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BRYOZOAN FOULING OF THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*) FOLLOWING THE 1999 DIE-OFF IN LONG ISLAND SOUND, USA

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ABSTRACT Bryozoan epibiosis on lobster hosts has rarely been reported. This study documents bryozoan fouling of the American lobster (*Homarus americanus* Milne Edwards, 1837) from the Connecticut portion of Long Island Sound, USA. A total of 168,664 lobsters were examined for epibionts from 2000 to 2013 following the lobster fishery crash in 1999. The lobsters were caught commercially for the State of Connecticut, Department of Energy and Environmental Protection lobster catch monitoring program. The lobster shell condition in four stages of its molt cycle was noted (i.e., from a soft new shell, hard new shell, hard shell, to ready to molt). Of the lobsters caught, 29% were fouled by epibionts. Of those, 88% were fouled by bryozoans, 20% by barnacles, 6% by tube worms, 3% by slipper shells, and <1% by mussels and sea squirts. The prevalence of fouling increased as time since last molt increased from <1% of soft new shells to 1% of hard new shells, 31% of hard shells, and 45% of those ready to molt. This prevalence of bryozoan fouling reported here was higher than that in other studies and may have been due to the poor health of the host lobsters and/or poor water quality.

KEY WORDS: lobster, Bryozoa, epibiosis, Atlantic, *Homarus americanus*

INTRODUCTION

Epibiosis has referred to the ecological association between organisms growing attached to a living surface such as the bryozoans on the lobsters in this study. This study used the terminology of Wahl (1989) and referred to the lobsters as basibionts (i.e., the motile host arthropod substrates) and the bryozoans as epibionts (i.e., the sessile organisms attached to the basibiont outer surface without trophically depending on it). Fouling refers to the more general colonization process of a solid surface, living or dead, by epibionts (Wahl 1989). Here, epibiosis and fouling were used interchangeably.

Understanding epibiosis has been important because fouling epibionts degrade the functionality of ship hulls, heat exchangers, and water intake pipes (Hellio & Yebra 2009). The presence of epibionts like bryozoans has covered host eyes, inhibited host wound healing, decreased the hydrodynamic efficiency of hosts, and resulted in an unappealing appearance of the affected lobster, which lowered their commercial value (Shields et al. 2006). This has been true for both aquaculture-raised (Fernandez-Leborans 2010) and wild-caught hosts (Welch 2014). As the duration in commercial American lobster impoundments increased, fouling increased above levels seen in the wild (McLeese & Wilder 1964). The unsightly nature of epibionts, as with epizootic shell disease (ESD), affected the commercial value of the lobsters (Shields et al. 2006, Gomez-Chiarri & Cobb 2012). This has been a problem not just for the Long Island Sound (LIS) American lobster fishery in this study (Landers 2005), but for crab, spiny lobster, and shellfish fisheries in general (Stentiford 2008, Watson et al. 2009, Zha et al. 2017).

Bryozoans have contributed to the fouling of both aquaculture-raised and wild-caught commercial hosts (Xixing et al. 2001). The bryozoan fauna of LIS was systematically described by Hutchins (1945) and Abbott (1973), but unfortunately, they only listed substrates as hard (i.e., shells and stones/pebbles) or soft and did not explicitly list lobsters as a substrate. More recent

work has shown that bryozoans typically foul hard substrates in LIS including commercial lobster fishing gear (Mercaldo-Allen et al. 2011, 2015). The bryozoan fauna east of the mouth of LIS has been better studied, and many bryozoan species have been reported fouling blue crabs, spider crabs, and horseshoe crabs, but not lobsters (Osburn 1912, Rogick & Croasdale 1949, Rogick 1964). In contrast, within LIS, bryozoan fouling of lobsters has been well documented (Dexter 1955, Dove et al. 2003, 2004, Hammerson 2004, Quinn et al. 2009) (Table 1).

Bryozoans have had a long evolutionary history of fouling lobsters. Bryozoans evolved the ability to live on palinurid lobsters by the Cretaceous period. Feldmann et al. (1977) reported the bryozoan *Berenicea* sp? fouling the Campanian lobster *Linuparus pustulosus* Feldmann et al., 1977. Bishop and Williams (1986) found the bryozoan *Membranipora* sp. fouling the Turonian lobster *Linuparus canadensis* (Whiteaves, 1884). Keep in mind that in fossils, it is hard to accurately measure the prevalence of epibiosis as postmolt lobsters often eat their exuviae/shed cuticle after molting to recover the lost calcium (Aiken 1980, Jernakoff et al. 1993, Lawton & Lavalli 1995). Also, one cannot rule out postmortem settlement of the bryozoan larvae on host exoskeletons (Tshudy & Feldmann 1988, Key et al. 2017). For example, the cyclostome *Berenicea* sp?. preserved growing on the carapace of *L. pustulosus* (Feldmann et al., 1977, pl. 3, fig. 10) may have happened after the host died and before its skeleton was buried. Before that in the Jurassic period, Robin et al. (2013) documented foraminiferans living epibiotically on an erymid lobster and Audo et al. (2019) reported brachiopods fouling a Jurassic polychelid lobster. By the end of the Cretaceous period, more epibionts (i.e., brachiopods, oysters, and serpulid worms) were fouling mecochirid, nephropid, palinurid, and pemphicid lobsters (Bishop 1981, 2016, Tshudy & Feldmann 1988, Robin et al. 2016). The diversification of motile arthropods with hard carapaces (e.g., lobsters) played a coevolutionary role in the diversification of sessile bryozoans (e.g., encrusting cheilostomes) over the last 250 Myr (Key & Schweitzer 2019).

In addition to lobsters (Table 1), bryozoans have fouled a variety of motile hosts including snails (Schwaha et al. 2019, Buttler & Taylor 2020), squid (Wyse Jackson & Key 2014, Wyse

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TABLE 1.
Known examples of extant epibiont bryozoans fouling lobster basibionts.

Bryozoan species	Bryozoan order	Host lobster species	Location	Where on host exoskeleton	Reference
Unidentified	Unidentified	<i>Homarus americanus</i>	Maine, USA	Carapace, antennae, eyes	Herrick (1895, 1911)
<i>Alcyonidium</i> sp.	Ctenostomata	<i>Munida gregaria</i>	Falkland Islands	Carapace, pereopods, abdomen, eyes	Rayner (1935)
<i>Alcyonidium polyoum</i>	Ctenostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	All surfaces	Dexter (1955)
<i>Bugula turrita</i>	Cheilostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	Ventral spines, seminal receptacle, carapace	Dexter (1955)
<i>Acanthodesia tenuis</i>	Cheilostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	Unidentified	Dexter (1955)
<i>Bowerbankia gracilis</i>	Ctenostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	Unidentified	Dexter (1955)
<i>Electra pilosa</i>	Cheilostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	Unidentified	Dexter (1955)
Unidentified	Unidentified	<i>H. americanus</i>	Atlantic provinces of Canada	Unidentified	McLeese and Wilder (1964)
Unidentified	Unidentified	<i>H. americanus</i>	Boothbay Harbor, ME, USA	Unidentified	Uzmann (1970)
Unidentified	Unidentified	<i>Nephrops norvegicus</i>	Isle of Man, UK	Unidentified	Farmer (1977)
Unidentified	Unidentified	<i>Jasus edwardsii</i>	Steward Island, New Zealand	Carapace, legs, sternum, and abdomen	McKoy (1983)
Unidentified	Unidentified	<i>Scyllarides latus</i>	Pico Island, Azores	Unidentified	Martins (1985)
<i>Triticella</i> sp.	Ctenostomata	<i>H. americanus</i>	Long Island Sound, CT, USA	Gills	Dove et al. (2003, 2004)
Unidentified	Unidentified	<i>H. americanus</i>	Long Island Sound, CT, USA	Unidentified	Hammerson (2004)
Unidentified	Unidentified	Unidentified	Unidentified	Cheliped	Waugh et al. (2004)
<i>Triticella flava</i>	Ctenostomata	<i>N. norvegicus</i>	Gullmarsfjorden, Sweden	Mouth parts	Funch et al. (2008)
Unidentified	Unidentified	<i>H. americanus</i>	St. Peters Bay, Canada	Unidentified	Bernier et al. (2009)
<i>Callopora</i> sp.	Cheilostomata	<i>H. americanus</i>	Long Island Sound, NY and Buzzards Bay, MA, USA	Unidentified	Quinn et al. (2009)
Unidentified	Unidentified	Unidentified squat lobster	Unidentified	Unidentified	Boyko and Williams (2011)
Unidentified	Unidentified	<i>Nephrops</i> spp.	Unidentified	Unidentified	Bell et al. (2013)
<i>Biflustra irregularata</i>	Cheilostomata	<i>Panulirus gracilis</i>	Gulf of California, Mexico	Barnacles on carapace	Key and Hendrickx (2022)
<i>B. irregularata</i>	Cheilostomata	<i>Panulirus inflatus</i>	Gulf of California, Mexico	Barnacles on carapace	Key and Hendrickx (2022)
<i>Caberea</i> sp. cf. <i>zelandica</i>	Cheilostomata	<i>J. edwardsii</i>	North Island, New Zealand	Carapace	Key et al. (2023)
Unidentified	Cheilostomata	<i>J. edwardsii</i>	North Island, New Zealand	Pleurons, uropods, pleopods	Key et al. (2023)
Unidentified	Ctenostomata	<i>S. latus</i>	Mediterranean Sea, Malta	Carapace and antenna	Key and Decker (2023)
<i>Crisia sigmoidea</i> or <i>C. oranensis</i>	Cyclostomata	<i>S. latus</i>	Mediterranean Sea, Malta	Carapace and antenna	Key and Decker (2023)
<i>Disporella</i> sp. or <i>Patinella radiata</i>	Cyclostomata	<i>S. latus</i>	Mediterranean Sea, Malta	Carapace and antenna	Key and Decker (2023)
Unidentified	Unidentified	<i>H. americanus</i>	Long Island Sound, CT, USA	Unidentified	This study

Taxonomic identifications are as listed in the original publication. Arranged by publication date.

Jackson et al. 2014), trilobites (Key et al. 2010), sea spiders (Key et al. 2013), isopods (Key & Barnes 1999), horseshoe crabs (Key et al. 1996a, 1996b, 2000), brachyuran crabs (Key et al. 1999, 2017, Winston & Key 1999), crayfishes (Đuriš et al. 2006), shrimps (Giri & Wicksten 2001, Farrapeira & Calado 2010), sea snakes (Key et al. 1995, 1996b), and sea turtles (Frazier et al. 1992). In all these cases, the permanence/longevity of the host external surface affected the occurrence of bryozoans. The

more frequently a host molted its exoskeleton or shed its skin, the less common fouling bryozoans were. As the time since last molt or shed increased, more time accrued for bryozoan larvae to settle on the host, and the more fouled the host became (Gili et al. 1993). In lobsters, the molt interval has increased with age (Phillips et al. 1980).

The objective of this study was to describe the prevalence of bryozoan fouling of *Homarus americanus* Milne Edwards, 1837,

especially in relation to the host lobster molt cycle. Compared with crabs (Key et al. 1999, 2017), lobsters tend to be much less frequently fouled by bryozoans (Key & Hendrickx 2022, Key & Decker 2023, Key et al. 2023). For example, along the northeast coast of the USA which includes LIS, Winston and Hayward (2012) reported 2% of bryozoan species fouling crabs but none on lobsters. In the literature, 21 studies were found that mention extant bryozoans growing on lobsters (Table 1). Of those, only nine identified the bryozoans. Of the bryozoans identified, they included at least 12 different bryozoan species (Table 1: 47% were cheilostomes, 40% ctenostomes, and 13% cyclostomes). The majority of the studies reported bryozoans on *H. americanus*, probably because it was the most studied lobster species due to its abundance and commercial value as the most productive lobster fishery in the world (Factor 1995, FAO 2019, 2022).

MATERIALS AND METHODS

The data for this study came from the State of Connecticut, Department of Energy and Environmental Protection (CTDEEP), Bureau of Natural Resources, Marine Fisheries Division commercial lobster catch monitoring program (Giannini & Howell 2013). All the lobsters were collected in the Connecticut portion of LIS from 40.96 to 41.38° N and 71.89 to 73.63° W (Fig. 1). Though the American lobster occurs further south in deeper cooler waters all the way to North Carolina, LIS is nearer the southern extent of its fished range in New Jersey (Williams 1984, Lawton & Lavalli 1995, Balcom & Howell 2006). Data for this project were collected following the fall of

1999 lobster fishery collapse in LIS (CTDEEP 2000). Lobsters were collected from 2000 to 2013 during routine trips by vessels of commercial lobstermen cooperating in the CTDEEP (2013) lobster catch monitoring program. The location of individual pots (Fig. 1) was recorded using a handheld GPS. Samples taken from participating commercial fishermen were scheduled seasonally so sampling effort would be proportional to the average landings over the time period 2001 to 2004. This resulted in 10–77 cruises annually by participating commercial fishermen ($n = 420$, mean = 32, SD = 20).

The following variables were scored or measured on each live lobster: carapace length, sex, relative fullness of egg mass, developmental stage of eggs, damage observations, missing appendages, presence and extent of shell disease, presence of macroepibionts, and shell hardness. Data from the first seven variables have been reported previously (e.g., Giannini & Howell 2010, 2013, CTDEEP 2013). For the purposes of this study, only the last two variables were used. First, the number of lobsters with bryozoans, barnacles, tube worms, mussels, slipper shells, and sea squirts were counted. For each lobster, the presence or absence of each macroepibiont was noted; the number of each kind was not counted. All data were collected by CT DEEP Fisheries staff. This study excluded the numerous less visible endosymbionts and microepibionts on *Homarus americanus* that have been long known due to their negative impact on commercial fisheries such as filamentous bacteria, stalked protozoans, diatoms, *Acanthocephala* parasitic worms, and parasitic nematodes (Montreuil 1954, Uzman 1967, Nilson et al. 1975, Stewart 1980, Bratley & Campbell 1985, Campbell & Bratley 1986).

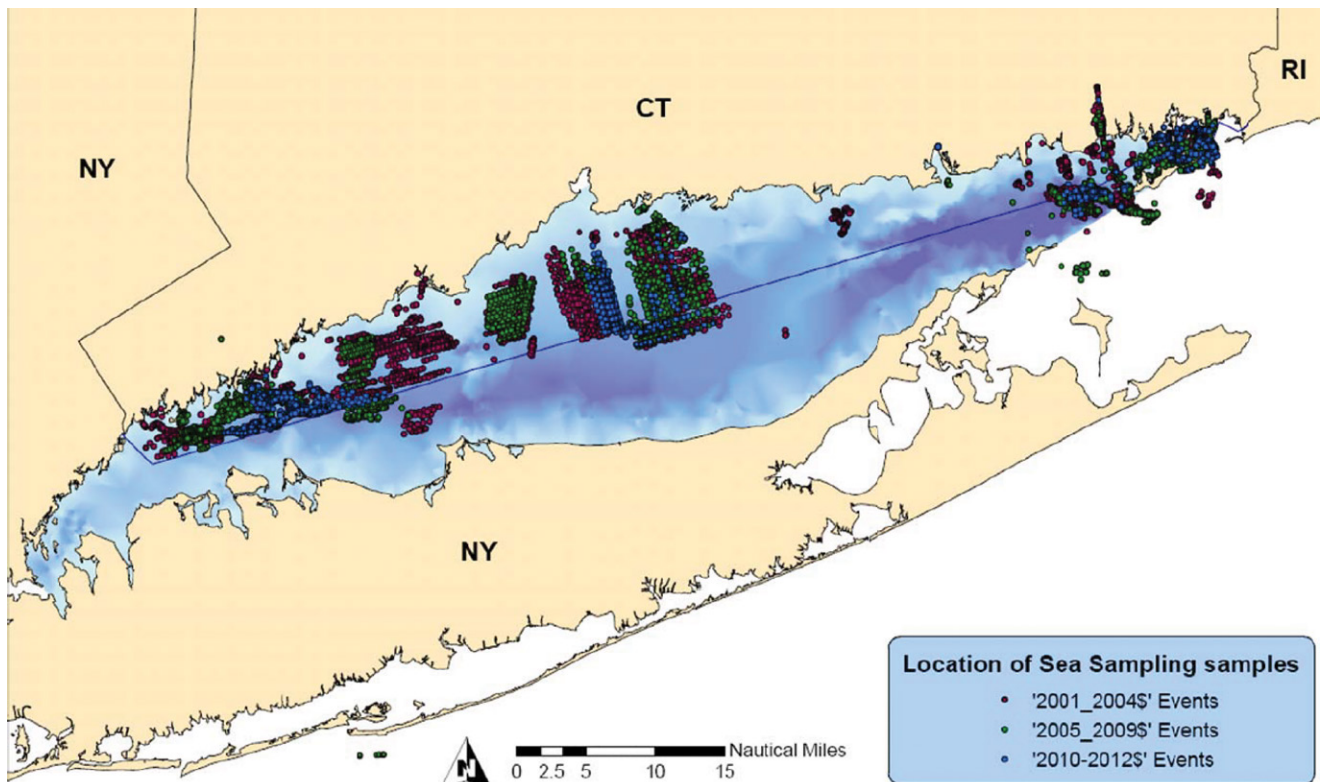


Figure 1. Bathymetric map of Long Island Sound showing locations of commercial fishery catches used in this study. Modified from CTDEEP (2013, fig. 1.2).

Second, shell hardness was used as a proxy for the molt stage. There are a variety of different methods to determine a lobster's molt stage. Due to the large number of animals in this study and despite its greater degree of subjectivity, the simpler field-based, hand-graded shell hardness classification system that is the standard assay used in the commercial trade was used. The hand-graded shell hardness system was applied by CT DEEP Fisheries staff to the carapace (i.e., the cephalothorax from the rostrum to the posterior end of the hard body shell anterior to the abdomen). Each lobster carapace was coded as one of four conditions from after molting to before molting: (1) soft new shell was a carapace that had recently molted that easily flexed under finger pressure, (2) hard new shell was a carapace that felt like it would crack if too much pressure was exerted, (3) hard shell was a carapace that did not crack under finger pressure, and (4) ready to molt shell was when the flexible membrane that joined the carapace and abdomen was stretched or starting to split.

RESULTS

A total of 168,664 *Homarus americanus* lobsters were caught from 2000 to 2013 as part of this study. The number of lobsters examined per year ranged from 724 in 2013 to 30,726 in 2001 (mean: 12,048, SD: 7,920). The number of lobsters caught declined significantly over the course of the study (Fig. 2; linear regression). Of the 168,664 lobsters, 96% were hard, 2% soft new, 1% each hard new, and ready to molt. Of the lobsters caught, 29% were fouled by an epibiont. This ranged annually from 17% to 38% (mean: 29%, SD: 6%) (Fig. 3). Of the fouled lobsters, 88% were fouled by bryozoans, 20% by barnacles, 6% by tube worms, 3% by slipper shells, and <1% by mussels and sea squirts. The prevalence of fouling by all epibionts and bryozoans declined throughout the study, but only significantly for the bryozoans (Fig. 3; linear regression). The prevalence of fouling by all nonbryozoan epibionts increased, but not significantly, over the course of the study (Fig. 3; linear regression). The prevalence of fouling increased through the molt cycle of the lobsters as time since last molt increased from <1% of soft new shells to 1% of hard new shells, 31% of hard shells, and 45% of those ready to molt (Fig. 4).

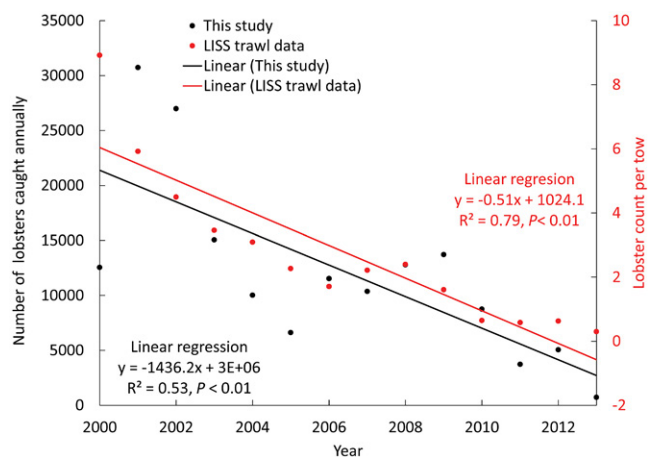


Figure 2. Number of *Homarus americanus* lobsters caught annually in Long Island Sound for this study and data standardized for sampling effort (LISS 2022).

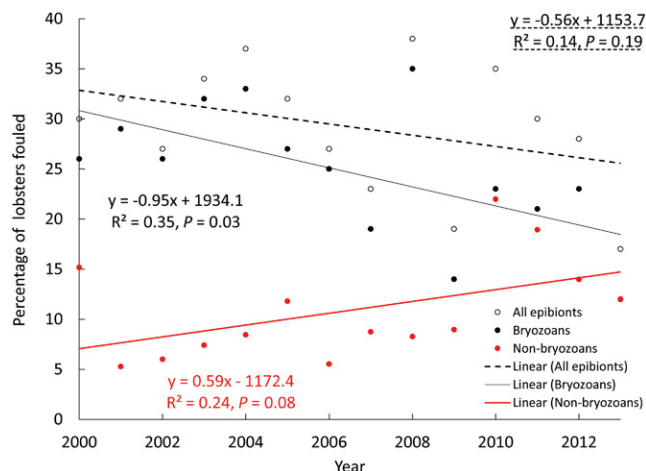


Figure 3. Annual prevalence of Long Island Sound *Homarus americanus* lobsters fouling by all epibionts, bryozoans, and nonbryozoans in this study.

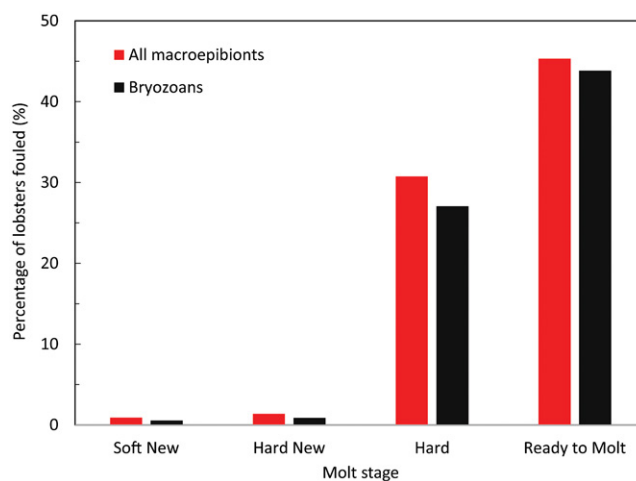


Figure 4. Increasing percentage of Long Island Sound *Homarus americanus* lobsters fouled by all macroepibionts and just bryozoans through stages of the molt cycle as time since last molt increases left to right.

DISCUSSION

Decreased Number of American Lobsters Caught in LIS Over the Course of this Study

There was a significant decline in the number of lobsters caught over the course of the 13 y of this study (Fig. 2). The LIS Study has been collecting data on the American lobster abundance in LIS since 1984 (LISS 2022). They annually record a fall and spring lobster count per research vessel trawl. From those data, a mean lobster count per trawl (i.e., standardized sampling effort) was calculated and plotted along with the count data from this study (Fig. 2). They both show a significant decline over the years of this study, 2000 to 2013. This gave confidence that the commercial pot fishery-based data used in this study was robust as it paralleled the research trawl-based data. The decline in the number of lobsters caught was real and not an artifact of decreasing sampling effort.

This decline followed the fall of 1999 when the LIS lobster population experienced a sudden and severe mortality event.

The initial event and continued decline in the lobster stock in LIS have been attributed to a variety of interrelated ecosystem-wide causes. These environmental, physiological, and biological stresses included higher seawater temperatures, lower concentrations of dissolved oxygen, pollutants (including nutrient runoff and alkylphenols), disease, and overfishing. According to Balcom and Howell (2006), the driving force of the 1999 die-off was sustained above average bottom water temperatures which resulted in a lower concentration of dissolved oxygen, which resulted in reduced ability for the lobster's immune defenses to overcome infection by pathogens. This environmental stress has been associated with multiple disease syndromes, especially ESD in the American lobster in southern New England (Smolowitz et al. 2005, Castro et al. 2012, Shields et al. 2012). Unfortunately, the challenges for the LIS lobster fishery are not going away anytime soon as global warming has led to warmer mean annual temperatures in LIS (Georgas et al. 2016, fig. 14) and more frequent marine heatwaves (Amaya et al. 2023).

Prevalence of Fouling of American Lobsters by Nonbryozoan Epibionts

The usual macroepibionts on *Homarus americanus* include red, brown, and green algae, sponges, hydroids, sea anemones, mussels, slipper shells, tunicates, annelids, and bryozoans (Herrick 1895, 1911, Dexter 1955). Of the lobsters caught in this study, 29% were fouled by an epibiont: 26% were fouled by bryozoans, 6% by barnacles, 2% by tube worms, 1% by slipper shells, and <1% by mussels and sea squirts. Dexter (1955) reported similar results from LIS lobsters with bryozoans as the most common epibionts followed in decreasing order by barnacles, jingle shells, sea squirts, mussels, tube worms, slipper shells, hydroids, sponges, and sea anemones. McLeese and Wilder (1964) reported Canadian *H. americanus* lobsters being fouled by bryozoans most frequently, then barnacles, jingle shells, limpets, mussels, and finally tube worms. Uzzmann (1970) reported the following epibionts from American lobsters: bivalves, barnacles, bryozoans, sea squirts, and tube worms. Two species of barnacles have been reported on *H. americanus*: *Trilasmis* (Lewis 1976) and *Balanus crenatus* Bruguière, 1789 (Dexter 1955). Ectoparasitic copepods have also been found (Shields et al. 2006, Wootton et al. 2011, Huys 2016).

These macroepibionts were in addition to the numerous less visible endosymbionts and microepibionts found on *Homarus americanus* but not part of this study. The commensal polychaete annelid *Histriobdella homari* Van Beneden, 1858 lives on the host branchial chambers and feeds on microorganisms in the respiratory current (Simon 1968, Jennings & Gelder 1976, Boghen 1978). Van Engel et al. (1986) reported that 18% of lobsters were fouled by the parasitic nematode *Ascarophis* sp. The cyclophoran *Symbion americanus* Obst et al., 2006 was reported to live on the host mouth parts (Obst et al. 2006).

Prevalence of Bryozoan Fouling of Lobsters

Few studies reported epizoid bryozoans on lobsters (Table 1). This may be a function of bryozoans being overlooked due to their removal to identify the host species (McDermott 2005, 2009), the lack of researchers to identify the bryozoans, and/or their small size (e.g., Hendrickx & Ramírez-Félix 2019, fig. 2), which sometimes leads to them being referred to as “moss” on epibiont surveys (Savoie et al. 2007). Unfortunately, the

bryozoans in this study were not identified, but that has been the norm in peer-reviewed fouling studies where only 43% of the studies did so (Table 1). There were even fewer studies that reported the prevalence of bryozoan fouling of lobsters. How did the prevalence of 26% of lobsters being fouled by bryozoans in this study compare with other studies? Dexter (1955) studied the prevalence of epizoid bryozoans on the American lobster in LIS in 1946. He found that the frequency of fouling bryozoans varied by species from 0.2% to 60% ($n = 5$, mean = 13%, SD = 24%). Bernier et al. (2009) similarly reported that 12% of American lobsters from St. Peters Bay, Canada, were fouled by bryozoans. The results in this study were twice that of the previous two studies.

One explanation for the higher prevalence of bryozoan fouling in this study compared with others is that water quality has degraded over time in LIS and fouling organisms are often associated with poorer water quality. This is true in aquaculture settings and locations with higher organic loads (Nilson et al. 1975). Lobsters from Canada may have a lower prevalence of bryozoan fouling as they inhabit less impacted waters (McLeese 1956). Water temperature might also play a role as temperatures in LIS are higher than those in the Gulf of Maine and Canada (McLeese 1956, Coastal Ocean Analytics 2016, fig. 1.22, Reardon et al. 2018).

The prevalence of bryozoan fouling of the American lobster reported here was lower than most other studies on crabs (Key et al. 1999, 2017). This was attributed to the lack of terminal anecysis in this host lobster. Shields (2011) noted that there were fewer fouling organisms on lobsters than on crabs, perhaps because many crab species have terminal molts whereas lobsters often do not. *Homarus americanus*, like most lobsters, does not have a terminal molt following reaching sexual maturity and mating (Phillips et al. 1980). As a result, it continues to molt throughout its life, but less frequently with increasing age (Phillips et al. 1980). Thus, epibionts continue to be discarded throughout its life, unlike most crabs that have terminal molts (Shields 2011).

As *Homarus americanus* grows, intermolt duration (i.e., period in days) increases exponentially with body size (i.e., carapace length in mm) (Mauchline 1977, Aiken 1980, fig. 7). As *H. americanus* molts throughout its life, its size (i.e., carapace length) increases exponentially (Shleser 1974, Aiken 1980, fig. 8). Therefore, as the lobsters grew, their target area for settling bryozoan larvae increased exponentially in size and time because of the last molt. Therefore, older/larger lobsters should be more fouled.

Larger/older lobsters were often not kept by commercial lobstermen for three reasons. First, in most commercial fisheries, there was a maximum legal size for lobsters [e.g., in Maine it is 5 in. (13 cm)]. Second, their meat was tougher/more leathery and not as sweet and generally only used for lobster chowder which was in less demand than live lobsters. Third, their exoskeletons were visually less attractive to consumers resulting from the increased time since they last molted. Due to this increased time since last molt, they tended to be more fouled, and they tended to have more ESD.

Why Did the Bryozoan Fouling Rate of Lobsters Decrease Significantly Over the Course of this Study?

Epibiotic communities have been known to vary interannually (Fernandez-Leborans & Gabilondo 2008). Including all

macroepibionts, the prevalence of fouling of lobsters in LIS did not change significantly over the 14 y of this study (Fig. 3). In contrast, the prevalence of bryozoan fouling of lobsters in LIS significantly decreased over the 14 y of this study (Fig. 3). In contrast, the nonbryozoan macroepibionts increased (Fig. 3). Perhaps the nonbryozoan macroepibionts were outcompeting the bryozoans for substrate space in response to increasing prevalence of ESD throughout this study (Castro et al. 2012, CTDEEP 2013, Giannini & Howell 2013). Epibionts tend to settle in the lesions associated with ESD in the American lobster (Smolowitz et al. 2005), including bryozoans (Dove et al. 2003, Gomez-Chiarri & Cobb 2012). Quinn et al. (2009) documented an association between the cheilostome bryozoan *Callopora* sp. and ESD lesions in *Homarus americanus* in eastern LIS and Buzzards Bay. More generally, heavy infestations of epibionts have been a useful indicator of the health of their host in addition to the presence of illness (Shields 2011). Compared with diseased lobsters and lobsters held in captivity, wild lobsters carried a lighter epibiotic load (Dove et al. 2003, Quinn et al. 2009).

Why Did the Prevalence of Fouling Increase through the Molt Cycle?

In this study, 96% of the lobsters examined were hard, 2% soft new, 1% each hard new, and ready to molt. The domination of the sample population by the hard shell condition was a function of how much time during a lobster molt cycle that it spent in that state relative to the timing of harvesting. In the American lobster, as with all lobsters, the frequency of molting decreases with increasing age (Phillips et al. 1980). On average *Homarus americanus* molts 10 times in their first year, three to four times in years 2–3, twice in year 4, and annually thereafter (Hughes & Matthiessen 1962, Comeau & Savoie 2001). According to Aiken (1980, table 1), *Homarus* spends on average 1% of each molt cycle in the soft stages A₁–A₂ (i.e., soft new shell in this study), 25% in the flexible stages B–C₃ (i.e., hard new in this study), 72% in the rigid stages C₄–D₂ (i.e., hard in this study), and 2% in the premolt stage D₃ (i.e., ready to molt in this study).

The prevalence of fouling by all macroepibionts increased through the molt cycle of the lobsters as time since last molt increased from <1% of soft new shells to 1% of hard new shells, 31% of hard shells, and 45% of those ready to molt (Fig. 4). The same was true for just the bryozoans which increased from <1% of soft new shells to 1% of hard new shells, 27% of hard shells, and 44% of those ready to molt (Fig. 4). As time since the last molt increased, the age of the host substrate increased, leading to increased epibiont load.

Previous studies of *Homarus americanus* have shown that endobiont load generally increases with host size and thus time since last molt (Boghen 1978, Bratney et al. 1985). A similar pattern has been documented for epibionts on crabs (Gili et al. 1993). This was only the second study that quantitatively related the prevalence of macroepibiont fouling to the molt stage in *H. americanus*. Dexter (1955), working in the Connecticut part of LIS, also found an increase in the prevalence of macroepibionts with increasing time because of the last molt. He reported that 26% of 1–2 mo old new-shell lobsters had macroepibionts, and this increased to 79% in nearly 2 y old shells of females in berry. Focusing on bryozoans, Dexter (1955) reported that 25% of 1–2 mo old new-shell lobsters caught in July–August

were fouled by the ctenostome bryozoan *Alcyonidium polyoum* (Hassall, 1841), and this increased to 60% in nearly 2 y old shells of females in berry caught in June. These results support those from this study that as time since last molt increased, epibiont load increased.

Other Factors Affecting the Prevalence of Bryozoans on Lobsters

The prevalence of bryozoans on their host lobsters may have been controlled by additional factors other than the time since the last molt. Bryozoan larvae are selective when it comes to choosing a hard living substrate upon which to settle rather than on an inert rock. Bryozoan larvae prefer certain biofilms and surface topographies when settling (Bers et al. 2010, Wahl et al. 2012). Perhaps bryozoan larvae and/or the biofilm community prefer or avoid certain chemical compositions of the lobster exoskeleton (Mergelsberg et al. 2019). Kunkel et al. (2012) showed that the chemistry of the lobster epicuticle can defend against microbes. Perhaps bryozoan larvae and/or the biofilm community prefer or avoid certain textures of the lobster exoskeleton. Finally, lobsters groom themselves to remove epizoans (Phillips et al. 1980, Atema & Voigt 1995) like crabs do (Tashman et al. 2018). Bauer (1981) reported that in addition to gill cleaning, the American lobster grooms its body using its anterior chelipeds and poster pereopods. Grooming would remove bryozoan larvae and reduce the prevalence of fouling bryozoans.

What Were the Costs and Benefits to the Fouling Bryozoans and Host Lobsters?

Many organisms have been known to foul the exoskeleton of lobsters. Some were opportunists that simply required a hard surface. Others were obligate symbionts or parasites. In small numbers, most epibionts had little if any effect on their host (Shields 2011). There were both costs and benefits to both the bryozoans and the lobsters for this symbiotic relationship.

There were a variety of potential costs to the bryozoans. The main one was living on an ephemeral substrate (i.e., the molting host lobster). If a bryozoan colony could not grow to large enough size to sexually reproduce before its host molted, there was no benefit. Once the exuviae was cast off, and often eaten (as mentioned above), the colony died. Additionally, the colonies could have been abraded or unable to feed when the host lobster mated or sheltered into rocky crevices or burrowed into soft substrates for protection (Cobb 1976, Cooper & Uzman 1980, Lawton & Lavalli 1995). During seasonal migrations, the host lobster could have taken the colonies into water bodies not conducive to the bryozoans (MacKenzie & Moring 1985).

There were a variety of potential benefits for a sessile bryozoan living on a motile host lobster. Hard substrate space has been a limiting factor for bryozoans, especially encrusting bryozoans (Jackson 1977, Lidgard & Jackson 1989, McKinney 1995, Taylor 2016). Therefore, any increase in hard substrate space (e.g., motile host lobster) should have reduced competition for substrate space and increased bryozoan diversity as documented by Balazy and Kuklinski (2013) and Key and Schweitzer (2019). Living on a motile host provided the sessile bryozoans with free transport for avoiding predators, improved gamete dispersal, and increased geographic range. By living on the carapaces of the host lobsters, the bryozoans could have

avoided one of their predators, the host itself. The main constituents of the diet of the American lobster have been crustaceans, molluscs, echinoderms, and fishes (Phillips et al. 1980, 2013, Sainte-Marie & Chabot 2002), but they have also eaten bryozoans (Lawton & Lavalli 1995). The Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758), has also eaten bryozoans (Chapman 1980). By fouling the carapace of the host lobster, they avoided predation. This relationship has similarly been documented for prey bryozoans fouling predatory sea spiders (Key et al. 2013).

Due to the small encrusting size of fouling bryozoan colonies, there were few potential costs to the lobsters such as increased drag from erect colonies. One cost that has been documented by other studies was when bryozoan colonies encrust over the eyes of their host lobsters. Herrick (1895) reported an unidentified bryozoan completely covering the eye of an American lobster. This is similar to the bryozoan *Alcyonidium* sp., known to foul the eyes of the squat lobster *Munida gregaria* (Fabricius, 1793), and in one case it obscured the cornea of the host eye (Rayner 1935).

There were probably no potential benefits to the host lobsters other than camouflage from prey or predators. *Homarus americanus* has been preyed upon by humans with northwest Atlantic landings increasing 5-fold over the last 50 y (Hvingel et al. 2021, fig. 4a). Camouflage from macroepibionts does not affect commercial lobster landings. The American lobster has also been preyed upon by a variety of fishes, especially cod (Lawton & Lavalli 1995). Perhaps the lobster could accrue the benefit of camouflage from these predators if enough of its carapace was covered by bryozoans. Martins (1985) suggested this for the bryozoan encrusted locust lobsters from the Azores.

Due to differing food sizes, there have been no studies about the removal of pathogenic microbes or the protection of microbes by macroepibionts.

CONCLUSION

In most epibiont-basibiont symbioses, the epibiont was a nonspecific substratum-generalist, and best classified as facultative (Wahl & Mark 1999). Like other documented examples of bryozoans fouling lobsters (Boyko & Williams 2011, Key & Hendrickx 2022, Key & Decker 2023, Key et al. 2023), this symbiotic relationship was classified as commensal where the fouling bryozoan benefited and the host lobster was unaffected. It was a facultative phoretic relationship (i.e., accidental hitchhiking).

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