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OBSERVATIONS ON A REEMERGING EPIZOOTIC OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*, RESOURCE

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ABSTRACT The Anaskid nematode, *Sulcascaris sulcata* has a worldwide distribution and utilizes benthic molluscs as an intermediate host with sea turtles (Chelonioidea) serving as definitive hosts. During the spring of 2015, sea scallops (*Placopecten magellanicus*) harvested along the mid-Atlantic Bight (MAB) presented with rust-colored lesions on the surface of the adductor muscles. Morphological and molecular investigations determined that the lesions were caused by an infection by third- and fourth-stage larval *S. sulcata*. Seasonal monitoring from 2015 to 2018 delineated a stable spatial distribution of infected scallops that corresponded to a large 2013 year-class of scallops and persistent utilization of this habitat by seasonally resident loggerhead turtles. Given the life cycle and etiology of *S. sulcata*, the risk to human health via direct infection or allergic reaction appears to be low, however, the spatiotemporal scale of nematode-infected scallops resulted in fishery-level impacts with respect to the spatial distribution of fishing effort in response to product quality and depreciation of the value of landed scallops. The long-term trajectory of the epizootic remains unclear and continued monitoring of the spatiotemporal distribution of nematode-infected scallops is warranted as *S. sulcata* spatial distribution is likely dependent upon sea scallop abundance, which is currently trending toward more northerly portions of the MAB.

KEY WORDS: Anisakidae, *Sulcascaris sulcata*, marine molluscs, spatiotemporal distribution, sea scallop fishery, *Placopecten magellanicus*

INTRODUCTION

The sea scallop, *Placopecten magellanicus*, is an epibenthic, bivalve mollusc distributed throughout the Northwest Atlantic Ocean from Virginia to the Canadian Maritimes (Shumway & Parsons 2016). Sea scallop distribution is mediated by thermal tolerance (upper lethal tolerance of 20°C–24°C), which restricts their distribution to the offshore, continental shelf waters along the mid-Atlantic Bight (MAB) (Dickie 1958). Farther north, sea scallops can be found on Georges Bank (GB) and near coastal areas in the Gulf of Maine. The species supports significant commercial fisheries throughout its range with the US fishery landing approximately 49 million pounds (adductor muscle) valued at $487 million in 2020 (NOAA 2022).

During the spring of 2015, the sea scallop industry reported the presence of rust-colored lesions on the exterior of harvested adductor muscles. The locus of the reports centered around the southern extent of the sea scallop resource, with the epicenter emanating from a newly reopened management area that had been closed to fishing for multiple years and contained dense concentrations of harvestable, adult scallops. Initial investigations suggested a nematode parasite was the likely cause as supported by historical observations from other molluscs along the East Coast of the United States presenting with similar pathologies (Lichtenfels et al. 1978, Barber et al. 1987, Deardorff 1989). Barber et al. (1987) described the prevalence and intensity of *Sulcascaris sulcata* larvae in calico scallops (*Argopecten gibbus*) collected off the southeastern US coast during the early 1980s. The current emergence of the parasite has raised concerns about the potential impacts on scallop product quality and food safety, as well as the potential longer-term population-level impacts on fishery productivity.

Anaskid nematodes are common, globally distributed helminth parasites in the marine environment (Kuhn et al. 2016). The nematode, *S. sulcata*, is the sole member of the genus and has a life history, physical characteristics, and etiology that have been well described by several authors (Cobb 1930, Lichtenfels et al. 1978, Lichtenfels et al. 1980, Berry & Cannon 1981). The species is characterized by four larval stages, with the third and fourth stages associated with marine molluscs as intermediate hosts. Whereas benthic molluscs act as intermediate hosts, several species of sea turtle including loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and Kemp's Ridley (*Lepidochelys kempii*) act as definitive hosts (Lichtenfels et al. 1978, Berry & Cannon 1981, Greiner 2013). Nematodes reside and become sexually mature in the gastrointestinal tract of sea turtles, shedding developing eggs to the benthos via feces (Barber et al. 1987, Deardorff 1989, Gračan et al. 2012, Greiner 2013). The first- and second-stage larvae enter benthic marine molluscs, presumably through filter-feeding activity, and become established in a variety of soft tissue structures where they progress through subsequent developmental stages (Berry & Cannon 1981, Barber et al. 1987, Deardorff 1989). Fourth-stage larvae become coiled within an encapsulated sheath in the soft tissue and present as brown, rust, or orange-colored lesions (Lichtenfels et al. 1978, Berry & Cannon 1981, Barber et al. 1987, Deardorff 1989). Fourth-stage larvae are passed to turtles when infected molluscs are ingested, thereby completing the life cycle (Berry & Cannon 1981, Barber et al. 1987, Deardorff 1989, Gračan et al. 2012).

The cosmopolitan distribution of sea turtles, coupled with the broad composition of prey species that comprise sea turtle diets have likely mediated the spread of *S. sulcata* into scallop species worldwide. The saucer scallop (*Amusium balloti*) in the tropical waters of Australia, the zigzag scallop (*Euvola ziczac*) in Brazil, and the Mediterranean scallop (*Pecten jacobaeus*) and queen scallop (*Aequipecten opercularis*) from the Adriatic Sea are global examples of scallop species that have been

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documented to have *S. sulcata* infections (Lester et al. 1980, Amato & Amato 1982, Marcer et al. 2020, Pretto et al. 2020). Along the East Coast of the United States, *S. sulcata* larvae have been observed in a range of benthic molluscs, including the surf clam (*Spisula solidissima*), calico scallop (*A. gibbus*), and bay scallop (*Argopecten irradians*) (Lichtenfels et al. 1978, Barber et al. 1987, Deardorff 1989). Whereas *S. sulcata* has been recognized as a common nematode parasite in marine bivalves worldwide, including numerous scallop species, it has not been definitively identified in *P. magellanicus* and the implications of the parasite with respect to population and fishery-level impacts remain unknown (Getchell et al. 2016).

The rapid emergence of sea scallops affected with symptoms consistent with infection by the nematode parasite *S. sulcata* has raised numerous concerns and questions about the potential impact on the fishery. The objectives of this study were to confirm the cause of lesions observed on the adductor muscle of sea scallops via a suite of histological, morphological, and molecular approaches. The spatiotemporal distribution of infected scallops over the course of 5 y, beginning with observations made during the spring of 2015, which represented the timing of the initial industry reports of affected scallops was also characterized. To begin to understand the possible relationship between sea turtles present in the system and affected sea scallops, the genetic similarities of nematode larvae obtained from both the infected sea scallops along the MAB and those recovered from the gastrointestinal tracts of moribund sea turtles were documented. Evidence of differences in the distribution of genetic variation among nematodes collected from sea scallops in different years and geographic regions was assessed.

MATERIALS AND METHODS

Data Collection

Observations that characterized the spatiotemporal distribution of infected sea scallops and material for molecular analyses were collected in conjunction with resource assessment surveys conducted annually by the Virginia Institute of Marine Science (VIMS). VIMS has conducted sea scallop dredge-based surveys of a large portion of the sea scallop resource, including the entire MAB and select portions of GB since 2015 (Fig. 1, Table 1). All surveys were conducted between May (MAB)

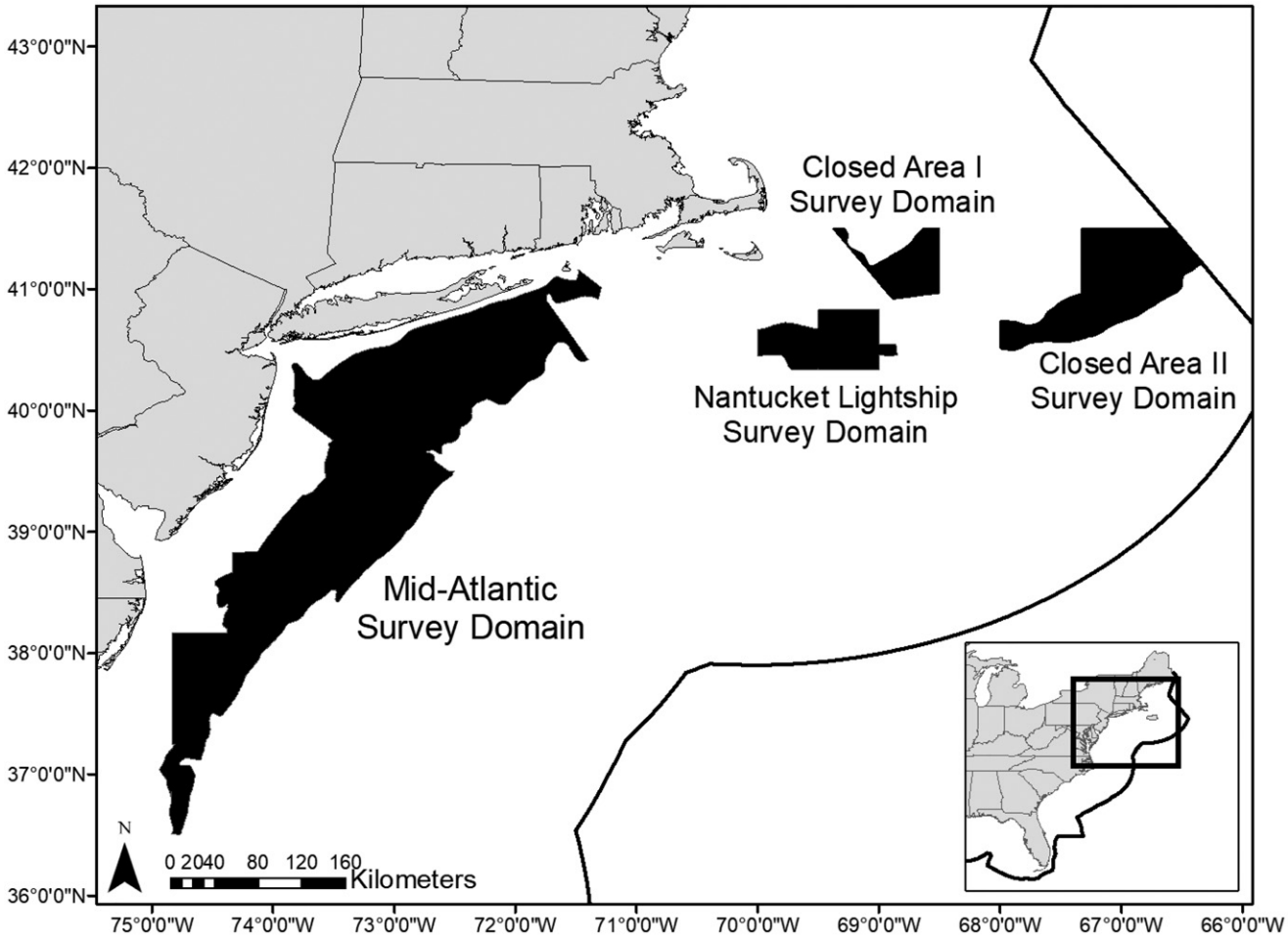

Figure 1. Survey domains (black polygons) sampled by the Virginia Institute of Marine Science where sea scallops were assessed for the presence of lesions in the adductor muscle. The Economic Exclusive Zone is indicated by the black line. The mid-Atlantic survey domain samples the mid-Atlantic Bight subunit of the resource. The Nantucket Lightship, Closed Area I, and Closed Area II survey domains are in the Georges Bank subunit of the resource.

TABLE 1.

Information on the number of sea scallops assessed for nematode infections from the mid-Atlantic survey, along with the number of sea scallops infected, mean prevalence of infections, and mean intensity of infections by year and latitudinal zone.

Year	Latitudinal zone	Number of scallop samples	Number of scallops infected	Prevalence	Intensity
2015	North	1,773	26	0.07% (0–3)	1.27 (0–3)
	Central	606	1	1.64% (0–22)	1 (0–1)
	South	1,433	300	21.43% (0–100)	2 (0–7)
2016	North	3,074	299	0.89% (0–20)	1.45 (0–5)
	Central	581	6	9.30% (0–46)	1.33 (0–2)
	South	1,895	854	46.74% (0–100)	2.45 (0–12)
2017	North	3,210	191	0.79% (0–20)	1.59 (0–5)
	Central	514	5	6.13% (0–66)	1 (0–5)
	South	2,026	719	35.43% (0–100)	2.40 (0–12)
2018	North	2,899	267	1.37% (0–27)	1.55 (0–7)
	Central	721	11	8.67% (0–60)	1.09 (0–2)
	South	1,793	743	42.23% (0–100)	2.64 (0–18)

Prevalence is defined as the number of sea scallops observed to be infected as a percentage of all sea scallops sampled. Intensity is defined as the mean number of lesions observed in infected sea scallops. Minimum and maximum prevalence and intensity values at the station level are in parentheses.

and June/July (GB) each year. Sampling stations were selected within a stratified random design with strata delimited by depth and latitude (NEFSC 2018).

At each sampling station that contained scallops, up to 15 animals were selected for biological sampling. Scallops were randomly selected to be representative of the overall size distribution of the animals encountered in the sample. Information recorded for each animal included: shell height (distance from the umbo to ventral margin), sex, maturity stage, meat quality, adductor muscle weight, and the occurrence of disease. The presence or absence of common sea scallop diseases was recorded, which included gray meat disease, shell blister disease, and nematode infections (Inglis et al. 2016, Shumway & Parsons 2016). Nematode lesions were visually identified and if at least one lesion was visible, a positive value was assigned. For each positive occurrence, the total number of visible lesions was also recorded. Samples of adductor muscle that contained visible lesions in 2016 and 2017 were preserved in 95% ethanol until lesions could be dissected in the laboratory and subsequent genetic analysis of nematodes found in dissected lesions.

Additional in-shell samples of sea scallops were obtained from commercial trips in areas affected by nematode infections during May and October of 2015. These samples provided material to further examine the larvae present and describe morphological characteristics to identify the nematode to the lowest possible taxonomic level. Data recorded included the location of lesions in all soft tissue, overall number of lesions per scallop, and size measurements of visually discernable larvae extracted from the muscle.

Histology

Macroscopic and microscopic examinations were initially completed to identify the larvae to species and document the larval stages of the parasite observed in the scallop adductor muscle. Fresh squash mounts were taken from infected scallops and processed to identify the species and document larval stages.

Genetics

Samples of 380 scallops positive for nematode infection based on visual inspection were randomly selected from the 2016 (n = 180) and 2017 (n = 200) surveys and tissue around the infection site was excised and preserved in 95% ethanol and held at −20°C until dissection and DNA extraction. In addition, 15 nematode samples were collected from the gastrointestinal tract of two necropsied loggerhead turtles and one Kemp's Ridley turtle found in Florida and preserved in 95% ethanol (Brian Stacy DVM, Ph.D., DACVP). Whereas these turtles were collected in Florida, the distribution of both species overlaps with that of *P. magellanicus* in the Northeast United States, as this region is used for migration and foraging (Murray 2011, Patel et al. 2016, Patel et al. 2018, Robinson et al. 2020). *P. magellanicus* has been identified as a prey item for loggerhead turtles (Smolowitz et al. 2015), and bay scallops have been documented in the gut content of Kemp's Ridley turtles in New York (Burke et al. 1994).

For the randomly selected genetic samples, ethanol-preserved tissue was dissected under an Olympus SZ61 stereomicroscope (Olympus, Waltham, MA) and nematodes were removed and placed into 95% EtOH until DNA was extracted using Chelex 100 following Walsh et al. (1991). For nematodes collected from turtles, DNA was extracted using the Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, CA). The mitochondrially encoded CO2 region (MT-CO2) was sequenced for all nematodes recovered from dissections using the PCR primers and parameters of Garbin et al. (2011). The MT-CO2 region was chosen for molecular identifications based on its higher level of variability as compared with other regions tested and the availability of sequences in GenBank. Amplification products from all loci were purified using a QIAquick PCR Purification Kit (Qiagen) following the manufacturer's protocol and quantified using a NanoDrop 2000 (Thermo Fisher Scientific, Waltham, MA). Purified PCR products were sequenced bidirectionally using the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) and sequencing reaction products

were electrophoresed on an ABI 3130xl Prism genetic analyzer (Applied Biosystems). Chromatograms of forward and reverse sequences were imported into SEQUENCHER v5.4.6 (Gene Codes Corporation, Ann Arbor, MI) for editing and creation of consensus sequences. Sequences for each individual were aligned in MACVECTOR v12.5.1 (MacVector Inc., Apex, NC) using the MUSCLE algorithm (Edgar & Edgar 2004) and compared with sequences deposited in GenBank (Sayers et al. 2019) using Basic Local Alignment Search Tool searches. Sequences were collapsed into haplotypes using FABOX v1.41 (Villesen 2007). To look for temporal and spatial differences in the distribution of haplotypes, samples were grouped by year and, alternately, by latitudinal zone and haplotype networks were generated using the median-joining algorithm of Bandelt et al. (1999) in POPART v1.7 (Leigh & Bryant 2015). Summary statistics for the sequence data including haplotype and nucleotide diversity, number of polymorphic sites, and mean number of pairwise differences between sequences were calculated using ARLEQUIN v3.5 (Excoffier & Lischer 2010). To test for significant differences in genetic divergence among groups, Φ_{ST} values based on the uncorrected distance between haplotypes were calculated in ARLEQUIN. Significance was assessed based on 10,000 permutations of the data.

Prevalence, Intensity, and Spatial Distribution

Data collected from the biological assessments conducted during the VIMS surveys were used to examine the prevalence, intensity, and spatial distribution of infected scallops. Prevalence was defined as the number of scallops observed to be infected as a percentage of all scallops sampled at a given station. Intensity was defined as the mean number of lesions observed in infected scallops at a given station. The survey domain was divided into three latitudinal zones to summarize prevalence and intensity across years. South of 38.8° N was classified as the South Zone, the Central Zone was between 38.8° N and 40.4° N, and the North Zone was the remaining survey area north of 40.4° N. The spatial distribution of nematode infections was estimated with an inverse distance weighted interpolation (IDW) for both prevalence and intensity. IDW was used to estimate infections for unsampled areas within the survey domain using point data from sampled stations (Fortin & Dale 2006). IDW was conducted in R with the gstat package (Gräler et al. 2015, R Core Team 2016). Maps depicting the spatial distribution were visually compared across all years (2015 to 2018) and an annual abundance-weighted mean location was calculated to assess spatiotemporal shifts in the distribution of infected scallops (Burt et al. 2009).

RESULTS

Histology

Histological examinations from in-shell samples collected from the commercial fishery and subsequently corroborated by the 2016 and 2017 genetic analysis in this study (see the following) suggested that the observed lesions were consistent with an infection by the nematode parasite *S. sulcata*. Macroscopic observations of the parasite showed that worms present in the lesions were typically elongated, ranging from 2 to 12 mm in length and 1–4 mm in width (Fig. 2). Typically, lesions were observed along the exterior edge of the adductor muscle between the mantle velar folds of both valves opposite the catch muscle (Fig. 2). Only two lesions were observed on the cut surface of the adductor muscle (where the right valve was removed). These lesions extended into the muscle between muscle fibers within 3 mm of muscle longitudinal surface. The deepest lesion observed was 5 mm below the muscle surface. The rust-, brown-, or orange-colored lesions were caused by melanization of the host granulomatous response around the encysted worms. Microscopic observations of the life stages of the nematode were consistent with observations from calico scallops, with only third- and fourth-stage larvae documented (Barber et al. 1987, Deardorff 1989) (Fig. 3). Infection intensity, lesion size, and larval *S. sulcata* length varied between the two time periods when in-shell scallops collected from the commercial fishery were examined. The May 2015 sampling, which corresponded to early initial reports of infected scallops, resulted in an intensity of 1–8 lesions per scallop. Recovered worms were similar in size (14–24 mm) and morphologically consistent with fourth-stage larvae (Fig. 3). Scallops collected during October 2015 had a higher intensity (2–12 lesions per scallop), greater variability in the size of individual lesions, and worms were more variable in size. Characteristics morphologically consistent with both third- and fourth-stage larvae were found in scallops collected during October 2015.

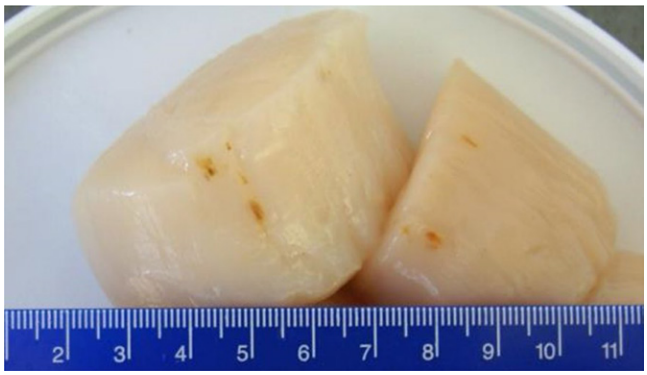

Figure 2. Picture of infected sea scallop adductor muscle. Lesions are rust/brown- or orange-colored imperfections on the adductor muscle.

Genetics

Of the 380 scallop samples selected for examination and genetic analysis during survey operations that ranged from Virginia to New York, individual nematode larvae were found in 184 samples (48%), with 77 (43%) in the 2016 samples and 107 (54%) in the 2017 samples. During dissection and examination of scallop adductor muscles with visible lesions, only two of the sampled scallops contained two nematode larvae with the remaining 182 containing a single larva. Whereas some adductor muscles presented with multiple lesions, no nematodes were visible in the remaining tissue samples, suggesting that either the nematode had exited the adductor muscle prior to collection, the larvae were too small to see under the dissecting microscope, or had disintegrated as part of the host response.

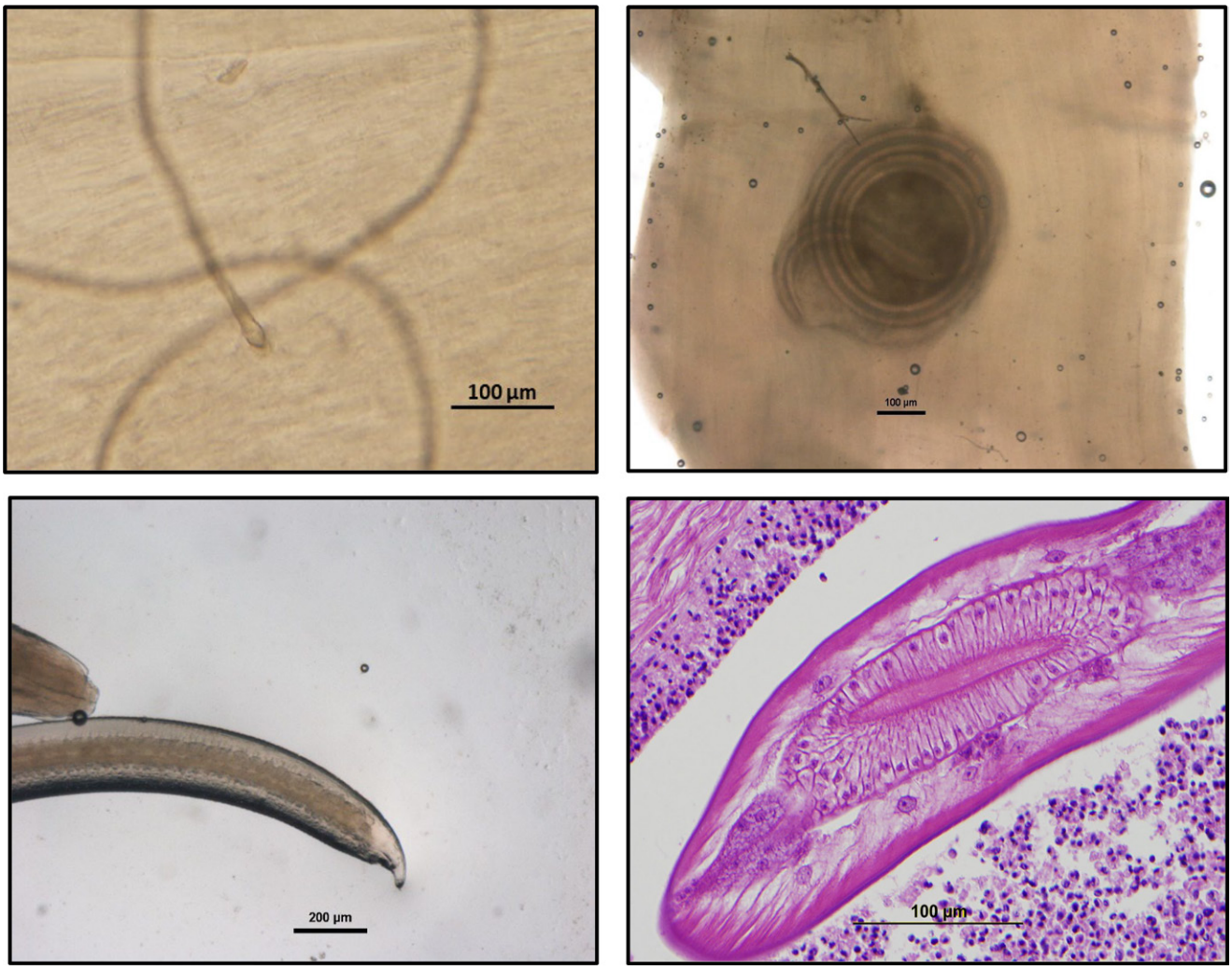

Figure 3. Fresh squash mount images of the parasitic nematode *Sulcascaris sulcata* in sea scallop adductor muscles. Top left: larvae uncoiled from adductor muscle sample; top right: larvae coiled in a sheath within the scallop adductor muscle of a lesion; bottom left: third-stage larvae tail of *S. sulcata*; bottom right: fourth-stage larvae of *S. sulcata* coiled in scallop adductor muscle.

A total of 158 nematode samples were successfully sequenced for 400 bp section of the MT-CO2 region. Alignment of all MT-CO2 sequences resulted in 47 haplotypes (unique sequences) with 37 variable nucleotide positions and a haplotype diversity of 0.87 ± 0.02. There were 20 transitions and no observed transversions across the 80 aligned sequences. Sequences were A-T rich with a nucleotide composition of 25% A, 43% T, 20% G, and 11% C across the 400 base pairs of the alignment. There were very few nucleotide differences between sequences; nucleotide diversity across all samples was 0.006 ± 0.0004. BLASTN searches used to compare sequences from this study to those available in GenBank were found to match *S. sulcata* sequences deposited in GenBank with high probability (>99% identity, *E*-value = 0), including sequences from nematodes collected from turtles and positively identified as *S. sulcata* based on morphology (genbank_HQ328505_1, Garbin et al. 2011). The sequences from infected scallops were also highly similar to and, in some cases, identical to sequences from the gut content of turtles collected from Florida and processed at VIMS (Fig. 4).

To look for temporal differences between sample collections, sequences were separated into three groups, 2016 survey (n = 58), 2017 survey (n = 86), and nematodes collected from turtle samples (n = 14). There were no significant differences in the sequence composition based on pairwise comparisons among the 2016 sample collection, the 2017 sample collection, and turtle collections based on 10,000 permutations of the data. Estimates of Φ_{ST} ranged from 0 between the 2016 and 2017 samples to 0.003 between the 2016 and samples collected from turtles ($P > 0.05$). To further explore the data, a minimum spanning network of the relationships among the haplotypes was constructed. All haplotypes recovered multiple times were recovered across both years (Fig. 4). The most common haplotype, haplotype 47, was present in 31.8% of samples from both years and was also found in nematodes recovered from the turtle samples (n = 4). The second most common haplotype, haplotype 13, was present in 15.9% of samples and was also found in nematodes sampled from turtles (n = 4). Twenty-five percent of haplotypes were unique.

To look for geographic differences, sequences were separated into three groups; South Zone (n = 102), Central Zone

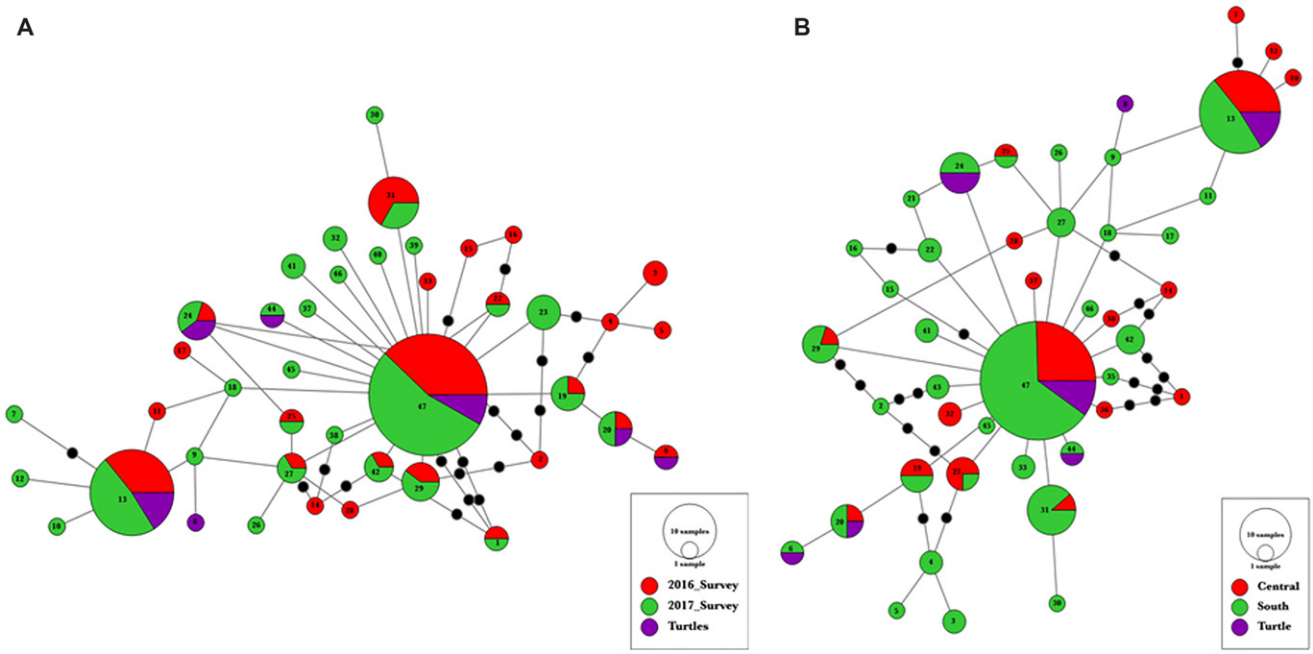

Figure 4. Minimum spanning network of the relationship among the 47 nematode haplotypes recovered during the analysis comparing the distribution of MT-CO2 haplotypes (A) data grouped by year: 2016 MAB survey trip (2016_Survey), 2017 MAB survey trip (2017_Survey), and sea turtle samples (turtles) and (B) data grouped by geographic region: Central Zone, South Zone, and sea turtle samples (turtles). Numbers represent distinct haplotypes and black circles represent 1-step edges.

(n = 42), and nematodes collected from turtle samples (n = 14) following the latitudinal zones delineated above. No nematodes were found in the North Zone samples. Estimates of Φ_{ST} were not significant between the Central Zone and turtle or the South Zone and turtle collections (Φ_{ST} = 0 and 0.008, respectively, $P > 0.05$. The comparison between samples from the South and Central zones, however, was significantly different (Φ_{ST} = 0.024, P = 0.03). Haplotypes recovered multiple (>4) times were not restricted to a particular geographic region, however, haplotype 31 was recovered multiple times (n = 8, 7.8% frequency) in the South Zone and only once (n = 1, 2.4% frequency) in the Central Zone and haplotype 24 was recovered in turtles (n = 3, 14.3% frequency) and in the South Zone (n = 3, 2.9% frequency), but was not recovered in the Central Zone. Haplotype (H) and nucleotide diversity (π) were not significantly different between the Southern Zone (H = 0.875 ± 0.027, π = 0.0055 ± 0.0034) and Central Zone (H = 0.862 ± 0.039, π = 0.0063 ± 0.0038) and were consistent with the values observed in turtles (H = 0.860 ± 0.055, π = 0.0062 ± 0.0040).

Prevalence, Intensity, and Spatial Distribution

Across all years of survey efforts, nematode-infected scallops were exclusively observed in the mid-Atlantic survey area that monitors the MAB sea scallop resource subunit. No visibly infected scallops were detected on GB. The number of scallops assessed annually during the mid-Atlantic surveys ranged from 3,812 in 2015 to 5,751 in 2017 (Table 1). For the GB surveys, a total of 8,453 scallops were examined across the three surveys and years. The maximum number of lesions observed on an individual scallop increased from 7 in 2015 to 18 in 2018 (Table 1). Prevalence, was variable across years, ranging from 9% to 21% of all scallops assessed for infection (Table 1). Intensity was relatively stable across the years with a mean of roughly two lesions observed per infected scallop (Table 1).

The interpolated spatial distributions of the prevalence and intensity of infected scallops by year are shown in Figures 5 and 6. Consistent with reports from the sea scallop industry, the highest percentage of infected scallops were found in the southern portion of the MAB resource area. There was a decline in prevalence as a function of increasing latitude across all years, with a similar pattern for intensity. The prevalence of infected scallops was highest in the South Zone, from Virginia through Delaware, where infection rates at some stations were 100% (Table 1). Scallops in the South Zone also had the greatest number of lesions per scallop observed (Table 1). Scallops off of New Jersey represented the Central Zone and had lower overall infection rates relative to the South Zone. Infection rates ranged from 1.6% in 2015 to a maximum of 9.3% in 2016 and the mean number of lesions was consistently one lesion per infected scallop (Table 1). Observations from off of Long Island or the North Zone, which represents the northernmost area of the mid-Atlantic survey domain, had the lowest infection prevalence (Table 1). Intensity was comparable to the Central Zone. Spatiotemporal changes in the distribution of infected scallops across the years were observed, although the spatial scale of the abundance-weighted mean center of the distribution was relatively small (Fig. 7). The initial center of the nematode-infected scallop distribution in 2015 was located off Delaware. This point moved approximately 22 km to the northeast in 2016 before settling between the 2015 and 2016 locations in both 2017 and 2018.

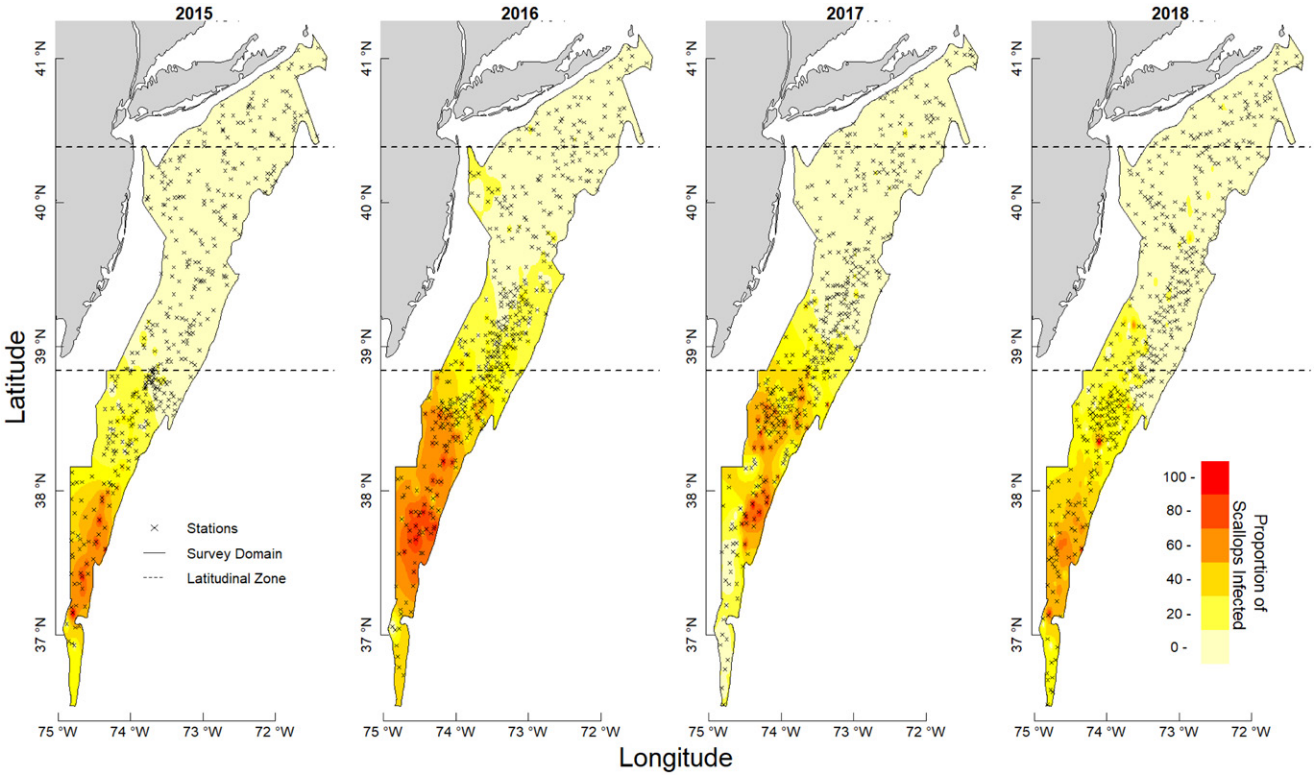

Figure 5. Inverse distance weighted interpolation of the prevalence of infected sea scallops in the mid-Atlantic survey area by year with station locations where biological assessments were conducted. Dashed horizontal lines indicate divisions between latitudinal zones. Prevalence is defined as the number of sea scallops observed to be infected as a percentage of all sea scallops sampled at a given station.

DISCUSSION

In many systems, disease and parasites can be significant modulators of population dynamics (Lafferty 2008). Scallops are no exception and are impacted by a suite of parasites and diseases that have the potential to impact resource and fishery productivity (Kristmundsson et al. 2015, Levesque et al. 2016, Stokesbury et al. 2019). This study verified the presence of the larval form of the Anaskid nematode (*S. sulcata*) in the sea scallop resource in the United States portion of the Northwest Atlantic Ocean. Whereas this is the first documented instance of *S. sulcata* in sea scallops, this parasite is endemic to the region and found across a range of benthic molluscs (Lichtenfels et al. 1978). Anecdotal reports from the early 2000s suggest that sea scallops were affected previously, although a lack of temporal continuity in the industry-based accounts indicates that the presence of the parasite was ephemeral prior to 2015. Since 2015, the parasite has become established throughout the southern and central portion of the MAB monitored for sea scallops with general stability in the spatial extent of its distribution.

Berry and Cannon (1981) described the life history of *S. sulcata* in detail and based upon those accounts and observations from this study, third- and fourth-stage larvae present in scallops are ingested by foraging loggerhead turtles that co-occur spatially and temporally on the scallop grounds (Smolowitz et al. 2015). Once ingested, the parasites attach to the gastrointestinal tract of the turtle where they become sexually mature, shedding eggs into the water column via defecation. The eggs hatch in roughly 5 days as third-stage larvae and enter benthic molluscs presumably via the inhalant siphon. Upon infection, third-stage larvae become established in various structures of the mollusc and develop into fourth-stage larvae 3–4 mo postinfection. Macroscopically, brown-colored lesions can be observed on the surface of the adductor muscle, although these lesions do not always contain a larval nematode necessitating caution regarding the interpretation of intensity values. It is at this stage that ingestion by the final host completes the life cycle. Observations from this study document variability in larval size, which suggests that infection is protracted over the course of a particular season and perhaps across seasons. These observations align with the ability of nematode larvae to encyst, which may provide the ability of fourth-stage larvae to persist over extended time periods and prolong the duration of the epizootic event (Sprent 1954).

The nematode, *S. sulcata*, has a cosmopolitan distribution that mirrors the worldwide distribution of its definitive host, marine sea turtles. Numerous economically important scallop species have been documented to be parasitized by *S. sulcata*. Australian saucer scallops (*A. balloti*), *P. jacobaeus*, and *A. opercularis* from the Mediterranean Sea and calico (*A. gibbus*) and bay (*A. irradians*) scallops from the western Atlantic represent the widespread spatial distribution of scallop species impacted by *S. sulcata* (Lester et al. 1980, Deardorff 1989, Marcer et al. 2020, Pretto et al. 2020). In addition to scallops, *S. sulcata* affects benthic molluscs generally and has been documented in other bivalves such as the surf clam (*S. solidissima*) as well as in marine gastropods (e.g., *Lunatia heros*, *Busycotypus*

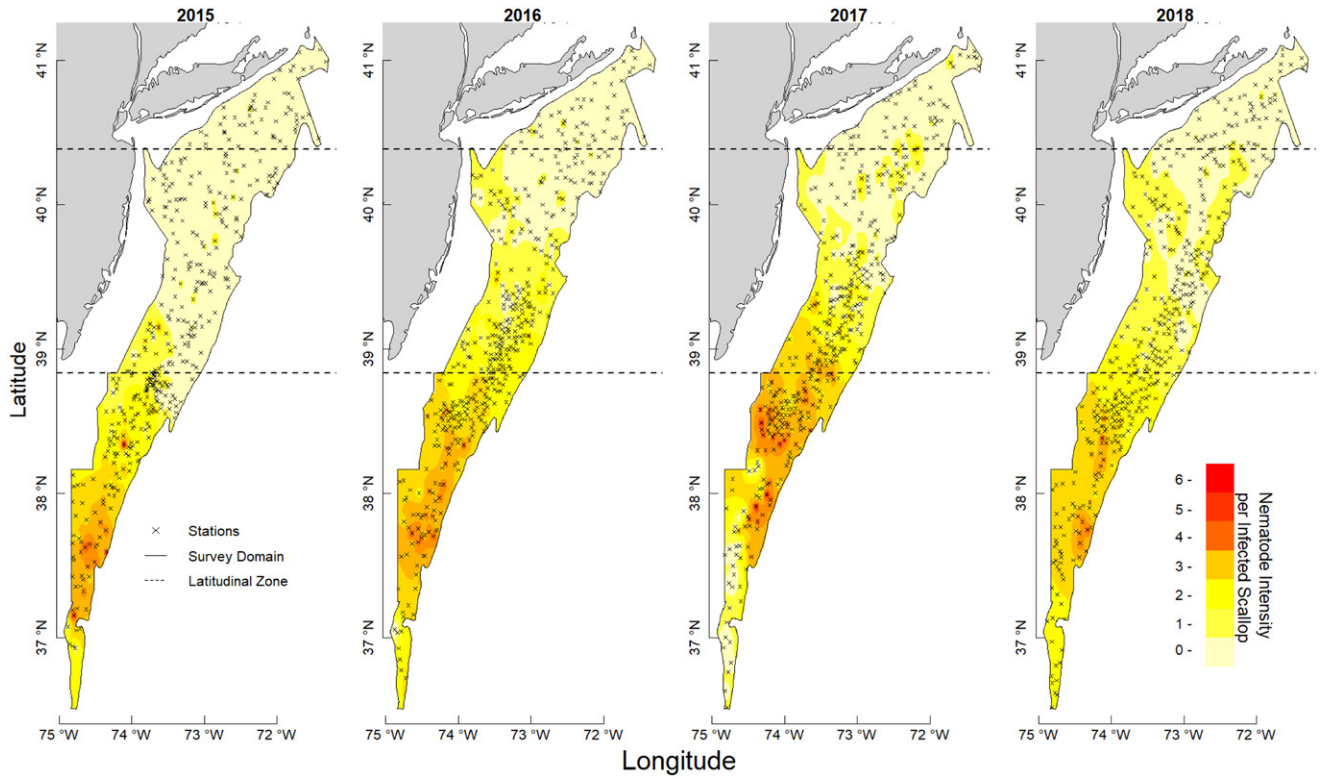

Figure 6. Inverse distance weighted interpolation of the intensity of infected sea scallops in the mid-Atlantic survey area by year with station locations where biological assessments were conducted. Dashed horizontal lines indicate divisions between latitudinal zones. Intensity is defined as the mean number of lesions observed in infected sea scallops at a given station.

canaliculatus, Bolinus brandaris) (Lichtenfels et al. 1978, Santoro et al. 2022). The diversity of affected molluscs reflects the varied diets of sea turtles and this generalist approach may provide a mechanism for the temporal persistence of *S. sulcata* observed over the course of this study (Lazar et al. 2011).

High genetic similarity was observed between *S. sulcata* samples obtained from infected sea scallops and samples obtained from moribund turtles in Florida. This result suggests that although the sampled turtles were geographically distant at the time of their stranding, *S. sulcata* infection is a common and persistent feature of sea turtle parasite loads and that this characteristic coupled with their seasonal, long-distance movements provide the biological basis for the observed epizootic. Winton et al. (2018) documented the spatial distribution and residence time of loggerhead turtles with the spatial overlap on the scallop beds where nematode infection was observed. Turtle residence on the sea scallop grounds is seasonal and generally corresponds to a preferred thermal range that allows the animals to forage on a suite of resources (Smolowitz et al. 2015, Patel et al. 2019). In the Mediterranean Sea, nematode prevalence in loggerhead turtles was higher in the Adriatic Sea, which has higher benthic forage biomass and diversity relative to adjacent areas in the basin (Santoro et al. 2019). The sea scallop resource is characterized by instances of episodic spatially explicit high recruitment that can be orders of magnitude higher than long-term averages for those same spatial areas. In 2013, a recruitment event that represented one of the highest biomass, most dense events on record occurred in the southern and central areas of the survey domain sampled (NEFSC 2018). Two years after this recruitment event, nematode-infected scallops were reported suggesting that the spatial and temporal co-occurrence of a transient but seasonally resident turtle

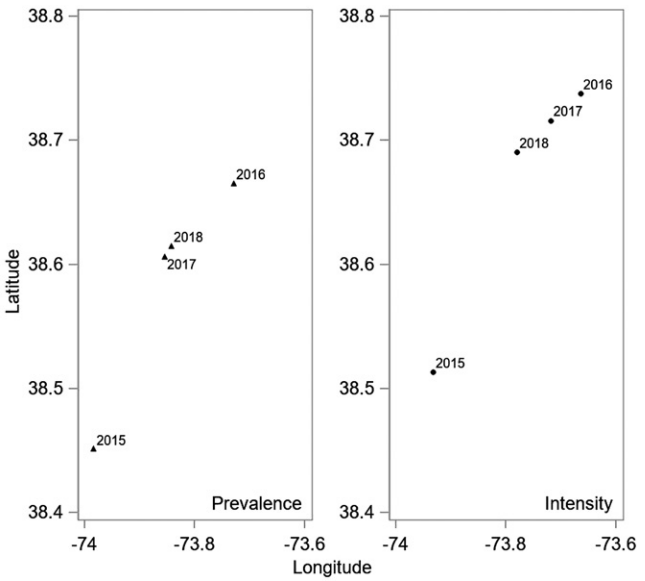

Figure 7. Weighted mean center of nematode distribution with respect to infection prevalence (left panel) and infection intensity (right panel). Individual years are plotted to demonstrate the spatial shift in nematode-infected scallops.

population and an exceptionally large recruiting year class of scallops created conditions that were favorable for the proliferation of *S. sulcata*. A small but significant genetic difference was observed between the South and Central Zone collections of *S. sulcata*. Although this difference was largely driven by a frequency difference for a single MT-CO2 haplotype and the data is from a single genetic locus, this result was consistent with the observation that the initial reports of infection were from the southern extent of the scallop resource. Higher resolution genomic methods and increased genetic sampling, including the sampling of additional affected species, could better document the spread of the parasite.

From an ecological perspective, the conditions favored an epizootic, which ultimately impacted the sea scallop fishery. Initial concerns were focused on product safety and marketability of landed scallop adductor muscles. Sea scallop adductor muscles are typically consumed after cooking and occasionally consumed raw. Based on the etiology of *S. sulcata*, and infection experiments conducted by Berry and Cannon (1981), the likelihood of this nematode infecting humans is low as the life history is specific to cold-blooded reptiles as the final host. Whereas *S. sulcata* is unlikely to infect homeothermic hosts, other nematode species (e.g., *Anasakis simplex* and *Anasakis pegreffii*) have been documented to contribute to an allergic response in some sensitive consumers, although there have been no documented instances of this type of response from *S. sulctata* (Nieuwenhuizen & Lopata 2013). Whereas a significant impact on human health as a result of *S. sulcata* infection is likely low, product marketability concerns related to adductor muscles presenting with visible lesions remain. Price depreciation of landed product was an anecdotally reported outcome, especially in the early stages of the epizootic. Fishery-level responses including avoidance of the affected areas and spatial redistribution of fishing effort at various scales were also observed. From a fishery management perspective, the movement of effort to adjacent areas has the potential to exacerbate localized depletion and an over-specification of annual quotas if a portion of the resource is not accessed because of product quality issues. Satellite-based vessel location data suggests that even though high levels of harvestable scallop biomass existed in the affected areas, fishing effort was disproportionately partitioned to areas of lower nematode prevalence (NEFSC 2018).

The emerging epizootic of the sea scallop resource of the MAB is the result of the nematode *S. sulcata* that appears to have been supported by the spatiotemporal overlap of the transitory, benthic foraging loggerhead sea turtle population and a high abundance of sea scallops resulting from an exceptionally large recruiting year class along the MAB. Genetic similarities across the range of infected scallop samples suggest that a common and persistent infection source is likely and larval morphological observations that observed a range of fourth-stage larvae sizes are a function of a protracted infection timeline. Whereas the risk to human health from infected scallops appears to be limited, product quality issues have resulted in fishery-level responses focused on the avoidance of nematode prevalent areas. The long-term trajectory of the epizootic remains unclear and continued monitoring of the spatiotemporal distribution of nematode-infected scallops is warranted. The two-host parasite infection dynamic is likely dependent upon the interaction between sea turtle loggerhead habitat utilization and the relative levels of sea scallop abundance that is currently trending toward more northerly portions of the MAB.

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