

## Northward expansion of the rhizocephalan *Loxothylacus panopaei* (Gissler, 1884) in the northwest Atlantic

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### Abstract

This report describes the first occurrence of the rhizocephalan *Loxothylacus panopaei* (Gissler, 1884) in North America, north of Virginia and the Chesapeake Bay. Of the panopeid mud crabs suitable for infection by *L. panopaei* (*Panopeus herbstii*, *Rhithropanopeus harrisi*, etc.), the parasite only infected *Eurypanopeus depressus*. In particular, *L. panopaei* disproportionately infected small *E. depressus* (20.5% of crabs with carapace width (CW) of 5–10 mm and 11.8% of crabs with 10–15 mm CW) but did not infect any crabs over 15 mm CW. Analysis of genetic data (COI sequences) suggests this Long Island Sound population could have derived from a range expansion from the mid-Atlantic, where the parasite is invasive. Given the parasite's disjunct distribution, human-mediated dispersal is the most likely vector for this northward range expansion.

**Key words:** estuarine; *Eurypanopeus depressus*; invasion; Long Island Sound; marine; panopeid; parasite

### Introduction

Parasites are common in marine and estuarine systems, but they can be easily overlooked or their roles poorly understood. This omission may stem from many parasites being neither conspicuous nor recognizable; consequently, their establishment in, or range expansions to, new regions may go unnoticed for some time (e.g. Carlton 1996). Here, we describe the discovery of *Loxothylacus panopaei* (Gissler, 1884) (Figure 1) in Long Island, NY (USA). *L. panopaei* is a parasitic, rhizocephalan barnacle that infects several species of panopeid crabs. The parasite's natural range extends throughout the Gulf of Mexico (GOM), the Caribbean, Venezuela, and along the Atlantic coast of Florida to Cape Canaveral (Boschma 1955; Hines et al. 1997). It was first described in 1884 as a parasite of the panopeid crab *Panopeus lacustris* Desbonne, in Desbonne and Schramm, 1867 collected in Tampa, FL (Gissler 1884; Hines et al. 1997). However, *L. panopaei* can

parasitize at least nine species of panopeid crabs (Hines et al. 1997), including *Eurypanopeus depressus* (Smith, 1869). *L. panopaei* was first noticed outside its native range in 1964 when infected panopeid crabs were found in the lower Chesapeake Bay (Van Engel 1966). The parasite was probably introduced with *E. depressus* or *Rhithropanopeus harrisi* (Gould, 1841) that had hitchhiked on oysters transplanted from GOM (Van Engel et al. 1966; Hines et al. 1997; Kruse et al. 2012; Carlton et al. 2011). From the Chesapeake Bay, *L. panopaei* has spread northeast to Chincoteague, Virginia (Hines et al. 1997) and south to North Carolina (Turquier and Payen 1978), Georgia, and Florida (Kruse and Hare 2007). In some locations, *L. panopaei* parasitizes over 90% of the available host population (Hines et al. 1997; Kruse and Hare 2007). Based on our review of the literature and personal communications (P. Foffonoff, Smithsonian Environmental Research Center, Edgewater, MD and J. Carlton Williams-Mystic, Mystic, CT), there appear to be no records of *L. panopaei* north of Virginia, USA (Hines et al. 1997).

**Figure 1.** The crab *Eurypanopeus depressus* displaying an externa of the parasite *Loxothylacus panopaei*. Photograph by ASF.



*Loxothylacus panopaei* has a highly modified life cycle (Hoeg and Lutzen 1995). The free-swimming, female cypris larva infects a crab by burying into the carapace, develops as an endoparasite (internal phase), and after about one month extrudes a virgin brood sac (externa) beneath the crab's abdomen. After fertilization by a free-swimming male cypris, the externa matures and produces several broods of thousands of naupli larvae. Both infection and emergence of the virgin externa usually occur after the host crab molts. From the moment of initial infection to the formation of this virgin externa, the crab undergoes a series of physiological and morphological changes in which *L. panopaei* assumes control over several of the crab's major biological functions, including molting and reproduction, while also compromising its immune system (Walker et al. 1992; Alvarez et al. 1995 and references therein).

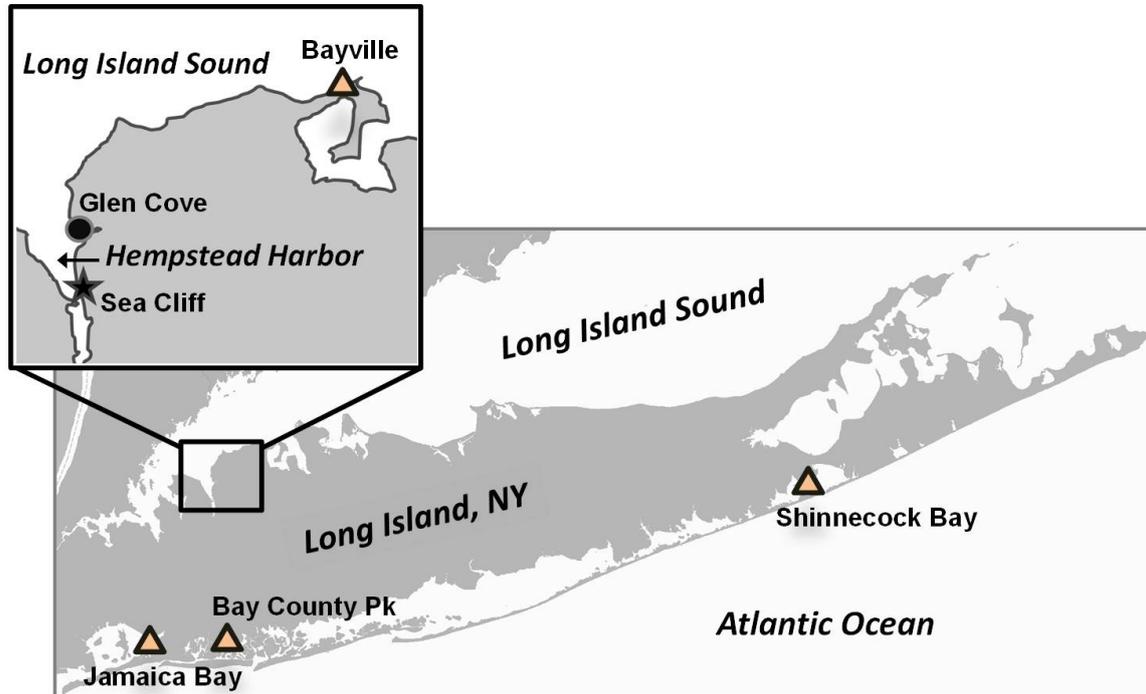
In past studies, genetic analysis of two genes (mitochondrial cytochrome oxidase I (COI) and nuclear cytochrome c) in *L. panopaei* has revealed a complex set of lineages (Kruse et al. 2012). Within Atlantic and GOM populations, at least two distinct lineages (deemed the 'ER' clade and 'P' clade) infect different crab species. The 'ER' clade infects both *E. depressus* and *R. harrisii*, while the 'P' clade infects at least 4

species of the genus *Panopeus* (Kruse and Hare 2007; Kruse et al. 2012). Recent genetic analysis has revealed that GOM, and Louisiana in particular, is the likely source region for the initial introduction of *L. panopaei* to the Atlantic coast (Kruse et al. 2012).

In this study, we describe the discovery of a new population of *L. panopaei* in Long Island Sound (LIS), its prevalence in host crabs, genetic evidence of its source population(s), and potential vectors for the species' range expansion.

## Methods

*Field Surveys:* In August 2012, we collected crabs at five sites on Long Island, NY (Figure 2). Each site was surveyed as follows: at randomly selected intervals, 15 1-m<sup>2</sup> quadrats were placed on the sand/cobble beach, below the mid-tide level during low tide. Each quadrat was then systematically searched for crabs by overturning rocks and digging through sediments for 5 minutes or until no additional crabs were discovered for > 1 minute. Any crabs > 5 mm carapace width (CW) were removed from quadrats, classified into 5 mm CW categories, and the presence of any egg masses or rhizocephalan externae recorded. Because the number of crabs



**Figure 2.** Map of Long Island, NY where surveys were conducted for *Loxothylacus panopaei* infections in panopeid mud crabs. Triangles indicate sites where panopeids were present but not infected. Circle and star indicate sites where parasitized mud crabs were found (Hempstead Harbor, map inset). In Hempstead Harbor crab surveys were conducted at Glen Cove and infected *Eurypanopeus depressus* for genetic analysis were collected from Sea Cliff.

in these 5-mm incremental categories (5–10mm, 10–15mm, etc.) was recorded for each quadrat, a median size for each category was used when calculating overall averages. When applicable, the prevalence of rhizocephalan infection was calculated by dividing the number of infected crabs by the total number of crabs sampled at a site.

**DNA sequencing and Genetic Analyses:** In August 2012, seven infected *E. depressus* were collected for genetic analysis during a haphazard survey at Sea Cliff, an intertidal site in Hempstead Harbor 2 km south of the Glen Cove crab survey site (Figure 2). Eight rhizocephalan externa were removed from seven infected *E. depressus* (one of these seven crabs had a double infection and both externa were removed for genetic analysis) and were extracted using a standard CTAB protocol (France et al. 1996). Extracted DNA was amplified using COI primers designed by Kruse et al. (2007). Samples were subjected to 95° C for 2 min followed by 29 cycles of 95° C for 45 s, 55° C for 45 s, and 72° C for 45 s, and a final extension at 72° C for 2

min. Sequencing was performed at the Smithsonian Institution's Laboratory of Analytical Biology (Suitland, MD). Sequences were aligned by eye using LaserGene DNASTar software (9.1.1 (4)) and collapsed into haplotypes using TCS1.21. We also included representative *L. panopaei* sequences from Kruse et al. (2012)'s population set, accession #: HQ848063-HQ848077. The latter sequences included invasive Atlantic and native GOM samples of *L. panopaei* from different panopeid host species (*R. harrisii*, *E. depressus*, *Panopeus* spp.) and also included four sequences from a related rhizocephalan, *Loxothylacus texanus* (Boschma, 1933), as an out-group. We incorporated the Kruse et al. (2012) population set with our eight sequences to identify if our sequences were indeed *L. panopaei* and if so, create a COI phylogenetic tree incorporating the LIS sequences into the Atlantic and GOM phylogeny. To do this, we constructed a neighbor-joining tree with PAUP\* v4.0b10 (Swofford 2001) and used TCS1.21 (Clement et al. 2000) to identify haplotypes that the LIS samples shared with those from the Kruse et al.

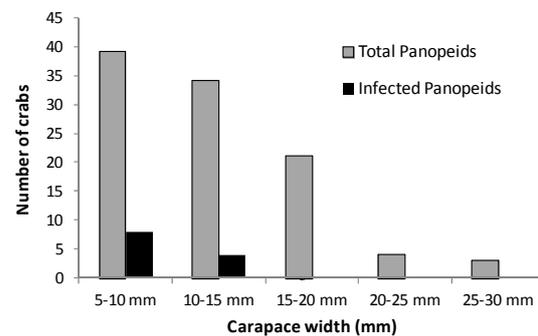
(2012) population set. In addition, we used Arlequin (v 3.1.5.2; Excoffier and Schneider 2005) to calculate fixation indices for population pairs using the combined data set. The latter analysis explored pairwise differences between haplotypes ( $\Phi_{ST}$ ) and tested for significance of differentiation.

Pairwise  $\Phi_{ST}$  patterns were further explored using a multidimensional scaling (MDS) analysis (with Primer 6, Plymouth Marine Laboratory, UK; Clarke 1993) to look for spatial patterns between and among the LIS, non-native Atlantic, native Atlantic, and native GOM populations of *L. panopaei*.

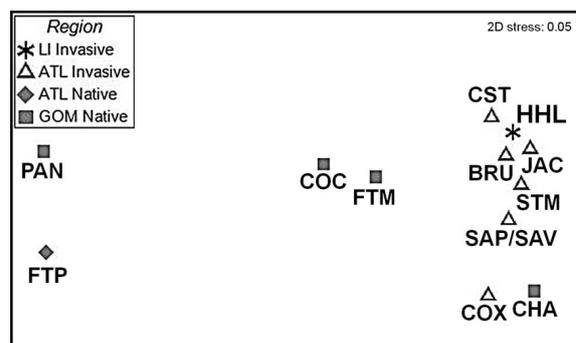
## Results

**Field Surveys:** In August 2012, *Loxothylacus panopaei* was discovered infecting panopeid crabs in Hempstead Harbor but not at our four other sampling sites (Shinnecock Bay, Jamaica Bay, Bayville, and Bay County Park; Figure 2). Of the 101 panopeid crabs found at Hempstead Harbor, only *E. depressus* were infected, and all 12 infected *E. depressus* were < 15 mm CW (Figure 3). The number of infections found in small *E. depressus* (< 15mm CW) was disproportionate to the number of infections in larger panopeids (> 15mm CW) (Chi-Squared likelihood ratio 8.397;  $P = 0.0038$ ). Based on close examination of 30 panopeids subsampled from Hempstead Harbor, *E. depressus* made up the majority of the panopeid population (approx. 90%), while two other species, *Panopeus herbstii* (approx. 3.3%) and *Dyspanopeus sayi* (approx. 6.7%) were also present. In addition, 223 Asian shore crabs (*Hemigrapsus sanguineus* De Haan, 1835) (Mean  $\pm$  SD: 17.3  $\pm$  8.2 mm CW) were found in our surveys at Hempstead Harbor, but none were parasitized with *L. panopaei* (which is unsurprising given that *L. panopaei* is specific to parasitizing panopeid mud crabs). Moreover, our prevalence calculations represent a conservative estimate because they are based on the presence of virgin and mature externae and do not account for early stage infections, which show no external evidence of rhizocephalan infection.

**Genetic Analyses:** Our eight samples corresponded to three of the eight haplotypes reported by Kruse et al. (2012). All eight sequences were located within the 'ER' clade defined in Kruse et al. (2012) as haplotypes 1 (n=1), 2 (n=4), and 3 (n=3). Of note is that the two externae extracted from a single crab represented two distinct haplotypes (hap1 and hap2), indicating a double infection by two



**Figure 3.** Size distribution of all panopeids and those infected by *Loxothylacus panopaei*. All infected panopeids were identified as *Eurypanopeus depressus*, however not all panopeids collected were identified to species.



**Figure 4:** MDS plot of pairwise results for the newly discovered invasive *Loxothylacus panopaei* Long Island population (LI Invasive) in Hempstead Harbor, the Atlantic invasive (ATL Invasive), the Atlantic native (ATL Native), and the native Gulf of Mexico populations (GOM Native). Three-letter abbreviations refer to the sample sites included in our analyses. From our study: HHL=Hempstead Harbor, Long Island (NY); From Kruse et al. (2012): BRU=Brunswick (GA), CHA=Chauvin (LA), COC=Cocodrie (LA), COX=Chesapeake Bay, Oxford (MD), CST=Chesapeake Bay, Queenstown (MD), FTM=Ft. Myers (FL), FTP=Ft. Pierce (FL), JAC=Jacksonville (FL); PAN=Panacea (FL), SAV=Savannah (GA), SAP= Sapelo (GA), STM=St. Mary's (GA). In the figure, SAP and SAV were genetically identical and thus cannot be distinguished from one another.

separate parasites. Our MDS  $\Phi_{ST}$  analysis based on pairwise differences demonstrated that all seven of the invasive Atlantic populations were not significantly (at  $p < 0.05$ ) differentiated from our Hempstead Harbor population (HHL), and the closest connections were from Chesapeake Bay (Queenstown, MD), Brunswick (GA), and Jacksonville (FL) (Figure 4). In contrast, all

native GOM and southern Florida parasite populations were significantly differentiated from our LIS population. Thus, the LIS population was more similar genetically to the invasive populations (MD, GA and FL) than to the native GOM populations, where the invasive populations originated.

## Discussion

In this paper, we document the northward expansion of the rhizocephalan *Loxothylacus panopaei* into LIS. At the LIS site where we observed the parasite, it exclusively infected small (<15 mm) *E. depressus* and derived from an 'ER' clade (infecting the mud crabs *Eurypanopeus* sp. and *Rhithropanopeus* sp.) in the parasite's invasive, Atlantic range (Kruse et al 2012). The disproportionate infection of small *E. depressus* that we observed (see also: Hines et al. 1997) is likely because crabs are most vulnerable to parasite infection soon after molting (i.e., when their carapace is soft and easier to penetrate) and small crabs (megalopae and juvenile stages) molt more frequently (Alvarez et al. 1995). Moreover, though initial infection can occur at a variety of sizes and infections may persist through multiple crab molts, infected crabs have higher mortality rates, thus crabs surviving to large size will be less often infected (Walker et al. 1992; Alvarez et al. 1995; Hines et al. 1997). Finally, once infected, the parasite halts the crabs' growth, contributing to the apparent high prevalence among small size classes (Alvarez et al. 1995).

Consistent with *L. panopaei*'s patchy distribution in other parts of the Atlantic coast (Hines et al 1997), we found the rhizocephalan at Glen Cove (in Hempstead Harbor), but no evidence of the parasite in Bayville, NY, an adjacent Long Island Sound harbor with a similar cobble and sand intertidal habitat (Figure 2). This may be because of patchy host distributions limiting opportunities for the parasite's dispersal (Hines et al. 1997), or perhaps it could indicate an early stage of invasion and the influence of Allee effects on mating success (e.g., Pringle et al. 2011; Chang et al., 2011). Because *L. panopaei* has a brief larval stage (at 25 °C, a 48 hour non-feeding planktonic nauplius), it must infect a crab host within 2–4 days. *L. panopaei* males that cannot find a female in this time may not recruit in the system, or may be swept downstream on prevailing currents (Walker et al. 1992; Hines et al. 1997). Thus, the parasite's

complex life cycle, as well as the availability of crab hosts, may influence its patchy distribution in the Atlantic, including the new populations in Long Island Sound.

If *L. panopaei*'s present northward expansion into LIS is derived from source populations in Virginia/Chesapeake Bay as our genetic data suggests, a natural current-driven spread into LIS would actually be against the prevailing southerly currents along the Middle Atlantic Bight in the Atlantic. While other analyses (e.g. Pringle et al. 2011) have shown that species can expand into upstream populations, this process is slow and typically requires large population sizes to alleviate Allee effects, or a series of retention zones to prevent larvae from advecting away from upstream populations. In the case of the new Hempstead Harbor population, Long Island itself is a large geographic barrier to natural dispersal from the middle Atlantic region into the LIS, and to date, we have found no record of *L. panopaei* at any other sites between Virginia and Long Island.

Human-mediated dispersal better explains the rhizocephalan's northward spread into LIS. In particular, several towns in Hempstead Harbor have hosted ship-based trade with various northwest Atlantic ports, especially New York City, for over two centuries (HMPHH 2004), and New York City itself is a major destination port for a substantial amount of North American shipping. Therefore, New York City may in fact serve as an introduction 'hub' for nearby LIS populations, such as Hempstead Harbor. In recent years, shipping (e.g., ballast water release and hull fouling) has been an important vector for establishing novel populations of invasive species throughout North American harbors (e.g., Ruiz et al 2000). In particular, hull fouling may transport larval and adult stages, perhaps including adult crabs infected by *L. panopaei*. For example, one of *L. panopaei*'s mud crab hosts (*R. harrisi*) is a globally invasive crab species and is suspected to have been transported to over 20 different countries by various means, including on ship hulls (Projecto-Garcia et al. 2010). Oyster translocation is believed to be responsible for the original introduction of *L. panopaei* to Chesapeake Bay (Van Engel et al. 1966) and could be another human-mediated vector for the parasite's northward movement into LIS. Though this vector has been identified as responsible for many marine bioinvasions around the globe (Carlton 1996), it may be less likely in this system because: 1) Hempstead Harbor shellfish

beds have been closed for most of the last 70 years due to industrial and residential run-off, making oyster seeding (from the Chesapeake) unlikely; and 2) New York State Department of Environmental Conservation limits any import of oysters to LIS from southern waters (S. Tettelbach, personal communication); however, illegal transport of oysters to Long Island from other populations cannot be ruled out.

*Loxothylacus panopaei* alters host behavior and lowers host survival rates (Alvarez et al. 1995), thus understanding the susceptibility of crab species to the parasite is important in predicting the parasite's impacts (Kruse et al. 2012). It also shows fairly high host generalization among mud crabs (Hines et al. 1997) and is able to cross-infect other native panopeid crabs (e.g. from *E. depressus* to *R. harrisii* in the laboratory) (Alvarez 1993). However, it is unlikely to infect other common coastal crab species found in LIS, including the alien European green crabs (*Carcinus maenas* (Linnaeus, 1758)) and Asian shore crabs, or the commercially important blue crab (*Callinectes sapidus* Rathbun, 1896). A congener, *L. texanus*, infects several crab species, including *C. sapidus* in the Gulf of Mexico, but at present, it is not established along the Atlantic coast (Briggs 1974; Shields and Overstreet 2003).

The potential for *L. panopaei* to attain epidemic population levels (as witnessed in other invasive populations; e.g., Hines et al. 1997) and impact host crab physiology and reproduction emphasizes the importance of continued and expanded surveys of the parasite's distribution in LIS and beyond. In particular, high levels of localized parasitism can occur due to the relatively short planktonic phase of *L. panopaei* larvae, especially in recently invaded areas and where there are large aggregations of panopeid mud crabs (Hines et al. 1997; Kruse and Hare 2007). Unfortunately, eradication of *L. panopaei* from LIS is not likely to feasibly control its spread because crabs can harbor internal infections that are not visible externally; e.g., the externa may drop off periodically, and a new externa emerges after the host molts (Alvarez 1993), or the crab may be recently infected and the female *L. panopaei* has not yet produced a virgin externa.

In conclusion, given the potential for *L. panopaei* to impact native mud crabs and spread to new crab hosts and new locations, we believe that it is highly important to obtain a better understanding of this invasion through the following: 1) determining the extent of the

parasite's invasion with extensive sampling in New Jersey, New York, and southern New England; 2) determining the prevalence of infections in all native panopeid species in these communities; 3) understanding how the infection could influence species interactions (native and invasive) in these communities; and 4) definitively determining its vector(s) of spread. With such information, we will be able to resolve many of the remaining questions surrounding the parasite's recent invasion.

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