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Biophysical transport model suggests climate variability determines distribution of Walleye Pollock early life stages in the eastern Bering Sea through effects on spawning

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ABSTRACT

The eastern Bering Sea recently experienced an anomalously warm period followed by an anomalously cold period. These periods varied with respect to sea ice extent, water temperature, wind patterns, and ocean circulation. The distributions of Walleye Pollock early life stages also differed between periods, with larval stages found further eastward on the shelf in warm years. Statistical analyses indicated that these spatial distributions were more closely related to temperature than to other covariates, though a mechanism has not been identified. The objective of this study was to determine if variable transport could be driving the observed differences in pollock distributions. An individual-based model of pollock early life stages was developed by coupling a hydrodynamic model to a particle-tracking model with biology and behavior. Simulation experiments were performed with the model to investigate the effects of wind on transport, ice presence on time of spawning, and water temperature on location of spawning. This modeling approach benefited from the ability to individually test mechanisms to quantitatively assess the impact of each on the distribution of pollock. Neither interannual variability in advection nor advances or delays in spawning time could adequately represent the observed differences in distribution between warm and cold years. Changes to spawning areas, particularly spatial contractions of spawning areas in cold years, resulted in modeled distributions that were most similar to observations. The location of spawning pollock in reference to cross-shelf circulation patterns is important in determining the distribution of eggs and larvae, warranting further study on the relationship between spawning adults and the physical environment. The different distributions of pollock early life stages between warm and cold years may ultimately affect recruitment by influencing the spatial overlap of pollock juveniles with prey and predators.

Introduction

The eastern Bering Sea shelf is one of the most biologically productive marine ecosystems in the world with marine resources that are integral to the culture and diet of native Alaskans and that comprise roughly 50% of the US commercial fish harvest. The continental shelf extends approximately 500 km westward from the Alaskan mainland coast to the Aleutian Basin shelfbreak and 1000 km northward from the Alaska Peninsula to the Bering Strait. The shelf can be divided into three regions based on bathymetry: inner shelf (<50 m), middle shelf (50–100 m), and outer shelf (>100 m; Coachman, 1986). The inner shelf is weakly stratified and influenced by freshwater runoff, while the middle and outer shelves are strongly stratified (Coachman, 1986). A large and highly variable portion of the shelf is ice-covered during winter, cooling the entire water column and resulting in a bottom layer of very cold water (the "cold pool") over much of the middle shelf that can persist through the summer. Offshore, the Bering Slope Current (Fig. 1) transports nutrient-rich waters along the slope to the northwest, replenishing nutrients on the shelf through cross-shelf exchanges associated with eddies (Mizobata et al., 2008), intrusions of water through canyons (Stabeno et al., 2008), and wind-forced cross-shelf flows (Stabeno et al., 2001; Danielson

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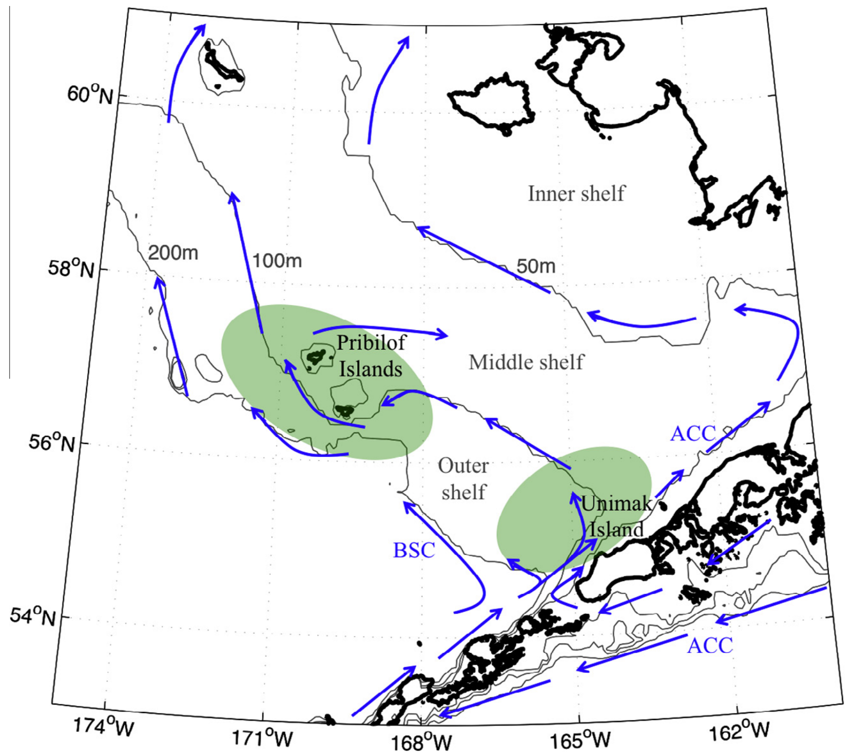

Fig. 1. The dominant currents (blue lines) and Walleye Pollock spawning areas (green ovals) of the eastern Bering Sea. The Alaska coastline is shown in black and the 50, 100, and 200 m isobaths in gray. ACC – Alaska Coastal Current; BSC – Bering Slope Current. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2011b). Mean circulation over the shelf is dominated by the Alaska Coastal Current, which is a seasonal current that flows roughly parallel to the 50-m isobath northeast along the Alaska Peninsula, around Bristol Bay, and continues to the northwest off of mainland Alaska towards the Bering Strait (Fig. 1). Cross-shelf and along-shelf flows provide important pathways for the planktonic stages of many species that spawn on the outer shelf or slope to reach suitable nursery areas (Lanksbury et al., 2007; Wespestad et al., 2000; Wilderbuer et al., 2013).

Walleye Pollock (*Gadus chalcogrammus*; hereafter pollock) is an ecologically and commercially important gadid in the eastern Bering Sea, supporting one of the largest single-species fisheries in the world. Adults are semi-demersal and occur primarily in regions 50–300 m deep (Duffy-Anderson pers. comm.). Females are iterative spawners with up to 10 batches of eggs per female per year (Duffy-Anderson pers. comm.). Pollock show fidelity to at least two spawning sites over the southeastern Bering Sea shelf (Fig. 1). Spawning begins nearshore north of Unimak Island in March and April and later near the Pribilof Islands from April through August (Jung et al., 2006; Bacheler et al., 2010). Egg production from these two locations is highest in April or May (Bacheler et al., 2010). Eggs can be found as deep as 300 m, but the center of the vertical distribution is <30 m (Smart et al., 2012). Depending upon water temperature, embryos hatch 18–34 days after fertilization and yolksac larvae are 4.6–5.7 mm standard length (SL) at hatch (Blood, 2002). Larvae develop in the upper 100 m of the water column and the depth of maximum abundance shifts deeper with age (Smart et al., 2013). Depth differences are related to flexion, which occurs between 10 and 17 mm SL (Matarese et al., 1989), after which larval swimming ability increases. Pollock transition from larva to pelagic juvenile when they are 30–40 mm SL (Matarese et al., 1989) and recruit into the fishery at age-3 to age-4 (Ianelli et al., 2012a).

The eastern Bering Sea recently experienced a prolonged warm period (2001–2005), followed by a prolonged cold period (2007–2012; Stabeno et al., 2012). During colder than average years, winter ice extends farther south and offshore, creating a more extensive cold pool that influences the distribution (Mueter and Litzow, 2008; Barbeaux, 2012; Ianelli et al., 2012a) and potentially the spawning ecology of pollock and other demersal fishes. The timing and location of pollock spawning affect the initial distribution of eggs, while their subsequent advection is a function of prevailing atmospheric and hydrographic conditions. Therefore both the initial distribution and advective forcing vary from year-to-year due to climatic variability. For example, strong northward flow and/or weaker cross-shelf flow have been observed at a hydrographic mooring over the middle shelf during the recent warm period compared to recent cold years that had strong westward flow (Stabeno et al., 2012), which could affect the dispersal of pelagic early life stages (ELS). Modeling results suggest generally enhanced on-shelf transport when winds blow predominantly from the southeast during winter (Danielson et al., 2011a). Such southeasterly winds coincided with warm temperatures from 2001 to 2005, while the following cold years were characterized by winds from the northwest. It has been speculated that these differences in advection influence the distributions of pollock ELS, whose centers are further inshore in warm years than cold years (Smart et al., 2012).

The observed variability in distribution could be the result of differences in physical transport as hypothesized, or they could be the result of biological responses to physical variation. Preliminary analysis of roe fishery harvest data and pollock fishery observer maturity data suggest that spawning extends further onshore in warm years (Barbeaux, unpub. data) and the onset of spawning is delayed in time by as much as 40 d in cold years (Jung et al., 2006; Smart et al., 2012). Differences in water temperature could impact not only where adults spawn, but also the development rates of ELS.

Mechanisms behind the spatial differences have not been identified, and effects of climate variation on the dispersal of pollock ELS are poorly understood. The differences in winds and water currents