations of *L. polyphemus* ranged from an average decrease in count per sample of 2.86–9.28% per year (Table 1).

An increasing proportion of females was observed in the Central Sound ($R^2 = 0.512$, F (df = 1; 20) = 21.01, $p = 0.00018$; in years prior to 2019, $R^2 = 0.670$, F (df = 1; 18) = 36.6, $p < 0.0001$) and a weak, marginally significant relationship was observed with time in Outer Norwalk Harbor (Fig. 4; $R^2 = 0.154$, F (df = 1; 17) = 3.102, $p = 0.09616$). An increase in mean prosomal width over time in the Central Sound was observed (linear regression, $R^2 = 0.327$, F (df = 1; 21) = 10.21, $p = 0.004$), but the relationship with time was less clear in the Outer Norwalk (Fig. 4; linear model, $R^2 = 0.124$, F (df = 1; 16) = 2.257, $p = 0.1524$). Removal of an outlier in 2020 identified from inspection of the Q-Q plot further weakened this relationship, suggesting that the observed increase was limited to the Central Sound ($R^2 = 0.0624$). The respective male and female prosomal widths have remained relatively unchanged over the same period (Fig. 5). In addition to increasing prosomal width in the Central Sound, an increase in *L. polyphemus* weight was observed over time in years prior to 2019 (Fig. 6; linear model, $R^2 = 0.70$, F (df = 1; 19) = 43.44, $p < 0.0001$). In years with a greater number of *L. polyphemus* caught per tow, the corresponding increase in weight per tow was found to increasingly deviate from a one-to-one relationship, indicating that in years with a higher count of *L. polyphemus*, relatively more smaller crabs were observed (linear regression, $R^2 = 0.809$, F (df = 1; 23) = 97.53, $p < 0.0001$). Linear regression results reported above met the assumption of normality of residuals (Shapiro–Wilk tests, $p > 0.05$ for all; inspection of Q-Q plots) and homoscedasticity (Breusch-Pagan tests, $p > 0.05$ for all).

Discussion

Horseshoe crabs have survived for 450 million years, but habitat loss, overexploitation, and environmental degradation are causing population declines globally[18–20]. By uniting datasets that have largely existed outside of the formally published literature, we show severe population decline in multiple locations for over 20 years.

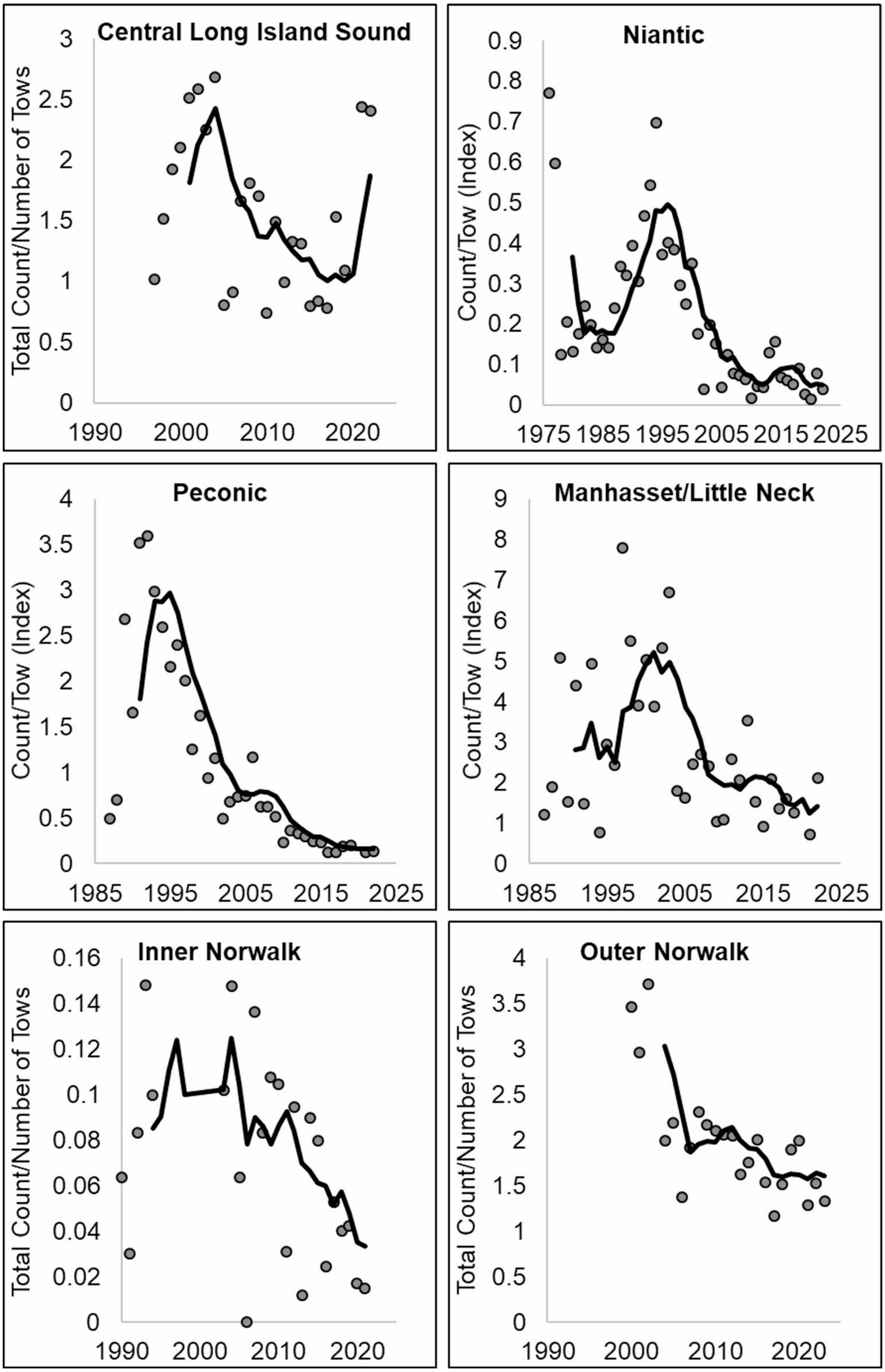

Fig. 3. Observational data on counts of *L. polyphemus* at six locations within the Long Island Sound region (CT DEEP's Long Island Sound Trawl Survey, Millstone Environmental Laboratory's Niantic Bay Survey, NYS DEC's Peconic East and Manhasset/Little Neck West Surveys, Harbor Watch's Inner Norwalk Harbor Survey, and The Maritime Aquarium's Outer Norwalk Harbor Survey). The "Count/Tow" Index is presented for three of the locations where raw data were not publicly available; for the other years, the value for each year shown represented the total number of *L. polyphemus* observed divided by the total number of trawls conducted in that year. Line represents a five-year running average.

	Slope (GLM)	Record start	Record end	Annual decrease in count per sample (%)	95% confidence interval
Manhasset/Little Neck	− 0.029	1987	2022	2.86	4.50–1.18%
Peconic	− 0.097	1987	2022	9.28	10.81–7.71%
Central Sound	− 0.041	1997	2022	3.98	7.21–0.64%
Niantic	− 0.051	1976	2022	4.98	6.03–3.92%
Inner Norwalk	− 0.032	2003	2021	3.18	5.30–1.01%
Outer Norwalk	− 0.047	2000	2023	4.58	7.34–1.74%

Table 1. Slope of individual sites from Gamma generalized linear models on the raw survey data for each dataset. Central Sound results only are reported from an analysis that excluded the 2 most recent years for which data were available, which were identified as a deviation from the trend of the majority of the dataset (2021–2022). Negative slope indicates a decline in horseshoe crab count per sample (trawl or seine). Slopes are on a log scale.

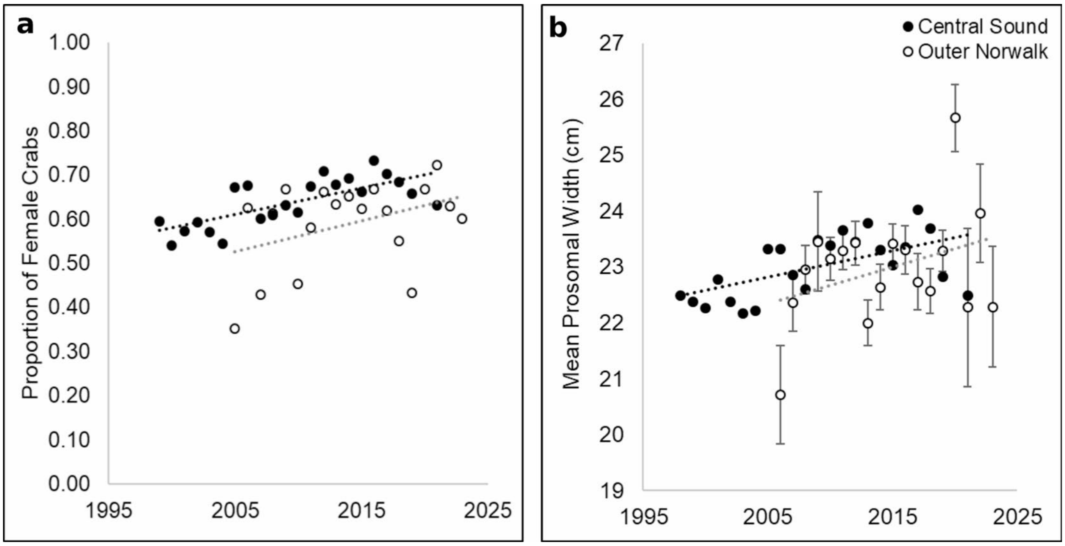

Fig. 4. **a** Proportion of female crabs caught in CT DEEP's Long Island Sound Trawl Survey (black dots ●, and black line; $R^2 = 0.512$, F (df = 1; 20) = 21.01, $p = 0.00018$; in years prior to 2019, $R^2 = 0.670$, F (df = 1; 18) = 36.6, $p < 0.0001$) and The Maritime Aquarium's Outer Norwalk Harbor Trawl Survey (white dots ○, and grey line; $R^2 = 0.154$, F (df = 1; 17) = 3.102, $p = 0.09616$). **b** Mean prosomal width over time in CT DEEP's Long Island Sound Trawl Survey (black dots, black line; $R^2 = 0.327$, F (df = 1; 21) = 10.21, $p = 0.004$) and The Maritime Aquarium's Outer Norwalk Harbor Trawl Survey (white dots ○, and grey line; $R^2 = 0.124$, F (df = 1; 16) = 2.257, $p = 0.1524$).

Declines in *L. polyphemus* count per sample occurred in all six Long Island Sound region datasets; these trends are further supported by long-term spawning beach surveys in New York[21,22]. Such population declines have been documented worldwide, driven by multiple mechanisms. Infrastructure development[23], pollution[19,24,25], and coastal armoring[13,18,26] are reshaping global coastlines and diminishing the extent of natural areas ideal for horseshoe crab spawning. Climate change and rising sea levels are further accelerating this loss of areas critical to horseshoe crab population viability[25,27–30]. However, our analysis also suggests a potential positive change in trajectory in the Central Sound since 2019; continued monitoring will be needed to assess whether the higher count per sample observations in 2021–2022 are anomalous or sustained, and if increases will be seen in the other areas under study throughout the region.

The change in sex ratio in two of the datasets also presents a potentially concerning trend. In Delaware Bay, sex ratio was found to be related to the density of spawning females, with a median sex ratio of 3.5 males per female at high spawning activity sites and fewer males per female at low spawning activity sites[31]. The mean size ratio of female to male crabs in the Central Sound dataset of 1.28 ± 0.01 was similar to the size ratio of 1.26 observed in Delaware Bay[32]. Previous work on Long Island Sound spawning beaches also found no increase in female prosomal width but did observe a significant decrease in male *L. polyphemus* size, as well as increasing relative proportion of female crabs[17]. Lower ratios of female to male *L. polyphemus* are typically observed on beaches during spawning events, as males tend to visit spawning beaches with greater frequency than females[33]. Operational sex ratios have been further found to vary over time, as well as with tidal height, tidal flow rate, and temperature[33].

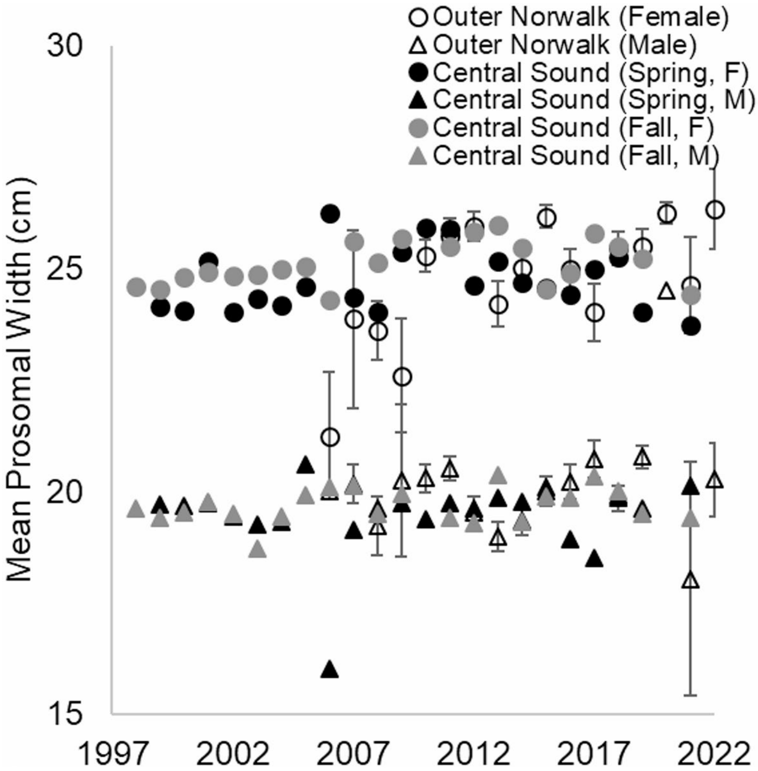

Fig. 5. *L. polyphemus* size over time for males (triangles, ▲) and females (circles, ●) in CT DEEP's Long Island Sound Trawl Survey (grey for fall and black for spring) and The Maritime Aquarium's Outer Norwalk Harbor Trawl Survey (white).

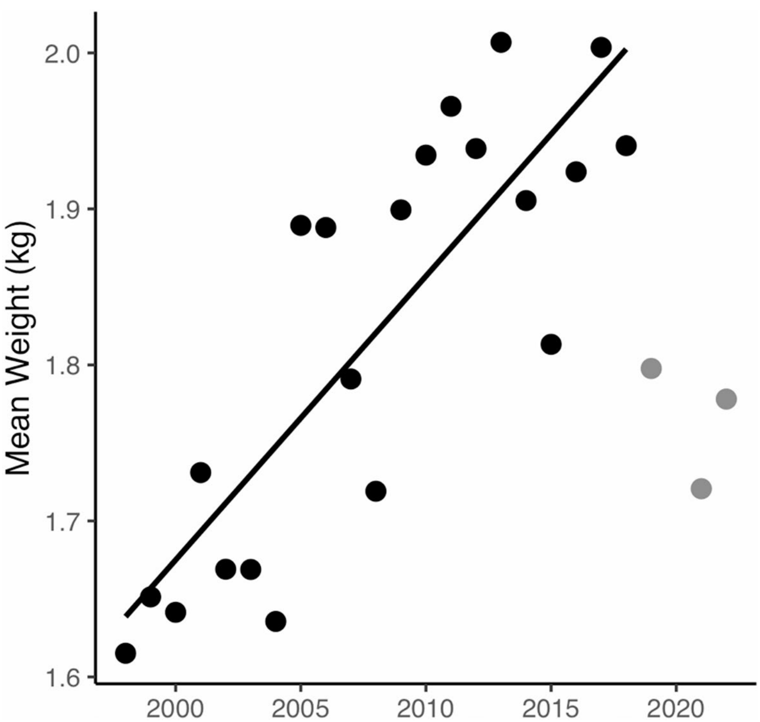

Fig. 6. Weight of *L. polyphemus* over time in the central Long Island Sound dataset (weight per trawl divided by count per trawl), showing the increasing average individual *L. polyphemus* weight over time in years prior to 2019 (linear model, $R^2 = 0.70$, F (df = 1; 19) = 43.44, $p = 0.0001$). Years 2019, 2021, and 2022 deviated from the increasing linear trend in prior years (shown in grey, omitted from analysis).

The driver of this apparent increase in the proportion of female crabs is unknown. In New York, survivorship was found to be lower for females, with modeled survivorship 11% lower on the North Shore of Long Island than males[12]. This suggests that some other factor is driving the apparent relative increase (e.g., behavior change, recruitment, migration patterns). However, this relative decrease in the number of male *L. polyphemus* is consistent with previous data that showed increasing numbers of single females and low incidence of polyandrous mating behavior on Long Island Sound spawning beaches[17]. As explored in that study, these Long Island Sound datasets similarly do not indicate an impact of preferential harvest of female crabs as is often found in bait and biomedical harvesting, which they suggest is due to a decline in the number of male *L. polyphemus* and low egg and/or juvenile survivorship[17]. The increasing proportion of females appeared to be driving an increase in mean prosomal width over time in the Central Sound, and potentially to a lesser extent in the Outer Norwalk Harbor (Fig. 4, 5, and see Beekey and Mattei 2015). However, this could also be caused by an aging population with fewer juveniles entering the population over time.

These trends suggest a need for urgent intervention. However, managing this species is complex. First, Long Island Sound is bisected by the jurisdictional boundaries of two states, Connecticut and New York. While harvest of *L. polyphemus* is regulated at the regional level on the United States Atlantic coast by a governing body, the Atlantic States Marine Fisheries Commission (ASMFC), Connecticut and New York also separately regulate harvest and habitat protection for this species. A stock assessment by the ASMFC in 2024 determined that the "New York" region population (which includes all of Long Island Sound in both Connecticut and New York) was in "poor" condition, in contrast with the population across the northeast being in "neutral" condition and the coastwide assessment reflecting "good" conditions[9]. The New York-Connecticut population received the worst rating out of all regions considered. Importantly, while the stock assessment describes the upward trend in the Central Sound data over the prior decade, the assessment did not include the 3 embayment datasets on the Connecticut side of the Sound, all of which remain on a downward trajectory more similar to the other datasets within the region. As such, not only does the incorporation of additional regional data further support the urgent need for additional protections, but it suggests that the condition of the population may in fact be even worse than it appears in the stock assessment.

With bait harvest restrictions implemented at the state level in Connecticut in 2023 (State of Connecticut Public Act No. 23–6) and no biomedical or for-consumption harvest known to be occurring within the Sound, the drivers of these continued declines warrant urgent evaluation. The same ASMFC 2024 stock assessment hypothesizes that the poor status in New York-Connecticut may reflect unsustainable bait harvest, a change in the habitat that has resulted in a decreased ability to support a larger population, or both.

While fisheries-independent surveys (like those presented in the ASMFC assessments and here) can provide important assessments of the adult population, catch per unit effort data have interpretive limitations. Interannual environmental factors may impact the catch rate of the population even with consistent methodology due to changes in animal behavior[34]. While not as large of a concern for *L. polyphemus* as for some other animals (like schooling fish), trawling and seining surveys are only representative of the population when that population is evenly distributed across space; aggregations of animals can skew count data (in either direction)[34]. Fortunately, the species-agnostic long-term monitoring programs reported on here do avoid many of the confounding factors inherent in the use of fisheries datasets[34,35]. Beyond these types of data, very limited data exist on other stages of the species' life history in the Sound, including survival during spawning, survival and viability of eggs, and survival during each juvenile stage. As such, it remains unclear where intervention may be most impactful on the overall abundance of the species. Additional research is needed on reproduction and juvenile dynamics that could inform more effective management. Furthermore, changes in abundance may be driven by local, regional, and larger-scale factors, complicating decision-making. For example, low counts observed in 3 of the datasets in 1985 could be temporally aligned with impacts from the North Atlantic Oscillation, but assigning causality to such relationships requires more robust longitudinal datasets.

Regardless of being able to identify a singular or primary driver of population decline, we demonstrate here that when reinforced by other local datasets for the Sound, the ASMFC's determination of the poor condition of the Long Island Sound population of *L. polyphemus* warrants additional protective measures. While Connecticut has banned the hand harvest of horseshoe crabs, similar legislation passed in New York in late 2024, but the Governor declined to sign it into law. Federal protection measures, including listing the species under the USA's Endangered Species Act, are also under consideration. The data presented here are suggestive of alarming trends in the abundance of *L. polyphemus* in Long Island Sound, alongside demographic changes that may hamper population recovery (e.g., sex ratio). Given these concerning trends, urgent action is needed to prevent loss of local populations in this important species.

Methods

CT DEEP's Long Island Sound Trawl Survey was conducted in the Central Sound, Millstone Environmental Laboratory's Niantic Bay Survey was conducted in Niantic, CT, NYS DEC's Peconic East, and Manhasset/Little Neck West Surveys were conducted in each of those harbors in Long Island, NY, Harbor Watch's Trawl Survey was conducted in Inner Norwalk Harbor, Norwalk, CT[36] (Supplementary Table S1), and The Maritime Aquarium at Norwalk's Survey was conducted in Outer Norwalk Harbor, Norwalk, CT (Supplementary Table S2). The Central Sound, Niantic Bay, Peconic Bay, Inner Norwalk Harbor, and Outer Norwalk Harbor data were reported to have been collected through trawl surveys and the Manhasset/Little Neck data were reported to have been collected through seine surveys. Summary data for the Central Sound, Niantic Bay, Manhasset/Little Neck Bay, and Peconic Bay were accessed from the Long Island Sound Study website (https://longislandsoundstudy.net/ecosystem-target-indicators/horseshoe-crab-abundance/) on August 14, 2024. Additional Central Sound data (number of tows, total count, and total weight) were accessed from "Marine Finfish Survey, Long Island Sound Trawl Survey Report (2022) Connecticut Department of Energy and Environmental Protection: 155 pp." from

Region	Gear type	Timing	Spatial design
Manhasset/Little Neck	Seine	May–October	Multiple specified sampling areas repeatedly sampled
Peconic	Otter trawl	May–October	Random from within grid overlaid on region
Central Sound	Otter trawl	Apri–June ("Spring"); September–October ("Fall")	Stratified random from within grid overlaid on region based on depth and sediment
Niantic	Otter trawl	Year–Round	Three specified stations repeatedly sampled
Inner Norwalk	Beam trawl	May–October	Stratified random from within grid overlaid on region based on inland, middle, and outermost regions of harbor
Outer Norwalk	Otter trawl	Year-Round	Single specified sampling area repeatedly sampled

Table 2. Summary of sampling methods used in each of the 6 datasets.

the CT DEEP website (https://portal.ct.gov/deep/fishing/fisheries-management/long-island-sound-trawl-survey) on August 14, 2024. The values of "count per trawl" were calculated manually from CT DEEP's report data; individual trawls are not reported, so the annual total count was divided by the annual total number of trawls. The raw data from Niantic Bay (Millstone Environmental Laboratory) and Manhasset/Little Neck and Peconic Bays (NYS DEC) associated with the data retrieved from the Long Island Sound Study website (Supplementary Table S3) are not known to the authors to be publicly available, so the summary "index" data are reported. The datasets from Norwalk Harbor were provided to the authors upon request from the collecting institutions. Data on prosomal width and proportion of females were sourced from CT DEEP and The Maritime Aquarium at Norwalk. Weight data were also sourced from CT DEEP's report data; 1997 was omitted as the reported count data represented fall only (Kurt Gottschall, CT DEEP, *Personal Communication*). The data for all six locations are shown in Tables S1-3.

Spatiotemporal design of sampling differed among the six regions[37–42] (Table 2). In Peconic Bay (1987–2022), the Inner Norwalk Harbor (2003–2021), and the Central Sound (1997–2022) a block design was used, in which the full potential sampling area was divided into a grid of boxes of the same dimensions (consistent within each region), from which sampling locations were randomly selected. In Niantic Bay (1976–2022), Manhasset/Little Neck Bay (1987–2022) and Outer Norwalk Harbor (2000–2023), specific stations were repeatedly resampled.

In Manhasset/Little Neck Bay, seining was conducted from May to October at fixed locations within each bay, with 5–10 seine sites sampled per date of sampling (1–2 times per month). In Peconic Bay, sampling locations were chosen by a random selection of 16 out of 77 sampling blocks, which were then sampled weekly from May to October. In the Central Sound, a stratified-random approach was used based on depth and sediment type (12 groups); 5 sites from each stratum were sampled each month, broken into "spring" and "fall" sampling periods. In Niantic Harbor, sampling was done year-round at each of 3 stations at specified geographic locations (with triplicate tows conducted per station from 1976 to 2016, and individual tows conducted since 2017). In the Inner Norwalk Harbor, a stratified-random approach was used with 20 blocks total, where on each day of sampling (May to October), one or more blocks haphazardly chosen from within each of 3 regions within the sampling area. In Outer Norwalk Harbor, all sampling locations were in one specific area (Sheffield Harbor), resampling approximately the same location during each trawl (year-round), though the specific line of tow within the harbor was determined by the captain based on prevailing conditions at the time of sampling.

The sampling technique also differed among the six regions. In Manhasset/Little Neck Bay, a 200 ft by 10 ft beach seine is used, which was deployed by boat and then pulled in to the shore by hand. In Peconic Bay, sampling was done using 16-ft semi-balloon shrimp trawl net with a 1-in mesh, with a 3/8-in mesh cod-end liner, attached to a 1 × 2-ft otter trawl. In the Central Sound, sampling was done using a 14 m otter trawl with a 51 mm mesh cod-end. In Niantic Harbor, a 9.1-m otter trawl with a 0.6-cm cod-end liner was used, towing a distance of 0.69 km during each trawl (a shorter trawl was sometimes required due to abundant macroalgae and detritus). In Inner Norwalk Harbor, a 1-m beam trawl with a 6.35 mm mesh was used, trawling for 3 min at 1.34 m s^{-1}. In Outer Norwalk Harbor, sampling was done using an otter trawl (12–13 ft mouth width, 4.33 ft mouth height) with a 2-in mesh; trawling was done at a speed of 1.8–2.2 knots for 10–30 min per trawl.

Prosomal width data were available for the Central Sound and Outer Norwalk Harbor datasets only, which is a measure of the widest part of the carapace of a horseshoe crab and is typically measured using calipers or a ruler. While prosomal width is only one aspect in the quantification of the size of *L. polyphemus*, and can have nonlinear relationship with weight and other morphological metrics, it is an easily-collected monitoring metric that can provide comparable data across studies[43,44].

In all datasets, omissions of data from certain stations and time periods did occur due to the logistical constraints involved with field research; none of these were reported to have been done in such a way that would bias the geographic or temporal resolution of the data or its interpretation.

Data analyses were conducted in R version 4.4.1 and R Studio[45]. To assess changes in the number of *L. polyphemus* observed (per trawl or seine), a generalized linear model with a Gamma distribution and log link was used, including year, site, and their interaction as predictors. The emmeans package in R was used to estimate the slope of year for each site individually (emtrends function), and tested whether these slopes differed significantly from zero[46]. For all linear models, normality and homogeneity of variance were checked using Shapiro–Wilk tests and review of residual versus fitted plots, respectively. Heteroskedasticity was tested using a Breusch-Pagan test. Linear regression was used to test for a relationship with time for the proportion of female crabs, weight of *L. polyphemus* per tow, and prosomal width; as those models met the required assumptions (checked using Shapiro–Wilk tests, Breusch–Pagan tests, and inspection of Q–Q plots). Due to evidence of a nonlinear relationship and heteroskedasticity when applying the linear model, the 3 most recent years of data (2019, 2021, 2022) were excluded when testing for a relationship between weight per individual (total weight divided by total number of horseshoe crabs) and time in the Central Sound dataset.

Data availability
Data used in the analyses are provided in Supplementary Tables 1, 2 and 3 to facilitate future use.

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Declarations

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