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Patterns of larval source distribution and mixing in early life stages of Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea

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ABSTRACT

Effective and sustainable management depends on knowledge of spawning locations and their relative contributions to marine fish populations. Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea aggregate at discrete spawning locations but there is little information on patterns of larval dispersal and the relative contribution of specific spawning areas to nursery habitats. Age-0 Pacific cod from two cohorts (2006 and 2008) were examined to address the following questions: (1) does size, age, and otolith chemistry vary among known capture locations; (2) can variation in elemental composition of the otolith cores (early larval signatures) be used to infer the number of chemically distinct sources contributing to juvenile recruits in the Bering Sea; and (3) to what extent are juvenile collection locations represented by groups of fish with similar chemical histories throughout their early life history? Hierarchical cluster (HCA) and discriminant function analyses (DFA) were used to examine variation in otolith chemistry at discrete periods throughout the early life history. HCA identified five chemically distinct groups of larvae in the 2006 cohort and three groups in 2008; however, three sources accounted for 80–100% of the juveniles in each year. DFA of early larval signatures indicated that there were non-random spatial distributions of early larvae in both years, which may reflect interannual variation in regional oceanography. There was also a detectable and substantial level of coherence in chemical signatures within groups of fish throughout the early life history. The variation in elemental signatures throughout the early life history (hatch to capture) indicates that otolith chemical analysis could be an effective tool to further clarify larval sources and dispersal, identify juvenile nursery habitats, and estimate the contributions of juvenile nursery habitats to the adult population within the southeastern Bering Sea.

1. Introduction

Knowledge of spawning and nursery locations and their relative contributions to marine fish populations, or stocks, is a fundamental component of sound fisheries management (Begg and Marteinsdottir, 2000; Jónsdóttir et al., 2007). However, there are numerous challenges to accurately identifying spawning and nursery areas, evaluating their output, and determining their relative contributions to a population. Demographic, genetic, and otolith structural and chemical approaches have been used to identify discrete aggregations and assess their relative contributions to adult populations (Wilimovsky et al., 1967; Miller et al., 2005; Cunningham et al., 2009; Svedang et al., 2010). Although each method has limitations, a combined approach has the potential to provide corroborative or complementary information on spawning contributions, larval sources, and essential fish habitats.

The Pacific cod fishery in the United States is currently managed as two components, the Gulf of Alaska stock and the larger Bering Sea – Aleutian Islands stock. Early work by Wilimovsky et al. (1967) reported geographic differences among Pacific cod using meristic measures, suggesting the potential for distinct stocks in southern British Columbia, southeast Alaska, and the Bering Sea. Additionally, several genetic studies (Grant et al., 1987; Cunningham et al., 2009; Spies, 2012) have observed isolation by distance across the species range throughout the North Pacific Ocean but no distinct boundaries within or between the current management areas.

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Pacific cod annually aggregate at discrete spawning locations throughout the Aleutian Islands, around the Pribilof Islands, north of Unimak Island, and along the shelf break near Zhemchug Canyon (Neidetcher et al., 2014). The degree of fidelity to each of these sites and the extent to which each of these spawning regions contribute to the Bering Sea population is unknown, and there is additional potential for larval Pacific cod to be transported from the Gulf of Alaska into the Bering Sea through the Unimak Pass (Siddon et al., 2011). Additionally, tagging studies of adult fish indicate that the Unimak Pass–Alaska Peninsula region may support the majority of spawning activity for Bering Sea Pacific cod (Shimada and Kimura, 1994). Pacific cod spawn demersal, non-adhesive eggs. Surveys of reproductive status of adults during winter in the Bering Sea from 2005 to 2007 indicate that spawning begins in February or early March and extends through early to mid-April (Neidetcher et al., 2014). Positively buoyant larvae hatch between 3 and 4 mm standard length (SL), are collected in surface waters, and transform into juveniles at 25–35 mm SL. In the Bering Sea, larvae have been most commonly collected from March to August along the Alaska Peninsula and the southeastern portion of the shelf, which is also when the majority of sampling effort has occurred (Matarese et al., 2003). Juveniles are most abundant in coastal waters along the Alaska Peninsula but also occur in pelagic waters over the broad continental shelf (Hurst et al., In review). However, little is known regarding patterns of larval dispersal, the relative contribution of specific spawning areas to the widely distributed nursery habitats, or the contribution of those nurseries to the adult population. Given that Pacific cod are fished on their spawning grounds, it is important to identify the factors that influence the abundance, distribution, and connectivity of stocks and to evaluate whether particular spawning sources are more critical than others in sustaining the productivity of populations within the Bering Sea.

Tracking larvae from spawning to settlement is challenging, particularly in widely distributed marine species. Small size and high rates of mortality make external tagging techniques impractical due to the large number of tagged individuals needed to ensure sufficient numbers are recovered (Jones et al., 1999, 2009; Almany et al., 2007). Similarly, the ability of traditional population genetic techniques is limited due to the low level of exchange required to maintain genetic homogeneity over ecologically relevant time scales (e.g., Slatkin, 1993), and more recent parentage approaches require representative sampling of parents and offspring which is not feasible in many marine species (Planes et al., 2009; Saenz-Aguledo et al., 2009; Christie, 2010). Isotopic and elemental analyses of otoliths have shown promise as a means to investigate spatial structure in fishes on ecological time scales and have been used to examine natal sources (Thorrold et al., 2001; Barbee and Swearer, 2007) and dispersal patterns in marine fishes (Swearer et al., 1999). This approach is feasible because the chemical composition of otoliths reflects the physical and chemical properties of the ambient water. When water masses have distinct physiochemical properties, then the elemental signature incorporated into the otoliths of individuals residing in those masses should also differ.

In this study, we used otolith structure and chemistry of juvenile Pacific cod to evaluate their potential to provide information on larval sources and early life histories in the southeastern Bering Sea. Specifically, we addressed the following questions: (1) do size, age, and otolith chemistry of age-0 Pacific cod vary among known capture locations; (2) can variation in elemental signatures in otolith cores (early larval signatures) be used to infer the number of chemically distinct sources contributing to juvenile recruits in the Bering Sea; and (3) to what extent are juvenile collection locations represented by groups of fish with similar chemical histories throughout their early life history, which could indicate cohesive dispersal patterns?

2. Methods

2.1. Study design

Juvenile (age—0) Pacific cod from 2 cohorts were collected throughout the southeastern Bering Sea to address the research questions presented above. First, we compared juvenile size and age among collection locations. Second, we examined the elemental signatures at the outer edge of the otoliths to evaluate the extent of spatial variation in elemental composition and assess the ability to classify fish to collection location based on otolith edge signatures. Third, we examined elemental signatures in the otolith core of those same juveniles, which represent their early larval stage, using a combination of hierarchical cluster and discriminant function analyses to identify chemically distinct groups of larvae. Fourth, we determined the spatial distribution of juveniles with distinct early larval elemental signatures. Finally, we evaluated how consistent otolith elemental signatures were during discrete periods of the early life history to provide an indication of potential mixing within the study area.

2.2. Sample collection

Juvenile Pacific cod were collected throughout their range in the southeastern Bering Sea (Hurst et al., 2012) from August–September 2006 and 2008 during the Alaska Fisheries Science Center's (AFSC) annual Bering-Aleutian Salmon International Survey (BASIS). Over the continental shelf, juveniles were collected with a 198-m mid-water rope trawl modified to sample the top 15 m of the water column and composed of hexagonal mesh wings and a body fitted with a 1.2-cm mesh codend liner (see Farley et al., 2005). Additional samples in both years were collected in the Bristol Bay region with a 3-m beam trawl (Cooper et al., 2014). Based on extensive sampling in 2012, fish collected with beam trawls in Bristol Bay and along the Alaska Peninsula are only slightly larger than fish collected with a surface trawl in deeper waters over the shelf (beam trawl: 66.6 ± 7.1 mm; surface trawl: 64.3 ± 9.2 mm TL), suggesting that summer collections are not influenced by a size-dependent habitat shift. Juveniles were frozen after capture and transported to the AFSC's Fisheries Behavioral Ecology laboratory in Newport, Oregon, for analysis. In both years, fish were selected from six trawl sites that covered the distribution of juveniles collected in the Bering Sea (Hurst et al., 2012); three samples were collected along the western, middle and eastern Alaska Peninsula (AP-W; AP-M; AP-E, respectively) and three samples were collected farther north over the western, middle and eastern Shelf (Sh-W; Sh-M; Sh-E; Fig. 1).

Additionally, in May of each sampling year, larval Pacific cod were collected in the vicinity of Unimak Pass in an attempt to relate the elemental signatures of otolith cores from fish collected as juveniles to signatures of larvae from a major known spawning region. However, those larvae averaged 19 d old with a mean hatch date of May 1. Therefore, it appears that the survey, which targets walleye pollock (*Gadus chalcogrammus*), does not coincide with the peak spawning of Pacific cod (Neidetcher et al., 2014). Given that the larval collections likely represent only the later spawners, we did not include them in subsequent analyses. Data on the spatial variation in otolith elemental composition of larval Pacific cod are presented in DiMaria (2011).

2.3. Age determination

Juveniles were weighed (to 0.01 mg) and measured (standard length SL, to 1.0 mm), and both sagittal otoliths were removed using standard methods to minimize contamination (Miller, 2009). Otoliths were photographed under a dissecting microscope and