Journal of Sea Research 111 (2016) 11–24

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Differential patterns of divergence in ocean drifters: Implications for larval flatfish advection and recruitment

Thomas Wilderbuer [a,*], Janet T. Duffy-Anderson [a], Phyllis Stabeno [b], Albert Hermann [b,c]

[a] Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle, WA 98115, United States
[b] Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, WA 98115, United States
[c] Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98105, United States

ARTICLE INFO

Article history:
Received 10 August 2015
Received in revised form 11 March 2016
Accepted 17 March 2016
Available online 19 March 2016

Keywords:
Drifters
Dispersion
Northern rock sole
Bering Sea
Larvae
Connectivity

ABSTRACT

In an effort to better understand the physics of the eastern Bering Sea shelf current as it relates to flatfish advection to favorable near-shore areas, sets of multiple, satellite-tracked, oceanic drifters were released in 2010, 2012 and 2013. The release sites and dates were chosen to coincide with known spawning locations for northern rock sole (*Lepidopsetta polyxystra*) and known time of larval emergence. The drifters were drogued 5-each at 20 and 40 m in 2010 and 2012, and 4 at 40 m and 2 at 20 m in 2013. The locations of drifters were used to calculate divergence over a 90-day period that corresponds to the larval pelagic duration of Bering Sea shelf northern rock sole. Results indicate that there are alternating periods of positive and negative divergence with an overall trend toward drifter separation after 90 days, roughly the end of the rock sole planktonic larval period. Examination of the drifter behavior at the hourly scale indicates that semi-daily tidal forcing is the primary mechanism of drifter divergence and convergence. Field observations of early-stage northern rock sole larval distributions over the same period indicate that predominant oceanographic advection is northerly over the continental shelf among preflexion stages, though juveniles are predominantly found in nursery areas located ~400 km eastward and inshore. Evidence from drifter deployments suggests that behavioral movements during the postflexion and early juvenile larval phases that optimize eastward periodicity of tidal cycles is a viable mechanism to enhance eastward movement of northern rock sole larvae to favorable nursery grounds. A regional ocean modeling system (ROMS) was implemented to track the different rates of dispersion in simulations both with and without tidal forcing, and was used to estimate effective horizontal eddy diffusion in the case of both isobaric (fixed-depth) and Lagrangian (neutrally buoyant) particles. The addition of tidal forcing had a pronounced effect on horizontal eddy diffusion, increasing its value by a factor of five in the case of fixed-depth floats, as compared with a factor of two in the case of neutrally buoyant floats. Further, the incorporation of diurnal vertical behavior in phase with favorable (on shelf) tides transported the "larvae" ~ 400 km within 40 days of their release date. Empirical drifter data coupled with model evidence suggest that semi-diurnal tidal forcing is the primary mechanism of eastward advection over the Bering Sea shelf, and larval observational data suggest that northern rock sole larvae can maximize their eastward transport to nursery grounds by synchronizing their vertical movements to tidal periodicity during the postflexion stage.

1. Introduction

Studies of the early life history in marine fish have shown that for some species there are large distances between adult spawning areas and preferred nursery habitat for offspring (Miller et al., 1991). In many cases the larvae of these species are advected to the nursery grounds by wind-driven currents, geostrophic currents, and tides (Boehlert and Mundy, 1988; Epifanio, 1988; Nakata et al., 2000), though risk of unfavorable advection is high. This risk is heightened among flatfishes that must rely on the broadly dispersive pelagic larval phase to bring offspring closer to juvenile nursery areas in time to coincide with their metamorphosis and assumption of demersal, bottom-dwelling existence (Duffy-Anderson et al., 2015). In Large Marine Ecosystems like the eastern Bering Sea, the distance from spawning grounds to nursery grounds may be hundreds of kilometers (Wilderbuer et al., 2002; Fig. 1) so the suite of interconnected events, spawning, transport, ontogenetic development, and settlement, is critical. In the case of Bering Sea northern rock sole (*L. polyxystra*), this process of advection from deep water spawning grounds (200 m) to shallow, inshore nursery areas (<50 m) occurs over a period of only 3–4 months.

The eastern half of the Bering Sea consists of a broad (>500 km), flat continental shelf. The Eastern Bering Sea (EBS) is bordered to the east by the Alaska mainland, to the south by the Alaska Peninsula and eastern Aleutian Islands, to the west by the Aleutian Basin, and to the north by Siberia and the Bering Strait (Fig. 2). Typically it is divided into three cross shelf domains (Coachman, 1986): coastal or inner shelf

---

* Corresponding author.

http://dx.doi.org/10.1016/j.seares.2016.03.003
1385-1101/Published by Elsevier B.V.

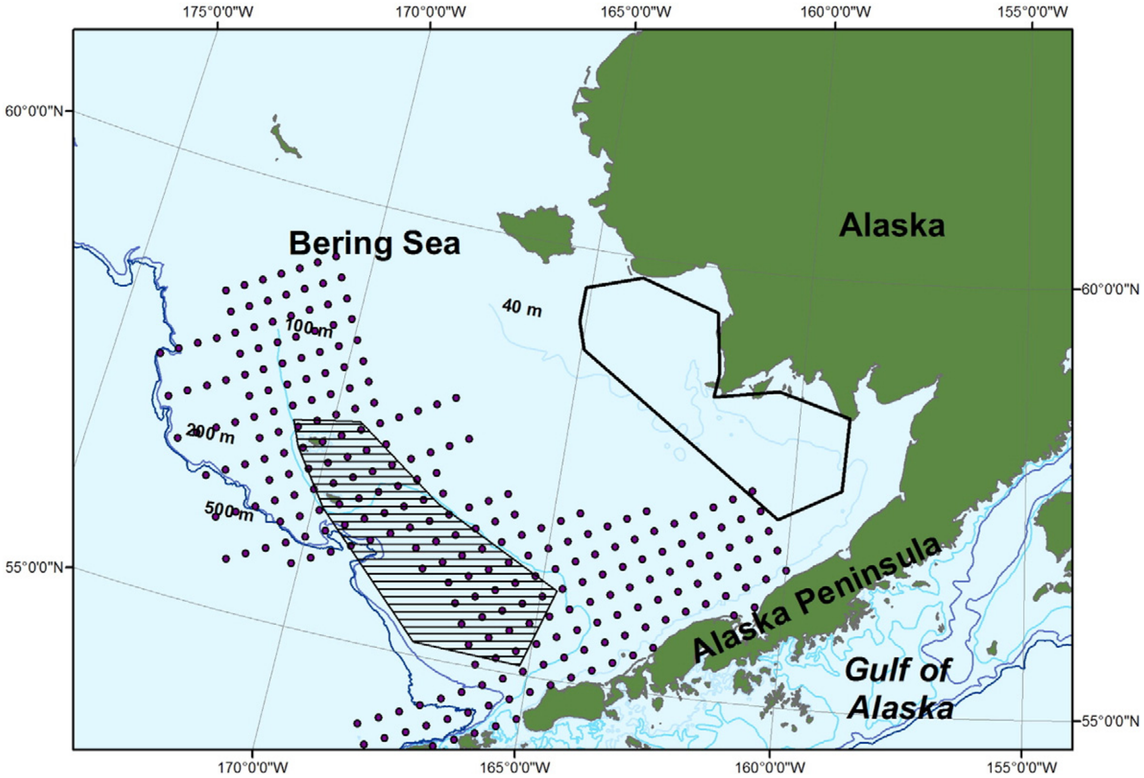

Fig. 1. Generalized spawning area 100–200 m depth (shaded) and age-0 nursery habitat <50 m depth (open) over the eastern Bering Sea shelf. Dots indicate maximum spatial extent of ichthyoplankton field collections (2005–2012). Distance from spawning to nursery areas is approximately 400 km.

(water depth < 50 m); middle (50 m to 100 m depth); and outer shelf (100 m to 180 m). The frontal or transition zones along the 50-m isobaths and 100-m isobaths act as barriers, limiting cross shelf flow between domains (Stabeno et al., 1999, 2002, 2012).

Water enters the Bering Sea through the many passes in the Aleutian Island chain (e.g., Amukta; Fig. 1). In the basin, the strong northeastward flowing Aleutian North Slope Current (ANSC) turns northwestward forming the Bering Slope Current (BSC). While flow along the slope is relatively strong (~20 cm s^{-1}), on the shelf annual mean currents are weak (<1 cm s^{-1}), with the exception of northeastward flow along the Alaska Peninsula (2–3 m s^{-1}), and northwestward flow along the 50-m isobaths paralleling the Alaskan coast (2 cm s^{-1}) and along the 100-m (10 cm s^{-1}) isobaths (Stabeno et al., 2016). Tidal currents are much stronger and dominated by semi-diurnal M_2 (21 cm s^{-1}) and diurnal K_1 (14 cm s^{-1}) (Stabeno et al., 2010). The tides play a critical role in mixing of the water column.

In the Bering Sea, spawning in northern rock sole occurs from December through March, and spawning grounds are located over the middle and outer continental shelves (Shubnikov and Lisovenko, 1964). Eggs are demersal, but hatched larvae are pelagic. A peak in rock sole larval abundance in the water column occurs in mid-April, and larvae are generally collected from along the Alaska Peninsula and around the Pribilof Islands. Settled juveniles occur in shallow water (<50 m) and inshore (Cooper et al., 2014), and a large nursery area has been identified off of Cape Newenham (Cooper and Nichol, 2016). The spawning and nursery areas described above are the largest, and best studied areas of northern rock sole production in the eastern Bering Sea. It is not conclusively known that these two important regions have a direct source-sink relationship, but given their proximity to one another, and the general regional oceanography in the area, it has been inferred (Cooper et al., 2013; 2014) that there is a relationship between the two, though we acknowledge that other high production areas may be present. Prior empirical and model studies that have examined connectivity of northern rock sole larvae from spawning areas to nursery areas in the Bering Sea have characterized baroclinic transport routes along the Alaska Peninsula and to the Pribilof Islands (Lanksbury et al., 2007; Cooper et al., 2013), and wind-driven, near-surface routes as influenced by stochastic atmospheric forcing (Wilderbuer et al., 2002). Cross-shelf advection as mediated by baroclinic flow across the shelf proper has been deemed unlikely due to sluggish current velocities (2–3 cm s^{-1}). Other mechanisms of cross-shelf transport have heretofore been unidentified, but it is unlikely that the mechanisms outlined above are the only means of cross-shelf connectivity.

A substantial modeling effort was made in 2009 to use a coupled biophysical individual-based model that incorporated ontogenetic changes in early-life history parameters to model larval dispersal of northern rock sole (pers. Comm. William Stockhausen). From designated spawning areas, larvae were allowed to disperse according to the stored output of 3-dimensional oceanographic currents at daily time steps from a Regional Ocean Modeling Systems (ROMS) oceanographic model (that did not include tidal forcing) for the North Pacific Ocean. Results showed that few larvae reached suitable nursery habitats (<50 m depth) within a larval drift period, and recruitment did not match year-class strengths calculated from age-structured stock assessment models. One factor that seemed to play a role in these results was that the version of the ROMS model employed in the larval dispersal simulation used a "terrain-following" vertical coordinate system that may inhibit the cross-isobath currents that are needed to disperse particles (larvae) from the mid-shelf to the inner-shelf nursery areas.

Northern rock sole larvae exhibit behavior that influences their vertical distribution in the water column (Lanksbury et al., 2007), and changing depth according to environmental conditions, which could potentially maximize their transport trajectory (e.g., selective tidal stream transport). Of course it has been shown that fish larvae also move in response to a variety of other environmental variables, but because we were interested to learn whether it was possible for rock sole larvae originating in the Unimak spawning area to move to the Newenham juvenile habitat area, we focused on putative vertical changes in response to circulation cues.