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Otolith chemistry of juvenile walleye pollock *Gadus chalcogrammus* in relation to regional hydrography: evidence of spatially split cohorts

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ABSTRACT: For many marine ecosystems, uncertainty about nursery locations and the spatial dynamics of juvenile fish impedes our understanding of fish production. Walleye pollock *Gadus chalcogrammus* occur throughout the coastal North Pacific Ocean and support some of the world's largest fisheries. We used otolith microchemistry to answer questions about whether cohorts of young-of-the-year (age-0) walleye pollock are spatially split in the western Gulf of Alaska (GOA). Demographics indicate a possible cohort split between habitat influenced by the Alaska Coastal Current (ACC) (Semidi regions) and habitat more influenced by oceanic influxes (Kodiak region). We used a stratified-random sampling design to select 204 age-0 juveniles collected with a small-mesh trawl during late summer 2007 and 2011. Laser ablation-inductively coupled plasma mass spectrometry was then used to measure the composition of elements assimilated into their otoliths within 1 wk of capture (otolith edge) and over their life histories (otolith edge to core). Otolith edge chemistry varied by region of capture, primarily in strontium:calcium (Sr:Ca), barium:Ca (Ba:Ca), and manganese:Ca (Mn:Ca). Semidi-region otoliths were discriminated from Kodiak otoliths by lower Sr:Ca and higher Ba:Ca and Mn:Ca with 78% (2007) and 79% (2011) success. We estimated that exchange between these 2 habitats was limited for ≥3 (2007) and ≥7 (2011) weeks, sufficient to explain observed demographic differences. We hypothesize that a Semidi–Kodiak split buffers the western GOA population against losses due to density-dependent mechanisms and downstream transport.

KEY WORDS: Juvenile walleye pollock · Otolith chemistry · Split cohort · Nursery · Connectivity

INTRODUCTION

Spatial and temporal resolution of variability in fish production is needed to advance our understanding of marine ecological processes and improve resource management. Spatial dynamics research, including connectivity between specific life stages and nursery locations (Gillanders et al. 2003, Dahlgren et al. 2006, Sheaves et al. 2006), provides context for recruitment-process studies (e.g. Jorde et al. 2007, Pineda et al. 2007, Skagseth et al. 2015, Whitfield & Pattrick 2015, André et al. 2016, Nagelkerken et al. 2017). Spatial structure in fish populations and movements often reflect environmental influence and can complicate our understanding of the recruitment process (Secor 2015). For example, cohorts (year classes) of white perch *Morone americana*, an anadromous species in the Patuxent River estuary, USA, spatially split into dispersive and retentive contingents whose proportional abundance relates to river flow (Kraus & Secor 2004, Kerr et al. 2010). The dispersive contingent moves to brackish-water habitat where juvenile

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*Corresponding author: matt.wilson@noaa.gov growth rates are relatively high and where episodic high survival can lead to strong year classes, whereas the resident contingent remains in fresh water and provides a relatively stable base of low recruitment (Kerr et al. 2010). This complicates the assignment of nursery value to the different habitats because each contingent contributes differently to overall population productivity, stability, and resilience (Kraus & Secor 2005, Secor 2007). Among marine species, spatial structuring of Atlantic cod *Gadus morhua* (Smedbol & Wroblewski 2002) and herring *Clupea harengus* (McQuinn 1997) populations has been described using metapopulation theory to better understand subpopulation interactions and overall population persistence. Spatial structuring has also been suggested for walleye pollock *Gadus chalcogrammus* in the North Pacific Ocean, but more empirical evidence is needed to better understand its role in the recruitment process (Bailey et al. 1999). Fish otoliths are well suited for studying environment-related spatial structure and movement of fish because the elemental composition of otoliths can vary with ambient water properties, effectively tagging (or 'fingerprinting') individuals in habitats of different hydrographic properties (Campana 1999, Chang & Geffen 2013, Kerr & Campana 2014).

Walleye pollock *G. chalcogrammus* (previously *Theragra chalcogramma*; Carr & Marshall 2008, Page et al. 2013) support some of the world's largest fisheries, contributing the greatest biomass of any marine species in 2014 (FAO 2016). Walleye pollock are common over the outer continental shelf and slope throughout the North Pacific Ocean (Bailey et al. 1999). They are a semi-pelagic schooling gadid; individuals can live 20 yr (Bailey et al. 1999) and reach 91 cm in total length (Mecklenburg et al. 2002). Their reproductive potential is great (e.g. Dorn et al. 2015), given that 50% maturity is attained at about age 5, fertilization is external, and fecundity is high. Early life-history stages are planktonic and easily dispersed (e.g. Kendall & Picquelle 1990, Hinckley et al. 1991). Populations are sustainably managed according to a precautionary approach (e.g. Dorn et al. 2015), but walleye pollock undergo large fluctuations in year-class strength (e.g. Bailey et al. 1999, Duffy-Anderson et al. 2016).

In the Gulf of Alaska (GOA), most walleye pollock occur west of 150° W longitude, reflecting the location of major spawning areas and coastal ocean transport (Mueter & Norcross 2002). While multiple spawning areas occur in the western GOA (Ciannelli et al. 2007), genetic structure within this western population has not been well investigated (Dorn et al. 2012). The largest and most intensively studied concentration of spawning adults is in the Shelikof sea valley (Bailey et al. 1999), where peak spawning occurs from March to May (Picquelle & Megrey 1993). Subsequent peak hatching occurs in April/May (Dougherty et al. 2007) and the larvae are about 4 mm standard length (SL) at hatch (Blood et al. 1994). Larvae are transported from the Shelikof sea valley southwestward over the shelf by the Alaska Coastal Current (ACC) (Hinckley et al. 1991), and population densities of larvae in these downstream areas can lead to density-dependent losses (Duffy-Anderson et al. 2002). As the putative major nursery for Shelikof-spawned juveniles, the inner and outer continental shelf regions between Shelikof Strait and the Shumagin Islands have received much research focus (e.g. Wilson 2009, Dougherty et al. 2012, Wilson et al. 2013); hereafter, we refer to these as the Semidi inner-shelf and outer-shelf regions (see Fig. 1). Hatch-date analysis in combination with circulation modeling indicates that many, but not all of the juveniles in these regions originate from the Shelikof sea valley (Dougherty et al. 2012). By late summer, young-of-the-year (age-0) juveniles (40 to 110 mm SL) are common in coastal areas throughout the entire western GOA (Brodeur & Wilson 1996a, Wilson 2000).

The spatial pathway of age-0 juvenile-to-adult recruitment has been difficult to resolve, but could be important to understanding overall population dynamics. A major challenge to resolving this pathway has been the widespread and variable geographic distributions of age-0 abundance (Brodeur & Wilson 1996a) and the existence of multiple spawning areas (Ciannelli et al. 2007, Quinn et al. 2011). However, demographic evidence is consistent with spatial segregation and lack of mixing between age-0 walleye pollock off the Gulf side of Kodiak Island (hereafter the Kodiak region) and those in the Semidi inner- and outer-shelf regions, creating a spatial split within year classes that results in a Kodiak contingent and a Semidi contingent. The natal origin(s) of the Kodiak juveniles is unknown, but could reflect local spawning and retention of larvae near shore (Wilson et al. 2005), downstream transport of larvae and immigration of juveniles from upstream spawning areas in the central GOA (Parada et al. 2016), or perhaps anomalous larval transport (Kendall & Picquelle 1990) and movement of some juveniles from Shelikof Strait. Age-0 juveniles in the Kodiak region are comparatively large (Wilson 2000) and in better condition energetically (Buchheister et al. 2006) than their Semidi-region counterparts. This is thought to reflect higher abundance of large, energy-rich krill *Thysanoessa* spp. (Mazur et al. 2007) in the Kodiak region (Wilson et al. 2013). Among juvenile fish, large individuals are less vulnerable to predation and starvation (Sogard 1997). Consequently, the Kodiak juveniles may have a size-related survival advantage over their smaller Semidi-region counterparts. Furthermore, contribution to the GOA population from the Semidi regions might be further diminished by downstream dislocation of small individuals due to their slower swim speed (Ryer et al. 2002) and greater exposure to the ACC. Downstream transport can potentially result in substantial loss of age-0 juveniles from the GOA (Parada et al. 2016). In fact, age-0 abundance in the Kodiak region better predicted subsequent Gulf-wide age-2 abundance than did age-0 abundance farther southwest (Wilson 2000). Conceivably, spatially split cohorts between the Kodiak and Semidi regions could have important consequences for overall population productivity, stability, and resilience to external forcing, but it might also similarly complicate the determination of nursery value as it did for white perch (Kraus & Secor 2005, Secor 2007).

Otolith microchemistry has potential for detecting whether cohorts split between the Kodiak and Semidi regions. Fish inhabiting hydrographically different water masses can often be distinguished (i.e. 'fingerprinted') by otolith microchemistry. The midwater habitat in the Kodiak region is colder and more saline than in the Semidi region due to oceanic influxes and less ACC influence (Stabeno et al. 2004, Ladd et al. 2005). Separating these and other water chemistry effects on otolith microchemistry can be difficult due to interaction (e.g. Bath et al. 2000, Elsdon & Gillanders 2004, Miller 2009, DiMaria et al. 2010), but our focus on a single species and life stage avoided additional taxonomic (Chang & Geffen 2013) and physiological (e.g. Sturrock et al. 2015) complications. Otolith microchemistry has been used to successfully differentiate geographic groups of juvenile walleye pollock in the Bering Sea (Mulligan et al. 1989) and GOA (Severin et al. 1995). Most recently, Fitzgerald et al. (2004) used laser ablation-inductively coupled plasma mass spectrometry (LA-ICPMS) to show geographic differences in otolith strontium:calcium (Sr:Ca), barium:Ca (Ba:Ca), and manganese:Ca (Mn:Ca) ratios. However, these studies did not include hydrographic information and focused on much larger geographic scales than the meso-scale, hydrographic focus of the present study.

We focused on the western GOA, where groups of juvenile walleye pollock inhabit different water masses in proximity and where uncertainty about spatial structure within the population impedes our understanding of their recruitment process. To fulfill our objective of determining whether age-0 walleye pollock from the Semidi and Kodiak regions represent unique groups without mixing (i.e. a spatial split of the age-0 cohort), we tested the null hypothesis of no difference in region-specific otolith microchemistry. When regionally distinct signatures were detected, we estimated the timing and duration of separation. This provided insight into the possible mechanism(s) underlying regional variation in otolith chemistry and responsible ecological processes, and allowed us to estimate region-specific growth rates from differences in body size.

MATERIALS AND METHODS

Study area

The present study was conducted in the western GOA over the continental shelf in the Kodiak region, and in the Semidi inner- and outer-shelf regions (Fig. 1). These 3 regions are under different hydrographic influences, which we hypothesized would produce distinct effects on otolith microchemistry. These hydrographic patterns are driven largely by the ACC, which is a buoyancy-structured, wind-driven current (Stabeno et al. 2004). Both freshwater input (which provides the buoyancy structure) and winds vary seasonally and interannually (Stabeno et al. 2004). The ACC flows down Shelikof Strait and through the Semidi regions, the putative nursery of Shelikof progeny (Fig. 1). In the Semidi regions, it is evident as a wedge of relatively low-salinity water along the coast (Schumacher & Reed 1986, Stabeno et al. 2004), and ACC water has been associated with cross-shelf gradients in the chemical composition of suspended particulates (Feely et al. 1979, Feely & Massoth 1981). Consequently, its influence on otolith microchemistry may differ between Semidi inner- and outer-shelf regions. In contrast, the midwater habitat of the Kodiak region is comparatively cold and saline due to greatly reduced ACC influence (Stabeno et al. 2004) and influxes of oceanic water through sea valleys with subsequent mixing over the shelf (Ladd et al. 2005).

Field sampling

Hydrographic data and fish were collected in the study area during surveys conducted by the Ecosystems and Fisheries-Oceanography Coordinated In-

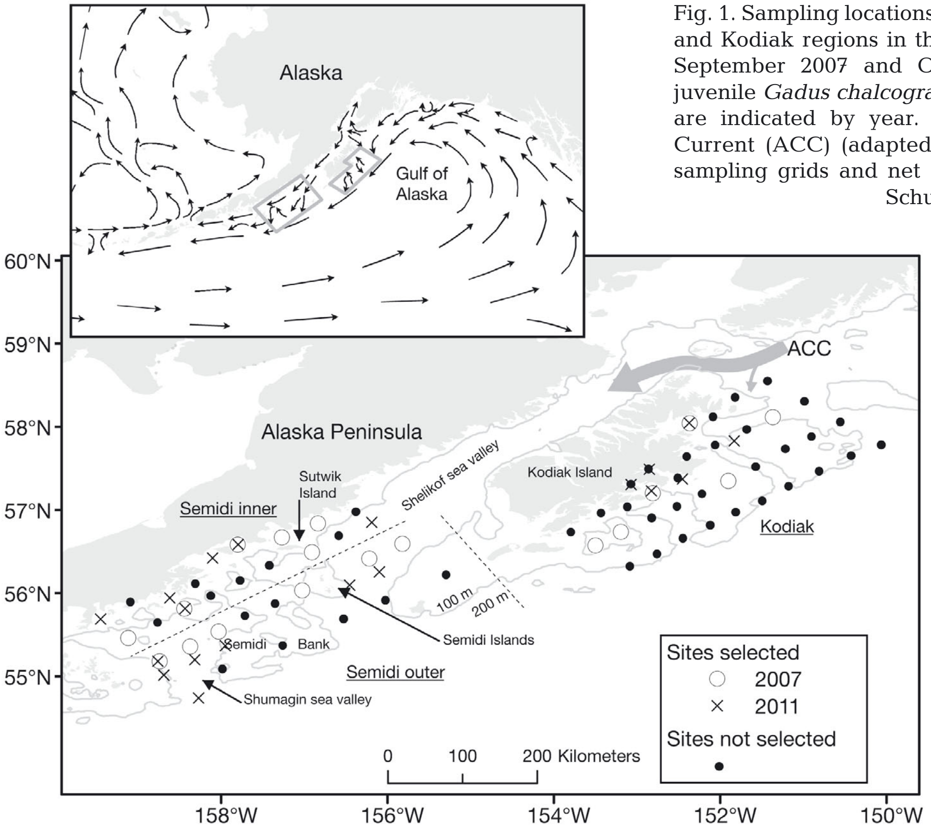

Fig. 1. Sampling locations in the Semidi-inner, Semidi-outer, and Kodiak regions in the Gulf of Alaska occupied during September 2007 and October 2011. Sites where age-0 juvenile *Gadus chalcogrammus* were selected for this study are indicated by year. Gray arrow: the Alaska Coastal Current (ACC) (adapted from Stabeno et al. 2004); inset: sampling grids and net current transport vectors (Reed & Schumacher 1986)

vestigations Program of the National Marine Fisheries Service. The survey targets small neritic fishes. The most geographically extensive sampling occurred during 2007 and 2011, when age-0 walleye pollock *Gadus chalcogrammus* were collected at 36 and 33 sites, respectively. From these collections, samples were selected for the present study using a stratified-random sampling design, with 6 fish from 6 randomly chosen sites per year (2007, 2011) and region (Semidi-inner, Semidi-outer, Kodiak) (Fig. 1) amounting to 212 fish; however, only 24 fish in total were collected in the Kodiak region during 2007. This resulted in 60 fish from Kodiak, 72 fish from Semidi-inner and 72 fish from Semidi-outer. The selected fish were collected between 6 and 15 September 2007 (mean collection date: 12 September 2007), and 3 to 13 October 2011 (mean collection date: 8 October 2011).

Operations were conducted without regard to time of day to collect fish and record water temperature and salinity as described by Wilson et al. (2013). Briefly, at each site, a small-mesh (3 mm codend liner) Stauffer midwater trawl (Wyllie-Echeverria et al. 1990) was fished over an oblique tow path (Wiebe et al. 2015) down to 200 m to collect age-0 walleye pollock. Age-0 walleye pollock were sorted from the catch and frozen (−80°C for 24 h, then held at −20°C) for subsequent examination in the laboratory. Sea-Bird Electronics (SBE)-19 and SBE-39 profilers were used to record water temperature and salinity over the water depths sampled by the trawl.

Otolith processing and data preparation

Both saccular otoliths (i.e. sagittae) were removed from each fish. Fish were measured for SL to the nearest mm. Otoliths collected in 2007 were extracted using surgical-grade steel forceps, cleaned in distilled de-ionized water (Milli-Q equivalent resistivity of 18 MΩ cm^{-1}), and stored dry in airtight vials. Otoliths collected in 2011 were extracted using plastic-tipped forceps to potentially minimize elemental contamination. The right otolith was arbitrarily chosen for chemical analysis.

Otoliths were randomized and prepared for elemental analysis. Each was cleaned ultrasonically in distilled de-ionized water for approximately 10 min, dried for ≥24 h, and embedded in Polytranspar Artificial Water resin. Each embedded otolith was then sectioned in the transverse plane using a Buehler Isomet saw, resulting in sections that were between 0.40 and 0.50 mm thick. Inclusion of the core region within each section was later confirmed microscopically. The resulting 204 sections were rinsed with deionized distilled water, dried, and affixed in randomized order to 5 standard microscope slides using Loctite 349. The sections on each slide were then batch-polished with 600, 800, and 1200 grit abrasive paper, and 0.05 µm Buehler Master-Prep alumina suspension to a common thickness (0.3 to 0.4 mm). Slides were then cleaned in distilled de-ionized water for 5 min in a Branson 1200 ultrasonic cleaner prior to elemental analysis.

We used LA-ICPMS to measure otolith elemental composition at Oregon State University's WM Keck Collaboratory for Plasma Spectrometry in Corvallis, OR, USA. A Thermo X-Series II Quadrupole ICPMS was coupled with a Photon Machines Analyte G2 laser system. The laser was set at a pulse rate of 7 Hz with a 30 µm diameter spot size and scan speed of 5 µm s^{-1}.

Each slide was loaded in random order into the laser-ablation chamber along with glass (National Institute of Standards and Technology, NIST 612) and carbonate (United States Geological Survey Microanalytical Carbonate Standard, MACS3) standards. The standards were included to correct for variation in instrument sensitivity and ablation rate, and to estimate precision (NIST 612; Pearce et al. 1997) and accuracy (MACS3). On each otolith section, 2 transects were ablated: (1) edge, and (2) life history (LH) (Fig. 2). The edge transect, which provided an estimate of the composition of elements assimilated within the region of capture, was approximately 300 µm in length and always situated along the ventral-distal edge (Fig. 2) to ensure consistent comparisons across individuals. The LH transect extended from the dorsal edge to the ventral edge, passing through the core area in order to ensure adequate sampling of the core and facilitate interpretation. However, only data from the core to the ventral edge are presented. Elemental composition of the standards was measured after every 10 otoliths. Background count rates were measured for 45 s pre-ablation and the system was flushed for 30 s post-ablation. Count rates of 16 analytes were recorded along all transects: ^{7}Li, ^{11}B, ^{24}Mg, ^{43}Ca, ^{47}Ti, ^{52}Cr, ^{55}Mn, ^{59}Co, ^{65}Cu, ^{66}Zn, ^{85}Rb, ^{86}Sr, ^{111}Cd, ^{138}Ba, ^{139}La, and ^{208}Pb. NIST glass measurements were used to convert count rates per second (cps) to elemental ratios, relative to Ca, following Kent & Ungerer (2005) and Miller (2007).

A total of 6 analytes were excluded from further analysis. The analytes ^{52}Cr, ^{59}Co, and ^{65}Cu were excluded due to high concentration in the embedding resin (>37% above background). The analytes ^{7}Li, ^{111}Cd, and ^{139}La were excluded due to cps < 3 standard deviations above background (Thomsen et al. 2003).

The remaining 10 elements were used in subsequent analyses of otolith chemical composition. Estimates of precision based on measurements of NIST 612 were: Ca (4%), B (17%), Mg (11%), Ti (18%), Mn (7%), Zn (11%), Rb (9%), Sr (4%), Ba (3%), and Pb (8%). The MACS 3 certificate of composition had information for estimating accuracy (±SD) for 7 ratios (n = 18 samples): Mg:Ca (22 ± 0.33%), Ti:Ca (25 ± 0.01%), Mn:Ca (10 ± 0.09%), Zn:Ca (25 ± 0.03%), Sr:Ca (3 ± 1.07%), Ba:Ca (20 ± 0.02%), and Pb:Ca (6 ± 0.03%).

Otolith edge analysis

We tested the null hypothesis of no region effect on otolith edge elemental composition by conducting a

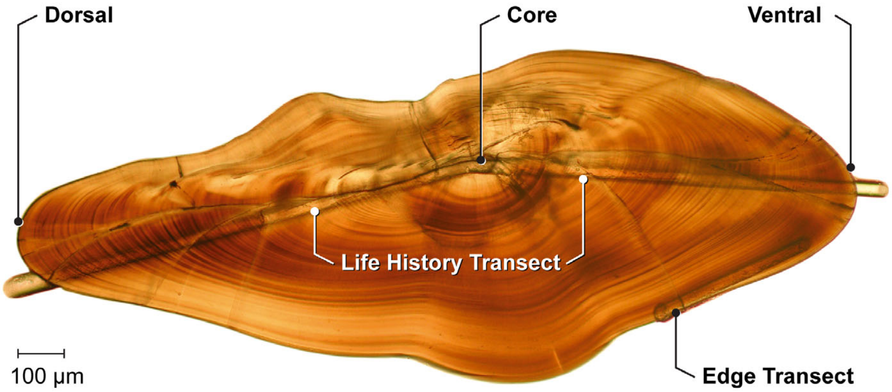

Fig. 2. Transverse section of a saccular otolith (sagitta) from an age-0 juvenile *Gadus chalcogrammus*, 92 mm standard length, collected at Site 'Si8' on 10 October 2011 (otolith ID# 12), showing the laser ablation track along the edge transect and along the life history transect (from the ventral edge through the core to the dorsal edge)

permutational multivariate analysis of variation (PERMANOVA). A PERMANOVA was appropriate as it (1) does not require the data to meet assumptions of normality because it is based on permutations rather than an *F*-distribution like MANOVA, and (2) allows for the inclusion of covariates, including in this case, fish SL. We used an unbalanced, 4 factorial mixed model in order to test for a region effect while accounting for other potential sources of variation:

$$y = \text{slide} + \text{year} + \text{region} + \text{year} \times \text{region} + \text{site}(\text{slide} \times \text{year} \times \text{region}) + \text{SL} \tag{1}$$

where y is the Euclidean distance between otoliths; slide was included as a randomized block (microscope slides 1 to 5); region (Kodiak, Semidi-inner, Semidi-outer) and year (2007, 2011) were included as fixed effects, with an interaction term included to allow regional differences to vary by year; site, a random effect, was nested within slide, year, and region. Fish SL was included as a covariate to account for possible confounding effects on elemental composition. The normalized Euclidean distance between otoliths was based on 4th root transformed element:Ca ratios. The transformation down-weighted Sr:Ca relative to other element ratios. The PERMANOVA test was followed by permutational analysis of multivariate dispersion (PERMDISP; Anderson 2006) which is analogous to the univariate Levene's test of heterogeneity of variances. All statistical analyses were run using the software PRIMER v7 with PERMANOVA+ add-on (Clarke & Gorley 2015).

To assess the performance of elemental composition to discriminate region, we conducted a permutational canonical discriminant analysis (CDA). This approach is a constrained ordination technique that finds components that maximize group variability, which is illustrated by ordination diagrams. As we were using a distance matrix, based on element:Ca ratios, the CDA procedure is actually applied to the principal components from a principal component analysis (PCA), and selects the subset of principal components that minimizes the misclassification rate. A cross-validation procedure (leave-one-out allocation of otoliths to regions) then evaluates discriminant function performance (Anderson & Robinson 2003). Performance was evaluated by the percentage of fish correctly assigned to collection region; model performance was chance-corrected using Cohen's kappa statistic (Titus & Mosher 1984).

Following the multivariate analyses, we conducted similarity percentage analyses (SIMPER) to evaluate the importance of each element to the average dissimilarity between regions within year (Clarke & Gorley 2015). This was conducted only for regions whose pairwise differences were significant. To further assess element importance to regional variation, we tested for a region effect on each of the elements that contributed most to the dissimilarity between regions. The univariate tests followed the same procedure as the multivariate tests.

Otolith life-history analysis

We examined the LH-transect data to determine when observed region-specific changes in otolith microchemistry occurred. Three-dimensional (3D) visualizations were constructed using (1) fish collection location and body size, (2) distance from the otolith edge, and (3) element:Ca ratio. As an exploratory exercise, we included data from 24 fish collected at 4 additional sites. One visualization was constructed for each of the elemental ratios that differed by region. Distance from the otolith edge was estimated by converting the elapsed time (ms) of each measurement (laser start time = 0 ms) along LH transects to distance (µm) using total transect length and total elapsed time. A 10 µm moving average smoothed element:Ca ratios along transects. To estimate timing of changes in otolith microchemistry, a random subsample of otoliths (n = 10) was selected to estimate mean width of daily growth increments over the outer portion of LH transects following Brown & Bailey (1992) and Wilson et al. (2005).

RESULTS

Near-surface salinities were lower in the Semidi regions than in the Kodiak region. The water at Semidi-inner sites was on average warmer and fresher than at collection sites farther offshore (Semidi-outer region) and off the Gulf-side of Kodiak Island (Kodiak region) (Fig. 3). Among the Semidi sites, near-surface temperatures were warmer in 2007 than in 2011; however, below ca. 40 to 50 m depth, temperatures were colder in 2007 than in 2011. Salinity appeared to be fresher during 2011 within the Semidi-inner region, but data were available from only 1 site. The lower near-surface salinities in the Semidi regions relative to Kodiak water were consistent with greater ACC influence.

Age-0 walleye pollock *Gadus chalcogrammus* were smaller in 2007 than in 2011. Lengths averaged (±SE) 60 ± 1.2 mm SL in 2007 and 83 ± 1.6 mm SL in 2011. This was consistent with the earlier sampling in

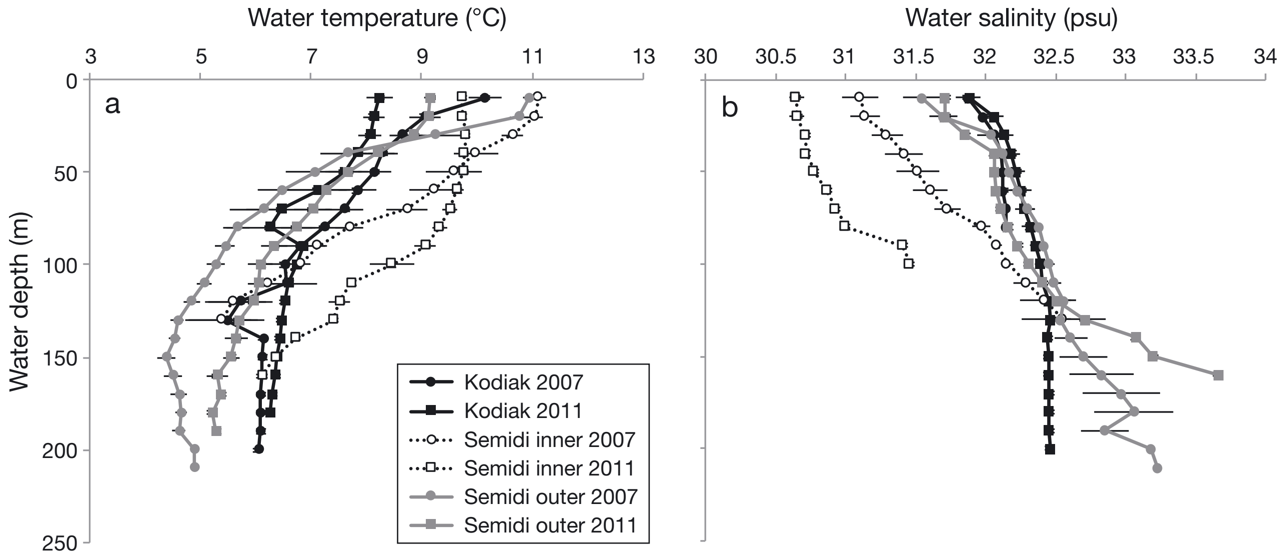

Fig. 3. (a) Water temperature and (b) salinity at 10 m depth intervals averaged (±1 SE) by year and region across sites where age-0 juvenile *Gadus chalcogrammus* were collected in the Gulf of Alaska during September 2007 and October 2011 for otolith chemistry analysis. Salinity profiles were available from only 5 sites during 2011

2007 (September) versus 2011 (October). During 2007, Kodiak fish (n = 24, $\bar{x}$ = 62 ± 1.3 mm) were similar in length to the Semidi-inner (n = 36, $\bar{x}$ = 62 ± 1.3 mm) and Semidi-outer (n = 36, $\bar{x}$ = 57 ± 0.9 mm) juveniles. In contrast, during 2011, Kodiak fish (n = 36, $\bar{x}$ = 96 ± 1.6 mm) tended to be longer than Semidi-inner (n = 36, $\bar{x}$ = 72 ± 1.0 mm) and Semidi-outer (n = 36, $\bar{x}$ = 80 ± 1.0 mm) juveniles.

Otolith edge analysis

Regional differences in otolith-edge elemental composition were detected but varied by year. The year × region interaction was significant (PERMANOVA, p = 0.025) (Table 1). The interaction was due to a difference between the Kodiak and Semidi-inner regions only during 2007 (post hoc pairwise comparison, p = 0.001) and not during 2011 (p = 0.337). Differences between the Semidi-inner and Semidi-outer regions (post hoc pairwise comparison: 2007, p = 0.001; 2011, p = 0.019), and between the Kodiak and Semidi-outer regions (2007, p = 0.001; 2011, p = 0.008) were significant for both years. The covariate, SL, and the randomized block, slide, accounted for significant amounts of variation (Table 1). There was no indication of unequal variance among regions for either year (PERMDISP, p > 0.05). Given that otolith elemental composition differed by region, we next evaluated its performance in discriminating region.

Elemental composition was a good predictor of fish membership to region as indicated by the leave-one-out cross-validation procedure from the CDA. This was evident as separation of regional groups in the associated CDA ordinations for 2007 and 2011 (Fig. 4). For 2007, the derived discriminant functions

Table 1. PERMANOVA results of otolith edge elemental composition among 204 age-0 juvenile *Gadus chalcogrammus* collected from 3 regions in the western Gulf of Alaska during September 2007 and October 2011. SL: standard length; p(perm): p-values based on permutations

Source	df	SS	MS	Pseudo-*F*	p(perm)	Perms	% variance explained
SL	1	74.39	74.39	15.66	0.001	999	5.3
Slide	4	99.24	24.81	4.70	0.001	997	7.6
Year	1	27.99	27.99	5.14	0.001	998	6.3
Region	2	140.83	70.42	12.57	0.001	998	16.6
Year × region	2	27.88	13.94	2.64	0.025	998	4.6
Site(slide × year × region)	105	478.59	4.56	1.78	0.001	999	20.2
Residual	87	225.24	2.56				39.4
Total	203	1074.20					

correctly assigned 73 % of the fish to region (Cohen's kappa = 59 % better than chance) (Table 2). Fish were assigned most successfully to the Semidi-inner region (86 % correct) in association with relatively high Ba:Ca (Fig. 4). For 2011, overall assignment accuracy was 63 % (Cohen's kappa = 44 % better than chance) with the highest success for Kodiak fish (72 % correct) (Table 2) in association with relatively high Sr:Ca (Fig. 4). Given that some elements were apparently more important than others in discriminating region, we next quantified the contribution of each element to regional differences in elemental composition.

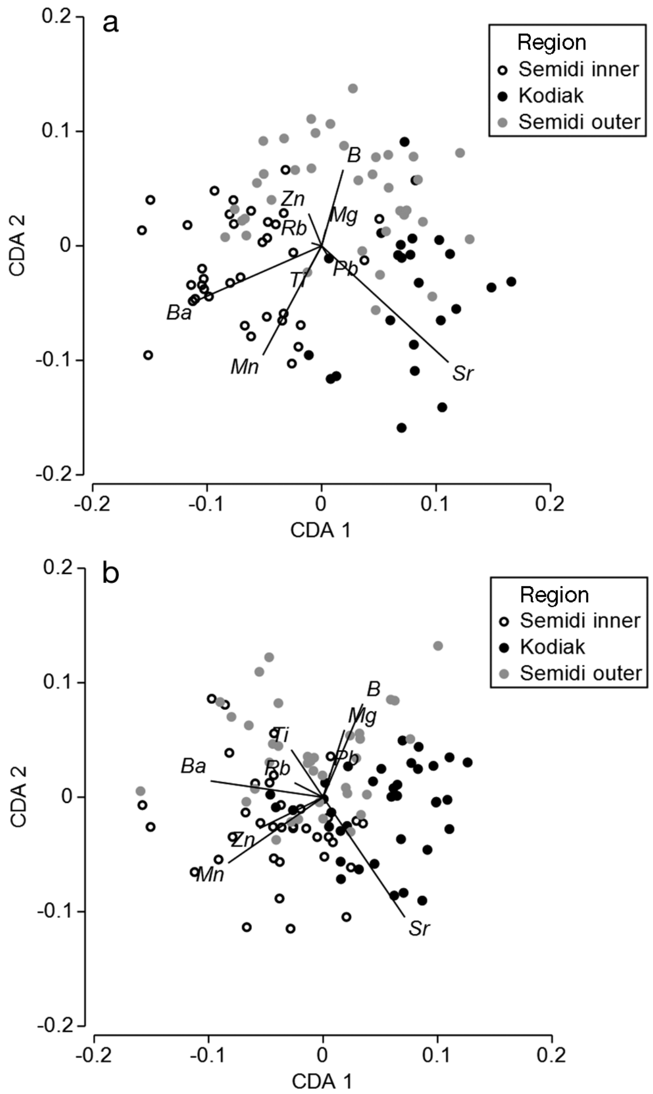

Fig. 4. Canonical discriminant analysis (CDA) ordinations of age-0 *Gadus chalcogrammus* based on otolith element composition. Fish were collected from 3 regions in the western Gulf of Alaska during (a) September 2007 and (b) October 2011. Vectors indicate correlation between element:Ca ratios and CDA axes

Table 2. Classification matrices from canonical discriminant analysis of elemental composition showing the number of correctly classified *Gadus chalcogrammus* by region (**bold** type on diagonal) and % correct for September 2007 (total correct: 70/96 = 73 %) and October 2011 (total correct: 68/108 = 63 %)

Original region	Kodiak	Semidi-inner	Semidi-outer	Total	% correct
2007					
Kodiak	**18**	2	4	24	75
Semidi-inner	1	**31**	4	36	86
Semidi-outer	7	8	**21**	36	58
2011					
Kodiak	**26**	7	3	36	72
Semidi-inner	7	**21**	8	36	58
Semidi-outer	7	8	**21**	36	58

The SIMPER analysis indicated that Sr:Ca, Ba:Ca, and Mn:Ca accounted for 61 to 81 % of the dissimilarity in elemental composition between regions. The greatest contribution was from Sr:Ca in 2007 (23–45 %) and 2011 (24–30 %) followed by Ba:Ca (2007, 13–30 %; 2011, 17–21 %), and Mn:Ca (2007, 13–17 %; 2011, 17–19 %). We next examined the variation of each of these elements at the otolith edge and then along LH transects.

For juveniles collected in the Kodiak region, otolith Sr:Ca was significantly greater than ratios in one or both Semidi regions, depending on year (Table 3, Fig. 5). The year × region interaction was significant (PERMANOVA, $p = 0.001$). Otolith Sr:Ca for juveniles in the Semidi-inner region was lower during 2007 than 2011.

The mean ratio of Ba:Ca was highest in the Semidi-inner region during 2007 (Table 3, Fig. 5). Although

Table 3. Mean ± SE *Gadus chalcogrammus* otolith-edge Sr:Ca and Ba:Ca ratios across collection sites ($n = 6$ for all sites) by region (Kodiak, Semidi-inner, Semidi-outer) and collection year (2007, 2011). Within each year and ratio, means with different superscripts are significantly different ($\alpha < 0.05$) based on PERMANOVA post hoc pairwise tests

Region	Sr:Ca (mg g^{-1}) $\bar{x}$	Sr:Ca (mg g^{-1}) SE	Ba:Ca (mg g^{-1}) $\bar{x}$	Ba:Ca (mg g^{-1}) SE
2007				
Kodiak	5.75^a	0.423	0.021^a	0.004
Semidi-inner	3.84^b	0.147	0.061^b	0.010
Semidi-outer	4.55^c	0.244	0.025^a	0.005
2011				
Kodiak	6.04^a	0.145	0.013	0.002
Semidi-inner	5.32^a	0.243	0.029	0.006
Semidi-outer	4.91^b	0.233	0.026	0.005

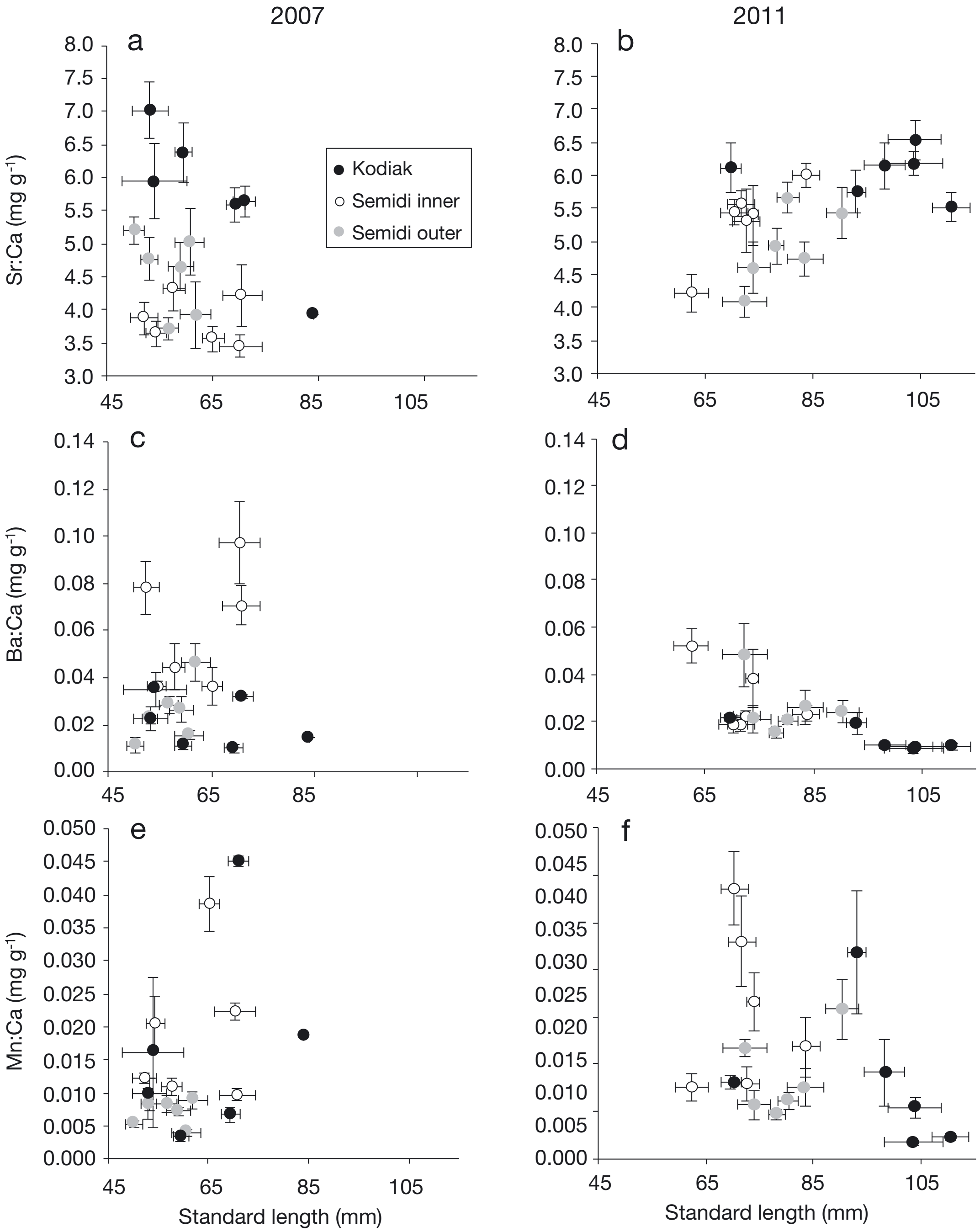

Fig. 5. Collection site means (±1 SE) of age-0 *Gadus chalcogrammus* otolith edge (a,b) Sr:Ca, (c,d) Ba:Ca, and (e,f) Mn:Ca ratios in relation to mean fish body length by collection region (Kodiak, Semidi-inner, Semidi-outer) and year (2007, 2011)

the among-region trend in 2011 was similar, differences between regions were not significant (post hoc, $p > 0.05$). Consequently, the year × region interaction was significant (PERMANOVA, $p = 0.006$).

The mean ratio of Mn:Ca was highest in the Semidi-inner region regardless of year. The year × region interaction was not significant (PERMANOVA, $p = 0.324$); thus, we report means for years combined: Semidi-inner, 0.017 ± 0.003 mg g^{-1}; Semidi-outer, 0.008 ± 0.001 mg g^{-1}; and Kodiak, 0.012 ± 0.004 mg g^{-1}. A separate plot for each year is shown in Fig. 5, despite no year × region interaction, simply to illustrate the similarity of regional variation between years.

Otolith life-history analysis

The most notable feature of the LH trajectories of element:Ca ratios was low Sr:Ca ratios (<4.3 mg g^{-1}) over long segments of the LH transects for 68% of the otoliths. The segment length over which Sr:Ca was low varied between 10 and 330 µm for otoliths in 2007, and between 10 and 770 µm for otoliths in 2011. For 2007, on average, the low Sr:Ca segments of LH transects were situated at 20 to 120 µm from the otolith edge. For 2011, they were situated at 140 to 320 µm. Thus, on average, these segments were closer to the otolith edge in 2007 (Fig. 6) than in 2011 (Fig. 7), when sampling occurred about 1 mo later and fish were larger. There was also an apparent inverse association between Sr:Ca and Ba:Ca, and to a lesser extent, Mn:Ca (Figs. 6 & 7). When arranged geographically, this 3-element signal was evidently more prevalent in the Semidi regions than in the Kodiak region (hereafter, the Semidi signal). The regional delineation, however, was not perfect; for example, compare Sr:Ca trajectories at Sites 'So5' and 'So6' to other Semidi-outer sites (Fig. 7). The overall success of the Semidi signal to discriminate the 204 fish by Semidi and Kodiak regions was 75% (Cohen's kappa = 41% better than chance) and 79% (Cohen's kappa = 53% better than chance) for 2007 and 2011, respectively.

Our estimates of signal timing were similar between years, but the estimated duration of limited population exchange was longer during 2011 than 2007. Mean daily increment width over the outer portion of LH transects did not vary by year (*t*-test, n = 10, p = 0.65) and averaged (±SD) 6.8 ± 0.53 µm. The date of mean signal formation onset was 22 August 2007 and 20 August 2011 (e.g. the distance from the otolith edge to the mean segment inner endpoint, 320 µm, divided by mean increment width, 6.8 µm, equals 47 d prior to capture in 2011). The approximate duration of limited exchange between the Semidi and Kodiak regions was therefore at least 3 and 7 wk prior to our sampling in 2007 and 2011, respectively. Assuming the regional differences in mean body length among our 204 fish materialized during these periods of limited exchange, we estimate that the Kodiak fish grew approximately 0.16 to 0.51 mm d^{-1} faster than the Semidi fish (i.e. the difference in mean fish length between regions divided by the estimated number of days of limited exchange).

DISCUSSION

We showed that age-0 juvenile walleye pollock *Gadus chalcogrammus* collected in different water masses over the GOA shelf could be discriminated with 78 to 79% success based on otolith Sr:Ca, Ba:Ca, and Mn:Ca ratios. We estimate that mixing between these populations was limited for at least 3 and 7 wk prior to capture in 2007 and 2011, respectively, and likely reflects recent differences in ambient conditions. If these groups were segregated earlier in their life history, such as due to divergent natal origin or transport of larvae, it was not evident in otolith chemistry, potentially due to similar ambient conditions regardless of proximity. The pronounced, common occurrence of the Semidi signal (low Sr:Ca, and high Ba:Ca and Mn:Ca) in the outer portions of the otoliths for Semidi but not Kodiak juveniles was indicative of a spatial split between these groups beginning in late August in the 2 years sampled. Our estimated Semidi–Kodiak differences in growth rate were slightly higher than bioenergetics-based estimates (0.02 to 0.37 mm d^{-1}; Wilson et al. 2013). We recognize that these estimates are sensitive to regional differences in fish size prior to our sampling. The low end of the range can be attributed to small fish size during 2007. Small fish may not benefit from residing in the krill-rich (*Thysannoesa* spp.) Kodiak habitat (Wilson et al. 2013) due to their mouth gape limitations (Brodeur 1998) and the large size of krill relative to most other prey (Wilson et al. 2011). Thus, limited exchange between regions of different habitat quality can reasonably explain the different demographics observed between the Semidi and Kodiak populations.

The proximate cause of the Semidi signal is unclear, but likely relates to water properties more than to body size or diet. Size does not explain the absence of the Semidi signal from the Kodiak fish, which were as big as or bigger than Semidi fish. Furthermore, although the diets of Semidi and Kodiak fish differ (Wilson et al. 2013), diet is thought to have only a minor effect on otolith chemistry (Chang & Geffen 2013). While water chemistry, temperature, and salinity are the likely cause, interactions among them (e.g. Bath et al. 2000, Elsdon & Gillanders 2004, Miller 2009, DiMaria et al. 2010) and our lack of data on seawater chemistry prevent further resolution of the specific cause.

The greater influence of the ACC in the Semidi regions is evident in the hydrographic differences between the Semidi and Kodiak regions. Vertical profiles of water temperature and salinity in the Semidi-inner and Semidi-outer regions indicated the presence of a warmer, low-salinity wedge of ACC water, similar to previous observations (Schumacher & Reed 1986). Freshwater inputs to estuaries and subsequent mixing into the ACC could increase Ba:Ca ratios (Guay & Falkner 1997, Yamamoto-Kawai et al. 2010)

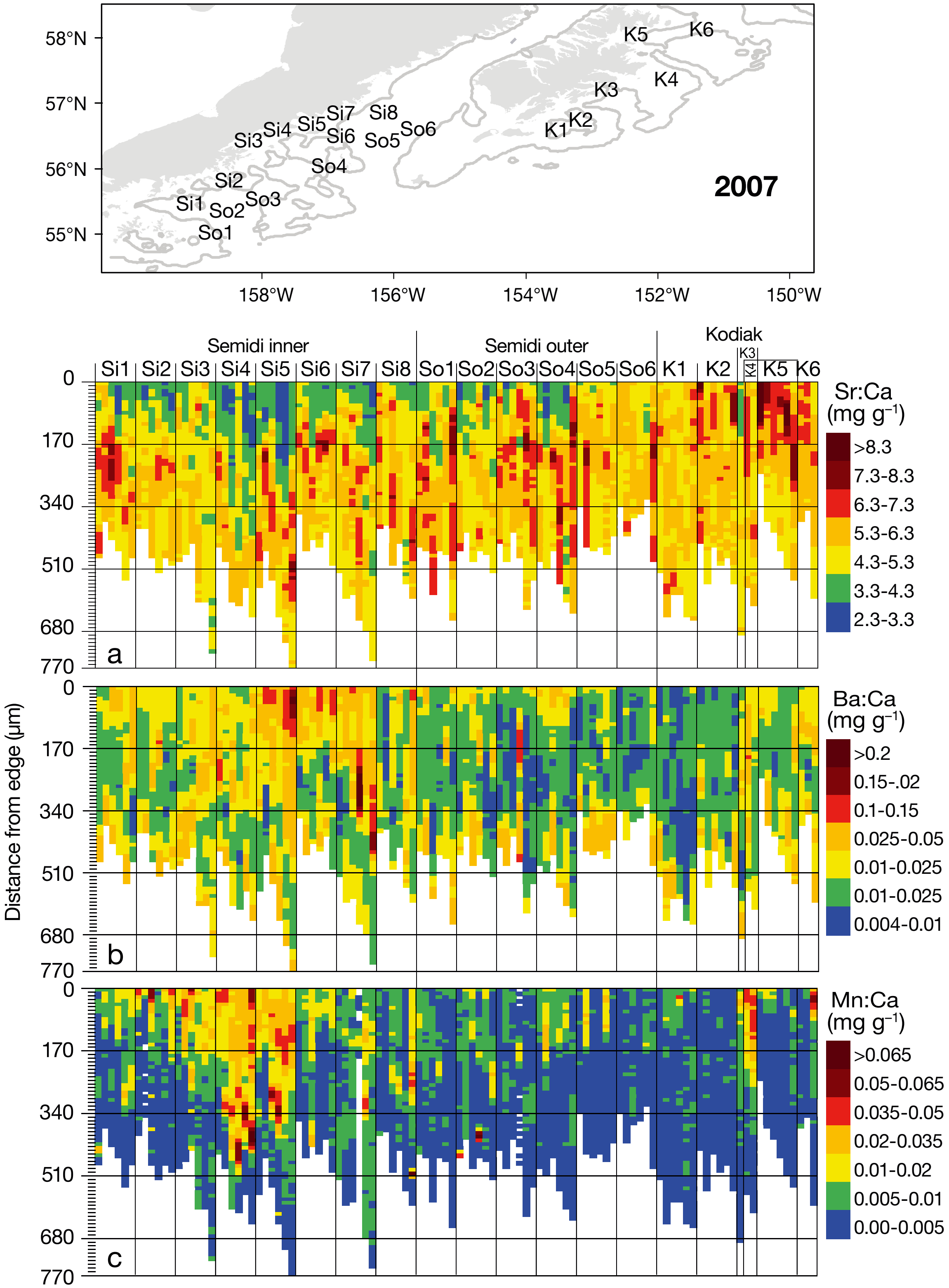

Fig. 6. Smoothed trajectories of otolith (a) Sr:Ca, (b) Ba:Ca, and (c) Mn:Ca along life history (LH) transects (ventral edge to core area) for 108 age-0 *Gadus chalcogrammus* collected between 6 and 15 September 2007 at 20 sites in the western Gulf of Alaska (inset map shows site locations). Each column of pixels represents 1 LH transect, pixel color represents the 10 µm bin mean of the smoothed ratios. Transects are ordered from left to right by region (Semidi-inner: Si; Semidi-outer: So; Kodiak: K), site (1 to 8), and increasing fish body length. We included exploratory data from 12 fish from Sites 'Si3' and 'Si8'

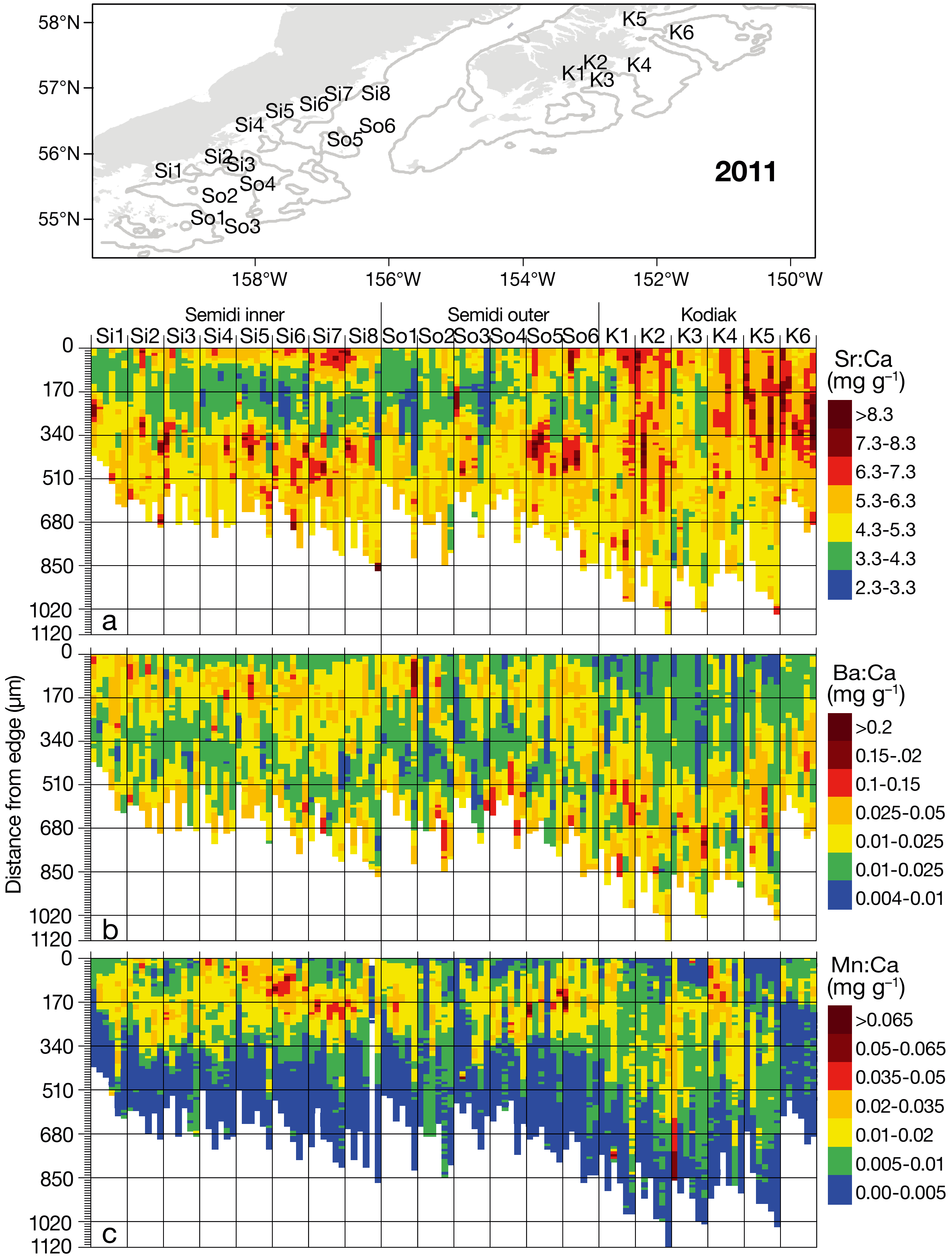

Fig. 7. Smoothed trajectories of otolith (a) Sr:Ca, (b) Ba:Ca, and (c) Mn:Ca along life history (LH) transects (ventral edge to core area) for 120 age-0 *Gadus chalcogrammus* collected between 3 and 13 October 2011 at 20 sites in the western Gulf of Alaska (inset map shows site locations). Each column of pixels represents 1 LH transect, pixel color represents the 10 µm bin mean of the smoothed ratios. Transects are ordered from left to right by region (Semidi-inner: Si; Semidi-outer: So; Kodiak: K), site (1 to 8), and increasing fish body length. We included exploratory data from 12 fish from Sites 'Si6' and 'Si7'

and may decrease Sr:Ca ratios (Brown & Severin 2009). It is unclear whether upwelling causes localized Ba:Ca enrichment in the GOA, although localized upwelling was reflected in the timing and location of enriched otolith Ba:Ca in juvenile rockfish *Sebastes jordani* off California (Woodson et al. 2013). While Mn:Ca contributed to regional variation in otolith chemistry, this is difficult to explain because the mechanisms governing its incorporation are poorly understood (e.g. Miller et al. 2006, Miller 2009). We suggest that the position and extent of the Semidi signal in otoliths reflect the exposure schedule of age-0 juveniles to ACC water. This would depend on their geographic location, their vertical position in the water column, which varies over diel (Brodeur & Wilson 1996b) and seasonal (Brodeur & Wilson 1996a) temporal scales, and the depth and extent of the wedge of ACC water (Schumacher & Reed 1986). We acknowledge, however, that otolith elemental composition varied within region, which warrants further investigation. Until the underlying mechanism is better understood, we caution against future assumptions that similar regional differences in otolith chemistry will occur within other cohorts.

Spatial contingents of age-0 walleye pollock in the Semidi and Kodiak regions could possibly buffer the western GOA population against regional effects on retention and survival. The Semidi regions are the putative nursery for juveniles spawned by the very large aggregation of adults in the Shelikof sea valley and they are exposed to the ACC. As such, their role as a nursery may suffer from density-dependent mechanisms (e.g. Duffy-Anderson et al. 2002) and transport-related losses. Coastal currents have long been associated with marine fish movements (Secor 2015). Off the Norwegian coast, year-class strength of spring spawning herring *Clupea harengus* appears to benefit from long-distance transport in the Norwegian Coastal Current to Barents Sea nurseries (Skagseth et al. 2015). In the western GOA, downstream movement of age-0 juveniles through the Semidi regions reflects southwestward ACC-related transport (Hinckley et al. 1991). Given the overlap between age-0 juvenile cruising speeds (1 to 2 body length s^{-1}; Ryer et al. 2002) and ocean current net velocities (3 to 28 cm s^{-1}; Schumacher & Reed 1986), years of high summer flow or poor growth might reduce the proportion of fish able to remain in favorable local habitat (e.g. Wilson 2009, Wilson et al. 2009) while increasing the proportion advected far downstream and perhaps exported from the GOA (Parada et al. 2016). It is noteworthy that the abundance of yearlings in the Shelikof sea valley, which abuts the Semidi regions, is a good predictor of year-class strength (McKelvey 1996, Dorn et al. 2015), perhaps further underscoring the importance of local retention to GOA recruitment.

The favorability of local habitat depends at least partly on nutrient and prey influxes that stimulate productivity and supplement the community of zooplankton consumed by age-0 walleye pollock. Nutrient enrichment can occur when nutrient-rich oceanic water enters sea valleys that transect the shelf and becomes vertically mixed in coastal areas (Ladd et al. 2005). The deep-sea valleys are also associated with relatively high population density of krill (e.g. Wilson 2009), which are an energy-rich, preferred prey of age-0 walleye pollock (Wilson et al. 2006, Mazur et al. 2007). The colder, more saline midwater habitat across the shelf in the Kodiak region, as compared to the Semidi regions, reflects greater oceanic influence. This has been associated with a relative abundance of large krill, and food-related benefits (i.e. krill-rich diet, large body size) to age-0 walleye pollock (Wilson et al. 2013). Additionally, Kodiak is the only region we know of that supports summer-spawned age-0 juveniles (Wilson et al. 2005), but the natal origin of these and the more abundant spring-spawned juveniles remains unknown. Nevertheless, spatial and temporal splitting of cohorts during the juvenile stage is of recognized importance in bet-hedging against local adverse environmental effects on fish survival (Secor 2007, 2015). A next step to resolving the importance of possible contingent structure would be to determine whether a disproportionate number of the yearlings and adults in the Shelikof sea valley exhibit the Semidi signal in their otolith microchemistry, and whether adults in the Kodiak region do not exhibit the signal. In other words, our future objective is to determine the nursery value of each region to each adult spawning aggregation (e.g. Kraus & Secor 2005). In the coastal North Atlantic Ocean, another gadid, Atlantic cod *Gadus morhua*, exhibits meso-scale spatial structuring to a degree that results in genetic structure (e.g. Smedbol & Wroblewski 2002, Jorde et al. 2007, André et al. 2016). To our knowledge, evidence of meso-scale spatial structure in population genetics or complex behavioral mechanisms such as philopatry (e.g. Secor 2015) have not been well examined for walleye pollock in the western GOA.

Our measurements integrated across multiple daily growth increments, reducing the temporal resolution of our results. Ablation depth and laser spot size can cause integration over the 3D structure of otolith growth increments (Hoover & Jones 2013). Curvature of growth increments over the depth of the ablation track was not apparent; however, effective laser spot size resulted in integration over approximately 7 daily growth increments (i.e. 1 wk). Post-ablation microscopic inspection indicated that the effective width and depth of ablation tracks was approximately 50 and 20 µm, respectively. While 50 µm is large relative to the minimum length of the Semidi signal (10 µm), it is small relative to the maximum length, and only 0.3 to 0.5 times the average length. Thus, while LA-ICPMS inherently reduced our temporal resolution, it did allow for signal detection and provided element:Ca ratios that were similar to those reported previously for juvenile walleye pollock (Severin et al. 1995, Fitzgerald et al. 2004).

In summary, a chemical signature in otolith Sr:Ca, Ba:Ca, and Mn:Ca (i.e. the Semidi signal) enabled 78 to 79% successful discrimination of individuals in the Semidi regions from those off the Gulf side of Kodiak Island. We estimate that exchange between these populations was limited for at least 3 and 7 wk prior to capture in September 2007 and October 2011, respectively. This spatial splitting of cohorts between habitats of differing quality can reasonably explain observed demographic differences. The low Sr:Ca and high Ba:Ca ratios of the signal might reflect fish schedules of exposure to ACC water, but additional information is needed. We hypothesize that spatial splitting of cohorts between the Semidi and Kodiak regions confers resilience to GOA walleye pollock against environmental conditions that adversely affect local retention and recruitment. Finally, by demonstrating that otolith chemistry differs between the Kodiak and Semidi regions, we now have a tool to address questions about contingent structure within the overall GOA walleye pollock population and perhaps determine the nursery value (Kraus & Secor 2005) of the Kodiak and Semidi regions with regard to each of the many spawning populations.

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LITERATURE CITED

Anderson MJ (2006) Distance-based test for homogeneity of multivariate dispersions. Biometrics 62:245–253

Anderson MJ, Robinson J (2003) Generalized discriminant analysis based on distances. Aust NZ J Stat 45:301–318

André C, Svedäng H, Knutsen H, Dahle G and others (2016) Population structure in Atlantic cod in the eastern North Sea-Skagerrak-Kattegat: early life stage dispersal and adult migration. BMC Res Notes 9:63

Bailey KM, Quinn TJ, Bentzen R, Grant WS (1999) Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. Adv Mar Biol 37:179–255

Bath GE, Thorrold SR, Jones CM, Campana SE, McLaren JW, Lam JWH (2000) Strontium and barium uptake in aragonitic otoliths of marine fish. Geochim Cosmochim Acta 64:1705–1714

Blood DM, Matarese AC, Yoklavich MM (1994) Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Alaska. Fish Bull 92:207–222

Brodeur RD (1998) Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. Environ Biol Fishes 51:175–186

Brodeur RD, Wilson MT (1996a) A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. Fish Oceanogr 5(Suppl 1):148–166

Brodeur RD, Wilson MT (1996b) Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can J Fish Aquat Sci 53: 1951–1963

Brown AL, Bailey KM (1992) Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. Mar Biol 112:23–30

Brown RJ, Severin KP (2009) Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Can J Fish Aquat Sci 66:1790–1808

Buchheister A, Wilson MT, Foy RJ, Beauchamp DA (2006) Seasonal and geographic variation in condition of juvenile walleye pollock in the western Gulf of Alaska. Trans Am Fish Soc 135:897–907

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297

Carr SM, Marshall HD (2008) Phylogeographic analysis of complete mtDNA genomes from walleye pollock (*Gadus chalcogrammus* Pallas, 1811) shows an ancient origin of genetic biodiversity. Mitochondrial DNA 19:490–496

Chang MY, Geffen AJ (2013) Taxonomic and geographic influences on fish otolith microchemistry. Fish Fish 14: 458–492

Ciannelli L, Bailey KM, Chan KS, Stenseth NC (2007) Phenological and geographical patterns of walleye pollock (*Theragra chalcogramma*) spawning in the western Gulf of Alaska. Can J Fish Aquat Sci 64:713–722

Clarke KR, Gorley RN (2015) PRIMER v7: user manual/tutorial. PRIMER-E, Plymouth

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM and others (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Mar Ecol Prog Ser 312:291–295

DiMaria RA, Miller JA, Hurst TP (2010) Temperature and growth effects on otolith elemental chemistry of larval Pacific cod, *Gadus macrocephalus.* Environ Biol Fishes 89:453–462

Dorn M, Aydin K, Barbeaux S, Jones D, Spalinger K, Palsson W (2012) Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska: assessment of the walleye pollock stock in the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK, p 53–182

Dorn M, Aydin K, Jones D, McCarthy A, Palsson W, Spalinger K (2015) Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska: assessment of the walleye pollock stock in the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK, p 49–172

Dougherty AB, Bailey KM, Mier KL (2007) Interannual differences in growth and hatch date distribution of age-0 year walleye pollock *Theragra chalcogramma* (Pallas) sampled from the Shumagin Islands region of the Gulf of Alaska, 1985–2001. J Fish Biol 71:763–780

Dougherty A, Bailey K, Vance T, Cheng W (2012) Underlying causes of habitat-associated differences in size of age-0 walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Mar Biol 159:1733–1744

Duffy-Anderson JT, Bailey KM, Ciannelli L (2002) Consequences of a superabundance of larval walleye pollock *Theragra chalcogramma* in the Gulf of Alaska in 1981. Mar Ecol Prog Ser 243:179–190

Duffy-Anderson JT, Barbeaux SJ, Farley E, Heintz R and others (2016) The critical first year of life of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea: implications for recruitment and future research. Deep-Sea Res II 134:283–301

Elsdon TS, Gillanders BM (2004) Fish otolith chemistry influenced by exposure to multiple environmental variables. J Exp Mar Biol Ecol 313:269–284

FAO (2016) The state of world fisheries and aquaculture 2016: contributing to food security and nutrition for all. FAO, Rome

Feely RA, Massoth GJ (1981) Major- and trace-element composition of suspended matter in the north-east Gulf of Alaska: relationships with major sources. Mar Chem 10:431–453

Feely RA, Baker ET, Schumacher JD, Massoth GJ, Landing WM (1979) Processes affecting the distribution and transport of suspended matter in the northeast Gulf of Alaska. Deep-Sea Res A Oceanogr Res Pap 26:445–464

Fitzgerald JL, Thorrold SR, Bailey KM, Brown AL, Severin KP (2004) Elemental signatures in otoliths of larval walleye pollock (*Theragra chalcogramma*) from the northeast Pacific Ocean. Fish Bull 102:604–616

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247:281–295

Guay CK, Falkner KK (1997) Barium as a tracer of Arctic halocline and river waters. Deep-Sea Res II 44:1543–1569

Hinckley S, Bailey KM, Picquelle SJ, Schumacher JD, Stabeno PJ (1991) Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can J Fish Aquat Sci 48:91–98

Hoover RR, Jones CM (2013) Effect of laser ablation depth in otolith life history scans. Mar Ecol Prog Ser 486:247–256

Jorde PE, Knutsen H, Espeland SH, Stenseth NC (2007) Spatial scale of genetic structure in coastal cod *Gadus morhua* and geographic extent of local populations. Mar Ecol Prog Ser 343:229–237

Kendall AW Jr, Picquelle SJ (1990) Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish Bull 88:133–154

Kent AJR, Ungerer CA (2005) Production of barium and light rare earth element oxides during LA-ICP-MS microanalysis. J Anal Atomic Spectrom 20:1256–1262

Kerr LA, Campana SE (2014) Chemical composition of fish hard parts as a natural marker of fish stocks. In: Cadrin SX, Kerr LA, Mariani S (eds) Stock identification methods, 2nd edn. Academic Press, San Diego, CA, p 205–234

Kerr LA, Cadrin SX, Secor DH (2010) The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecol Appl 20:497–507

Kraus RT, Secor DH (2004) Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279:247–259

Kraus RT, Secor DH (2005) Application of the nursery-role hypothesis to an estuarine fish. Mar Ecol Prog Ser 291:301–305

Ladd C, Stabeno P, Cokelet ED (2005) A note on cross-shelf exchange in the northern Gulf of Alaska. Deep-Sea Res II 52:667–679

Mazur MM, Wilson MT, Dougherty AB, Buchheister A, Beauchamp DA (2007) Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. J Fish Biol 70:816–836

McKelvey D (1996) Juvenile walleye pollock, *Theragra chalcogramma*, distribution and abundance in Shelikof Strait — What can we learn from acoustic survey results? In: Brodeur RD, Livingston PA, Loughlin TR, Hollowed AB (eds) Ecology of juvenile walleye pollock, *Theragra chalcogramma*: papers from the workshop 'The importance of prerecruit walleye pollock to the Bering Sea and North Pacific ecosystems'. Seattle, WA, 28–30 October 1993. NOAA Tech Rep NMFS 126, US Department of Commerce, Seattle, WA, p 25–34

McQuinn IH (1997) Metapopulations and the Atlantic herring. Rev Fish Biol Fish 7:297–329

Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society. Bethesda, MD

Miller JA (2007) Scales of variation in otolith elemental chemistry of juvenile staghorn sculpin (*Leptocottus armatus*) in three Pacific Northwest estuaries. Mar Biol 151:483–494

Miller JA (2009) The effects of temperature and water concentration on the otolith incorporation of barium and manganese in black rockfish *Sebastes melanops.* J Fish Biol 75:39–60

Miller MB, Clough AM, Batson JN, Vachet RW (2006) Transition metal binding to cod otolith proteins. J Exp Mar Biol Ecol 329:135–143

Mueter FJ, Norcross BL (2002) Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. Fish Bull 100:559–581

Mulligan TJ, Bailey K, Hinckley S (1989) The occurrence of larval and juvenile walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea with implications for stock structure. In: Proc Int Symp Biol Manage walleye pollock, Anchorage, AK, 14 to 16 November 1988. Alaska Sea Grant Report No. 89-1, University of Alaska, Fairbanks, AK, p 471–489

Nagelkerken I, Huebert KB, Serafy JE, Grol MGG, Dorenbosch M, Bradshaw CJA (2017) Highly localized replenishment of coral reef fish populations near nursery habitats. Mar Ecol Prog Ser 568:137–150

Page LM, Espinosa-Pérez H, Findley LT, Gilbert CR and others (2013) Common and scientific names of fishes from the United States, Canada, and Mexico, 7th edn. American Fisheries Society, Special Publication 34, Bethesda, MD

Parada C, Hinckley S, Horne JK, Curchister E (2016) Modeling connectivity of walleye pollock in the Gulf of Alaska: Are there any linkages to the Bering Sea and Aleutian Islands? Deep-Sea Res II 132:227–239

Pearce NJG, Perkins WT, Westgate JA, Gorton MP, Jackson SE, Neal CR, Chenery SP (1997) A compilation of new and published major and trace element data for NIST SRM 610 and NIST SRM 612 glass reference materials. Geol Newsl 21:115–144

Picquelle SJ, Megrey BA (1993) A preliminary spawning biomass estimate of walleye pollock, *Theragra chalcogramma*, in the Shelikof Strait, Alaska, based on the annual egg production method. Bull Mar Sci 53:728–749

Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography (Wash DC) 20:22–39

Quinn TJ II, Ianelli JN, Cadrin SX, Wespestad V, Barbeaux SJ (2011) Report on a workshop on spatial structure and dynamics of walleye pollock in the Bering Sea. AFSC Processed Report 2011-04. Alaska Fisheries Science Center, NOAA, National Marine Fish Service, Seattle, WA

Reed RK, Schumacher JD (1986) Physical oceanography. In: Hood DW, Zimmerman ST (eds) The Gulf of Alaska: physical environment and biological resources. Ocean Assessment Division, NOAA, Washington, DC, p 57–75

Ryer CH, Lawton A, Lopez RJ, Olla BL (2002) A comparison of the functional ecology of visual vs. nonvisual foraging in two planktivorous marine fishes. Can J Fish Aquat Sci 59:1305–1314

Schumacher JD, Reed RK (1986) On the Alaska Coastal Current in the western Gulf of Alaska. J Geophys Res 91: 9655–9661

Secor D (2007) The year-class phenomenon and the storage effect in marine fishes. J Sea Res 57:91–103

Secor D (2015) Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore, MD

Severin KP, Carroll J, Norcross BL (1995) Electron microprobe analysis of juvenile walleye pollock, *Theragra chalcogramma*, otoliths from Alaska: a pilot stock separation study. Environ Biol Fishes 43:269–283

Sheaves M, Baker R, Johnston R (2006) Marine nurseries and effective juvenile habitats: an alternative view. Mar Ecol Prog Ser 318:303–306

Skagseth Ø, Slotte A, Stenevik EK, Nash RDM (2015) Characteristics of the Norwegian Coastal Current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L.). PLOS ONE 10:e0144117

Smedbol RK, Wroblewski JS (2002) Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. Fish Res 55:161–174

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60: 1129–1157

Stabeno PJ, Bond NA, Hermann AJ, Kachel NB, Mordy CW, Overland JE (2004) Meteorology and oceanography of the northern Gulf of Alaska. Cont Shelf Res 24:859–897

Sturrock AM, Hunter E, Milton JA, EIMF, Johnson RC, Waring CP, Trueman CN (2015) Quantifying physiological influences on otolith microchemistry. Methods Ecol Evol 6:806–816

Thomsen V, Schatzlein D, Mercuro D (2003) Limits of detection in spectroscopy. Spectroscopy 18:112–114

Titus K, Mosher JA (1984) Chance-corrected classification for use in discriminant analysis: ecological applications. Am Midl Nat 111:1–7

Whitfield AK, Pattrick P (2015) Habitat type and nursery function for coastal marine fish species, with emphasis on the Eastern Cape region, South Africa. Estuar Coast Shelf Sci 160:49–59

Wiebe PH, Dicky A, Kennedy M, Moncoiffé G (2015) A vocabulary for the configuration of net tows for collecting plankton and micronekton. J Plankton Res 37:21–27

Wilson MT (2000) Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988. Fish Bull 98:823–834

Wilson MT (2009) Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. Mar Ecol Prog Ser 392:223–237

Wilson MT, Brown AL, Mier KL (2005) Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): Evidence of mesoscale variation in nursery quality? Fish Bull 103:207–218

Wilson MT, Jump CM, Duffy-Anderson JT (2006) Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. Mar Ecol Prog Ser 317:245–258

Wilson MT, Jump C, Buchheister A (2009) Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to krill standing stock and the physical environment. Mar Ecol Prog Ser 392:239–251

Wilson MT, Buchheister A, Jump C (2011) Regional variation in the annual feeding cycle of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Fish Bull 109:316–326

Wilson MT, Mier KL, Jump CM (2013) Effect of region on the food-related benefits to age-0 walleye pollock (*Theragra chalcogramma*) in association with midwater habitat characteristics in the Gulf of Alaska. ICES J Mar Sci 70: 1396–1407

Woodson LE, Wells BK, Grimes CB, Franks RP, Santora JA, Carr MH (2013) Water and otolith chemistry identify exposure of juvenile rockfish to upwelled waters in an open coastal system. Mar Ecol Prog Ser 473:261–273

Wyllie-Echeverria T, Lenarz WH, Reilly CA (1990) Survey of the abundance and distribution of pelagic young-of-the-year rockfishes off central California. NOAA Technical Memorandum NMFS-SWFC-147, US Department of Commerce, La Jolla, CA

Yamamoto-Kawai M, Carmack EC, McLaughlin FA, Falkner KK (2010) Oxygen isotope ratio, barium and salinity in waters around the North American coast from the Pacific to the Atlantic: implications for freshwater sources to the Arctic throughflow. J Mar Res 68:97–117

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