



Cyclical trends in the biomass and mean body weight indices of two Northwest Atlantic squid species and their synchronies with Gulf Stream latitudinal positions

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Abstract

Autoregressive spectral analysis revealed underlying cyclical trends in the highly variable biomass and mean body weight indices of two Northwest Atlantic squid species with opposing life histories. *Doryteuthis pealeii* attaches its egg masses to the seabed in shallow waters on the Northeast USA shelf. The broader-ranging *Illex illecebrosus* uses the Gulf Stream (GS) to transport its pelagic egg masses and paralarvae from the Southern (USA shelf) to the Middle (Scotian Shelf) and Northern (Grand Banks) Fishery Regions. We compared significant spectral peaks, or cycles, between the 1993–2016 survey indices, GS latitudinal positions (at 74°, 70°, 65°, 60°, 55° and 50°W) and winter North Atlantic Oscillation (NAO) indices to reveal any synchronicities. Positive NAO anomalies associated with northward GS position shifts were predominant. NAO indices exhibited 2–3-year, 4–5-year, and near-decadal cycles. GS position periodicities included 2–3-year, 3–4-year, and both timescales for west of 65°W (Western Segment), east of 60°W (Eastern), and from 65° to 60°W, respectively. *I. illecebrosus* indices exhibited stock-wide 3–4-year cycles and 2–3-year cycles for the Middle and Southern Fishery Regions that were synchronous with GS latitudinal positions for the Eastern and Western GS Segments, respectively. *D. pealeii* biomass cycles varied seasonally. Spring 4–5-year cycles were synchronous with the NAO, and fall near-decadal cycles were synchronous with the NAO and all GS locations analyzed. Our findings of inter-annual biomass and body weight cycles from 2 to 3 years to near-decadal are remarkable given the sub-annual lifespans of both species, but confirm the tight coupling between recruitment, body size, and cyclical environmental forcing factors.

Keywords *Illex illecebrosus* · Squid biomass and body weight · Autoregressive spectral analysis · *Doryteuthis pealeii* · Gulf Stream · NAO

Introduction

Most squid species are semelparous and have lifespans of less than one year (Boyle and Rodhouse 2005). Due to these characteristics, combined with the strong influence of environmental factors on their recruitment, maturation and

growth rates (Pierce et al. 2008), high inter-annual variability in biomass, abundance, and mean body size is common amongst squid stocks. This high variability makes trends in stock size and productivity difficult to identify, thereby hindering stock assessments needed for managing squid resources (Arkhipkin et al. 2020). Such is the case for two fished Northwest Atlantic (NWA) squid species, *Illex illecebrosus* (Northern shortfin squid) and *Doryteuthis (Amerigo) pealeii* (longfin inshore squid), whose relative abundance and growth rates are affected by environmental conditions (Brodziak and Hendrickson 1999; Hatfield et al. 2001; Hatfield and Cadrin 2002; Hendrickson 2004; Hendrickson and Holmes 2004; Jacobson 2005). Therefore, the application of a method that can be used to characterize biomass and mean body size trends for these species will help identify which environmental variables have similar trends and might be useful predictors of stock size.

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Both squid species have sub-annual lifespans and spawn year-round with two peaks that result in summer-hatched and winter-hatched intra-annual cohorts (Brodziak and Macy 1996; Dawe and Beck 1997; Macy and Brodziak 2001; Hendrickson 2004). In addition to supporting fisheries, both species are voracious predators on commercial fish species and important prey for top-level predators as well as commercial fish species (Hendrickson and Holmes 2004; Jacobson 2005). However, the two species have opposing life history strategies and also differ in geographic range, annual migration pattern, habitat preferences, and spatial distribution (Hendrickson and Holmes 2004; Jacobson 2005).

Illex illecebrosus

I. illecebrosus is a nerito-oceanic ommastrephid that inhabits a broad latitudinal range in the NWA, from the east coast of Florida to southern Greenland and Iceland (about 29°N–66°N; Roper et al. (2010)). However, abundance is

highest on the continental shelf between Newfoundland, Canada (CA) and Cape Hatteras, North Carolina (NC) in the United States of America (US) where the fisheries occur (Fig. 1). Throughout this range, the species is considered to comprise a single stock (Hendrickson 2004; Martinez et al. 2005; Arkhipkin et al. 2015).

Onset and duration of the fisheries are limited by the species' seasonal on-shelf availability within three Fishery Regions located in catch reporting Subareas (SA) 3, 4 and 5+6 of the Northwest Atlantic Fisheries Organization (NAFO). For ease of recollection, we refer to these three Subareas as the Northern, Middle and Southern Fishery Regions, respectively (Fig. 1). During early spring, individuals migrate northward along the upper slope from Cape Hatteras and farther south, then move onto the continental shelf between Newfoundland and Cape Hatteras (O'Dor and Dawe 1998; Hendrickson 2004), where they are fished; generally during June–October in the Southern and Middle Fishery Regions and July–November in inshore Newfoundland

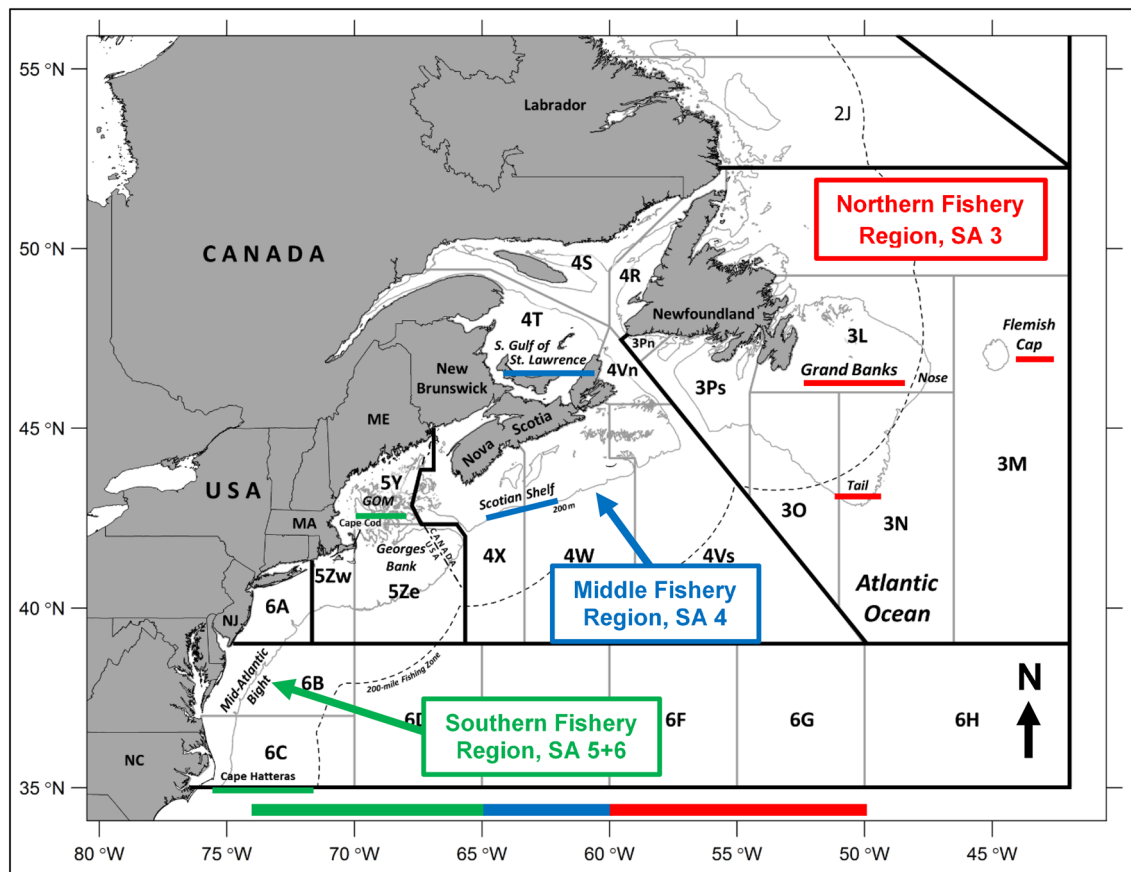


Fig. 1 Northwest Atlantic Fisheries Organization (NAFO) catch reporting Subareas (SA) 3, 4 and 5+6 (thick black lines) are referred to as the Northern (N), Middle (M), and Southern (S) Fishery Regions, respectively. Groupings of the six longitudinal locations used for the Gulf Stream latitudinal position time series are shaded green, blue and red in the horizontal bar and represent the Western,

Middle and Eastern Gulf Stream Segments, respectively. Bottom trawl survey areas (underlined), defined by NAFO Division (thin grey lines), show locations of the surveys used to derive squid indices. Spring and fall surveys conducted on the USA shelf (Subareas 5+6) extend from the Gulf of Maine (GOM) to Cape Hatteras, North Carolina (NC)

waters in the Northern Fishery Region (Arkhipkin et al. 2015).

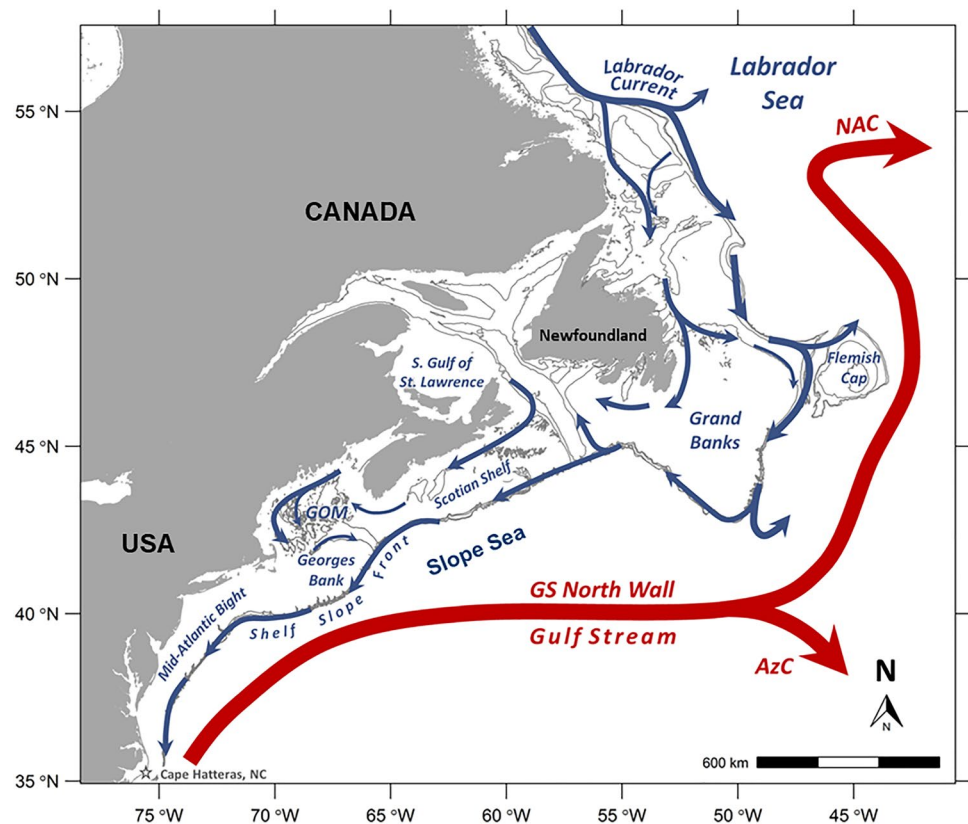
Of the two intra-annual cohorts, only the spawning area of the winter cohort has been confirmed by the capture of mated and spawning females. The winter cohort spawns during summer near the US shelf-break, in the Mid-Atlantic Bight where the US fishery occurs (Hendrickson 2004; Hendrickson and Hart 2006). During late fall, individuals from all three Fishery Regions migrate off the shelf and southward to spawn during winter at an unknown location in warmer southern waters on the US shelf (O’Dor and Dawe 1998). For individuals from the Northern Fishery Region, these long-distance spawning migrations can cover distances of up to 2000 km (O’Dor and Dawe 1998).

The age range of juveniles collected on the US shelf (69 to 108 days) indicates that most of the species’ 6–7-month lifespan (Hendrickson 2004) is spent on the shelf. However, individuals experience a broad range of oceanographic conditions during their short lifespans because this neritic phase is preceded by a brief oceanic phase involving the early life stages (O’Dor and Dawe 1998; Perez and O’Dor 1998).

During winter, paralarvae surveys conducted in the shoreward edge of the Gulf Stream (GS) and in the Slope Sea (Fig. 2), within an area located between the Northeast US and southern Nova Scotia, *Illex* (cf. *illecebrosus*) paralarvae (assumed to be *I. illecebrosus* because they were sampled

north of the ranges of two congeners (Roper et al. (2010)) were most abundant near the GS North Wall (GSNW) and the GS-Slope Water “convergence zone” (Hatanaka et al. 1985). Based on these findings and those from other winter paralarvae and juvenile surveys (e.g. Dawe and Beck 1985), the GS is believed to be the primary mechanism for north-eastward transport of paralarvae, and presumably the species’ pelagic egg masses (O’Dor and Balch 1985), from the winter spawning grounds on the southern US shelf (O’Dor and Dawe 1998). However, similar GS paralarval transport from the summer spawning grounds on the Mid-Atlantic Bight shelf has not been documented. Another GS-related mechanism for the transport of *I. illecebrosus* paralarvae can occur within the periphery of warm-core rings (WCRs; (Dawe and Beck 1985)). These anticyclonic eddies develop from GS meanders and spend most of their lifespan in the Slope Sea (Chaudhuri et al. 2009). However, WCRs can inhibit northeastward dispersion of *I. illecebrosus* paralarvae due to their southwestward trajectories (Bakun and Csirke 1998), and when located close to the shelf-break, they can transport entrained Shelf Water and any associated paralarvae off the shelf (Flierl and Wroblewski 1985; Joyce et al. 1992; Dawe et al. 2000). During spring, the growth rates of young juveniles increase in a shoreward direction as they migrate from the GS Front, where warm water temperatures result in high metabolic costs, to the more productive

Fig. 2 Schematic of general circulation routes of major currents in the Northwest Atlantic Ocean in relation to the 200, 400, 900 and 1000-m isobaths. NAC, AzC, GS and GOM represent the North Atlantic Current, Azores Current, Gulf Stream and Gulf of Maine, respectively



Shelf-Slope Front that also offers increased conversion efficiency at cooler temperatures (Perez and O'Dor 1998).

Doryteuthis pealeii

In contrast to *I. illecebrosus*, *D. pealeii* is a neritic loliginid whose entire life cycle occurs on the continental shelf. *D. pealeii* also prefers warmer water temperatures than *I. illecebrosus* (Brodziak and Hendrickson 1999) and is distributed from southern Nova Scotia, Canada to the Gulf of Venezuela (Cohen 1976), with rare occurrences off southern Newfoundland (Dawe et al. 2007). Abundance is highest on the US shelf between Georges Bank and Cape Hatteras, NC (Fig. 1) where bottom trawl fisheries occur throughout the year. The *D. pealeii* population that is distributed in shelf waters between the Gulf of Maine and Cape Hatteras is managed as a single stock based on the results of genetics studies and age composition data which indicate that the winter cohort produces the summer cohort and vice versa (Arkhipkin et al. 2015). The fisheries follow the species' annual migration pattern; near the shelf edge generally during November through April and inshore along the coast during May–October; time periods which also define the hatching periods of the winter and summer cohorts, respectively (Brodziak and Macy 1996; Macy and Brodziak 2001).

During late spring, individuals migrate inshore to spawn in shallow water from southern Nova Scotia and the Bay of Fundy to Cape Hatteras, NC throughout the summer (Jacobson 2005). Mating behaviour is elaborate and spawning individuals are highly aggregated (Hanlon and Messenger 1996) when the small-mesh bottom trawl fishery occurs on the summer spawning grounds. In contrast to the pelagic egg masses of *I. illecebrosus*, *D. pealeii* attaches its egg masses to the seabed, vegetation and fixed objects, presumably in locations where water temperatures and food resources are optimal for embryonic and paralarval survival and growth. These shallow spawning areas also serve as juvenile nursery areas during summer and early fall. An offshore migration to the shelf edge and upper slope occurs during late fall and is followed by winter spawning at an unknown location; probably near Cape Hatteras where winter bottom temperatures are warm enough for normal embryonic development (Jacobson 2005).

Study area oceanographic conditions

Oceanographic conditions within our broad-ranging study area are primarily driven by interactions between two dominant currents that flow in opposite directions. Warm, high-salinity water of the GS, a rapid Western Boundary Current that flows northeastward from Cape Hatteras, converges with the cold, low-salinity water of the southward-flowing limb of the Labrador Current (Loder et al. (1998); Fig. 2). The

GS exhibits two modes of variability that consist of meanders and latitudinal shifts in its position (Lee and Cornillon 1996). Our study focuses on latitudinal fluctuations in the GS path because of its direct effects on the winter transport of the early life stages of *I. illecebrosus* and its indirect effects on the circulation dynamics and physical water mass characteristics of the continental shelf and upper slope habitats of both squid species.

The strength of the North Atlantic Oscillation (NAO) directly influences patterns in atmospheric and oceanic variability in the North Atlantic and is defined as the difference in atmospheric pressure at sea level between the Icelandic Low and the Azores High (Hurrell 1995). Multiple studies have shown that negative (positive) NAO phases are associated with southward (northward) latitudinal displacements of the GS path, as summarized in Frankignoul et al. (2001) and Chaudhuri et al. (2011). These latitudinal displacements and the NAO affect circulation dynamics and physical water mass characteristics within the study area and both exhibit cyclical trends at multiple timescales (Taylor and Stephens 1998; Gangopadhyay et al. 2016).

Broad-scale changes in the NWA have been documented during our 1993–2016 study period. For example, ongoing rapid sea surface (Friedland and Hare 2007; Chen et al. 2020) and benthic warming (Kavanaugh et al. 2017), as well as changes in GS dynamics, have affected the habitats of both study species. During 2008, the Gulf Stream migrated closer to the “Tail” of the Grand Banks and reduced the supply of cold, fresh Labrador Current waters to the shelf, which contributed to subsurface warming that propagated southwestward throughout the Northwest Atlantic Shelf (Neto et al. 2021). The annual mean path of the GS between 65°W and 50°W showed a southward secular trend during 1993–2013 (Bisagni et al. 2017) and the GS produced an increased number of WCRs during 2000–2016 (Monim 2017). In addition, the point of destabilization in the GS path shifted westward of the New England Seamount Chain, during 1993–2014, which brought the meandering Gulf Stream closer to the MAB shelf and slope (Andres 2016), where both squid species support US fisheries. Because we are interested in using our study results to inform the development of future stock size forecast models for *I. illecebrosus* and *D. pealeii*, we have focused our study on this recent period of increased variability in the NAO and GS dynamics.

Models that incorporate near real-time, high-frequency spatiotemporal fishery data have been implemented for in-season stock assessment and management of the *Illex argentinus* and *Doryteuthis gahi* squid stocks in the Falkland Islands (Arkhipkin et al. 2020), which have life histories that are very similar to *I. illecebrosus* and *D. pealeii*, respectively (O'Dor and Dawe 1998). In lieu of in-season assessment and management of squid stocks, near-term stock size forecasts with environmental covariates have been recommended

(Moustahfid et al. 2021). Our study is a first step towards a longer-term objective of developing such a forecast model for both squid stocks because the results will improve our understanding of their natural fluctuations in stock size and productivity.

We hypothesize that cyclical trends may underlie the high inter-annual variability in the biomass and mean body size indices of both squid species because several broad-scale climatic and physical drivers of oceanographic conditions within their habitats have been shown to be cyclical (Hurrell 1995; Taylor and Stephens 1998; Frankignoul et al. 2001; Petrie 2007) and this may result in a biophysical response involving their population dynamics. To address this hypothesis, our study objectives are to: (1) investigate whether inter-annual biomass and mean body weight indices, for the two intra-annual cohorts of each species exhibited cyclical trends during 1993–2016, a period of increasing environmental variability in the NWA; (2) and if so, to determine if any of these cycles were synchronous with those of the Gulf Stream's mean latitudinal positions and/or the winter NAO indices during the same time period; and (3) to characterize similarities and differences in the periodicities of biomass and mean body size indices between species as well as their synchronicities with the winter NAO indices and GS latitudinal displacements given their opposing life history strategies.

Materials and methods

In overview, we used autoregressive spectral analysis to identify and characterize significant inter-annual peaks (i.e. cycles or periodicities) in: (1) biomass and mean body weight indices, from seasonal bottom trawl surveys, for both squid species; (2) GS mean latitudinal positions,

at six longitudes that generally span the survey areas; and (3) winter NAO indices during 1993–2016. Survey areas encompassed the continental shelf and upper slope habitats of both squid species within the three Fishery Regions. Statistically significant spectral peaks were compared between all-time series to identify any synchronicities, and correlation analysis was used to determine the significance, strength and direction of associations between all pairs of variables within and amongst species.

Squid survey indices

The study domain extends from the Grand Bank to Cape Hatteras, North Carolina (52° 30'N to 35°N) and from slightly east of Cape Hatteras to the Flemish Cap (74°W to 45°W; Fig. 1). *I. illecebrosus* biomass and abundance indices were derived using data from seven stratified, random research bottom trawl surveys conducted during various seasons within each of the three *I. illecebrosus* Fishery Regions (Fig. 1, Table 1). These surveys captured the distribution of the two dominant intra-annual cohorts of each species. Biomass and abundance indices were computed as stratified mean kg per tow and numbers per tow, respectively, except for the Div. 3M and Divs. 3NO survey indices, which were provided to us as swept-area biomass estimates (tonnes). Relative abundance indices were solely used to compute stratified mean body weight (g) indices, as the quotient of stratified mean kg per tow divided by stratified mean number per tow indices, then converted to grammes. Mean body weight indices were not computed for the Divs. 3NO and Div. 3M surveys. For the SA 5+6 (Southern Fishery Region) spring and fall shelf-wide surveys (Fig. S1) conducted by the Northeast Fisheries Science Center (NEFSC), biomass indices were derived separately for all sizes combined and pre-recruits (≤ 10 cm dorsal mantle length, representing the

Table 1 Characteristics of stratified, random bottom trawl surveys, by Fishery Region, from which data were used to derive *Illex illecebrosus* and *Doryteuthis pealeii* stratified mean biomass, abundance and body weight indices. Surveys were conducted by: the Department of Fisheries and Oceans, Canada in Northwest Atlantic Fisheries Organ-

ization (NAFO) Divisions (Divs.) 3LNO, 4VWX and 4T; European Union (EU)-Spain in Divs. 3NO; EU-Spain and Portugal in Div. 3M; United States–Northeast Fisheries Science Center in Subareas 5+6 and the Massachusetts (MA) Division of Marine Fisheries in inshore MA waters

Fishery Region	Survey Name (Division or Subarea)	Survey Area (depth range)	Survey Period
Northern	3LNO	Grand Bank (30–730 m)	Spring (Apr–June), 1996–2016 Fall (Oct–Dec), 1995–2016
Northern	3M	Flemish Cap (120–730 m)	Summer (July), 1993–2016
Northern	3NO	“Tail” of Grand Bank (56–1400 m)	Summer (June), 1995–2016
Middle	4T	S. Gulf of St. Lawrence (20–274 m)	Fall (Sept), 1993–2016
Middle	4VWX	Scotian Shelf (30–400 m)	Summer (July), 1993–2016
Southern	Subareas 5+6 (shelf-wide)	Gulf of Maine to Cape Hatteras (27–366 m)	Spring (Mar–Apr), 1993–2016 Fall (Sept–Oct), 1993–2016
Southern	Subareas 5+6 (inshore MA)	Within 3 nmi of MA coast (6–89 m)	Spring (May), 1993–2016 Fall (Sept), 1993–2016

sizes not recruited to the US bottom trawl fishery). Survey designs, vessels, gear types, sampling protocols and strata used to derive the survey indices are presented in Hendrickson and Showell (2019). All time series included data from 1993 to 2016, except for the Divs. 3LNO spring surveys and both the Divs. 3LNO fall and 3NO summer surveys, which began in 1996 and 1995, respectively. The initial year selected for all of the other time series was 1993, in order to include the Grand Bank survey indices from the Northern Fishery Region, and thereby enable a comprehensive, stock-wide study. Second, it enabled inclusion of the Archiving, Validation and Interpretation of Satellite Oceanographic (AVISO) sea surface height time series that began in 1992, and third, as previously discussed, 1993–2016 encompassed a period of rapid change in oceanographic conditions in the NWA that is still ongoing.

Biomass, abundance and mean body weight indices were also derived for *D. pealeii* using data from two surveys conducted in SA 5+6 during spring and fall in the Southern Fishery Region during 1993–2016 (Table 1). Biomass and mean body weight indices were derived separately for all sizes combined and pre-recruits (≤ 8 cm dorsal mantle length) for both surveys and mean body weights were computed for the combined size biomass indices. One of the two surveys was the shelf-wide NEFSC bottom trawl survey, which covers a set of offshore strata with a depth range of 27 to 366 m (Fig. S1; shaded with diagonal lines) and a set of inshore strata with a depth range of 18–27 m (Fig. S1; the single series of unshaded strata abutting the offshore strata). Data from the shallowest two series of depth strata (< 18 m) were not used to calculate the survey indices because they were not sampled during 2009–2016. *D. pealeii* indices for the NEFSC surveys were derived in accordance with the methods used for the stock assessment (NEFSC 2011).

The same three time series of survey indices were also derived using data from spring and fall bottom trawl surveys conducted within inshore Massachusetts (MA) waters (Table 1, Fig. S1 inset) by the MA Division of Marine Fisheries (MA DMF). These indices, referred to here as the “inshore MA” survey indices were included in the study because the spring surveys are conducted when inshore spawning occurs within the survey area (i.e. south and west of Cape Cod; Fig. S1). During the fall surveys, this area serves as nursery habitat for juveniles (Jacobson 2005). Data from all survey strata (Fig. S1 inset) were used to derive the *D. pealeii* indices. Survey design, gear and vessel characteristics and sampling protocols for the inshore MA surveys are described in King et al. (2010).

GS latitudinal positions and winter NAO indices

For comparison with spectral signatures of the survey biomass and mean body size indices for both species, we

conducted spectral analyses on the annual mean latitudinal position of the GS at six representative longitudes (74°, 70°, 65°, 60°, 55° and 50°W). These longitudes capture the spatial variability of the GS path's behaviour along its axis from 75°W to 50°W reasonably well, and although the GS is a continuous path, its spectral behaviour in between each of the six longitudes is synchronous (Gangopadhyay et al. 2016).

The six GS latitudinal position time series were derived using mapped satellite altimetry data (daily, $\frac{1}{4}^\circ \times \frac{1}{4}^\circ$ resolution), based on the 35-cm sea surface height (SSH) contour, and were obtained from the AVISO website: <https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/ssha.html>. Details of the altimetry data processing and archiving methodology are available from the Copernicus Marine Service website (<http://marine.copernicus.eu>). The 25-cm SSH contour has been used for understanding the GS path's behaviour in multiple previous studies (e.g. Pena-Molino and Joyce 2008; Andres 2016; Seidov et al. 2018), considering it to be representative of the axis of the GS. Previously, Gangopadhyay et al. (2016) used the 50-cm SSH contour for their path analysis, which is closer to the axis and compared that variability with other well-known GS path indices, such as the Taylor–Stephens Index (Taylor and Stephens 1998) and the Joyce Index (Joyce et al. 2000). A comprehensive discussion on different metrics of GS path indices is provided in Chi et al. (2019). Here, we used the 35-cm SSH contour as the representation of the GS path. As shown in Fig. 1a of Chi et al. (2019), the distance between the 50-cm and 25-cm SSH contours (with 35 cm falling within this range) is only about 17 km compared to the overall width of 150 km for the Gulf Stream.

Our spectral analyses also included the winter, station-based Hurrell NAO Indices, averages of the NAO anomalies for December through March (Hurrell 1995), during 1993–2016. These indices were obtained from the website of the Climate Analysis Section of the National Center for Atmospheric Research (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>).

Spectral analyses

Spectral analysis involves the decomposition of a time series into its underlying sine and cosine functions, of different frequencies, in order to identify the frequencies that are especially strong. The conventional Fourier Transform (FT) method is often inapplicable for time series that are short (i.e. 17–55 data points) or that have spatial or temporal data gaps, and when applicable, may provide dubious results (Gangopadhyay et al. 1989, 2016). All but two of our time series included 24 data points. As a result, we used linear autoregressive (AR) spectral analysis (Kay

and Marple 1981) rather than the FT method to identify the presence of inter-annual periodicities or cycles in the time series that we analyzed: *I. illecebrosus* and *D. pealeii* biomass and mean body weight indices, GS mean latitudinal positions at the six longitudes previously specified and winter NAO indices. Following the recommendations of Gangopadhyay et al. (2016) for time series of less than 100 points, and to be consistent with all of our time series, we used sixth-order AR models for our spectral analyses because the shortest time series in our study was 21 years (Table 1). The same study also found that the spectra resulting from sixth-order and eighth-order AR models were consistent with one another for the GS and NAO time series; the difference being a very slight shift of less than one year. Therefore, we discuss commonalities and differences between the significant spectral peaks of all of the analyzed time series in terms of “structured groupings” of peaks for a band of years, rather than choosing or specifying a particular yearly peak (e.g. we considered a 3–4-year peak to be synonymous with both a 3-year and a 4-year peak).

All time series were standardized prior to conducting the spectral analyses, to facilitate spectral estimate comparisons amongst time series. Each time series was de-trended, to remove any long-term trends, and then divided by its standard deviation after subtracting the mean. These operations produced a transformed data set with a unit standard deviation and zero mean.

Confidence intervals (CI) for the spectral peak estimates were based on approximate statistics and remained constant across the spectrum because of the form of the variance (Kay and Marple 1981). The variance depends on the factor $(2p \cdot N^{-1})^{1/2}$ for a p th-order model of an N -point time series. As in Gangopadhyay et al. (2016), we determined the CIs using the Burg (1977) algorithm provided in the MATLAB Scientific Toolbox and followed the methodology described by Eq. (6.4.20) of Jenkins and Watts (1968). Using the Bartlett Window Formulation (refer to Table 6.6 of Jenkins and Watts (1968), the number of degrees of freedom for our N -year time series and a p th-order AR model was determined to be $3N \cdot p^{-1}$. The sixth-order model thus allows for higher degrees of freedom than an eighth-order model for the same time series. We used the 95% CI to determine which spectral peaks of ≤ 10 years were statistically significant. The 95% CIs, computed based on 10–12 degrees of freedom, were included in the spectra plots of each time series. Peaks greater than 10 years were considered spurious, because such peaks are close to or beyond the Nyquist limit, given that most of the time series analyzed were in the 24-year range.

Correlation analyses

Spearman’s Rank Order Correlation analyses were conducted using the “proc corr” function in SAS (SAS Institute Inc., Cary, NC, USA) to determine the strength and direction of associations between all pairs of *I. illecebrosus* and *D. pealeii* biomass and mean body weight indices and GS mean latitudinal position and winter NAO time series for 1993–2016. Pairs that were statistically significant at the 0.05 alpha level were reported.

Results

Gulf Stream latitudinal positions and winter NAO indices

During 1993–2016, variability in GS mean latitudinal position increased in an easterly direction between 74°W and 50°W (Fig. 3a). North–south displacement trends were similar for 74°, 70° and 65°W until 2010, when the GS position at 74°W shifted from its southernmost position to an increasingly northward position, concurrent with the largest negative NAO anomaly for the study period (Fig. 3b). A similar northward shift propagated in an easterly direction along the GS path, except for 65°W, during the following year. In each case, the shift occurred after the GS was at or near its

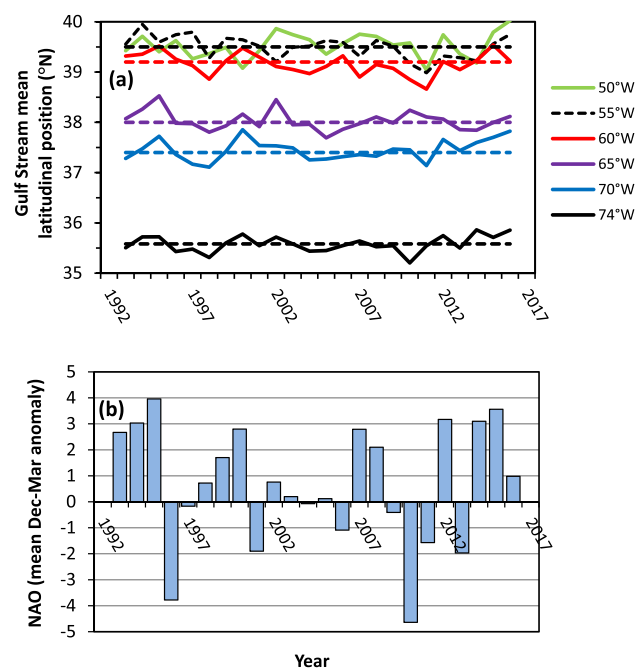


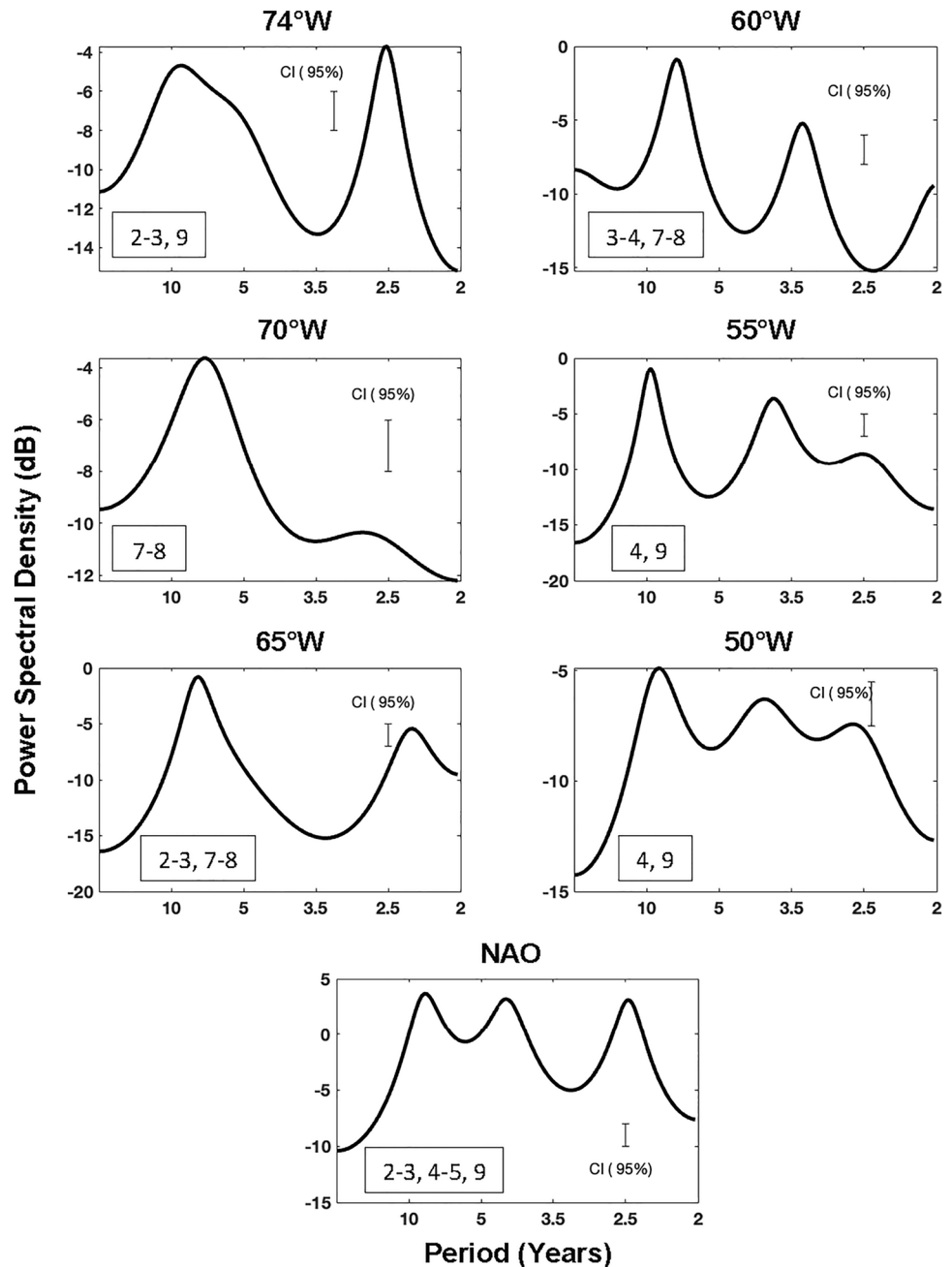
Fig. 3 Mean latitudinal positions of the Gulf Stream at 74°, 70°, 65°, 60°, 55°, and 50°W and their time series means (a) and winter NAO indices (mean of Dec–Mar anomaly) (b) during 1993–2016. The time series means for 55° and 50°W were the same

southernmost position for each respective time series. The second highest negative anomaly occurred during 1996 but were low during the other seven years with negative anomalies. The magnitudes of positive anomalies were generally much greater those of negative anomalies during most years (Fig. 3b).

Statistically significant spectral peaks (i.e. periodicities or cycles) for the six GS latitudinal position time series differed along the GS path between 74°W and 50°W (Fig. 4), but formed three distinct GS Segments (Fig. 1). The Middle

GS Segment extends from 60°W to 65°W and the Western and Eastern GS Segments extend from west of 65°W to 74°W and east of 60°W to 50°W, respectively. The Western GS Segment (which spans the Southern Fishery Region), exhibited a 2–3-year peak, whereas the Eastern GS Segment exhibited a 3–4-year peak. The Middle GS Segment represented a transition zone that consisted of both 2–3- and 3–4-year spectral peaks. Thus, periodicities for GS latitudinal positions increased in an easterly direction.

Fig. 4 Spectral signatures (power spectral density, in dB) from sixth-order autoregressive spectral analysis models of annual mean latitudinal positions of the Gulf Stream at 74°, 70°, 65°, 60°, 55° and 50°W and winter North Atlantic Oscillation (NAO) indices (mean of December–March anomalies) during 1993–2016. Statistically significant spectral peaks (shown in boxes) were identified based on the 95% confidence intervals shown



The NAO was in a positive phase during most of 1993–2016 (Fig. 3b) and the indices exhibited spectral peaks at near-decadal, 4–5- and 2–3-year timescales (Fig. 4). The near-decadal NAO peak was synchronous with peaks for GS mean latitudinal positions at all six longitudes, but the 2–3-year NAO peak was only synchronous with those of the GS latitudinal positions west of 65°W (Table 2); the Western GS Segment. The NAO and GS latitudinal position time series were most strongly correlated at the westernmost longitudinal boundary of the study area, at 74°W ($p < 0.0001$, $n = 24$, $r = 0.721$), where near-decadal and 2–3-year GS periodicities were exhibited (Tables 2 and 3). The NAO indices were moderately correlated with GS positions for the Middle

and Western GS Segments, at 70°W ($p = 0.019$, $n = 24$, $r = 0.473$) and 60°W ($p = 0.010$, $n = 24$, $r = 0.514$).

Illex illecebrosus

I. illecebrosus biomass indices were highly variable, regardless of season, in all three Fishery Regions; often increasing or decreasing by multiple orders of magnitude from one year to the next (Fig. 5).

Mean body weight indices were less variable than the biomass indices and trends for the Southern Fishery Region differed from those of the other two Fishery Regions. Fall mean body weight indices for the Southern Fishery Region showed an overall decreasing trend and

Table 2 Significant spectral peaks (years) from linear, sixth-order autoregressive spectral analysis models of *Illex illecebrosus* biomass indices (stratified mean kg per tow), for all sizes and pre-recruits (≤ 10 cm dorsal mantle length), and stratified mean body weight indices, by season and bottom trawl survey, during 1993–2016. Significant spectral peaks of Gulf Stream mean latitudinal positions, at the

six longitudes shown in the grey boxes (listed from east to west), and winter North Atlantic Oscillation (NAO) indices (mean of December–March anomalies) during 1993–2016 are shown for comparison. NSP denotes no significant peaks ≤ 10 years at the 0.05 significance level. Color codes for spectral peak bands: blue (near-decadal); magenta (4–5-year); green (3–4-year); and yellow (2–3-year)

Time Series	Spectral Peaks (Years)					
Northern Fishery Region						
Spring 3LNO biomass						4
Spring 3LNO mean body weight		7		3		
Fall 3LNO biomass			5	3		
Fall 3LNO mean body weight			5		2-3	
Summer 3NO biomass	9					
Summer 3M biomass						
Gulf Stream latitudinal positions at:						
50°W	9					4
55°W						
60°W		7-8		3-4		
Middle Fishery Region						
Fall 4T biomass						
Fall 4T mean body weight						2-3
Summer 4VWX biomass						2-3
Summer 4VWX mean body weight				4		2-3
Gulf Stream latitudinal positions at:						
60°W		7-8		3-4		
65°W		7-8				2-3
Southern Fishery Region						
Spring SA 5+6 biomass						4
Fall SA 5+6 biomass						4 2-3
Spring SA 5+6 pre-recruit biomass						
Fall SA 5+6 pre-recruit biomass						4 2-3
Spring SA 5+6 mean body weight	10					
Fall SA 5+6 mean body weight						2-3
Gulf Stream latitudinal positions at:						
65°W		7-8				2-3
70°W		7-8				
74°W	9					2-3
NAO Indices	9		4-5			2-3

Table 3 Significant Spearman ranks order correlations from tests between all pairs of *Illex illecebrosus* biomass indices (stratified mean kg per tow), for all sizes and pre-recruits (≤ 10 cm dorsal mantle length), stratified mean body weight indices, Gulf Stream annual mean latitudinal positions at 74°W, 70°W, 65°W, 60°W, 55°W and 50°W, and winter North Atlantic Oscillation (NAO) indices (mean of December–March anomalies) during 1993–2016. Significance level = 0.05. **N** = Northern, **M** = Middle and **S** = Southern Fishery Regions

Time Series 1	Time Series 2 (<i>p</i> -value, <i>n</i> , <i>r</i>)
Spring 3LNO biomass– N	74°W (0.002, 21, – 0.620) and 70°W (<0.0001, 21, – 0.747)
Fall 4T biomass– M	74°W (0.041, 24, – 0.418) and 70°W (0.001, 24, – 0.614)
Summer 3M biomass– N	70°W (0.008, 24, – 0.523)
Summer 4VWX biomass– M	70°W (0.023, 24, – 0.460)
Summer 3NO biomass– N	70°W (0.002, 22, – 0.607) and 60°W (0.002, 22, – 0.613)
Fall 3LNO mean body weight– N	70°W (0.001, 22, – 0.643) and 60°W (0.011, 22, – 0.529)
Fall SA 5+6 mean body weight– S	55°W (0.019, 24, 0.473)
Winter NAO indices	74°W (<0.0001, 24, 0.721), 70°W (0.019, 24, 0.473) and 60°W (0.010, 24, 0.514)
Northern Fishery Region	
Spring 3LNO biomass	Summer 3M biomass– N (<0.0001, 21, 0.812)
Spring 3LNO biomass	Summer 3NO biomass– N (0.006, 21, 0.571)
Spring 3LNO biomass	Fall 3LNO mean body weight– N (0.004, 21, 0.590)
Spring 3LNO biomass	Summer 4VWX biomass– M (0.027, 21, 0.480)
Spring 3LNO biomass	Spring SA 5+6 pre-recruit biomass– S (0.032, 21, – 0.467)
Spring 3LNO biomass	Fall SA 5+6 biomass– S (0.009, 21, 0.553)
Summer 3M biomass	Summer 3NO biomass– N (<0.0001, 22, 0.737)
Middle Fishery Region	
Fall 4T biomass	Summer 3M biomass– N (<0.0001, 24, 0.728)
Fall 4T biomass	Summer 3NO biomass– N (0.0006, 22, 0.672)
Fall 4T biomass	Fall 3LNO mean body weight– N (0.008, 22, 0.547)
Fall 4T biomass	Spring 3LNO biomass– N (0.0004, 21, 0.702)
Fall 4T biomass	Fall SA 5+6 biomass– S (0.025, 24, 0.455)
Summer 4VWX biomass	Fall 4T biomass– M (0.0005, 24, 0.655)
Summer 4VWX biomass	Summer 3M biomass– N (0.005, 24, 0.547)
Summer 4VWX biomass	Summer 3NO biomass– N (0.005, 22, 0.566)
Summer 4VWX biomass	Fall SA 5+6 mean body weight– S (0.009, 24, 0.520)
Southern Fishery Region	
Fall SA 5+6 biomass	Summer 3M biomass– N (0.021, 24, 0.465)
Fall SA 5+6 pre-recruit biomass	Spring SA 5+6 mean body weight– S (0.001, 24, – 0.603)

were mainly below the mean during 2010–2016, whereas the spring indices varied about the mean but were mainly below it during 2008–2016 (Fig. 6a). In contrast, the mean body weight trends for the Northern (fall Divs. 3LNO) and Middle (summer Divs. 4VWX and fall Div. 4T) Fishery Regions were similar to one another, but did not show the same overall decrease as during fall in the Southern Region. (Fig. 6b). The spring Divs. 3LNO mean body weight indices varied without trend (Fig. 6c).

One or more significant spectral peaks were exhibited for all but three of the *I. illecebrosus* biomass and body weight time series, but there were no significant peaks for the fall Div. 4T (Middle Fishery Region) and summer Div. 3M (Northern Fishery Region) biomass indices and the SA 5+6 spring (Southern Fishery Region) pre-recruit biomass indices (Table 2, Fig. 7).

Spectral peaks of 3–4 years were common to one or more series of *I. illecebrosus* biomass and body weight indices across all Fishery Regions, regardless of season,

and were synchronous with those of GS latitudinal positions for the Eastern and Middle GS Segments (Figs. 4, 7 and 8, Table 2).

Biomass and mean body weight indices for both the Middle and Southern Fishery Regions exhibited 2–3-year peaks, during summer and fall, respectively. This 2–3-year cycle was synchronous with those of both the NAO and GS latitudinal positions for the Western and Middle GS Segments (Figs. 7 and 8, Table 2). Fall (Divs. 3LNO) biomass and mean body weight indices for the Northern Fishery Region exhibited the only 5-year peaks for this species.

Only a few of the *I. illecebrosus* indices exhibited the near-decadal peaks that were common to those found along the entire studied GS path and the NAO indices. These included spring mean body weight indices for the Northern and Southern Fishery Regions and biomass indices for Divs. 3NO on the “Tail” of the Grand Bank during summer (Table 2, Fig. 4).

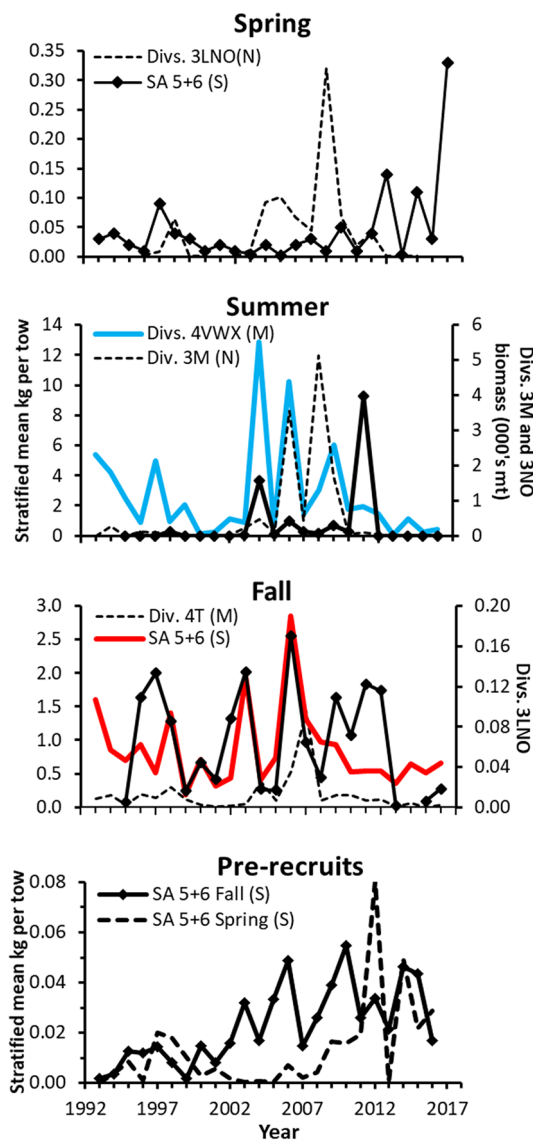


Fig. 5 *Illex illecebrosus* biomass indices (stratified mean kg per tow) for all sizes combined, by season, and pre-recruits (≤ 10 cm dorsal mantle length) during 1993–2016. Surveys began during 1995 in Divs. 3LNO fall and 3NO and during 1996 in Divs. 3LNO spring. Sampling coverage was inadequate for the 2014 Divs. 3LNO fall survey. N=Northern, M=Middle and S=Southern Fishery Regions

All of the *I. illecebrosus* biomass indices from the Northern Fishery Region were positively correlated with one another and with indices for both the Middle and Southern Fishery Regions, regardless of season (Table 3). Strong correlations were found between the spring Divs. 3LNO biomass indices (Northern Fishery Region) and biomass indices from the two most isolated locations in the study area, the Flemish Cap (Div. 3M) and Southern Gulf of St. Lawrence (Div. 4T), as well as the “Tail” of the Grand Bank (Divs. 3NO); r values ranged from 0.702 to 0.812 (Table 3). Correlations between the Northern and Southern Fishery

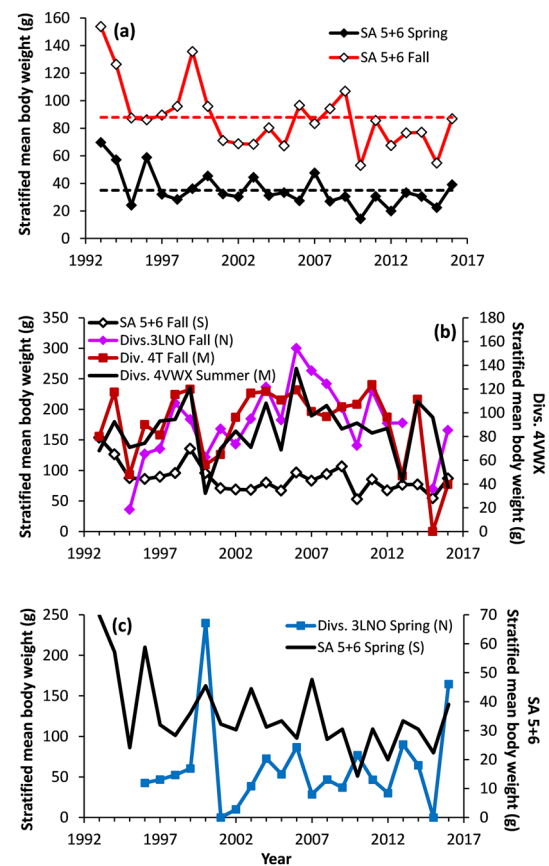
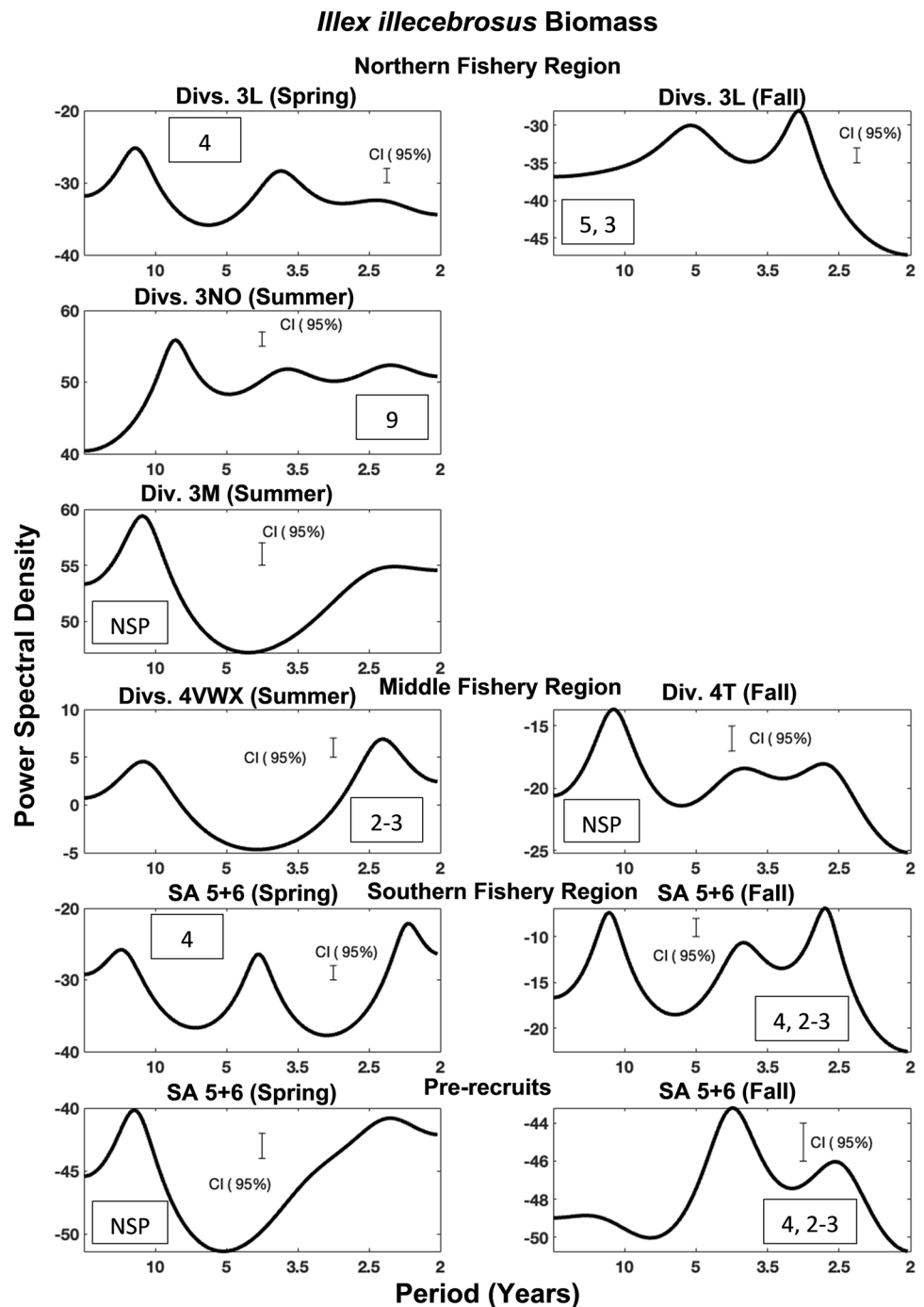


Fig. 6 *Illex illecebrosus* stratified mean body weight indices (g) for the Southern Fishery Region (a) and for summer and fall (b) and spring and fall bottom trawl surveys (c) during 1993–2016. No catches—2001 and 2015 Divs. 3LNO spring and 2015 Div. 4T surveys. N=Northern, M=Middle and S=Southern Fishery Regions

Regions were weak to moderate and were negative between the spring Divs. 3LNO biomass and spring SA 5+6 pre-recruit biomass, but positively correlated with the fall SA 5+6 biomass.

Negative correlations between *I. illecebrosus* indices were only found in the Southern Fishery Region between spring mean body weight and fall pre-recruit biomass indices ($p=0.001$, $n=24$, $r=-0.603$) and between pre-recruit biomass indices for the Southern Region and biomass indices (Divs. 3LNO) for the Northern Region during spring ($p=0.032$, $n=21$, $r=-0.467$; Table 3). Regardless of season, only the biomass indices for the Northern Fishery Region were correlated with GS latitudinal positions (i.e. at 74°W , 70°W and 60°W). All of these correlations were negative and several were strongly correlated (Table 3). The only positive correlation between GS positions and *I. illecebrosus* indices was between fall mean body weight in the Southern Fishery Region and GS positions at 55°W . NAO indices were not correlated with any *I. illecebrosus* indices (Table 3).

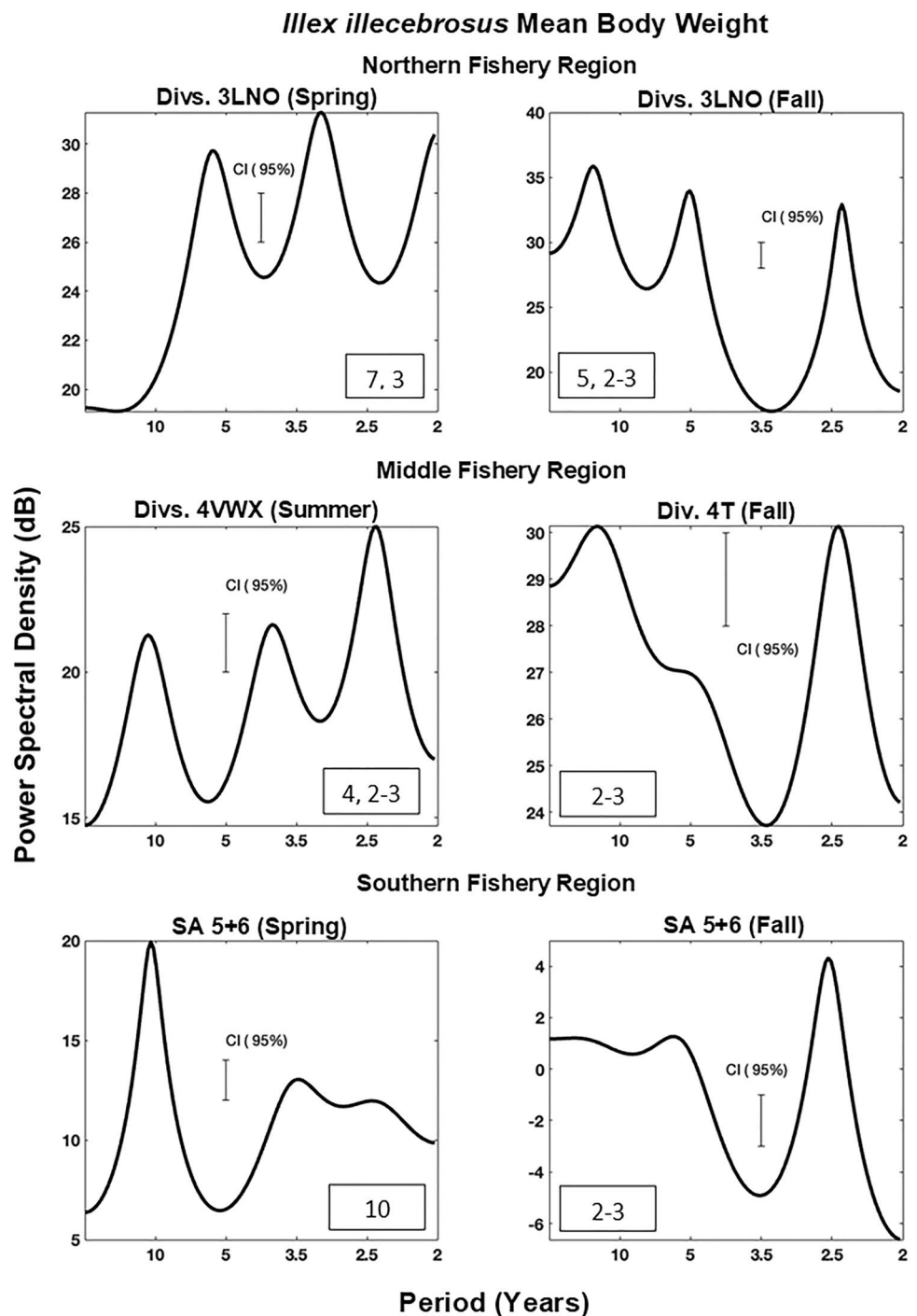
Fig. 7 Spectral signatures (power spectral density, dB) from sixth-order autoregressive spectral analysis models of *Illex illecebrosus* biomass indices (stratified mean kg per tow; all sizes and pre-recruits (≤ 10 cm dorsal mantle length)), by bottom trawl survey and Fishery Region, during 1993–2016. Statistically significant spectral peaks (shown in boxes) were identified based on the 95% confidence intervals shown. NSP denotes no significant peaks ≤ 10 years



In summary, 3–4-year cycles were common to one or more of the *I. illecebrosus* indices across all three Fishery Regions. These cycles linking all three Fishery Regions were synchronous with those of GS positions for the Eastern and Middle GS Segments. A 2–3-year cycle was common to *I. illecebrosus* indices for the Southern Fishery Region and was synchronous with the 2–3-year cycles for GS positions of the Western and Middle GS Segments and the NAO indices. The near-decadal cycles identified for all GS Segments were lacking for all but spring mean body weights for the

Northern and Southern Fishery Regions and summer biomass on the “Tail” of the Grand Bank (Divs. 3NO). The 4–5-year NAO cycle was only synchronous with fall biomass and mean body weight indices for the Northern Fishery Region. Strong correlations were found between all biomass indices for the Northern Fishery Region and moderate to strong correlations were found between one or more series of *I. illecebrosus* indices from all three Fishery Regions. There was a strong negative correlation between spring mean body weight and fall pre-recruit biomass indices for the Southern

Fig. 8 Spectral signatures (power spectral density, dB) from sixth-order autoregressive spectral analysis models of *Illex illecebrosus* stratified mean body weight indices for the Northern (Divisions (Divs.) 3LNO, 3M, 3NO), Middle (Divs. 4VWX and 4T) and Southern (SA 5+6) Fishery Regions, by bottom trawl survey, during 1993–2016. Statistically significant spectral peaks (shown in boxes) were identified based on the 95% confidence intervals shown



Fishery Region and a moderate negative correlation between spring pre-recruit biomass indices for the Southern Fishery Region and spring biomass indices for the Northern Fishery Region. GS latitudinal positions for the Western GS Segment were all negatively correlated with biomass indices for the Northern Fishery Region.

Doryteuthis pealeii

Interannual variability of the *D. pealeii* biomass indices was also very high (Fig. 9). Biomass trends for the inshore MA and shelf-wide surveys were similar during spring but not fall. Similar to the *I. illecebrosus* mean body weight for the Southern Fishery Region, but less pronounced, *D. pealeii* mean body weights were higher during the first few years of the inshore and shelf-wide spring and fall surveys.

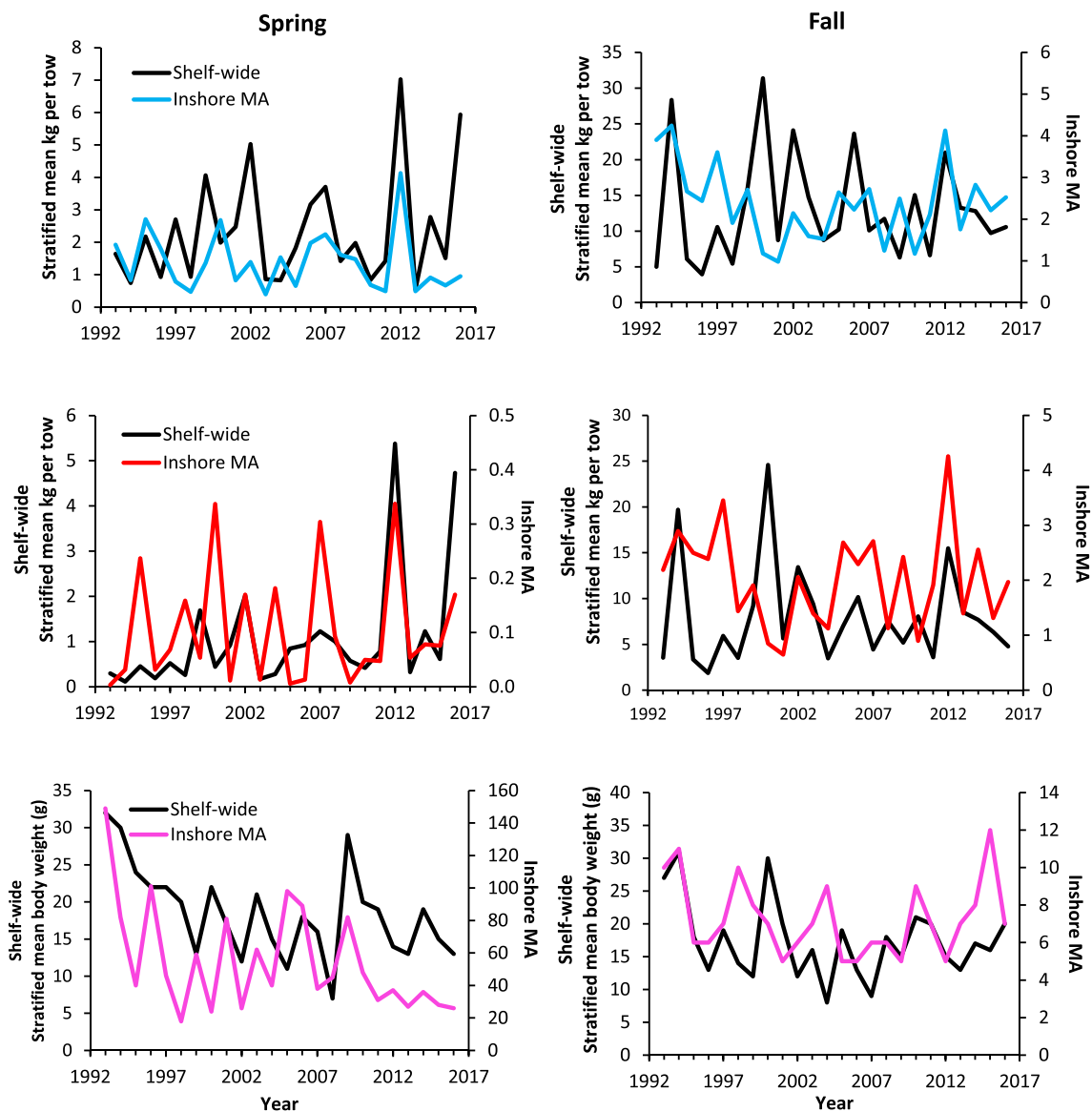


Fig. 9 *Doryteuthis pealeii* spring (left column) and fall (right column) biomass indices (stratified mean kg per tow) for all sizes combined (top panels) and pre-recruits (≤ 8 cm dorsal mantle length; middle panels), and stratified mean body weight indices (g), for bot-

tom trawl surveys conducted in the Southern Fishery Region, during 1993–2016. Inshore MA and shelf-wide bottom trawl surveys were conducted by the Massachusetts (MA) Division of Marine Fisheries and Northeast Fisheries Science Center, respectively

Thereafter, the two surveys exhibited different trends. The spring and fall shelf-wide surveys both showed a gradual decrease, but unlike *I. illecebrosus*, it did not persist throughout the time series (Figs. 5 and 9). Individuals from the spring inshore surveys weighed more than those from the shelf-wide surveys, but this relationship was reversed during fall.

Significant spectral peaks were identified for all *D. pealeii* indices, but timescales varied by season. Spring biomass indices for both surveys were dominated by 5-year peaks that were synchronous with the 4–5-year NAO peak (Table 4,

Fig. 10). In contrast, shelf-wide fall biomass and mean body weight indices exhibited near-decadal peaks, which were synchronous with the GS positions for all GS Segments. Spring and fall indices exhibited 2–3- and 3–4-year peaks. The 2–3-year peaks were only exhibited for the inshore MA biomass and body weight indices and they were synchronous with the 2–3-year NAO peak and GS position peaks for the Western and Middle GS Segments. The 3–4-year peaks were exhibited for all of the fall shelf-wide survey indices, as well as the spring mean body weight indices, and were synchronous with the Eastern and Middle GS Segments.

Table 4 Significant spectral peaks (years) from linear, sixth-order autoregressive spectral analysis models of *Doryteuthis pealeii* biomass (stratified mean kg per tow), for all sizes and pre-recruits (≤ 8 cm dorsal mantle length), and stratified mean body weight indices, by bottom trawl survey (shelf-wide versus inshore Massachusetts (MA)) conducted in the Southern Fishery Region, during 1993–2016. Significant spectral peaks for Gulf Stream (GS) mean latitudinal positions, at the

longitudes shown in the grey box (listed from east to west), and winter North Atlantic Oscillation (NAO) indices (mean of December–March anomalies) during 1993–2016 are shown for comparison. GS latitudinal position locations between 74°W and 65°W coincide with the longitudinal boundaries of the Southern Fishery Region. Significance level is 0.05. Color codes for spectral peak bands: blue (near-decadal); magenta (4–5-year); green (3–4-year); and yellow (2–3-year)

Time Series	Spectral Peaks (Years)
Spring shelf-wide biomass	5
Spring inshore MA biomass	5
Spring shelf-wide pre-recruit biomass	5
Spring inshore MA pre-recruit biomass	5, 2-3
Spring shelf-wide mean body weight	3
Spring inshore MA mean body weight	4, 2-3
Fall shelf-wide biomass	8, 3
Fall shelf-wide pre-recruit biomass	8, 3
Fall shelf-wide mean body weight	8, 3
Fall inshore MA biomass	4, 2-3
Fall inshore MA pre-recruit biomass	10, 2-3
Fall inshore MA mean body weight	5
Gulf Stream latitudinal positions at:	
50°W	9, 4
55°W	9, 4
60°W	7-8, 3-4
65°W	7-8, 2-3
70°W	7-8
74°W	9, 2-3
Winter NAO indices	9, 4-5, 2-3

The only negative correlations occurred between the fall mean body weight indices for the inshore MA survey and both spring biomass ($p=0.022$, $n=24$, $r=-0.462$) and pre-recruit biomass indices for the shelf-wide survey ($p=0.027$, $n=24$, $r=-0.449$; Table 5). Spring biomass indices for the inshore and shelf-wide surveys, which exhibited 5-year periodicities, were correlated ($p=0.013$, $n=24$, $r=0.495$). All spring and fall shelf-wide survey indices were positively correlated with GS latitudinal positions at 74°W.

Similarities and differences between species in the Southern Fishery Region

Spectral peaks for biomass and mean body weight indices differed between species, by season, in the Southern Fishery Region (Tables 2 and 4). All fall *D. pealeii* indices for the shelf-wide surveys exhibited near-decadal peaks, whereas *I. illecebrosus* only exhibited a near-decadal peak for spring mean body weight indices. All spring *D. pealeii* biomass indices exhibited 5-year cycles (for inshore and shelf-wide surveys) that were synchronous with the 4–5-year NAO cycle. However, none of the *I. illecebrosus*

survey indices for the Southern Region exhibited 4–5-year cycles.

Both species exhibited 2–3- and 3–4-year periodicities for biomass and/or body weight indices that were synchronous with the Western and Eastern GS segments, respectively, and the Middle GS Segment. However, during fall, biomass and mean body weight indices exhibited 2–3-year periodicities for *I. illecebrosus* and 3–4-year periodicities for *D. pealeii* (shelf-wide indices only). The 2–3-year periodicities exhibited by *D. pealeii* during the fall were only present for the inshore MA biomass indices.

Discussion

Autoregressive spectral analysis revealed underlying cyclical trends in the biomass and mean body weight indices of two squid species that were otherwise masked by their high inter-annual variability. The presence of inter-annual cycles at timescales ranging from 2 to 3 years to near-decadal is remarkable given the sub-annual lifespans of both species, but confirms the tight coupling between squid recruitment

Doryteuthis pealeii

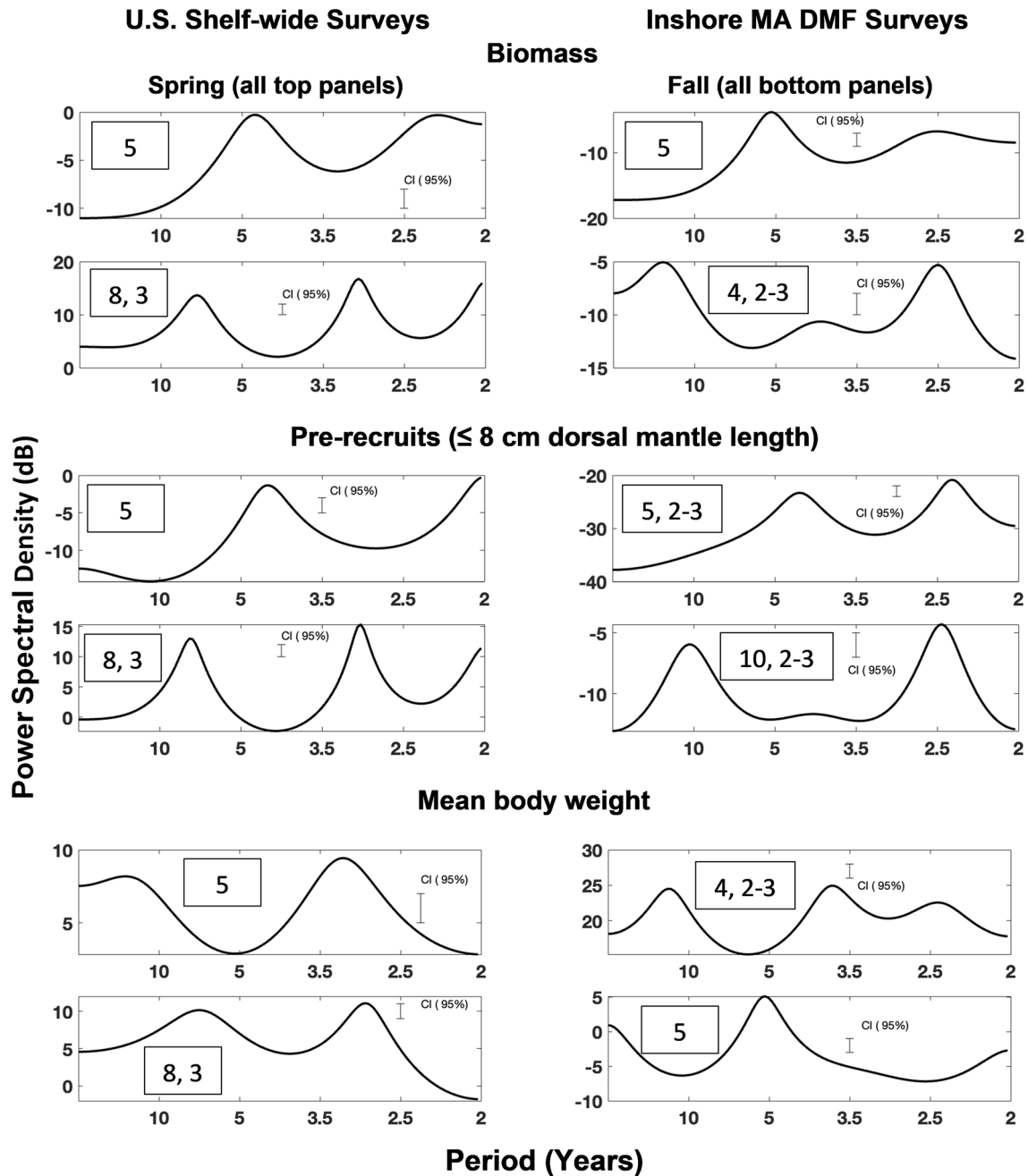


Fig. 10 Spectral signatures (power spectral density, in dB) of *Doryteuthis pealeii* biomass indices (stratified mean kg per tow; all sizes and pre-recruits) and stratified mean body weight indices (g), by bottom trawl surveys conducted in the Southern Fishery Region, during 1993–2016. Inshore MA DMF and U.S. shelf-wide surveys represent

the Massachusetts Division of Marine Fisheries and Northeast Fisheries Science Center bottom trawl surveys, respectively. Statistically significant spectral peaks (shown in boxes) were identified based on the 95% confidence intervals shown

and cyclical environmental forcing factors. For example, we found that inter-annual biomass periodicities were synchronous with one or more periodicities of the Gulf Stream’s latitudinal position, but at specific GS Segments, along its path between and 74° and 50°W.

GS latitudinal position and NAO periodicities

We identified multi-scale periodicities for the GS position and NAO time series, but only the near-decadal periodicity was exhibited at all six of the GS position locations between

Table 5 Significant Spearman Ranks Order Correlations from tests between all pairs of *Doryteuthis pealeii* biomass indices (stratified mean kg per tow), for all sizes and pre-recruits (≤ 8 cm dorsal mantle length), and stratified mean body weight indices for shelf-wide versus inshore Massachusetts (MA) bottom trawl surveys conducted

Time Series 1	Time Series 2 (<i>p</i> -value, <i>r</i>)
Fall shelf-wide biomass	74°W (0.029, 0.444)
Spring shelf-wide biomass	74°W (0.002, 0.597)
Fall shelf-wide pre-recruit biomass	74°W (0.042, 0.417)
Spring shelf-wide pre-recruit biomass	74°W (0.015, 0.486)
Spring inshore MA pre-recruit biomass	74°W (0.039, 0.422) and NAO (0.011, 0.506)
Fall shelf-wide mean body weight	65°W (0.044, 0.413)
Spring inshore MA biomass	60°W (0.032, 0.437) and NAO (0.050, 0.403)
Fall inshore MA biomass	NAO (0.015, 0.487)
Spring inshore MA biomass	Spring shelf-wide biomass (0.013, 0.495)
Spring shelf-wide biomass	Fall inshore MA mean body weight (0.022, - 0.462)
Fall inshore MA mean body weight	Spring shelf-wide pre-recruit biomass (0.027, - 0.449)
Winter NAO indices	74°W (<0.0001, 0.721), 70°W (0.019, 0.473) and 60°W (0.010, 0.514)
<i>D. pealeii</i> spring shelf-wide biomass	<i>I. illecebrosus</i> spring shelf-wide biomass (0.033, 0.434)
<i>D. pealeii</i> spring shelf-wide mean body weight	<i>I. illecebrosus</i> fall shelf-wide mean body weight (0.035, 0.430)
<i>D. pealeii</i> spring shelf-wide pre-recruit biomass	<i>I. illecebrosus</i> spring shelf-wide pre-recruit biomass (0.015, 0.486)
<i>D. pealeii</i> fall inshore MA biomass	<i>I. illecebrosus</i> spring shelf-wide biomass (0.023, 0.592)
<i>D. pealeii</i> fall inshore MA pre-recruit biomass	<i>I. illecebrosus</i> spring shelf-wide biomass (0.031, 0.440)

in the Southern Fishery Region, Gulf Stream (GS) mean latitudinal positions at 74°W, 70°W, 65°W, 60°W, 55°W and 50°W, and winter North Atlantic Oscillation (NAO) indices (mean of December–March anomaly) during 1993–2016. Correlations between species are also presented. Significance level is 0.05

74° and 50°W as well as the NAO indices. Previous studies of the NWA have linked this near-decadal GS periodicity to basin-wide forcing by the NAO (e.g. summarized in Chaudhuri et al. 2009 and 2011). GS latitudinal position moves northward (southward) during positive (negative) NAO phases, with a lag of one to two years (Taylor and Stephens 1998; Joyce et al. 2000).

The biomass and mean body weight indices of both species exhibited fewer significant near-decadal peaks than expected, especially for *I. illecebrosus*, given the species' direct association with GS paralarval transport during winter. We attributed this finding to the shortness of our 24-year time series. We specifically truncated our time series from 1993 onward because it would have omitted the Grand Bank *I. illecebrosus* indices (Divs. 3LNO) which were derived with data from the largest survey area in the Northern Fishery Region. Inclusion of these indices was critical to our objective of understanding the stock-wide synchronicity of biophysical variability, given recent large-scale changes in the hydrologic conditions of the NWA (Sanchez-Franks et al. 2014; Gawarkiewicz et al. 2018; Gangopadhyay et al. 2019; Neto et al. 2021). In addition, analysis of longer time series would have required the use of a composite GS index (i.e. the use of a single metric to represent the entire GS path) for the spectral analysis because the AVISO dataset only extends back to 1992.

Stock-wide continuity of *I. illecebrosus* biomass/mean body weight periodicities

Irrespective of season, one or more of the biomass and mean body weight indices from all three *I. illecebrosus* Fishery Regions shared a common periodicity of 3–4 years, which was synchronous with the periodicity of GS latitudinal shifts for the Eastern and Middle GS Segments. This common stock-wide periodicity indicates that all three Fishery Regions are linked by one or more environmental factors associated, either directly (e.g. dispersal of eggs and paralarvae) and/or indirectly (e.g. changes in Slope Water characteristics), with movements of the Eastern Segment of the GS path, where its inter-annual variability is the highest (Bisagni et al. 2017; Seidov et al. 2019). This finding lends further support to the designation of the population as a single stock.

Similarities and differences between species in the Southern Fishery Region

Despite their opposing life history strategies, the biomass and mean body weight indices of both species shared some common periodicities in the Southern Fishery Region.

On the US Shelf, periodicities of multiple biomass and mean body weight indices for both squid species were synchronous with the 2–3-year and 3–4-year periodicities of

the GS positions of the Western and Eastern GS Segments, respectively, in addition to the Middle Segment. For *D. pealeii*, the 2–3-year periodicity was limited to the inshore survey indices, but persisted during both spring and fall. In contrast, for *I. illecebrosus*, the 2–3-year periodicity was only present during fall, but for both biomass and body weight indices.

We also found highly significant negative correlations between GS latitudinal positions, at 74°, 70° and 60°W, and *I. illecebrosus* biomass indices in the Northern and Middle Fishery Regions, only one positive correlation; between GS latitudinal positions at 55°W and the *I. illecebrosus* fall mean body weight indices in the Southern Fishery Region. In contrast, all correlations between *D. pealeii* spring and fall biomass indices and GS latitudinal positions were positive and occurred at 74°W. The negative association between *I. illecebrosus* biomass increases (decreases) in the Middle and Northern Fishery Regions and southward(northward) displacements of the Middle and Western GS Segments is especially interesting and warrants further investigation.

The more pronounced seasonality of the *D. pealeii* biomass and mean body weight periodicities reflects the year-round presence of this species on the US shelf where there is a strong seasonal temperature cycle associated with the physical and biological processes in this Fishery Region (Friedland and Hare 2007). All of the spring *D. pealeii* biomass indices exhibited a 4–5-year periodicity that was synchronous with the NAO and most of the fall biomass periodicities. Unexpectedly, *D. pealeii* biomass indices also exhibited more near-decadal periodicities than *I. illecebrosus*, but only during the fall. These near-decadal periodicities were expected to be more likely to occur during spring when the population is distributed near the shelf-break in the Mid-Atlantic Bight where GS-related interactions frequently occur (Joyce et al. 1992; Zhang and Gawarkiewicz 2015; Gawarkiewicz et al. 2012). The influence of physical drivers of biomass and mean body weight other than GS latitudinal displacements must certainly be investigated for both squid species.

We note that the biomass and mean body weight indices included in our study were derived from surveys conducted during different seasons. However, inter-annual variabilities of the seasonal GS paths exhibit similar cycles when compared to the annual GS paths (Seidov et al. 2017, 2018). A more comprehensive study where seasonal GS paths are linked with seasonal squid biomass indices in a lag-correlation framework is beyond the scope of this study, but we plan to investigate these linkages as an important next step towards identifying specific environmental drivers of biomass and body weight that exhibit the same periodicities found in the subject study. Nevertheless, it is remarkable that our results show similar inter-annual periodicities of biomass and mean body weight indices across the three *I.*

illecebrosus Fishery Regions despite survey differences in season, spatial coverage, gear characteristics, vessels and sampling protocols.

Two previous studies involving climate and oceanographic effects on *I. illecebrosus* relative abundance produced conflicting results with respect to the statistical significance of GS latitudinal position (Dawe et al. 2000, 2007). One reason may have been that these studies used a composite GS index that does not take into account variability in the GS position along its path (Gangopadhyay et al. 2016). These studies also did not involve a comprehensive investigation between GS position and *I. illecebrosus* abundance indices across seasons and all three Fishery Regions. Abundance indices for the Northern Fishery Region and spring indices for all Fishery Regions were not included in either study. Consequently, an important objective of our study was to determine whether squid throughout the range of the stock exhibited similar interannual biomass and mean body weight periodicities and whether such periodicities were synchronous with those of GS positions at specific GS Segments. Similar to our study, Dawe et al. (2007) also found that the different life history strategies between *I. illecebrosus* and *D. pealeii* resulted in differences in the environmental variables that affect their relative abundance.

Oceanographic variability during the study period

Both species exhibited cyclical trends in biomass and mean body weight despite the increased variability in oceanographic conditions that occurred in the study area during 1993–2016. For example, the rapid, ocean warming that has been occurring in the NWA has affected GS dynamics, such as the southward shift of the GS path from its mean latitudinal position during 1993–2013 (Bisagni et al. 2017). In addition, the destabilization point of the GS path downstream of Cape Hatteras has recently moved westward (Andres 2016). This westward destabilization and other factors (e.g. internal GS dynamics and atmospheric forcing) might have resulted in the formation of more warm-core rings (Gangopadhyay et al. 2019), an increase in the number of filaments to break-off from the GS, and thus, more warm-core ring-shelf interactions which are known to affect on-shelf and off-shelf larval fish populations (Flierl and Wroblewski 1985; Cohen et al. 1988; Hare et al. 2001).

Mean body weight periodicities

In the Southern Fishery Region, *I. illecebrosus* mean body weight indices exhibited a 2–3-year periodicity during the fall and a longer, decadal periodicity during the spring. These seasonal periodicity differences suggest that recruitment in the winter and summer intra-annual cohorts are influenced by different environmental factors. During the

study period, a gradual decrease in *I. illecebrosus* mean body weight occurred in the Southern Fishery Region for squid caught in both the spring and fall surveys (i.e. for both intra-annual cohorts), but was more pronounced during fall when mean body weights were larger than in the spring (Fig. S2a). In contrast, *D. pealeii* mean body weights for the same two surveys were similar to one another in trend and values during 1993–2016 and did not show the same consistent decrease exhibited by *I. illecebrosus* (Fig. S2b).

Collapse of the *I. illecebrosus* resource occurred in the Northern and Middle Fishery Regions (O’Dor and Dawe 1998) in 1982, following a multi-year period of the highest exploitation rates on record (Hendrickson and Showell 2019). Thereafter, landings from these two Fishery Regions remained at low levels for 34 years, due to low recruitment, whilst landings from the Southern Fishery Region, where quotas were much lower, remained stable (Hendrickson and Showell 2019).

As described in Hendrickson and Showell (2019), *I. illecebrosus* mean body weights in both the Southern Fishery Region during fall and Middle Fishery Region during summer were the highest during the 1976–1981 high productivity period, but were lower during the 1982–2016 low productivity period (Fig. S3). However, squid from the Southern Fishery Region exhibited a gradual, multi-decadal decrease in mean body weight during 1982–2016 (Fig. S3a). During this same period, *I. illecebrosus* mean body weight trends for the Middle Fishery Region, did not show the same consistent decrease (Fig. S3b).

Why did this long-term decrease in *I. illecebrosus* mean body weight only occur in the Southern Fishery Region? This is an important question because of the positive correlation between potential fecundity and body weight (Laptikhovsky and Nigmatullin 1993), which affects egg-per-recruit model results (Hendrickson and Hart 2006). Therefore, we investigated this question by determining the spatial extent of the decrease in mean body weight across the species’ latitudinal range (i.e. 10°) on the US shelf and whether the decrease was present in both pre-recruits and recruits. To do so, we extended the same spring and fall mean body weight time series back to 1968 and derived mean body weight indices for three sub-regions; the Mid-Atlantic Bight, Southern New England-Georges Bank and the Gulf of Maine. At the time of the spring surveys, few individuals have migrated into the Gulf of Maine so spring mean body weight indices could not be computed for this subregion. We also derived separate mean body weight indices for pre-recruits and recruits (for combined subareas) during both spring and fall.

Similar mean body weight decreases occurred in all sub-regions, after 1982, during both spring and fall (Fig. S4a and 4b). During the fall, the decreasing trends were similar between squid from the Mid-Atlantic Bight and Southern

New England, but the trend differed for individuals from the cooler waters located farther north in the Gulf of Maine. The latter showed a more variable decreasing trend through 1995 with an increase during 2004–2016. Gulf of Maine squid also weighed more than squid from the other two sub-areas, due to the latitudinal cline in *I. illecebrosus* mean body weight that increases from south to north with decreasing water temperature (Hendrickson 2004). In addition, the decreasing mean body weight trends only occurred for recruits (the sizes caught by the US fishery), which dominated the survey catches during both spring and fall (Fig. S4c and d). In summary, these additional analyses demonstrated that the mean body weight decrease only occurred on the US shelf and for both intra-annual cohorts, but was this mean body weight decrease species-specific?

When examined a longer time series of *D. pealeii* mean body weight indices for the spring and fall inshore MA and shelf-wide surveys, we discovered that high and low productivity regimes occurred during 1978–2016 and that their durations varied by survey and were more pronounced during spring (Fig. S5). Similar to *I. illecebrosus*, the spring and fall shelf-wide surveys showed a decreasing trend following the high productivity period, but the inshore MA surveys did not. This finding of decreasing trends in mean body weight for both species, and for both intra-annual cohorts (Fig. S6), suggests that a cyclical environmental driver that operated specifically on the US shelf led to the observed reductions in mean body weights of both species.

The specific causal relationships for synchronicities between the NAO and GS position periodicities and those of the biomass and mean body weight indices of our study species are beyond the scope of this paper, but there are many possibilities. For example, in the Southern Fishery Region, the response of the mean percentage of Labrador Slope Water entering the Gulf of Maine (at depths of 150–200 m) to the NAO was substantially reduced during 1990–2008, as NAO indices increased (Mountain 2000). Through an analysis of bottom water temperatures, Petrie (2007) found that Labrador and Newfoundland bottom water temperatures were cooler (warmer) during periods of high(low) NAO indices and were the opposite on the Scotian Shelf and in the Gulf of Maine. Latitudinal variability in GS position is strongly correlated with changes in sea surface temperature (SST) and circulation in the Slope Sea. During 1993–2007, the GS position was correlated with Slope Water SST anomalies whereby positive anomalies (i.e. warming of the Slope Water) preceded northward shifts of the GS position by about one year (Pena-Molino and Joyce 2008).

Our findings demonstrate that environmental factors which persist over much longer timescales than the sub-annual lifespans of these squid species are major

determinants of their stock size and productivity. The specific timescales of the spectral peaks identified also provide new insights into which environmental factors may be useful to investigate as potential drivers of their recruitment and growth. The mechanisms that govern interactions between Gulf Stream processes and the biomass and mean body weight indices of these species require further investigation so that accurate, near-term forecast models can be derived for both of these commercially valuable species.

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Author contributions All authors contributed to the study's conception and design. Material preparation, data collection and analyses were performed by LCH and AG. The manuscript was written primarily by LCH with assistance from AG. All authors commented on and approved the version of the manuscript submitted for publication in the Marine Biology journal.

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Data availability The data analyzed in this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest to disclose.

Ethical approval All of the squid catch data used in our study were obtained from the Northeast Fisheries Science Center's multispecies bottom trawl survey database. The survey's sampling and animal handling protocols were carried out in compliance with the United States National Marine Fisheries Service's (NMFS) Institutional Animal Care and Use Policy (NMFS Policy 04-112) and Scientific Research Permit #23001.

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