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The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management

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Abstract

The American sand lance (*Ammodytes americanus*, Ammodytidae) and the Northern sand lance (*A. dubius*, Ammodytidae) are small forage fishes that play an important functional role in the Northwest Atlantic Ocean (NWA). The NWA is a highly dynamic ecosystem currently facing increased risks from climate change, fishing and energy development. We need a better understanding of the biology, population dynamics

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and ecosystem role of *Ammodytes* to inform relevant management, climate adaptation and conservation efforts. To meet this need, we synthesized available data on the (a) life history, behaviour and distribution; (b) trophic ecology; (c) threats and vulnerabilities; and (d) ecosystem services role of *Ammodytes* in the NWA. Overall, 72 regional predators including 45 species of fishes, two squids, 16 seabirds and nine marine mammals were found to consume *Ammodytes*. Priority research needs identified during this effort include basic information on the patterns and drivers in abundance and distribution of *Ammodytes*, improved assessments of reproductive biology schedules and investigations of regional sensitivity and resilience to climate change, fishing and habitat disturbance. Food web studies are also needed to evaluate trophic linkages and to assess the consequences of inconsistent zooplankton prey and predator fields on energy flow within the NWA ecosystem. Synthesis results represent the first comprehensive assessment of *Ammodytes* in the NWA and are intended to inform new research and support regional ecosystem-based management approaches.

KEYWORDS
Ammodytes, ecosystem-based management, forage fish, life history, sand lance, trophic ecology

1 | INTRODUCTION

Sand lances and sandeels (*Ammodytes* sp.) are considered a "quintessential forage fish" in the Northern Hemisphere (Robards, Willson, Armstrong, & Piatt, 1999). Despite their ecological importance, most aspects of their ecology, population dynamics and vulnerability to current and future stressors in the Northwest Atlantic Ocean (NWA) are poorly understood. A few key historical studies of the biology, life history, distribution and ecology of *Ammodytes* exist in the region. However, recent and projected environmental and ecological changes (Alexander et al., 2018; Saba et al., 2016; Thomas et al., 2017) are making some of this information obsolete as most of it was collected in the 1970s and 1980s (Nelson & Ross, 1991; Scott, 1968, 1973; Winters, 1981, 1983). The NWA is a highly dynamic ecosystem currently facing myriad impacts from climate change, fishing, aquaculture, oil and gas development, as well as emerging and unknown risks from alternative energy sources (e.g., offshore wind energy facilities), nearshore and shoreline alterations from activities such as sand mining and coastline armouring (Fisheries & Oceans Canada, 2009; Pershing et al., 2015; Saba et al., 2016). *Ammodytes* may be vulnerable to changes brought about by any one or combination of these anthropogenic threats. Currently, we have an incomplete understanding of what drives high spatio-temporal variability in distribution and density of *Ammodytes*, which severely limits our ability to make predictions and assess risk. Although we can draw on experiences elsewhere (e.g., North Sea and Pacific Northwest) where the species and its habitats are well studied, the set of challenges to *Ammodytes* in the NWA region is unique. These knowledge gaps further impede the evaluation of cascading indirect impacts and trophic consequences of *Ammodytes* variability on predators, co-occurring forage species and their sensitivity to disturbances in the greater community.

The objective of this synthesis is to summarize the current state of knowledge and identify information gaps, about the two primary species, *A. dubius* and *A. americanus* (hereafter collectively referred to as NWA *Ammodytes)* throughout their range in continental shelf waters of the NWA from North Carolina (USA) to Greenland. A range of basic and applied questions related to the life history, trophic ecology and vulnerability to growing anthropogenic threats were identified by a diverse working group of scientists, natural resource managers and conservation practitioners from state, federal, academic and non-governmental organizations with interests and expertise in NWA *Ammodytes* ecology or their predators. Although previous literature syntheses have covered *Ammodytes* on a global scale (Robards, Willson, et al., 1999) and in the Northeast Atlantic Ocean (Green, 2017), to the best of our knowledge this is the first comprehensive assessment in the NWA region. Results are intended to inform new research, and to help guide conservation and management efforts by regional Fishery Management Councils, regulatory agencies, fishing communities, conservation organizations and coastal development groups, all of whom share responsibilities and interests in NWA *Ammodytes* and their predators.

2 | LIFE HISTORY

The family Ammodytidae contains 33 described species globally, with eight in the genus *Ammodytes* (Fricke, Eschmeyer, & Van Der Laan, 2019; Orr et al., 2015). The genus *Ammodytes* is composed of zooplanktivorous fishes that span coastal temperate to polar waters in the Northern Hemisphere. Their occurrence depends on the presence of coarse-grained sand from which they emerge on diel and seasonal cycles to feed in the water column (Auster & Stewart, 1986; Holland, Greenstreet, Gibb, Fraser, & Robertson, 2005; Reay, 1970; Robards, Piatt, & Rose, 1999; Scott, 1968; Wright, Jensen, & Tuck, 2000).

There are two phenotypically similar, congeneric NWA species: the American sand lance *Ammodytes americanus* (DeKay 1842) and the Northern sand lance *A. dubius* (Reinhardt 1837). Their distinction is primarily based on differences in distribution, maximum size and a few meristic (i.e., countable) traits. *A. americanus* primarily occurs in shallow nearshore habitats (<20 m, though often <2 m) from Delaware, USA, to the Labrador coast, Canada (Auster & Stewart, 1986; Nizinski, 2002; Nizinski, Collette, & Washington, 1990). In contrast, *A. dubius* tends to occur in deeper, more offshore waters (2–100 m, though often > 20 m) between Cape Hatteras, USA, and Greenland (Nizinski et al., 1990). While the smaller *A. americanus* rarely exceeds 20 cm in standard length, *A. dubius* appears to be deeper-bodied and can grow to over 30 cm (Nizinski et al., 1990). In addition, *A. dubius* generally shows higher meristic counts of certain morphological features than *A. americanus*, with a greater number of plicae (folds of the skin around the lateral musculature) and vertebrae (Nizinski et al., 1990; Scott, 1968). The meristic separation between the two species appears to increase with latitude, thereby aiding identification in the more northern locations of their range.

The subtle differences between *A. dubius* and *A. americanus* have likely been confused in the literature. For example, Meyer, Cooper, and Langton (1979) referred to *Ammodytes* on Stellwagen Bank as *A. americanus*, yet the offshore specimens (and probably nearly all those observed in the study) were *A. dubius* owing to the depth of the bank and its distance from shore. The difficulty in distinguishing the species morphologically has likely also confounded genetic differentiation between the two species. For example, previous studies suggest that the mitochondrial genomes of *A. dubius* and *A. americanus* are nearly identical, and standard DNA barcoding techniques using the cytochrome oxidase 1 (COI) gene cannot be used to differentiate between them (Horne, Mcbride, Lighten, Bradbury, & Bentzen, 2016; McCusker, Denti, Van Guelpen, Kenchington, & Bentzen, 2013; Orr et al., 2015); however, morphological characters used to identify these specimens were not provided. In contrast, COI sequence data for *Ammodytes* collected from waters along the east coast of the USA grouped into two distinct clusters (D. Richardson, personal observation). One grouping matched sequences currently reported as *A. dubius* and *A. americanus* in public databases (GenBank and Boldsystems). The second group of sequences differed by ~4% from the first, was a close match to *A. hexapterus* (Ammodytidae) from the Pacific and Arctic, and came from specimens with the meristics of *A. americanus*. These results suggest that it is possible to genetically differentiate these two species.

2.1 | Growth and reproduction

Little is known about the biology and life history of *A. dubius* and *A. americanus* in the NWA. A few studies were conducted in the 1970s and 1980s to assess age distributions, growth rates and reproduction, but may now be out of date given the rapid environmental changes occurring in the region during recent decades (Friedland et al., 2018; Pershing et al., 2015; Thomas et al., 2017). Indeed, *Ammodytes* populations that are in close proximity (<60 km) to each other but experience different ocean temperature regimes can exhibit markedly different age compositions or growth rates (Robards, Rose, & Piatt, 2002). Growth rates can also vary markedly among just a few years with strong temperature fluctuations (von Biela et al., 2019). During the 1980s, NWA *Ammodytes* populations in Northeast U.S. continental shelf waters were generally ≤5 years of age, primarily age 1–3 (Nelson & Ross, 1991). More northerly populations, including those on the Scotian Shelf, were found to potentially live longer, with reported maximum ages of 8 and 12 years for *A. dubius* and *A. americanus*, respectively, during the late 1960s–1970s (Brêthes, Saint-Pierre, & Desrosiers, 1992; Winters, 1981). Age at maturity may also differ between northern and southern populations of *A. dubius*, with populations along the Northeast USA reaching 50% maturity at age 2 and populations in the Grand Banks subregion reaching maturity at age 3 (Nelson & Ross, 1991; Winters, 1983). NWA *Ammodytes* from the Grand Banks demonstrated faster growth rates than those from Georges Bank and further south. This suggests a reduction in growth rate with decreasing latitude consistent with counter-gradient latitudinal growth (Baumann & Conover, 2011), although the exact mechanisms behind this pattern are not understood (Nelson & Ross, 1991; Winters, 1983).

Both species of *Ammodytes* in the NWA are gonochoristic (i.e., reproductively distinct between sexes) and exhibit 1:1 sex ratios (Nelson & Ross, 1991). The diameter of oocytes is unimodal for *A. americanus*, suggesting once-a-year spawning for this species (Westin, Abernethy, Meller, & Rogers, 1979), which is consistent with recent observations for *A. dubius* from Stellwagen Bank (H. Baumann, personal observation). Both species spawn in fall and winter along the Northeast USA: *A. dubius* and *A. americanus* develop ripe gonads in the fall, and larvae are prevalent in the water column throughout the winter and spring (Dalley & Winters, 1987; Nelson & Ross, 1991; Potter & Lough, 1987; Walsh, Richardson, Marancik, & Hare, 2015). Near Greenland, the timing of spawning for *A. dubius* occurs earlier in the year, likely due to the colder temperatures and a truncated foraging season in this northern region (Danielsen, Hedeholm, & Grønkjær, 2016). The duration of spawning times of *A. americanus* and *A. dubius* is unknown. The historical literature suggests a long spawning season ranging from December through May on the Grand Banks (Dalley & Winters, 1987); however, a recent analysis of *A. dubius* captured on Stellwagen Bank in 2016 and 2017 indicates that this species has a truncated spawning period, lasting ~1–2 weeks in late November (Murray, Wiley, & Baumann, 2019).

2.2 | Early life history

Fertilized eggs of NWA *Ammodytes* are demersal and adhesive, and are thought to develop on sandy substrates over the course of a two month period (Smigielski, Halavik, Buckley, Drew, & Laurence, 1984). Time to hatch in the wild has been observed in a single study in the Gulf of Alaska at 67 days of total incubation (Robards, Piatt, et al., 1999). Laboratory studies revealed that development is highly temperature-dependent for *A. americanus* and the European congener *A. marinus*, which can result in interannual and regional variability in hatch phenology for these species (Régnier, Gibb, & Wright, 2018; Smigielski et al., 1984). Yolk-sac larvae begin to appear in ichthyoplankton tows in February in Nova Scotia and in December on Georges Bank, Nantucket Shoals, and Stellwagen Bank, though peak hatching is in January for these more southerly regions (Dalley & Winters, 1987; Potter & Lough, 1987; J. Llopiz, unpublished data). Larvae range from 4 to 7 mm at hatch, and *A. americanus* larvae in Long Island Sound consume phytoplankton at first feeding before shifting to copepod species such as *Temora* sp. and *Acartia* sp. throughout their early life history (Auster & Stewart, 1986; Monteleone & Peterson, 1986). In the laboratory, first feeding in *A. americanus* can occur up to 16 days post-hatch, indicating they may be resilient to short-term delays in accessing food during the first few weeks of life (Buckley et al., 1984). NWA *Ammodytes* larvae live in the water column for the first 3–4 months until reaching sizes of 35–50 mm, at which point they begin to settle into demersal habitats (Auster & Stewart, 1986; Scott, 1973). Historically, settlement has occurred in May along the Northeast USA and June to July in Nova Scotia (Potter & Lough, 1987; Scott, 1973); however, observed shifts of later winter larval phenology during recent decades in the NWA (Walsh et al., 2015) could affect settlement timing.

2.3 | Diet and key prey

The adult diet of *Ammodytes* in the NWA is poorly known, with most existing studies focusing on *A. dubius* (Danielsen et al., 2016; Meyer et al., 1979) and the last comprehensive foraging study within Northeast U.S. shelf waters conducted in the late 1970s (Bowman, 2000). Where diets have been characterized, large and energy-rich copepods, primarily members of the genus *Calanus*, are prominent and thought to affect recruitment success and productivity (Bowman, 2000; Danielsen etal., 2016; van Deurs, van Hal, Tomczak, Jónasdóttir, & Dolmer, 2009; van Deurs, Jørgensen, & Fiksen, 2015; Lindegren et al., 2018; Régnier et al., 2018; Scott, 1973). Of ecological significance, in areas where NWA *Ammodytes* are particularly abundant, such as Georges Bank, they can exhibit top-down effects on zooplankton, consuming significant proportions of total annual production (Gilman, 1994).

Calanus species, notably *C. finmarchicus* (Calanidae), were historically abundant in the deep waters (>75 m depth) of the Gulf of Maine (Bigelow, 1926; Durbin, Gilman, Campbell, & Durbin, 1995; Runge & Jones, 2012), where densities have been as high or higher than anywhere across the NWA, even though this area represents the southernmost margin of their subarctic range (Melle et al., 2014). *C. finmarchicus* exhibits high interannual and seasonal variability in the Gulf of Maine (Record et al., 2019). Historically, older stages were transported from the Gulf of St. Lawrence during summer and fall into the eastern Gulf of Maine, with contributions by the subsurface Labrador Subarctic Slope Water (Head, Harris, & Petrie, 1999; MERCINA Working Group et al., 2001; Record et al., 2019) in the Nova Scotia Current (Appendix S1: Supplemental 1) (Kane, 2007; Pershing et al., 2005). However, shifts in seasonal oceanographic conditions, circulation and the phenology of lower trophic level species are affecting established patterns in regional timing and availability of resources (see Sections 4.1 and 4.2; Staudinger et al., 2019; Thomas et al., 2017). Production from the Maine Coastal Current also supplied predators, including NWA *Ammodytes*, in the western Gulf of Maine during summer and fall with lipid-rich older stages of *C. finmarchicus* (Ji et al., 2017; Runge et al., 2015). In Greenland waters, late-stage *Calanus* have been found to constitute the majority of the summer diet of *A. dubius* (Danielsen et al., 2016). Smaller copepods, such as *Centropages typicus* (Centropagidae), *Temora longicornis* (Temoridae), *Oithona* sp. (Oithonidae) and *Pseudocalanus* sp. (Clausocalanidae), are also known prey of NWA *Ammodytes*, particularly *A. americanus*, likely due to overlapping occurrence in coastal habitats (Bowman, 2000).

2.4 | Influences on abundance and distribution

In European waters, environmental variables (e.g., water velocity and bottom temperature) as well as top-down and bottom-up forcings have been associated with *Ammodytes* (*A. marinus*, *A. tobianus* and *Hyperoplus lanceolatus*, Ammodytidae) distribution and abundance (Frederiksen, Edwards, Richardson, Halliday, & Wanless, 2006; van der Kooij, Scott, & Mackinson, 2008; Tien et al., 2017). Bottom-up effects were postulated where significant correlations existed between *A. marinus* recruitment in the North Sea and the production of *Calanus* eggs (van Deurs et al., 2015; Régnier et al., 2018). Intraguild trophic relationships among forage fishes may also contribute to oscillations in relative abundances (Irigoien & de Roos, 2011). Such dynamics have been suggested in the NWA region where Atlantic herring (*Clupea harengus*, Clupeidae) and Atlantic mackerel (*Scomber scombrus*, Scombridae) abundances were observed to oscillate out of phase with NWA *Ammodytes* during 1969–2010 (Fogarty, Sissenwine, & Cohen, 1991; Richardson, Palmer, & Smith, 2014; Sherman et al., 1981) as well as for capelin (*Mallotus villosus*, Osmeridae) and *A. hexapterus* in Alaskan waters (Sydeman et al., 2017). This out-of-phase oscillation is noteworthy given its consistency over such a long time span. Because NWA *Ammodytes*, Atlantic mackerel and Atlantic herring diets differ appreciably throughout much of the region, competition for prey is unlikely to be the primary driver of this oscillation (Bowman, 2000; Suca et al., 2018). However, when diet overlap is high among zooplanktivorous predators, the prey base can be reduced to the point where all forage fish growth and survival are compromised (Purcell & Sturdevant, 2001). Top-down control is more likely as both Atlantic herring and mackerel are known to prey on larval NWA *Ammodytes* (Fogarty et al., 1991; Suca et al., 2018; also see Section 3). When Atlantic herring and mackerel are at low population levels, NWA *Ammodytes* can be released from predation, resulting in a competitive advantage, and vice versa (Polis, Myers, & Holt, 1989). Further, intercohort cannibalism (adult *Ammodytes* consuming larvae) can occur in regions and years with low abundances of alternative prey (Eigaard et al., 2014, North Sea). Because generalist predators typically consume the most abundant prey available, out of phase cycles of NWA *Ammodytes* with other forage fishes in the region could have important trophic effects on higher-level predators. Indeed, in past decades predator diets (e.g., Atlantic cod) have mirrored trends in oscillating abundances of NWA *Ammodytes* and Atlantic herring (Fogarty et al., 1991; Nelson & Ross, 1991; Richardson et al., 2014). Environmental drivers and fishing pressure likely influence these complicated species interactions directly and indirectly (Figure 1).

The availability of NWA *Ammodytes* appears to be highly patchy across temporal and spatial scales and differs substantially from that of other forage fishes, in part due to habitat requirements for coarse-grained sandy bottom substrates that allow them to bury and hide from predators (Nizinski, 2002). In comparison, Atlantic herring make broad movements throughout the year and are less confined to a single type of substratum, making them more widely distributed across continental shelf habitats, except during the fall spawning season (Jech & Stroman, 2012; Munroe, 2002). Dependency on sandy substrates leads to high densities of NWA *Ammodytes* in regions such as the northwest and southwest corners of Stellwagen Bank in the Gulf of Maine. High densities of NWA *Ammodytes* in a predictable location attracts (Hazen et al., 2009; Richardson et al., 2014) and is likely advantageous to predators, both resident and those that move to occupy such habitats during times of peak food abundance. Further, changes in higher-level predator abundance can create strong top-down pressures that control NWA *Ammodytes* dynamics in areas where they are concentrated. Predatory release due to overfishing of Atlantic cod (*Gadus morhua)* and other piscivorous fishes was one explanation for observed population increases in NWA *Ammodytes* in Canadian waters from 1990 to 2010 (Frank et al., 2013; Frank, Petrie, Fisher, & Leggett, 2011); however, this remains an open question as changes in the vertical distribution of pelagic forage fishes provides an alternative explanation, and gear bias may have confounded interpretation of demographic trends (Jech & McQuinn, 2016; McQuinn, 2009).

Gathering reliable data on NWA *Ammodytes* abundance, distribution and population dynamics in the region has been difficult. In addition to the absence of fishery-dependent data, *Ammodytes* are not caught consistently or detected readily in state and federal bottom trawl survey methods due to the mesh sizes used (Miller et al., 2010; Politis, Galbraith, Kostovick, & Brown, 2014). Their narrow, anguilliform morphology and burrowing behaviour also make *Ammodytes* especially difficult to capture with routine bottom trawl gear. NWA *Ammodytes* are captured during ichthyoplankton surveys (Figure 2) and incidentally in bottom trawl gear (Figure 3), and thus, some insights can be gained into population trends from similar gear type collections that go beyond presence/absence. For example, ichthyoplankton collections were used to estimate spawning stock biomass between 1974 and 1980 at 1 million metric tons, similar to that of Atlantic herring abundances in peak years (Morse, 1982). Richardson et al. (2014) assessed coherence in interannual NWA *Ammodytes* abundance anomalies across ichthyoplankton, bottom trawl and diet surveys as an index to ameliorate the biases in determining population trends based on a single survey (Figure 1). Anomalies in the spring National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) Bottom Trawl Survey collections closely track the trends found by the index.

A common pattern among members of the genus *Ammodytes* is a dormancy period lasting up to a few months. For most species within the genus, dormancy occurs in fall and winter, centred around spawning for *A. personatus* in the Northeast Pacific, and occurring post-spawning for *A. marinus* and *A. tobianus* in the Northeast Atlantic (Winslade 1974; Ciannelli 1997; Van Deurs, Christensen, Frisk, & Mosegaard, 2010; van Deurs, Hartvig, & Steffensen, 2011. *Ammodytes japonicus* (Ammodytidae) in the Northwest Pacific, however, undergoes aestivation in the late summer through fall prior to spawning, indicating that dormancy strategies are variable according to species and climate (Inoue, 1967; Kuzuhara et al., 2019; Sekiguchi, 1977). A winter dormancy period has been suggested for

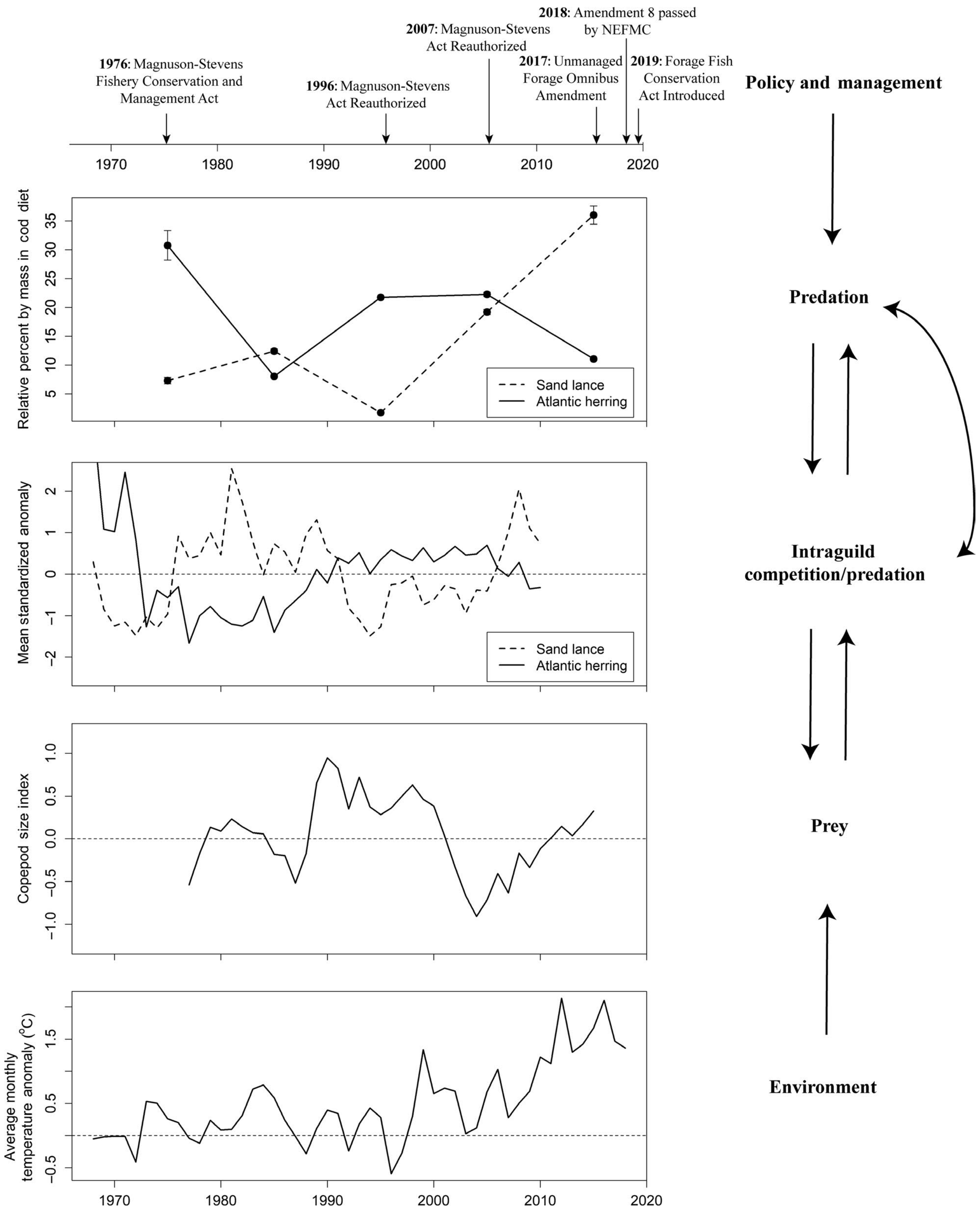
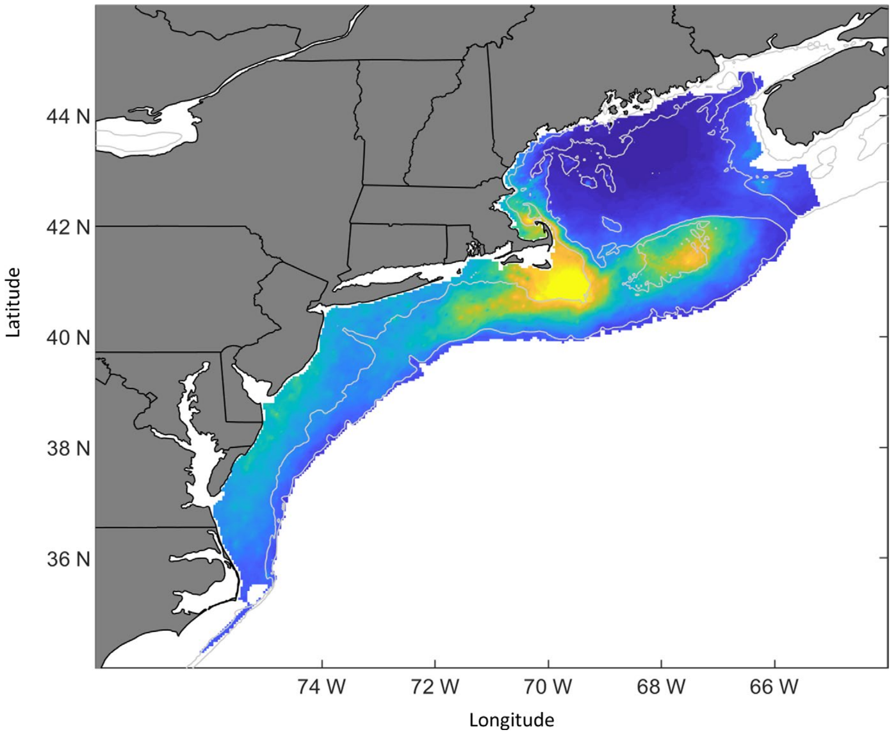


FIGURE 1 Diagram of top-down and bottom-up controls on Northwest Atlantic (NWA) *Ammodytes*. Panels from bottom to top: **Environment**—Average monthly temperature anomaly (°C) for the Gulf of Maine calculated from NOAA's Extended Reconstructed Sea Surface Temperature V5. **Prey**—Copepod size index data (small copepod-large copepod; average across Northeast U.S. Shelf) are adapted from Perretti et al. (2017). **Intraguild Competition/Predation**—Mean standardized anomaly in NWA *Ammodytes* and Atlantic herring indices are adapted from Richardson et al. (2014). **Predation**—Cod diet data represent per cent herring and NWA *Ammodytes* by mass in the diet of cod (with 95% confidence interval) collected by the Northeast Fisheries Science Center Food Web Dynamics Program. **Policy and Management**—historical management decisions impacting NWA *Ammodytes* and other forage fishes

FIGURE 2 Map showing the average spatial distribution of larval Northwest Atlantic (NWA) *Ammodytes*, with bathymetry lines, between 1977 and 2018. NWA *Ammodytes* are winter spawners, and data coincide with the months when larvae are present in the water column and before they attain body sizes (typically in spring) whereby they are capable of evading survey gear. Note that distribution changes annually. Data were collected by the Northeast Fisheries Science Center Ecosystem Monitoring (EcoMon) sampling programme and were provided courtesy of David Richardson



A. dubius, yet no rigorous study of dormancy timing currently exists in the NWA region (Gilman, 1994). In each case, vigorous feeding prior to dormancy appears to contribute to maturation and survival, thus making this genus potentially vulnerable to changes in the spatio-temporal dynamics of their zooplankton prey (Kuzuhara et al., 2019; Nishikawa, Nakamura, Okamoto, & Ueda, 2019; Van Deurs, Christensen, Frisk, & Mosegaard, 2010; van Deurs, Hartvig, & Steffensen, 2011; von Biela et al., 2019;).

3 | ROLE AS PREY

Although *Ammodytes* are recognized as important forage fish, a comprehensive evaluation of the extent and variation of their role as prey in the diets of higher trophic levels has not been completed for the NWA region. To address this need, we synthesized available literature and diet datasets associated with three major predator groups: fishes, seabirds and marine mammals. Using Web of Science and Academic Search Premier, the scientific and common names of known predator species were searched in combination with "diet" and "prey." In addition, we queried "*Ammodytes*," "*Ammodytes americanus*" and "*Ammodytes dubius*," on their own and in combination with "prey." Studies were reviewed for relevance (i.e., geographical scope), and dietary metrics describing consumption of *Ammodytes* (e.g., % mass) were compiled. In addition, a query of the long-term NMFS/NEFSC Food Web Dynamics Program database (Smith & Link, 2010; https://inport.nmfs.noaa.gov/inport/hierarchy/1368) yielded detailed information on 40 predatory fishes. Data were identified by searching for all records where "*Ammodytes*" was identified as a prey item in a predator stomach. Predation was summarized as the relative proportion with 95% confidence intervals (CI) of *Ammodytes* (by % mass in grams) consumed by each species by season, region and decade (Table 1; Appendix S1: Supplemental 2–4). Summary statistics are based on a minimum of 205 stomach samples for each predator and factor. Dietary studies conducted at seabird colonies managed by the U.S. Fish and Wildlife Service, the National Audubon Society Seabird Restoration Program, state agencies and non-governmental organizations throughout the Northeast USA and Gulf of Maine were also compiled and summarized based on the frequency of occurrence (% FO) or per cent mass (% M) in the provisioned chick diets of each seabird species at a given location (Appendix S1: Supplemental 8). No routine diet datasets were found for marine mammals, and assessments were purely based on the results of the existing published literature.

In total, 45 species of fishes, 2 squids, 16 seabirds and 9 marine mammals were reported to consume *Ammodytes* in the NWA region. The methodology for assessing predator diets varied from direct observations of stomach contents to visual assessments of prey deliveries and observations of surface foraging behaviours (Figure 4). Fish predator data yielded the most quantitative assessments of diet followed by seabird predators. In contrast, information on marine mammal diets was often based on opportunistic assessments and largely qualitative.

3.1 | Importance to fishes and squids

Fish and squid predators captured in the NEFSC survey between 1973 and 2015 and containing notable amounts (≥5% M) of NWA *Ammodytes* in their stomach contents included Atlantic cod, longhorn sculpin (*Myoxocephalus octodecemspinosus*, Cottidae), winter skate (*Leucoraja ocellata*, Rajidae), alewife (*Alosa pseudoharengus*,

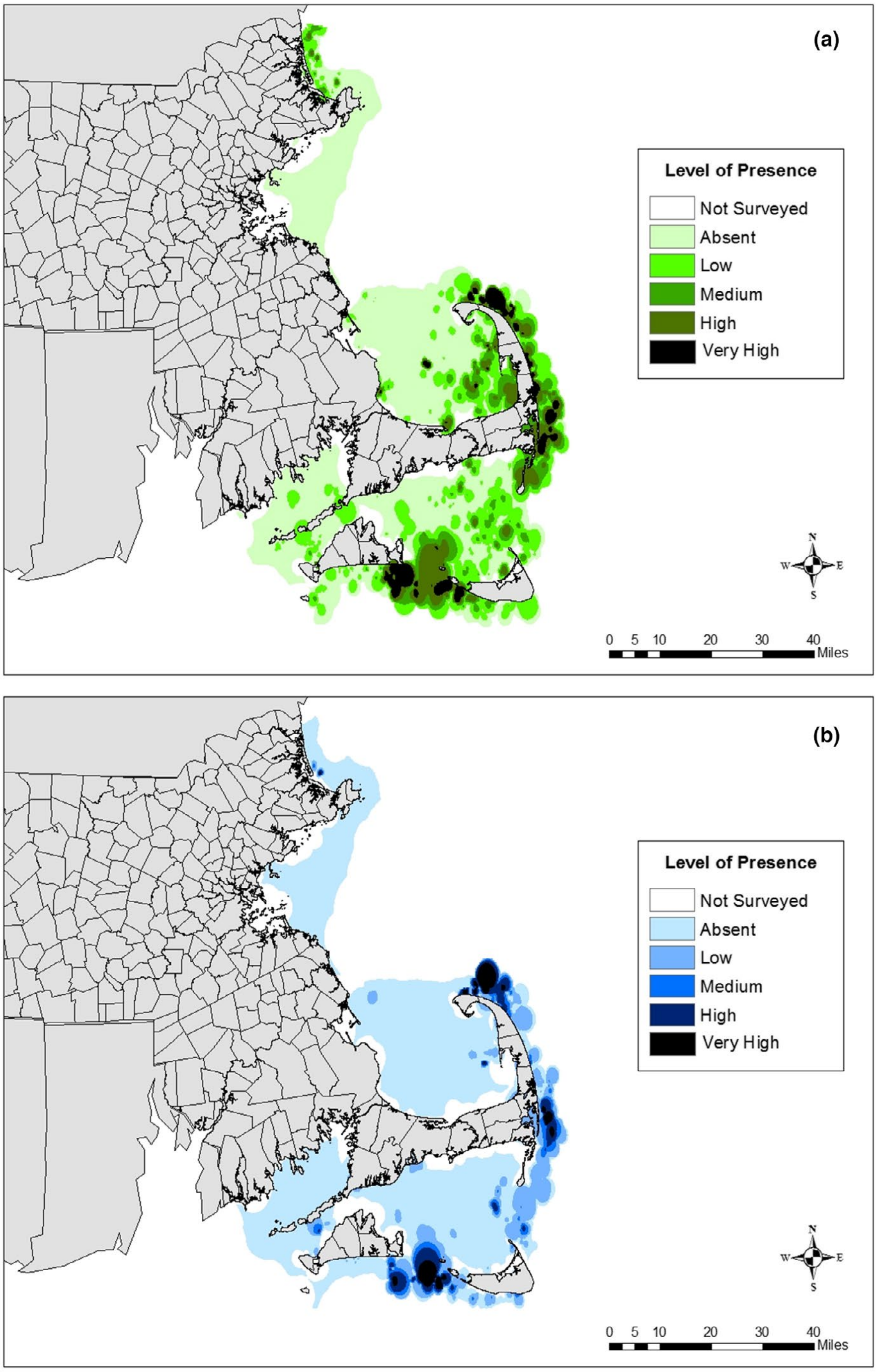


FIGURE 3 Spatial distribution of Northwest Atlantic *Ammodytes* during A) spring and B) fall caught during the Massachusetts Department of Marine Fisheries resource trawl survey. Data reflect occurrences between 1978 and 2016 on a relative scale ranging from absent (light colour) to very high numbers (dark colour). Maps courtesy of Amanda Davis and the Massachusetts Wildlife Climate Action Tool (For interactive data go to: climateactiontool.org)

Clupeidae), haddock (*Melanogrammus aeglefinus*, Gadidae), windowpane flounder (*Scophthalmus aquosus*, Scophthalmidae), striped searobin (*Prionotus evolans*, Triglidae) and northern kingfish (*Menticirrhus saxatilis*, Sciaenidae) (Table 1). However, the importance of NWA *Ammodytes* as prey to these and other predators varied substantially with season, geography, decade and ontogeny.

On a seasonal basis, NWA *Ammodytes* were consumed by the greatest diversity of fish species ($N_{\text{predators}} = 33$) in moderate (5%–10% M) to high (≥10% M) proportions during fall (September–December) (Figure 5; Appendix S1: Supplemental 2). Winter skate, striped bass (*Morone saxatilis*, Moronidae), clearnose skate (*Raja eglanteria*, Rajidae), haddock, windowpane and summer flounder (*Paralichthys dentatus*, Paralichthyidae) were among the top consumers of NWA *Ammodytes* during this season. A similar diversity of fish species ($N_{\text{predators}} = 28$) foraged on NWA *Ammodytes* in spring; however, most contained low proportions (<5% M) in their diets, with the exception of alewife, longhorn sculpin, Atlantic cod, winter skate and pollock (*Pollachius virens*, Gadidae). Survey effort was relatively low during the winter (January–March) and summer (June–August) seasons compared to spring and fall and likely influenced results for these periods ($N_{\text{predators}} = 11$ in both seasons). During winter, NWA *Ammodytes* was only found in trace amounts (<2% M)

TABLE 1 A summary of all fish predators caught by the Northeast Fisheries Science Center on the Northeast Continental Shelf from 1973 to 2015 and the percentage by mass (% Mass) and 95% Confidence Intervals (CI) of their overall diets found to contain Northwest Atlantic *Ammodytes*

Common name	Scientific name	% Mass	CI	Mean predator length (cm)	Range (cm)	Mean prey length (mm)	Range (mm)
Alewife	*Alosa pseudoharengus*	18.32	3.93	19.3	18–23	38.8	28–50
American shad	*Alosa sapidissima*	0.04	0.00	–	–	–	–
Atlantic cod	*Gadus morhua*	17.01	0.19	60.4	17–130	130.7	10–270
Atlantic croaker	*Micropogonias undulatus*	0.15	0.01	–	–	–	–
Atlantic halibut	*Hippoglossus hippoglossus*	0.45	0.04	69.0	49–87	148.9	80–215
Atlantic herring	*Clupea harengus*	0.51	0.01	22.4	12–36	33.8	10–120
Atlantic mackerel	*Scomber scombrus*	1.46	0.04	25.7	20–40	55.3	11–158
Barndoor skate	*Dipturus laevis*	0.38	0.01	65.3	56–85	88.3	73–118
Black sea bass	*Centropristis striata*	0.94	0.02	46.4	24–51	88.7	80–100
Bluefish	*Pomatomus saltatrix*	4.66	0.08	58.5	18–85	111.8	11–200
Clearnose skate	*Raja eglanteria*	4.67	0.17	57.8	42–73	86.3	28–170
Fourspot flounder	*Paralichthys oblongus*	1.56	0.01	31.2	22–43	95.8	45–150
Goosefish	*Lophius americanus*	0.45	0.01	44.4	12–90	152.5	60–275
Haddock	*Melanogrammus aeglefinus*	7.25	0.18	49.9	18–80	102.5	40–180
Little skate	*Leucoraja erinacea*	0.92	0.00	44.0	28–53	78.3	12–215
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	22.06	0.23	28.5	15–36	130.8	19–195
Northern kingfish	*Menticirrhus saxatilis*	5.34	0.65	35.0	35–35	107.7	95–118
Northern searobin	*Prionotus carolinus*	1.61	0.05	26.0	23–29	97.5	95–100
Ocean pout	*Macrozoarces americanus*	<0.01	0.00	45.0	45–45	126.0	126–126
Pollock	*Pollachius virens*	3.70	0.09	55.8	23–106	139.8	40–230
Red hake	*Urophycis chuss*	0.65	0.00	37.7	19–54	104.3	10–209
Rosette skate	*Leucoraja garmani*	0.15	0.01	–	–	–	–
Scup	*Stenotomus chrysops*	0.06	0.00	28.3	20–33	104.0	76–115
Silver hake	*Merluccius bilinearis*	0.88	0.01	32.4	9–53	117.1	11–250
Sea raven	*Hemitripterus americanus*	2.10	0.02	26.0	14–40	124.6	25–230
Smooth dogfish	*Mustelus canis*	0.22	0.00	96.5	55–122	105.5	10–180
Smooth skate	*Malacoraja senta*	0.04	0.00	–	–	–	–
Spiny dogfish	*Squalus acanthias*	2.31	0.03	76.9	23–105	126.6	12–388
Spotted hake	*Urophycis regia*	0.61	0.01	20.9	10–31	92.9	25–195
Striped bass	*Morone saxatilis*	3.34	0.30	58.1	32–81	129.8	100–195
Striped searobin	*Prionotus evolans*	5.51	0.36	31.5	25–37	136.3	120–160
Summer flounder	*Paralichthys dentatus*	3.45	0.02	41.2	28–62	115.9	11–260
Thorny skate	*Amblyraja radiata*	1.40	0.03	65.5	21–81	123.7	74–180
Weakfish	*Cynoscion regalis*	1.00	0.02	37.3	23–77	109.7	70–152
White hake	*Urophycis tenuis*	0.10	0.00	31.0	22–51	76.5	16–140
Windowpane flounder	*Scophthalmus aquosus*	6.20	0.07	29.4	17–38	89.6	11–190
Winter flounder	*Pseudopleuronectes americanus*	0.03	0.00	30.7	16–38	94.7	54–120
Winter skate	*Leucoraja ocellata*	19.80	0.12	77.8	22–106	125.0	10–380
Yellowtail flounder	*Limanda ferruginea*	4.54	0.09	31.0	20–41	78.3	40–135

across predator diets, suggesting lower predation pressure, or reduced availability, possibly a result of winter dormancy in NWA *Ammodytes*. In contrast, haddock, windowpane flounder and winter skate consumed very high amounts (>31% M) of NWA *Ammodytes* during summer.

Geographically, NWA *Ammodytes* was consumed by the greatest diversity of fishes in Southern New England ($N_{\text{predators}} = 28$) waters. A few notable predators were seasonal migrants to the region (striped bass and bluefish (*Pomatomus saltatrix*, Pomatomidae)). Most fish diets from

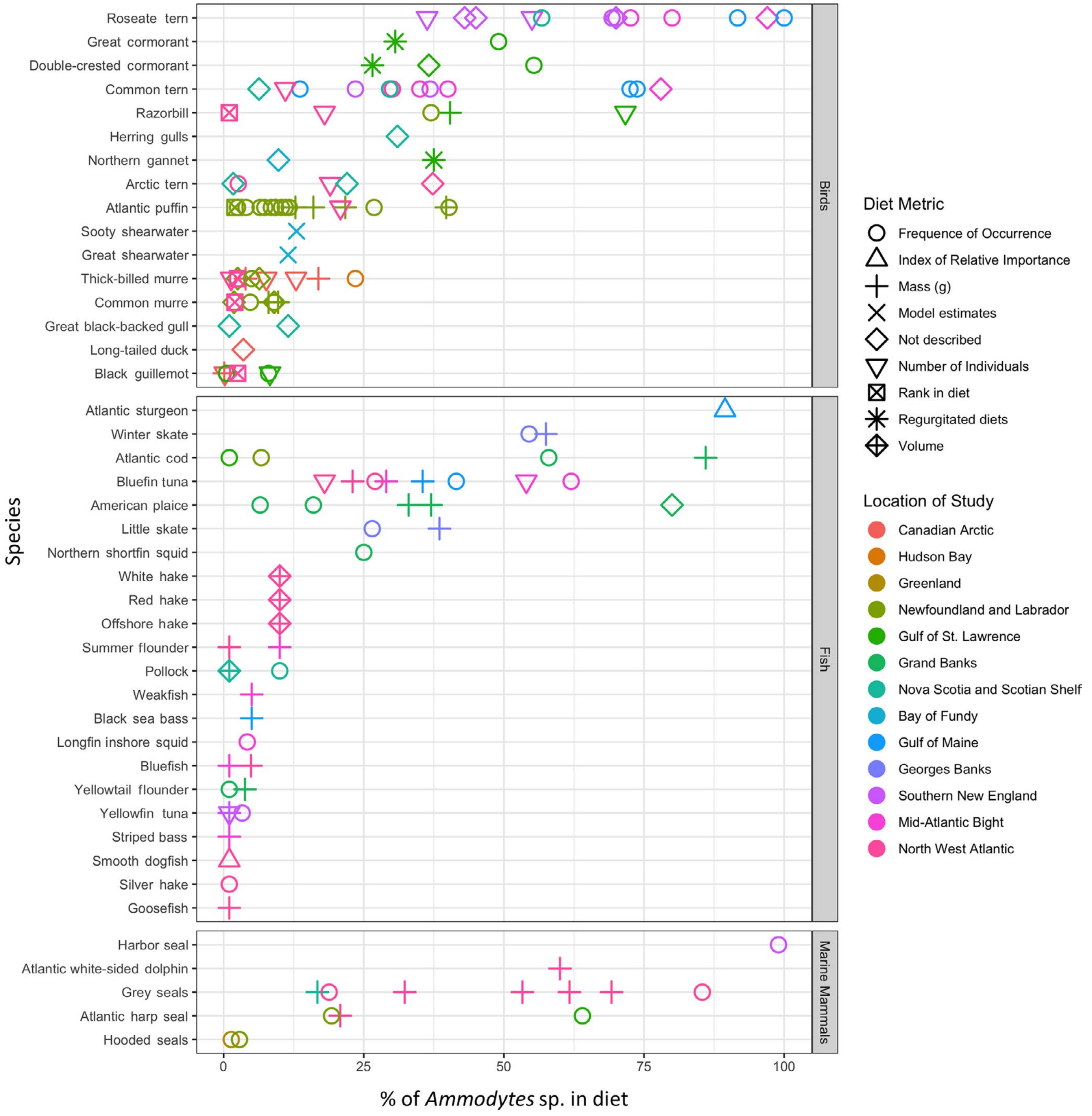


FIGURE 4 Proportion of Northwest Atlantic *Ammodytes* in seabird, fish, squid and marine mammals diets based on the results of a systematic literature review. Species within each taxonomic group are generally ordered from highest to lowest importance of *Ammodytes* sp. in their respective diets. Diet metrics are indicated by symbols, and study locations are indicated by colour. Exact dietary values and other study details can be found for fishes and squids in Appendix S1: Supplemental Table 6, for seabirds in Appendix S1: Supplemental Table 7, and for marine mammals in Appendix S1: Supplemental Table 9

the Mid-Atlantic Bight ($N_{\text{predators}}$ = 23) contained relatively low (<5% M) amounts of NWA *Ammodytes*, except for silver hake (*Merluccius bilinearis*, Merlucciidae) and winter skate (Figure 6; Appendix S1: Supplemental 3). In the northern regions of Georges Bank ($N_{\text{predators}}$ = 25) and the Gulf of Maine ($N_{\text{predators}}$ = 20), NWA *Ammodytes* were consumed in relatively higher proportions than in other regions. For example, the diets of winter skate on Georges Bank, as well as longhorn sculpin and Atlantic cod in the Gulf of Maine, contained 25%–47% M of NWA *Ammodytes*. Few predators (*N* = 7) consumed NWA *Ammodytes* on the Scotian Shelf and only in trace amounts (<2% M).

Seventeen species of fish predators were found to consume NWA *Ammodytes* during all five decadal periods sampled (Figure 7; Appendix S1: Supplemental 4). During the 1970s, 1980s and 1990s, fewer species consumed NWA *Ammodytes* overall (22–23 predator

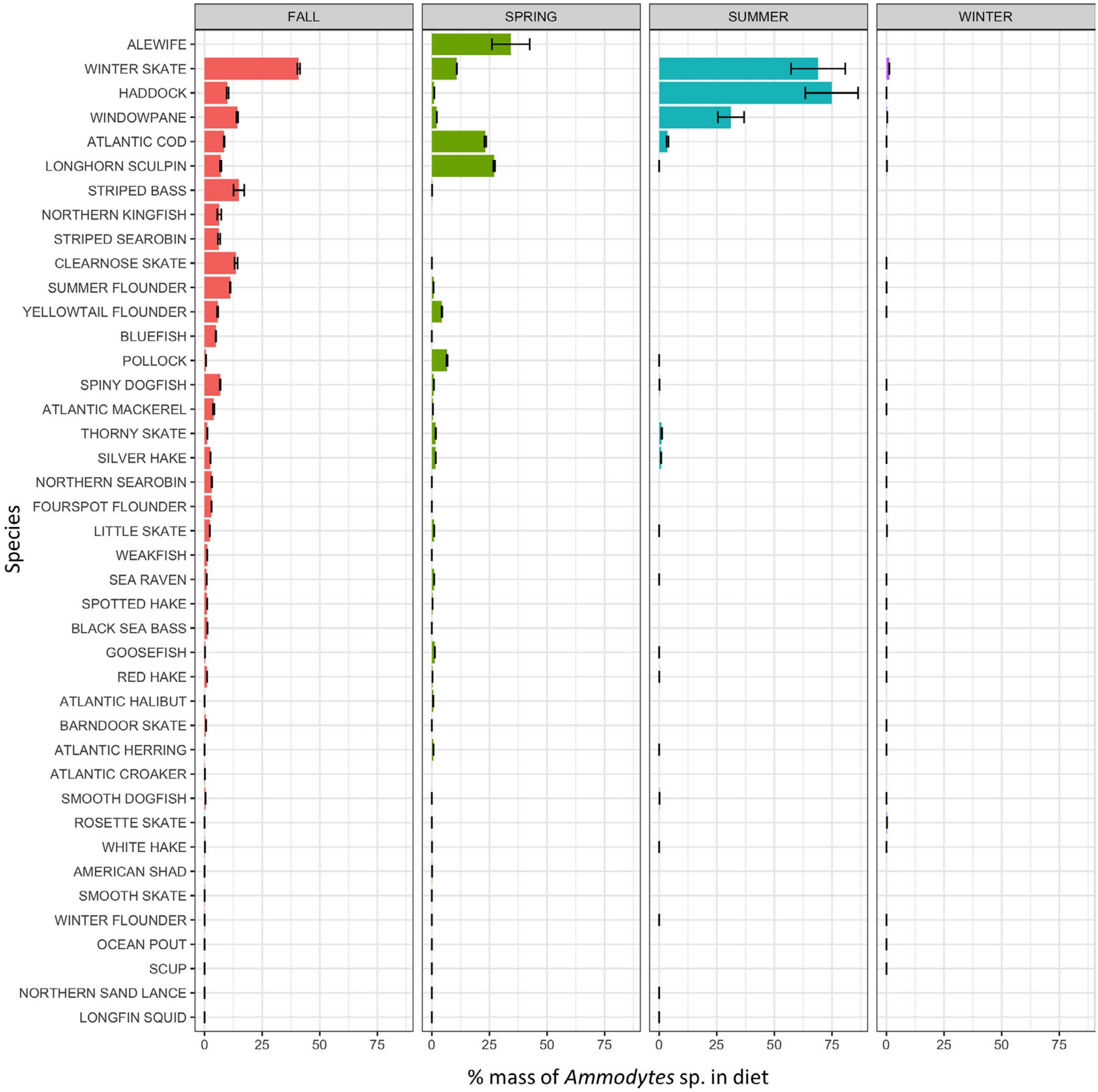


FIGURE 5 Per cent by mass of Northwest Atlantic *Ammodytes* in fish diets by season. Data were collected by the Northeast Fisheries Science Center on the Northeast Continental Shelf from 1973 to 2015

species) compared to more recent decades (N_{2000s} = 36 predators; N_{2010s} = 26 predators). Fish diets during the 1970s and 1980s contained greater proportions of NWA *Ammodytes* compared to the 1990s and 2000s, before increasing again during the most recent decade (2010s). A noticeable drop in predation was evident during the 1990s, when NWA *Ammodytes* was only found in trace amounts (≤2% M) across all predator diets, except for winter skate, whose diet contained low to moderate amounts (<10% M) compared to all other time periods (22%–45% M). These results are consistent with previous studies that have identified the 1990s (and the 1960s) as a time period of low NWA *Ammodytes* availability (Figure 1; Richardson et al., 2014).

NWA *Ammodytes* have gone through periods of importance as prey to other forage fishes including: alewife in the 1980s during spring; and to a lesser extent, American shad during the 2000s in spring in the Gulf of Maine; Atlantic herring from the 1980s to present during spring primarily in the Georges Bank region; and scup (*Stenotomus chrysops*, Sparidae) in Southern New England during fall in the 1970s. Clearnose (*R. eglanteria*, Rajidae), barndoor (*Dipturus laevis*, Rajidae) and rosette (*L. garmani*, Rajidae) skates, as well as striped and northern (*P. carolinus*, Triglidae) sea robins, were not documented as predators of NWA *Ammodytes* prior to the 2000s in the NMFS trawl survey, but were found thereafter to consume them in

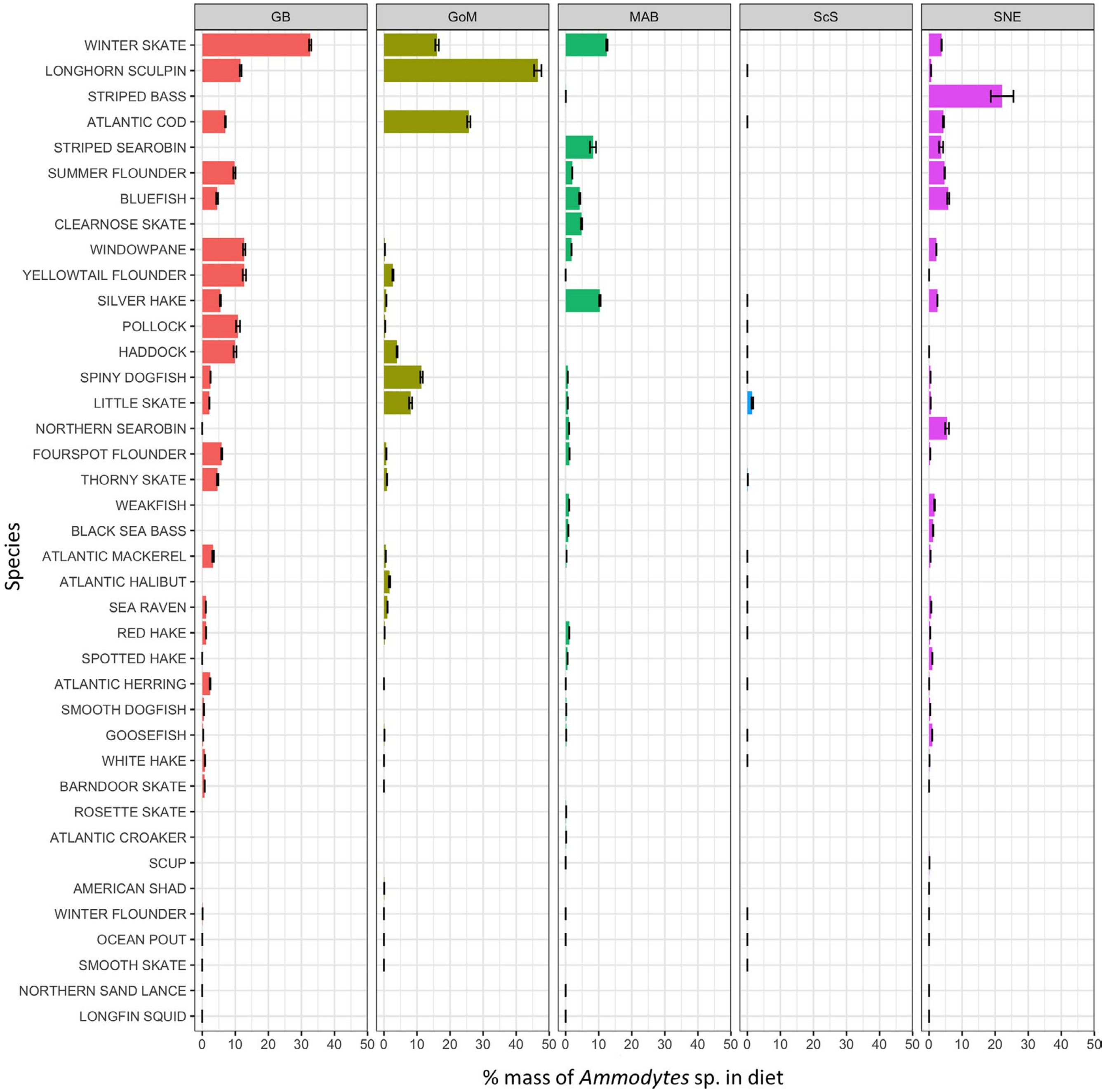


FIGURE 6 Per cent by mass of Northwest Atlantic *Ammodytes* in fish diets by geographical area. GB, Georges Bank; GoM, Gulf of Maine; MAB, Mid-Atlantic Bight; SNE, Southern New England; and ScS, Scotian Shelf. Data were collected by the Northeast Fisheries Science Center on the Northeast Continental Shelf from 1973 to 2015

low to moderate amounts (<10% M of total diets), particularly during spring and fall across multiple regions. However, this may have been a sampling artefact of the survey as sampling intensity has changed over time due to commercial and ecological interest in certain species (Smith & Link, 2010).

Predator-prey body-size data were available for 35 fishes in the NMFS trawl series (Table 1). The mean size ± *SD* of NWA *Ammodytes* consumed by all predators across all years was 117.3 ± 46.7 mm. Based on size-at-age estimates from Monteleone and Peterson (1986) and Nelson and Ross (1991), the majority of NWA *Ammodytes* consumed across the region were post-metamorphosis young-of-the-year (YOY) and year-1 and year-2 fish. Few predators consumed NWA *Ammodytes* > 180 mm TL. The smallest NWA *Ammodytes* on average were found in the diets of Atlantic herring, alewife, Atlantic mackerel, white hake (*Urophycis tenuis*, Phycidae), yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) and several species of skates (Table 1). Atlantic herring and alewife consumed mostly larval and young-of-the-year NWA *Ammodytes*, but early life stages of NWA *Ammodytes* were found in the diets of most other fishes, except ocean pout (*Macrozoarces americanus*, Zoarcidae), striped bass and

FIGURE 7 Per cent by mass of Northwest Atlantic *Ammodytes* in fish diets by decade. Data were collected by the Northeast Fisheries Science Center on the Northeast Continental Shelf from 1973 to 2015

striped searobin, which consumed individuals ≥100 mm. Goosefish (*Lophius americanus*, Lophiidae), Atlantic halibut (*Hippoglossus hippoglossus*, Pleuronectidae), pollock, striped searobin, longhorn sculpin and Atlantic cod consumed the largest NWA *Ammodytes* on average (≥130 mm TL). Across all regions, the smallest individuals were consumed during summer, intermediate sizes were consumed in fall, and slightly larger and equivalent sized NWA *Ammodytes* were consumed in winter and spring (Table 2). Size distributions of larger NWA *Ammodytes* were related to cohort growth rates and availability, possibly due to changes in activity levels (e.g., spawning aggregations). Across regions, the smallest sized individuals were consumed in the Scotian Shelf and Gulf of Maine, while the largest were consumed in the Gulf of Maine and Mid-Atlantic Bight (Table 2). The average size of NWA *Ammodytes* consumed across all predators decreased from 124.3 to 112.2 mm from the early 1970s to 2015. The majority of predators consumed increasingly larger individuals with (predator) growth; however, a few consumed a consistent range of body sizes throughout their ontogeny, including bluefish, goosefish, longhorn sculpin, red and white hake (Appendix S1: Supplemental 5).

Information from the literature revealed six additional fish species—American plaice (*Hippoglossoides platessoides*, Pleuronectidae), Atlantic salmon (*Salmo salar*, Salmonidae), Atlantic

TABLE 2 Mean body sizes (mm) of Northwest Atlantic *Ammodytes* consumed by all fish predators caught by Northeast Fisheries Science Center on the Northeast Continental Shelf from 1973–2015 by season, region and decade

Factor	*N*	Mean length (mm)	Std Dev
Season			
Fall	1707	113.4	35.7
Spring	2,655	121.2	52.2
Summer	378	105.2	42.9
Winter	199	122.3	51.7
Region			
GB	2,400	116.3	41.5
GoM	378	141.6	38.6
MAB	1,192	123.0	49.5
ScS	19	84.0	32.1
SNE	948	103.8	53.0
Decade			
1970s	630	124.3	44.8
1980s	2008	117.5	49.2
1990s	1,307	117.3	48.4
2000s	763	112.8	37.7
2010s	231	112.2	44.3

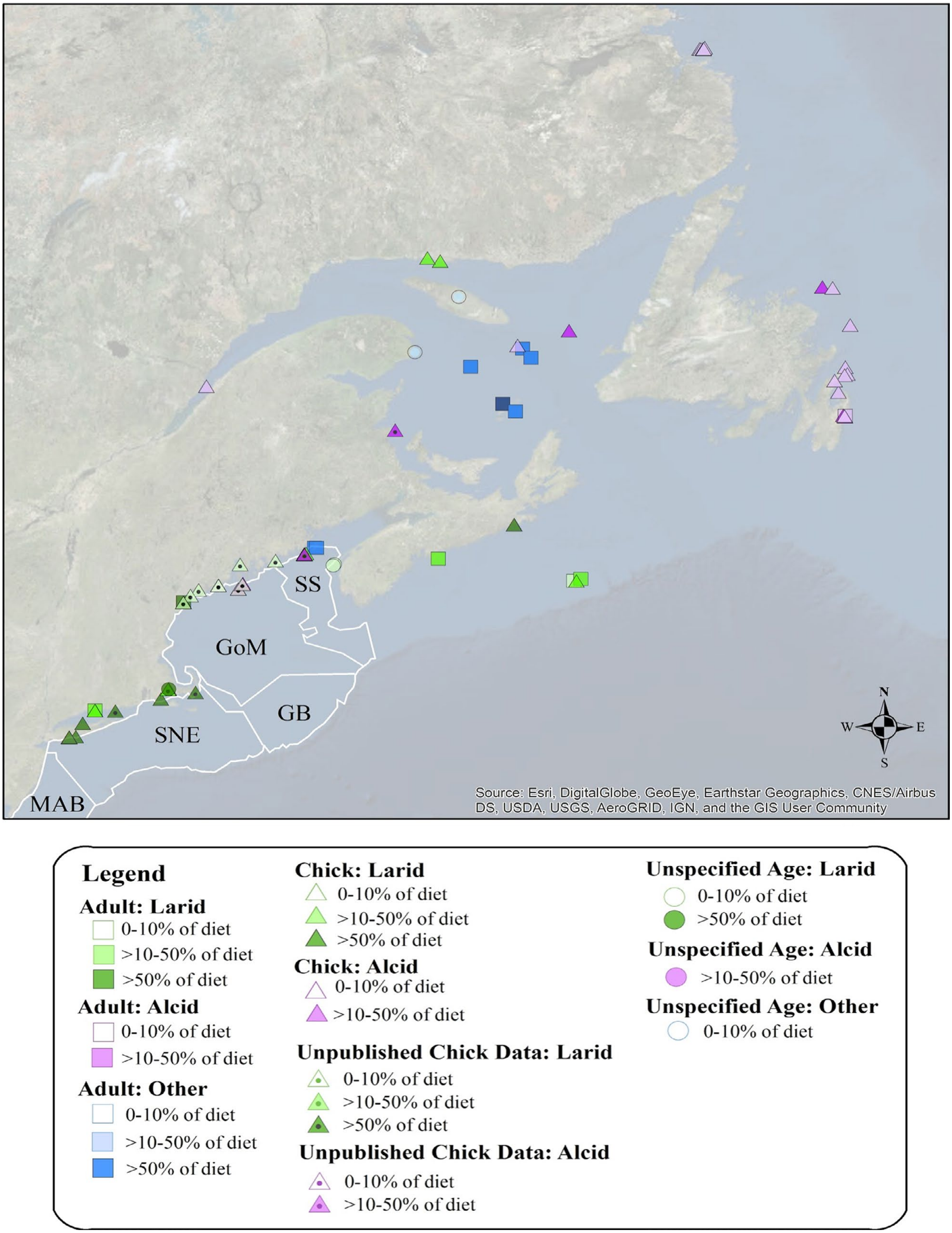
Abbreviations: GB, Georges Bank; GoM, Gulf of Maine; MAB, Mid-Atlantic Bight; SNE, Southern New England and ScS, Scotian Shelf.

sturgeon (*Acipenser oxyrinchus oxyrinchus*, Acipenseridae), offshore hake (*M. albidus*, Merlucciidae), bluefin (*Thunnus thynnus*, Scombridae) and yellowfin (*T. albacares*, Scombridae) tunas, as well as northern shortfin (*Illex illecebrosus*, Ommastrephidae) and longfin inshore (*Doryteuthis pealeii*, Loliginidae) squids—consumed NWA *Ammodytes* in the region (Figure 4; Appendix S1: Supplemental 6). Six previously published studies used data from the NMFS trawl survey, but augmented sampling of certain species across seasonal periods including red (*U. chuss*, Phycidae), offshore, silver and white hakes (Garrison & Link, 2000; Link, Lucey, & Melgey, 2012), little (*L. erinacea*, Rajidae) and winter skates (Smith, Collie, & Lengyel, 2014), scup and black sea bass (*Centropristis striata*, Serranidae) (Byron & Link, 2010), Atlantic mackerel and Atlantic herring (Suca et al., 2018), as well as summer flounder, bluefish, goosefish (Staudinger, 2004) and longfin inshore squid (Hunsicker & Essington, 2006). The remaining studies represented predator diets from inshore and estuarine habitats (Gelsleichter, Musick, & Nichols, 1999; Novak, Carlson, Wheeler, Wippelhauser, & Sulikowski, 2017; Wuenschel, Able, Vasslides, & Byrne, 2013), offshore areas of the continental slope and pelagic waters (Chase, 2002; Logan, Golet, & Lutcavage, 2015; Logan et al., 2011; Teffer, Staudinger, & Juanes, 2015), as well as Canadian waters (Carruthers, Neilson, Waters, & Perley, 2005; Dawe, Dalley, & Lidster, 1997; Hanson & Chouinard, 2002; Kelly & Hanson, 2013; Zamarro, 1992). A few notable areas where predation on NWA *Ammodytes* was extremely high included the Saco River Estuary in the Gulf of Maine, where the diets of juvenile and adult Atlantic sturgeon between 2013 and 2014 contained 85%–96% (Index of Relative Importance, IRI) of *A. americanus* (Novak et al., 2017). In coastal waters off New Jersey in summer and fall during the mid-2000s, summer flounder consumed low to high (3%–17% M) amounts of NWA *Ammodytes* (Wuenschel et al., 2013). American plaice in Newfoundland waters also showed historically high amounts (16% FO) of *A. dubius* during the 1990s (Zamarro, 1992), as well as pollock (7%–13% FO) in the Bay of Fundy in the 1950s and 1960s (Carruthers et al., 2005). Several studies determined that bluefin tuna, especially smaller and younger fish (Logan et al., 2011, 2015), relied heavily (up to 69% M of their diet) on NWA *Ammodytes* during summer and fall in the Mid-Atlantic Bight, Southern New England, Gulf of Maine and Georges Bank regions during the late 1980s to early 2000s (Chase, 2002; Logan et al., 2011, 2015), while low amounts (<5% M) were found in sympatric yellowfin tuna in the early 2000s (Teffer et al., 2015).

In summary, NWA *Ammodytes* were found in the diets of several fishes of high conservation concern including Atlantic cod, Atlantic salmon, thorny skate, barndoor skate, alewife, Atlantic sturgeon and bluefin tuna. While contributions to some of these predator diets were either episodic (alewife in the 1980s) or in relatively low amount (skates), NWA *Ammodytes* have comprised substantial proportions of the collective diets of Atlantic cod, Atlantic sturgeon, and bluefin tuna across historical periods (1960s–2000s) and spatial scales (U.S. and Canadian waters). Results suggest NWA *Ammodytes* contribute substantially to their overall nutrition and could influence abundance, distribution and population recovery (where they are depleted).

3.2 | Importance to seabirds

A total of 16 species of seabirds including terns, alcids, gulls, cormorants, murres, shearwaters, gannets and some ducks were reported to consume NWA *Ammodytes* in notable amounts, according to published (Appendix S1: Supplemental 7) and unpublished (Appendix S1: Supplemental 8) sources. This was either as adults or as provisioned to chicks along the eastern coasts of the United States and Canada (Figure 8). Long-term dietary studies conducted at 13 managed colonies between New York and Nova Scotia showed common terns (*Sterna hirundo*, Laridae), Arctic terns (*S. paradisaea*, Laridae) and roseate terns (*S. dougallii*, Laridae), as well as Atlantic puffins (*Fratercula arctica*, Alcidae) and razorbills (*Alca torda*, Alcidae) fed NWA *Ammodytes* to their chicks on a regular basis (Appendix S1: Supplemental 8). Some species such as double-crested cormorants (*Phalacrocorax auritus*, Phalacrocoracidae), common terns, razorbills and roseate terns specialized on NWA *Ammodytes*, with diets containing 40%–100% M, FO or N across sampling periods (Appendix S1: Supplement 7). Roseate terns nesting in Southern New England and the Gulf of Maine demonstrated the highest reliance. For example, chick diets at Great Gull Island (Long Island Sound, NY) consisted of 97% FO NWA *Ammodytes* in 2016 (M. Abemayor, unpublished data), while those on Bird Island (Buzzards Bay, MA) averaged 69% FO between



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

FIGURE 8 Proportion of Northwest Atlantic *Ammodytes* in marine bird diets, by seabird family (Larid: terns, gulls, and skimmers; Alcid: murres, guillemots, auklets, puffins and murrelets; Other: cormorants, shearwaters, etc.), mapped across the region. Refer to Appendix S1: Supplemental 7 for additional details on species-specific diet metric, location and time periods of studies. GB, Georges Bank; GoM, Gulf of Maine; MAB, Mid-Atlantic Bight; SNE, Southern New England and SS, Scotian Shelf

2009 and 2011 (Goyert, 2015). Common terns at colonies in MA and NY fed their chicks 30%–78% FO NWA *Ammodytes* during similar time periods (Appendix S1: Supplemental 8). Adult terns at colonies in the northern Gulf of Maine and Nova Scotia, Canada, delivered a combination of (mainly) NWA *Ammodytes*, Atlantic herring, and hake to their chicks (Kirkham, 1986; Rock, Leonard, & Boyne, 2007a, b; Shealer & Kress, 1994; Yakola, 2019). Regional populations of common and roseate terns staging (i.e., pre-migratory) on Cape Cod, MA, were observed feeding almost exclusively on NWA *Ammodytes* for up to six weeks in late summer and early fall before departing for South America (Althouse, 2016; Jedrey, Harris, & Ray, 2010; J. Spendelow, personal communication).

In the Gulf of Maine and Georges Bank, a diversity of non-breeding adult and immature seabirds were found to consume NWA *Ammodytes* during the late 1970s to early 1980s, particularly during the summer and fall, including great shearwaters (>50% IRI, *Ardenna gravis*, Procellariidae), Cory's (*Calonectris borealis*, Procellariidae) and sooty shearwaters (10%–50% IRI, *A. grisea*, Procellariidae), as well as black-legged kittiwakes (*Rissa tridactyla*, Laridae) (Powers & Backus, 1987). Between 2005 and 2009 in the Bay of Fundy, NWA *Ammodytes* were also important to staging (i.e., the period of time post-breeding and pre-migration to wintering sites when birds congregate) sooty and great shearwaters, in some years acting as one of the top two forage fishes and comprising nearly one third of their overall diet (Ronconi, Koopman, McKinstry, Wong, & Westgate, 2010) (Figure 4). Recent telemetry studies (2005–2014) of tagged great shearwaters suggested that movements reflecting foraging trips frequently overlap with NWA *Ammodytes* habitat in the southern Gulf of Maine (Powers, Wiley, Allyn, Welch, & Ronconi, 2017).

Ammodytes provide a highly nutritional source of lipids and proteins to seabirds (and other predators). Post-larval NWA *Ammodytes* showed higher caloric content than capelin (Baillie & Jones, 2003) and Atlantic herring (Hislop, Harris, & Smith, 1991) of comparable length. Over the last two decades in the Gulf of Maine, herring has frequently been replaced by high-lipid NWA *Ammodytes* in the diets of Atlantic Puffin, Razorbill and Common Murre (Scopel, Diamond, Kress, & Shannon, 2019). While larger seabirds (e.g., alcids) are able to dive and access adult *Ammodytes* throughout the water column, smaller species (e.g., *Sterna*) are limited to foraging at the sea surface where YOY and juveniles are more likely to occur (Breton & Diamond, 2014; Chapdelaine & Brousseau, 1996). Small-sized *Ammodytes*, although of lesser nutritional value compared to larger individuals, may be selected because of their availability, size or morphology; smaller individuals are also easier for adults to carry and for chicks to swallow (Bradstreet & Brown, 1985; Burger & Piatt, 1990; Burke & Montevecchi, 2008; Gaston & Woo, 2008).

Consumption of NWA *Ammodytes* by several seabird species (common murres, razorbills and great shearwaters) was shown to vary based on their abundance relative to other forage fishes and proximity to key habitats such as nesting colonies (Brown, Barker, Gaskin, & Sandeman, 1981; Overholtz & Link, 2006; Piatt, 1987; Pratte, Robertson, & Mallory, 2017; Regular et al., 2014). The spatial distribution of NWA *Ammodytes* had a positive effect on seabird foraging behaviours, where availability impacted foraging ranges (e.g., razorbills and kittiwakes; Gaston & Woo, 2008; Jodice et al., 2006) and persistence influenced fidelity to areas of high abundance (e.g., roseate terns and Atlantic puffins; Goyert, 2015; Jessopp et al., 2013). Seasonality is also important to regional breeding populations such as herring gulls, which feed in more inshore habitats during summer (Ronconi, Steenweg, Taylor, & Mallory, 2014), and to non-breeding birds (e.g., great shearwaters) that migrate through the Gulf of Maine during summer and fall (Brown et al., 1981).

Ammodytes role as prey in the NWA ecosystem has important implications for seabirds of conservation concern. State wildlife management agencies in New England have recently identified 11 Species of Greatest Conservation Need (SGCN) that consume NWA *Ammodytes* as part of their diets or provisioning activities: roseate tern, Arctic tern, Atlantic puffin, razorbill, common murre (*Uria aalge*, Alcidae), great cormorant (*P. carbo*, Phalacrocoracidae), great shearwater, Cory's shearwater, sooty shearwater, northern gannet (*Morus bassanus*, Sulidae) and red-throated loon (*Gavia stellata*, Gaviidae). Roseate terns are listed as federally endangered in both Canada and the USA, including in all six north-eastern states. In the past decade, 90% of the north-eastern roseate tern population nested on only three islands (Great Gull Island, NY, Bird and Ram Islands, MA; C. Mostello, unpub. data), and NWA *Ammodytes* dominated (≥57% FO) chick diets across those colonies (M. Abemayor, unpublished data; Goyert, 2015). As *Ammodytes* specialists, roseate terns show limited flexibility in their foraging strategies, which makes them particularly vulnerable to changes in availability (Goyert, 2015). During the breeding season, feeding areas have been documented within 10–30 km of breeding colonies (Heinemann, 1992), but recent tagging studies suggest that adults may travel as far as 50 km to find suitable prey (Loring et al., 2019). Productivity and chick survival rates of roseate terns have been attributed primarily to the availability of high-quality prey (Kirkham, 1986), and thus, changes in the abundance and distribution of NWA *Ammodytes* relative to breeding colonies and staging locations could significantly affect their population dynamics and breeding success if they are not able to exploit an alternative prey source of comparable nutrition. In addition, direct links between dietary importance and productivity have yet to be quantified explicitly in the region.

3.3 | Importance to marine mammals

NWA *Ammodytes* are generally known to be important prey to a number of marine mammals (Anonymous, 2006; Fisheries & Oceans Canada, 2009; L. A. Smith, Link, Cadrin, & Palka, 2015). Quantitative and qualitative reports of dietary exploitation of NWA *Ammodytes* were found for four species of pinnipeds: Atlantic harp (*Pagophilus groenlandicus*, Phocidae), grey (*Halichoerus grypus*, Phocidae), harbour (*Phoca vitulina concolor*, Phocidae) and hooded (*Cystophora cristata*, Phocidae) seals; two small-sized cetaceans: Atlantic white-sided dolphin (*Lagenorhynchus acutus*, Delphinidae) and harbour porpoise (*Phocoena phocoena*, Phocoenidae); and three large whale species: humpback (*Megaptera novaeangliae*, Balaenopteridae), minke

(*Balaenoptera acutorostrata*, Balaenopteridae) and fin (*B. physalus*, Balaenopteridae) whales (Figure 4; Appendix S1: Supplemental 9). Four of these species (humpback whales, fin whales, harbour porpoise and harbour seals) were identified as SGCN within USA by state wildlife management agencies and one (fin whales) was listed as endangered by the U.S. Endangered Species Act.

For most marine mammals, diet data were scarce, and the only direct observations are derived from by-caught animals from various gillnet fisheries or stranded individuals. Grey seals were the best-studied marine mammal in the region, with estimates of NWA *Ammodytes* contributing between 15%–70% by M and FO to their diets (Appendix S1: Supplemental 9). DNA analysis of grey seal faeces from two locations (Muskeget and Monomoy Islands) in MA between 2016 and 2017 found a very high FO (85%) of NWA *Ammodytes* in their diets (Z. Olson, personal communication, September 3, 2020). In waters off Muskeget and Monomoy Islands in Nantucket Sound, NWA *Ammodytes* dominated grey seal diets between 2004 and 2008 (53% M, Ampela, 2009). During the 1990s in the Sable Island region of Canada, the diets of grey seals contained between 17% M (Beck, Iverson, Bowen, & Blanchard, 2007) and 88% M (Bowen & Harrison, 1994, 2006) NWA *Ammodytes* across age and sex classifications. Movement studies in the NWA as well as Sable Island region confirmed repeated visitation and high use of nearshore areas and substrates typical of burrowing NWA *Ammodytes* (Breed, Bowen, & Leonard, 2013; Moxley, Skomal, Chisholm, Halpin, & Johnston, in press).

In other pinnipeds, dietary inclusion of NWA *Ammodytes* varied over geographical scales. Harbour seal diets contained between <5%–99% FO of NWA *Ammodytes* depending on geography in the Southern New England and Gulf of Maine regions (Bowen, Tully, Boness, Bulheier, & Marshall, 2002; Payne & Selzer, 1989). The Monomoy area of Cape Cod and Sable Island, Nova Scotia, were particularly important areas during the 1980s and 1990s, with harbour seal diets almost exclusively containing NWA *Ammodytes* (*A. dubius*, Bowen et al., 2002; *A. americanus*, Payne & Selzer, 1989). Using animal-borne video cameras, behavioural studies of harbour seals documented effective feeding strategies on burrowing NWA *Ammodytes* whereby individuals consumed substrate containing prey, regurgitated the contents and re-consumed fish drifting in the water column (Heaslip, Bowen, & Iverson, 2014). In Atlantic harp seals, diet proportions of *A. dubius* ranged from 19% to 64% FO among studies conducted between 1980 and 2004 (Appendix S1: Supplement 9), with subadults and pups generally consuming greater amounts compared to adults (Lawson & Stenson, 1997). Hooded seal diets contained lesser amounts of *Ammodytes*, generally <5% FO in waters off Greenland and Newfoundland during the 1990s–early 2000s (Haug, Tormod Nilssen, Lindblom, & Lindstrøm, 2007; Tucker, Bowen, Iverson, Blanchard, & Stenson, 2009).

From the little diet evidence that exists for other marine mammal species, as well as reports from areas outside the NWA, *Ammodytes* is inferred to be a key prey item. There have been limited direct observations of white-sided dolphins consuming NWA *Ammodytes* in coastal New England waters (Weinrich, Belt, & Morin, 2001); however, Craddock, Polloni, Hayward, and Wenzel (2009) documented high amounts (60% M) in the stomach contents of a stranded animal off of Cape Cod, MA, using multiple diet metrics. Other evidence of delphinid reliance on NWA *Ammodytes* is indirect but highly suggestive. For instance, white-sided dolphin seasonal distribution and habitat use, based on surveys from 1978 to 1988, has been shown to mirror that of NWA *Ammodytes*, leading to conclusions that they were likely major prey (Kenney, Payne, Heinemann, & Winn, 1996; Selzer & Payne, 1988).

Harbour porpoises are posited to consume NWA *Ammodytes* (COSEWIC, 2006), despite the absence of direct evidence of consumption. In the NWA, stomach content studies have been limited to the Bay of Fundy, Canada (Recchia & Read, 1989), where herring may be more important to cetaceans. However, in areas outside the NWA, such as in the North Sea, harbour porpoise distribution and abundance correlated positively with *Ammodytes* fisheries (Herr, Fock, Kock, & Siebert, 2008; MacLeod, Pierce, & Santos, 2007; MacLeod, Santos, Reid, Scott, & Pierce, 2007), and starvation events coincided with *Ammodytes* declines (but see Thompson et al., 2007).

Diet determination of large whales is inherently difficult and often limited to (as well as biased by) visual observation of surface feeding and any prey or other non-prey species flushed to the surface (Hain et al., 1995). Published observations confirmed 3 species of baleen whales feed on NWA *Ammodytes* (humpback, fin, and minke), and regionally, the strongest dietary link exists for humpback whales. The distribution and abundance of humpback whales between 1978 and 1988 on Georges Bank and in the Gulf of Maine (at least in the Stellwagen Bank National Marine Sanctuary) mirrored that of NWA *Ammodytes* (Payne, Nicolas, OBrien, & Powers, 1986; Payne et al., 1990). Recent technological advances using hydroacoustic measurements and real-time sensor tags that track fine-scale diel movements showed the surface and bottom foraging behaviours of humpback whales were dependent on the distribution of *NWA Ammodytes* in the water column (Friedlaender et al., 2009; Hazen et al., 2009). Humpback whales use bubble nets to feed on NWA *Ammodytes* in the water column during the day and follow them to the bottom at night and hunt them using a characteristic side-roll behaviour (Friedlaender et al., 2009; Hazen et al., 2009; Ware et al., 2014; Wiley et al., 2011). Periods of greater humpback whale exchange between primary feeding grounds in the Gulf of Maine and off Eastern Canada during the early 1990s were linked to forage availability, including NWA *Ammodytes* (Stevick et al., 2006). Humpback whale calf survival after weaning in the Gulf of Maine has also been linked to the availability of NWA *Ammodytes* and Atlantic mackerel (Robbins, 2007). Information on other large whales was indirect and derived from relating whale occurrences with known locations of NWA *Ammodytes* or their habitat (Overholtz & Nicolas, 1979; Payne et al., 1986, 1990; Weinrich, Martin, Griffiths, Bove, & Schilling, 1997).

One of the only areas in the NWA with direct diet data for minke whales is in Greenland. NWA *Ammodytes* were found in 92% FO of whale diets from offshore areas of West Greenland in the 1980s; however, they were less important during the early 1990s and replaced by capelin (Neve, 2000). In one study of individually identified minke whales off the coast of MA, sightings were less common in years when local NWA *Ammodytes* abundance was low, providing indirect evidence of their possible dietary importance (Murphy, 1995). Evidence from other areas of the world (e.g., Japan, Iceland and Norway) shows that minke whales consume adult *Ammodytes* (Lydersen, Weslawski, & Øritsland, 1991; Murase et al., 2009; Sigurjónsson, Galan, & Víkingsson, 2000; Tamura et al., 2009; Víkingsson et al., 2015). In waters off Scotland, minke whale diets contained high amounts (66% Number, 62% M) of *A. marinus* (Pierce, Santos, Reid, Patterson, & Ross, 2004), and their distribution in surrounding waters corresponded to *Ammodytes*-associated habitats (Macleod et al., 2004; Olsen & Grahl-Nielsen, 2003). A body condition study off Iceland did not successfully link minke whale blubber thickness with trends in *Ammodytes* abundance, but this was considered likely due to there being multiple prey species of importance (Christiansen, Víkingsson, Rasmussen, & Lusseau, 2013).

3.4 | Interspecific interactions

Within the broader NWA food web, the predictability and persistence of forage species such as *Ammodytes* is highly important to the multiple predator groups that specialize on them (e.g., Atlantic sturgeon, roseate terns and harbour seals; Figure 4, Appendix S1: Supplements 6–9). Interspecific interactions may provide additional opportunities for socially flexible and opportunistic predators. The pelagic realm is a dynamic environment where prey aggregations (e.g., bait balls) can attract multiple predators that engage in facilitative (e.g., commensal) or competitive feeding frenzies (Goyert et al., 2018; Goyert, Manne, & Veit, 2014). During these social interactions, predatory fishes (e.g., tunas) and marine mammals can drive prey upwards towards seabirds feeding at the air–sea interface (Safina, 1990; Veit & Harrison, 2017). In addition, fish, seabird and marine mammal predators may feed cooperatively on large aggregations through social facilitation, by providing cues to each other as to where NWA *Ammodytes* (and other aggregations of forage species) are located. This may be especially important for predators to take advantage of spatiotemporally persistent hotspots of NWA *Ammodytes*, which occur in areas such as Stellwagen Bank National Marine Sanctuary (Silva et al., 2019). Therefore, access, connectivity and communication pathways surrounding such hotspots have the potential to affect facilitative or competitive interactions from multiple functional groups in the region. Our understanding of similar types of facilitative or competitive interactions of predators in the NWA region, especially over and at the seafloor when *Ammodytes* enter and exit sand refugia (Hobson, 1986 for *A. hexapterus*), is extremely limited.

4 | THREATS AND RELATED VULNERABILITIES

Ammodytes play a clear and significant ecological role in natural systems of the NWA, and like other forage species (Hunsicker, Essington, Watson, & Sumaila, 2010) provide ecosystem services that directly and indirectly support humans in unrecognized and unexpected ways (Alder, Campbell, Karpouzi, Kaschner, & Pauly, 2008; Pikitch et al., 2004; Section 5 of this synthesis). Existing and emerging threats from climate change, fishing pressure, aquaculture, mining of sand deposits, energy exploration and infrastructure, and other anthropogenic activities have the potential to impact NWA *Ammodytes* either directly through harvest or habitat degradation, or indirectly through altered food web relationships. Depending on the vulnerability of each *Ammodytes* species to these stressors, there could be radiating effects on regional human-ecological systems that increase the need for their explicit consideration, especially to avoid tipping points, in management and conservation initiatives.

4.1 | Changes in regional climate and oceanographic patterns

The NWA region is experiencing rapid warming due to climate change, with rates as high as 0.4–0.3°C per decade since the 1980s (Brickman, Hebert, & Wang, 2018; Pershing et al., 2015; Thomas et al., 2017). Regional warming has been observed during all seasons, with the greatest increases during summer (Baumann & Doherty, 2013; Thomas et al., 2017). The timing of spring and fall conditions have shifted, with spring arriving earlier and fall ending later, which has resulted in decreasing winter duration (Friedland et al., 2015; Thomas et al., 2017). Changes in winter and spring are particularly important to NWA *Ammodytes* since they complete their early life history and feed vigorously as adults during these periods. *Ammodytes dubius* are associated with cold water habitats of 2–7°C during winter and 7–15°C during summer (Nelson & Ross, 1991), which are projected to warm substantially over the coming decades (Alexander et al., 2018; Saba et al., 2016). Observed and projected changes in regional precipitation and hydrology affect the delivery of fresh water, sediments and nutrients into nearshore coastal areas (Groisman, Knight, & Zolina, 2013; Guilbert, Betts, Rizzo, Beckage, & Bomblies, 2015; Rawlins, Bradley, & Diaz, 2012; Walsh et al., 2014) with implications for the conditions supporting *A. americanus*, in particular. Seasonal variation in wind forcing, freshwater run-off and water mass influx into the Gulf of Maine creates substantial seasonal and interannual differences in circulation flows (Pettigrew et al., 2005; Smith, Pettigrew, Yeats, Townsend, & Han, 2012). These physical patterns and drivers are key underlying influences on the regional distribution and occurrence of planktonic early life history stages of NWA *Ammodytes*, as well as primary and secondary production (Churchill, Runge, & Chen, 2011; Ji, Davis, Chen, & Beardsley, 2009; Ji et al., 2017). *Ammodytes* and other forage species that exhibit boom and bust cycles are likely driven, at least in part, by large-scale environmental changes (Dickey-Collas et al., 2013), and when conditions become unfavourable, there is an increased risk of stock collapse due to the interactive effects of climate change and other stressors (e.g., fishing pressure or habitat disturbance; Pinsky, Jensen, Ricard, & Palumbi, 2011).

4.2 | Fluctuations in primary prey resources

Since 2010, evidence points to a shift in the external source that supplies *C. finmarchicus*, NWA *Ammodytes*' primary prey during the spring season, into the Gulf of Maine as more warm and saline (*Calanus*-poor) Atlantic slope water and less cold (*Calanus*-rich) Nova Scotia shelf current enters at depth through the Northeast Channel (Record et al., 2019). The shift in deep water salinity and temperature anomalies in deep-eastern Gulf of Maine waters corresponds to the recent weakening of Atlantic Meridional Overturning Circulation and northward shift of the Gulf Stream (Caesar, Rahmstorf, Robinson, Feulner, & Saba, 2018). Since 2010, observed abundances of lipid-rich stages of *C. finmarchicus* in the Maine Coastal Current and Wilkinson Basin have declined by about 30%, consistent with a lower supply in the eastern Gulf of Maine and partial amplification of the coastal current (Record et al., 2019).

In addition to changes in supply and transport, *C. finmarchicus* abundance is also driven by changes in the timing and magnitude of local primary production. One source of variability is the match or mismatch of food available to *C. finmarchicus* emerging from diapause in spring, which has already advanced in time, and is predicted to continue advancing, due to earlier spring warming (Maps et al., 2011; Pierson, Batchelder, Saumweber, Leising, & Runge, 2013). Shifts in the timing of seasonal events during recent decades are linked to changes in primary productivity and growth cycles leading to large earlier cohorts of *C. finmarchicus*, despite reduced overwintering stock (Record et al., 2019; Staudinger et al., 2019). Changes in spring production affect the supply of *C. finmarchicus* in subsequent seasons, particularly on Stellwagen Bank, Georges Bank and elsewhere in coastal waters of Southern New England (Greene & Pershing, 2007). Whether this favourable match between primary and secondary production in the western Gulf of Maine continues in the future is uncertain. Long-term habitat modelling (that does not take into account advective supply) suggests a long-term decline in regional *C. finmarchicus* abundance (Grieve, Hare, & Saba, 2017). As *C. fin*marchicus represents the primary source of lipids to pelagic consumers in the Gulf of Maine, a reduction in its availability may have consequences not only for NWA *Ammodytes* but also for the broader regional food web (Johnson et al., 2011). Substantially, lower abundances of *C. finmarchicus* observed in the eastern Gulf of Maine have already been implicated in shifting the foraging distribution of North Atlantic right whales (*Eubalaena glacialis*, Balaenidae), which also rely on *C. finmarchicus* as a principal food source (Record et al., 2019).

4.3 | Climate change impacts

NWA *Ammodytes* have been ranked as “moderately vulnerable” to climate change relative to 81 other marine fishes and invertebrates along the Northeast USA (Hare et al., 2016). Under a high emissions scenario (RCP 8.5) for the time period of 2005–2055, NWA *Ammodytes* are expected to have high climate exposure from increasing sea surface temperatures (high–very high exposure), ocean acidification (very high) and sea level rise (high), among other factors (Hare et al., 2016). Biological and ecological attributes that influence their sensitivity to climate impacts confer moderate-to-high restrictions on mobility, and moderate habitat specificity. This is due to their strong association with sandy sediments, often with patchy and ephemeral distribution, located in relatively shallow water depths of <100 m. It remains unresolved how changes in coastal hydrology could impact habitat suitability, particularly for *A. americanus*. Aspects of their spawning cycle, early life history and sensitivity to increasing temperatures also influence their moderate-to-high climate vulnerability ranking (Hare et al., 2016). However, projections of future variability and long-term changes in circulation are uncertain (Brickman et al., 2018). Similarly, acidification trends of Gulf of Maine waters and parts of the greater NWA shelf have so far been masked by the unusually strong temperature and salinity increases (i.e., lower CO_2 solubility and higher alkalinity, buffering capacity; Salisbury & Jönsson, 2018). A reversal of these decadal trends, combined with predicted increases in freshwater input, could lead to a more rapid acidification of NWA coastal shelf waters in the coming decades, as compared to current model predictions for this region (~−0.35 pH units by 2099, Bopp et al., 2013).

Emerging research on *A. dubius* indicates that this species exhibits biological characteristics that may make them particularly vulnerable to ocean warming and acidification, more so than previously thought. As a fall/winter spawner, NWA *Ammodytes* release embryos and larvae into cold and cooling water; warmer temperatures in fall may affect hatch timing and survival characteristics with uncertain consequences (Laurel, Hurst, Copeman, & Davis, 2008). Recently, Murray et al. (2019) compared the CO_2 × temperature sensitivity during the embryo stage between *A. dubius* and a nearshore forage fish, Atlantic silverside (*Menidia menidia*). While high CO_2 conditions of ~ 2,000 µatm reduced embryo survival in silversides by 6%–15% (Baumann, Cross, & Murray, 2018), in *A. dubius* these reductions were more than an order of magnitude greater (80%–350%), making this the most CO_2-sensitive fish species tested to date. Moreover, acidified conditions delayed hatching, reduced remaining endogenous energy reserves at hatch and reduced embryonic growth. Importantly, while silverside embryos showed no clear temperature dependency in their CO_2 sensitivity (Murray & Baumann, 2018), survival of *A. dubius* embryos showed a synergistic negative effect of temperature and CO_2. These assessments require further empirical support that should extend to larval and early juvenile NWA *Ammodytes* stages.

A large number of fish stocks in the NWA have shown strong responses to changing climate conditions over historical periods through shifts in distribution, range, and phenology (Nye, Link, Hare, & Overholtz, 2009; Walsh et al., 2015). These studies provide important evidence and insights on the sensitivity and adaptive capacity of species to climate impacts (Beever et al., 2016). The centre of biomass of 24 out of 36 (67%) fish stocks generally shifted either poleward and/or to greater depth in the NWA Shelf ecosystem (Nye et al., 2009). Catch data from the NMFS bottom trawl survey (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013) indicate that NWA *Ammodytes* showed high interannual variation, but no detectable shifts in latitude or depth (p-values > .05) since the late 1960s; however, low catchability and gear changes preclude definitive conclusions. Comparisons of larval and adult occurrence in the NWA ecosystem between 1977–1987 and 1999–2008 showed a significant shift in spatial distribution and seasonal phenology of larval *Ammodytes* in the region (Walsh et al., 2015). Timing of larval NWA *Ammodytes* occurrence was significantly later during winter and showed a simultaneous spatial shift in distribution northward and to deeper waters along the continental shelf; changes in the distribution of adult NWA *Ammodytes* were also evaluated but showed no trend (Walsh et al., 2015), possibly due to the high dependency of older life stages on specific bottom substrates. Projected changes in the centre of biomass for *A. dubius* suggest poleward shifts in latitude of 92.8 km ± 59.3 under a low carbon emissions (RCP 2.6) scenario and 256.4 km ± 135.8 under a high (RCP 8.5) scenario over the coming century (Morley et al., 2018). Concurrent decreases in suitable thermal habitat available to *A. dubius* were estimated at −23.0% ± 15.5 and −64.9% ± 24.3 under the low and high climate scenarios, respectively (Morley et al., 2018).

Collectively, these results suggest that larval stages of *Ammodytes* in the NWA are responding to changing environmental conditions. The lack of evidence for shifts in distribution, range and phenology of adults could be a function of stochasticity or data scarcity. Alternatively, adult NWA *Ammodytes* may lack the capacity to adapt their distribution or behaviour to track optimal conditions, or perhaps they are adapting in place (Parmesan, 2007). If NWA *Ammodytes* are not able to keep pace with changing environmental conditions at any life stage, they will be at increased risk of population declines given projections of declining suitable habitat (Morley et al., 2018).

4.4 | Fisheries

There are currently no large-scale commercial fisheries directly targeting *Ammodytes* in the NWA. However, they are caught as by-catch in some small-scale bait fisheries off the Northeast USA (no fishery exists in Canada). Regulations developed by the Mid-Atlantic and New England Fishery Management Councils restrict commercial harvest of NWA *Ammodytes* in federal waters (i.e., 3–200 nautical miles from shore). A 1,700-pound possession limit (either as aggregate or for individual species) applies to commercial harvest of NWA *Ammodytes* and over 50 additional forage species in federal waters of the Mid-Atlantic region (i.e., from New York through Cape Hatteras, NC; MAFMC, 2017). In federal waters of New England, NWA *Ammodytes* possession limit for the exempted fisheries is zero, although the New England Fishery Management Council (NEFMC) could consider allowing possession under existing policies. Small-mesh fisheries in this area are allowed, but mesh size regulations designed to minimize by-catch in the groundfish fishery are effective in limiting targeted fishing on NWA *Ammodytes*. Overall, restrictions in federal and state waters (e.g., gear restrictions) limit the potential for the development of large-scale commercial harvest of NWA *Ammodytes* at the present time. Nonetheless, fishing has historically been opportunistic in nature (Branch, Lobo, & Purcell, 2013); as such, there are concerns by the conservation and management community an *Ammodytes* fishery could still be pursued in the NWA as a replacement species (e.g., for bait) or new industry (e.g., fish oil), and if this happened there would be detrimental consequences on the broader community of predators known to rely on them as prey.

Stock assessments of species like *Ammodytes* that undergo boom and bust cycles in a Maximum Sustainable Yield context require understanding the implications of highly stochastic recruitment dynamics (Arnott, Ruxton, & Poloczanska, 2002; Deyle et al., 2013). This is difficult to estimate and subject to high uncertainty; therefore, precautionary and ecosystem-based management approaches that account for direct and indirect sources of fishing and other mortality will be important (see Section 5 of this synthesis). In addition, changes in bottom trawl fisheries could have unintended impacts on *Ammodytes*, even when they are not directly targeted. For example, flatfish and shrimp fisheries in Europe were hypothesized to have a negative effect on *A. marinus*, *A. tobianus* and *H. lanceolatus* presence due to disturbance and incidental mortality caused by fishing gear to bottom habitats (Tien et al., 2017). Strong associations with certain bottom substrates increase the risk of *Ammodytes* to localized depletion, particularly when capture rates remain high during low abundance years in areas where fish exhibit dense aggregations (Csirke, 1988). Bottom fishing gear can also disturb the demersal eggs of *Ammodytes* during developmental periods and older individuals during winter dormancy when they are buried in the sediment.

Recently, the Mid-Atlantic Fishery Management Council has taken steps to move towards an ecosystem-based approach to fisheries management. For example, they recognized forage species as key components of the regional ecosystem and increased protections by implementing a possession limit to prevent the development of large-scale commercial fisheries for over 50 previously unmanaged forage species (MAFMC, 2017). New large-scale fisheries or the expansion of existing directed fisheries for these species are now effectively prohibited in federal waters off of NY through Cape Hatteras, NC. The New England Fishery Management Council has also begun to take steps towards more holistic approaches, although actions to date have been limited to managed forage fishes such as Atlantic herring. In 2018, the NEFMC approved Amendment 8 (https://www.nefmc.org/library/amendment-8-2), a control rule that caps fishing mortality on Atlantic herring at 80% of sustainable levels when biomass is relatively healthy, and much lower levels if biomass declines. This control rule is intended to better address uncertainty in interannual variation in biomass estimates of the species. The rule explicitly recognizes the role of Atlantic herring as forage within the ecosystem. Amendment 8 also proposes to prohibit vessels fishing with midwater trawl gear in nearshore waters (within 12 nautical miles) from Maine through the Rhode Island/Connecticut border. In addition, the New England Council is developing a draft Fishery Ecosystem Plan for Georges Bank as an example to consider adopting such an approach (Applegate et al., 2019). Early drafts and modelling consider and include the effects of forage on prey abundance and vice versa. The Forage Fish Conservation Act (introduced to the U.S. House as HR 2236 in April 2019) is emerging legislation that builds upon the Magnuson-Stevens

Fishery Conservation and Management Act to strengthen key protections and promote responsible management of forage fishes nationally. All of these efforts could benefit regional populations of NWA *Ammodytes*, though indirect effects (e.g., to intraguild feedback loops with Atlantic herring) can be complicated and have unintended outcomes that require regular data collection to determine outcomes and effectiveness (Fogarty et al., 1991; Sherman et al., 1981).

4.5 | Energy development and resource extraction

During recent decades, energy development and exploration in the U.S. Atlantic has increased, at least in part as a result of U.S. policy. In an effort to identify shared risks and opportunities across seascapes, regional ocean partnerships such as the Northeast Regional Ocean Council (established in 2005) and Mid-Atlantic Regional Council on the Ocean (established in 2009, now the Mid-Atlantic Committee on the Ocean) formed to provide comprehensive, multi-use planning frameworks. Construction, dredging and resource mining (e.g., sand) all have the potential to directly impact *Ammodytes* populations. Offshore sand mining could potentially expand due to the need for substrate to replenish and elevate beaches and other shoreline habitats experiencing increased erosion and flooding from sea level rise and coastal storms (Desprez, 2000; Slott, Murray, Ashton, & Crowley, 2006). Since *Ammodytes* have demersal eggs, and older individuals bury within the substrate, disturbances to bottom habitats are likely to affect them disproportionately, relative to other forage fishes, and result in decreased production. The usability and amount of upper shoal habitat, preferred by *Ammodytes* (Rutecki et al., 2014), can be impacted by offshore dredging depending on varying scenarios (Dibajnia & Nairn, 2011). Offsetting sand mining or dredging activities during times of high *Ammodytes* abundance and spawning periods can lessen impacts (e.g., winter in the Mid-Atlantic Bight; Slacum et al., 2010).

Offshore infrastructure development and construction projects can transform the coarse-grain sediment habitats that *Ammodytes* rely on into artificial reef habitat that supports hard-bottom associated communities (Lindeboom et al., 2011). This would exclude *Ammodytes* from previously occupied areas. Indirect effects of these activities may also impact *Ammodytes*; for example, it has been hypothesized that artificial reef effects lead to an increase in predators that exert additional top-down pressure on *Ammodytes* (e.g., by Atlantic cod; Lindeboom et al., 2011). The cumulative effects from multiple closely located development sites would pose additional risk (Leonhard, Stenberg, & Støttrup, 2011). The development has the potential to act at different time scales by altering *Ammodytes* habitats immediately through direct disturbance, and then incurring lagged ecological effects as the community stabilizes (Gray, 2006; Petersen & Malm, 2006).

Alternatively, some development activities could have neutral or positive effects. In the North Sea, the presence of *A. marinus and A. tobianus* was assessed before and after the construction of wind turbines. Short-term effects of the facilities were either not observed (Lindeboom et al., 2011) or showed increases in density at wind development sites after construction (Degraer, Brabant, Rumes, & Vigin, 2016; Leonhard et al., 2011; Stenberg et al., 2015; van Deurs et al., 2012; Vandendriessche, Hostens, Courtens, & Stienen, 2011). Positive short-term effects were attributed to increased or neutral effects on sediment quality, increases in juvenile abundance, associations of midwater feeding schools with structure and/or reductions in predators during construction (Leonhard et al., 2011; van Deurs et al., 2012). Reductions in fishing activities during construction and operation of wind farms also have the potential to benefit *Ammodytes*, though this could lead to localized increases in competitors and predators that experience concomitant reductions in fishing mortality. Alternatively, these patterns could be due to, or in synergy with, the aggregation effects of the offshore structures through flow or shade effects. No long-term effects on *Ammodytes* were seen in such areas, despite an increase in species diversity due to artificial reef effects (Degraer et al., 2016; Leonhard et al., 2011; Stenberg et al., 2015; van Deurs et al., 2012).

Development, accidents (e.g., oil spills) or run-off from facilities can have other unintended consequences that need to be carefully considered if they are undertaken in proximity to key NWA *Ammodytes* habitats (see Fisheries & Oceans Canada, 2009). Under normal conditions, toxicity burdens of heavy metals (primarily mercury) in NWA *Ammodytes* show mid-range Hg levels compared to other forage fishes such as bay anchovy, mackerel, butterfish and herring in coastal Northeast U.S. waters (Staudinger, 2011). NWA *Ammodytes* live within or near sandy bottom habitats, which generally do not retain contaminants as much as silty, muddy habitats. This aspect of their life history plus their relatively low position in the food chain likely limits exposure. However, following oil spills and other chemical disasters, *Ammodytes* have accumulated toxic chemicals from fuel oils and dispersants (Calbet, Saiz, & Barata, 2007; Hansen, Altin, Olsen, & Nordtug, 2012). Such exposure can have immediate lethal or long-term chronic sublethal effects on *Ammodytes* and their predators (Hjermann et al., 2007). Negative effects of oil spills on *Ammodytes* include physiological haemorrhaging when *Ammodytes* burrow into oil-contaminated sands and reduced time buried in oil-contaminated sand, which increases exposure to predators (*A. hexapterus*, Pearson, Woodruff, Sugarman, & Olla, 1984; Pinto, Pearson, & Anderson, 1984), as well as mass die-offs in response to oil and/or the subsequent detergents that are used to contain or clean up spills (e.g., Torrey Canyon clean up in the United Kingdom; Reay, 1970; Simpson, 1968). Additional toxic burdens (e.g., paralytic shellfish poisoning associated with red tides) have led to mass mortalities of higher trophic level predators of conservation and management concern (Jessup et al., 2009).

The interactive impacts of a changing climate and other anthropogenic stressors on *Ammodytes* are largely unknown, but as a key prey species, these cumulative effects warrant careful consideration.

5 | ECOSYSTEM SERVICES AND ECOSYSTEM-BASED MANAGEMENT

In marine systems, increasing attention has been focused on characterizing the direct and indirect ecosystem services provided by forage fishes (Alder et al., 2008; Pikitch et al., 2004). As demonstrated by this synthesis, NWA *Ammodytes* provide extensive support to higher trophic levels through energetic transfer. Many of the 72 predators that rely on NWA *Ammodytes* directly contribute to regional economies and food resources through commercial and recreational fisheries, as well as cultural and other recreational benefits such as tourism and viewing activities (Nelson et al., 2013). The bottom-up contributions of NWA *Ammodytes* to the landings of commercially exploited fish predators in the NWA are likely substantial. Their indirect value may outweigh any commodity services arising from direct harvest and sale of NWA *Ammodytes* if a large-scale commercial fishery was ever pursued in the region. A formal valuation analysis of existing supporting and projected commodity services (e.g., based on harvest targets), derived from NWA *Ammodytes*, would be an important preliminary step to assess potential trade-offs, stakeholder conflicts and competing demands within the NWA region (Hunsicker et al., 2010; Koehn et al., 2017).

Ecosystem services are crucial for developing ecosystem-based management (EBM) and ecosystem-based fisheries management (EBFM) plans and are increasingly being integrated into sustainability efforts in the world's oceans (Altman, Boumans, Roman, Gopal, & Kaufman, 2014; Francis, Hixon, Clarke, Murawski, & Ralston, 2007; Patrick & Link, 2015; Ruckelshaus, Klinger, Knowlton, & DeMaster, 2008). EBFM approaches to resource management incorporate interactions among species (e.g., predator-prey, competitive) and with their environment (e.g., climate change), account for direct and indirect effects of human activities and view humans as an integral component of ecosystems (Boumans, Roman, Altman, & Kaufman, 2015; Patrick & Link, 2015; Van Dyne, 1969). Important steps have been taken by the United States and Canada to move towards implementation of EBFM in the NWA (Link et al., 2011) through policy (Mid-Atlantic Management Council, 2019; National Ocean Council, 2013), regional planning initiatives (Northeast Regional Planning Body, 2016) and recent fishery management council actions (MAFMC, 2017). These actions recognize the need for integrative approaches to protect the long-term function of ecosystem pathways and balance multiple stakeholder objectives.

Minimum realistic models (MRMs) that account for natural predation and fishing mortality rates provide an example of how ecosystem considerations have been approached in the NWA region (Gamble & Link, 2009; Link et al., 2011). This type of model has been used to answer research questions pertaining to some forage fishes including Atlantic herring, Atlantic mackerel and butterfish; however, they have yet to be directly linked to species stock assessments or management actions. To date, the role of NWA *Ammodytes* as prey has not been explicitly accounted for in stock assessments, despite their apparent importance in years of low Atlantic herring and mackerel abundance (Gamble & Link, 2009; Link & Sosebee, 2008; Moustahfid, Link, Overholtz, & Tyrrell, 2009; Overholtz, Jacobson, & Link, 2008; Overholtz & Link, 2006; Tyrrell, Link, & Moustahfid, 2011). Further analyses are needed to determine NWA *Ammodytes* contributions to the energetic demands, condition, marketability and population dynamics of commercially important predators as well as in relation to other forage fishes and regional species of conservation concern (Golet, Cooper, Campbell, & Lutcavage, 2007; Logan et al., 2015). Because Atlantic cod, summer flounder, winter skate, common terns and grey seals rely heavily on NWA *Ammodytes* as prey on a seasonal basis and have robust diet and productivity/fecundity data series, these species are ideal candidates to model energetic links and flow, non-linear functional responses and foraging thresholds that different predators may exhibit in response to changes in prey availability.

Preliminary efforts to incorporate NWA *Ammodytes* as prey into ecosystem models were conducted using the Massachusetts Multiscale Integrated Model of Earth Systems (MIMES). This predicted a decrease in the abundance of humpback whales under forecasted simulations of fishing pressure on NWA *Ammodytes* (Boumans et al., 2015). Efforts are underway to incorporate environmental variables and the effects of climate change into projections of food web dynamics over the coming century. However, NWA *Ammodytes* remain underrepresented in many regional EBM plans, and their explicit consideration would improve overall understanding of ecosystem dynamics in the NWA.

Scaling reference points based on confidence in scientific knowledge and assessments is recommended (Pikitch et al., 2012) and currently used to set regional catch limits. Since NWA *Ammodytes* are unmanaged forage fishes, information on their biology and population dynamics is woefully inadequate compared to managed species (e.g., Atlantic herring). Lastly, the Magnuson-Stevens Fishery Conservation and Management Act identifies the maintenance of forage fishes for all components of the ecosystem as an important consideration in setting optimal yields for harvested species. In support of these conservation and management goals, we conclude this synthesis by outlining remaining gaps in knowledge and high-priority basic and applied research needs for NWA *Ammodytes* populations in the NWA region.

6 | A PATH FORWARD: RESEARCH NEEDS

Compared to *Ammodytes* species in the NWA, knowledge of the life history, population dynamics and trophic ecology of European congeners (*A. marinus* and *A. tobianus*) is significantly greater. This is in part because a targeted commercial fishery exists in Northeast Atlantic waters where stock assessment data are collected regularly (Ellis, Milligan, Readdy, Taylor, & Brown, 2012). A comparison of what is known across the two regions helps identify critical knowledge gaps and research needs in the NWA.

The industrial fishery for *A. marinus* began in the 1950s in the North Sea and expanded rapidly in the following decades, growing to become the region's largest single-species fishery at around 0.8 million metric tons annually. More recently, yields exhibited strong declines, with annual catch reduced to around 313,000 metric tons between 2003–2010 and localized depletion occurring in multiple areas (ICES, 2010). Fishing on *A. marinus* had broad ecosystem effects throughout the North Sea (Green, 2017; Wanless, Harris, Newell, Speakman, & Daunt, 2018). Statistical and ecological modelling studies have investigated the trophic implications of long-term changes in *Ammodytes* population size structure, abundance and nutrition, revealing direct links to seabird breeding success at multiple sites in the North Sea (Frederiksen, Wanless, Harris, Rothery, & Wilson, 2004, Frederiksen, Elston, Edwards, Mann, & Wanless,2011; Wanless, Wright, Harris, & Elston, 2004; Wanless et al., 2018).

Similar to the NWA, the North Sea is experiencing rapid warming due to climate change (Rutterford et al., 2015), which has been linked to several detrimental effects on *Ammodytes* populations. Warming has been associated with increases in the metabolic rate of YOY *Ammodytes* and subsequent reductions in growth and energy reserves, which compromise their ability to attain adequate body sizes needed to survive overwintering (van Deurs, Hartvig, & Steffensen, 2011). Increasing temperatures have also been shown to reduce the reproductive potential of adults (Wright, Orpwood, & Scott, 2017). In addition, climate change is altering the availability of key *Ammodytes* prey in the North Sea where *C. finmarchicus* is being replaced by a warmer water conspecific, *C. helgolandicus* (Calanidae). *Calanus helgolandicus* differs in phenology, size, and nutrition (Frederiksen et al. 2011, van Deurs et al., 2009; van Deurs et al., 2015), which has implications for energy flow to higher-level predators (von Biela et al., 2019). Examples from the Northeast Atlantic presented here and throughout this synthesis show how the competing demands from the commercial fishery relative to fish, marine mammal and seabird predators can be managed (Furness, 2002) when *Ammodytes* are explicitly considered. Further, regional fisheries management in the North Sea provides guidance on the tools and data needed to advance research and conservation in the NWA.

An immediate and high-priority need in the NWA is to resolve long-term patterns and drivers of *Ammodytes* abundance and distribution. Ichthyoplankton surveys (e.g., NEFSC Ecosystem Monitoring (EcoMon)) have effectively tracked the distribution and abundance of early life stages of NWA *Ammodytes*, as well as co-occurring plankton and oceanographic conditions (Sherman et al., 1981; Walsh et al., 2015). Continued support for this programme is imperative to prevent data gaps in one of the few long-term time series of NWA *Ammodytes*. However, catchability remains a limiting factor in most bottom trawl surveys as NWA *Ammodytes*, particularly post-larval YOY and age-1 fish, are not reliably assessed. The observed trend of declining NWA *Ammodytes* body size in predator diets is an important finding from our analysis of the NEFSC dataset. Preliminary examination of *Ammodytes* caught in the NEFSC trawl survey provided complementary evidence of decreases in maximum body size over similar time periods, but additional analysis is needed before definitive conclusions can be made about how size-related changes may affect habitat use and vulnerability to predation.

Catchability issues have also precluded reliable estimates of some aspects of the life history of NWA *Ammodytes*. An updated and thorough assessment of the reproductive biology (e.g., gonadal development schedules), timing, duration and locations of spawning are needed throughout their NWA range. Population connectivity and growth relative to adjacent regions (e.g., Canadian and Arctic regions) remain largely unresolved and crucial to identify and protect source and sink populations. Increased seasonal coverage of *Ammodytes* populations could yield new insights into factors affecting survival and recruitment during critical life phases. Studies during summer are important because this is the time period when YOY *Ammodytes* have just transitioned to relying on sand habitats and overlap is maximized spatially with many demersal and pelagic predators. In addition, a focus on NWA *Ammodytes* winter ecology is needed to resolve spawning duration times, larval distribution and recruitment, winter dormancy behaviour and risk to predation.

The trophic consequences of high spatiotemporal variability in NWA *Ammodytes* populations and relative to other forage fishes are likely to affect predators in different ways depending on a variety of constraints, including predator mobility, overlap, behaviour and physiological factors (e.g., dietary needs, energy transfer rates). Some predators may exhibit strong localized correlations with NWA *Ammodytes* distributions; however, because these predators forage over broad spatial areas and can switch prey based on relative availability, long-term population dynamics may show weak associations (Smith, Ligenza, Almeida, & Link, 2007). In contrast, specialist predators (e.g., nesting seabirds, particularly those with high foraging site-fidelity, and habitat-associated piscivorous fish) may be more dependent and at greater risk to shifts in NWA *Ammodytes* abundance and distribution, particularly as climate change and other broad-scale processes alter their availability and energetic value across interannual scales (von Biela et al., 2019; Erikstad, Reiertsen, Barrett, Vikebø, & Sandvik, 2013; Óskarsson, 2008). Studies are needed to fully comprehend *Ammodytes*' trophic role in the NWA, particularly to increase our understanding of (a) when predators switch to alternative prey, (b) what thresholds lead to detrimental spatiotemporal mismatches and (c) how changes in energetic pathways affect the fitness/condition and breeding/spawning success of higher-level predators. As has been seen in the Northeast Atlantic, such information could guide management decisions of harvest amounts during low and high NWA *Ammodytes* abundance years (Furness, 2002) as well as the potential impacts from other human activities that could disturb *Ammodytes* habitat (e.g., sand mining, dredging).

Because inshore habitats are not well sampled by the NEFSC bottom trawl survey, there is a limited understanding of the ecological role of NWA *Ammodytes* in these systems. A few studies suggest that certain species specialize on NWA *Ammodytes* in these areas (e.g., Atlantic sturgeon, Novak et al., 2017) but were limited in geographical and temporal scope. Additional population and food habits data exist from inshore surveys conducted by state fisheries agencies and research institutions. To determine whether discrete sampling efforts are representative of broader regional importance, the analyses undertaken here could be augmented by synthesizing existing datasets from long-term sampling programmes that target regional bays and estuary habitats (e.g., Northeast Area Monitoring and Assessment and Chesapeake Bay Multispecies Monitoring and Assessment Programs (NEAMAP and CheMMAP)).

The NWA region is of critical importance to the life cycles of many long-distance seasonal migrants that come to feed on *Ammodytes* and other forage resources during the summer and fall months (Diamond, 2012; Staudinger et al., 2019). Data from seabird provisioning studies likely reflect nearshore availability of NWA *Ammodytes* (Goyert, 2014), but are skewed towards chick diets during the summer rearing season. Despite their apparent importance in some areas (e.g., to roseate terns in MA and NY), direct links between NWA *Ammodytes* availability and chick productivity have yet to be established. Largely absent from the literature are diet data on adults during the breeding and non-breeding seasons, both within and outside the NWA region. Reliance on NWA *Ammodytes* during the critical post-migration (fall) and pre-breeding (spring) periods are of particular importance to migrating seabirds, given their high nutritional demands that support survival, recruitment and productivity.

Our synthesis found relatively few accounts of large (e.g., tunas and marine mammals) and small (e.g., clupeids, Atlantic mackerel) pelagic predators; however, the few studies that were identified suggest NWA *Ammodytes* are important to these groups over seasonal and decadal scales. A better understanding is needed of the relationship between NWA *Ammodytes* and Atlantic herring, particularly how Atlantic herring declines, recovery and sustainability may affect the interplay between these two species and other regional forage fishes. Large data gaps are also evident for marine mammals throughout most NWA subregions and historical periods. Diet data are largely qualitative, opportunistically collected (often from a few stranded individuals), or derived from indirect observations of movements. Based on studies from other regions, some marine mammals rely heavily and likely specialize on *Ammodytes* (e.g., humpback and minke whales); nonetheless, there is currently insufficient evidence in the published literature to support strong conclusions for NWA populations. Emerging genetic and ecological tools such as eDNA, barcoding, stable isotope and fatty acid analyses have high potential to increase knowledge on data-poor predators within NWA food webs, especially those for which regular direct sampling has been prohibitive due to accessibility issues (e.g., at sea adult seabirds; rorqual whales, endangered and listed species).

The sensitivity and adaptive capacity of NWA *Ammodytes* to climate change remains an area of high uncertainty due to a lack of regional and species-specific studies. It is currently unknown if *A. dubius* and *A. americanus* are exposed and respond to environmental stressors equally. Climate change impacts on *Ammodytes* have been reasonably well investigated in the Pacific Northwest (von Biela et al., 2019; Robards, Anthony, Rose, & Piatt, 1999; Robards et al., 2002) and the North Sea (Arnott & Ruxton, 2002; von Biela et al., 2019; Burthe et al., 2012; Burthe, Wanless, Newell, Butler, & Daunt, 2014; Wanless et al., 2004, 2018). In contrast, very few studies have directly evaluated climate impacts on *Ammodytes* in the NWA (Danielsen et al., 2016; Dixon, Dempson, Sheehan, Renkawitz, & Power, 2017). Preliminary evidence suggests *A. dubius* may be a critical indicator of climate change and system thresholds. Early-stage development appears to be highly sensitive to ocean acidification and temperature (Murray et al., 2019) and is likely to affect other aspects of life history that influence vulnerability (Hare et al., 2016).

There is strong concern about climate-induced shifts in *C. finmarchicus* distribution in northern areas of the NWA (Record et al., 2019). *Ammodytes* populations that are heavily reliant on *Calanus* sp. are expected to be relatively more vulnerable to changes in availability and nutrition, particularly during spring (Friedland et al., 2015; Morse, Friedland, Tommasi, Stock, & Nye, 2017; Thomas et al., 2017), and may be indicators of shifting ecosystem dynamics and energy transmission processes, as has been suggested for the Northeast Pacific congener *A. personatus* (von Biela et al., 2019). Climate-induced changes in the distribution and availability of *C. finmarchicus* could also intensify competitive interactions between NWA *Ammodytes* and planktivorous whales such as the critically endangered North Atlantic right whale (Payne et al., 1990). Although orders of magnitude different in size, the presence of NWA *Ammodytes* as well as other forage fishes (e.g., herring, mackerel) inhibits their feeding behaviour.

Current management measures, including the possession limit implemented in the Mid-Atlantic region in 2017, and small-mesh and exempted fishery regulations in New England, have likely kept regional fishing mortality rates on NWA *Ammodytes* low; however, their designation as an unmanaged forage species and absence of a species stock assessment has, until recently, precluded the acquisition of basic biological data, assessments of mortality rates and accurate quantitative population assessments. Based on what is known from systems outside the NWA (e.g., North Sea), *Ammodytes* may be highly vulnerable to overfishing. The sandy substrates preferred by NWA *Ammodytes* are relatively resilient to physical disturbance (Auster & Langton, 1999) and may be repopulated after acute fishing or construction events. However, timelines to recovery and further consequences are not well understood (Green, 2017; Wanless et al., 2004, 2018). Catches could initially remain high, even after repeated fishing attempts in the same area, while inflicting long-term impacts, such as increased dispersal and exposure to predation as fish relocate in search of undisturbed habitat. In addition, if fishing, dredging, sand mining or offshore development activities occur during spawning periods, these disturbances could disrupt early life history through damage to eggs laid in/on the substrate.

7 | CONCLUSIONS

This synthesis provides a comprehensive summary of the current state of knowledge of *Ammodytes* populations in the NWA. A diverse set of at least 72 species of predators were found to rely on NWA *Ammodytes* as prey. Collectively, these results show that changes in the availability and distribution of NWA *Ammodytes* could affect numerous regional species that are highly valued as commercial fisheries (e.g., bluefin tuna, Atlantic cod), as endangered species (roseate terns, Atlantic salmon, Atlantic sturgeon), and iconic wildlife that support cultural and recreational activities throughout the region (e.g., humpback whales, Atlantic puffins). The amassed data are readily available to calculate key metrics, populate initial models and facilitate broad-scale assessments of NWA *Ammodytes*, their dependent predators, and linked human systems (Smith et al., 2011). Ecosystem (e.g., Ecopath with Ecosim, Atlantis) and empirical dynamic models are potential tools to explore the connections and consequences of previously unresolved community changes (e.g., top-down versus bottom-up controls; intraguild competitive relationships) and disturbance scenarios (e.g., climate and fishing levels) on NWA *Ammodytes* populations (Glaser et al., 2014; Klein, Glaser, Jordaan, Kaufman, & Rosenberg, 2016; Plagányi & Essington, 2014). However, reliable estimates from any new research initiatives are dependent on filling the remaining data gaps outlined here. Several predator groups require expanded diet data to fully comprehend their dependence on NWA *Ammodytes*, including all marine mammals, adult seabirds, estuarine and inshore fish predators, and small pelagic/intraguild competitors. Updated evaluations are also needed to understand ecosystem changes occurring during the most recent two decades (2000-present) that capture potentially unprecedented changes in trophic interactions due to rapid warming in the region (Saba et al., 2016; Thomas et al., 2017). NWA *Ammodytes* have been consistently abundant and were consumed by the greatest diversity of fish predators in the Southern New England region, making this an ideal focal area for targeted sampling and analyses of population size structure and related changes in predatory demand and energy transfer.

Paramount to resolving almost all of the remaining questions outlined in this study is the need for information on the underlying environmental and ecological factors driving NWA *Ammodytes*' spatial and temporal variability over multiple scales. Retrospective analyses of the conditions surrounding periods of peak abundance (e.g., the early 1980s, and around 2010) and at known sites of locally high abundance (e.g., Stellwagen Bank) could provide important insights. In addition, new data collected from alternative and novel approaches such as hydroacoustic surveys (Hazen et al., 2009), geospatial analytical techniques (Friedlaender et al., 2009), composite indices and predators as biological samplers (Piatt et al., 2018; Richardson et al., 2014) could address vertical and horizontal availability over diel, seasonal and interannual scales. Finally, recent (MAFMC, 2017) and pending (Applegate et al., 2019; HR 2236, 2019) legislation requiring information on the ecosystem role of forage fish may provide newfound support for achieving the outstanding research, conservation and management goals for *Ammodytes* and dependent predators in the NWA region.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available in National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC) Food Web Dynamics Program database at https://inport.nmfs.noaa.gov/inport/hierarchy/1368.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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