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Larval fish assemblages in the eastern and western Gulf of Alaska: Patterns, drivers, and implications for connectivity

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ABSTRACT

As stewardship goals in marine environments expand to encompass ecosystem dynamics, our comprehension of ecological structure must incorporate complex interactions among ecosystem components to define linkages and spatial boundaries for management. For example, the Gulf of Alaska (GOA) is currently considered a single Large Marine Ecosystem (LME), yet the GOA spans a large geographic domain, suggesting that ecosystem linkages may vary depending upon population, community, or process-based assessments. We used six years of larval fish assemblage data (2010–2015), co-collected oceanographic data, satellite-tracked drifters, adult fish trawl surveys, and an individual-based biophysical model to determine the processes that structure larval fish assemblages in the GOA focusing on 1) the local physical environment, 2) seasonality, 3) oceanographically-driven connectivity, and 4) adult fish distributions. Larval assemblages occurred along an eastern to western longitudinal gradient with regionally distinct assemblages in the spring and to a lesser degree in the summer. Assemblage patterns were largely driven by regional spring spawning events and only minimally influenced by temperature, salinity, and bottom depth over the continental shelf. Assemblage analyses and modeled particle trajectories suggest that longitudinal gradients in larval assemblages across the LME are influenced by the prevailing currents that promote connectivity despite variability in species-specific life-history characteristics such as spawning location and pelagic larval duration. Divergences in eastern and western GOA assemblages during the spring, and similarities in the summer, were consistent across most study years, but there were shifts in larval assemblages in the western GOA and not the eastern GOA during 2013 and 2015. Such geographic decoupling of assemblages in recent years highlights the potential for differential regional responses to environmental change across the GOA. Patterns in larval fish assemblages underscore the complex processes that structure pelagic ecosystems and suggest that assemblages diverged along a longitudinal gradient resulting in distinct communities in the eastern and western GOA. We propose that the influence of environmental or climatic variability on regional larval assemblages and life-history traits such as pelagic larval duration and phenology may alter future ecosystem linkages in rapidly changing environments.

1. Introduction

Determining relevant spatial scales of dynamic ecological processes is a major challenge to the management of marine ecosystems and one that requires comprehensive knowledge of the physical and biological environment through space and time (Spalding et al., 2007; Toonen et al., 2011). Recent shifts in research and management from population level processes (Gerber et al., 2003) toward community and ecosystem dynamics necessitates a holistic understanding of ecosystem processes and an evaluation of regional delineations of management areas (Baker and Hollowed, 2014; Mollmann et al., 2014). However, efforts toward these goals are often constrained by a lack of knowledge of the physical, biological, and ecological linkages between ecosystem components (Thorpe et al., 2015), and by a poor understanding of the temporal and spatial scales of such linking processes. Better understanding of spatial and temporal variability, and the cumulative interrelationships among ecosystem components (oceanography, primary production, population and community dynamics, anthropogenic influences) can help to further ecosystem approaches to management (Borja et al., 2014).

Globally, several Large Marine Ecosystems (LMEs) have been delineated for management purposes such as fisheries and socioeconomic

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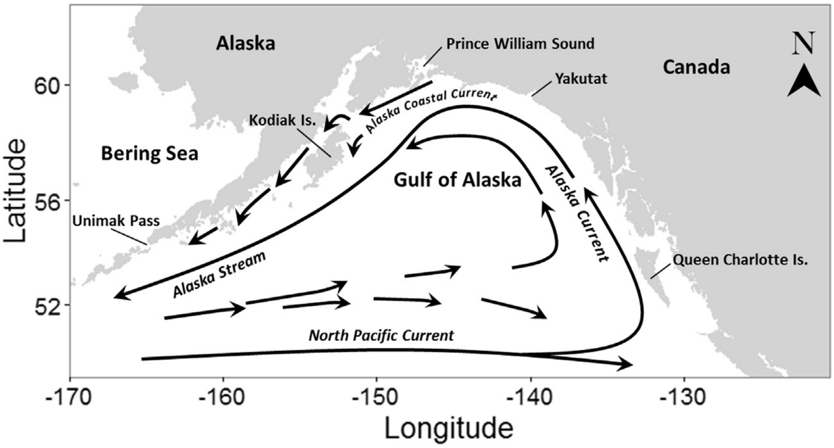

Fig. 1. Map of the Gulf of Alaska showing major oceanographic currents based on Stabeno et al. (2004). Names of currents are in italics and the prevailing current directions are depicted by arrows.

sustainability (Lubchenco, 2012), inclusive of the Gulf of Alaska (GOA). The GOA LME spans a longitudinal distance of nearly 3000 km and was designated as a single LME based on bathymetry, hydrography, productivity, and trophic relationships (Sherman, 1991). Indeed, several processes suggest ecosystem connectivity and congruence across the GOA, despite its expansive size. The GOA is influenced by downwelling favorable winds (Ladd et al., 2005), and studies have shown that temporal variations in wind estimates are correlated across the full extent of the LME (Spies and Cooney, 2007). The major currents in the GOA flow across the entire span of the LME and serve to connect the eastern and western regions by westward flows. The Alaska Current (AC, 5–15 cm s^{-1}), a northward flowing eastern boundary current, becomes the Alaska Stream (AS, 50–100 cm s^{-1}) that primarily flows from east to west along the shelf break (Fig. 1; Stabeno et al., 2016, 2004), influencing the GOA ecosystem over its entire pathway. On the shelf, the Alaska Coastal Current (ACC, 50–100 cm s^{-1}) is responsible for westward along-shelf transport (Stabeno et al., 1995) and is a conduit for east-west transport of nutrients, zooplankton, and larval fish (Stabeno et al., 2016). Biogeographically, a variety of species inclusive of fish, birds, and mammals occur throughout the full geographic range of the GOA (Gaichas et al., 2011; Spies, 2007). Finally, physical, biophysical, and trophic models suggest broad-scale connectivity (Coyle et al., 2013; Hermann et al., 2016; Hinkley et al., 2009; Parada et al., 2016), providing ecological evidence that supports the designation of a single LME for the entire GOA.

Despite this large-scale ecosystem connectivity, the GOA is a dynamic environment and transient conditions and local oceanographic features may interrupt, regionalize, or otherwise disconnect the LME across its span. To the east, the AS is influenced by mesoscale eddies with diameters of ~ 200 km that primarily form in the eastern GOA and propagate westward, influencing ecosystem dynamics (Ladd, 2007). Eddy formation in the GOA can promote local retention that can influence species distributions by affecting transport and east-west connectivity (Henson and Thomas, 2008; Xiu et al., 2012). Temporally, the formation and persistence of anticyclonic eddies in the eastern and western GOA has been asynchronous over the past few decades, potentially leading to regional differences in chlorophyll concentrations and species assemblages for multiple trophic levels (Ladd, 2007; Atwood et al., 2010). The ACC, which contributes to east-west transport across LME, is influenced by local winds, regional bathymetry, seasonal variability in river discharge, and interactions with tidal currents that can create discontinuities in the strength or direction of the current (Stabeno et al., 2016). Near Kodiak Island, the ACC is frequently disrupted by winds that blow offshore through mountain gaps with the highest prevalence in the winter months. This disruption decreases water velocities in the inshore area of the shelf (Ladd et al., 2005), potentially altering larval transport from the eastern Gulf of Alaska (EGOA) to the western Gulf of Alaska (WGOA; Ladd et al., 2016). Bathymetrically, the WGOA has a wider continental shelf than the EGOA and is intersected by numerous submarine troughs that facilitate shelfward movement of nutrient-rich water and tidal vertical mixing that increases on-shelf productivity (Ladd et al., 2005; Stabeno et al., 2016). This topographic variability and perturbations to the GOA system suggest ecosystem discontinuities and differential regional-scale processes that may have consequences to fish populations, communities, and ecosystem management.

Management within the GOA has historically focused on targeted single-species fisheries with most assessments based on the premise that the stock is continuous across the LME, though there have been more recent efforts to incorporate ecosystem dynamics (Witherell, 2000; Zador and Yasumiishi, 2016). These more recent ecosystem considerations argue for separating the eastern and western regions of the GOA LME into subunits (Zador and Yasumiishi, 2016). Rationale for regional partitioning is evidenced by community-level patterns of adult groundfish distributions that indicate potential temporal changes in community dynamics and a possible breakpoint in species assemblages near the longitudinal mid-point of the GOA at Prince William Sound (Mueter and Norcross, 2002). Other studies have demonstrated east-west dissimilarities among lower trophic levels including along shelf gradients in chlorophyll (Brickley and Thomas, 2004) and zooplankton (Rand and Hinch, 1998; Cooney, 2007). Finally, historical work has identified that the eastern GOA is influenced by the California Current coastal upwelling ecosystem to a greater degree than the western GOA, suggesting differing biogeography and ecosystem processes (Brodeur et al., 2007; Fisher et al., 2007; Ware and McFarlane, 1989).

The pelagic larval stages of marine fish may be useful indicators of LME homo- or heterogeneity because they are affected by both large-scale and local-scale processes including climate patterns (Koslow et al., 2013; Guan et al., 2015), environmental variability at seasonal or interannual time scales (Auth, 2008; Doyle et al., 2009; Doyle and Mier, 2015; Duffy-Anderson et al., 2006), adult distributions (Walsh et al., 2015), phenology (Doney et al., 2012), and larval transport and connectivity (Cowen and Sponaugle, 2009). Consequently, seasonal and interannual patterns in larval fish assemblages can help to discern the influence of differential forcing mechanisms and environmental variability on ecosystem dynamics that are relevant to management (Baker and Hollowed, 2014). In this study, we use six years of larval fish assemblage data from the GOA to determine ecosystem linkages and discontinuities that can inform ecologically relevant spatial delineations for management by focusing on (1) interannual and seasonal variability in larval fish assemblages in the eastern and western GOA, and (2) key processes that may influence larval assemblages (local

Table 1
Shipboard larval collection information showing eastern (EGOA) and western (WGOA) regional designations of the sampling area and the survey year, season, dates, and research cruise. N_{total} is the total number of stations sampled, and N_{phys} refers to the number of stations sampled that included physical data. Dashes denote regions and seasons for which no samples were collected.

Year	Season	EGOA			WGOA		
		Dates	Cruise	N_{total}, N_{phys}	Dates	Cruise	N_{total}, N_{phys}
2010	**Spring**	Apr 15-Apr 24	1NW10	44, 43	May 22-June 1	3DY10	163, 160
	Summer	July 4-July 22	2NW10	68, 0	–	–	–
2011	**Spring**	Apr 30-May 21	1TT11	114, 102	Apr 26-May 11	1TX11	46, 44
					June 2-June 9	2DY11	72, 65
	Summer	July 3-July 17	1NW11	49, 36	Aug 2-Aug 21	2NW11	53, 40
2012	**Spring**	–	–	–	–	–	–
	Summer	July 3-July 22	1NW12	65, 38	Aug 3-Aug 20	2NW12	61, 53
2013	**Spring**	Apr 6-Apr 24	DY1304	113, 101	Apr 26-May 10	1TX13	26, 25
					May 17-June 1	DY1306	226, 216
	Summer	July 3-July 21	1NW13	68, 45	Aug 3-Aug 22	2NW13	52, 47
					Aug 26-Aug 30 & Sept 4-Sept 17	DY1308	224, 121
2014	**Spring**	–	–	–	–	–	–
	Summer	July 7-July 24	NW1402	66, 49	–	–	–
		Aug 5-Aug 25	NW1404	71, 38			
2015	**Spring**	–	–	–	May 15-June 4	DY1505	281, 274

physical environment, seasonality, larval connectivity, and adult distributions). Determining patterns and processes that affect larval fish assemblages is a step toward understanding complex ecosystem dynamics that can be applied to ecosystem delineations and potentially adaptive management strategies in changing environments.

2. Methods

2.1. Sample collection and processing

Larval fish were collected during 19 research cruises in the spring and summer months of 2010–2015 in the GOA with expanded survey efforts that encompassed both the EGOA and WGOA in spring and summers of 2011 and 2013 in association with the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP). Survey data were not available for the spring of 2012 and 2014, or the summer of 2015 (Table 1, Fig. 2). Larvae were collected using a paired 60-cm bongo net (505 μm mesh) that was towed obliquely from the surface to 10 m off-bottom or to a maximum depth of 200 m. All nets were equipped with flow meters to quantify volume filtered. One net was selected for ichthyoplankton processing and larval fish counts were standardized to catch per unit effort (CPUE: catch 10 m^{-2} surface area calculated based on the maximum depth of the tow and volume filtered; Matarese et al., 2003). Ichthyoplankton samples were preserved in a 5% formalin-seawater solution buffered with sodium borate and sent to the Plankton Sorting and Identification Center in Szczecin, Poland, where larval fish were identified to the lowest taxonomic level possible and measured to the nearest 0.1 mm standard length (SL). Verification and additional identification to lower taxonomic levels took place at the National Oceanographic and Atmospheric Administration, Alaska Fisheries Science Center (NOAA AFSC) in Seattle, WA, USA. Detailed shipboard sampling, handling, and identification protocols are described in Matarese et al. (2003). Physical oceanographic data including temperature (°C) and salinity (Practical Salinity Units) were co-collected for the majority of net tows (Table 1) using either a sensor that was attached in-line with the plankton nets (Sea-Bird SeaCAT SBE 16 Plus, Sea-Bird SeaCAT SBE 19 Plus, or Sea-Bird SBE 49 FastCAT) or a CTD cast (Sea-Bird SBE 25 Sealogger, Sea-Bird SBE 911 plus) immediately prior to net deployments, and bottom depth (meters) was recorded at each station. Additionally, satellite-tracked (Argos instrument) drifters drogued at 40 m were deployed in 2011 (release time: 5/10/2011 14:24:00 GMT) and 2013 (release time: 4/16/2013 13:23 GMT) to track oceanographic currents (Fig. A.1; EcoFOCI Drifter Data: http://www.ecofoci.noaa.gov/drifters/efoci_drifterData.shtml). For all analyses, the GOA was divided into eastern (EGOA) and western (WGOA) regions at Prince William Sound (Mueter and Norcross, 2002; Siddon et al., 2016) with a longitudinal break at 146.0°W (Figs. 1, 2).

2.2. Assemblage patterns

To discern spatial and temporal patterns in larval fish assemblages, a non-metric multidimensional scaling analysis (NMDS) was performed using CPUE for taxonomic groups from each cruise and station from 2010 to 2015 (Table 1, Fig. 2). Dissimilarity matrices were constructed using the Bray-Curtis index that was selected based on the high frequency of zeros and the lack of a normal distribution in the dataset (Anderson et al., 2011; Clarke et al., 2006). NMDS ordination is an iterative algorithm that converges on a solution that most closely matches the Bray-Curtis index and the final ordination converges on a solution that minimizes the stress statistic (Clarke, 1993). The number of NMDS axes was selected as the minimum number that resulted in a stress statistic < 0.2. Seven outlier stations with NMDS scores that obscured all other relationships were identified and excluded from the final analysis, and rare species that were only observed once were removed from the dataset resulting in 93 taxonomic groups selected for analyses out of a total of 119. CPUE data were fourth root transformed to reduce the influence of highly abundant species on site scores (Anderson et al., 2011). Patterns in larval assemblages were visualized using a biplot of the first two NMDS axes and species scores were depicted based on weighted averages. To visualize changes in larval assemblage patterns through time, the mean (± standard error) was computed for NMDS scores in the spring and summer in the EGOA and WGOA from 2010 to 2015 for all NMDS axes.

2.3. Environmental drivers

2.3.1. Local physical environment

The influence of the local physical environment on structuring larval fish assemblages was determined using a subset of sample locations at which local physical data were co-collected from 2010 to 2015 (Table 1, Fig. A.2). Data were analyzed using a partial distance-based redundancy analysis (p-dbRDA) with the Bray-Curtis dissimilarity index using the same criteria for rare species as NMDS analyses resulting in 87 taxonomic groups for the data subset.

P-dbRDA is a multivariate analog to partial regression and is an extension of distance-based redundancy analysis that can be used to partition the total variation into components to determine the amount of variability that can be attributed to explanatory variables by

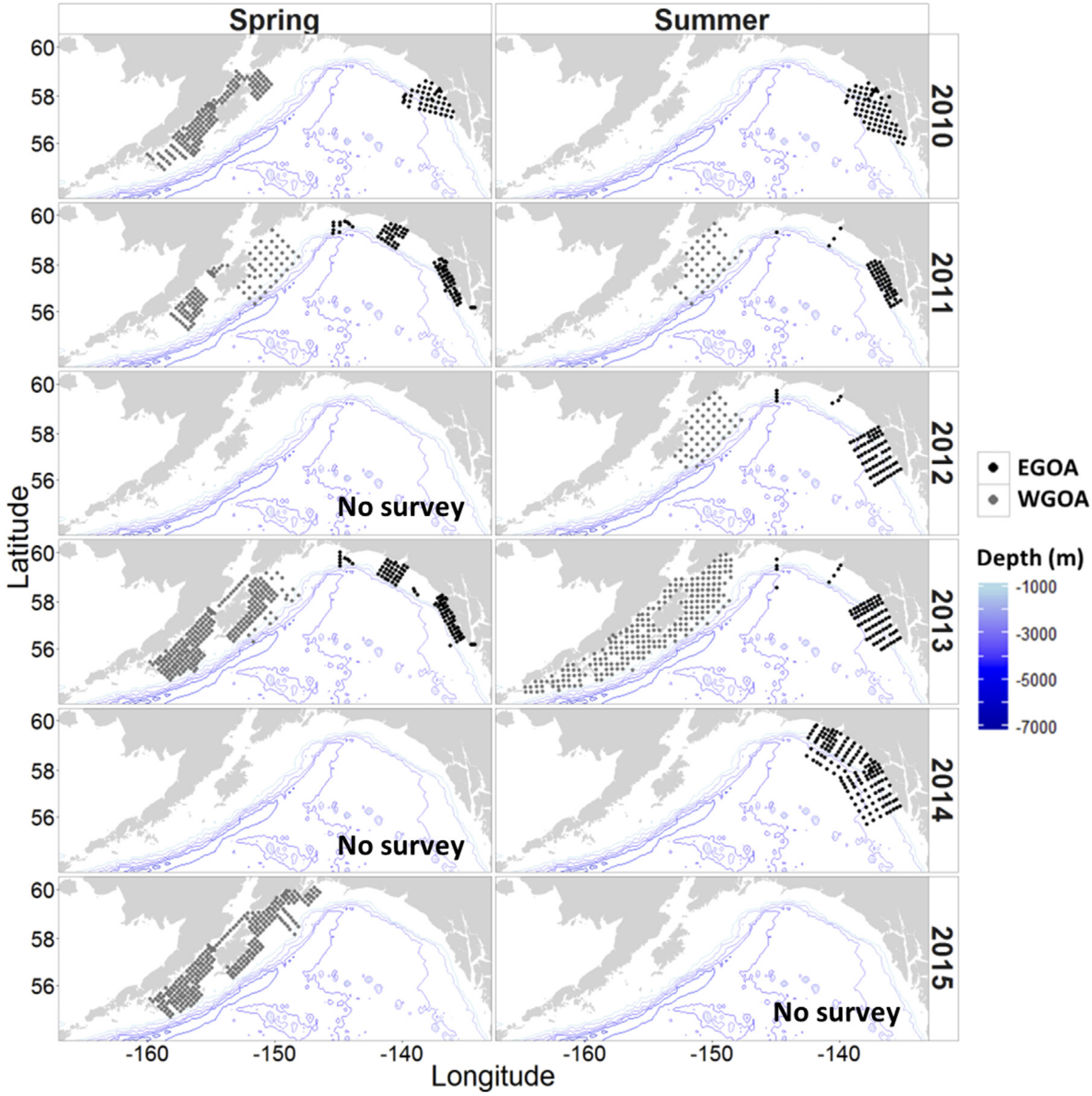

Fig. 2. Map of the Gulf of Alaska showing station locations from 2010 to 2015 in the spring and summer seasons in the eastern (EGOA) and western (WGOA) Gulf of Alaska. Regions were based on a longitudinal divide at 146.0°W (−146°). Bathymetry contours are from Amante and Eakins (2009). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

removing the effects of co-variables by multiple linear regression (Borcard et al., 1992). Like other constrained ordination methods, p-dbRDA canonical axes maximize the linear correlation between explanatory and response variables (Legendre and Legendre, 2012). P-dbRDA analyses can be based on an ecologically meaningful distance matrix such as Bray-Curtis (Legendre and Legendre, 2012) by performing a principle coordinate analysis (PCoA) on the distance matrix followed by redundancy analysis on the eigenvalues obtained from the PCoA (Legendre and Anderson, 1999). For all analyses, models were selected based on examination of variance inflation factors (VIF) and using a forward selection procedure. To minimize type I error, the forward selection procedure first tests the significance of the global model ($\alpha = 0.05$), then proceeds until the adjusted coefficient of multiple determination (R^2_{adj}) is exceeded by the candidate model or if no additional variables are significant based on permutation tests (*packfor* package in R statistical software; Blanchet et al., 2008; Borcard et al., 2011).

To determine the relative role of the local physical environment in structuring larval fish assemblages, p-dbRDA was performed for the full set of environmental variables that were collected at all stations: bottom depth, water temperature and salinity above 40 m depths, and water temperature and salinity below 40 m. A depth of 40 m was selected based on the average depth of the pycnocline (~ 40 m in summer; Weingartner, 2007) and the average depth of the euphotic zone (~ 50 m; Childers et al., 2005) in the GOA. To account for unmeasured environmental processes and the effects of spatial gradients across multiple scales on structuring larval assemblages, Moran's eigenvector maps (MEM; historically Principle Coordinate of Neighborhood Matrices) analyses were performed and incorporated as co-variables in p-dbRDA analyses. MEM is a method of eigenvalue decomposition that extracts eigenvectors from a truncated matrix of geographic distances using PCoA. The truncation distance selected for analyses was the longest link along a minimum spanning tree (Borcard et al., 2011). Each MEM eigenfunction can be interpreted as a spatial scale of variability from broad-scale (smaller variable numbers) to fine-scale (larger variable numbers) patterns. MEM variables can then be selected based on a forward selection (Borcard et al., 2011) for inclusion in univariate or multivariate models (Duarte et al., 2012; Dray et al., 2006; Borcard et al., 2004; Borcard and Legendre, 2002).

Covariables were included in the p-dbRDA analysis to isolate the influence of the proximal physical environment and water mass characteristics on larval fish assemblages in absence of seasonal influences and year effects. Accordingly, co-variables included day of the year to account for the influence of seasonality on species assemblages and year to address inter-annual variability in assemblages. Forward selection resulted in 70 significant MEM variables out of which only 5 variables with R^2 values > 0.01 (MEM: 1–3, 7, 9) were included in the model. Further model variables were selected based on the forward selection procedure outlined above. Following inclusion of variables based on forward selection, variables and interaction terms were sequentially removed from the model based on examination of VIFs using a cutoff value of 5, and finally, a permutation to test for the significance of model variables and interactions. Inspection of VIFs also ensured that MEM spatial variables did not co-vary substantially with measured local physical parameters that may also have a spatial component. Longitude and latitude were not included in the model based on the inclusion of MEM spatial variables that were correlated with geographic coordinates; indicating that spatial patterns were sufficiently represented by MEM variables. Based on selection criteria the final p-dbRDA model was:

$$\sqrt[4]{CPUE} \sim D + T_b + S_s + MEM + D{*}T_b + D{*}S_s + Conditional(J + Y)$$

where Bray-Curtis dissimilarity index was calculated based on the fourth root of CPUE (larvae 10 m^{-2}), D is bottom depth (m), T_b is average temperature in the water column deeper than 40 m calculated for each net tow, S_s is average salinity in the water column shallower than 40 m calculated for each net tow, MEM refers to 5 separate MEM variables, J is day of the year, and Y refers to the 6 separate study years that were included as factors in the model. Variance partitioning was performed based on adjusted R^2 values from the p-dbRDA to determine the relative role of each explanatory variable or group of variables in structuring fish assemblages (Borcard et al., 2011). Variables were divided into four groups for variance partitioning: local physical (D, T_b, S_s), inter-annual (Y), seasonal (J), and unmeasured spatial processes (MEM).

2.3.2. Seasonality

The influences of regional species composition and spawning seasonality on structuring larval fish assemblages were determined by comparing assemblage composition within each region (EGOA or WGOA), season (spring or summer), and year (2010–2015). Analyses focused on dominant taxonomic groups that comprised > 5% of the species composition to contrast seasonal and interannual changes in dominance patterns that reflect spring or summer spawning.

2.3.3. Advective processes and transport

To test whether species assemblages across the GOA may be linked to movement of a water mass and transport from the EGOA to the WGOA, individual drifter tracks deployed in 2011 and 2013 were included in multivariate analyses. For each respective sampling year (2011 and 2013) all station locations within a 150-km radius of the drifter track were selected for analysis (Fig. A.1). This buffer distance included most sample locations but excluded those that were far beyond the western end of each drifter track. For each sample station, a Euclidean distance from the drifter track was calculated based on distance in space and time from the sampling location to the closest point along the drifter track to calculate a Euclidean space-time variable for each station that described the distance of that collection from the drifter or water mass (Fig. A.1). This analysis assumes that sample stations in close proximity (spatially and temporally) to the drifter track will have similar assemblages regardless of whether they are located in the EGOA or WGOA if the assemblages are moving as a cohesive unit along with a water mass. Prior to calculating the Euclidean space-time distance, values were centered and scaled to give equal weight to space and time.

To quantify the potential influence of water mass movement on species assemblages, Euclidean space-time variables were included in p-dbRDA analyses with Bray-Curtis dissimilarity index for 2011 and 2013. Rare taxonomic groups were removed following the same criteria outlined for NMDS analyses, and models were selected based on forward selection criteria and VIFs. Fine-scale, and not broad-scale, MEM variables were included in the model to account for spatial autocorrelation at small spatial scales (detected by Mantel correlograms; Legendre and Legendre, 2012), that may co-vary with Euclidean distance from the drifter track, without removing the effects of longitudinal gradients because longitude was explicitly included in the model. Forward selection procedures resulted in fine-scale and broad-scale MEM variables with R^2 values > 0.01. Of the variables that met selection criteria, four fine-scale variables (33–35, and 38) were included in the p-dbRDA model for 2011 and broad-scale variables (1–5) were excluded. For 2013, 6 variables met the selection criteria, of which 2 fine-scale variables (21 and 89) were included in model and 4 broad-scale (1–4) variables were excluded. The cut-off between broad and fine-scale MEM variables was chosen based on natural breaks in the variables that met the selection criteria (Borcard et al., 2011). Local physical environmental parameters were not included in the full model based on weak correlations between the local physical environment and assemblages (see Section 3) and strong correlations between spatial and temporal variables with depth and temperature reflected in VIFs. The final models for 2011 and 2013 were:

$$\sqrt[4]{CPUE} \sim Distance + L + Conditional(J + MEM_{fine})$$

where Bray-Curtis dissimilarity index was calculated based on the fourth root of CPUE (larvae 10 m^{-2}), Distance is Euclidean space-time distance, L is Longitude, J is day of the year, and MEM_{fine} is forward-selected fine-scale MEM variables. Day of the year was included as a co-variable in the model to control for the influence of seasonal changes in assemblage patterns that may co-vary with drifter movement. Variance partitioning included Euclidean space-time distance, Longitude, day of the year, and MEM_{fine}.

The feasibility of larval transport across the GOA was verified using the Dispersal Model for Early Life Stages (DisMELS), a three dimensional individual-based model (IBM) coupled with daily averaged output from Regional Ocean Modeling System (ROMS). The ROMS hydrodynamic model is a primitive equation three-dimensional ocean circulation model driven by atmospheric forcing. The nested models used for this study had a 20–40 km resolution (NPac), a 10 km resolution (NEP), and a 3 km resolution (CGOA), where coarser grids set boundary conditions for the finer resolution nested grids (https://www.myroms.org/, Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008; Hermann et al., 2009; Coyle et al., 2013; Stockhausen et al. 2018). DisMELS was developed at NOAA AFSC and has been parameterized and applied to multiple studies (Cooper et al., 2013; Duffy-Anderson et al., 2013). For the present study, DisMELS was run for the year 2011 based on the available ROMS output and was used primarily as a particle tracking model to determine whether assemblage patterns and relationships to a single drifter could be corroborated by the particle trajectories. Therefore, DisMELS was not parameterized for any particular species; rather it was intended to simulate general drift and potential connectivity. The model was run using four different scenarios that differed in depth of particle release and hypothetical preferred depth ranges to obtain an overview of potential larval assemblage transport across the GOA given a wide range of life-histories and larval depth ranges (Table 2). In all model runs, particle release locations coincided with EGOA bongo collections in the spring of 2011 (Fig. 2 and Fig. A.3), and 100 particles were released from each location. The IBM was primarily developed to assess the plausibility and duration of larval fish transport from the EGOA to the WGOA and does not include biological complexity associated with variability in spawn times. The

Table 2
Individual-based biophysical model (IBM) scenarios using multiple particle release depths and constrained depth ranges of particles to encompass potential variability in life-history traits.

Model Run	Description	Release depth (m)	Depth range (m)
1	Surface	20	10–30
2	Shallow (mimic drifter)	40	30–50
3	Mid-depth	60	50–70
4	Deep	5 m from the benthos	70–500

particle release locations that were near the start of the drifter track (easternmost grid location) were released at the same time as the drifter on May 10, 2011 at 14:24:00. Particles were released from the second grid (farther west) on July 10, 2011 at 12:00:00 based on the time at which the drifter track crossed the sampling area (Fig. A.1 and Fig. A.3). All model scenarios were run for 180 days in accordance with the approximate time that it took for a drifter to traverse the GOA (Fig. A.4) and a maximum larval duration of ∼ 6 months (Bouwens et al., 1999). In addition, all model runs included vertical and horizontal diffusion rates of 0.001 m^2 s^{-1} and larvae were assigned a vertical swimming speed of 0.003 m s^{-1} following values from the literature (Sohn, 2016) to maintain preferred depth ranges. Model outputs were plotted as heat maps depicting the number of larvae that crossed 0.2° latitude by 0.2° longitude grids cells.

2.3.4. *Spawning location*

Spatial distributions of adults, spring and summer larvae, and larval length-frequency distributions of case-study species, *Lepidopsetta bilineata* (southern rock sole) and *Isopsetta isolepis* (butter sole) in 2013, were examined to complement assemblage analyses and further evaluate the potential role of transport and species-specific life histories in structuring larval fish assemblages. The assumptions of this analysis were that locally-spawned or locally-retained larvae would be spatially co-located with the centers of adult distributions. For species with spring spawning and long pelagic larval durations, evidence of transport from the EGOA to the WGOA could be identified if larvae and adults are co-located in the spring, but summer larval distributions shift westward. Species that were selected for analyses met the following criteria: 1) spawning occurred in the EGOA in the spring, 2) individuals were present in the WGOA in the summer with > 1% of their abundance present in summer to exclude species that were likely transitioning from pelagic larvae to juvenile stages during the collection period, and 3) species were present in both larval and adult datasets. One assumption of the spatial comparisons of adult and juvenile distributions is that larvae will be transported away from adult spawning grounds. Therefore, pleuronectid species were selected because they typically have distinct adult and juvenile habitat constraints, presumably favoring directed transport from spawning grounds to juvenile nursery habitats rather than self-recruitment (Duffy-Anderson et al., 2014).

To isolate the influences of larval movement and additional spawning events on distributions, length-frequency distributions of spring and summer larvae were plotted with the assumption that larvae spawned in the EGOA and transported to the WGOA would shift toward larger individuals as a result of maturation, and fewer individuals due to mortality. Lengths were measured for a subset of individuals, therefore length-frequency distributions were scaled to CPUE to reflect relative abundance and plotted as kernel density estimates reflecting CPUE.

Adult distributions were obtained from groundfish trawl data from biennial surveys conducted during the spring and summer months by NOAA's AFSC Groundfish Assessment Program (http://www.afsc.noaa.gov/RACE/groundfish/). To show general patterns in distributions, kernel density distributions were calculated based on positive observations (presence) for each life stage. Adult distributions from trawl data incorporated annual survey data and larval distributions were calculated for spring and summer separately.

All analyses were performed using R version 3.3.0 (R Core Team, 2016) and multivariate analyses were performed in the vegan package (Oksansen et al., 2017).

3. Results

3.1. *Assemblage patterns*

Larval fish assemblages based on NMDS analyses with the Bray-Curtis index had a non-metric fit of 0.98 and a stress statistic of 0.13 with a three-dimensional solution, showing an acceptable level of agreement between the dissimilarity matrix and reduced dimensionality data. General patterns showed both regional and seasonal separation of larval assemblages for the years 2010–2015 with seasonal

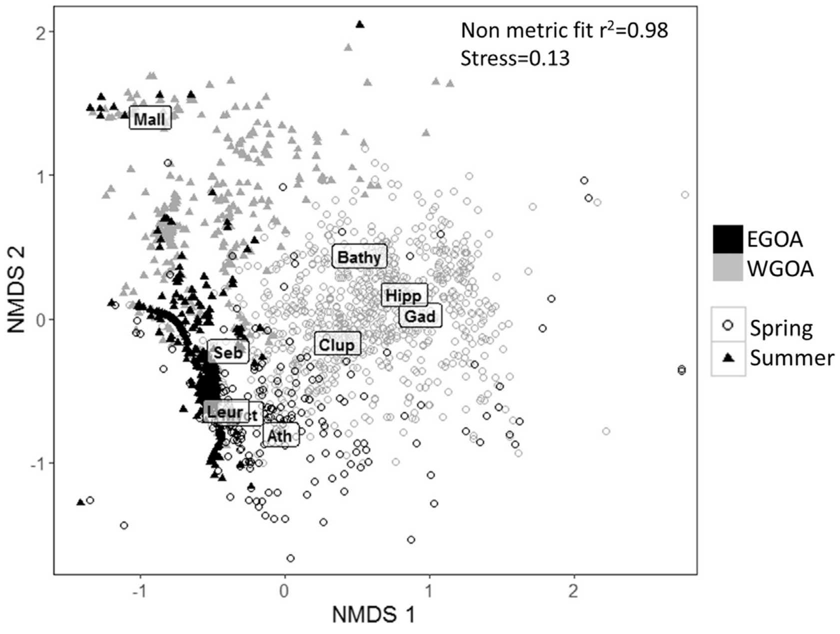

Fig. 3. Plot of the first two axes of a non-metric multidimensional scaling analysis of larval fish assemblages in the Gulf of Alaska (GOA) from 2010 to 2015. The points depict station locations, the gray scale represents regions within the GOA (EGOA = eastern GOA and WGOA = western GOA), and the shapes correspond to spring and summer seasons. The taxonomic groups that comprised > 5% of the total percent composition within each respective year and season (see Fig. 5) are plotted based on weighted average scores (Ath = *Atheresthes stomias*, Bathy = Bathymasteridae, Clup = *Clupea pallasi*, Gad = *Gadus chalcogrammus*, Hipp = *Hippoglossoides elassodon*, Leur = *Leuroglossus schmidti*, Mall = *Mallotus villosus*, Myct = Myctophidae (obscured by Leur), Seb = *Sebastes* spp.).

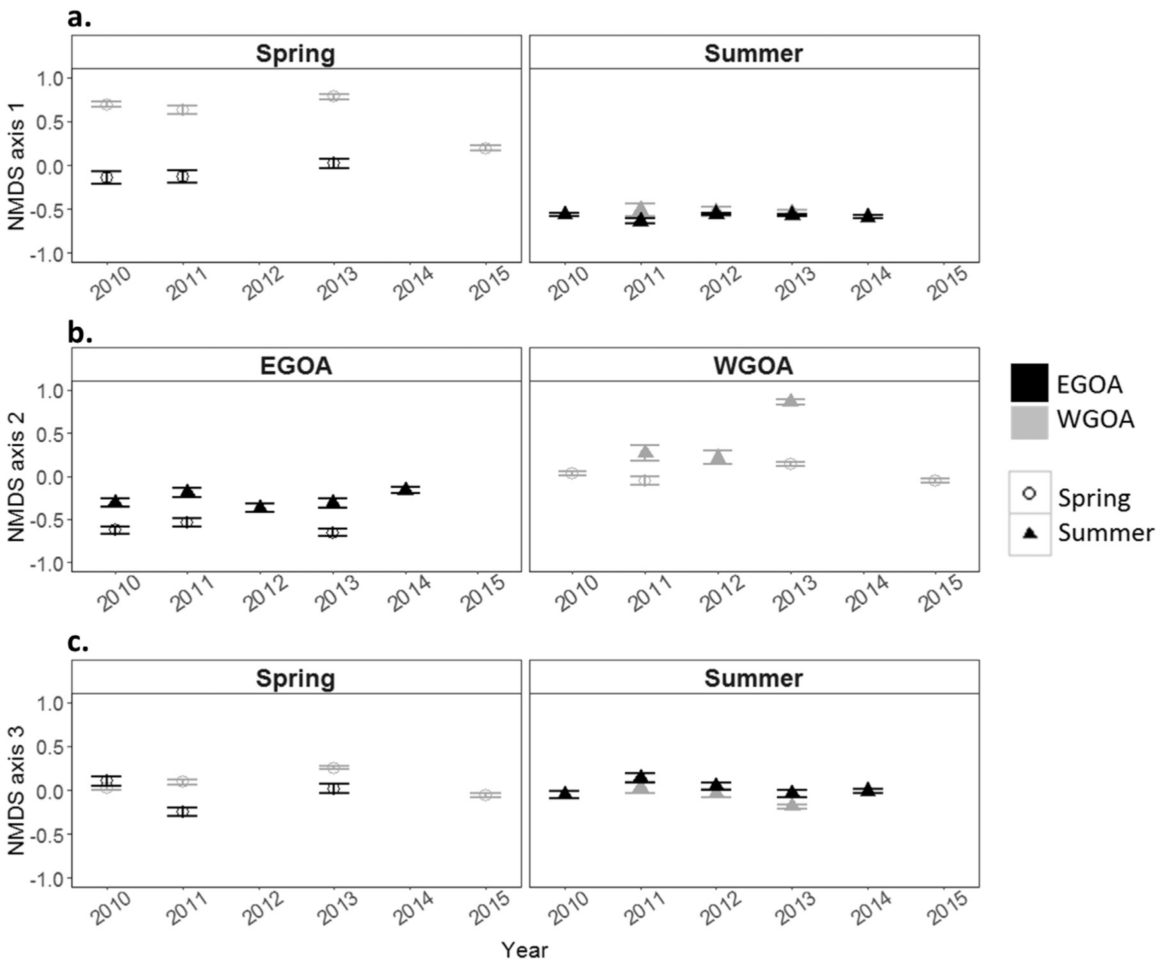

Fig. 4. (a-c) Average (± SE) non-metric multidimensional scaling (NMDS) analysis site scores showing annual (2010–2015), regional (color; EGOA = eastern Gulf of Alaska and WGOA = western Gulf of Alaska), and seasonal (shape; spring and summer) patterns for NMDS axes 1–3 (a-c, respectively). Missing data points correspond to years or seasons during which no surveys were conducted.

patterns primarily separating along the first NMDS axis and regional patterns along the second (Fig. 3). *Mallotus villosus* was highly associated with the summer months, and several taxa, particularly *G. chalcogrammus*, *H. elassodon*, and Bathymasteridae, were primarily associated with spring in the WGOA. A comparison of mean (± SE) NMDS axis 1 scores across all sample years and seasons revealed a large separation between EGOA and WGOA assemblages in spring for all years except 2015, and consistently similar summer NMDS axis 1 scores between the EGOA and WGOA (Fig. 4a). No spring EGOA survey was conducted in 2015, but WGOA scores more closely resembled the EGOA than previous years (Fig. 4a). NMDS axis 2 revealed seasonal separation within the EGOA and WGOA independently, and a general pattern of lower scores in the EGOA than the WGOA in both spring and summer (Fig. 4b). Based on NMDS axis 2 scores, larval assemblages in the WGOA in summer were unique in 2013 compared to other years (Fig. 4b). NMDS axis 3 showed temporal stability and some differences between regions and seasons but to a lesser degree than other axes (Fig. 4c).

3.2. Environmental drivers

3.2.1. Local physical environment

The local physical environment played a minor role in structuring larval fish assemblages based on p-dbRDA analyses that included data from 2010 to 2015. After controlling for the influences of seasonality (day of the year) and year, constrained axes (local physical parameters and MEM) explained ~ 16% of the variability in the dataset with CA 1 and CA 2 explaining ~ 9.4% and 1.3% of the variability, respectively. A significant amount ($p < 0.05$) of variability was associated with the local physical environment (temperature, depth, salinity, and interactions among them) as well as spatial MEM variables. Based on variable selection criteria, the MEM variables that most substantially correlated with fish assemblages primarily encompassed broad-scale, rather than small-scale spatial processes (MEM variables 1–3, 7, and 9 out of 70 significant variables). The combination of all co-variables and conditional variables explained ~32% of the variability in the dataset leaving ~ 68% unexplained (Table 3). Variance partitioning showed that year and season influenced larval assemblages to a greater degree than the local physical environment, but most variability was explained by unmeasured spatial processes. Co-variation between the local physical environment and unmeasured spatial processes explained an additional ~ 3% of the variability in the dataset, suggesting that there was a small degree of co-variability among local physical parameters and broad spatial patterns (Table 3).

3.2.2. Seasonality

Percent composition of the most common taxonomic groups showed that spring and summer assemblages and regional assemblages were dominated by different taxa from 2010 to 2015 with some commonalities (Fig. 5 and Fig. A.5). Larvae of *Sebastes* spp. (rockfishes) comprised a large proportion of the assemblages in each region, season, and year except for summer in the WGOA in 2013. Taxonomic dominance in spring assemblages in the EGOA was variable with up to 5 groups present in the spring of 2013. In addition to larvae of *Sebastes* spp.,

Table 3
Variance partitioning for partial distance-based redundancy analyses (p-dbRDA). The p-dbRDA from 2010 to 2015 (Local physical) included the local physical environment (LP: depth, temperature below 40 m, and salinity above 40 m), Year (Y), day of the year (J), and spatial patterns from Moran's eigenvector maps (MEM). P-dbRDA analyses for the years 2011 and 2013 (Spatial) included the Euclidean distance from the drifter track (D), Longitude (L), day of the year (J), and fine-scale MEM variables (MEM). Values correspond to the proportion of variability explained by each explanatory variable in isolation or the additional joint variability that is co-explained by a combination of variables based the adjusted coefficient of multiple determination (R^2_{adj}). Total variability refers to the total amount of variability explained (incorporating both positive R^2_{adj} values that are listed in the table and negative R^2_{adj} values that are not shown in the table) for all explanatory variables and combinations.

Local physical	**LP**	**Y**	**J**	**MEM**	**LP, Y**	**LP, J**	**LP, MEM**	**Y, J**	**Y, MEM**	**LP, Y, MEM**	**Y, J, MEM**	**LP, Y, J, MEM**	**Total variability**
2010–2015	2.5	4.0	6.3	10.9	0.58	1.1	2.6	1.6	1.7	1.2	0.5	0.4	∼32
Spatial	**D**	**L**	**J**	**MEM**	**D, L**	**D, J**	**D, MEM**	**L, J**	**D, L, J**	**D, L, MEM**	**D, J, MEM**	**D, L, J, MEM**	**Total variability**
2011	2.5	9.9	6.0	5.4	10.9	0.4	0.2	–	1.6	–	0.1	0.1	∼37
2013	1.8	7.2	8.0	1.1	14.6	7.6	0.1	3.5	–	0.1	0.2	–	∼37

assemblages in the EGOA included myctophids (lanternfish) and *Atheresthes stomias* (arrowtooth flounder) as dominant taxa in more than one sampling year. In the WGOA in spring, *Sebastes* spp. comprised a large proportion of species assemblages as well as *Gadus chalcogrammus* (walleye pollock), *Hippoglossoides elassodon* (flathead sole), and bathymasterids (ronquils). Both the EGOA and WGOA had a maximum of two dominant groups in summer, *Sebastes* spp. in both, and myctophids in the EGOA, and *Mallotus villosus* (capelin) in the WGOA (Fig. 5).

3.2.3. Advective processes and transport

Euclidean space-time distance from drifter tracks and longitude were both significantly ($p < 0.05$) related to larval assemblages after accounting for the influence of seasonality (day of the year) as well as fine-scale spatial patterns in 2011 and 2013 (Fig. 6a, b). Euclidean space-time distance and longitude explained just over 20% of the variability in the dataset (Table 3) in 2011, the majority of which was associated with longitude and correlations between Euclidean distance and longitude along constrained axis 1 (CA1; Fig. 6a). A large portion of the variability in assemblage patterns (∼63%) could not be explained by the full model including co-variables (Table 3). Longitude had a greater influence on assemblages than Euclidean distance based on variance partitioning (Table 3), and that was reflected in assemblage separation between the EGOA and WGOA along CA 1 (Fig. 6a). However, the overlap between Euclidean distance and longitude explained an additional 10.9%, indicating that the two variables co-varied, but together they were strongly related to assemblage patterns (Table 3). In 2013, Euclidean distance and longitude were again significant and negatively correlated. Constrained axes again explained over 20% of the variability in the dataset, the vast majority of which was associated with longitude along CA 1 (Table 3, Fig. 6b). Separation between the EGOA and the WGOA was less defined in 2013 than 2011, particularly as a result of summer assemblages in the WGOA that grouped midway between EGOA and WGOA spring assemblages, and spring assemblages in the EGOA that were dispersed along CA 1 and CA 2 (Fig. 6b). The relationship between larval assemblages and Euclidean distance was strongly driven by assemblages in the WGOA in the spring as evidenced by the separation between WGOA spring stations and other stations, as well as the proximity of those points to the Euclidean distance vector in the ordination plot (Fig. 6b). Variance partitioning revealed that longitude played a large role in structuring assemblages, and that Euclidean distance alone was again associated with ∼ 2% of the variability

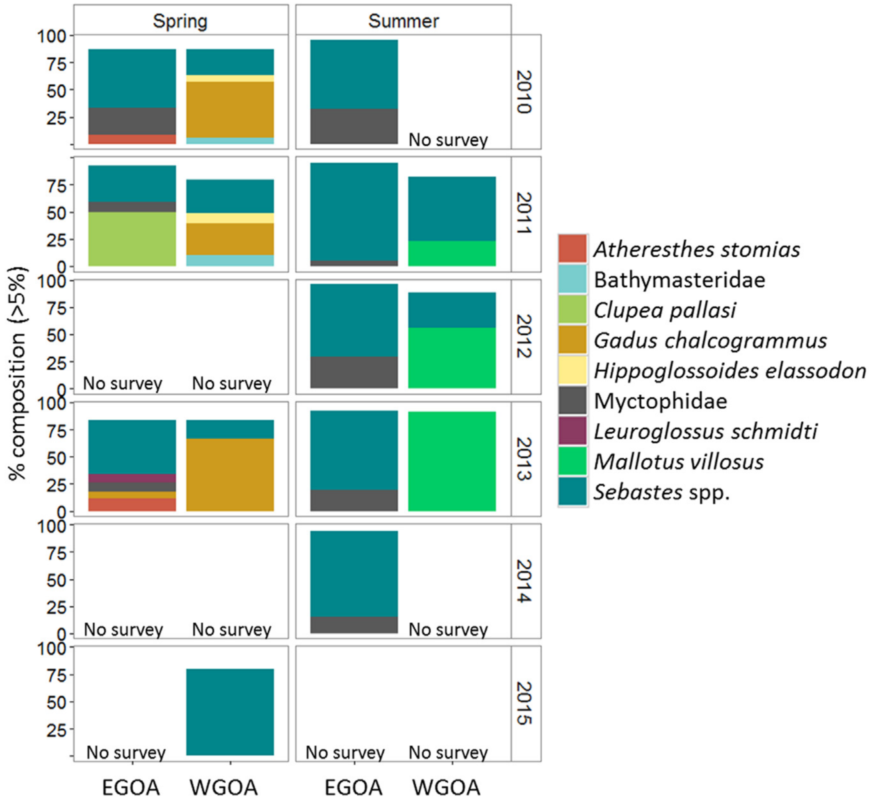

Fig. 5. Percent composition of dominant taxonomic groups of larval fishes (comprised > 5% of the total percent) within each respective year (2010–2015), season (spring and summer), and region (EGOA = eastern Gulf of Alaska and WGOA = western Gulf of Alaska). “No survey” corresponds to years, regions, or seasons in which no surveys were conducted. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

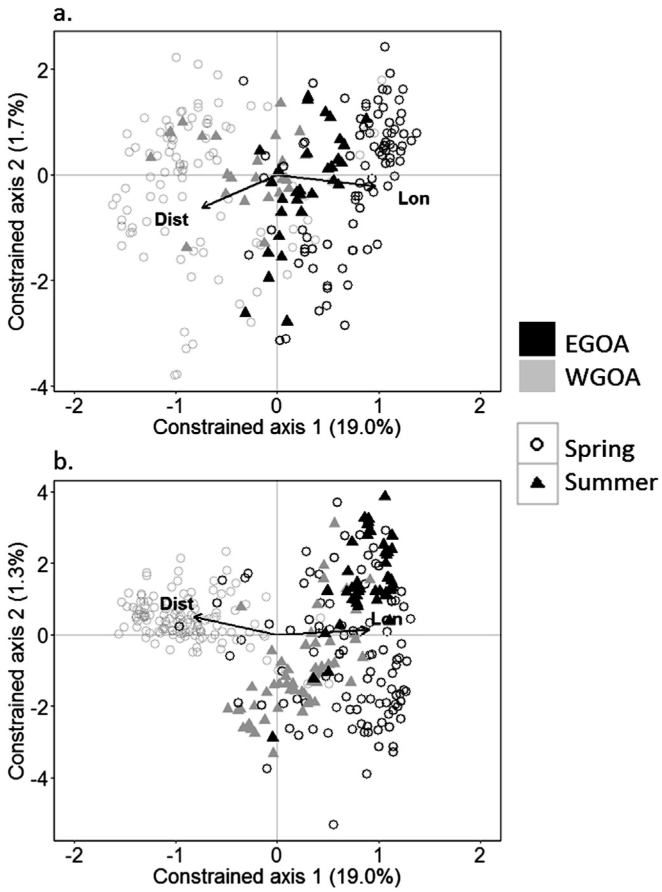

Fig. 6. The relationship between longitude, Euclidean distance from a drifter track, and larval fish assemblages in the eastern (EGOA) and western (WGOA) Gulf of Alaska during (a) 2011 and (b) 2013. Results are from partial distance-based redundancy analyses. Lon refers to longitude and Dist is Euclidean space-time distance. Percentages correspond to the amount of variability in the dataset associated with each constrained axis.

in assemblages (Table 3). The overlap between longitude and Euclidean distance explained 14.6% of the variability in assemblages, indicating that the two variables co-varied, but together they are correlated with larval assemblage patterns in the GOA (Table 3).

In all biophysical modeling scenarios using DisMELS, particles traversed from the release grid locations in the eastern GOA and dispersed into the western GOA within 6 months of particle release (Fig. A.3). The two release grid locations in the EGOA led to similar particle transport pathways, although some particles from the easternmost release grid were dispersed into the basin and to the southeast of their release locations, opposing the prevailing east-west flow in the GOA (Fig. A.3). Particles typically remained on the continental shelf, but there was evidence of enhanced offshore dispersal in the shallow release (10–30 m) and the deepest release scenarios (5 m off bottom; Fig. A.3). In contrast to other model scenarios, particles that were constrained to the 70–500 m depth range (deep release scenario) did not travel to the north or west of Kodiak Island (Fig. A.3d). In accordance with the drifter track that remained northward of Kodiak Island, many particles in the 40 m release scenario (matching the depth of the drifter drogue) traveled northward of Kodiak Island rather than following the southern bifurcation of the current (Fig. 7). In addition, the westward movement of IBM particles temporally corresponded with the drifter track, indicating that the IBM output from the 30–50 depth range captured the general flow patterns during the study year (Fig. A.4).

For model scenarios with preferred particle depth ranges < 70 m, many modeled particles remained on the continental shelf throughout much of the 6 month dispersal period, in agreement with the spatial coverage of larval collections that were restricted to the continental shelf (Fig. 7 and Fig. A.3a-c). Biophysical modeling results for the 30–50 m larval depth range visually corresponded to larval fish assemblages based on multivariate p-dbRDA CA1 scores (see Section 3.2.3.; Fig. 7 and Fig. A.3b) such that the gradient in larval assemblage composition across the GOA qualitatively corresponded with the diminishing IBM particle counts from east to west (Fig. 7). At finer spatial scales, the heatmap of particle counts showed spatial overlap in the central GOA (~ between −140° to −150° longitude) for particles sourced from both release grids (Fig. 7), indicating a region of particle accumulation. Particle accumulation in the central GOA was corroborated by larval assemblage composition in the central GOA that resembled those in the EGOA (CA1 scores of ~0–1; Fig. 7). Westward of this region of accumulation, modeled larval trajectories from the easternmost release grid bifurcated before reaching Kodiak Island. This bifurcation spatially coincided with a transition from assemblages that closely resembled those in the east toward WGOA assemblages (CA1 scores shift to negative numbers) between approximately −147° and −151° longitude. This transition from "eastern" to "western" GOA assemblages coincided with the scarcity of modeled particles from the easternmost release grid immediately adjacent to Kodiak Island (Fig. 7). Similarly, to the west of Kodiak Island, where bifurcated modeled particle trajectories re-join (~156° to −158° longitude), spring assemblages showed a slight reverse gradient from east to west toward more positive CA1 scores that resembled EGOA assemblages.

The biophysical model output from the 40 m release depth scenario visually coincided with larval assemblage patterns and captured the general timing and trajectory of the drifter track (Fig. A.4). Notably, the drifter track and IBM particles that were released starting on May 10 reach the central rather than the WGOA by mid-August, but larval fish sample collections began on April 30, 2011 in the EGOA and concluded on Aug 21, 2011 in the WGOA (Table 1, Fig. A.4c,d). This result indicates that while the Euclidean distance from the drifter track used for p-dbRDA analyses encompasses the general timing of ichthyoplankton collections and east-west transport from spring to summer, there is some temporal offset that may obscure assemblage cohesion across the GOA in p-dbRDA analyses (Fig. 7, Fig. A.4). Nevertheless, the duration of east-west transport across the GOA from the IBM indicated that the 4-month time window of sample collections (April 30, 2011-August 21, 2011, Table 1) is sufficient to capture larval transport across the entirety of the GOA from spring to summer (Fig. A.4d,e). The presence of "eastern" assemblages in the WGOA in summer coincides with the 4-month duration of transport from the easternmost release grid (Fig. 7 and Fig. A.4d). Larvae spawned from the more western release grid reach the WGOA within ~2 months (Fig. A.4c,d), corresponding with the ~2 month time window of spring sampling (April 30-June 9; Table 1) and corroborates the evidence of "eastern" fish assemblages just east of Kodiak Island in the spring (Fig. 7).

3.2.4. *Spawning location*

Few taxonomic groups included larvae that were present in both spring and summer (2011: 16 out of 40, 2013: 28 out of 73). Length frequency distributions of larval *L. bilineata* revealed the highest larval CPUE in the spring in the WGOA with the size distribution skewed toward smaller individuals. In the summer, there were fewer larvae and the size distribution was bimodal and included similar frequencies of small and large individuals (Fig. 8a inset). Distributions of adult *L. bilineata* and larvae in the spring were co-located, both with distributional centers in the WGOA and to a lesser degree in the EGOA. Larvae collected in summer were only found in the WGOA at the center of both the adult and spring larval distributions (Fig. 8a). Length frequency distributions of larvae of *I. isolepis* showed high frequencies of small larvae in both the EGOA and the WGOA in the spring, but in summer larvae were only present in the WGOA. While few larvae were collected, length distributions also had a bimodal pattern in summer

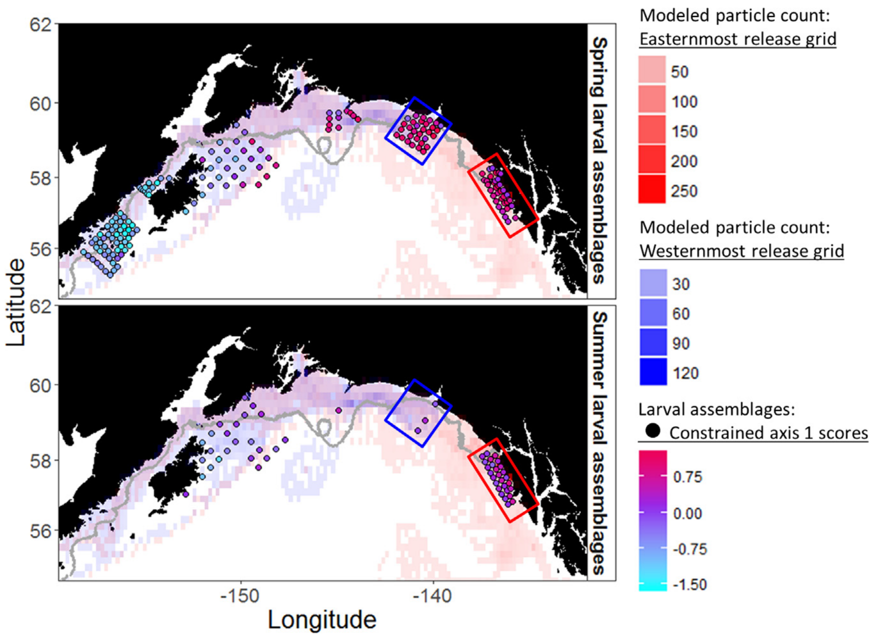

Fig. 7. Spatial depiction of community patterns of larval fishes from the partial distance based redundancy analysis (p-dbRDA) and particle trajectories from the DisMELS individual-based biophysical model (IBM) for 2011. The color gradient of points shows p-dbRDA constrained axis 1 scores (see Fig. 6a). The IBM output (grid cells) shows particle counts from 2011 based on the IBM with a particle release depth of 40 m (see Table 2). Grid color represents the particle release locations from the easternmost and westernmost release grids (outlined in red and blue, respectively; see Fig. A.3 for details), and opacity is the number of particles (count) that traversed each grid cell during the duration of the model run (180 days). The upper and lower panels are based on larval assemblages from spring and summer collections, respectively, but show the same modeled particle trajectory and drifter track (gray line) because the trajectories were continuous and spanned both spring and summer. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

(Fig. 8b inset). Adult spatial distributions peaked in the WGOA; and larvae collected in spring co-occurred with adults. In summer, *I. isolepis* larvae were found in the WGOA and near the central GOA, but did not directly co-occur with adult or spring larvae distributional centers (Fig. 8b).

4. Discussion

Examination of variability and consistencies in larval fish assemblages in the GOA across seasonal, inter-annual, or greater time scales can provide a holistic perspective of ecosystem patterns and linkages that are rooted in fundamental ecological processes. Larval distributions suggest that the separation of eastern and western regions of the GOA LME occurs along a spatial continuum that ultimately results in unique regional assemblages. Spatial and temporal patterns indicate that assemblages are largely related to longitude and spawning season, and that oceanographic transport and connectivity contribute to spatial gradients in species assemblages across large spatial domains such as the GOA. Such patterns in larval assemblages can provide insight into the mechanistic processes that may also be linked with ecosystem change such as oceanographic currents, phenology, temperature related life-history traits, and geographic distributions (Walther et al., 2002). Regional congruence or disparities in larval assemblages, or fluctuations in response to environmental change, can inform Large Marine Ecosystem delineations and management by building an understanding of the influences of environmental processes on community and ecosystem structure.

Divergence in spring and convergence in summer larval fish assemblages revealed the role of seasonality in structuring regional congruence between the EGOA and WGOA. Throughout the GOA the majority of fish species spawn in late winter (Jan-Feb) and early spring (Mar-Apr), with maximum numbers of larval species observed in late spring (May-June); larval abundances reach their peak at this time as well (Matarese et al., 2003). This spring peak in occurrence and abundance probably reflects the production of offspring by the community of spawning adults in each location. Given the relatively short time between spawning and sampling, agents of mortality that act to remove individuals from the larval assemblage have not fully manifested and disparate larval fish assemblages in spring are likely a reflection of the regionally distinctive adult groundfish community (Mueter and Norcross, 2002). By summer however, other physical and biological processes have acted on larval assemblages over time, serving to diminish the number of species. Ontogenetic development is manifested and selected larval species transition out of the plankton (ex: flatfishes, demersal species, nearshore species) reducing the number of individuals in the assemblage matrix and homogenizing the community over broad regional scales. The number of summer spawning species in the GOA is markedly fewer, resulting in lower taxonomic diversity in summer larval assemblages once spring larvae are removed from the planktonic community through mortality, ontogeny, or other processes. Spawning by the diverse and abundant *Sebastes* spp. group is a notable exception where summer larvae reflect numerous species and spring larvae are primarily Pacific Ocean Perch (*Sebastes alutus*; Siddon et al., 2016). Given that regional ecosystem heterogeneity is substantially influenced by the timing of biological processes (Gray and Miskiewicz, 2000) we might expect differing seasonal influences on eastern and western GOA assemblages as a result of similarities in summer spawning taxa compared to regionally disparate spring spawning taxa with species-specific life-histories and vulnerabilities.

In addition to spawning seasonality and adult distributions, the physical and biological environment experienced by a larval fish in the planktonic environment can influence survival, distributions, and assemblage patterns which may have been a factor in summer larval assemblage homogenization across the GOA. The results of this study suggest that the local physical environment played only a minor role in structuring larval assemblages in comparison to broad-scale spatial processes. In the GOA, the westward flowing AS and ACC (Stabeno et al., 2004) may influence larval spatial distributions and create the potential for connectivity across the basin for species with a 3–6 month pelagic larval duration (Bouwens et al., 1999; Doyle and Mier, 2015). Correspondingly, biophysical modeling studies of walleye pollock and arrowtooth flounder indicate that larvae that are spawned in the spring in the EGOA may be transported to the WGOA by the summer (Parada et al., 2016). Regional differences in spring assemblages were dampened during the summer months when WGOA assemblages more closely resemble those in the EGOA. This assemblage change from spring to summer was likely influenced by adult distributions interacting with spawning seasonality, but gradients in larval assemblages suggest that east to west transport may have also contributed to regional congruence during the summer months. Drifter tracks that were utilized to assess assemblage cohesion were based on a single

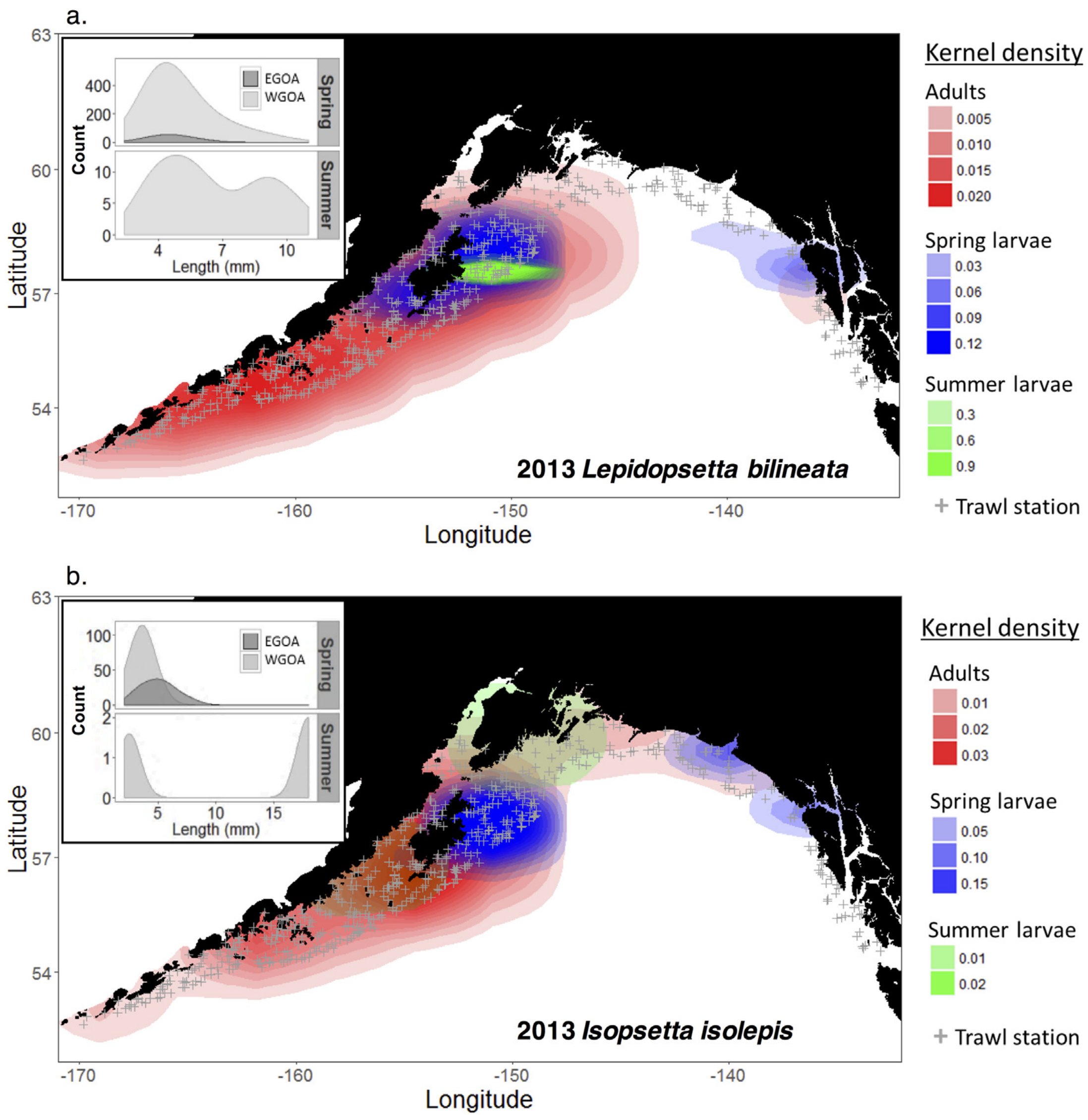

Fig. 8. Kernel density plots based on presence of adults from trawl data (red), larvae in spring (blue), and larvae in summer (green) for (a) *Lepidopsetta bilineata* and (b) *Isopsetta isolepis* in 2013. Opacity corresponds to frequency of occurrence. Gray symbols show the starting locations of adult trawl survey tows to show the spatial coverage of the survey. Insets show larval length frequency distributions in spring and summer in the eastern (EGOA) and western (WGOA) Gulf of Alaska based on a spatial break at 146.0° W (−146°). Larval length-frequency distributions were based on Catch Per Unit Effort (larvae 10 m^{-2}) and the scale of the y-axes are different to highlight size distributions. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

deployment in each year and showed a slight temporal offset from the ichthyoplankton collections. However, the drifter track encompassed the general timing of spring to summer ichthyoplankton collections from east to west across the GOA, and ~70% of the transport of the ACC continues along the northern side of Kodiak Island (Stabeno et al., 2004), suggesting that the drifter tracks were representative of the westward transport in the region. While the strength of conclusions and ability to disentangle the influence of location and transport are restricted by the strong negative correlation between Euclidean distance from a drifter and longitude, convergences in summer assemblage in the EGOA and WGOA as well as cohesion among larval assemblages along a drifter track suggest that basin-wide east to west transport may contribute to broad-scale spatial patterns such as longitudinal gradients in assemblage composition.

The influence of transport on assemblages was supported by the particle tracking model that showed connectivity between the EGOA and WGOA within a 2- to 6-month time window, and spatial patterns that coincided with east to west gradients in larval assemblages. In addition to basin-wide connectivity, few particle trajectories traversed the region immediately adjacent to the eastern side of Kodiak Island where larval assemblages diverged from those in the EGOA, suggesting a region of larval accumulation and a transitional zone between the EGOA and WGOA. Larval accumulation near Kodiak Island is congruent with the formation of eddies off Yakutat in the winter months, and propagation along the shelf until they reach Kodiak Island in the spring where they can have long residence times (Ladd et al., 2005). Divergences in assemblages, trajectory bifurcations, and the accumulation of larvae near Kodiak Island are also consistent with the branching of the ACC (Ladd et al., 2005) as well as local oceanography that disrupts east-west flow such as eddies and gap winds (Ladd, 2007; Ladd et al., 2016; Stabeno et al., 2004). This region of accumulation is apparent in both spring and summer, despite evidence that transport across the entire GOA takes ~5–6 months based on the drifter track and IBM modeling. This pattern does not preclude connectivity between the eastern and western GOA and the biophysical model highlights the potential for within-season transport across shorter distances and timescales, and the probable role of more westward spawning locations within the EGOA that promote regional connectivity. Oceanographic features can be important for maintaining larval assemblages (Atwood et al., 2010; Cowen et al., 1993), and our results suggest that local disruptions in prevailing currents promote regional divergences in assemblages while broader-scale oceanographic transport contributes to gradients in larval assemblages across large spatial domains.

Notably, assemblages in the EGOA also differed between spring and summer, but to a lesser degree than those in the WGOA. The Gulf of Alaska is often considered ecologically distinct from more southerly regions in the North Pacific (Coyle and Pinchuk, 2003; Doyle et al., 2002). However, the seasonal patterns in the EGOA may be influenced by the influx of larvae from upstream spawning locations. For example, the dominant summer taxa, *Sebastes* spp. and Myctophidae, have distributions that extend southward to the Northern California Current Ecosystem off Oregon, USA (Auth, 2008). While the majority of the surface flow along the North Pacific coastline is southward during the summer months (Freeland, 2006; Hickey, 1979), the bifurcation of the North Pacific Current can vary in latitude and may influence transport routes for larvae sourced from the south (Sydeman et al., 2011). Additionally, eddies in the EGOA may retain larvae (Stabeno et al., 2016) and maintain assemblage patterns between spring and summer (Atwood et al., 2010). While larval sources located upstream of the EGOA were not assessed in this study, spatial and seasonal fluctuations in larval distributions and assemblage composition highlight the potential for regional variability in larval sources, import, and export.

Regional connectivity between EGOA and WGOA is likely for species with a range of life-history traits; however, single-species distributions highlight the potential importance of spawning location and pelagic larval duration on larval transport. In comparison to the total number of taxa identified, few species had pelagic larvae that were present in the water column in both spring and summer, indicating that assemblage cohesion along the drifter track may be the result of a small subset of taxa with long pelagic larval durations. For many species, connectivity and transport across the entirety of the GOA may be restricted by pelagic larval duration. For example, *Lepidopsetta bilineata* spawn demersal eggs from winter through summer on the continental shelf (< 120 m deep; Matarese et al., 2003; Stark, 2002a, 2002b), and a bimodal length-frequency distribution in the summer suggests both summer spawning and that larvae that were spawned in spring may remain in the water column until summer. The spatial co-occurrence of adults and summer larvae in the WGOA suggests that larvae may have been locally spawned and retained rather than transported from the EGOA to the WGOA. Characteristics such as shallow spawning depths and demersal eggs that are hypothesized to limit offshore advection (Bailey et al., 2005; Riginos et al., 2011) may promote local retention for this species, highlighting the probable role of life-history characteristics in determining transport and connectivity. In contrast, *Isopsetta isolepis* (butter sole) adults were more broadly distributed across the GOA than *L. bilineata*, and spawn pelagic eggs at reported depths of ~30–60 m (Levings, 1968), primarily in the spring (Matarese et al., 2003). *Isopsetta isolepis* larvae collected in the summer did not co-occur spatially with the peak distributions of adult or spring larvae, suggesting that the presence of larvae in the WGOA in the summer may reflect oceanographic transport rather than local spawning and retention. Summer larvae were also located nearshore, coinciding with the drifter track and the typical trajectory of the ACC (Stabeno et al., 2004), further supporting the influence of transport on larval distributions and regional connectivity. Species-specific case studies are not exhaustive analyses of the influence of life-history characteristics on dispersal and connectivity, and while many other species in the GOA also spawn from spring through summer on the continental shelf (yellowfin sole, starry flounder, capelin), other taxa such as arrowtooth flounder and Pacific halibut spawn in deeper waters in the winter (Doyle and Mier, 2012). Thus, the two-example species represent a subset of life-history traits, and elicit additional hypotheses regarding the interacting roles of oceanography and life-history characteristics such as spawning location, depth, and potentially egg type in determining transport and connectivity across large geographic domains.

Larval assemblages showed several persistent spatial and temporal patterns, suggesting the probable influences of spawning location, seasonality, and transport on structuring eastern and western GOA larval fish distributions. Despite primarily consistent patterns, there were subtle shifts in larval assemblages that emerged during the summer of 2013 and the spring of 2015 in the WGOA and not the EGOA. While the definitive causes of atypical larval assemblages in the western GOA cannot be directly identified from the present study, anomalous warm water temperatures, or the “Warm Blob”, developed during the latter years of this study, starting in the North Pacific during the fall of 2013 and spreading throughout the GOA in the winter of 2013/2014 and through much of 2015 (Bond et al., 2015). This warm anomaly affected multiple trophic levels from primary productivity to large marine mammals (Cavole et al., 2016; Di Lorenzo and Mantua, 2016). Pelagic organisms such as larval fishes are sensitive to environmental fluctuations, and warmer temperatures can affect egg production, phenology, food availability, and larval mortality (Beaugrand, 2005; Smart et al., 2012; Visser and Both, 2005). Notably, assemblages in the summer of 2013 and spring of 2015 in the WGOA were dominated by taxonomic groups (*Mallotus villosus* and *Sebastes* spp., respectively) that are sensitive to temperature variability and associated with warm water conditions (Daly et al., 2013, 2017; Rose, 2005). Many of the biological and physical processes that influence larval assemblages in the GOA, particularly spawning seasonality and pelagic larval duration, are influenced by temperature (Genner et al., 2010; O’Connor et al., 2007; Visser and Both, 2005; Asch, 2015), suggesting that changes in regional larval assemblages may reflect regionally distinct environmental variability or differential responses to change.

5. Conclusions

The movement toward ecosystem management should encompass an understanding of processes that influence individual organisms, species, communities, and interactions among ecosystem components. Discerning such processes for a suite of organisms with distinct life-histories presents unique challenges in dynamic oceanographic environments. In complex systems, a multi-species approach such as assemblage patterns of larval fish can reflect community variability and cohesion, signal ecosystem change or transitions, and can be applied to ecosystem delineations of geographically and ecologically distinct regions (Baker and Hollowed, 2014; Toonen et al., 2011).

Larval assemblages in the GOA reflected a combination of spatial and temporal processes that, together, influence assemblage patterns and regional continuity. Regional spawning mediated by transport resulted in an east to west gradient in assemblage structure with an area of accumulation near the eastern side of Kodiak Island. This dominant east to west spatial gradient in assemblages was punctuated by seasonal patterns that underscore the influence of phenology on assemblage structure and ecosystem linkages and discontinuities, and the importance of temporal processes in Large Marine Ecosystem delineations. While larval assemblage patterns across the GOA showed primarily consistent spatial gradients across the LME throughout the 6-year study period, there was evidence of regional discontinuities and assemblage shifts in recent years in the WGOA, suggesting the influence of environmental variability on larval distributions.

Assemblages and metacommunity dynamics can help to explain or predict spatial patterns in diversity in marine systems and can reflect large-scale ecosystem change (Guichard, 2005; Guichard et al., 2011). Distributional patterns of fish larvae in the GOA underscore the relevance of assessing ecosystem and community dynamics across various levels of complexity and a range of spatial and temporal scales that reflect the appropriate resolution for management challenges. Larval fish assemblage patterns are the endpoint of multiple biological and physical processes that are susceptible to climate variability (Genner et al., 2010; O'Connor et al., 2007; Visser and Both, 2005; Asch, 2015), suggesting that while larval fish assemblage composition indicates unique eastern and western regions, future ecosystem and climate change may alter species' distributions and linkages across the GOA.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2018.09.003.

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