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Effects of seasonal and interannual variability in along-shelf and cross-shelf transport on groundfish recruitment in the eastern Bering Sea

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ABSTRACT

The Bering Sea responds rapidly to atmospheric perturbations and over the past several decades has experienced extreme variability in both its physical and biological characteristics. These changes can impact organisms that inhabit the region, particularly marine fishes, as normal current patterns to which reproductive habits are tuned can be disrupted, which, in turn, may influence recruitment and population dynamics. To understand the influence of ocean circulation on groundfish recruitment in the eastern Bering Sea, we examined transport along and across the Bering Slope derived from 23 years (1982–2004) of simulations from a Regional Ocean Modeling System (ROMS) ocean circulation model. We expected that changes in the strength and position of the Bering Slope Current (BSC) would affect recruitment in selected species (Pacific cod, walleye pollock, Greenland halibut, Pacific halibut, and arrowtooth flounder), and that circulation features along and across the shelf edge would be strongly influenced by atmospheric forcing. Variability in along-shelf transport at three transects along the path of the BSC, cross-shelf transport across the 100 and 200 m isobaths, and transport through Unimak Pass were examined. Strong seasonal and interannual variations in flow were observed, with transport typically highest during fall and winter months, coinciding with timing of spawning activity in the five species. Significant correlations were found between transport, BSC position, and groundfish recruitment. Pacific cod, in particular, benefitted from decreased along-shelf and on-shelf flow, while Pacific halibut recruitment increased in relation to increased on-shelf transport through southern canyons. The results of this study improve our understanding of variability in circulation and associated effects on groundfish recruitment in the eastern Bering Sea.

1. Introduction

Numerous studies have shown that transport plays an important role in population regulation in marine fishes and have linked larval transport with variability in year-class strength (Parker, 1989; Van der Veer et al., 1998; Van der Veer and Witte, 1999; Wilderbuer et al., 2002; Mueter et al., 2006). Since adult spawning and juvenile settling locations are often geographically separated, early life history stages must rely on transport and retention features, as well as their own behavior, to move them toward or keep them within appropriate habitats for successful recruitment to the juvenile phase (Norcross and Shaw, 1984). Many species undergo a long dispersal stage from their source (e.g., fish spawning areas) to nursery locations (e.g., juvenile settling locations). During this period, eggs and larvae experience high mortality, which strongly influences recruitment variability (Cowen, 2002; Houde, 2008). Over time, organisms have likely adapted to optimize dispersal success and reduce mortality loss by taking advantage of local physical and biological conditions (Iles and Sinclair, 1982; Bailey and Picquelle, 2002; Bailey et al., 2008). Further, deviations from average conditions may be a source of population fluctuations (Bailey et al., 2005a, 2005b) when the normal current patterns to which reproductive habits are tuned are disrupted (Bakun, 1985).

A major source of transport in the eastern Bering Sea (EBS) is the Bering Slope Current (BSC). The BSC exists as either a series of eddies and meanders, or as a more uniform northwestward flowing current (Stabeno et al., 1999; Schumacher et al., 2003), with exchange across the shelf break likely dependent on which

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flow pattern is dominant. Recent work by Ladd (2014) has shown that the BSC has a strong seasonal cycle and is typically not a continuous, cohesive feature outside of the winter months. On-shelf flow can also vary as a result of wind-driven advection, interaction of the BSC with topography, and the funneling effect of canyons (Springer et al., 1996; Stabeno and Van Meurs, 1999; Clement Kinney et al., 2009). Several large submarine canyons incise the EBS slope margin, including Bering Canyon to the south, which is long with a wide valley (> 400 km), and Pribilof and Zhemchug canyons to the north, which are steeper and have trough-shaped basins. These canyons are believed to enhance the flux of heat, salt, and water from the Aleutian Basin to the EBS shelf (Stabeno et al., 1999, 2008; Clement Kinney et al., 2009), and are thought to be important spawning locations for several species of marine fishes (Seitz et al., 2007; Sohn et al., 2010; Neidetcher et al., 2014).

Circulation in the EBS has been shown to vary with large-scale atmospheric features. In particular, the Arctic Oscillation (AO: Thompson and Wallace, 1998; Overland et al., 1999) and the Pacific Decadal Oscillation (PDO: Mantua et al., 1997) influence the distribution and intensity of winter storms, represented by the position and intensity of the Aleutian Low (AL: Wilderbuer et al., 2002). The AL influences surface winds in the EBS, which can affect advection (Ladd, 2014) and mixing of the upper ocean (Ladd and Stabeno, 2012), the production and advection of ice, and heat flux (Schumacher et al., 2003), as well as timing of the spring phytoplankton bloom, the degree of pelagic-benthic coupling, and the match-mismatch of prey production for larval fish (Napp et al., 2002). The El Niño-Southern Oscillation (ENSO) can also influence circulation through its positive correlation with the AL (Schumacher et al., 2003). Atmospheric circulation is an important determinant of water mass movement on the EBS shelf (Wespestad et al., 2000), with flows being highly sensitive to the surface forcing specific to each year (Hermann et al., 2002). Recent work by Ladd (2014) suggests that interannual variability of the BSC is wind-driven, with strong interannual variability in the strength of the BSC correlated with the North Pacific Index (NPI, Trenberth and Hurrell, 1994) and Multivariate ENSO Index (MEI, Wolter and Timlin, 1998). The extent of sea ice coverage over the shelf and timing of sea ice retreat are also believed to be important factors influencing transport and flow in the region (Stabeno et al., 2012).

The purpose of the present work is three-fold: (1) to investigate seasonal and interannual variations in hydrodynamic circulation in the EBS, (2) to relate observed transport variability to recruitment of slope- and shelf-spawning groundfish species, and (3) to discern the atmospheric features that modulate variation in flow. We characterized seasonal and interannual variability of along-shelf and cross-shelf transport in the EBS, along with changes in the position of the BSC, using 23 years of output from the Regional Ocean Modeling System (ROMS) ocean circulation model. We then compared results to recruitment indices of five groundfish species whose early life stages have shelf break crossings: age-0 Pacific cod (cod, *Gadus macrocephalus*), age-1 walleye pollock (pollock, *Gadus chalcogrammus*), age-1 Greenland halibut (*Reinhardtius hippoglossoides*), age-2 Pacific halibut (*Hippoglossus stenolepis*), and age-2 arrowtooth flounder (*Atheresthes stomias*) to determine the potential effects of oceanographic variability on recruitment. The species selected for this study are both commercially and ecologically important, and may be vulnerable to changes in circulation, as they spawn during winter months when storm activity is high (Stabeno et al., 1999) and have relatively long pelagic larval durations (3–4 months for cod and pollock; 5–8 + months for Greenland halibut, Pacific halibut, and arrowtooth flounder). Cod and pollock are largely considered shelf-spawners, though spawning may also occur along the outer continental shelf and slope region, while the three flatfish species are considered

slope-spawners. Our analyses focus primarily on winter months to examine how recruitment in the different groundfish species varies in relation to transport during the various spawning seasons (cod: January–April (Bakkala, 1993; Neidetcher et al., 2014); pollock: February–April (Bacheler et al., 2010); Greenland and Pacific halibut: November–March (St-Pierre, 1984; Sohn et al., 2010); arrowtooth flounder: fall through winter (Blood et al., 2007, and references therein). Finally, we compared results from the circulation analysis to leading oceanic and atmospheric variables to resolve which climate variables are important to circulation-mediated recruitment.

2. Data and methods

2.1. Study area

The eastern Bering Sea consists of a broad (> 500 km), shallow shelf extending approximately 1000 km from the Alaska Peninsula north to Bering Strait, with a narrow continental slope adjoining the extensive Aleutian Basin. Patterns of wind and tidal energy divide the shelf into three domains during spring, summer, and fall: coastal (0–50 m depth), middle (50–100 m) and outer (100–200 m), each having its own characteristic hydrography, circulation, and assemblage of fauna and food webs (Coachman, 1986; Springer et al., 1996; Stabeno et al., 1998). In the winter and spring, a substantial portion of the shelf is covered by ice. The duration and extent of ice coverage is highly variable from year to year (Stabeno et al., 2012), which can strongly influence the timing of the spring bloom and transfer of energy to higher trophic levels (Hunt et al., 2002, 2011; Sigler et al., 2014).

Inflow from the Alaskan Stream through the Aleutian Islands feeds the cyclonic circulation pattern observed in the basin. Two currents dominate the eastern side of the Aleutian Basin, the Aleutian North Slope Current (ANSC), which flows eastward along the north side of the Aleutian Islands, and the BSC, which flows northwestward along the continental slope (Fig. 1). Before flowing northward into the BSC, the ANSC changes direction sharply in the southeast corner of the basin and accelerates, becoming unstable and generating eddies that can impinge upon the shelf (Stabeno and Van Meurs, 1999). Unimak Pass serves as the only major connection between the shelves of the North Pacific and the EBS, with inflow following the 50 and 100 m isobaths as it travels along the shelf (Reed and Stabeno, 1996; Stabeno et al., 2002). Cross-
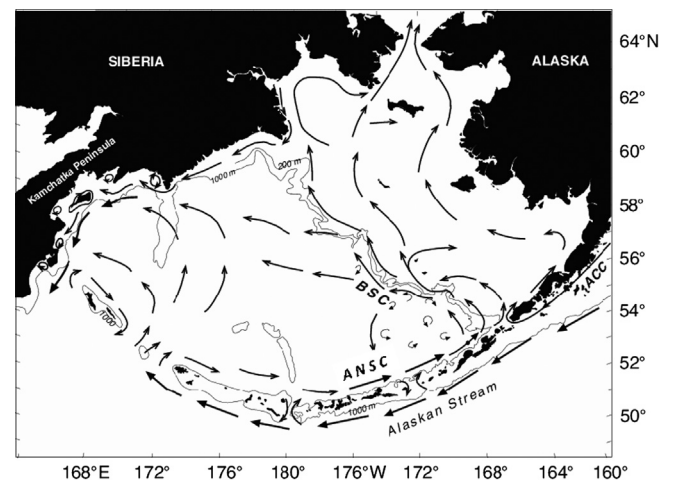

Fig. 1. Schematic diagram of flow in the Bering Sea at 40 m. BSC: Bering Slope Current, ANSC: Aleutian North Slope Current, ACC: Alaska Coastal Current. Modified from Stabeno et al. (1999).

shelf currents vary seasonally, with weakest flows during late spring and summer (< 0.5 cm s^{-1}) and stronger flows during the remainder of the year (1–2 cm s^{-1}) (Stabeno et al., 2012).

2.2. Modeled circulation

Output from the Regional Ocean Modeling System (ROMS) Northeast Pacific version 4 (NEP4) model from 1982–2004 was used to examine variation in transport along and across the EBS slope and shelf. ROMS is a state-of-the-art, free-surface, terrain-following, primitive equation model that is driven by atmospheric forcing, and has been widely used to examine the effects of climate and hydrography in the North Pacific and other oceans (Haidvogel et al., 2000; Curchitser et al., 2005; Shchepetkin and McWilliams, 2005; Di Lorenzo et al., 2008; Fiechter et al., 2009; Hermann et al., 2009). The NEP4 model, which includes the EBS, uses 10 km horizontal grid spacing with 42 levels in the vertical, and is nested in a larger, lower resolution North Pacific model. The model is forced with daily winds, heat, and freshwater fluxes, and includes a three-layer ice module. While the model is eddy-permitting, it cannot resolve the smallest eddies at this grid size and does not include tides. Despite these limitations, this circulation model generates the correct seasonal to interannual large-scale variability and represents the climatic signals of interest in the eastern Pacific Ocean (Curchitser et al., 2005).

2.2.1. Along-shelf analysis

Along-shelf transport was quantified across three transects placed perpendicular to the mean path of the BSC at 30 m depth, which represents the bottom of the wind-mixed surface layer. The mean path of the BSC was determined by averaging velocities over the 1995–2004 period. Transects were positioned north of Bering,

Pribilof, and Zhemchug canyons (hereafter South, Central, and North transects, respectively) to examine how transport varied along the path of the BSC (Fig. 2). Each transect was subdivided into three sections, with Main sections bracketing mean flow greater than 0.02 m s^{-1}, Basin sections extending over the Aleutian Basin, and Shelf sections extending shelf-ward to approximately the 100 m isobath. Volume transport (in Sverdrups, Sv $= 10^6$ m^3 s^{-1}) was calculated for each entire transect and each section (Main, Basin, and Shelf) down to 500 m depth or the bottom, whichever was shallowest, and standardized to transect length in order to facilitate comparisons among transects. A general index (BSC Index) characterizing along-shelf flow was created by averaging standardized transport anomalies for the three BSC transects.

In addition to examining variation in the strength of the BSC, the three BSC transects were used to characterize the position of the BSC, defined by the location of the maximum current velocity from the ROMS output. In several cases, the maximum current velocity was found to occur close to the transect origin over the Aleutian Basin for the South and Central transects. Therefore, to represent positional changes in the main BSC flow closer to the shelf break, the location of maximum velocity along the South transect was calculated only in the region east of 168.55°W, and for the Central transect in the region east of 174°W. No restrictions were imposed for the North transect.

2.2.2. Cross-shelf analysis

Cross-shelf transport was characterized by analyzing transport across the 100 and 200 m isobaths (Fig. 2). The 100 and 200 m isobath transects were further divided into 7 and 12 sections, respectively, to explore finer scale variations in transport across the EBS shelf, and to examine variations in transport along each isobath. Sections followed the natural contour of each isobath along
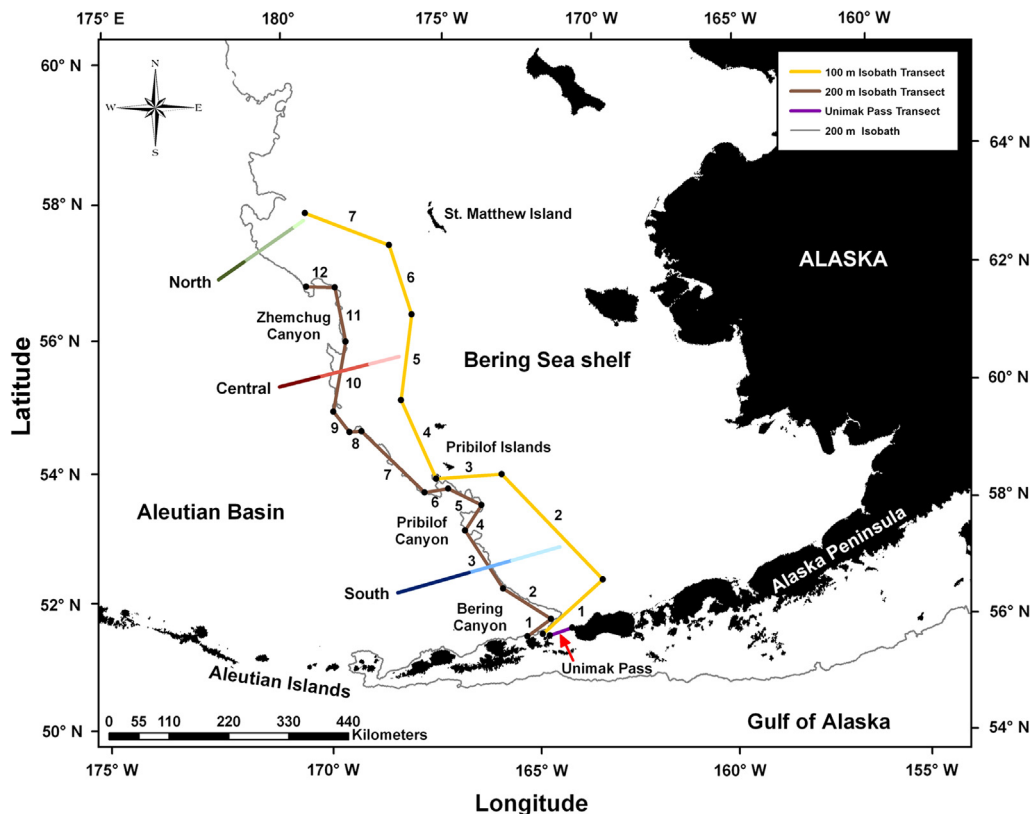

Fig. 2. Locations of the South, Central, and North BSC transects, the 100 and 200 m isobath transects, and the Unimak Pass transect used to examine variability in EBS circulation. Numbers denote 100 and 200 m isobath transect sections. Shading of BSC transects denotes Basin (dark), Main (medium), and Shelf (light) sections. The 200 m isobath is shown for reference.

the shelf to approximately 56–58°N. Sections were numbered consecutively, starting with Section 1 at the southernmost end of each isobath transect (Fig. 2). Cross-shelf transport was calculated over each section and standardized to section length and depth to facilitate comparisons between sections. General indices of cross-isobath flow were created by summing transport across all sections of each isobath transect for each year. Transport across the 200 m isobath was summed over Bering (Sections 1–2), Pribilof (Sections 4–6), and

Zhemchug (Sections 10–12) canyons to create three canyon indices, as these canyons are known regions of shelf/slope exchange (Springer et al., 1996; Stabeno and Van Meurs, 1999; Clement Kinney et al., 2009) and were expected to be important to groundfish recruitment.

Transport through Unimak Pass (Fig. 2) was also calculated. Variability in the northward flow of the Alaska Coastal Current (ACC) onto the shelf through Unimak Pass was expected to strongly influence transport in the region.
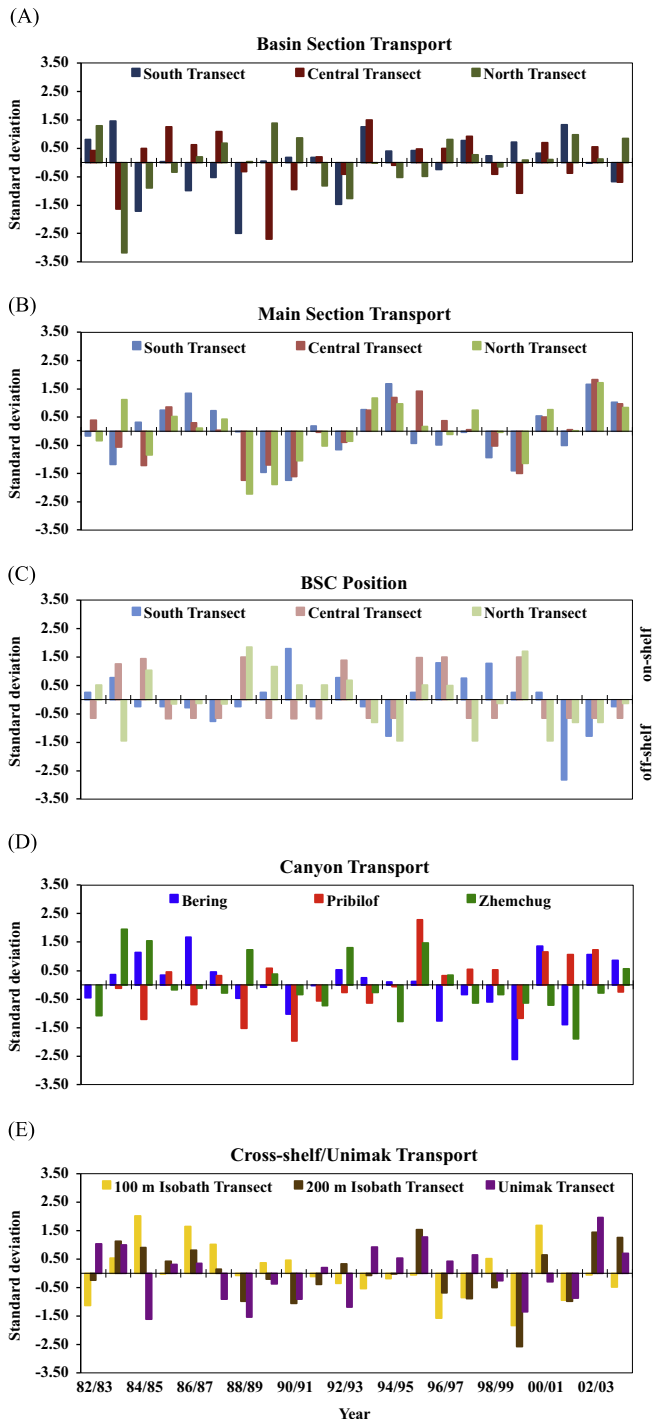

Fig. 3. December 1st–January 31st values from 1982/83 to 2003/04 used in the correlation analyses for (A) Basin transect transport, (B) Main transect transport, (C) BSC Position, (D) canyon transport, and (E) cross-shelf (100 and 200 m isobath) and Unimak transport indices. Anomalies are deviations from the mean transport or BSC position normalized by the standard deviation. Negative (positive) values for the BSC Position Index refer to an off-shelf (on-shelf) shift in the BSC.

Fig. 4. February 1st–March 31st values from 1982 to 2004 used in the correlation analyses for (A) Basin transect transport, (B) Main transect transport, (C) BSC Position, (D) canyon transport, and (E) cross-shelf (100 and 200 m isobath) and Unimak transport indices. Anomalies are deviations from the mean transport or BSC position normalized by the standard deviation. Negative (positive) values for the BSC Position Index refer to an off-shelf (on-shelf) shift in the BSC.
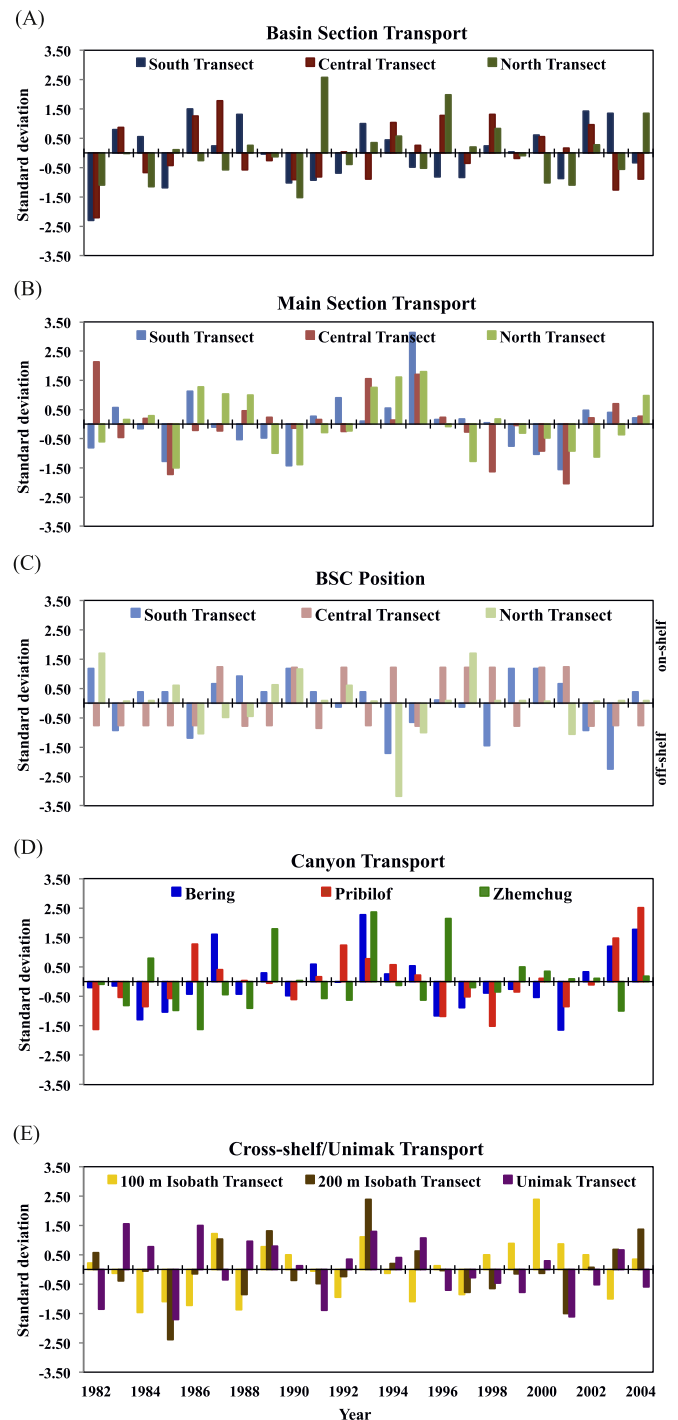
2.2.3. Time periods evaluated

Annual and monthly transports were quantified for all transects to determine seasonal and interannual patterns. Winter transport, defined here as transport from Nov. 1st–Mar. 31st, was of particular interest as it coincides with timing of spawning activity and/or larval pelagic period of the selected groundfish species examined. Bi-monthly (Dec. 1st–Jan. 31st, Feb. 1st–Mar. 31st, and Apr. 1st–May 31st) transport indices were also derived to further resolve whether groundfish recruitment was influenced by circulation throughout the early life history stages, which can develop over the course of several months. Transport and BSC Position indices were developed from anomalies for each time period examined, and were calculated as deviations from the 1982–2004 mean transport (or mean position) normalized by the standard deviation (Fig. 3, December–January; Fig. 4, February–March; Fig. 5, April–May).
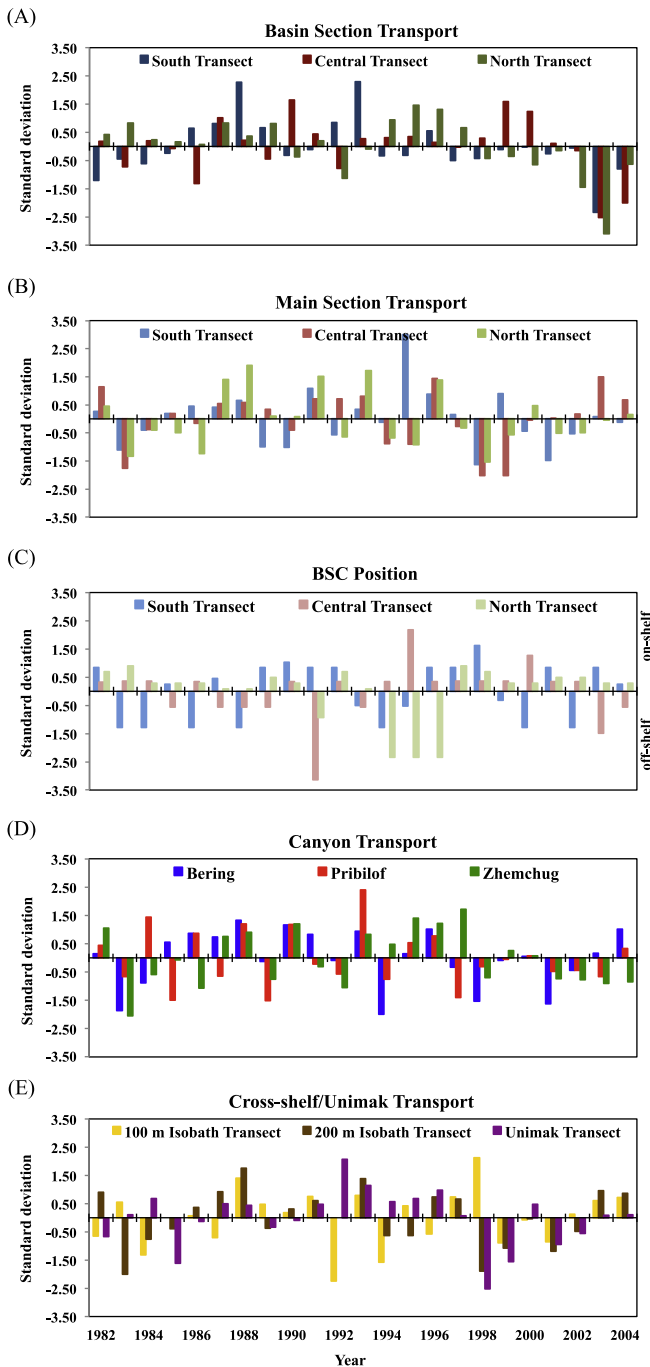

Fig. 5. April 1st–May 31st values from 1982 to 2004 used in the correlation analyses for (A) Basin transect transport, (B) Main transect transport, (C) BSC Position, (D) canyon transport, and (E) cross-shelf (100 and 200 m isobath) and Unimak transport indices. Anomalies are deviations from the mean transport or BSC position normalized by the standard deviation. Negative (positive) values for the BSC Position Index refer to an off-shelf (on-shelf) shift in the BSC.
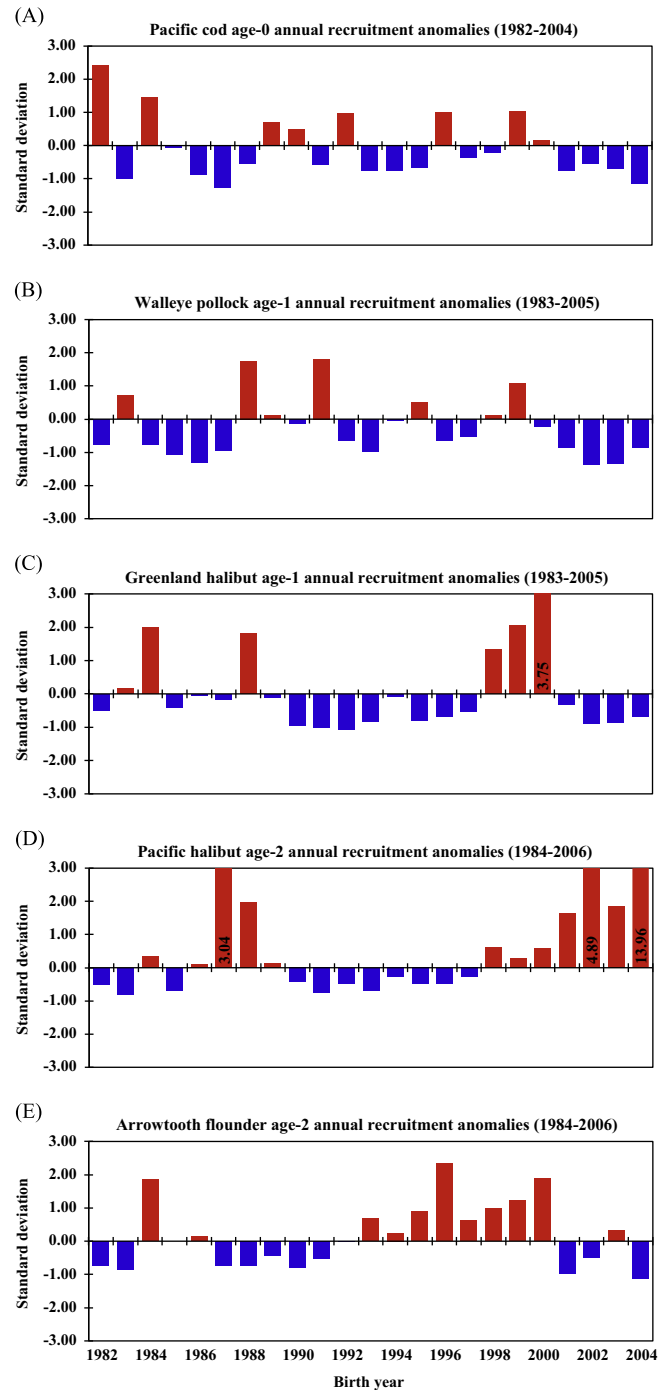
Fig. 6. Annual recruitment anomalies of (A) age-0 Pacific cod (1982–2004), (B) age-1 walleye pollock (1983–2005), (C) age-1 Greenland halibut (1983–2005), (D) age-2 Pacific halibut (1984–2006), and (E) age-2 arrowtooth flounder (1984–2006), with birth year shown on the x-axis (1982–2004). Recruitment anomalies are deviations from the mean normalized by the standard deviation. Values greater than three standard deviations from the mean are shown within their corresponding columns.

2.3. Correlations with groundfish recruitment

Recruitment indices for age-0 cod, age-1 pollock, age-1 Greenland halibut, and age-2 arrowtooth flounder (Fig. 6A–C and E) were obtained from NOAA's Bering Climate website, and are based on model estimates of the recruitment-at-age (millions) from the Alaska Fisheries Science Center's (AFSC) Stock Assessment and Fishery Evaluation (SAFE) Reports for each species. The recruitment anomalies are deviations from the mean value for the 1981–2000 period (1971–2000 for pollock) normalized by the standard deviation. Recruitment estimates for arrowtooth flounder in 2004–2006 are from estimates of abundance of fish less than 25 cm in length. Further information on the recruitment indices can be found at http://www.beringclimate.noaa.gov/data/index.php. The recruitment index for Pacific halibut (Fig. 6D) was derived from catch of age-2 fish (20–30 cm fork length (FL), Clark and Hare, 2006) in the AFSC's EBS bottom trawl shelf survey between 1982 and 2009, with recruitment anomalies as deviations from the mean value for the 1982–2000 period normalized by the standard deviation.

Groundfish recruitment indices were compared to selected indices representing flow along and across the EBS slope and shelf. Preliminary data analysis indicated that several transport indices were strongly correlated with each other. Thus, to reduce collinearity among covariates and the probability of making a Type I error, four transport indices were removed from the analysis. The BSC Index, which was strongly correlated with transport in the Main sections of all three transects, was removed, along with the three Shelf indices, which were strongly correlated with transport in their adjacent Main sections, as well as with transport through Unimak Pass. Along-shelf indices included in the analysis were the Basin, Main, and BSC Position indices for the North, Central, and South transects. Indices representing on-shelf flow were: transport over Bering, Pribilof, and Zhemchug canyons, and transport across the 100 and 200 m isobaths. Transport through Unimak Pass was also included in the analysis to account for inflow of larvae from the Gulf of Alaska and flow across Shelf sections. Correlations between groundfish recruitment indices and transport were calculated over bi-monthly time periods using Pearson's Product Moment Correlation, for a total of 15 comparisons per species per time period. Recruitment was lagged by one year for pollock and Greenland halibut (1983–2005), and two years for Pacific halibut and arrowtooth flounder (1984–2006) to correspond with transport at the time of spawning, while no lag was necessary for cod recruitment (1982–2004).

2.4. Correlations with oceanic, atmospheric, and climate indices

To determine possible mechanisms influencing groundfish recruitment, transport and position indices that were significantly correlated (here, $p < 0.1$) with recruitment were compared to atmospheric, oceanic, and climate indices thought to influence circulation in the EBS. Large-scale climatic drivers examined were the AL, represented by the NPI, ENSO, represented by the MEI, and the winter PDO. The Ice Cover Index (ICI) was selected to represent the influence of sea ice in the region and is a measure of the average ice concentration for January 1st–May 31st in a $2° \times 2°$ box (56–58°N, 163–165°W). All indices were obtained from NOAA's Bering Climate website (http://www.beringclimate.noaa.gov/data/index.php). To examine how surface winds influenced transport along and across the Bering Slope, along-shelf and cross-shelf wind indices were developed. Monthly mean u- and v- surface (0.995 sigma level) winds (NCEP/NCAR Reanalysis, Kalnay et al., 1996) were rotated in the along-shelf direction (blowing from the northwest, 315°) and averaged over the area 54.5–57.5°N, and 167.5°–175.0°W for each bi-monthly time period. Preliminary data analysis indicated that the winter PDO was strongly correlated with the MEI. To account for multiple comparisons

and reduce the probability of making a Type I error, the PDO was removed from the analysis, which resulted in a total of 15 comparisons per index per time period.

3. Results

3.1. Along-shelf analysis

Analysis of flow across the South, Central, and North BSC transects revealed differences in average annual transport among transects and also among years. In the annual mean, transport across the South transect was more variable than transport across the Central and North transects (Table 1). Significant differences were found between mean transport across the South and Central transects (Welch's t test: $t_{(df=41.21)}=4.99$, $p \ll 0.001$) and the Central and North transects ($t_{(df=43.35)}=-5.70$, $p \ll 0.001$) but not between the South and North transects ($t_{(df=43.12)}=-0.24$, $p=0.81$).

Strong interannual variability in flow was observed in the Basin and Main sections of all three BSC transects, while lower variability was found across the Shelf sections (Table 1; Fig. 7). Transport was predominantly to the northwest (NW) across the Basin sections of the South and North transects, though directionality changed in some years (Fig. 7A). Annual transport across the Basin section of the South transect was to the southeast (negative) approximately 9% of the time, while for the North Basin transect, flow reversals occurred 30% of the time (Fig. 7A). The 1982–2004 mean direction of transport in the Central Basin section was southeastward (Table 1; Fig. 7A). Standardized flow across the Basin section of the Central transect differed significantly from Basin flow across the South ($t_{(df=38.11)}=4.64$, $p \ll 0.001$) and North ($t_{(df=43.97)}=-3.03$, $p < 0.01$) transects, which is likely due to higher mesoscale variability across the Central transect. Transport through the Main and Shelf sections of all three BSC transects was primarily northwestward (positive), however southeastward (negative) mean flow did occur in some years (Fig. 7B and C). Flow across the Main and Shelf sections differed significantly between all three transects ($p < 0.05$), with transport per km increasing as it flows to the NW through the Main sections. Transport along the adjacent shelf weakens from SE to NW, implying that BSC flow becomes more concentrated toward the north.

Strong seasonal variation in along-shelf flow was found across the Basin (not shown) and Main (Fig. 8A) sections of all three BSC transects, while little variation was observed across the Shelf sections (not shown). Transport in the BSC tended to be higher during fall and winter months (Table 1; Fig. 8A), as was also found from an analysis of surface currents derived from altimetry (Ladd, 2014). Winter, December–January, and February–March transport across the Central Basin section was to the NW, which contrasted with the mean annual southeastward flow (Table 1). Transport decreased drastically during April–May along all three transects, but especially across the Central transect (Table 1).

The position of the BSC was most variable across the South transect for all time periods examined (Table 2). Little variation was found in the BSC position across the Central and North transects. Winter and bi-monthly BSC positions were off-shelf of the mean annual position. The greatest variability in the position of the BSC was found during April–May, which is likely due to increased eddy activity in the region.

3.1.1. Cross-shelf analysis

Both the 100 and 200 m isobath transects exhibited net on-shelf transport, though off-shelf transport occurred across some sections (Table 1). On-shelf transport was highest across sections found on the north side of canyons (Sections 2, 6, and 12) for the 200 m isobath transect. For both isobath transects, flow was predominantly on-shelf

Table 1

Mean annual, winter (Nov. 1st–Mar. 31st), and bi-monthly (D–J=Dec. 1st–Jan. 31st, F–M=Feb. 1st–Mar. 31st, A–M=Apr. 1st–May 31st) volume transport (in Sv) for BSC (South, Central, and North), isobath (100 and 200 m), and Unimak Pass transects, with standard deviation shown in parentheses. Positive values represent northwestward/on-shelf transport; negative values represent southeastward/off-shelf transport.

Transect	Length (km)	Annual mean transport direction	Annual mean transport 1982–2004 (SD)	Winter mean transport (Nov. 1st–Mar. 31st) 82/83–03/04 (SD)	D–J mean transport (Dec. 1st–Jan. 31st) 82/83–03/04 (SD)	F–M mean transport (Feb. 1st–Mar. 31st) 1982–2004 (SD)	A–M mean transport (Apr. 1st–May 31st) 1982–2004 (SD)
BSC South	304.03	NW	2.62 (0.96)	4.48 (1.49)	4.67 (1.91)	5.17 (2.01)	3.02 (1.71)
Basin	137.00	NW	1.14 (1.05)	1.92 (1.26)	1.89 (1.79)	2.63 (1.27)	1.98 (1.29)
Main	80.00	NW	1.00 (0.51)	1.99 (0.68)	2.20 (0.88)	1.97 (1.11)	0.63 (0.91)
Shelf	87.03	NW	0.48 (0.07)	0.57 (0.11)	0.59 (0.15)	0.57 (0.17)	0.41 (0.13)
BSC Central	224.00	NW	1.36 (0.73)	3.55 (1.06)	4.28 (1.60)	3.32 (1.39)	0.29 (1.81)
Basin	75.00	SE	−0.36 (0.87)	1.18 (0.93)	1.64 (1.00)	1.09 (1.53)	−0.97 (1.88)
Main	95.00	NW	1.58 (0.35)	2.17 (0.51)	2.46 (0.80)	1.99 (0.81)	1.12 (1.04)
Shelf	54.00	NW	0.14 (0.02)	0.19 (0.05)	0.19 (0.06)	0.24 (0.07)	0.14 (0.05)
BSC North	194.24	NW	2.68 (0.83)	4.83 (0.98)	5.46 (1.50)	5.05 (1.76)	2.82 (2.09)
Basin	58.00	NW	0.32 (0.69)	0.77 (0.51)	1.03 (0.92)	0.56 (0.83)	0.74 (1.37)
Main	111.00	NW	2.27 (0.38)	3.96 (0.99)	4.34 (1.41)	4.37 (1.38)	1.98 (1.41)
Shelf	25.24	NW	0.09 (0.03)	0.10 (0.05)	0.09 (0.07)	0.13 (0.07)	0.11 (0.06)
100 m isobath	1144.45	On-shelf	0.24 (0.14)	0.38 (0.25)	0.40 (0.41)	0.31 (0.41)	0.20 (0.24)
1	151.55	Off-shelf	−0.51 (0.09)	−0.61 (0.13)	−0.65 (0.17)	−0.66 (0.19)	−0.51 (0.16)
2	261.56	On-shelf	0.24 (0.04)	0.32 (0.09)	0.36 (0.17)	0.32 (0.12)	0.20 (0.08)
3	116.73	On-shelf	0.39 (0.05)	0.51 (0.08)	0.53 (0.12)	0.51 (0.14)	0.36 (0.11)
4	157.87	Off-shelf	−0.17 (0.04)	−0.22 (0.05)	−0.25 (0.08)	−0.19 (0.09)	−0.12 (0.07)
5	163.57	Mixed On-/Off-shelf	−0.01 (0.03)	−0.06 (0.06)	−0.06 (0.11)	−0.10 (0.12)	0.02 (0.07)
6	134.42	On-shelf	0.04 (0.03)	0.05 (0.05)	0.05 (0.08)	0.03 (0.10)	0.04 (0.05)
7	158.75	On-shelf	0.26 (0.03)	0.39 (0.06)	0.42 (0.08)	0.40 (0.10)	0.22 (0.05)
200 m isobath	958.58	On-shelf	1.58 (0.21)	2.06 (0.32)	2.17 (0.47)	2.03 (0.43)	1.42 (0.43)
1	54.21	On-shelf	0.07 (0.02)	0.06 (0.03)	0.05 (0.04)	0.05 (0.04)	0.05 (0.04)
2	99.54	On-shelf	0.39 (0.09)	0.54 (0.11)	0.60 (0.16)	0.41 (0.17)	0.19 (0.16)
3	125.88	On-shelf	0.47 (0.12)	0.61 (0.15)	0.71 (0.20)	0.56 (0.24)	0.41 (0.24)
4	58.17	Off-shelf	−0.69 (0.18)	−0.87 (0.22)	−1.00 (0.29)	−0.78 (0.27)	−0.51 (0.33)
5	64.92	On-shelf	0.31 (0.07)	0.40 (0.07)	0.46 (0.11)	0.40 (0.08)	0.25 (0.12)
6	42.77	On-shelf	0.67 (0.14)	1.00 (0.23)	1.08 (0.27)	0.94 (0.35)	0.57 (0.33)
7	156.14	Off-shelf	0.20 (0.12)	−0.39 (0.14)	−0.44 (0.15)	−0.29 (0.24)	−0.13 (0.32)
8	21.45	On-shelf	0.24 (0.10)	0.42 (0.16)	0.46 (0.21)	0.41 (0.22)	0.19 (0.22)
9	46.07	Off-shelf	−0.27 (0.11)	−0.40 (0.11)	−0.40 (0.16)	−0.38 (0.18)	−0.25 (0.21)
10	135.46	Off-shelf	−0.35 (0.14)	−0.48 (0.18)	−0.59 (0.25)	−0.43 (0.25)	−0.23 (0.28)
11	102.60	Off-shelf	−0.04 (0.04)	−0.06 (0.07)	−0.07 (0.09)	−0.04 (0.10)	−0.02 (0.07)
12	51.37	On-shelf	0.99 (0.18)	1.22 (0.19)	1.31 (0.23)	1.18 (0.24)	0.90 (0.33)
Unimak	42.67	On-shelf	0.66 (0.10)	0.79 (0.14)	0.84 (0.18)	0.82 (0.21)	0.68 (0.17)

north of Bering Canyon (100 m isobath: Sections 2 and 3; 200 m isobath: Sections 1–3, 5, 6), off-shelf north of Pribilof Canyon (between 56 and 58°N; 100 m isobath: Sections 4 and 5; 200 m isobath: Sections 7, 9–11), and on-shelf north of Zhemchug Canyon (north of 58.5°N; 100 m isobath: Sections 6 and 7; 200 m isobath: Section 12) (Table 1; Fig. 2).

Cross-shelf transects exhibited strong seasonal signals along some sections, while transport across other sections remained fairly constant throughout the year (Fig. 8B). On-shelf transport was highest during the winter months (Table 1), while transport during April–May was lower than the other periods examined and highly variable. Transport direction remained consistent for each bi-monthly period examined (Table 1).

3.2. Correlations with groundfish recruitment

Results from the correlation analyses suggest seasonal differences in circulation may differentially affect recruitment in the five species examined (Table 3). The species most correlated with flow along and across the Bering Slope was cod, especially during the February–March period. In general, cod recruitment declined in relation to increased NW transport, specifically in the Basin sections of the South and Central transects, and the Main section of the North transect. The species least correlated with flow indices was pollock, with weakly significant correlations found only with

along-shelf flow across the Central transect during April–May. Recruitment of pollock increased in relation to increased NW transport in the Basin Section, but decreased in relation to increased NW transport in the Main section. Similar results were found for Greenland halibut recruitment during the same time period. In contrast, Pacific halibut recruitment decreased as NW transport over the Central Basin section increased. Arrowtooth flounder recruitment was most strongly correlated with transport during December–January, with decreased recruitment associated with increased NW transport over the Basin section of the North transect (Table 3).

Cod recruitment increased with a more shelf-ward position of the BSC across the South and North transects. While Greenland halibut recruitment decreased in relation to a more shelf-ward position of the BSC across the South transect, arrowtooth flounder recruitment increased as the BSC moved closer to the shelf along the Central transect. Neither pollock nor Pacific halibut recruitment were associated with a shift in the BSC position (Table 3).

Cod recruitment was negatively correlated with increased on-shelf transport through Bering and Pribilof canyons. However, Pacific halibut showed the opposite trend, with recruitment increasing in relation to increased on-shelf transport through these canyons during February–March (Table 3). Over the same time period, recruitment in arrowtooth flounder was positively correlated with increased on-shelf flow through Zhemchug Canyon. Recruitment in Greenland halibut declined in relation to increased
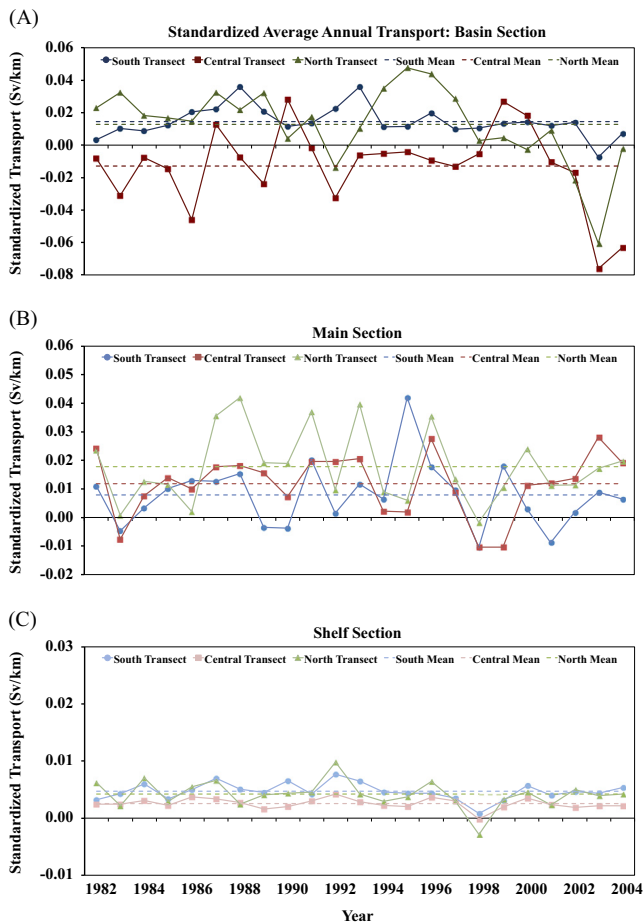
Fig. 7. Average annual transport in the BSC for the (A) Basin, (B) Main, and (C) Shelf sections of the South, Central, and North BSC transects. The 1982–2004 mean transport for each transect is also shown (dashed lines). Transport has been standardized to transect length (Sv/km) to facilitate comparison between transects. Positive values represent northwestward transport; negative values represent southeastward transport. Note different scales on vertical axes.

on-shelf transport through Bering Canyon and across the 200 m isobath during December–January (Table 3), while cod recruitment decreased in relation to increased on-shelf transport across the 100 m isobath during April–May (Table 3). No significant correlations were found with pollock, Pacific halibut, or arrowtooth flounder recruitment and transport across either the 100 or 200 m isobaths. Similarly, no significant correlations were found with transport through Unimak Pass for any of the species examined (Table 3).

3.3. Correlations with oceanic, atmospheric, and climate indices

Indices representing environmental variability in the EBS were correlated (here, $p < 0.1$) with transport and BSC Position indices found to be important to groundfish recruitment. In general, the NPI was negatively correlated with NW along-shelf transport indices from December–March, while the MEI was positively correlated with increased NW along-shelf transport over the same time period (Table 4). Increased ice cover was negatively correlated with NW along-shelf transport, except during April–May across the Central Basin section, similar to the NPI. Increased northwesterly winds were associated with a decrease in NW transport in the Basin sections of both the South and Central transects, except during February–March for the Central Main section where transport increased. Similarly, along-shelf transport
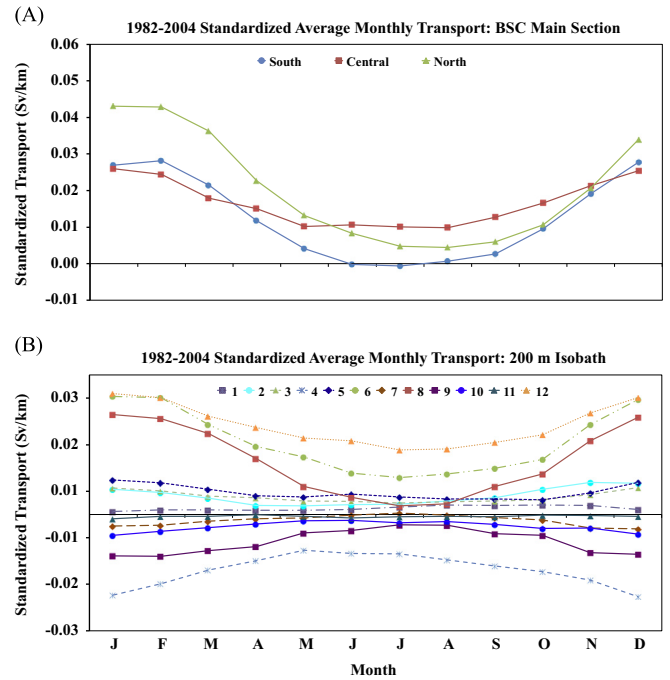

Fig. 8. Seasonal variation in (A) along-shelf and (B) cross-shelf transport. The 1982–2004 average monthly transport across Main sections of the three BSC transects (A) and the 200 m isobath transect (B) are shown. Transport has been standardized to transect length (Sv/km) to facilitate comparisons between transects. Positive values represent northwestward/on-shelf transport; negative values represent southeastward/off-shelf transport. Note different scales on vertical axes. Similar seasonal patterns were observed in other along-shelf sections and isobath transects.

Table 2

Mean location of maximum velocity in the BSC across the South, Central, and North transects, with transect length (in km) provided for reference. Locations are given as distances (in km) from the western origin of each transect, with standard deviation shown in parentheses. Mean locations were calculated over 1982–2004 (annual, Feb. 1st–Mar. 31st, Apr. 1st–May 31st) and 1982/83–2003/04 (winter, Dec. 1st–Jan. 31st).

Transect length (km)	South 304.24	Central 224.00	North 194.24
Annual	183.40 (8.96)	112.57 (2.87)	108.98 (4.16)
Winter (Nov. 1st–Mar. 31st)	168.72 (17.38)	109.48 (2.08)	106.95 (4.79)
Dec. 1st–Jan. 31st	174.22 (11.81)	109.49 (2.08)	105.93 (5.89)
Feb. 1st–Mar. 31st	162.22 (20.03)	109.84 (2.24)	104.53 (7.19)
Apr. 1st–May 31st	163.00 (31.32)	110.85 (4.87)	103.39 (19.10)

decreased in relation to increased southwesterly on-shelf winds between December–March (Table 4).

Positive correlations were found between the NPI and the South and North transect BSC Position indices, indicating a more shelf-ward position during a strong NPI (Table 4). The MEI was associated with shift in the BSC position towards the Aleutian Basin across both the South and Central transects, while ice cover showed no significant correlations with any of the BSC Position indices. In general, southeasterly along-shelf winds and southwesterly on-shelf winds were associated with a shelf-ward shift in the BSC position (Table 4).

The NPI showed mixed correlations with on-shelf transport through canyons, being negatively correlated with flow through Pribilof Canyon during December–January, but positively correlated with on-shelf flow through Zhemchug Canyon during April–May (Table 4). In contrast, the MEI was negatively correlated with on-shelf transport through Zhemchug Canyon. Ice cover was strongly and negatively correlated with on-shelf transport through Bering

Table 3

Groundfish recruitment correlations with transport and BSC Position indices. D–J=Dec. 1st–Jan. 31st; F–M=Feb. 1st–Mar. 31st; A–M=Apr. 1st–May 31st. Positive along-shelf flow is toward the NW, while positive cross-shelf flow is on-shelf. Cell shading corresponds to significance of correlation (Dark gray: p-value ≤ 0.05, Light gray: 0.05 < p-value ≤ 0.10, White: no significant correlation, p-value > 0.10). Bold font represents a significant correlation. Italicized font represents a significant negative correlation.

	Transect	Pacific cod F-M	Pacific cod A-M	Pollock F-M	Pollock A-M	Greenland halibut D-J	Greenland halibut F-M	Greenland halibut A-M	Pacific halibut D-J	Pacific halibut F-M	Pacific halibut A-M	Arrowtooth flounder D-J	Arrowtooth flounder F-M	Arrowtooth flounder A-M
Along-shelf	**South**													
	Basin	*-0.49*	-0.13	-0.04	0.22	0.26	0.33	0.10	-0.07	0.15	-0.15	0.32	0.13	0.00
	Main	-0.31	-0.05	0.04	0.25	-0.29	-0.31	-0.14	0.32	0.00	-0.10	-0.29	0.16	0.25
	Central													
	Basin	*-0.40*	0.28	-0.07	**0.39**	-0.08	0.16	**0.39**	-0.08	-0.05	*-0.42*	-0.06	0.22	0.24
	Main	0.23	0.10	0.06	*-0.38*	-0.31	-0.28	*-0.42*	0.28	0.00	0.20	0.06	0.01	-0.15
	North													
	Basin	-0.26	0.06	0.32	0.35	-0.21	-0.24	0.02	0.27	0.20	-0.31	*-0.59*	0.07	0.08
	Main	*-0.41*	0.02	0.14	0.18	0.02	0.07	-0.04	0.29	0.16	0.07	0.18	0.10	-0.04
Position	**BSC**													
	South	**0.43**	0.22	0.22	-0.09	0.24	0.27	*-0.43*	-0.33	0.02	-0.03	0.26	-0.08	-0.15
	Central	0.00	0.20	-0.15	-0.17	0.20	0.06	0.28	-0.27	-0.15	-0.13	**0.54**	0.19	**0.37**
	North	**0.51**	0.10	-0.10	-0.22	0.01	-0.10	0.18	-0.19	-0.05	0.15	-0.06	-0.05	-0.35
Cross-shelf	**Canyon**													
	Bering	*-0.43*	0.03	-0.07	0.00	*-0.38*	-0.34	-0.19	0.21	**0.41**	0.19	-0.32	-0.28	-0.06
	Pribilof	*-0.52*	0.14	-0.19	0.03	-0.11	-0.23	0.14	0.08	**0.53**	0.01	0.21	-0.23	0.24
	Zhemchug	0.35	0.19	-0.10	0.12	0.00	0.04	-0.06	-0.07	-0.02	-0.23	0.29	**0.39**	0.25
	Isobath													
	100 m	-0.01	*-0.42*	-0.02	0.28	-0.15	0.25	0.03	-0.04	0.15	0.17	-0.30	0.01	-0.14
	200 m	-0.05	-0.03	-0.18	-0.13	*-0.39*	-0.18	-0.25	0.26	0.28	0.20	-0.06	0.02	-0.13
	Unimak	-0.23	-0.04	0.07	-0.02	-0.16	0.15	-0.21	0.12	-0.16	-0.05	0.21	0.14	0.11

Table 4

Environmental correlations with transport and BSC Position indices. D–J=Dec. 1st–Jan. 31st; F–M=Feb. 1st–Mar. 31st; A–M=Apr. 1st–May 31st. Positive along-shelf flow is toward the NW, while positive cross-shelf flow is on-shelf. Southeasterly along-shelf winds are positive, while southwesterly on-shelf winds are positive. Cell shading corresponds to significance of correlation (Dark gray: p-value ≤ 0.05, Light gray: 0.05 < p-value ≤ 0.10, White: no significant correlation, p-value > 0.10). Bold font represents a significant correlation. Italicized font represents a significant negative correlation.

	Transect	NPI D-J	NPI F-M	NPI A-M	MEI D-J	MEI F-M	MEI A-M	ICI D-J	ICI F-M	ICI A-M	Along-shelf wind D-J	Along-shelf wind F-M	Along-shelf wind A-M	Cross-shelf wind D-J	Cross-shelf wind F-M	Cross-shelf wind A-M
Along-shelf	**South**															
	Basin	-0.32	*-0.48*	0.07	0.18	0.25	0.02	0.22	-0.08	0.10	*-0.67*	0.18	-0.17	*-0.46*	*-0.41*	-0.24
	Main	*-0.37*	-0.29	0.19	**0.37**	**0.44**	-0.09	*-0.41*	0.09	0.13	0.02	0.24	-0.09	-0.14	*-0.42*	-0.27
	Central															
	Basin	*-0.40*	*-0.43*	**0.42**	0.28	0.20	-0.25	-0.17	-0.05	**0.41**	0.00	0.12	*-0.36*	-0.10	-0.19	-0.21
	Main	*-0.56*	0.25	0.18	**0.36**	0.04	-0.22	*-0.43*	-0.04	*-0.50*	-0.14	**0.41**	0.26	*-0.43*	-0.04	-0.05
	North															
	Basin	0.14	0.15	0.21	0.22	0.10	-0.10	-0.18	-0.10	0.02	-0.16	0.08	-0.27	-0.03	0.14	-0.28
	Main	*-0.54*	-0.31	0.34	0.30	**0.40**	-0.17	-0.23	-0.08	-0.29	-0.22	0.09	-0.03	*-0.48*	*-0.49*	-0.15
Position	**BSC**															
	South	0.09	**0.47**	0.17	-0.15	*-0.49*	0.05	0.28	0.17	-0.13	**0.37**	-0.08	0.21	0.04	0.26	**0.47**
	Central	0.26	-0.09	-0.17	*-0.55*	0.04	-0.05	0.07	-0.02	0.34	**0.53**	-0.04	0.05	0.21	-0.07	-0.17
	North	**0.41**	0.17	-0.24	-0.32	-0.14	0.05	0.09	0.21	0.13	**0.46**	0.22	**0.40**	**0.39**	0.28	**0.39**
Cross-shelf	**Canyon**															
	Bering	-0.27	0.04	0.27	0.23	0.35	-0.22	*-0.60*	-0.28	-0.09	0.28	**0.37**	0.26	0.08	0.09	0.06
	Pribilof	*-0.39*	-0.13	-0.05	0.05	0.14	0.01	-0.27	-0.23	0.03	-0.30	0.15	-0.01	-0.06	-0.33	-0.34
	Zhemchug	0.24	0.35	**0.48**	*-0.42*	*-0.41*	-0.26	-0.19	-0.13	0.09	**0.76**	**0.47**	0.00	0.19	0.20	-0.10
	Isobath															
	100 m	0.09	0.24	-0.04	-0.12	-0.24	0.28	-0.29	-0.06	-0.01	0.22	**0.42**	0.26	0.36	**0.55**	**0.51**
	200 m	-0.32	0.07	0.23	0.09	0.08	-0.16	*-0.64*	-0.25	-0.29	0.35	**0.70**	0.24	-0.16	0.01	-0.02
	Unimak	*-0.62*	*-0.40*	-0.07	**0.43**	**0.36**	0.13	-0.28	0.06	-0.15	-0.14	0.33	0.05	*-0.65*	*-0.67*	*-0.74*

Canyon ($r = -0.60$, $p < 0.01$). On-shelf transport through Bering and Zhemchug canyons increased as southeasterly along-shelf winds increased, while no significant correlations were found between on-shelf canyon transport and cross-shelf winds. Southeasterly along-shelf winds were positively correlated with transport across both the 100 and 200 m isobaths, while southwesterly on-shelf winds were positively correlated with transport across the 100 m isobath (Table 4). Increased ice cover was negatively correlated with transport across the 200 m isobath ($r = -0.64$, $p < 0.01$).

Transport through Unimak Pass, although not correlated with groundfish recruitment indices, decreased during a positive NPI, but increased during a positive MEI. Strong negative correlations were found between transport through Unimak Pass and increased southwesterly on-shelf winds for all bi-monthly time periods (Table 4), consistent with previous analyses showing enhanced northward transport through Unimak Pass during easterly wind anomalies along the Alaska Peninsula (Bond and Overland, 2005).

4. Discussion

We found that changes in the strength and position of the BSC were associated with changes in along-shelf and cross-shelf flow, which may differentially influence recruitment in the five EBS groundfish species examined. Additionally, we noted that changes in circulation were modulated by climate variability. Northern edges of canyons were identified as regions of increased on-shelf transport, in accordance with generalized canyon circulation, where upwelling typically occurs over the axis and downstream wall of the canyon (Hickey, 1995).

4.1. Transport variability and recruitment

In general, increased northwestward flow in the BSC during February–March was associated with decreased cod recruitment. Major spawning aggregations of cod are found north of Unimak Pass, southwest of the Pribilof Islands along the shelf (Shimada and Kimura, 1994), and at the shelf break near Zhemchug Canyon (Neidetcher et al., 2014). Spawning activity in cod occurs from January through April (Bakkala, 1993; Neidetcher et al., 2014), and takes place predominantly over the outer shelf, most often between 100 and 200 m depth (Neidetcher et al., 2014). Eggs sink to the bottom after fertilization, and are somewhat adhesive, in contrast to the pelagic eggs of the other species examined in this study. Reduced along-shelf transport during this time would likely further reduce northward dispersal of cod early life stages, which could potentially lead to enhanced connectivity with shelf nursery areas in the months following. While cod recruitment was negatively correlated with on-shelf flow from February through May, pelagic juveniles settle in shallow Alaskan coastal waters in July (Blackburn and Jackson, 1982; Laurel et al., 2007), which suggests that the transition to the shelf may occur in late spring or early summer, outside of the time periods examined in this study.

Spawning concentrations of pollock occur near Bogoslof Island, north of Unimak Island and the Alaska Peninsula, and around the Pribilof Islands, as suggested from egg distributions (Bacheler et al., 2010). Two major temporal pulses of eggs have been identified during February–March and April–May (Bacheler et al., 2010), and pollock eggs and larvae would likely be sensitive to flows during this time. Previous research that modeled dispersal of pollock eggs and larvae from a major spawning concentration near Unimak Pass found distinct differences in transport patterns between weak, strong, and average year classes (Wespestad et al., 2000). We found that pollock recruitment was weakly correlated with April–May along-shelf transport, but no other significant correlations were apparent. Flow through Unimak Pass

showed no correlations with recruitment, which was surprising given its proximity to pollock spawning locations and its influence over flow on the shelf. The weak correlations with flow suggest that other factors likely influence pollock recruitment. For example, overwinter survival may be an important mechanism controlling their recruitment (Heintz et al., 2013).

For Greenland halibut in the EBS, spawning is believed to occur along the continental slope from Unimak Pass to as far north as Cape Navarin mainly between November and March (Musienko, 1970; Alton et al., 1988; Sohn et al., 2010). While Sohn et al. (2010) have suggested that Bering and Pribilof canyons are important conduits for transport of Greenland halibut larvae to shelf nursery areas, we found that on-shelf flow through Bering Canyon was associated with a decline in recruitment. Furthermore, Greenland halibut recruitment declined when the BSC shifted closer to the shelf south of Pribilof Canyon, which suggests that larvae may not connect with nursery areas via the southern shelf. Distributions of newly-settled age-0 individuals in the vicinity of St. Matthew Island support this conclusion (Sohn et al., 2010; Lauth, personal communication). Flow north of Pribilof Canyon may be important to Greenland halibut recruitment, and possibly to pollock recruitment as well. Eddy energy is known to be particularly strong in the spring near Zhemchug Canyon (Ladd et al., 2012). The opposing flow regimes observed there during April–May, which are indicative of meanders and eddies, could potentially enhance retention of larvae. Indeed, Greenland halibut and pollock larvae and juveniles recruit to these domains (Sohn et al., 2010; Smart et al., 2012).

For species with a long pelagic larval duration like Greenland halibut (Sohn et al., 2010), slowed northwestward transport may allow sufficient time for larval development prior to transitioning to nursery areas located on the shelf. Duffy-Anderson et al. (2013) showed that Greenland halibut connectivity could be negatively impacted by premature advection to the continental shelf. That study suggested that Greenland halibut could be advected to presumed nursery areas prior to the period of settlement competency, after which time larvae would not reconnect with suitable settlement habitat. Moreover, prolonged entrainment in the BSC reduces the exposure of vulnerable larvae to the variable thermal regimes and wind events over the shallower continental shelf in winter (Stabeno et al., 2012), providing some insulation from shelf-associated environmental stochasticity.

Spawning of Pacific halibut appears to be concentrated in relatively discrete winter spawning grounds near the edge of the continental shelf in the southeast Bering Sea to Pribilof Canyon (St-Pierre, 1984; Seitz et al., 2007). Juveniles settle along the northern Alaska Peninsula, near the Pribilof Islands, especially around St. Paul Island, and near St. Matthew Island (Skud, 1977; St-Pierre, 1989). Our results indicate that Pacific halibut larvae likely connect to shelf nursery areas through Bering and Pribilof canyons, and catches of age-0 individuals in the vicinity of the Alaska Peninsula and Unimak Island support this conclusion (Cooper, personal communication). Several studies have suggested that Pacific halibut larvae are transported into the Bering Sea via inflow of Gulf of Alaska coastal waters through island passes (Best, 1977; Skud, 1977; St-Pierre, 1984, 1989). If Pacific halibut spawned in the Gulf do indeed contribute to EBS recruitment, significant correlations between indices related to inflow from the Gulf of Alaska (e.g., Unimak Pass) and recruitment would be expected. Interestingly, we found no such correlations for any of the time periods examined, which suggests that most of the Pacific halibut in the recruitment index were spawned in the EBS and that delivery of larvae through the Aleutian Passes does not contribute meaningfully to their overall recruitment in the Bering Sea. However, Unimak Pass is narrow (16–35 km; Stabeno et al., 2002), and is not well-resolved by the ROMS model. A more accurate assessment of the relative importance of delivery of propagules through Unimak Pass to small-scale aggregations in the Unimak

vicinity might be a local index of Pacific halibut age-0s along the Alaska Peninsula.

Little is known about arrowtooth flounder spawning timing and location in the EBS, though several studies suggest that spawning occurs in deep waters along the outer continental shelf and slope during fall and winter months (Blood et al., 2007, and references therein). Our results suggest that arrowtooth flounder may connect with shelf nursery areas between Pribilof and Zhemchug canyons. Recruitment increased in relation to a more shelf-ward position of the BSC across the Central transect and on-shelf flow through Zhemchug Canyon, but decreased in relation to increased NW along-shelf flow north of Zhemchug Canyon. However, high numbers of juveniles (≤ 100 mm FL) have also been found on the middle and outer shelves between Bering and Pribilof canyons (Cooper, personal communication), making it likely that arrowtooth flounder also connect to the shelf via southern locations.

4.2. Influence of atmospheric forcing on recruitment-relevant flow

The influence of the dominant modes of climate forcing on groundfish recruitment can be understood by examining their influence on EBS circulation. During a strong AL (negative NPI), warm air is pumped northward and sea ice extent is limited, which results in warmer than normal winters in the EBS (Hollowed and Wooster, 1995; Stabeno et al., 2001; Benson and Trites, 2002). A strong AL is associated with a strong sub-polar gyre, as evidenced by the increase in NW along-shelf transport found in our study, and gyre spin-up may generate more eddy activity in this region (Ladd et al., 2012). Eddies are believed to increase on-shelf transport while in the proximity of the shelf-break (Stabeno and Van Meurs, 1999; Mizobata et al., 2008; Clement Kinney et al., 2009). Eddies, which move downstream at slower rates than the mean currents, can aid in delivering retained larvae to nursery areas (Hinckley et al., 2001); however, they can also transport water from the outer shelf into the basin (Okkonen et al., 2004; Ladd et al., 2012). We found that a weak AL (positive NPI) was associated with a shelf-ward shift in the BSC position, likely due to a more uniformly flowing BSC with fewer eddies. On-shelf transport through Pribilof Canyon decreased, while that through Zhemchug Canyon increased, which again may be indicative of a more regular flow pattern during a positive NPI. Recruitment in cod was most closely associated with along-shelf and on-shelf transport patterns related to the NPI, ice cover, and wind indices. Areas of high intensity spawning have recently been identified for cod around the Pribilof Islands and along the shelf break near Zhemchug Canyon (Neidetcher et al., 2014). Strong northward advection of cod eggs and larvae away from these spawning areas would likely result in transport to unfavorable northern habitats, while a more shelf-ward position of the BSC would likely increase connectivity with nursery areas on the shelf.

Northwesterly along-shelf winds were associated with increased along-shelf transport across sections over the Aleutian Basin for the South and Central transects, while southeasterly winds were associated with increased transport in the main BSC north of Pribilof Canyon. Off-shelf Ekman transport during northwesterly winds may explain the increase in NW transport observed over the basin. However, a recent study of Bering Sea circulation by Danielson et al. (2012) found no evidence of increased off-shelf transport during northwesterly winds. Their study, which used the newer NEP6 ROMS model, found that southeasterly winds were associated with large on-shelf Ekman transport across most of the shelf break (Danielson et al., 2012). Similarly, we found that on-shelf transport through canyons and across isobaths increased when southeasterly along-shelf winds increased. Stronger on-shore flow over Bering Canyon and the shelf-break during winter may benefit a more southerly-distributed species, like Pacific halibut, while a more shelf-ward flow over Pribilof and Zhemchug canyons may benefit species like cod and arrowtooth flounder. In fact, stronger alongshore and cross-shelf winds during winter have been found to generate transport conditions favorable to survival of Pacific halibut, resulting in the production of strong year-classes (Parker, 1989).

Increased southeasterly along-shelf and southwesterly on-shelf winds were also associated with a more shelf-ward position of the BSC. Recent work by Ladd (2014) suggests that mesoscale variability is likely responsible for interannual shifts in BSC position. Large on-shelf Ekman transport generated by strong southeasterly winds may also be responsible for a more shelf-ward shift in BSC position, at least at the surface. Additionally, stronger on-shelf winds may push the BSC closer to the shelf break, and the resulting increased southeastward Ekman transport can potentially impede BSC flow at the surface, as evidenced by the reduced NW along-shelf flow found in our study.

Stronger flow close to the shelf-break during the winter has been observed from satellite altimetry (Ladd, 2014) and model results (Overland et al., 1994). However, we found that the BSC position shifted off-shelf of the mean annual position during the winter and spring. One possible explanation for this discrepancy is that the position calculation may be obscured by the prevalence of eddies in the summer, as the BSC is largely a system of eddies during this time and is not a particularly significant current (Ladd, 2014). Another explanation is that variability in BSC position may not be resolvable with our 10 km gridscale model output. Alternatively, satellite altimetry data measures surface currents, while our study examined changes in the BSC down to 500 m depth. Modeled maximum current velocities were often found at depth, sometimes as deep as 250 m. Interestingly, stronger and deeper flow in the BSC during winter may enhance vertical mixing at the shelf break, which may benefit deep water (> 400 m), slope-spawning species like Greenland halibut, Pacific halibut, and arrowtooth flounder that require both vertical and horizontal connectivity with shelf nursery habitats.

High ice cover was associated with reduced along-shelf flow, likely because both ice and circulation are influenced by winds. Increased ice cover was also associated with reduced on-shelf transport through Bering Canyon and across the 200 m isobath, which would likely benefit species associated with the outer shelf (e.g., cod and Greenland halibut). Significant along-shelf transport was associated with warmer conditions on the Bering Sea shelf, namely a strong AL (negative NPI), and a positive MEI. Previous research has found that strong year classes of pollock occur during warm years when juveniles are transported inshore and away from cannibalistic adults in spring (Wespestad et al., 2000), though this was not confirmed by our results. Poor correlations between pollock and indices related to flow suggest that other factors may influence pollock survival (see Wespestad et al., 2000; Hunt et al., 2002, 2011; Mueter et al., 2006), and recent evidence suggests strong age-1 cohorts may be more the result of total energy condition at the end of their first summer (Heintz et al., 2013) than by transport conditions during the larval phase.

Atmospheric forcing largely controls the extent of sea ice over the EBS shelf, and sea ice extent and timing of retreat are believed to be important physical factors influencing circulation on the shelf (Stabeno et al., 2012). We expected stronger correlations between sea ice and modeled flow patterns, especially since preliminary data analysis indicated that ice cover was positively correlated with recruitment in all species, except for Pacific halibut. However, ice extent may not have much influence on BSC variability, and the link between sea ice and recruitment may be related to factors other than flow. For example, ice cover and extent can affect stratification of shelf waters and timing of the spring-phytoplankton bloom (Hunt and Stabeno, 2002; Hunt et al., 2002, 2011; Sigler et al., 2014), which can impact the match-mismatch of prey production for larval fish. Sea ice characteristics represent an integrated measure of winter atmospheric forcing (Schumacher et al., 2003) and clear relationships with indices related

to flow may be difficult to establish. Still, some speculation as to the relationship between sea ice and currents deserves mention. The freezing and melting of sea ice is known to influence baroclinic flow in the EBS (Stabeno et al., 1999), with circulation often opposing the direction of ice motion (Zhang et al., 2010). During years with high ice cover and strong, cold winds out of the north, the BSC could potentially be pushed off-shelf resulting in reduced along- and on-shelf flow, which may benefit species like cod and Greenland halibut.

4.3. Uncertainties

Despite the fact that strong correlations between flow and recruitment were not found for most of the species examined, except for cod, transport during the early life history stages still likely plays an important role in their recruitment variability. Transport has been shown to be important to year-class formation in Pacific halibut and arrowtooth flounder in the Gulf of Alaska (Bailey and Picquelle, 2002), while in the EBS, transport-mediated spatial separation of juvenile and adult pollock can influence year-class size (Wespestad et al., 2000; Mueter et al., 2006). Other studies have shown that strong year-classes of several flatfish species in the EBS, namely Pacific halibut, flathead sole (*Hippoglossoides elassodon*), northern rock sole (*Lepidopsetta polyxystra*), and arrowtooth flounder, occurred following periods of wind-driven on-shelf transport (Parker, 1989; Wilderbuer et al., 2002).

Recruitment in marine fishes is known to be highly variable, and is influenced by both biological and physical processes operating at changing spatial and temporal scales (Hollowed et al., 2001; Bailey et al., 2005a, 2005b). In addition, the relationships between climate forcing and marine biological responses at higher trophic levels are not as clear as those at lower trophic levels (Hollowed and Wooster, 1995; Hollowed et al., 2001). For example, climate can indirectly affect fish populations through changes in predator distribution and abundance (Bailey, 2000; Benson and Trites, 2002) and also through prey availability or prey quality (Hunt et al., 2002, 2011; Grebmeier et al., 2006; Heintz et al., 2013). Interestingly, we found that age-0 cod recruitment showed the strongest correlations with flow indices, while the correlations for other species were less pronounced. This may be a result of differences in reproductive strategies, as cod are semi-demersal spawners with negatively-buoyant semi-adhesive eggs that remain on or near the bottom (Hurst et al., 2009), while the other species are deep pelagic spawners with pelagic eggs (Doyle et al., 2009; Sohn et al., 2010). Additionally, attempting to correlate flow indices that affect larval abundances to recruitment at age-1 and age-2 may prove especially challenging, as survival to these ages can be influenced by many factors, such as temperature (Houde, 2008), ocean conditions at time of first feeding (Lasker, 1978, 1981), match-mismatch of prey (Cushing, 1974, 1990), predation (Leggett and Deblois, 1994; Wespestad et al., 2000; Mueter et al., 2006), as well as prey quality and quantity (Coyle et al., 2011; Hunt et al., 2011; Mueter et al., 2011). Indeed, it is widely understood that many processes act together over the early life stages and that recruitment variability is not controlled by a single process, mechanism, or factor (Houde, 2008). Another factor that makes it difficult to resolve underlying relationships between recruitment and transport are the recruitment indices themselves. The indices used in this study, except that for Pacific halibut, were derived from modeled estimates of recruitment-at-age. These are back-calculated from catches of older-aged individuals for which more data are available by assuming a constant mortality rate. However, mortality rates can change dramatically during the early life stages (Houde, 2002) and indices derived from older-aged fish may not represent true recruitment at the ages examined here. Similarly, the Pacific halibut recruitment index was derived from survey catch estimates of abundance and may not accurately reflect true recruitment, as smaller-sized Pacific halibut are not well-represented in the groundfish surveys. Finally, it is important to note that recruitment is often poorly correlated with measures of environmental variability, and is usually only significantly correlated for populations at the limit of a species' geographical range (Myers, 1998).

Biases inherent in the circulation model may also further obscure relationships between recruitment, transport, and drivers of environmental variability. While the NEP4 model captures the observed major current systems in the region and represents climatic signals of interest in the eastern Pacific Ocean (Curchitser et al., 2005), simulated currents are weaker and more topographically steered than observations, though current directions are in good agreement with observations (Duffy-Anderson et al., 2013). Another potentially confounding influence on transport estimates are eddies, which are prevalent in the Bering Sea (Stabeno and Van Meurs, 1999; Johnson et al., 2004; Clement Kinney et al., 2009). Since the ROMS model cannot fully resolve eddies at this grid size, on- or off-shelf transport resulting from eddy activity may be underestimated. These biases should be taken into consideration when interpreting the results of this study; however, future modeling efforts may improve upon our results, as the next generation of models under construction have finer spatial resolution.

5. Conclusion

Variability in ocean circulation patterns is likely a key factor in determining year-class strength of marine fishes (Van der Veer et al., 1998). Interannual variations in wind and current patterns may advect eggs and larvae in different directions, with substantial losses occurring when they are transported beyond typical habitat boundaries. Research into the causal relationships between environmental variability and recruitment in marine fishes has important practical and predictive applications (Norcross and Shaw, 1984), especially as climate change over the next century is expected to alter the dominant modes of climate variability and their influence upon circulation and biological processes in the Northeast Pacific (Capotondi et al., 2009; Overland et al., 2010). We found strong variations in the strength and position of the BSC. Changes in along-shelf and cross-shelf flow were associated with changes in recruitment in the groundfish species examined. Pacific cod, in particular, benefitted from decreased along-shelf and on-shelf flow, as did Greenland halibut to a lesser extent. In contrast, Pacific halibut recruitment benefitted from increased on-shelf transport through Bering and Pribilof canyons. Variability in transport and BSC position was strongly influenced by winds, ice cover, and large-scale climatic drivers. The present work aids in understanding how shifts in atmospheric and hydrographic forcing influences recruitment in several commercially and ecologically important groundfish species in the EBS, and may be informative when developing effective fishery management strategies that take a changing climate into account.

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