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The critical first year of life of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea: Implications for recruitment and future research

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Abstract

Walleye pollock (*Gadus chalcogrammus*) support a large commercial fishery in the eastern Bering Sea despite large interannual and decadal swings in population abundance. These oscillations challenge the fishery, prompting significant effort directed to understanding the species and its recruitment. Conceptual paradigms of walleye pollock recruitment recognize that understanding the factors affecting survivorship during the first year of life is central to understanding population fluctuation. Since the first year is critical to year-class strength of this key economically and ecologically important species, we review the state of knowledge of pre-recruit walleye pollock ecology in the eastern

Bering Sea during this critical first-year period, including spawning, changes in vertical and horizontal distributions, feeding, growth, body condition, transport, and predation. We then critically examine the recruitment paradigms based on component processes that have been proposed to explain mechanisms of recruitment control. We identify paradigm strengths or weaknesses relative to our current state of knowledge, discussing relevance and validity. Finally, we identify gaps in knowledge and propose areas of future research effort.

Keywords

Walleye pollock, eggs, larvae, juveniles, Bering Sea, recruitment, climate

1. Introduction

Walleye pollock (*Gadus chalcogrammus*, previously *Theragra chalcogramma*, Carr and Marshall 2008; Page et al., 2013), is a sub-arctic gadid found from Japan to the Chukchi Sea to central California. Walleye pollock (hereafter, pollock) occur over continental shelves, 50 – 300 m depth, migrate in large schools, and form seasonal spawning aggregations February – June. A major fishery for the species exists in the Pacific subarctic, where catches have ranged from approximately 0.7 – 1.7 million metric tons in the Eastern Bering Sea (EBS) and Gulf of Alaska (GOA) since 1984 (Hiatt et al., 2010). First-sale value for these catches has been in excess of \$1 billion US per year over the last decade. Fishery products include roe in the winter and fillets throughout the spring and summer. Not only are pollock of significant commercial interest, they are also a central component of the food web in the eastern Bering Sea, serving as prey for fish,

marine mammals, and seabirds (Livingston, 1993; Napp et al., 2000; Wespestad et al., 2000; Sinclair et al., 2008). Since pollock are both economically and ecologically valuable, there is significant interest in understanding their recruitment, determining how and when recruitment is set, discerning the associated effects on demographics, and establishing the influences on the overall community structure, with the ultimate goal of developing appropriate management and conservation strategies for the species.

Recruitment strength in pollock is particularly sensitive to events that occur during the early life phases because high abundances of small-sized offspring are more vulnerable to mortality than older, more established life stages (Houde, 1987; 1989).

In an effort to better understand recruitment in pollock, it is appropriate to take a careful look at events occurring during the first year of life. This paper will review the current understanding of pollock ecology during the first year (spawning to age-1 juveniles), focusing on populations occurring in the EBS. The EBS was chosen as the system of study as it supports a major pollock fishery and it is experiencing a shift in atmospheric and oceanographic conditions (Stabeno et al., 2012), which may influence ecosystem dynamics and function, including pollock recruitment. The review focuses on pollock populations in the EBS, but makes reference to pollock in other large marine ecosystems in an effort to highlight differences or expand conceptual thought. This review will also identify areas of research that are needed to improve our understanding of EBS pollock recruitment, and provide comments on past and current EBS pollock recruitment paradigms that focus on the first year of life.

We define several early life history terminologies to describe young pollock ontogeny that are variously used throughout the pollock literature. Here, *egg* describes

the life stage that occurs from spawning to hatching, also described as the embryonic phase of development (Miller and Kendall, 2009). The *yolk-sac stage* begins immediately after hatching and yolk is present for internal nourishment of the animal. Pollock larvae rely on maternally-provisioned yolk for several days to weeks and yolk exhaustion occurs when larvae are 5 – 7 mm standard length (SL). *Early-stage larvae* describe larvae in the developmental period between exhaustion of the yolk sac and flexion of the notochord, a stage also referred to as *preflexion* in the literature (Dunn and Matarese, 1987). *Late-stage larvae* (also referred to as *postflexion*) are those stages between notochord flexion (10 – 17 mm SL) and the development of the full, adult complement of fin rays. The term *age-0 juveniles* (also, *young-of-the-year*) refers to individuals with a full complement of fin rays (transformation typically occurs 30 – 40 mm SL; Brown et al., 2001) that are less than 1 year old, and *age-1 juveniles* refers to those individuals that have experienced their first birthdays.

Collections of pollock during the first year of life in the EBS date from 1979, providing a rich historical data source from which observations are derived. Ichthyoplankton (eggs and larvae) have been collected using obliquely towed 60-cm bongo nets, 1-m² Tucker nets, and 1-m² depth-discrete Multiple Opening and Closing Net and Environmental Sensing Systems (MOCNESS, 333 or 505- μ m mesh) by the National Oceanic and Atmospheric Administration (Alaska Fisheries Science Center) as well as by numerous academic institutions (University of Alaska, University of Washington, Oregon State University, among others). Age-0 juveniles have been collected with large rope trawls and with small-mesh trawls, (both of which typically use a set of trawls doors to open the net) and Methot nets (a fixed-frame mounted net) towed in the midwater and

at the surface. Age-1 pollock have been collected from bottom trawl surveys and from midwater trawl surveys that are conducted in conjunction with acoustic surveys.

Generally, spring surveys in the EBS collect pollock eggs and early-stage larvae, summer surveys collect late-stage larvae and transforming juveniles, and autumn surveys collect age-0 juveniles. There are no overwinter collections and age-1 individuals have been collected in spring and summer the year after spawning (Table 1). For the purpose of this review, focus will be on ecology of egg – age-0 pollock; age-1 pollock will only be addressed as they pertain to emergent overwintering age-0s.

2. Review

2.1 Oceanographic characteristics of the eastern Bering Sea shelf

The 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 Bering Strait (Fig. 1). The continental shelf is very broad (~500 kilometers). Northwest flow is driven by the Alaska Coastal Current and flow through Aleutian passes (Napp et al., 2000). East-west flow is driven by the Aleutian North Slope Current. Together these two currents drive flow northward over the shelf. The EBS shelf can be divided into three bathymetric domains during spring and summer, each with its own characteristic hydrography (Coachman, 1986). The inner shelf (or coastal domain, < 50 m depth) is weakly stratified and influenced by freshwater run-off; the middle shelf (50 – 100 m depth) is strongly stratified; and the outer shelf (100 – 200 m depth) is an area of intermittent upwelling in the spring and summer, high productivity, and stratification (Hunt et al., 2002). Ocean thermal conditions are often categorized as warmer- or colder-

than-average (hereafter “warm year” and “cold year,” respectively), based on sea-ice extent, timing of sea-ice retreat, water temperatures, and the extent of a pool of cold bottom water (Cold Pool, $< 2\text{ }^{\circ}\text{C}$) over the middle shelf during the summer (Stabeno et al., 2012). Currents also vary between cold and warm years; during cold years, currents are predominantly westward, while in warm years current direction is variable and seasonal, with northward flow during winter and weak flow in other seasons (Danielson et al., 2012; Stabeno et al., 2012).

2.2 Spawning Ecology

Pollock exhibit fidelity to general spawning regions and spawning occurs within predictable time intervals; however, small-scale spatio-temporal variability exists within broad-scale spawning regions and known spawning periods that is believed to be dependent on oceanographic conditions. Pollock are iterative spawners, releasing up to 10 cohorts of eggs each year per individual female (Brodeur et al., 1996). Maturity occurs at 3 – 4 years of age and female fecundity is in the millions (Hinckley, 1987). In the EBS, several active pollock spawning grounds have been identified (Fig. 1). Over the shelf, pollock spawn north of the Alaska Peninsula in the vicinity of Unimak Island in March – April, and proximal to the Pribilof Islands April – August (Jung et al., 2006; Bacheler et al., 2010). Over the slope, pollock spawn in the vicinity of Bogoslof Island February – April, although spawning stock biomass in this area has declined since the early 1990s (Bacheler et al., 2010). Farther north, a potential fourth spawning aggregation has been identified near Zhemchug Canyon, although the phenology of this aggregation is unknown (S. Barbeaux, unpublished data). Likewise, a very large, historical spawning

aggregation over the Aleutian Basin, “The Donut Hole” aggregation, was depleted in the 1970s and 1980s, and there remains only a marginal, remnant population in the basin that does not contribute significantly to the shelf stock (Bailey, 2013). Spawning stock biomass on the EBS shelf increased substantially in the 1980s due to an influx of large year classes in the late 1970s and early 1980s (Ianelli et al., 2013). Large recruitment events continued through the 1980s and 1990s resulting in high spawning stock biomass during this period. It is believed that strong recruitment and a resultant increase in spawning biomass was due to a regime shift within the EBS in 1977 favoring juvenile pollock survival (Bailey, 2000; Hunt et al., 2002). Although a period of poor recruitment and continued fishing from 2001 to 2005 resulted in a decline in pollock spawning biomass through 2008, recent data suggest that favorable recruitment events in 2006 and 2008 and lower fishing quotas have led to an increasing spawning biomass trend since 2009 (Ianelli et al., 2013).

Previous work using egg and yolk-sac larval data has suggested a latitudinal cline in pollock spawning phenology (Hinckley 1987; Bachelier et al. 2010). This phenomenon can also be investigated using pre-spawning data. The commercial roe fishery separates pollock roe into grades of different value; and hydrated roe can be applied as a proxy for spawning activity. The tonnage of roe recovered by week and grade was available from the EBS pollock commercial fishery (2001 – 2006) and we combined these data with weekly centroids of vessel fishing locations. A generalized additive model with the proportion of hydrated roe as the dependent variable and latitude and week by year as independent variables was fit using 2-dimensional cubic splines (Wood, 2006). The model explained 62% of the deviance. In general, hydration, taken as a proxy for

spawning, occurred earlier in the south and later in the north, with 50% hydrated roe occurring 1 – 5 weeks earlier at 54°N than at 58°N latitude (Fig. 2). This was true for all but two years; in 2004 and 2006 there was little difference in the timing of hydration from north to south. Interannual differences in timing were also apparent with 50% hydrated roe occurring at 56°N as early as week 10 (mid-March) (2004 – 2006) and as late as week 14 (mid-April) (2001 – 2002). Results confirm the latitudinal cline in pollock spawning phenology but also demonstrate interannual plasticity in timing of spawning, the latter likely related to ocean thermal differences among years examined. Climate-mediated shifts in spawning phenology can influence density-independent mortality of pre-recruit life stages through variations in the timing of larval fish production relative to zooplankton production (match-mismatch hypothesis, Cushing, 1981) or variable dispersal of larvae relative to seasonally-established oceanographic features. Density-dependent mortality of older stages as a downstream result of phenological shifts can be manifested through temperature-mediated effects on growth, species interactions and predation, or juvenile condition.

Early studies suggested the existence of several stocks of pollock within the Bering Sea (Mulligan et al., 1989; Mulligan et al., 1992; Bailey et al. 1999), though more recent work on genetic differentiation of pollock populations demonstrated only a weak cline in population structuring from Puget Sound, Washington, USA, to Funka Bay, Japan (Canino et al., 2005). Nevertheless, Canino et al. (2005) suggested the existence of self-recruiting populations at moderate geographic scales, though whether these populations might contribute significantly to the overall population (Smith et al., 1990) remains unresolved. Other unknowns regarding pollock spawning ecology in the EBS

include surprisingly little spatio-temporal information for how spawning aggregations are formed, or from which spawning locales resultant larvae are derived. Moreover, there has been work in other parts of the world to show that gadid fecundities are influenced by environmental factors (Marshall, 2009; Kjesbu et al., 1998), but comparable studies are lacking for pollock in the EBS. Increased research into the spawning ecology of adults will help to inform studies on the survival and recruitment of their offspring.

2.3 Fertilized Eggs

Eggs appear in the water column in the EBS as early as February in the Bogoslof Island area (Bacheler et al., 2010). Based on a 17-year time series of ichthyoplankton tows, the peak in the egg production cycle for the EBS population occurs in April and May, with most eggs produced by the spawning aggregation north of the Alaska Peninsula and Unimak Island (Smart et al., 2012a). Egg mortality has been estimated on one occasion, in 1977, and was found to be approximately 0.6 d^{-1} in April and 0.3 d^{-1} in May (Jung et al. (2006). Eggs collected in the EBS tend to be larger than eggs collected from the Gulf of Alaska, and developmental rates at low temperatures are accelerated in the EBS relative to the Gulf (Blood, 2002) suggesting the EBS population is adapted to colder temperatures associated with winter ice cover. Normal development occurs at temperatures ranging from 0.4 to 3.8 °C. Below 0 °C development is abnormal and mortality is high.

The timing of peak abundance of pollock eggs occurs earlier in warm years compared to cold years (Smart et al., 2012b; Table 2), which likely is attributable to either earlier spawning (see Section 2.2) or temperature-dependent effects on hatching

and development (Blood, 2002). In the EBS, eggs are found throughout the water column, occurring to depths as deep as 300 m (Smart et al., 2013), but also present in the neustonic layer (Waldron and Vinter, 1978). Sampling to document the deepest extent of pollock eggs in the Aleutian Basin has not occurred, but generally eggs collected over the basin are deeper than those collected over the continental shelf (Kendall, 2001). Over the continental shelf pollock eggs are found ≤ 30 m over all domains, but centers of distribution are < 30 m over the shelf and ≥ 100 m over the slope (Smart et al., 2013).

2.4 Larvae

2.4.1 Distribution

Pollock early- and late-stage larvae are found in the vicinity of spawning areas as well as hundreds of kilometers away from spawning grounds. Over the EBS shelf, larvae are concentrated near the Pribilof Islands, probably due to local anti-cyclonic circulation patterns (Stabeno et al., 2008) that act to retain larvae, and north and east of the Alaska Peninsula following transport by the Alaska Coastal Current (Stabeno et al., 1999) from spawning grounds located in the vicinity of Unimak Island. Very few late-stage larvae have been collected in proximity to the spawning grounds at Bogoslof Island, despite the prevalence of yolk-sac and early-stage larvae there (Smart et al., 2012a). This could be the result of low sampling intensity in this area in late spring when older larvae would be present in the water column, or it could indicate high mortality or transport away from this island along the Aleutian Island chain (Fig. 1). Large aggregations of larvae north of the Pribilof Islands have not been documented, but recent evidence of the occurrence of spawning-condition adult pollock over the outer shelf at latitudes north of 58°N (S.

Barbeaux, personal communication) suggests that pollock larvae may be concentrated there in late spring. Increased sampling effort over the outer shelf north of the Pribilof Islands is warranted.

Pollock larvae smaller than ~ 15 mm SL can be collected efficiently with several types of ichthyoplankton nets (primarily bongo or MOCNESS) with mesh sizes as small as 333 μm . Fish longer than ~ 50 mm SL (age-0 juveniles) are increasingly adept at avoiding capture by plankton nets but can still be collected by midwater trawls. A problematic area of research on larval pollock occurs at the juncture in lengths between fish collected efficiently with ichthyoplankton nets, and those sizes that are collected in small mesh trawls (age-0s, described below). Postflexion larvae 15 – 30 mm SL are relatively rare in collections by any presently-employed gear types, and constitute a portion of the size population that is significantly understudied. As such, there is little information on distribution, vertical distribution, diet, or growth of larvae within this size range.

During cold years in the EBS, centers of distribution of pollock eggs and larvae are located farther west (outer domain) within the general spawning region than in warm years (middle domain, Fig. 3; Smart et al. 2012b). In cold years, the Cold Pool persists over the southern middle shelf through the summer months (Maeda, 1977; Reed, 1995), but in warm years, the Cold Pool is restricted to the northern shelf. Pollock adults avoid water $< 2\text{ }^{\circ}\text{C}$ (Wyllie-Echeverria and Wooster, 1998) and egg development and hatching is diminished at temperatures $\leq 0\text{ }^{\circ}\text{C}$ (Blood, 2002). An extensive Cold Pool likely reduces the available shelf habitat for spawning and for successful embryo development, and can also impact feeding success, as recent work has shown that zooplankton prey

composition is shifted over the middle shelf in warm years compared to cold (Stabeno et al., 2012; Eisner et al. in press).

Pollock larvae in the EBS are found in the upper 100 m of the water column and depths of occurrence become shallower with ontogeny (Smart et al., 2013). Yolk-sac larvae are found throughout the upper 100 m of the water column, and non-feeding stages show no evidence of diel vertical migration. Late-stage larvae do exhibit diel vertical behavior, with most migration of feeding larval stages occurring above the pycnocline (~30 m in the EBS). Larvae are generally deeper during the day (10 – 40 m) than at night (0 – 20 m; Fig. 4), and movements are postulated to be dependent on prey levels, light levels, and predator presence. For comparison, feeding larvae collected from the Gulf of Alaska tended to be deepest at midday and shallowest at dusk, indicating a crepuscular pattern of movement (Kendall et al., 1987; Kendall et al., 1994). Depth occurrences of larvae have implications for variability in transport trajectories, which can ultimately influence the distribution of larvae. Pollock larvae spawned in the vicinity of Unimak Island are subject to a bifurcated flow, either northward along the 100 and 200 m isobaths of the EBS, or eastward along the 50 m isobath. Entrainment below the mixed layer depth (~25 – 30 m) increases the likelihood of northward transport ($5 - 8 \text{ cm s}^{-1}$) to the middle and outer shelves, while entrainment above the mixed layer increases the chance of eastward drift ($2 - 4 \text{ cm s}^{-1}$) and delivery to the middle and inner shelves (Stabeno et al., 1999). Near-surface entrainment increases exposure to wind-forced circulation, which has the potential to transport larvae far from nursery areas. Indeed, Danielson et al. (2011) and Stabeno et al. (2012) have both demonstrated that variability in circulation over the EBS shelf is influenced by changes in wind direction.

2.4.2 Feeding Ecology and Growth

Pollock first-feeding larvae (preflexion stage, 4.5 – 6.5 SL) over the outer shelf primarily consume copepod eggs and nauplii (Hillgruber et al., 1995). As larvae grow and develop improved swimming capability and larger mouth gapes, the diets diversify to include copepodites, particularly those of *Pseudocalanus* spp. (Strasburger et al., 2014), barnacle cyprids, and euphausiid calyptopis. In 1995 (a cold year), pollock larvae were found at high densities in mid-May, but prey concentrations were below a hypothesized critical density of 20 prey l⁻¹ derived for Shelikof Strait, Gulf of Alaska (Napp et al., 2000). However, critical prey abundances may be lower for Bering Sea larvae due to the cooler temperatures and lower metabolic rates of larvae. Theilacker and Porter (1995) did not find evidence of starvation at low prey densities in field-caught larvae in the Bering Sea. More recent work using a flow cytometric assay to identify starving larvae in the field suggests that pollock larvae collected over the EBS slope and basin were healthy, though a risk of food limitation (6% of individuals) was noted among larvae collected from over the adjacent shelf (Porter and Bailey, 2011). Finally, in a recent analysis of the Match/Mismatch Hypothesis (Cushing, 1981) for pollock larvae and their *Pseudocalanus* spp. prey, no relationship was found between an index of spatial mismatch and subsequent recruitment to age-1 (De Forest et al., in revision). Taken collectively, there is presently little evidence for mass starvation of pollock larvae in the EBS, though it is cautioned that weak or starving individuals are ready predation targets, making a true assessment of the food-limited fraction of population difficult to obtain. Larvae collected from the field are those that are healthy, and best able to avoid predator encounter and

capture; mortality has already removed the others. In order to better assess the role of food limitation among larval pollock, laboratory studies of critical densities of prey needed over a range of larval sizes and temperatures, with models to describe consequent metabolism and growth, are required.

Energy allocation strategies in larval and juvenile fish reflect competing physiological demands of somatic growth versus lipid storage (Post and Parkinson, 2001) and are a response to differing survival constraints. By maximizing growth and transitioning through the larval period rapidly, larvae minimize exposure to size-dependent predation during this stage. However, overwinter survival is hypothesized to be higher in fish that are both larger and have increased lipid reserves, indicating that energy allocation during the juvenile stage will favor lipid storage while also increasing fish size (Beamish and Mahnken, 2001; Heintz and Vollenweider, 2010). Differing energy allocation strategies for larval (< 25 mm SL) and juvenile (25 mm $< X < 100$ mm SL) pollock indicate that distinct ontogenetic stages face different survival constraints. Larval fish favor energy allocation to somatic growth and development, presumably in order to escape size-dependent predation, while juvenile fish begin to allocate energy to lipid storage in late summer (Siddon et al., 2013a; Fig. 5).

Historical laboratory efforts to estimate growth suggest rates of $0.1 - 0.7$ mm d^{-1} (Davis and Olla, 1992; Porter and Bailey 2007; Hurst et al. 2013), while field estimates derived from otoliths suggest nearly 0.4 mm d^{-1} (Walline, 1985). Dell 'Arciprete (1992) developed an age-length key from pollock otoliths collected in the EBS in 1988 and used this to estimate growth rates for $4 - 8$ mm larvae at 0.21 mm d^{-1} . There is some evidence for temperature-mediated growth, a phenomenon that has significant import to studies of

atmospheric and oceanographic thermal variability on pollock. For example, Jung et al. (2006) used age-length keys to show that larvae collected in 1976 and 1977 (cold years) grew more slowly (0.12 mm d^{-1}) than larvae collected in 1979 (warm year, 0.23 mm d^{-1}), but suggested that differences were at least partly due to variations in timing of sampling, fish size, and length-specific growth. Smart et al. (2012b) estimated larval growth rates by assuming that most larvae collected in consecutive cruises belonged to the same or dominant cohort. They found that growth rates were dependent on water temperature, and showed that growth rates in cold years tended to be approximately half those of warm years (0.1 mm d^{-1} and 0.2 mm d^{-1} , respectively). Few studies have examined the consequences of short-term thermal stochasticity or longer, more gradual increases in ocean temperature on growth rate, and work to incorporate those consequences into a predictive framework is lacking.

2.4.3 Predation

Predation is likely a significant source of pollock pre-recruit mortality in the eastern Bering Sea; larvae are consumed by vertebrates and invertebrates alike. Most research on invertebrate predation of young pollock has been done either in the laboratory or in the Gulf of Alaska, where it has been shown that euphausiids are consumers of yolk-sac larvae (Bailey et al. 1993; Brodeur and Merati, 1993). Gelatinous macrozooplankton are predators of fish larvae in other marine systems, and their numbers appear to be increasing in the EBS, in particular the large jellyfish, *Chrysaora melanaster* (Brodeur et al., 2002; Brodeur et al. 2008), but we suggest they are not likely to be major predators of pollock eggs and larvae since the timing of production of jellyfish and larvae

is mis-matched, with jellyfish occurring at small sizes in early spring when larvae are most vulnerable. Vertebrates certainly consume pollock early life stages. Spawning adult pollock in the EBS are cannibals of pollock eggs (Schabetsberger et al., 1999) and adult pollock, Pacific cod (*Gadus macrocephalus*) and arrowtooth flounder (*Atheresthes stomias*) all consume pre-recruit pollock (Livingston and Juado-Molina, 2000; Bailey 2000). The minimum size of larval pollock in the diets of piscivorous fishes typically ranges from 10 – 20 mm SL, depending on species of predator. Predation and food limitation (section 2.4.2, above) are likely synergistic factors that act remove pollock larvae from the population, with predators selectively preying on undernourished, weaker, and slower swimming or poorly-reactive individuals. Rates of predation on weaker individuals are not well documented but are likely quite high.

2.5 Age-0 Juveniles

2.5.1 Distribution

In their first summer, larvae transition to age-0 juveniles prior to reaching 40 mm SL (Brown et al., 2001). Juvenile pollock have been observed across the southeastern Bering Sea (Winter and Swartzman, 2006; Moss et al., 2009; Hollowed et al., 2012), with the area around the Pribilof Islands identified as an essential nursery habitat (Walters et al., 1988; Traynor and Smith, 1996; Brodeur et al., 1997; Hunt et al., 2002). In that region, age-0s are concentrated in inshore rather than offshore areas, despite better potential feeding conditions in offshore areas (Ciannelli, 2002). Patchiness in the distribution of age-0s is common with aggregations ranging in size from meters to kilometers (Benoit-Bird et al., 2013a). During late summer and early fall Parker-Stetter et

al. (2013) found that in 2006 – 2010, age-0 pollock were distributed across the EBS, primarily within the middle and outer shelf regions. In 2006 – 2008, years that were classified as “average” or “cold” based on sea surface temperature (Stabeno et al., 2012), high numbers of age-0 pollock were associated with the pycnocline in the upper 30 m of the water column throughout the EBS (Fig. 6, Fig. 10 in Parker-Stetter et al., 2013) as previously identified in other studies (Bakkala et al., 1985; Swartzman et al., 2002; Moss et al., 2009; Hollowed et al., 2012). In 2009 and 2010, years that were colder than 2006 – 2008, higher numbers of age-0 pollock were observed in deep water below the pycnocline (Fig. 6, Fig. 10 in Parker-Stetter et al., 2013). The presence of age-0 pollock in midwater during summer has previously been observed in the EBS (Miyake et al., 1996; Tang et al., 1996) and in the Gulf of Alaska (Brodeur and Wilson, 1996) and has been attributed to survey timing coinciding with the ontogenetic transition from pelagic to demersal habits, and not due to water column attributes or differences in fish length (Brodeur and Wilson, 1996; Parker-Stetter et al. in review 1).

Two recent studies (Hollowed et al., 2012; Parker-Stetter et al., in review 2) have evaluated the horizontal distribution of age-0 pollock relative to physical, biological, and climate factors. Bottom depth and temperature were important predictors of both near-surface age-0 pollock presence and density in Hollowed et al. (2012). In contrast, Parker-Stetter et al. (in review 2) found that depth, quantity of zooplankton prey, and spring winds were important predictors of near-surface age-0 pollock presence and density. Previous studies have suggested that other factors such as prey abundance and/or predator overlap (Swartzman et al., 1999; Ciannelli et al., 2002a; Winter and Swartzman, 2006;

Winter et al., 2007), habitat energetics (Ciannelli, 2002b), bottom depth (Brodeur et al., 1999), and temperature (Brodeur et al., 1999) are also important.

Age-0 pollock exhibit diel vertical migration, moving from the pycnocline or deeper into the near-surface waters at night. Swartzman et al. (2002) concluded that migration patterns were dependent on stratification, depth, zooplankton prey, and age-0 pollock size. Schabetsberger et al. (2000) suggested that vertical movements by age-0s were motivated by feeding potential and demonstrated that age-0 pollock and their prey had similar vertical distribution patterns. Bailey (1989) noted that shifts in vertical distribution of age-0s had significant implications for inter-cohort cannibalism, with age-1 and older fish feeding on age-0s occurring at similar depth strata.

2.5.3 Feeding Ecology and Growth

Diet of early age-0 juveniles (30 – 50 mm TL) includes small adult copepods (e.g. *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp.), euphausiids, amphipods, and chaetognaths (Brodeur, 1998; Brodeur et al., 2000; Strasburger et al., 2014). Feeding and body condition vary spatially, around frontal regions and across habitats (Brodeur et al., 2000; Brodeur et al., 2002; Ciannelli et al., 2002a; Ciannelli et al. 2002b; Swartzman et al. 2002; Schabetsberger et al. 2003), and interannually, which appears related to thermal conditions and associated changes in prey base (Heintz et al., 2013). Age-0 juveniles (30 – 100 mm SL) collected by surface trawls in 2003 – 2006, which were warm years, fed mainly on small copepods and euphausiids. In 2007 – 2009, which were cold years, age-0 juveniles within the same size range fed mainly on euphausiids and large copepods (Coyle et al., 2011). This shift is most likely the result of variation in prey availability

rather than feeding ability as juveniles collected in surface trawls in 2004 and 2005 (warm years) were longer with larger mouth gapes than those collected in surface trawls in 2006 and 2007 (an average and a cold year respectively; Moss et al., 2009). A diet shift occurs after approximately 50 mm TL, and larger-sized age-0 juveniles feed on larger prey including euphausiids and large copepods (*Calanus* spp.) (Brodeur, 1998). The switch in diet coincides with the increased swimming speeds that allow predators to pursue larger, more evasive prey, as well as an increase in gape size that permits consumption of larger, higher-quality prey items. Moss et al. (2009) suggested that juveniles 100 – 130 mm TL are piscivorous and cannibalistic during warmer-than-average conditions, though it remains unclear if any larger pollock in their study might have been small-sized age-1s. Cannibalism has been documented among age-1 pollock in the EBS (Bailey, 1989; Duffy-Anderson et al., 2003).

Prey quality and availability relative to juvenile age-0 pollock energetic condition may also influence recruitment as a function of environmental conditions. Climate effects on prey field composition (Coyle et al., 2011) have been shown to lead to the consumption of high lipid diets in cold years (Heintz et al., 2013; Fig. 7). Estimates of total energy in late summer integrate the effects of climate, diet, growth, and prey abundance and quality at the end of the first growing season. The effects of climate on diet quality and condition of age-0 pollock are consistent with observations of a generally inverse relationship between late summer sea surface temperatures and survival (Mueter et al., 2011).

Prey resources for age-0 juvenile pollock decline in autumn and reduced foraging opportunities coupled with near-freezing temperatures during winter heighten the

importance of body size and physiological condition prior to winter onset. In high latitude systems, winter is a period of low light, cold temperatures, and reduced prey availability, and is therefore a significant source of mortality and a determinant of recruitment success of marine fishes (Hurst, 2007a). Availability of lipid-rich prey during this period is important as age-0 pollock face severe energy deficits during winter (e.g., Sogard and Olla, 2000). The window of time during which pollock can provision themselves with lipid occurs between the completion of metamorphosis in early August and the onset of oceanographic winter (Wilson et al., 2011; Siddon et al., 2013a). Those individuals that can consume high lipid prey during this critical period are expected to survive winter better than individuals consuming leaner prey. The energetic status of age-0 pollock in late summer is recognized as a predictor of age-1 abundance during the following summer in the EBS (Heintz et al., 2013). Therefore, late summer (July – September) represents a critical period for energy storage in age-0 pollock, and subsequent energy levels provide an early metric for the prediction of overwinter survival and recruitment success to age-1.

2.5.2 Predation

Age-0 juvenile pollock are preyed upon by a wide variety of predators. Age-0s <100 mm SL are eaten by older pollock, yellowfin sole *Limanda aspera*, arrowtooth flounder, and Pacific cod (Livingston, 1993). Most consumption by adult pollock and arrowtooth flounder on age-0 pollock occurs late in the day (Lang et al., 2000). Some authors have contended that cannibalism is the most important source of mortality of age-0 juvenile pollock in the EBS (Livingston and Jurado-Molina, 2000). Hunsicker et al.

(2013) found that arrowtooth flounder population abundance and temperature synergistically affect the spatial overlap of predator (arrowtooth flounder) and prey (pollock) suggesting that the magnitude of the primary source of predation of young pollock, arrowtooth flounder, may shift if projections of a warmer EBS become reality. Predation (and cannibalism) by fishes has been hypothesized to be the most significant contributor of age-0 juvenile mortality (Bailey, 1989; 2000; Livingston and Jurado-Molina, 2000) and an important regulator of overall recruitment, but recent work suggests a significant role for feeding, body condition, and overwinter survival.

Marine birds and mammals constitute a significant, although less pronounced, source of predation on juveniles (Livingston, 1993). Benoit-Bird et al. (2013b) showed that predation on age-0 juvenile pollock by seabirds and northern fur seals (*Callorhinus ursinus*) was dependent not on overall prey biomass, but on small-scale prey density.

2.6 Models

2.6.1 Biophysical Models

Several generations of biophysical models have been used to explain factors affecting distribution and abundance of young pollock over the Bering Sea shelf. Spatially explicit, coupled biological-physical models simulate dispersal of the early life stages and the biological processes that occur during this period (Table 3). One of the first biophysical models of the early life stages of pollock in the Bering Sea was used to test the effect of advection and sub-grid scale diffusion on the distribution of larvae (Walsh et al., 1981). The two-dimensional (2-D) physical model tracked distribution of two life history stages, non-feeding and feeding larvae, in the vicinity of Unimak Island.

The results of model simulations supported the idea that spawning date affected the drift trajectory and mortality of individuals.

Later, 2-D float-tracking models developed in the 1990s described near-surface wind-driven transport of pollock larvae in the EBS, but they contained no biological component (Wespestad et al., 1997; Wespestad et al. 2000) and pollock larvae do not typically occur at the surface. These models were used to examine how surface advection during the early life stages related to recruitment success by characterizing annual circulation as good or bad, with the effects of circulation on recruitment feeding into a stock assessment model for pollock. This model was further used to analyze how wind-driven transport affected the distribution of juvenile pollock in relation to the distribution of adults (Wespestad et al., 2000). Strong year classes, which often occurred in warm years, coincided with transport of early life stages to the north and onshore, which separated juveniles from adults. Average year classes corresponded with transport to the NW along the shelf, whereas weaker year classes resulted from little transport, which left juveniles on the outer shelf near adults.

A more complex biophysical model has recently been used to examine stage-specific, 3-D transport trajectories of pollock larvae over the EBS (Petrik et al., in press). The physical model used a version of the 3-D Regional Ocean Modeling System (ROMS) for the North East Pacific (NEP; Curchitser et al. 2010; Danielson et al., 2011) that included the EBS domain. Daily averages of velocity, diffusivity, and temperature were generated with ROMS-NEP6 and used to force the particle-tracking, biological model, TRACMASS (Döös, 1995), which simulated the development, growth and vertical behavior of pollock eggs and larvae. Results showed that shifts in spawning location,

rather than changes in current patterns or temporal shifts in spawning time, contributed most to spatial shifts of larvae and juveniles observed over the EBS shelf. It was concluded that field-observed differences in distributions of eggs and larvae over the continental shelf between warm and cold years most likely occur because adults modify their use of spawning habitat in response to changes in the presence and extent of sea ice. Direct observations from the field are necessary to verify this hypothesis.

How has understanding of pollock early life ecology been shaped by biophysical modeling studies? Until only recently, physical models were primarily 2-D and incorporated little or no pollock-specific biology. Larvae were considered passive particles since there was limited ability to account for species-specific variations in physiological and behavioral characteristics within the model framework. While early models certainly had utility as predictive tools for evaluating horizontal dispersal relative to mean flow, and they had the advantage of modest computational requirements, their value for enhancing understanding of pollock biology was significantly hampered by the inability to account for species-specific attributes that have the potential to influence, or even change, the dispersal outcome. The legacy of biophysical modeling in the study of pollock biology has been vastly improved since the development of spatially-explicit, 3-D circulation models coupled to Lagrangian particle tracking and behavioral models, and they have the potential for further advancement with the more recent development of full life cycle models than span generations (reviewed by Lett et al., 2010). As they exist now, biophysical models of pelagic fishes, inclusive of pollock, provide powerful tools with which to evaluate long-term shifts in growth, distribution, and recruitment. Use of biophysical models of pollock in the Bering Sea in recruitment prediction scenarios is

forthcoming (C. Petrik and F. Mueter, personal communication), but remain regional and single species.

2.6.2 Trophic Models

Trophic models have been developed that link age-0 pollock juveniles with other components of the EBS ecosystem in an effort to determine energy flows, relative importance, and consequences on pollock survivorship and subsequent recruitment. All too often however, these models minimize large portions of the first year period, typically egg and larval, favoring to model those life history phases as dispersed propagules rather than treating them as part of the larger trophic framework. This approach assumes that primary sources of larval mortality are density-independent, an assumption that is increasingly turning out to be biased. While evidence for mass starvation of pollock larvae in the Bering Sea is equivocal (section 2.5.3, above), the role of predation upon larvae weakened by poor nutrition should not be overlooked. For decades predation has been acknowledged to be a major source of mortality among marine fish larvae (Hunter et al. 1981; Bailey and Houde 1989; Leggett and Deblois 1994; Houde, 2002; Gallego et al. 2012), and predation likely plays a critical role in structuring age-0 pollock cohort strength. Knowledge of the links and energy pathways that put larvae at risk of predation, including prey availability, foraging capability, feeding, temperature, biochemical condition, swimming competency, and sensory development provides critical mechanistic understanding of how young pollock interact with the environment, which factors are strongly limiting, and over what developmental stages recruitment controls are likely to act. Given the importance of the first year of life to recruitment

success, we encourage development of trophic models that are specifically focused on the first year to better understand mechanisms regulating early life survival and connections between vulnerable young fish and the broader ecosystem.

Despite the limitations described above, trophic models have been successful in identifying energy flows from the age-0 juvenile phase forward. Earlier food web models that included young pollock in the EBS took the form of mass balance food web approaches, such that flow of juvenile age-0 biomass entering and leaving the ecosystem was tracked and accounted for, allowing biomass loss or gain by the system to be realized (Aydin et al., 2007). Mass balance models achieved success in identifying and quantifying key sources of juvenile pollock mortality in the EBS (cannibalism), determining the sensitivity of pollock to fluctuations in prey availability, and identifying key energy flows to upper trophic levels that rely on juvenile pollock production.

Physiological trophic modeling approaches have been applied in the EBS to test the hypothesis that variability in pollock growth and survival is structured, in part, by climate-driven, bottom-up control of zooplankton composition. To this end, the broadly applied Wisconsin bioenergetics modeling approach (Kitchell et al., 1977; Ney, 1990) has been adapted for pollock (Ciannelli et al., 1998; Mazur et al., 2007; Holsman and Aydin, in review). The spatially-explicit model estimates temperature- and weight-specific consumption and assesses changes in predicted growth under varying prey or climate conditions. Model results suggest variability in age-0 pollock growth rates relative to hydrographic features which may influence prey availability and food supply (Ciannelli et al., 2002), and pronounced, thermally-induced changes in the relative

foraging rates and daily ration of arrowtooth flounder and Pacific cod (Holsman and Aydin, in review).

A mechanistic, 3-D individual-based trophic model (IBM) has also been developed and applied to age-0 juvenile pollock to predict growth over geographic area. The IBM, based on that of Kristiansen et al. (2009), predicts growth using a mechanistic prey selection component that simulates the feeding behavior of age-0 juvenile pollock on zooplankton. The simulated feeding ecology depends on age-0 development (e.g., swimming speed, gape width, eye sensitivity) and vertical behavior, prey densities and size, as well as light and physical oceanographic conditions. This approach has been used to examine mechanisms underlying observed differences in juvenile pollock energy content between warm and cold years in the EBS (Siddon et al., 2013b). Model results revealed that poor growth conditions resulted from spatial mismatches between juvenile pollock and spatial hot spot areas that are conducive to growth, and were correlated to interannual variations in pollock recruitment.

Most recently, efforts have focused on fully integrated model frameworks, in which output from one model feeds another in a vertical suite of model hierarchies. Efforts such as the Bering Sea Integrated Ecosystem Research Program (<http://bsierp.nprb.org/>) have provided a platform for the development of linked biophysical-energetics models that offer the opportunity to evaluate spatial predictions of fisheries based on Intergovernmental Panel on Climate Change scenario inputs (2000–2050). At its base, hindcast (1970 – 2005, for model validation) or forecast climate scenarios force a 3-D, 10-km resolution physical oceanographic model (ROMS) that contains an embedded Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD)

component. Upper trophic level dynamics are modeled through the age-length based bioenergetics model FEAST (Forage-Euphausiid Abundance in Space and Time), which adopts a layered landscape approach to modeling foraging, growth, movement, and survival of 15 distinct fish groups (I. Ortiz, personal communication). FEAST provides two-way feedback between the NPZD model and the fish groups so that it can capture bottom-up and top-down influences on ecosystem dynamics.

Finally, multi-species stock-assessment models (MSMs) quantify the indirect effects of fisheries harvest on populations and evaluate management trade-offs for fisheries that target several species. MSMs include population dynamics models for each stock and link these through annual predation mortality rates (Jesus-Molina and Livingston, 2004). Holsman et al. (in review) recently used this approach to demonstrate that interactions between fishing pressure and Pacific cod and arrowtooth flounder predation on age-0 juvenile pollock strongly influence adult pollock population biomass. These authors have clearly shown that trophic interactions and harvest rates affect biomass estimates, so the ultimate goal would be to incorporate this information into stock assessment.

2.6.3 Model Caveats

It should be cautioned that the output of any model is only as sound as the input data used in its parameterization and the observational data used in model validation. Therefore, while model efforts have certainly helped researchers understand factors influencing pollock connectivity, trophic interactions, phenology, distribution, survival, and recruitment in the EBS, their value remains contingent upon the supporting

laboratory and fieldwork that are indispensable for model success. In the Bering Sea, key observational data are lacking in several critical areas, which compromises the value of hypothesis testing using a model context. One crucial consideration is the need for stage-specific information, given that different developmental stages have varied physiological requirements, behaviors, and ecological constraints that potentially influence model outcomes. Basic information by developmental stage that is wanting includes robust temperature- and size-dependent growth rates, information on prey preferences, consumption rates as a function of prey type, prey biomass, and temperature, assimilation rates, resting metabolism as a function of size and temperature, and maximum growth rates under unlimited food conditions. In order to be fully operative, studies must be conducted across the range of temperatures experienced during the larval period and with prey sources that represent the natural mix of zooplankton encountered in the field.

Of course, the argument could be made that rich data sources exist for congeneric species, particularly Atlantic cod, *Gadus morhua*, which could be used as proxy data in model development, or that field work from other ecosystems, namely from studies of pollock from the Gulf of Alaska, are ready substitutes for the data-poor Bering Sea. This tactic should be approached with caution, as species-specific or regional differences in physiology, development, ecology, and behavior all have the potential to influence model-predicted outcome. An exercise conducted for the purposes of this review highlights these constraints. Growth rates (mm d^{-1}) across temperatures were derived from the literature for gadids from the Bering Sea, Gulf of Alaska, Funka Bay, Gulf of Maine, and Norwegian Sea and plotted relative to one another. Derivations were based on either original empirical models fit to laboratory estimates or otolith derived estimates

of age/length, or growth rates back-calculated from field-observed lengths (or weights converted to length using published algorithms). Results show significant differences in temperature-dependent growth among species, within regions, and across ecosystems (Figure 8A). Moreover, comparative age-length plots (Figure 8B) show that growth trajectories vary greatly among species examined, with several species reaching asymptotic size thresholds at temperatures that are well within the optional thermal range for others.

Other examples of subtle but meaningful differences include regional differences in egg buoyancy (Kendall, 2001), which can impact drift rate and trajectory in depth-specific currents, durations of larval development and the pelagic larval period (Auditore et al., 1994), which affect time in the plankton and dispersal potential, vertical movements of juveniles in response to environmental cues (Brodeur and Wilson, 1996; Smart et al., 2013), which influence growth and survival, and predation risk (as reviewed in Ottersen et al., 2014) as it has the potential to control predicted recruitment biomass (Hunsicker et al., 2013). Use of data derived from other sources may be necessary at times, such as when model predictions are the only option for making fisheries management decisions despite incomplete understanding. In these cases, careful consideration and thorough vetting a must when results are to be applied in a predictive framework.

3. Recruitment paradigms

The term recruitment generally refers to the age at which a fish species becomes vulnerable to the fishery; in the case of pollock this is typically age 3 – 4 (Ianelli et al.,

2013). To ecologists however, recruitment is a general term that describes survival from one phase in the life cycle to another. For the purposes of this work, we use recruitment to refer to the survival of an annual cohort to the second year of life (age-1). Here we review the recruitment hypotheses that center on the cohort success of pollock during the first year of life, focusing on hypotheses that affect transport, variability in nutritional status, and vulnerability to predation, to better understand the role of fish early life history in population fluctuation of pollock in the EBS.

3.1 Transport

The Transport-Cannibalism Hypothesis predicts that strong pollock year classes are produced in years that support high rates of juvenile transport away from the adult habitat (Wespestad et al., 2000; Yamamura, 2005; Sakurai, 2007), reducing the distributional overlap of age-0 pollock with cannibalistic adults. This hypothesis assumes that vertical distributions of predators and prey are similar as well, which has been shown to be the case among cannibalistic age 1+ pollock in the EBS (Duffy-Anderson et al., 2003). Cannibalism of young pollock in the EBS is indeed high; Aydin et al. (2007) estimated that cannibalism accounted for nearly 40% of the total mortality of juvenile pollock in the 1990s. The Transport-Cannibalism hypothesis assumes that 1) juvenile distribution patterns are determined by passive drift of eggs and larvae in the upper water column, and 2) warmer-than-average ocean conditions are associated with transport to the middle and inner shelves where the presence of adults is reduced. Recent evidence suggests eastward distributional shifts in pollock eggs, larvae, and early juveniles in warm years (Smart et al., 2012b), but concomitant eastward shifts in the distribution of

adults (Kotwicky et al., 2005) may, in fact, maintain the overlap between adults and juveniles. Generally however, we find that the Transport-Cannibalism Hypothesis retains its applicability to the present. The EBS is broad, flat, and relatively homogeneous, providing little landscape refuge for vulnerable age-0 pollock to shelter from large, cannibalistic adults. Empirical and theoretical evidence (Danielson et al., 2012; Stabeno et al., 2012; Wilderbuer et al., 2013) document the differential oceanographic currents that act to disperse larvae, and studies have shown that overlap indices of adult and juvenile pollock can explain up to 50% of recruitment variability (Mueter et al., 2006). Environmental conditions can modify the strength of predator-prey overlap as has been shown between predatory arrowtooth flounder and age-1 pollock (Hunsicker et al., 2013), but the interplay of spatial co-occurrence and top-down predation clearly continues to measurably modify juvenile pollock survivorship and subsequent recruitment.

The Recruitment Routes Hypothesis was developed to understand recruitment variability in the Oyashio ecosystem off of Japan (Suzaki et al., 2003), but may have application to the Bering Sea. This hypothesis explores the link between physical oceanographic shifts and changes in distribution and abundance of pollock, suggesting that differential transport of eggs from spawning grounds underlies shifts in recruitment success. These authors proposed that when the southward flow of the Oyashio Current was strong and nearshore, successful transport to the Doto nursery resulted in average or good recruitment due to the presence of feeding conditions that favor growth potential. When the Oyashio Current was weakened and offshore, poor year classes were observed. The Recruitment Routes idea has been applied to the EBS to describe factors that

contribute to the fluctuation of flatfish populations (Wilderbuer et al., 2002), and is currently under investigation for pollock in the EBS (Petrik et al., in prep.).

3.2 Nutrition and condition

The Production-Competition Hypothesis predicts that strong year classes in the EBS are produced in years with strong storm activity in the summer (Bond and Overland, 2005) based on the observation that four out of five high recruitment years from 1977 to 2000 included warm and windy summers. Storms that occur after the establishment of summer stratification promote mixing of nutrients from below the thermocline into the euphotic zone where nutrients enhance a prolonged period of primary productivity (Sambrotto et al., 1986; Whitley et al., 1986). Prolonged productivity then may be converted to high availability of preferred prey for larval pollock, reducing competition. Indeed, increased abundances of late larvae have been associated with moderate to vigorous summer wind mixing, and high abundances of early juveniles were associated with high summer wind mixing from 1988 – 2008 (Smart et al., 2012a). Increased abundances of feeding larvae and early juveniles were associated with high concentrations of copepods in these years as well. However, recent warm and windy years (2003, 2004, 2005) have not produced strong year classes (Coyle et al., 2011) and not all warm and windy years prior to 2000 produced strong year classes (Bond and Overland, 2005). The Production-Competition Hypothesis is probably only partially valid in that bottom-up forcing plays a role in pollock larval survivorship, but agents of mortality acting between the larval stage and recruitment to age-1 can modify or even nullify effects. As an example, Gann et al. (in revision) found that a weak year class of

pollock was derived from 2007, despite lower trophic level conditions that initially appeared favorable for recruitment, due to weak summer wind patterns that led to poor mixing, high stratification, and low nutrient replenishment.

The Oscillating Control Hypothesis (OCH; Hunt et al., 2002) predicts that the EBS ecosystem alternates between primarily bottom-up control in cold phases and primarily top-down control in warm phases. Warm years are predicted to be favorable to pollock recruitment. This hypothesis is based on the impact of interannual variation in the timing of sea-ice retreat on spring and summer temperature conditions and the extent of the Cold Pool, similar to the Production-Competition Hypothesis. The OCH diverges from the Production-Competition Hypothesis in that zooplankton production is not tied to the onset or persistence of the spring bloom, but rather zooplankton production is directly tied to the water temperature in which zooplankters are grazing on the spring bloom. During cold periods with late ice retreat, there is an ice-associated spring bloom while during warm periods there is an open-water spring bloom, so prey availability for zooplankton is not necessarily limiting in either scenario. In cold periods, however, zooplankton grazing rates, subsequent growth rates, and the onset of reproduction are diminished by temperature (Walsh and McRoy 1986; Huntley and Lopez 1992), thus reducing availability of zooplankton prey to larval fish. Biomasses of copepods that serve as the primary prey items for pollock larvae (*Calanus marshallae*, *Pseudocalanus* spp., and *Acartia* spp.) were reduced in the cool springs of 1980 and 1981 relative to the warm springs of 1997 and 1998 (Stockwell et al., 2001; Napp et al., 2002). The hypothesis predicts that several successive warm years producing strong year classes of fish contribute to a build-up on the pollock population in the EBS. However, limitations of the

hypothesis were realized after the failure of several successive warm-year year classes (2001 – 2005), and the success of several pollock year classes produced from a series of cold years (2006 – 2009). A recent modification (Hunt et al., 2011) to the original OCH suggests a more dynamic interplay of temperature, sea ice, copepod production, and young pollock than originally conceived, and predicts that cold years are favorable to pollock recruitment. In the revised view, early ice retreat and warm waters still enhance primary, and in turn secondary, production contributing to large numbers of age-0 pollock in spring and summer. However, a lack of large, lipid-rich copepod species during warm years is a factor in poor body condition of age-0 pollock in autumn, contributing to high overwinter mortality and poor survival to age-1.

The Critical Size Hypothesis is similar to ideas outlined in the OCH but also recognizes the need for juvenile fish to store energy prior to winter (Beamish and Mahnken, 2001; Heintz et al., 2013). The OCH states that recruitment of a cohort depends on both the size and diet of the fish during the period in which they provision themselves prior to their first winter. The time at which larval transformation is complete is a direct function of temperature (Smart et al., 2012b), so under warm spring and summer conditions age-0 pollock should complete larval development early, increasing the length of the provisioning period. However, fish must also encounter abundant and energy-rich food in order to meet the metabolic demands of growth while maximizing energy storage (Siddon et al., 2013a). Actively finding food is particularly important for smaller fish with reduced energy reserves compared to a larger fish with ample stored energy and reduced incentive to search for prey. Failure to encounter food of sufficient quality will produce fish entering winter with lower levels of stored energy. Therefore,

the conditions that maximize survival beyond the first summer of life are those that lead to early larval transformation, production of abundant energy-rich prey, spatial overlap between pollock and prey, and maximal energy storage in the form of lipids.

While the body of evidence supporting the link between pre-winter condition and survivorship is building (Sogard and Olla, 2000; Heintz and Vollenweider, 2010), critical questions remain unanswered that complicate the two hypotheses outlined above.

Laboratory studies rearing larval pollock at low temperatures (<2 °C) indicate that pollock not only survive extreme thermal conditions, but are capable of growth during the winter (T. Hurst, personal communication). This observation is supported by results from spatially-explicit bioenergetics models of young-of-the-year pollock in the Bering Sea suggesting that age-0 juveniles grow at temperatures as low as 2 °C (Ciannelli et al., 1998; Siddon et al., 2013a). If at least some growth can occur over the winter, it may be possible for overwintering fish to compensate for poor initial condition. Metabolic adjustments may be possible, and certainly behavioral thermoregulation is documented for overwintering pollock (Sogard and Olla, 1996; Hurst, 2007b), leaving open the possibility that age-0s could offset some of the expense of small initial body size or poor condition. Additionally, in the absence of good *in situ* measurements, it is difficult to know how much spatial plasticity of food resources exists overwinter, which can potentially offer low, but growth-sustainable, levels of localized prey resources to small age-0s. Of course, though small fish have reduced metabolic requirements they also have lower overall energy reserves, so the potential to deplete energy stores faster than larger pollock remains. Nevertheless, small, winter-emergent juvenile pollock are collected in spring, indicating that survival of small fish does occur overwinter. Finally, the influence

of winter severity on survivorship has not been investigated, but mild winter temperatures could preclude winter starvation if sufficient food resources persist. In light of these unresolved issues, the risk of overwinter mortality due to small body size or poor condition needs further investigation.

The Gas Tank Hypothesis (Sigler et al., in review) builds from the Critical Size Hypothesis to recognize that timing of production across trophic levels is critical to pre-winter conditioning success in pollock during the first year of life. This theory maintains that timing of the spring phytoplankton bloom is central to phytoplankton-zooplankton-pollock energy transfer, but is careful to recognize that dynamics in summer and autumn, particularly temperature-metabolic requirements and predation, remain important to pre-recruit production. Moreover, the hypothesis maintains that production is also dependent upon spatial co-occurrences of phytoplankton-zooplankton-pre-recruit pollock, and that successive warmer-than-average or colder-than-average conditions over the EBS shelf influence overall trophic control of recruitment success to age-1.

3.3 Predation

Conceptual models of pollock recruitment as related to predation impacts on age-0s have been best developed in the Gulf of Alaska. The Shifting Control Hypothesis (Bailey, 2000) suggests that control of pollock recruitment in the Gulf shifted from bottom-up control of abiotic parameters acting on feeding and survival of pollock larvae in spring, to top-down control by large piscivorous predators, most notably arrowtooth flounder and Pacific cod feeding on age-0 pollock in summer and autumn. Increases in biomass of these and other piscivores, coupled with the Gulf of Alaska's narrow

continental shelf and constricted landscape geography that acts to bring predators and pollock into close proximity, makes this a feasible hypothesis in the Gulf system but less likely to exert population level control in the EBS. Biomass of predator species is increasing in the EBS, but the broad continental shelf allows for greater spatial separation of predators and prey, making top-down predation control by piscivores less problematic unless factors act to bring predators and prey into close proximity (ex: Cold Pool presence/absence, Transport Cannibalism Hypothesis). Multi-species modeling efforts in the EBS suggest that top-down recruitment control is possible, but caution that it is temporally variable and dependent upon predator population levels (Livingston and Jurado-Molina, 2000).

A corollary to the Shifting Control Hypothesis is the Climate-Biology Hypothesis (Ciannelli et al., 2005). In this refinement of the original Shifting Control idea, the authors proposed that the dominant mechanisms of juvenile pollock mortality (predation) in the Gulf of Alaska could change over contrasting climate regimes, suggesting a dynamic interplay of climate and predation pressure. They demonstrated that during ecosystem phases characterized by elevated sea surface temperatures and high predation on juvenile pollock, pollock recruitment variability and abundance were below average. In contrast, periods characterized by low temperatures and relaxed predation were associated with high pollock abundance and high population variability. The recognition of the interplay of physical and biological forcing factors on pollock recruitment is not unique, but has important implications for the management of the species in the Gulf of Alaska and elsewhere.

4. Data Gaps

Even after nearly 40 years of active research, basic information on pollock early life dynamics in the EBS remains unresolved. Researchers have disentangled certain aspects of the complex ecology of young pollock, though changes in climate, oceanography, trophic structure, and food web dynamics act synchronously to interrupt, modify, or break down known relationships, prompting a continuing need to re-evaluate and redefine conceptual frameworks. The following sections identify gaps in knowledge of pollock early life ecology, and reflect on the variables that are appropriate for continued monitoring as they may either be uniquely influenced by changing ecosystem dynamics or exert disproportionate control on pollock recruitment.

4.1 Spawning location

The vast geographic area over which pollock spawning grounds are located, coupled with the large spatial discontinuities in their locations, make comprehensive sampling of putative pollock spawning locations in the Bering Sea extremely difficult. Moreover, logistical constraints of sampling during late winter and early spring when storms are frequent and sea ice is present complicate complete pre-spawning and spawning sampling. Recent work (De Robertis and Cokelet, 2012) suggests that pollock shift their distribution away from areas of cold water and extensive ice cover, indicating spawning under the ice is probably minimal. There is indirect evidence of spawning north of 60 °N latitude over the outer shelf in the vicinity of Zhemchug Canyon (see section 2.2), but direct evidence is lacking. Critical questions linger: Does spawning area

expand and contract interannually with variable thermal conditions? Does spawning habitat become fragmented by the presence of the Cold Pool? What happens to spawning activity when the preferred spawning area is covered by ice? Pollock in the BS exhibit broad-scale spawning site fidelity, but do they move into deeper water over the basin where temperatures are warmer and sea ice is lacking, thus spawning in locations where currents are less conducive to on-shelf transport of offspring? Continued monitoring of spawning populations, complemented by long-term observations of egg and early larval distributions, is critical to elucidating environmental tolerances of adult pollock during spawning, and potential effects on recruitment.

Climate-induced variability in timing of spawning has been suggested in several studies but questions remain. Predominant currents in the EBS are seasonally altered due to the early spring establishment of the Inner Front along the Alaska Coastal Current (Stabeno et al., 1999; Kachel et al. 2002), which has major implications for transport and distribution of larvae and ultimately for spatial distribution of age-0 juveniles. Pollock adults that spawn in the vicinity of Unimak Island produce larvae that are entrained in one of two major flows, the cross shelf flow of the Alaska Coastal Current that delivers propagules over the southeastern middle shelf, and the northward flowing current along the 100 and 200 m isobaths (Fig. 1) delivering larvae over the outer shelf. Set up of the Inner Front typically occurs in late spring (Kachel et al., 2002), a month or more after the presumed spawning time for pollock in that vicinity (March). Shifts in spawning time relative to establishment of the Inner Front have the potential to affect the proportion of offspring that are delivered to the middle and outer shelves.

Some progress can be made in addressing the questions posed above with regard to spawning ecology by examining long-term variations in maturity scales and by examining shifts in distributions of eggs. Collections of ovaries from annual pre-spawning acoustic surveys have suggested differences in timing of gamete development with thermal regime (Smart et al, 2012a) and differences in spawning time between warm and cold periods in the EBS have been inferred through examination of timing of peak abundances of pollock eggs (Smart et al., 2012b). These approaches suggest that spawning can be delayed by up to a month during cold years. In addition, multi-year surveys of egg distribution can provide indirect evidence for spatial shifts in spawning areas due to climate and oceanographic shifts, as has been shown for Arcto-Norwegian cod (Sundby and Nakken, 2008).

Finally, until now we have not had the technology to localize the natal area for any particular juvenile pollock collected at sea. This information would be extremely valuable in clarifying stock origin, resolving the degree of mixing among Bering Sea source areas (Bogoslof, Unimak, Pribilof, Zhemchug), and answering source-sink connectivity questions. Analysis of otolith elemental composition could help to resolve these issues since otoliths incorporate trace metals into their growth rings that can be related to environmental conditions at the time of the growth period. Otoliths have been used to resolve natal origin, connectivity, and nursery habitat for anadromous species (Thorrold et al., 1998; Kennedy et al., 2002), reef fishes (Ruttenberg et al., 2008), and flatfishes (Cuveliers et al., 2010), but the effort for pelagic fishes has been complicated by the temporal scale of residency relative to dispersal potential (Gillanders, 2011). However, recent work using gadoids shows some promise. Thorisson et al. (2010) were

able to trace natal areas of age-0 Atlantic cod in a year with limited oceanic mixing, DiMaria et al. (2011) determined that elemental signatures in larval Pacific cod (*Gadus macrocephalus*) could reflect thermal as well as chemical variations in rearing water, and a pilot study using pollock collected from the Gulf of Alaska indicated that broad-scale geographic differences in residency may be resolved among age-0s (Fitzgerald et al., 2004). These approaches, if successfully applied in the EBS, would be extremely valuable to begin addressing questions such as, “Which source areas contribute significantly to the overall population biomass?”; “To what degree does pollock input from the Gulf of Alaska affect EBS population structure?;” “What are the connectivity links, rates, and routes between larval, juvenile, and adult fish?;” and “How much local recruitment is there?”. The EBS, with its broad, homogenous seascape and well-mixed water column during the pollock spring-spawning period present challenges, but continued efforts are encouraged.

4.2 Ageing

Ambiguities in ability to accurately assign daily ages to larvae and age-0 juveniles from otoliths have hampered early life studies of walleye pollock in the EBS. Determining ages of larval and age-0 pollock in the EBS is of significant interest as several studies indicated the existence of multiple cohorts (Walline, 1985; Nishimura et al., 1996). However, difficulties determining growth increments for fishes at low temperatures are well documented (Campana and Neilson, 1985), and it appears that pollock larvae may not consistently accumulate daily otolith rings in the EBS (K. Bailey, personal communication), a phenomenon that has been demonstrated for other larval fish

species as well (Geffen, 1982; McGurk, 1987; Collins et al., 1989). More research into improved or new approaches to assigning daily ages to larval and age-0 pollock in the EBS is an area of much-needed effort.

Another area in which ageing information is needed is to determine whether 100 – 150 mm TL juvenile pollock collected in late-summer are large age-0 fish that have not experienced a first winter or small age-1 fish that have undergone a slow-growth period. Typically, inferences of age are made based on fish size and length-frequency histograms, but size alone is not a reliable indicator of age. Moreover, length-frequency histograms are confounded in the EBS where offspring are produced from multiple spawning events over a wide geographic area, and length-based separations into year classes are often imprecise. Examination of otoliths for the presence of a winter hyaline zone (winter check) is possible, but unusual growth zones over the otolith occasionally confound that interpretation (T. Helser, personal communication). Historically-collected pollock (70 – 150 mm TL) from the EBS are available at the Alaska Fisheries Science Center and can be examined for the presence of overwinter signatures, as determined by relative ratios of stable oxygen isotopes. Studies of Atlantic cod demonstrate that peaks in $\delta^{18}\text{O}$ concentrations in the otolith indicate the animal experienced winter conditions (Gao, 2002), and a similar approach for juvenile pollock would help to resolve age discrepancies. Such information is extremely useful as it can not only help to resolve year classes in the EBS, but it can also be used to determine whether there are spatial or temporal shifts in the size range of age-0s with varying environmental conditions (prey availability, temperature, etc).

4.3 Maternal history

It is not presently known what the influence of maternal history is on resultant offspring. Significant work on other species has shown varying oceanographic conditions experienced by the female affect the traits of their offspring, including size at hatching, larval growth, behavior, and survival (Solemdal, 1997; Berkeley et al., 2004). Abiotic influences such as temperature and photoperiod as well as biotic factors such as maternal age, crowding, prey availability, and habitat quality exert measurable phenotypic effects on progeny. Once thought to be comparatively inconsequential to overall population structure, phenotypic effects have been shown to have the potential for demographic influences propagated by variations in offspring performance, including how young experience food limitation, predator encounters, thermal stress, and oceanographic shifts. Moreover, recent work to examine whether pollock reproductive biology affects stock productivity among Gulf of Alaska pollock has shown that weight-specific relative fecundity and maternal weight-at-age influence stock status, which in turn have the potential to influence estimation of fisheries harvest points (Spencer and Dorn, 2013). Accordingly, more effort to quantify the effects of maternal history on population differences in progeny is recommended.

4.4 Condition and overwinter success

Work to examine links between environmental conditions and recruitment has focused on the role of juvenile condition and overwintering success. Field work on EBS age-0 pollock provides evidence of a link between survivorship and condition of YOY

pollock in near-surface waters. However, it is known that large aggregations of juvenile pollock school below the pycnocline (30 m), and these deeper fish may have different energy content relative to counterparts near surface. It has been hypothesized that poor condition pollock occur in near surface waters during daylight hours because they do not possess the energy reserves to vertically migrate. Vertically-migrating age-0 pollock may have higher energy contents since they remain in close proximity to vertically migrating zooplankton prey. A pilot study which included directed, paired sampling of pollock from the surface and midwater regions suggests no at-station differences in energy content from fish collected above and below the pycnocline (Parker Stetter et al., 2013) but additional work is needed to fully resolve whether there are differences in energy content of age-0s collected across vertical strata.

Some laboratory work has been done to examine compensatory growth among food-limited age-0 pollock at optimal temperatures (Sogard and Olla, 2002), but work specifically examining the potential for accelerated growth under simulated late autumn/winter conditions is needed. If prey quality and quantity regulates size and body condition prior to first winter onset then the capacity to compensate for inadequate provisioning during summer seems likely. Spawning in the Bering Sea is seasonally protracted and occurs over several spawning areas, yielding multiple groups of larvae spawned months apart that co-mingle in the water column. Can late-spawned, smaller juveniles catch up to early-spawned larger-sized individuals under low-thermal, winter-simulated conditions if prey resources are available? Or are all the smaller, late-spawned cohorts fated to disproportionate overwinter mortality? If not, and overwinter compensatory growth is possible, are there associated costs?

If size- or condition-selective overwinter mortality occurs in juvenile pollock, a significant body of research is needed to determine demographic effects on the resultant population. For example, are early-spawned progeny that have a protracted opportunity for growth prior to winter onset selected for, potentially scaling the population for early reproduction? If late-spawned cohorts are subject to high rates of overwinter mortality, is there a competitive growth release from population-level density-dependent regulation among survivors? If factors act to delay spawning, or limit habitat areas over which early spawning can take place (e.g., sea ice), what are the effects on resultant overwintering juveniles? Are there tendencies toward expedited or disproportionate energy allocation prior to or during the overwintering period? Are demographic effects modulated by interactions between growth and/or predation? Are effects propagated as the population ages? These and other questions remain unanswered, but warrant attention and study.

4.5 Multi-species interactions

Pollock research has benefited from significant single-species attention, but more could be done to investigate interactions between pollock and other species. As an example, it is known that young pollock and Pacific cod spatially and temporally co-occur during the first year of life, but larval pollock and Pacific cod show dissimilarities in diet (Strasburger et al., 2014), while age-0 diets are similar (Farley et al., in press). Do initial diet dissimilarities and resource partitioning help to mitigate the effects of ontogenetic convergence later on? Are diet convergences at the age-0 stage constrained or modulated by habitat separations between demersal Pacific cod and pelagic pollock? Are these relationships maintained during oscillating thermal phases of the EBS

ecosystem? Further, studies from the Gulf of Alaska have demonstrated that capelin have a similar prey base as age-0 pollock (Logerwell et al., 2010), and studies in the Bering Sea that examine the relationship between pollock and other midwater zooplanktivores (capelin, eulachon, Pacific herring, jellyfish) are warranted. Multispecies studies that examine these and other interactions, both at the local and broad-scale level, are necessary to better understand community response to climate variation and effects on recruitment potential.

5. Conclusions and Recommendations

Factors affecting production, growth, and survivorship of pollock during the first year of life underlie population fluctuations in the species, so it remains critical to continue to monitor and study pollock during this period. Because the Bering Sea represents the northern end of their latitudinal range, environmental constraints have the potential to exert significant control over intrinsic rates of pollock population increase. Understanding these processes is critical given that climate conditions in the EBS are changing, with documented increases in air and ocean temperatures, changes in frequency and intensity of storms, declines in sea ice thickness and extent, and affects to ocean stratification, to name only a few. In order to effectively understand the complex ecological processes governing EBS pollock population variability, we must seek mechanistic understanding of the factors influencing processes occurring over the first year of life. To do so we recommend, in order of importance,:

- 1) Development and implementation of a seasonal monitoring program to examine pollock ecology and dynamics over the entire first year of life, through the winter

- to the ensuing spring (age-1), with focus on process-oriented research that can resolve mechanistic linkages and pathways of recruitment control;
- 2) Studies directed to examining predation dynamics and trophic consequences of predation, with particular emphasis on the relationship between food availability and food quality, larval and juvenile body condition, and vulnerability to predators;
 - 3) Studies that focus on larval and age-0 juvenile diet and condition, as well as studies that examine physiological and behavioral responses to prey shifts;
 - 4) Investment in additional laboratory studies to resolve stage-specific baseline information such as temperature-dependent growth, compensatory growth, prey preferences, consumption rates, assimilation rates, and rates of metabolism that can be used to parameterize models;
 - 5) Development of spatially-explicit, mechanistic biophysical, bioenergetics, and trophic models that specifically focus on the first year of life to resolve energy flows, connectivity, trophic constraints, and sources of mortality that may be indistinct using present approaches;
 - 6) Development of stage-specific predictive models (statistical, trophic, and biophysical) to assess implications of variable early life mortality to future recruitment;
 - 7) Work to resolve critical production areas (spawning areas, feeding grounds, nursery habitats) of pre-recruit pollock;
 - 8) Evaluation of potential effects of competition throughout the first year of life from species such as Pacific cod, capelin, Pacific herring, and jellyfish; and

- 9) Development of novel approaches to resolving daily ages of larval and age-0 juvenile pollock in the Bering Sea.

The importance of factors influencing the growth and survival of early life stages on recruitment potential has been recognized since the earliest days of Hjort (1914), and certainly recruitment variability during early life remains a leading factor in determining year class strength (Ottersen et al., 2014). For walleye pollock occurring in the Bering Sea, a myriad of influences, environmental, trophic, and intrinsic, act in concert over a suite of developmental phases throughout the critical first year to influence recruitment variability and regulate recruitment strength. Future research should move toward mechanistic understanding of how survival is modulated throughout the first year of life and strive for inclusion in predictive methodologies that can be used in successful management of the species.

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Figure 1. The southeastern Bering Sea with schematic representation of the major flows over the Aleutian Basin and adjacent shelf. Walleye Pollock spawning areas (known and putative) indicated as shaded ellipses.

Figure 2. Proportion of harvested roe that is hydrated from the commercial fishery by latitude (LAT) and week of the year (Week) for 2001 through 2006. The surfaces were derived from a 2-dimensional cubic splines fit within a generalized additive model (GAM) for latitude and week by year as the independent variables. Points are the data used in the GAM for each year. Color ramp indicates density.

Figure 3. Centers of distribution of Walleye Pollock early life history stages over the eastern Bering Sea shelf under years of warm (light grey) and cold (black) oceanographic conditions. Bars indicate +/- one standard deviation. Eg = Egg, YL = Yolksac larvae, PL = Preflexion larvae, LL = late larvae, JV = Juvenile.

Figure 4. Vertical distribution of feeding stages of Walleye Pollock larvae (preflexion, late larvae, early juvenile) during day and night. Bars represent 1 standard deviation; n indicates the number of positive tows.

Figure 5. Generalized additive mixed model (GAMM) regression analysis showing the estimated effect of standard length (SL; mm) on energy density (kJ/g dry mass) for age-0 Walleye Pollock. Dashed lines denote 95% confidence interval. Energy densities are plotted as anomalies because actual values depend on location and year of sampling. Adapted from Siddon et al. (2013).

Figure 6. Horizontal distribution of late-juvenile pollock in 2008-2010. The top panel shows shallow (surface to pycnocline) and bottom panel shows deep (pycnocline to bottom) distributions. Deep data were not available for 2008. Bubble size is proportional to density, a thin black line shows 0 density, and a thin grey line indicates that data were not available for this section of transect. Adapted from Parker-Stetter et al. (2013).

Figure 7. Relationship between the average energy content of age-0 walleye pollock sampled in September and their subsequent survival to age-1 in the eastern Bering Sea. Symbol colors reflect the ice/temperature regime in the eastern Bering Sea at the time of sampling. Index of survival (age-1 recruits per spawner) is from Ianelli et al. (2013).

Figure 8. A. Temperature-dependent growth in length (mm d⁻¹) and B. Age-dependent growth-in-length at four temperatures derived for Bering Sea pollock (BSP; Petrik et al. in press), Gulf of Alaska Pacific cod (GOAPC; Hurst et al. 2010), Norwegian Coastal cod (NCC; Otterlei et al., 1999), Northeast arctic cod (Otterlei et al.; 1999), Norwegian cod (NC; Folkvord 2005), Norwegian arctic cod (NAC; Folkvord 2005), Shelikof Strait pollock (SSP K; Kendall et al., 1987), Shelikof Strait pollock (SSP Y&B; Yoklavich and Bailey 1990), Funka Bay pollock (FBP; Nishimura and Yamada, 1984), Gulf of Maine haddock (GOMH; Campana and Hurley, 1989), and Gulf of Maine cod (GOMC; Campana and Hurley, 1989).

Table 1. Collections of the early life stages of walleye pollock in the eastern Bering Sea. Eco-FOCI = Ecosystems and Fisheries Oceanography Coordinated Investigations, EMA = Ecosystem Monitoring and Assessment, MACE = Midwater Assessment and Conservation Engineering, UAF = University of Alaska Fairbanks, UW = University of Washington.

Life Stage	Program	Years	Season	Biological Sampling Gear	Physical Sampling Gear
Eggs, larvae	Eco-FOCI	1988-present	Spring	60 cm bongo, 1m ² MOCNESS, Tucker nets	CTD, Seacat
Larvae, age-0 juveniles	Eco-FOCI, UAF	2008-2010	Spring, Summer	1m ² MOCNESS	CTD, Seacat
Larvae, age 0 juveniles	Eco-FOCI, Hokkaido University	1995-2001	Summer	Methot trawl	Seacat
Age-0 juveniles	EMA, UW	2001-present	Summer	CanTrawl, acoustics, midwater trawl	CTD, Seacat
Pre-spawning adults	MACE		Spring	Midwater trawl, acoustics	
Age-1 juveniles	MACE		Winter & summer the following year	Midwater trawl, acoustics	

Table 2. Phenological shifts in temporal distributions of walleye pollock early life stages showing day of year when each life stage appears over the eastern Bering Sea shelf. NA: not available to seasonal sampling limitations. Adapted from Smart et al. 2012a.

Life history stage	WARM			COLD		
	Start	Peak	End	Start	Peak	End
Egg	NA	65	130	NA	105	150
Yolksac	NA	100	170	100	145	180
Early larval	NA	125	185	100	145	195
Late larval	100	150	210	125	180	240
Juvenile	120	200	NA	135	225	NA

Table 3. Hydrodynamic models used to examine walleye pollock early life ecology in the eastern Bering Sea (EBS).

Model	Domain; Dimensions	Physical model and forcing	Biology	Results/Outputs
Walsh et al. 1981	EBS; 2D	Wind stress, bottom friction, topography, Coriolis force, geostrophic pressure gradient	2 stages (nonfeeding, feeding); Growth; Mortality	Trajectories and mortalities based on spawning date
Wespestad et al. 1997; Wespestad et al. 2000	EBS; 2D	OSCURS; Sea level pressures, mean geostrophic currents, satellite-tracked drifter speed coefficients	1 stage; No biology	Relate year-class success to wind-driven advection and spatial overlap of final distributions with adults
Petrik et al. in press; in preparation	EBS; 3D	ROMS	4 stages (egg, yolk sac, preflexion, late); Growth; Vertical behavior	Trajectories, distributions, patchiness, and connectivity as influenced by environmental and spawning conditions

















