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FINAL REPORT

Surface trawl survey acoustics

NPRB BSIERP Project B59 Final Report

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Abstract

Forage fish, which include capelin, herring, and early life stages of walleye pollock and Pacific cod, are food for many fish, birds, and mammals in the Bering Sea. While little is known about specifics of their horizontal and vertical movements, evidence suggests that forage fish distributions can change from year to year and may be influenced by a variety of factors. This study was undertaken to characterize forage fish distributions and evaluate which factors may affect those distributions. We used active acoustics (echosounders) and trawling (surface and midwater) to map distributions of forage fish between BASIS (Bering Aleutian Salmon International Survey) survey stations in 2008-2010. The analysis was expanded to include archived acoustic data from 2006-2007. In 2008, age-0 pollock were primarily found in the surface water (<35 m depth). In both 2009 and 2010, highest densities were found in dense schools in midwater (>35 m below the surface). Both age-0 Pacific cod and capelin had high densities in the surface in 2010 but no or low densities in the midwater. We tested hypotheses on whether local, annual, and/or regional factors affected forage fish distributions. Models varied by species but, in general, temperature, bottom depth, and/or zooplankton prey were important predictors of forage fish presence and density. Interestingly, annual variables, such as storminess in June and sea ice extent, were sometimes as or more important than local conditions at a station. This work underscores the need for dedicated studies of forage fish and an increased focus on explaining distributions to support climate predictions and modeling efforts.

Key Words

Bering Sea, forage fish, acoustics, trawling, distribution, biophysical coupling, oceanography, age-0 walleye pollock, age-0 Pacific cod, capelin

Citation

Table of Contents

Abstract.......................................................................................................................... 2
Key Words......................................................................................................................... 2
Citation............................................................................................................................ 2
Study Chronology............................................................................................................ 7
Introduction.................................................................................................................... 7

Overall Objectives ........................................................................................................ 9
  Original objectives from progress reports................................................................. 9
  Objective 1 .................................................................................................................. 9
  Objective 2 ................................................................................................................ 10
  Objective 3 ................................................................................................................ 10

Manuscripts..................................................................................................................... 10

Chapter 1. Summer distributions of forage fish in the eastern Bering Sea.................... 11
  Citation....................................................................................................................... 11
  Abstract..................................................................................................................... 12
  Keywords................................................................................................................... 12
  1. Introduction........................................................................................................... 13
  2. Methods................................................................................................................ 14
    2.1. Survey design..................................................................................................... 14
    2.2. Acoustic data collection.................................................................................... 15
    2.3. Trawling and target identification..................................................................... 15
    2.4. Acoustic data analysis....................................................................................... 16
      2.4.1. Acoustic data processing........................................................................... 16
      2.4.2. Depth zones............................................................................................... 17
      2.4.3. Data threshold............................................................................................ 18
      2.4.4. Horizontal distribution of fish backscatter................................................. 19
      2.4.5. Acoustic species proportions..................................................................... 19
      2.4.6. Trawl assignments...................................................................................... 20
      2.4.7. Species densities....................................................................................... 20
      2.4.8. Species distributions................................................................................... 20
      2.4.9. Percentage of fish in the surface zone....................................................... 21
  3. Results...................................................................................................................... 21
    3.1 Trawling results .................................................................................................. 21
    3.2. Acoustic general results ................................................................................... 22
    3.3 Forage fish densities and distributions............................................................... 23
      3.3.1. Capelin ....................................................................................................... 23
Study Chronology

Project BSIERP-B59 was initiated on 1 February 2008 and was initially scheduled to be completed 30 December 2012, with the report due 28 February 2013. The funding of a complementary project, NPRB-1006 (“Assessing age-0 walleye pollock distributions for cohort strength and response to climate change”) increased the amount of data and number of analyses that were included in BSIERP-B59.

Due to unforeseen delays, a no-cost extension for NPRB-1006 was requested in September 2011, extending the project to 30 June 2013 and the report deadline to 30 August 2013. As data analysis for BSIERP-B59 and NPRB-1006 were being conducted simultaneously, in February 2013 we received a no-cost extension for BSIERP-B59, with both the project and report due on 30 June 2013.

Introduction

Ecosystem-based approaches to fisheries management (EBFM) are advocated in the scientific literature and mandated in the management of aquatic resources (Pikitch et al., 2004; Livingston et al., 2005). Implicit in the development of EBFM is an increased understanding of ecosystem function and process, which should lead to prediction of inter-species interactions and environmental influences on species abundances (Pikitch et al., 2004). Expanded surveys and assessment of biota and the environment are a necessary first step, but financial and logistic constraints make the monitoring of all species, species interactions, and physical variables impossible. Although long-term, multi-trophic level datasets are rare, studies that include environmental measures through upper trophic level responses have shown concordance over a wide range of spatial and temporal scales (e.g., Aebischer et al., 1990).

In marine ecosystems, monitoring some trophic levels is easier than others. Environmental variables thought to influence primary production (e.g., sea surface temperature, atmospheric pressure, wind speed, wind direction) can be monitored remotely. Many commercially important fish stocks are surveyed on a regular basis and additional population size and structure information can be obtained using fishery data. Among apex predators such as marine mammals and seabirds, measures of population size, reproductive effort, and occasionally diet, is often monitored at rookeries and colonies. A critical component missing from many ecosystem datasets is non-commercial species, especially the abundance and distribution of juvenile and adult pelagic fish and large zooplankton (e.g., krill). This trophic guild, commonly called forage fish, fuels production of commercial fish stocks and apex predators (Springer & Speckman, 1997), and can respond to environmental forcing (e.g., Barber & Chavez, 1983). Information on associations between the environment, primary/secondary production, and forage fish is a necessary prerequisite to
formulate ecosystem models. A mechanistic understanding of how changes in forage fish dynamics propagate up to apex predators is essential for successful EBFM.

Forage fish are a critical component of the northeast Bering Sea ecosystem, yet the understanding of their distributions and dynamics is incomplete. As an example, the Gulf of Alaska capelin population abundance has been estimated using food habits (i.e. diet) data from piscivorous predators (Conners & Guttormsen, 2005, Yang et al., 2005) and mass-balance models (Ormseth & Vollenweider, 2007). The importance of forage species as harvestable resources (e.g. herring, capelin) and as prey to apex predators (e.g. adult gadoid fish, marine mammals, seabirds) emphasizes the need to understand biological and physical processes influencing forage fish population dynamics and interactions with predators.

This project was designed to contribute to BSIERP hypotheses 1-4, specifically bottom-up (1.c, 3.a-c, 4.a) and top-down (2.b-d) hypotheses.

1. Climate-induced changes in physical forcing will modify the availability and partitioning of food for all trophic levels through bottom-up processes. Specifically:
   c. Earlier spring transition will lengthen the period of time of organized onshore flow along the Alaska Peninsula, thus transporting larvae away from outer domain piscivores.

2. Climate and ocean conditions influencing water temperature, circulation patterns and domain boundaries impact fish reproduction, survival and distribution, the intensity of predator-prey relationships and the location of zoogeographic provinces through bottom-up processes. Specifically:
   b. Reduced cold pool extent will increase overlap of inner domain forage fish and outer domain piscivores.
   c. Strength of frontal boundaries will weaken due to absence of the summer cold pool, allowing expansion of the inner domain and juvenile and forage fish habitat there. Weaker winds will enhance this effect.
   d. Sporadic reversals to cold conditions (e.g., 1999) will have strong effects on the subarctic community and result in increased interannual variability in abundance and pelagic productivity of piscivorous fish, seabirds and marine mammals.

3. Later spring phytoplankton blooms as a result of early ice retreat will increase zooplankton production, thereby resulting in increased abundances of piscivorous fish (pollock, cod and arrowtooth flounder) and a community controlled by top-down processes [Oscillating Control Hypothesis] with the possible trophic consequences:
   a. Competition with abundant, piscivorous fish species for forage species will lead to a decline in murres, kittiwakes and fur seals.
b. Growing populations of humpback and fin whales increasingly will both consume and compete with forage fish (juvenile pollock) for zooplankton (euphausiids and copepods). By reducing the prey base of forage fish, whales not only reduce the amount of forage fish available to other predators, but also their quality (lipid content).

c. In a top-down control community, fishing will reduce the degree of top-down control of forage species (including juvenile pollock) by adult pollock, cod and arrowtooth flounder. Owing to light exploitation rates, top-down control by arrowtooth flounder will increase, as will their level of competition with piscivorous fish, seabirds and marine mammals. As a result of these two processes, arrowtooth flounder will determine ultimate community composition, such that the climax community will be arrowtooth flounder-dominated (similar to the Gulf of Alaska).

4. Climate and ocean conditions influencing circulation patterns and domain boundaries will affect the distribution, frequency and persistence of fronts and other prey-concentrating features and thus the foraging success of marine birds and mammals largely through bottom-up processes. Specifically:

a. Climate-ocean changes will displace predictably located, abundant prey (hot spots) necessary for successful foraging by central place (seabirds and fur seals while nurturing young) and hot spot (baleen whales, walrus) foragers.

Distribution data supported hypotheses on potential climate change effects and predator-prey interactions. Density and abundance estimates were used to examine forage fish responses to environmental conditions. These data contributed to identifying species or predator-prey interactions susceptible to climate change. The forage fish distribution and abundance data are being used to evaluate seabird distributions and are available for use in modeling, spatially-explicit bioenergetics, and the predator-prey dynamics.

**Overall Objectives**

**Original objectives from progress reports**

1. Map density distributions of forage fish (e.g. juvenile pollock, capelin, herring, and myctophids) in the Bering Sea from 2008-2010.

2. Examine relationships between oceanography and forage fish distribution and abundance

3. Contribute to the examination of how forage fish distribution/abundance may affect apex predator distributions and abundances.

**Objective 1**

Data were collected for this objective in August-October of 2008-2010 as part of an existing survey, the NOAA-NFMS Bering Aleutian Salmon International Survey (BASIS). Sampling was performed on both
the NOAA ship Oscar Dyson and the chartered fishing vessel FV Epic Explorer. The funding of NPRB-1006 (“Assessing age-0 walleye pollock distributions for cohort strength and response to climate change”) allowed us to include archived data from 2006 and 2007 to our analyses. Distributions of forage fish (primarily age-0 walleye pollock, age-0 Pacific cod, capelin) were mapped using active acoustics. Trawling (surface and midwater) was conducted to obtain species composition and length frequency data. Forage fish distributions in 0.5 nmi horizontal bins were quantified in the surface zone (~top 35 m, accessible to the surface trawl), the midwater zone (>35 m to the bottom), and the water column (surface + midwater zones).

Objective 2
Data from Objective 1 were used to test hypotheses about what physical, biological, and/or climate-related factors influence forage fish distributions. We used an information-theoretic approach to evaluate hypotheses generated by previous studies, discussions with colleagues at meetings, and our biological knowledge to guide the formulation of a hypothesis set to test. In addition to statistically comparing individual hypotheses, we also ran a full model selection to determine if our hypotheses had missed any important combinations of factors. Data analysis was conducted to evaluate forage fish probability of occurrence and density.

Objective 3
Forage fish densities were provided to Kathy Kuletz (USFWS) and Rob Suryan (Oregon State University) for use in analyzing distributions of post-breeding seabirds relative to their prey. Parker-Stetter has worked closely with Suryan and Kuletz for this effort. This analysis is ongoing and the target dates for completion and submission are to be determined. Additional information can be found in progress reports and the final report for project BSIERP-B64 “Seabird broad-scale distribution.”

Manuscripts
Two manuscripts are included with this report:

Chapter 1 is entitled “Summer distributions of forage fish in the eastern Bering Sea” and this has been published in Deep Sea Research Part II: Topical Studies in Oceanography.

Chapter 2 is entitled “Factors affecting summer distributions of Bering Sea forage fish: comparing hypotheses” and will be sent to colleagues for a courtesy review prior to submission.
Chapter 1. Summer distributions of forage fish in the eastern Bering Sea

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Abstract

Juvenile and small adult fish, typically called forage fish, are an important but poorly studied part of the eastern Bering Sea (EBS) ecosystem. Acoustic and trawl data from a non-target survey were used to evaluate distributions of capelin (*Mallotus villosus*), age-0 Pacific cod (*Gadus macrocephalus*), and age-0 walleye pollock (*Theragra chalcogramma*, herein pollock) in 2006-2010. Within the surface zone (15 m to ~35 m, evaluated 2006-2010), capelin occurred throughout the EBS but primarily in the middle shelf. Capelin were also present in the midwater zone (~35 m to 0.5 m off-bottom) in both 2009 and 2010 (evaluated 2009-2010), and resulted in water column zone (15 m to 0.5 m off-bottom) distributions that differed from surface zone characterizations. Age-0 Pacific cod occurred primarily in the surface zone of the middle and outer shelf regions in all years. As midwater and surface zone age-0 Pacific cod were often coincident, water column zone distributions in 2009-2010 were similar to surface zone distributions. Age-0 pollock were found in the EBS surface zone in all years, primarily in the middle and outer shelf regions. High densities of age-0 pollock occurred in the midwater zone in 2006-2007 and 2009-2010. Water column zone distributions of age-0 pollock were similar to surface zone distributions in 2006-2007, but differed in 2009-2010 due to low numbers of age-0 pollock in the surface zone and presence of high densities in the midwater zone of the outer shelf region. While general patterns in capelin distribution in the surface zone were similar between the present and the previous studies, the acoustic-trawl characterization suggested that capelin densities were high in the middle shelf region. As expected, surface zone distributions of age-0 Pacific cod and age-0 pollock were similar to previous characterizations. Observed high densities of midwater age-0 pollock have not been described by previous studies. Annual abundance indices based on bottom or surface trawl data alone will not be sufficient in all years. Data and conclusions from non-target surveys may be constrained compared to dedicated survey efforts, but can provide baseline distributions, potential abundance indices, and insight for planning future research.

Keywords: Bering Sea, forage fish, walleye pollock, Pacific cod, capelin, distribution
1. Introduction

Juvenile and small pelagic adult fish, commonly referred to as forage fish, are a critical component of the eastern Bering Sea (EBS) ecosystem (Springer and Speckman, 1997), yet our understanding of their distributions and dynamics is incomplete. Implementation of ecosystem-based approaches to fisheries management (Pikitch et al., 2004; Livingston et al., 2005; Pikitch et al., 2012) and future predictions of biological response to climate change in the EBS (e.g. Mueter and Litzow, 2008) will require comprehensive distribution and abundance data for this important trophic guild.

Unlike commercially-important fish populations, information on EBS forage fish has typically been extracted from large-scale surveys designed to sample other species. Recent data sources have included systematic bottom or surface trawl surveys (e.g. Moss et al., 2009, Hollowed et al., 2012; Hurst et al., 2012), midwater trawl surveys (e.g. Traynor and Smith, 1996), or opportunistic data collected during other assessments (e.g. Bakkala et al., 1985; Walters et al., 1988). While these data can be used to derive abundance or biomass indices, surveys using fixed-opening trawl gear only sample a portion of the water column, may not sample the bulk of forage fish distribution (Hollowed et al., 2012), and cannot typically adapt to compensate for vertical and/or horizontal changes in fish distributions related to environmental conditions.

An alternate sampling strategy combines active acoustics with trawling to map distributions and estimate abundances of pelagic or semi-demersal fish species. An example of this approach by Hollowed et al. (2012) examined the distribution of age-1 walleye pollock (Theragra chalcogramma, herein pollock) in the EBS. Echosounders continuously sample the water column along the survey vessel’s path and trawl samples are used to verify species compositions and to provide length frequency distributions. Large geographic ranges and systematic transect designs typical of acoustic-based surveys also ensure that variations in vertical and/or horizontal distributions can be detected over time or if environmental conditions change.

Dedicated acoustic assessments of forage fish species in the EBS have not been conducted, but acoustic data collected during non-target surveys can be used to increase knowledge of forage fish distributions. Analyses using acoustic and trawl data from non-target surveys may be constrained compared to those from dedicated survey efforts, but can provide an analytic starting point and a baseline for evaluating future research and appropriate survey designs.
This study was undertaken to characterize late-summer distributions of three forage fish species in the
EBS using non-target acoustic and trawl survey data from 2006-2010. In some cases, surface trawl data
from the existing survey have been used to evaluate EBS forage fish (e.g. Moss et al., 2009; Hollowed et
al., 2012; Hurst et al., 2012). We build on these results by using acoustic data collected continuously
between trawl stations and by evaluating densities within and below the surface trawl zone. Our specific
objectives were to: (1) use acoustics and trawling to characterize spatial distributions of capelin (*Mallotus
villosus*), age-0 Pacific cod (*Gadus macrocephalus*), and age-0 pollock, and (2) to compare acoustic
characterizations with previously published distributions.

2. Methods

2.1. Survey design

Data were collected during the 2006-2010, mid-August to early-October Bering-Aleutian Salmon
International Survey (BASIS) research surveys in the EBS (Fig. 1). The BASIS survey was initially
designed as a systematic surface trawl survey to sample salmon species (*Oncorhynchus* spp.) throughout
the EBS (Helle et al., 2007). In 2008 through 2010, the addition of active acoustics, limited midwater
trawling on acoustic targets, and modifications to survey transect sampling enabled estimates of forage
fish densities throughout the water column. Archived acoustic data from 2006-2007 (see Farley et al.,
2009 for survey description) were also used in this study, but trawling during those survey years was
limited to surface waters.

The spatial extent and timing of the surveys (Fig. 1), and the resolution of surface trawl stations sampled
varied among years (Fig. 2) due to variation in available funding and ship time. During 2006, 2007, and
2010, surface trawl stations were spaced ~35 nautical miles (nmi, 1 degree longitude, 0.5 degree latitude)
(Fig. 2). During the 2008 and 2009 surveys, BASIS stations were spaced ~65 nmi (2 degrees of
longitude) in the east-west direction and ~35 nmi (0.5 degree latitude) in the north-south direction. The
range of sampling dates also varied across years, with the 2008 and 2009 surveys starting in September
rather than the more typical mid- to late-August start date in other years (Table 1). Survey operations
occurred from approximately 0630 to 2200 Alaska Daylight Time (ADT).

BASIS surveys generally sampled in waters with bottom depths ranging from 25 to 400 m, with bottom
depths during the truncated 2008 survey limited to 25 to 100 m (Fig. 1). Based on supplementary
information in Harvey and Sigler (2013), the survey area included stations and transects within the inner
shelf (< 50 m bottom depth range), inner front (transition zone between the inner and middle shelf
regions), middle shelf (50-100 m), middle front (transition zone between the middle and outer shelf
regions), outer shelf (100-200 m), and a small portion of the shelf break and off-shelf (> 200 m) regions. For brevity, north of 60°N is referred to as the North EBS (NEBS) and south of 60°N is referred to as the South EBS (SEBS, Fig. 1).

2.2. Acoustic data collection

Acoustic data were collected from three different chartered fishing vessels in 2006-2010 using hull-mounted Simrad ES-60 echosounders (Kongsberg Maritime) operating at 38 kHz (Table 1). In 2008-2010, acoustic data were also collected from the NOAA ship Oscar Dyson’s Simrad EK-60 split-beam echosounders (18, 38, 70, 120, and 200 kHz) mounted on a 3 m retractable centerboard that extends transducer faces to 9.15 m below the water surface. Only 38 kHz data were used in these analyses. All split beam ES38-B kHz transducers had 7° beamwidths (measured at half power points) and the single-beam ES38-200 had a 13° beamwidth. All acoustic data were collected using a pulse duration of 1.024 msec and a ping rate of 1 pulse/sec. Data from chartered fishing vessels were collected at speeds of 3.1 to 4.6 m/s (6-9 kt). Data from the Oscar Dyson were collected at speeds of 5.1 to 6.2 m/s (10-12 knots). All echosounders were calibrated prior to and/or following each survey using reference sphere methods described in Foote et al. (1987).

2.3. Trawling and target identification

Fish were sampled using a Cantrawl 400/601 rope trawl (20-25 m vertical opening, 1.2 cm cod-end liner) equipped with 5 m alloy trawl doors (for details see Farley et al., 2009). Three types of trawls were performed: standard BASIS surface trawls, surface target identification trawls, and midwater target identification trawls. Three to four BASIS surface trawls were performed per day during daylight hours. A single midwater or surface target identification trawl was typically performed each day.

For standard BASIS surface trawls (2006-2010) and surface target identification trawls (2008-2010), floats were attached to the headrope of the Cantrawl to ensure the headrope remained at or near the surface. The duration of BASIS surface trawls was 30 minutes once the net was fishing. Surface target identification trawl times varied from 5 to 30 minutes. Autonomous depth loggers (Vemco Minilog-TD and Wildlife Computers Mk9) were deployed on the head and footrope during all net deployments in 2009-2010 to verify fishing depths and net openings. Based on headrope/footrope measurements taken from the Oscar Dyson in 2010, the average maximum footrope depth during fishing was 35 m. BASIS surface trawls occurred at regularly spaced stations. Surface target identification trawl locations were selected based on observed echosounder patterns.
Midwater target identification trawls (2008-2010) were used to identify observed acoustic patterns below the vertical sampling range of the surface trawl. For midwater trawls, floats were removed and net depth and opening were monitored in real time using a Simrad FS-70 sonar attached to the headrope of the trawl. Midwater trawl times varied between 5 and 57 minutes depending on fish densities observed on the echosounder and headrope sonar displays. Midwater target identification trawls were conducted at locations with bottom depths sufficient to safely trawl and selected based on echosounder patterns. Contamination of midwater trawl catch by surface species was assumed negligible.

Trawl catches were sorted to species, weighed, and sampled for length frequency distributions. If catch weight was 1 tonne (t) or less, the entire catch was processed. If the catch weight exceeded 1 t, then the entire catch was weighed and a ∼1 t subsample was randomly selected for sampling. Fork lengths of at least 50 individuals from each species or age-group (i.e. juvenile or adult) were measured to the nearest mm. Catches were divided into four classes: capelin, age-0 Pacific cod, age-0 pollock, and non-target fish species. Proportional catch composition was calculated for each trawl by dividing the number of fish in each class by the total number of non-salmonid fish in the catch.

2.4. Acoustic data analysis

2.4.1. Acoustic data processing

Acoustic data analysis was restricted to the use of 38 kHz data as the chartered fishing vessels were typically equipped with only 38 kHz echosounders (Table 1). Echoview 4.70 (Myriax Pty Ltd) was used to process all acoustic data. The ES-60 triangle wave error was removed prior to data processing (Keith et al., 2005). In the SEBS, sound speeds and absorption coefficients were set at 1470 m/s and 0.00998 dB/m. In the NEBS, where water column properties were more variable, sound speed and absorption coefficients were calculated using CTD data (range 1473-1482 m/s, 0.00992-0.00986 dB/m). Noise spikes and empty pings, where a transmitted pulse was not received due to vessel motion, were manually removed. Vessel noise levels (range -145 to -113 dB re 1 m⁻¹ @ 1 m across vessels and years) were estimated using passive data collections and removed from the acoustic data using linear subtraction (Watkins and Brierley, 1996; Korneliussen, 2000). Data cells that did not meet a 6 dB signal-to-noise ratio threshold were also removed from the analysis. Acoustic data near evening or morning crepuscular periods were only included if echogram patterns were consistent with daytime data. Across years, 73% to 100% of the acoustic transect data were collected during the daytime.

Data within 15 m of the surface were excluded from analysis to account for maximum transducer depth (9.15 m on the Oscar Dyson) and twice the near-field range of the 38 kHz transducers (2 × 2.54 m). The
seafloor was initially detected using the bottom detection algorithm in Echoview and then manually corrected. All data within 0.5 m of the corrected bottom were excluded from the analysis.

In 2008-2010, acoustic transect data between north-south BASIS stations in the SEBS and between east-west stations in the NEBS were used in analyses. In 2006 and 2007, when acoustic data collection was not included in the survey design and data quality was variable, any acoustic data (north-south or east-west) which had low vessel noise spikes in the water column were included in the analysis.

2.4.2. Depth zones

Patterns observed on the echosounder were combined with trawl sampling and bottom depth ranges to divide the study area into surface, midwater, and whole water column depth zones. These zones, while selected to facilitate data analysis, also enable comparisons between this study and previous characterizations of forage fish distributions.

The “surface zone” (15 to ~35 m, herein surface zone) was sampled by BASIS surface and surface target identification trawls. The upper edge of the surface zone was set to 15 m based on acoustic near-field constraints (Section 2.4.1.). In the stratified middle, outer, and off-shelf regions, high backscatter values were observed in an acoustically-detected shallow layer (c.f. Wolliez et al., 2012) typically associated with the mixed layer at 20 to 30 m depth (Ladd and Stabeno, 2012). The base of this acoustically-detected layer was set as the lower edge of the surface zone. A semi-automated edge detection routine, consisting of a 0.5 m vertical by 10 ping horizontal resample window, a -75 dB re 1 m⁻¹ (herein dB, MacLennan et al., 2002) S, minimum threshold, a Sobel edge detection operator (Gonzalez and Woods, 2007), and manual correction by an analyst were used to define the lower edge of the layer. When no layer was detected, the lower edge of the surface zone was set at 35 m based on the mean maximum fishing depths of the surface trawl (Section 2.3.). In much of the inner shelf, fish were dispersed between the surface and the bottom. Therefore this region was considered to be effectively sampled by the surface trawl, with the acoustic upper edge set to 15 m and the lower edge set to 0.5 m from the bottom (Section 2.4.1.). Acoustic estimates within the surface zone enable a comparison with previous characterizations of forage fish distributions based on surface trawl data.

The “midwater zone” (herein midwater zone), sampled using only midwater trawls, was defined from the lower edge of the surface zone to 0.5 m from the acoustically-detected bottom (Section 2.4.1.). As no midwater trawling was performed in 2006 and 2007, midwater zone fish density estimates in those years were not possible for any species except age-0 pollock (see Section 2.4.6). In this analysis, midwater
trawl catches were considered to be representative of species composition and length distributions within sampled regions and observed backscatter patterns. Sections of acoustic transects with backscatter patterns that were inconsistent with trawl sampled patterns were designated “unknown” and excluded from calculations. Unknown regions typically included near- or on-bottom aggregations that could not be sampled with the trawl, or midwater zone backscatter patterns consistent with sampled jellyfish. Acoustic estimates within the midwater zone represent a depth zone that has not been characterized in previous surface trawl studies and provides a comparison for previous studies using bottom trawl data.

The “water column zone” (herein water column zone) was defined from 15 m below the surface to 0.5 m above the acoustically-detected bottom (Section 2.4.1.). This zone combined information from the surface and midwater zones for all species in 2009-2010 (water column zone = surface zone + midwater zone). If backscatter from the midwater zone was classified as unknown, no water column zone estimate was made. Acoustic water column zone estimates provide a full water column distribution of pelagic forage fish that has not been previously reported.

2.4.3. Data threshold

To select appropriate volume backscatter thresholds (i.e. minimum $S_v$ values) that included forage fish and excluded jellyfish, sections of acoustic data from the 2008 field season were used as training sets to determine backscatter characteristics of forage fish (based on age-0 pollock) and jellyfish (dominated by Chrysaora melanaster). Acoustic target strengths of jellyfish species found in the northeast Pacific have not been fully documented. Using trawl catches to guide selection, regions of echograms that contained dense surface zone age-0 pollock (n = 52 regions), surface zone jellyfish (n = 99), or midwater zone jellyfish (n = 23) were identified. $S_v$ values from samples within each section were exported and a negative log likelihood function was used to generate a mean and standard deviation of $S_v$ values for surface zone age-0 pollock (-51.2 ± 9.7 dB) and jellyfish (-82.8 ± 8.6 dB), and midwater zone jellyfish (-86.3 ± 12.7 dB). Fitted curves, based on the negative log likelihood, for the three groups intersected at -67 dB. The -67 dB threshold was validated using data from 2009. Standard scores (i.e. $z$-scores) were used to compare areas of curves above or below the -67 dB intersection: 5.2% of the age-0 pollock occurred below the -67 dB intersection and 3.3% of the surface zone jellyfish and 6.4% of the midwater zone jellyfish occurred above the -67 dB intersection. The fish minimum $S_v$ threshold was set at -67 dB in all data sets. Backscatter < -67 dB was removed from the analysis to exclude jellyfish.
2.4.4. Horizontal distribution of fish backscatter

Fish area backscatter values \(s_A, \text{m}^2/\text{nmi}^2\), MacLennan et al., 2002) for surface zone and midwater zones were integrated and exported at the -67 dB threshold in 0.926 km (0.5 nmi) horizontal bins. Backscatter above -67 dB, but classified as unknown, was also exported to evaluate the amount of unclassified backscatter in the analysis. No additional vertical binning was applied. The average bottom depth within each 0.5 nmi bin was calculated.

2.4.5. Acoustic species proportions

A trawl-derived acoustic species proportion was calculated for each trawl using surface and/or midwater trawl catches. All pelagic species captured in the trawl were included in the calculations except salmon \((Oncorhynchus\ spp.,\ primarily\ juvenile,\ few\ immature\ or\ adult)\) and adult Pacific herring \((Clupea\ pallasii)\). These two groups were excluded as they were considered to be within the 15 m acoustic surface exclusion zone (Section 2.4.1) and not measured by the echosounder. As a check on this assumption, trawl catches from 12 paired surface and sub-surface (headrope 8 to 18 m) trawls during the 2008-2010 surveys were compared. Salmon were captured in 9 surface trawls, but in 0 sub-surface trawls. In the same 12 paired trawls, adult Pacific herring were captured in 5 surface trawls, but in 0 sub-surface trawls. Multiple analyst inspection of acoustic data in regions with high surface trawl catches of salmon or adult Pacific herring suggested that findings from the paired trawls were representative of the broader survey area.

For all pelagic species captured in trawls, an acoustic target strength was calculated from its measured length using a target strength versus length equation from the literature (Table 2). For fish lacking a species-specific equation it was necessary to use an equation from a similar species or a generalized equation. Target strength \((TS, \text{dB re } 1 \text{ m}^2, \text{herein dB, MacLennan et al., 2002})\) to length \((L, \text{cm})\) equations were identified for all non-salmonid fish captured in trawls (Table 2). The target strength (dB) for each fish was calculated and converted to linear echo amplitude \((\sigma_{bs}, \text{m}^2\text{where } \sigma_{bs} = 10^{TS/10}, \text{MacLennan et al.}, 2002)\)

Linear echo amplitudes were summed for each trawl (i.e. sum of \(\sigma_{bs}\) for all species, total echo amplitude) and for each species within the trawl (i.e. sum of \(\sigma_{bs}\) for each species, species echo amplitude). The trawl-derived acoustic species proportion for each trawl was then calculated by dividing the species echo amplitude by the total echo amplitude for the trawl.
2.4.6. Trawl assignments

Fish backscatter within each 0.5 nmi horizontal acoustic bin was assigned the trawl-derived acoustic species proportion from the nearest trawl location using a nearest neighbor function (ArcMap 10.0, ESRI Inc.). Only trawls that sampled the surface zone or midwater zone were used to partition backscatter within that zone. Since no midwater trawling was performed in 2006 or 2007, and only a single midwater trawl was performed in 2008, it was not possible to estimate midwater zone densities of capelin or age-0 Pacific cod. As midwater zone age-0 pollock were found in large aggregations in 2009-2010, scrutiny by three analysts was used to identify “analyst-based pollock” (herein analyst-based pollock) midwater zones in 2006-2008 that were consistent with echosounder patterns from 2009-2010. This approach assumed that echosounder patterns from 2009 and 2010 were representative of previous years and that if not, the introduced bias was small and consistent.

2.4.7. Species densities

Species backscatter ($s_A$) within 0.5 nmi horizontal bins was calculated by multiplying the total fish $s_A$ in each 0.5 nmi bin (Section 2.4.4.) by its assigned trawl-derived acoustic species proportion (Sections 2.4.5., 2.4.6.). This was then used to calculate final densities (fish/nmi$^2$) by dividing the species $s_A$ in each 0.5 nmi bin by a mean echo amplitude ($\sigma_{sp}$, m$^2$; derived from $\sigma_{bs}$ through the equation $\sigma_{sp} = 4\pi \cdot \sigma_{bs}$, MacLennan et al., 2002) for that species (Section 2.4.5.). Mean echo amplitudes were calculated for each year, to account for potential inter-annual differences in fish length, and were weighted by length measurements from trawl catches. Densities were calculated for the surface zone, midwater zone, and water column zone (surface zone + midwater zone).

2.4.8. Species distributions

Distributions of density (fish/nmi$^2$) in surface zones were plotted for capelin, age-0 Pacific cod, and age-0 pollock for 2006 to 2010. Midwater zone and water column zone densities were plotted for capelin and age-0 Pacific cod in 2009-2010. Midwater zone and water column zone densities were plotted for age-0 pollock in 2006-2008 using analyst-based pollock and for 2009-2010 from acoustic data validated using midwater trawl samples. Within the stratified middle, outer, and off-shelf regions, water column zone results were only plotted when estimates were available for both the surface zone and the midwater zone.

Minimum, maximum, and mean density values were calculated to facilitate comparisons among years and depth zones. For consistency among years, calculations were restricted to 0.5 nmi bins with bottom depths ranging from 20 to 200 m. Maximum density values were identified for all years (2006-2010) and depth zones (surface, midwater, water column). Minimum values were identified for the surface zone in all years (2006-2010), but for midwater and water column zones in only 2009-2010 as analyst-based
pollock estimates in 2006-2008 were biased against low densities. Mean densities, standardized by
bottom depth, were generated for the same zones and years in a three-step calculation. First, the bottom
depths within all 0.5 nmi horizontal bins (Section 2.4.4.) were classified into 10 m bottom depth
categories. Second, a mean for each bottom depth category was calculated. Finally, the mean density
was calculated by averaging the bottom depth category means. This standardization was necessary as
sampling effort across bottom depths was unequal within and among years. While this approach
standardized for sampling effort, it did not account for differences in survey extent, such as the limited
spatial distribution of acoustic data in 2006 or the lack of transects in bottom depths > 105 m in 2008, or
for potential shifts in species’ distributions outside the surveyed area.

2.4.9. Percentage of fish in the surface zone
The percentage of fish in the surface zone was calculated for middle, outer, and off-shelf using 0.5 nmi
bins that had density estimates for both the surface zone and the midwater zone. Percentage of shallow
fish was calculated by dividing the density of fish in the shallow zone by the density of fish in the water
column zone and multiplying by 100. Calculations were not performed for 0.5 nmi bins where midwater
zone backscatter was classified as unknown or for bins where the water column zone density of the
species of interest was zero. The mean percentage of fish in the surface zone was only calculated for
2009 and 2010, as analyst-based pollock estimates in 2006 and 2007 were biased high. Percentages of
surface zone fish were mapped to facilitate spatial comparisons. For comparison, values for the inner
shelf, where the percentage of surface zone fish was analytically-defined at 100% (Section 2.4.2.), were
also mapped.

3. Results
3.1 Trawling results
Four-hundred and eighty-one trawls were used to characterize species proportions and lengths in the
surface zone in 2006-2010, with 65 in 2006, 114 in 2007, 41 in 2008, 104 in 2009, and 157 in 2010 (Fig.
2). Additional BASIS surface trawls were conducted in 2006 (n = 86) and 2007 (n = 17), and are shown
in Fig. 2 to illustrate patterns in species distribution, but were not used in the acoustic analysis as they
were outside the area where acoustic data were available. 2008 had the highest mean surface zone
catches of jellyfish in the SEBS east of 170ºW (mean ± 1 standard deviation, 305 ± 883 kg/30 minute
tow, n=39) in the five data years, and was used to develop the volume backscatter threshold to exclude
jellyfish. Jellyfish mean catches were a factor of 2 to 6 lower in all other years. Non-target fish species
were captured in the trawls in all years: Atka mackerel (*Pleurogrammus monopterygius*), Bering wolfish
(*Anarhichas orientalis*), Pacific sand lance (*Ammodytes hexapterus*), Pacific sandfish (*Trichodon*
trichodon), prowfish (Zaprora silenus), rainbow smelt (Osmerus mordax dentex), threespine stickleback (Gasterosteus aculeatus aculeatus), and age-1+ pollock. Additional non-target fish species were found only in some years, likely influenced by survey extent: Arctic cod (Boreogadus saida, 2006, 2010), age-1+ Pacific cod (2006, 2007), ninespine stickleback (Pungitius pungitius, 2006, 2007, 2009), juvenile rockfish (Sebastes spp., 2006-2009), adult rockfish (2010), and saffron cod (Eleginus gracilis, 2006, 2007, 2009, 2010) (Fig. 2). Of the trawl locations and catches shown in Fig. 2, BASIS surface trawl results for fish have been summarized for some years (Moss et al., 2009; Hollowed et al., 2012; Hurst et al., 2012).

A total of 31 trawls were used to characterize species proportions and lengths in the midwater zone in 2008-2010, with 1 in 2008, 22 in 2009, and 8 in 2010 (Fig. 3). Limited midwater trawling effort in 2008 resulted from a compressed survey effort and a lack of midwater zone targets. In 2010 few trawls in the midwater zone were performed due to a lack of midwater zone targets. Age-0 pollock dominated the midwater catches, with non-target species including age-1+ pollock (2009), prowfish (2009), and Pacific sandfish (2009, 2010). Midwater zone jellyfish catches were similar to or less than surface catches in 2009 and 2010.

3.2. **Acoustic general results**

A total of 11,028.5 nmi (20,425 km), equivalent to 22,057 0.5 nmi horizontal bins, of acoustic transect data were collected in 2006-2010 (Table 1). The 2006 and 2007 data quality was variable, with sections of data omitted due to the presence of vessel noise spikes. The smallest acoustic dataset occurred during 2008 and did not include bottom depths > 105 m. Although 2006 had 1768.5 nmi of data, the entire study area is not represented as acoustic data were not recorded during sections of the survey. The number of 0.5 nmi bins that contained unknown backscatter in the midwater zone was 1093 (63% of all 0.5 nmi bins with a midwater zone, 2006), 2421 (81%, 2007), 1026 (100%, 2008), and 1998 (80%, 2010). Backscatter ($s_A$) values within these cells ranged from 1-14,637 (2006), 0.1-5486 (2007), 1-3226 (2008), and 0.1-2659 m$^2$/nmi$^2$ (2010). Of those cells containing unknown backscatter, the entire midwater zone was classified as unknown in 993 (2006), 2411 (2007), 1026 (2008), and 1633 (2010) 0.5 nmi bins. A total of 1286 regions within 0.5 nmi horizontal bins were identified as analyst-based pollock (743 in 2006, 543 in 2007, and 0 in 2008) and used in further analysis. The base of the acoustically-detected layer varied among years, from just below the 15 m acoustic surface exclusion line to a maximum of > 50 m (Fig. 4). Using only those 0.5 nmi horizontal bins where the layer was detected, and excluding those that were assigned to 35 m in the absence of a layer, 96% (2006, n = 716 total layer observations), 95% (2007, n = 1759),...
97% (2008, n = 1026), 63% (2009, n = 1505), and 78% (2010, n = 1826) of layer depths were less than or equal to the 35 m mean maximum footrope depth of the surface trawl (Fig. 4).

3.3 Forage fish densities and distributions

3.3.1. Capelin

Capelin were distributed across the surface zone of the study area in all years, but were primarily found in the middle shelf in the SEBS and the inner and middle shelves in the NEBS (Fig. 5). In all years, capelin were not detected in the surface zone of the outer shelf. In years with sampling in both the NEBS and SEBS, capelin were located in both regions. The highest single estimate of capelin density in the surface zone \((1.10 \times 10^8 \text{ fish/nmi}^2)\) occurred in the middle shelf in 2009. Mean surface zone densities during 2009 and 2010 (49,644 and 85,045 fish/nmi\(^2\)) were higher than in 2006-2008 (5844-11,230 fish/nmi\(^2\), Fig. 5).

Capelin occurred in the midwater zone out to the off-shelf region in 2009 and 2010, with the highest densities in the outer shelf region (Fig. 6). No direct comparison of 2009 and 2010 distributions is possible as large sections of the 2010 midwater zone were classified as unknown. The mean midwater zone density of capelin was higher in 2009 (76,263 fish/nmi\(^2\)) than in 2010 (10,687 fish/nmi\(^2\), Fig. 6).

Combining the surface and midwater zone estimates, high water column zone densities of capelin were found in the middle and outer shelf regions in 2009 (Fig. 7). While the 2010 distribution map is incomplete, high densities in that year also occurred in the middle, outer, and off-shelf regions (Fig. 7). The highest single water column zone density estimate \((1.10 \times 10^8 \text{ fish/nmi}^2)\) for capelin occurred at the same location as the highest surface zone estimate in 2009. The mean water column zone densities of capelin were similar between 2009 (118,732 fish/nmi\(^2\)) and 2010 (116,421 fish/nmi\(^2\), Fig. 7).

3.3.2. Age-0 Pacific cod

Age-0 Pacific cod in the surface zone were distributed across a wide range of bottom depths, with middle and outer shelf regions containing the highest densities (Fig. 8). While some age-0 Pacific cod were estimated in the NEBS, higher and more consistent surface zone densities occurred in the SEBS. The highest single surface zone density of age-0 Pacific cod \((7.48 \times 10^7 \text{ fish/nmi}^2)\) was observed in 2006 near the inner front. Age-0 Pacific cod were scarce in 2009 (Fig. 8). The highest surface zone mean density of age-0 Pacific cod occurred in 2010 (426,548 fish/nmi\(^2\)), with the lowest in 2007 (9667 fish/nmi\(^2\), Fig. 8). In the midwater zone, age-0 Pacific cod occurred primarily at the middle front or outer shelf region in 2009 (Fig. 6). While the 2010 midwater zone data are incomplete, high densities of age-0 Pacific cod...
were also found in the same regions. Mean midwater zone age-0 Pacific cod densities were higher in 2010 (120,888 fish/nmi$^2$) than in 2009 (495 fish/nmi$^2$, Fig. 6).

Combining surface and midwater zone density estimates, age-0 Pacific cod water column zone distributions in 2009 and 2010 were similar to surface zone distributions, with the highest densities occurring in the outer shelf and lower densities in the middle shelf (Fig. 7). As high densities of age-0 Pacific cod in the 2010 water column zone were observed on either side of unknown regions (where the midwater zone was classified as unknown), it is possible that the distribution was continuous across that area (Fig. 7). The highest single water column zone density of age-0 Pacific cod ($3.19 \times 10^7$ fish/nmi$^2$) occurred in the outer shelf in 2010. Mean water column zone densities of age-0 Pacific cod were higher in 2010 (610,310 fish/nmi$^2$) than in 2009 (64,177 fish/nmi$^2$, Fig. 7).

3.3.3. Age-0 pollock

Age-0 pollock within the surface zone were widely distributed in the survey area during all years, with the highest densities in the SEBS (Fig. 9). The maximum single age-0 pollock surface zone density observation ($5.77 \times 10^7$ fish/nmi$^2$) occurred in the middle shelf in 2006. The highest mean surface zone density for age-0 pollock was in 2006 (785,652 fish/nmi$^2$), with the lowest occurring in 2009 (13,109 fish/nmi$^2$, Fig. 9). Surface zone densities of age-0 pollock were similar in 2007, 2008, and 2010.

Age-0 pollock occurred in the midwater zone of the study area in 2006 (analyst-based pollock), 2007 (analyst-based pollock), 2009, and 2010 (Fig. 10). No analyst-based pollock regions were detected in the limited 2008 study area, but were observed in deeper water outside the study area (Parker-Stetter, unpublished data). The highest single density of midwater zone age-0 pollock was measured in the middle shelf in 2007 ($1.15 \times 10^8$ fish/nmi$^2$) northwest of St. Paul Island. Mean densities for midwater zone age-0 pollock were similar in 2009 (994,788 fish/nmi$^2$) and 2010 (972,078 fish/nmi$^2$, Fig. 10).

While maps of age-0 pollock water column zone distributions are fractured by unknown midwater zone data regions in 2006, 2007, and 2010 (Fig. 11), additional information can be gained from this partial dataset. In 2006 and 2007, water column zone distributions were similar to surface zone distributions as age-0 pollock in the surface zone were often coincident with midwater zone age-0 pollock (Fig. 11). The presence of high densities of midwater zone pollock in 2009 and 2010 weight the water column zone distributions to the outer and off-shelf regions (Fig. 11). The highest single water column zone estimate of age-0 pollock occurred in 2007 ($1.15 \times 10^8$ fish/nmi$^2$), at the same location as the highest midwater
zone density estimate. Mean water column zone densities of age-0 pollock were similar between 2009 (949,519 fish/nmi$^2$) and 2010 ($1.13 \times 10^6$ fish/nmi$^2$), Fig. 11).

3.4 Percentage of fish in the surface zone

Capelin were primarily found in the surface zone of the middle shelf in 2009 (mean 65%) and 2010 (mean 92%, Fig. 12). All capelin in the outer and off-shelf regions were observed in the midwater zone. With the exception of the off-shelf region in 2009, some age-0 Pacific cod were located in the surface zone of all shelf regions in 2009 and 2010 (17-100%, Fig. 12). More age-0 Pacific cod were located in the surface zone during 2010 than 2009. Age-0 pollock distribution patterns were similar to those of age-0 Pacific cod, but with lower overall percentages of fish in the surface zone (Fig. 13). Some fish were found in all regions of the surface zone in 2009-2010 (8-48%) with the exception of the off-shelf region in 2009 (Fig. 13). More age-0 pollock were located in the surface zone in 2010 (26-48%) than during 2009 (0-18%). Distributions and proportions of analyst-based pollock in 2006 and 2007 were similar, with low percentages in the surface zone of the outer shelf region (Fig. 13).

4. Discussion

This study provides annual estimates of densities and distributions of important EBS forage fish species in 2006 through 2010 using acoustic-trawl data collected during an existing survey. Even though acoustic transect layouts and midwater trawling strategies did not conform to a traditional acoustic survey design, distributions derived from these surveys are believed to be representative and can be used to compare observed distributions to those reported in previous studies.

Capelin were located in the surface zone in the inner and middle shelf regions in all years, with the highest densities in the SEBS. Resulting distributions were generally similar between the acoustic-trawl data in this study and characterizations based on bottom trawl (Hollowed et al., 2012) data, with the notable exception that highest capelin densities in the SEBS during 2007, 2009, and 2010 typically occurred in the middle and not the inner shelf. While the difference in locations, and associated water depths, may be attributed to differences in sampling dates (May-July for bottom trawl, August-October for acoustic-trawl), distributions of capelin based on “thermal gateways” predict high capelin densities to occur in the middle shelf during cold conditions (Ciannelli and Bailey, 2005), such as those during the present study and 2007-2009 in the Hollowed et al. (2012) study. Differences in distributions characterized using acoustic-trawl (i.e. surface and midwater) and bottom trawl data may be due to the proportion of the water column sampled and location of gear relative to capelin vertical distribution. In the inner shelf region, fish were typically distributed throughout the water column, potentially within the sampling range of bottom trawls. In contrast, in the middle, outer, and off-shelf regions, capelin were
located predominantly within the surface zone and would only be sampled by a bottom trawl during
deployment and retrieval. Acoustic-trawl data used in this study would exclude capelin within 0.5 m of
the bottom, which could result in density estimates of capelin being biased low within the inner shelf.
This potential bias cannot be quantified with our data. Capelin in the midwater zone occurred over a
larger area in 2009 than in 2010. As a result, capelin water column zone distributions differed from
surface zone distributions and from bottom trawl characterizations (Hollowed et al., 2012).

Age-0 Pacific cod were primarily distributed in the surface zone of the middle and outer shelf regions in
the SEBS. The surface zone distribution of age-0 Pacific cod has also been evaluated using BASIS
surface trawl data (Hurst et al., 2012). Distribution patterns in the two studies were expected to be similar
as the same surface trawl data were used to partition surface acoustic backscatter at, and between, surface
trawl stations in the present study. Analysis of the surface trawl (Hurst et al., 2012) and the acoustic-
trawl data identified low-density, limited distributions of age-0 Pacific cod in 2007 and 2009. The
reduced spatial extent of surface zone age-0 Pacific cod in 2008 (Hurst et al., 2012) may be due to the
limited survey area that year. In contrast age-0 Pacific cod densities in 2010, which were not evaluated in
Hurst et al. (2012), were the highest observed in all study years. The observed distribution in 2010 was
more similar to 2006 than any other year in the present study. In this study, midwater zone age-0 Pacific
cod contributed to water column zone densities in a limited area during 2009 and 2010. As high densities
of fish in the midwater zone typically occurred at the same location as high densities in the surface zone,
the resulting water column zone maps are similar to those generated using surface zone data only. There
is limited previous information on age-0 Pacific cod distribution in the SEBS, but shallow (typically < 40
m below the surface) trawls targeting age-0 pollock, also contained up to 5% age-0 Pacific cod in the
catch and age-0 Pacific cod were often spatially coincident with age-0 pollock (Bakkala et al., 1985;
Walters et al., 1988).

Distribution maps characterized age-0 pollock densities as being highest in the stratified middle and outer
shelf regions in all years. While the area around the Pribilof Islands has frequently been associated with
high densities of age-0 pollock (e.g. Walters et al., 1988; Traynor and Smith, 1996; Swartzman et al.,
2005), results from the present study suggest that high age-0 pollock densities were also observed on
transects throughout the SEBS in all study years. Our findings support observations that age-0 pollock in
surface waters were more abundant in layers within the middle and outer shelf regions (Bakkala et al.,
1985; Moss et al., 2009; Hollowed et al., 2012) than in the inner shelf (Miyake et al., 1996; Swartzman et
al., 2005). While age-0 pollock densities in surface waters have been described as being typically highest
in water < 120 m deep (e.g. Bakkala et al., 1985; Walters et al., 1988), we observed age-0 pollock out to
the shelf break (i.e. 200 m isobath) in 2006, 2007, and 2010. As the same surface trawl data were used to partition surface zone acoustic backscatter in the present study as in previous studies (Moss et al., 2009; Hollowed et al., 2012), distribution patterns near surface trawl stations were expected to be similar. The acoustic-trawl data collected between stations suggested that surface zone age-0 pollock distributions were generally continuous throughout the surveyed area, but that densities could vary by an order of magnitude between surface trawl stations. Our approach cannot account for potential shifts in species composition between stations as species composition was assigned to acoustic data based on the nearest trawl station. Net-based abundance indices that interpolate densities between stations may not account for spatial heterogeneity within the survey area domain.

While high densities of age-0 pollock were observed and captured in the surface zone, the present study suggested that fish in the midwater zone were also an important component of water column zone densities. High densities of midwater zone age-0 pollock occurred in 2006 and 2007 (analyst-based evaluation) and in 2009 and 2010 (survey data). As estimated midwater zone densities frequently exceeded surface zone estimates, the water column zone distribution maps of age-0 pollock differed from those generated using surface zone data only, and from other characterizations using only surface trawl data (e.g. Moss et al., 2009; Hollowed et al., 2012). In 2006, 2007, and 2010, midwater zone age-0 pollock increased overall water column zone densities, particularly in the outer and off-shelf regions. In 2009, a year with very low densities of surface zone age-0 pollock, midwater zone fish dominated the water column zone distribution. It is important to note that although age-0 pollock densities in surface waters may decrease in cold relative to warm years (as defined in Brodeur et al., 2002a; Moss et al., 2009), water column zone densities may remain stable in deeper water due to the presence of midwater zone age-0 pollock.

The presence of midwater zone age-0 pollock has been noted in previous studies, with position in the water column attributed to differences in fish lengths. During the day, fish shorter than 60 mm have been caught in shallow water, within or near the pycnocline (Bailey, 1989; Swartzman et al., 1999; Swartzman et al., 2002). Larger fish were typically located below the pycnocline, often migrating to the surface at night (Bailey, 1989; Swartzman et al., 2002). Miyake et al. (1996) hypothesized that age-0 pollock inhabit progressively deeper water as length increases. Brodeur and Wilson (1996) observed that the mean depth of capture for age-0 pollock in the Gulf of Alaska increased from July/August to October. Only Tang et al. (1996), working in the Aleutian basin and not on the EBS shelf, observed all age-0 pollock (with a mean body length of 40.2 mm) in deep water during the day migrated to the surface at night. We observed age-0 pollock above/within (surface zone) and below (midwater zone) the
pycnocline, often in the same location. While age-0 pollock lengths varied spatially, the largest fish were not typically found at the deepest depths, and lengths of surface zone and midwater zone fish were similar (Parker-Stetter, unpublished data). This observation suggests that the explanation for the vertical location of age-0 pollock in the SEBS is more complex than length alone.

The acoustically-detected layer was a consistent feature in all 2006-2010 datasets. The location of the layer was related to the oceanographic mixed layer depth (i.e. depth of the top of the pycnocline) through the function: Acoustically-detected layer depth base = 0.81 ∙ Mixed layer depth + 10.32 (R² = 0.59, n = 670, Parker-Stetter unpublished data). The 10.32 intercept approximates the upper limit of the 2 to 8 m late-summer pycnocline thickness range for 2006-2010 in the southern Bering Sea (Stabeno et al., 2012a). The pycnocline is a strong density gradient that separates surface and bottom water masses, each with different temperature, salinity, nutrients, and chlorophyll-a properties (Kachel et al., 2002). The aggregation of organisms near or within the pycnocline may be due to increased concentrations of phytoplankton or zooplankton prey. Using samples in June and July from the SEBS, Wolliez et al. (2012) describe this layer as containing pollock and euphausiids, likely jellyfish, and potentially fish larvae or macroplankton. Trawl samples in August to October suggested that the layer primarily contained larval and age-0 fish, age-1+ forage fish, and jellyfish. The potential contribution of macrozooplankton could not be evaluated. As suggested in Wolliez et al. (2012), a dedicated effort is needed to determine the composition and relative abundance of organisms within the layer.

Recognizing that all sampling gears and survey designs can bias data, we examine potential biases and caveats associated with our effort to characterize forage fish distributions. We consider the results from the present study to be robust and that any biases in the data do not obfuscate observed distribution patterns. As this work serves as an initial assessment of forage fish distributions in the EBS, discussion of assumptions and potential biases is prudent and will inform future use of these data and the design of additional studies.

The use of a single acoustic frequency for data collection necessitated a simplified analytic scheme that may have introduced bias from non-target organisms such as jellyfish. In the eastern Bering Sea jellyfish wet weight biomass can be more than 2 orders of magnitude greater than that of age-0 pollock (Schabetsberger et al., 2000; Brodeur et al., 2002b), and age-0 pollock are sometimes observed to be in association with the jellyfish, swimming among their tentacles during the day (Brodeur 1998). To minimize the contribution of jellyfish backscatter, the present study used areas of dense age-0 pollock and jellyfish backscatter in the development of our empirically-based -67 dB minimum threshold. Previous
studies of jellyfish within the genus *Chrysaora* have reported mean *in situ* target strengths at 38 kHz in the range of -63.9 dB (Graham et al., 2010) to -65.5 dB (Brierley et al., 2004) with potential changes > 10 dB due to variation in shape and orientation during swimming. This target strength variability complicates the selection of a single volume backscatter threshold. By limiting the analysis to strong backscatter regions, our intention was to bias fish estimates low. In cells where jellyfish backscatter exceeded the -67 dB threshold, that backscatter would have been included as fish backscatter and biased fish density estimates high. In contrast, in cells with low densities of fish and corresponding backscatter values less than -67 dB, those fish would have been excluded from the analysis, biasing fish density estimates low. As an additional filter, acoustic cells suspected of containing high jellyfish backscatter, based on scrutiny by three analysts, were labeled unknown and removed from the analysis. Jellyfish backscatter may also have been included in analyst-based pollock classifications for 2006-2008 survey data. If analyst-based classifications were incorrect, then spatial distribution of midwater zone age-0 pollock may be biased. The magnitude of the bias associated with jellyfish inclusion or fish exclusion cannot be quantified with available data, particularly since trawl retention of jellyfish and the vertical distribution of jellyfish are unknown. As the biomass and potentially packing densities of jellyfish in the EBS vary annually and may be influenced by sampling gear (e.g. Cieciel et al., 2012; Lauth and Hoff, 2012), testing the validity of a single volume backscatter threshold to exclude backscatter from jellyfish will require a dedicated study conducted across a range of jellyfish densities. We recommend that future projects focus on this issue using multi-frequency acoustic data and directed trawl samples to quantitatively evaluate the contribution of jellyfish to regions of backscatter that contain forage fish.

As target strength to length relationships were not available for all species of forage fish, it was necessary to use non-target equations in our analysis. The use of generalized equations or those from similar species may bias target strength estimates and the resulting acoustic partitioning, but were necessary when species-specific equations were not available. In some cases, equations were developed using larger specimens than those in the present study. Depending on the mismatch between the species or length range, the use of non-target, target strength to length equations may bias fish estimates low or high. In our approach, which used target strengths and trawl catch to proportion acoustic energy, an underestimate of the target strength of one species will affect density estimate of other species in the sample. In other words, the total acoustic proportions for a trawl sum to one, so underestimating one causes another to be overestimated. The potential for bias introduced by using non-target equations cannot be quantified. Dedicated development of target strength to length equations for EBS forage fish species is a daunting, but necessary analytic need for accurate density estimates.
Two assumptions enabled the use of surface trawl data as species verification samples for the partitioning of acoustic backscatter in the surface zone. With the exception of salmon and adult Pacific herring, it was assumed that fish in the surface zone were equally available to the echosounder below 15 m. This assumption was checked using surface and sub-surface paired trawls and inspection of acoustic echograms. If this assumption was not met, acoustic species composition could be biased and densities may be erroneously estimated for species caught in surface trawls, but not measured by the echosounder. If fish were vertically stratified within the surface zone, and the surface trawl did not sample the entire zone, then species proportions used in the acoustic analysis would be biased toward the shallowest species. We also assumed that contamination of surface trawl catches by fish below the acoustically-detected layer was negligible. No paired trawls were performed to validate this assumption as there was typically little backscatter immediately below the acoustically-detected layer on which to trawl. Visual inspection of echograms suggested that negligible contamination of surface trawls by midwater fish was likely a valid assumption. If this assumption was not met, then acoustic species compositions could be biased. Validation of these assumptions would require an analysis using fine-scale, depth-stratified trawling.

We assumed that trawl data adequately sampled forage fish species composition and length distributions. Retention of specific species or a restricted length range by a net may lead to selectivity biases (e.g. Nakashima, 1990; Godo and Sundanna, 1992; Williams et al., 2011). This assumption is common in trawl-based analyses and affects acoustic-based surveys using trawl catches to validate backscatter patterns. We did not assume that surface trawl data were representative of abundance, but that catch compositions were proportional to abundance. If the trawl did not proportionally sample species composition and lengths, then acoustic density estimates may be biased toward lengths or species that were captured in the trawl. This assumption could not be tested. Normal distributions of fish lengths and the retention of macrozooplankton (e.g. amphipods) suggest that the assumption was reasonable; however, estimates of species compositions and lengths from the trawl are uncertain. The catch composition of a similar midwater trawl was shown to be biased toward larger animals (Williams et al., 2011). A dedicated study of selectivity by the Cantrawl, as has been done for the Aleutian wing trawl (Williams et al., 2011), is needed to validate this assumption and to improve confidence in forage fish density estimates.

Time constraints during BASIS surveys limited the number of midwater trawls used to verify species composition and sample fish length distributions in 2008-2010. Areas where non-sampled midwater zone backscatter patterns did not match backscatter patterns that were sampled were classified as unknown and removed from analyses. While this approach reduced the size of midwater zone acoustic datasets (e.g. no
midwater zone estimate for 2008), it increased our confidence in species backscatter allocations based on available trawl data. Although visual classification of acoustic data is less desirable than validation using direct samples, comparisons of midwater zone age-0 pollock distributions across years are possible, given appropriate caveats. Future efforts to estimate midwater forage fish densities will require additional trawling effort for target verification, and depth-stratified trawling to validate assumptions about distribution homogeneity.

Although the present study surveyed much of the EBS shelf, the sample domain may not have included the entire range of forage fish distributions. Studies have reported observations of age-0 pollock in both shallower (e.g. Wilson et al., 1996) and deeper (e.g. Tang et al., 1996) water depths than those sampled in the present study. As densities of capelin, age-0 Pacific cod, and age-0 pollock in this study generally tapered off before the ends of survey transects were reached, it is likely that the 2006-2010 surveys covered a representative range of depths occupied by these species. Failure to capture the entire distributional range would result in a biased (low or high) estimate of mean density and a biased characterization of spatial distribution.

Despite the fact that survey durations ranged from 17 (2008) to 49 (2007, 2010) days, all distribution data were treated as a snapshot of forage fish densities in the southeastern Bering Sea. This assumption implies that there was no directional movement by fish that resulted in an over- or underestimate of any fish density (Simmonds and MacLennan, 2005). As the range of sampling dates varied across years, we also assumed that no date-related temporal changes in horizontal distributions or ontogenetic shifts in vertical distribution affected density estimates between years. This assumption is consistent with other fixed-date surveys.

The 2006-2010 surveys coincided with a period of average (2006) and cold (2007-2010) ocean temperatures in the eastern Bering Sea (Stabeno et al., 2012b). A comparison of fish vertical and horizontal densities across years suggested that temperature-related conditions may have influenced horizontal and vertical distributions. As predicted by “thermal gateways” (Ciannelli and Bailey, 2005), capelin were widely distributed in the surface zone and had the highest densities in the coldest years, 2009 and 2010. Both surface zone age-0 Pacific cod and age-0 pollock were absent from much of the surveyed areas in 2009, a year in which the temperature in the top 20 m was the coldest of the 2006-2010 period (Stabeno et al., 2012b). In 2010, surface zone age-0 pollock were concentrated near the Alaska Peninsula and Unimak Island rather than spread between the 50-100 m contours as they were in 2006-2008 and during the 2004-2005 warm years (Moss et al., 2009; Hollowed et al., 2012). Despite the limited
midwater zone observations, the highest densities of age-0 pollock, which dominated the biomass in 2009
and 2010, were found in deeper waters of the SEBS, likely outside the extensive cold pool (Stabeno et al.,
2012b). As distributions may be related to water temperatures, observed forage fish distributions in the
present study are thought to reflect average and cold year conditions, and may not be representative of
distributions during warm years.

Shifts in vertical and/or horizontal distributions by Bering Sea forage fish in response to water
temperature or other climate-related conditions must be considered when planning surveys and/or
analyzing existing data. While the present study did not include acoustic data from warm years, we
would predict that if forage fish vertical distribution shifts shallower in the water column, then acoustic-
based abundance indices may be biased low. Reduction of the acoustic exclusion zone below 15 m
reduces this potential bias. Given observed changes in the depth of the acoustically-detected layer within
and across years, surface trawl-based indices of abundances may be biased. Similarly, the presence of
high densities of midwater age-0 pollock suggest that surface trawl data alone will not characterize their
abundance and may not sample the bulk of the biomass in some years. This discrepancy is predicted to be
most severe during cold water conditions such as those observed in 2009 and 2010. The integration of
acoustic and trawl sampling is recommended to ensure accurate characterization of forage fish species
throughout the water column (e.g. McQuinn et al., 2005).

Understanding horizontal and vertical distributions of forage fish is needed to effectively manage the
Bering Sea ecosystem. Baseline distribution patterns from the present study quantify the 2006-2010
range of spatial distributions and densities under cold and average water temperatures. When combined
with previous observations during warm years, it is possible to begin to evaluate potential influences of
climate-related physical and biological factors on distributions, recruitment, and potential competition
among forage fish species in the EBS.

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represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA. This paper is NPRB publication number 420 and BEST-BSIERP Bering Sea Project publication number 97.

References


**Figure Legends**

Fig. 1. Survey extents for 2006-2010. Bathymetric contours and the corresponding shelf regions referred to in the text are labeled. Inset map shows the location in Alaska, U.S.A.

Fig. 2. Catch composition for trawls that sampled the surface zone in 2006-2010. Proportional catches of focal and non-target species are shown.

Fig. 3. Catch composition for trawls that sampled the midwater zone in 2008-2010. Proportional catches of focal and non-target species are shown.

Fig. 4. Distribution of the depth of the base of the acoustically-detected layer in 2006-2010.

Fig. 5. Surface zone densities (fish/nmi$^2$) of capelin in 2006-2010. Minimum (Mn), mean (Me), and maximum (Mx) densities, based on 20-200 m bottom depths, are shown. The number of 0.5 nmi bins (#) and % zero values (% 0) used in the calculations of Mn, Me, and Mx are listed in the inset table.

Fig. 6. Midwater zone densities (fish/nmi$^2$) of (A) capelin and (B) age-0 Pacific cod in 2009 and 2010. Sections of transects classified as unknown are identified. Minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.

Fig. 7. Water column zone densities (fish/nmi$^2$) of (A) capelin and (B) age-0 Pacific cod in 2009 and 2010. Bins where a water column zone estimate could not be made (midwater zone was unknown) are identified. Minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.

Fig. 8. Surface zone densities (fish/nmi$^2$) of age-0 Pacific cod in 2006-2010. Minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.

Fig. 9. Surface zone densities (fish/nmi$^2$) of age-0 pollock in 2006-2010. Minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.

Fig. 10. Midwater zone densities (fish/nmi$^2$) of age-0 pollock in 2006-2010. Sections of transects classified as unknown are identified. When calculated, minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.
Fig. 11. Water column zone densities (fish/nmi²) of age-0 pollock in 2006-2010. Bins where a water column zone estimate could not be made (midwater zone was unknown) are identified. When calculated, minimum (Mn), mean (Me), and maximum (Mx) densities and inset table as in Fig. 5.

Fig. 12. Percentage of (A) capelin and (B) age-0 Pacific cod in the surface zone in 2009 and 2010. Inner shelf bins, where the percentage is analytically defined at 100%, are shown for reference. Mean percentages for middle (Mid), outer (Out), and off-shelf (Off) regions are given with number of 0.5 nmi bins included in the calculation (#).

Fig. 13. Percentage of age-0 pollock in the surface zone in 2006-2010. Inner shelf bins, where the percentage is analytically defined at 100%, are shown for reference. Mean percentages for middle (Mid), outer (Out), and off-shelf (Off) regions are given with number of 0.5 nmi bins included in the calculation (#) are shown when calculated.
Fig. 1. Survey extents for 2006-2010.
Fig. 2. Catch composition for surface trawls, 2006-2010.
Fig. 3. Catch composition for midwater trawls, 2008-2010.
Fig. 4. Depth of the acoustically-detected layer, 2006-2010.
Fig. 5. Surface zone densities of capelin, 2006-2010.
Fig. 6. Midwater densities of capelin and age-0 Pacific cod, 2009-2010.

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Fig. 7. Water column densities of capelin and age-0 Pacific cod, 2009-2010.
Fig. 8. Surface zone densities of age-0 Pacific, 2006-2010.
Fig. 9. Surface zone densities of age-0 pollock, 2006-2010.

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Fig. 10. Midwater densities of age-0 pollock, 2006-2010.
Fig. 11. Water column densities of age-0 pollock, 2006-2010.
Fig. 12. Percentage of capelin and age-0 Pacific cod in the surface, 2009-2010.
Fig. 13. Percentage of age-0 pollock in the surface zone, 2006-2010.

- **2006**
  - Age-0 pollock
  - NEBS
  - SEBS
  - 200 m
  - Calculation used analyst-based pollock

- **2007**
  - NEBS
  - SEBS
  - 200 m
  - Calculation used analyst-based pollock

- **2008**
  - NEBS
  - SEBS
  - 200 m
  - Calculation used analyst-based pollock

- **2009**
  - NEBS
  - SEBS
  - 200 m
  - Mid 18% (1215)
  - Out 8% (717)
  - Off 0% (90)

- **2010**
  - NEBS
  - SEBS
  - 200 m
  - Mid 48% (58)
  - Out 26% (710)
  - Off 47% (87)

Percent of fish in surface zone:
- 0 - 25%
- 26 - 50
- 51 - 75
- 76 - 100
- 100% (analytically defined)
- No age-0 pollock present
- Unknown
**Table 1. Survey, vessel, and acoustic summary**

Survey dates, vessel, Simrad transducer model, transducer input power (Power, W), and amount of acoustic transect data (Dist, nmi) for 2006-2010 surveys.

<table>
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<th>Transducer</th>
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<th>Dist (nmi)</th>
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Chapter 2. Factors affecting summer distributions of Bering Sea forage fish: comparing hypotheses

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Abstract

Hypotheses on how physical, biological, and climate-related factors affect forage fish distributions are commonly proposed but rarely evaluated using a comprehensive suite of variables. Using 24 predictor variables, we tested hypotheses and calculated average models for Bering Sea capelin, age-0 Pacific cod, and age-0 pollock in 2006-2010. Distribution was evaluated with a two stage approach: presence/absence and density when fish were present. Local hypotheses/variables varied within and among years and evaluated whether distributions were related to conditions at individual stations. Annual variables were constant within but varied among years, accounting for the possibility that distributions were random but that overall presence/absence or densities changed with annual conditions. One regional variable, distance to the location of preflexion larvae earlier in the year, was evaluated for age-0 pollock. Capelin distributions were best predicted by local variables such as bottom depth, temperature, and salinity. Conversely, annual climate (May sea surface temperature (SST), sea ice extent anomaly) and wind (June wind speed$^3$) variables were often important for age-0 Pacific cod in addition to local variables (temperature and depth). Surface, midwater, and water column age-0 pollock distributions were best described by a combination of local (depth, temperature, salinity, zooplankton) and annual (May SST, sea ice anomaly, June wind speed$^3$) variables. Our results corroborated some previous hypotheses but suggested that in some cases, the overall presence/absence or density of forage fish may be more closely related to annual variables than to local ones. Ultimately, the collective understanding of what factors affect forage fish distributions in the Bering Sea may not be as complete as previously thought.

Keywords: capelin, walleye pollock, Pacific cod, distribution, information theoretic approach, Bering Sea
Introduction

There is increased recognition that forage fish are a critical part of aquatic ecosystems (Pikitch et al., 2012). This is particularly true in marine systems where a limited number of forage fish species may support an abundant and diverse group of upper trophic predators (Bakun et al., 2006). The increased focus on ecosystem-based resource management (e.g., Christensen et al., 1996; McLeod et al., 2005) suggests that forage fish management benefits both fisheries and ecosystem health (Smith et al., 2011; Pikitch et al., 2012). Yet increased efforts to enumerate forage fish as potential targets of commercial fisheries and as prey to upper trophic level predators have not greatly increased our knowledge of what factors influence distributions and dynamics of forage fish.

Forage fish distributions have been linked to physical, biological, and climate-related conditions across global marine ecosystems (e.g. Maravelias et al., 2000; Paramo et al., 2003; Bellido et al., 2008; Hollowed et al., 2012). The continued interest in defining essential fish habitat (e.g. Valavanis et al., 2008; Johnson et al., 2012) and predicting ecosystem responses to climate change (e.g. Doney et al., 2012; Fernandes et al., 2013), underscores the importance of understanding how spatial and temporal variability influence the distribution and abundance of forage fish.

In the southeastern Bering Sea (SEBS), the environment varies spatially and is influenced by annual climate conditions. The broad continental shelf is characterized by three domains: inner (well-mixed, ~ < 50 m bottom depth), middle (stratified 2-layer, ~50-100 m bottom depth), and outer (3+ layer with well mixed surface and bottom layers, ~100-200 bottom depth) (Kinder & Schumacher, 1981; Coachman, 1986; Sigler & Harvey, 2013). The three domains retain characteristic oceanographic properties (Kinder & Schumacher, 1981; Coachman, 1986), but boundaries between domains and characteristics within domains vary among years (cf. Kachel et al., 2002; Stabeno et al., 2012a). One biologically-relevant, physical factor that influences domain boundaries is a cold (<2°C) pool of bottom water that varies in spatial extent among years (Stabeno et al., 2001; Sigler et al., 2011; Zhang et al., 2012). The southern extent of the cold pool reflects the extent of sea ice the prior winter/spring. A warming trend and a reduction in sea ice, as predicted by the Intergovernmental Panel on Climate Change (Hollowed et al., 2009), will potentially alter habitat available for both demersal and pelagic fish (Mueter & Litzow, 2008; Spencer, 2008; Stabeno et al., 2012b), and ultimately affect the balance between benthic and pelagic productivity (Hunt & Stabeno, 2002). Understanding how environmental factors influence the distribution of SEBS forage fish will inform management of forage fish stocks, and upper trophic level species that depend on forage fish as prey.
Numerous relationships between SEBS forage fish distributions and the environment have been hypothesized and/or tested in the literature. Studies have inferred, but not directly tested, that temperature (Miyake et al., 1996; Moss et al., 2009), proximity to fronts (Schabetsberger et al., 2003; Swartzman et al., 2005), extent of the cold pool (Wyllie-Echeverria & Wooster, 1998), and zooplankton abundance (Swartzman et al., 2002) may influence forage fish distributions. Other studies have statistically evaluated relationships using a subset of explanatory variables, suggesting that EBS forage fish distributions are related to bottom depth (Brodeur et al., 1999; Hollowed et al., 2012; Hurst et al., 2012), temperature (Brodeur et al., 1999; Ciannelli & Bailey, 2005; Hollowed et al., 2012; Hurst et al., 2012), prey abundance and/or overlap with predators (Swartzman et al., 1999; Ciannelli et al., 2002; Winter & Swartzman, 2006; Winter et al., 2007), habitat energetics (Ciannelli, 2002); cohort size (Hurst et al., 2012), thermal regime (Ciannelli & Bailey, 2005; Hurst et al., 2012), and latitude (Hurst et al., 2012).

With the addition of proximity to the capture location of egg or larval stages earlier in the year (Hinckley et al., 1991; Brodeur & Wilson, 1996) and ocean current speed (Wilson, 2009), similar explanations for environmental influences on forage fish distributions have been proposed for the Gulf of Alaska (Wilson et al., 1996; Wilson, 2009). Such relationships, combined with annual climate indices, have been extended to evaluate forage fish condition and recruitment (Bond & Overland, 2005; Mueter et al., 2006; Coyle et al., 2011; Hunt et al., 2011; Mueter et al., 2011). Most of these studies found relationships between the variables they evaluated and the distribution of forage fish. But because each study used different datasets with non-overlapping sets of explanatory variables, it is difficult to determine whether significant variables in one study are more, less, or equally useful for predicting the presence/absence or density of forage fish. To address the mismatch between studies, we use a large, comprehensive dataset to simultaneously evaluate the importance of local, annual, and regional variables that are thought to influence the distributions of forage fish in the EBS.

Given the large number of potential explanatory variables used in previous studies, we adopted an information-theoretic hypothesis comparison approach to evaluate the influence of predictor variables on forage fish distributions. The information-theoretic approach to model selection has been advocated in the literature as an alternative method that avoids many of the biases inherent to traditional model selection procedures (Burnham & Anderson, 2002). Traditional model selection methods, such as stepwise regression, have several shortcomings: they ignore uncertainty in choosing a model, produce biased parameter estimates, and use a large number of null-hypothesis significance tests (NHST), which inflate the probability of Type-I error (Whittingham et al., 2006). The information-theoretic approach circumvents these problems by using a filter criterion such as Akaike’s information criterion (AIC, Akaike, 1974) to compare a small set of models selected a priori, thereby reducing the number of
variables and/or models whose utility is hard to measure or are biologically-meaningless (Burnham &
Anderson, 2002). The results can then be used to guide robust inference and prediction based on model
averaging.

In this study, we evaluate how physical, biological, and climate-related factors influenced spatial
distributions of forage fish species in the SEBS from 2006-2010. Our specific objectives were to:

1. Compare *a priori* hypotheses on relationships between local, annual, and regional variables and
   the distributions of capelin (*Mallotus villosus*), age-0 Pacific cod (*Gadus macrocephalus*), and
   age-0 walleye pollock (*Theragra chalcogramma*, herein pollock),

2. Construct an average model from an exhaustive set of possible variable combinations, enabling
   multimodel inference and assessment of the relative importance of individual variables, and

3. Compare well-supported hypotheses and model-averaging results with assumed and previously-
published characterizations of forage fish distributions

**Methods**

**Survey design and study area**

Data were collected in the eastern Bering Sea as a part of the 2006-2010 Bering Aleutian Salmon
International Survey (BASIS). Chartered fishing vessels (2006-2010, FV Sea Storm, FV Northwest
Explorer, FV Epic Explorer) or the NOAA ship Oscar Dyson (2008-2010) were used to collect data
between August and October (cf. Table 1 in Parker-Stetter *et al.*, 2013) of each year. Survey extent and
station spacing varied among years (Fig. 1).

**Oceanographic data collection and processing**

Oceanographic data were collected using Sea-Bird Model 25 or Sea-Bird Model 9 (Seabird Electronics,
Bellevue, WA) Conductivity-Temperature-Depth (CTD) sensors with a chlorophyll a fluorometer (Wet
Labs Wet Star) calibrated with discrete chlorophyll a samples. Water column casts to 5-10 m from the
bottom were made at all station locations in 2006-2010 (Fig. 1). Downcast data were checked for errors
and all variables were averaged into 1 m vertical bins.

The Rossby radius (R) was used to estimate the horizontal distance from each CTD cast location; within
the Rossby radius water properties were assumed homogeneous (cf. Alenius *et al.*, 2003). The two-layer
Rossby radius of deformation (Rossby, 1938; Gill, 1982) was calculated for each CTD cast station as:

\[ R = \sqrt{gD/f} \]
where, $D$ is the depth (in m) of the upper layer, $f$ is the Coriolis parameter (s$^{-1}$), and $g'$ is the reduced gravity, given by:

$$g' = \frac{g (\rho_2 - \rho_1)}{\bar{\rho}}$$

where $g$ is the acceleration due to gravity (m s$^{-2}$), $\rho_1$ and $\rho_2$ are the mean densities (kg m$^{-3}$) in the upper and lower layers, and $\bar{\rho}$ is the mean density (kg m$^{-3}$) over the whole water column.

**Zooplankton collection and processing**

A 0.1 m$^2$ Juday net with 168 μm mesh was used to sample small zooplankton biomass. A vertical tow, from near bottom to the surface at a rate of 1 m s$^{-1}$, was completed at each station. Three sieves (0.5, 1.2, 3-4 mm mesh) were used to separate the sample into small (<0.5 and <1.2 mm) and large (>3-4 mm) size fractions. The entire large fraction was counted, a Bogorov chamber was used to count the small size fractions, the abundance estimate was corrected for net avoidance, and density was scaled to biomass using values from the literature (Volkov, 1996; Volkov et al., 2007; cited in Coyle et al., 2011).

A pair of 60 cm, 505 μm mesh bongo nets was used to sample large zooplankton biomass at each station. Double oblique tows were conducted from near bottom to the surface at a rate of 1 m s$^{-1}$ and volume of water filtered was measured using a flowmeter (General Oceanics, Miami, FL). A 5% formalin/seawater solution was used to preserve samples. Specimens were processed according to Coyle et al. (2008), identified to the lowest taxonomic stage (genus or species), and weighed (wet weight, g). Zooplankton biomass (grams wet weight m$^{-3}$) was calculated for each sample, not including euphausiids as they were not effectively sampled by this method (Coyle et al., 2011).

**Acoustic data collection and processing**

Acoustic density estimates (fish nmi$^{-2}$) of capelin, age-0 Pacific cod, and age-0 walleye pollock were taken from Parker-Stetter et al. (2013). Density estimates were available for three vertical sampling zones: “water column” was defined from 15 m depth to 0.5 m above the bottom; “surface” was defined from 15 m depth to the base of the pycnocline-associated layer in the stratified middle and outer domains and from 15 m depth to 0.5 m above the bottom within the inner domain, and; “midwater” was defined from the base of the pycnocline-associated layer to 0.5 m above the bottom in the middle and outer domains (Parker-Stetter et al., 2013). Density estimates were based on measurements by a Simrad (Kongsberg Underwater Technology Inc., Lynnwood, WA) EK-60 38 kHz split- or single-beam
echosounders and targeted trawling for species identification using a surface or midwater trawl (see Parker-Stetter et al., 2013 for details).

We identified all 0.5 nmi acoustic horizontal bins whose midpoint was within estimated Rossby radii from CTD stations. Only those CTD stations that had coincident zooplankton information available at the time of analysis were used. Density estimates for surface capelin, age-0 Pacific cod, age-0 pollock, midwater age-0 pollock, and water column age-0 pollock within those 0.5 nmi bins were included in our analysis (cf. Parker-Stetter et al., 2013 for density calculations). As acoustic data were not available within the Rossby radius of all CTD stations, some locations were not used in the analysis.

**Hypothesis models**

*A priori* hypotheses were generated to characterize potential relationships between local, annual, and regional factors and forage fish distributions (viz. Burnham & Anderson, 2002). We assumed that our 2006-2010 data represent snapshots of forage fish distributions, without spatial reference. We also assumed that the relationships between factors and fish presence/absence and density say something about the “true” physical-biological processes that generated that observed distribution of fish. All of our models are heuristic approximations of the true processes.

A preliminary analysis of the data showed that forage fish distributions were patchy, containing both dense aggregations and gaps between aggregations (i.e., zero-inflation and right-skew). To incorporate these distribution characteristics in the analysis, we used a two-stage approach: hypotheses were evaluated for both fish presence/absence and for density of fish when fish were present (Stefánsson, 1996; Hollowed et al., 2012). In this context, both presence/absence and density may represent preference and/or survival under a given set of conditions. Density also serves as a relative index of abundance.

Ten hypotheses were common to capelin, age-0 Pacific cod, age-0 pollock and an eleventh was added for age-0 pollock (Table 1). Hypotheses are shown in the text in **bold italics**. These hypotheses address local, annual, and regional conditions.

Local hypotheses. Hypotheses included depth and physical/biological oceanographic factors, which varied within and among years. The *Depth* hypothesis evaluated the idea that forage fish occur over a predictable range of bottom depths, regardless of oceanographic conditions. The *Water Column* and *Stability* hypotheses represented the notion that forage fish occur in predictable oceanographic conditions. The *Total Prey*, *Prey Groups*, *Energetics*, and *Predators* hypotheses represented the idea that forage fish
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are found where prey or predator conditions were favorable. The \textit{Comfort} hypothesis represented the idea that forage fish are associated with predictable oceanographic, prey, and predator conditions (Table 1). These hypotheses account for the possibility that presence/absence and density depend on physical or biological conditions at an individual station.

Annual hypotheses. Hypotheses included climate/wind factors that were constant within but vary among years. The \textit{Climate} hypothesis represented the perspective that forage fish were more likely to be present and abundant under specific climate conditions. Similarly, the \textit{Wind} hypothesis represented the idea that favorable wind conditions resulted in more abundant and widespread forage fish (Table 1). These hypotheses can be seen as “null” models, which account for the possibility that distributions are random but that overall presence/absence or density depends on annual factors.

Regional hypothesis. The final hypothesis, \textit{Early Life Stage}, was evaluated only for age-0 pollock (Table 1). This hypothesis accounts for the possibility that age-0 pollock presence and density are highest near the last measured location for preflexion larvae earlier in the year.

\textbf{Predictor variables}

Variables used in hypotheses were selected to be representative of conditions at individual locations, while limiting collinearity among variables. From an initial set of 47 potentially important variables, a principal component analysis and evaluation of correlation matrices within each hypothesis were used to identify and remove collinear variables. If two variables within a hypothesis were correlated >0.90, one variable was eliminated. Final hypotheses were based on a reduced set of 23 predictor variables and an additional variable for age-0 pollock (Table 1). Calculation details are provided for variable groups with abbreviated variable names shown in the text in \textbf{bold}.

Local variables. Local variables reflected conditions at individual locations. Bottom depth (\textit{Depth}) was the mean depth within the 0.926 km (0.5 nmi) horizontal acoustic bin. The $\textit{Depth}^2$ term was also included to account for the possibility that fish abundance was highest at an intermediate depth rather than increasing monotonically towards shallow or deep water. Depths can be characterized as belonging to Bering Sea oceanographic domains (Sigler & Harvey, 2013).

Eight oceanographic variables were derived from CTD cast data at each station. The mixed layer depth was identified as the region where water density was within 0.2 kg/m$^3$ of the surface value (the average density within the top 10 m). Mean values were taken above and below the mixed layer for temperature
(TempAbove, TempBelow) and salinity (SalAbove, SalBelow). Above/below and surface/bottom measurements were highly correlated (>0.95), so above/below values were used in models as fish densities occurred within the water column, not at the water surface or bottom interfaces. Water column stability (WC-Stab) was calculated using the potential energy anomaly $\varphi$ (J m$^{-2}$, Simpson, 1981):

$$\varphi = \frac{1}{h} \int_{-h}^{0} (\bar{\rho} - \rho) gz \, dz$$

where $\rho$ is density, $\bar{\rho}$ is mean density through the water column, $g$ is gravity, and $h$ is water depth. This quantity represents the energy (per unit area) required to fully mix a stratified water column.

Chlorophyll-a (Chlor-a) was taken as the mean concentration of chlorophyll-a ($\mu$g L$^{-1}$, calculated from calibrated CTD fluorescence data) in the top 50 m of the water column.

Zooplankton biomass (grams wet weight/m$^3$) from each station was square root transformed to reduce the influence of a few large values. Species were classified in large and small categories following Eisner et al. (2013). Total biomass was calculated for small (SmZoops) and large (LgZoops) species. Species were also broken into copepods (SmCope, LgCope), chaetognaths (LgChaet), and other (SmOther, LgOther) based on diet preferences of age-0 pollock (Coyle et al., 2011). Using cold-year lipid contents for large and small copepods (Heintz et al., 2013), PreyEnergy was calculated as an index of potential available energy at a station as:

$$\text{PreyEnergy} = \text{SmCope} \cdot \text{lipid content small copepods} + \text{LgCope} \cdot \text{lipid content large copepods}$$

An index of predator density (Preds) was calculated using summer (June-August) bottom trawl data for age-1+ pollock from 1982-2011 (data were prepared by Matt Baker, NOAA Alaska Fisheries Science Center, Seattle, WA). A map of data grids and explanation of methods are presented in Baker & Hollowed (in revision). Predator catch-per-unit-effort (CPUE) was calculated for each bottom trawl station and stations were then separated into 10 m bottom depth bins and 0.1°C bottom temperature bins. CPUE was then averaged within depth-temperature bins and a generalized additive model (GAM, Hastie & Tibshirani, 1986) was fit to the data using log(CPUE + 1) as the response variable; with a tensor smooth of temperature and depth as the predictor variable. The fitted model was used to predict Preds at
each station based on TempBelow and Depth attributes. Antilogs of the calculated Preds values were used in model fits for the hypotheses.

Annual variables. Three annual climate variables were used as indicators of ocean conditions. All of our data were collected during “cold” ocean conditions (Stabeno et al., 2012a). Pre-bloom May sea surface temperature (MaySST) and the anomaly of sea ice extent (SeaIce) values were taken from the NOAA Bering Climate website (http://www.beringclimate.noaa.gov/data/index.php) for all years in the study. The day of year on which the percentage of ice cover in the northern portion of the study area (169-171°W, 57-60°N) dropped below 20% (Ice20%) was calculated using National Snow and Ice Data Center special sensor microwave/imager data (data were prepared by Sigrid Salo, NOAA-Pacific Marine Environmental Laboratory, Seattle, WA).

Three annual wind variables, as indicators of potential productivity, were calculated for 2006-2010: Mean wind speed cubed (an estimate of wind mixing) in June (JuneWind$^3$) and July (JulyWind$^3$) were used as proxies for annual storminess (Stabeno et al., 2004). The third variable was the percentage of time in upwelling-favorable winds which is linked to onshore and offshore flows (see Danielson et al., 2012 for details) between October (of the previous year) and April (%UpOctApr). Wind data were calculated using the 3-hourly NARR model hindcasts (http://www.emc.ncep.noaa.gov/mmb/rreanl/, data were prepared by Seth Danielson, University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, AK).

Regional variable. Distance from each observation to the mean location of preflexion larvae capture in cold years (Smart et al., 2012) (Preflex) was used as a variable in this analysis. As all early life stages (egg, yolksac larvae, late-larvae, and juveniles) cold-year loci were highly correlated (>0.95), the preflexion stage was selected based on consultation with Smart et al. (2012) coauthors. Mean early life stage locations were not available for capelin or age-0 Pacific cod.

Hypothesis model comparison for presence/absence and density

A two-stage model approach was used (Stefánsson, 1996; Hollowed et al., 2012). Presence/absence was modeled using a generalized linear model (GLM, cf. McCullagh & Nelder, 1989) with a logistic link function and a binomial error structure. Density was log-transformed and modeled using a Gaussian linear model, since non-zero fish densities were approximately lognormally distributed.

Hypotheses were compared using an information-theory approach (Burnham & Anderson, 2002). We used the small-sample version of AIC (AICc, Hurvitch & Tsai, 1989) as our model filter criterion. For
each hypothesis, we fit the corresponding model using maximum likelihood and then calculated its delta-
AIC\_c value (Δ\_i), the difference between its AIC\_c value and the best hypothesis/model in the set of
hypotheses/models, as well as its Akaike weight (w\_i, Burnham & Anderson, 2002). The Akaike weight
for model \( i \) is that model’s likelihood divided by the sum of the likelihoods of all \( R \) models in the
hypothesis set. Because the likelihood is proportional to \( \exp(-0.5 \Delta_i) \), Akaike weights were computed as:

\[
W_i = \frac{e^{-0.5 \Delta_i}}{\sum_{r=1}^{R} e^{-0.5 \Delta_r}}
\]

Each Akaike weight represents the probability of that model being selected as the best one if the model
selection was conducted with new data (Whittingham et al., 2006). Both presence (binary 0, 1) and
density (numeric, fish nmi\(^{-2}\)) models were fit for each hypothesis, using the R language’s glm() function
(R Development Core Team, 2011). To assess goodness-of-fit, we also calculated an R\(^2\) value for each
model fit. For the binomial presence/absence models, where R\(^2\) values based on the residual sum of
squares cannot be calculated, we used McFadden’s (1974) pseudo-R\(^2\), based on the likelihood ratio of the
fitted and null models. We determined which hypothesis model was the ‘best’ and which models were
included in the cumulative 90, 95, and 99% confidence sets to estimate the probability that the best
approximating model occurred within that set of models (Johnson & Omland, 2004).

**Full model selection for presence/absence and density**

As a post-hoc exploratory analysis, we repeated the procedure above on an expanded set of models that
included every possible combination of up to 5 variables (the greatest number included in any of our
hypotheses). This set of models was used to calculate an average coefficient for each of the 24 variables.
If the estimated coefficient for variable \( k \) in model \( i \) is \( \hat{\theta}_{ki} \), then the average coefficient for variable \( k \) is

\[
\bar{\hat{\theta}}_k = \sum_{i=1}^{R} W_i \hat{\theta}_{ki}
\]

The goodness-of-fit of the average models was calculated and compared with the hypothesis models. We
also calculated variable relative importance weight for each variable, where the importance weight was
calculated as the sum of the Akaike weights of all models in which the variable occurs, divided by the
number of models in which it occurs. Within each hypothesis set, variables were normalized by the most
important variable, so that all values range between 0.00 and 1.00 and they can be compared. Species-specific distributions and densities predicted by average models were compared with observed data.

Results

Data summary

Forage fish densities were available within the Rossby radii of 264 CTD cast locations during 2006-2010 surveys (Table 2). The highest number of CTD locations (n=86) occurred in 2009 and the lowest were in 2006 (n=30) and 2008 (n=31). In the surface zone, 1,356 of the 0.5 nmi acoustic bins were located within the radii of 264 CTD casts, 401 of the 0.5 nmi acoustic bins occurred within the radii of 63 CTD casts in the midwater zone, and 952 of the 0.5 nmi acoustic bins were within the radii of 193 CTD casts in the water column zone (Table 2).

Hypothesis models and model-averaged prediction for presence/absence and density

Hypothesis model results listed in Tables C, E, and G include the metrics Delta AICc, Akaike weights, R-squared values, and inclusion in the 90, 95, or 99% confidence sets. Model-averaged prediction results in Tables D, F, H, I, and J include the mean linear regression coefficient, standard error, and the standardized (0.00-1.00) variable relative importance weight for each explanatory variable. As it can be misleading to interpret the coefficients of individual variables from a multiple-regression model when the variables are partially correlated, all descriptions of specific covariates’ effects have been checked to ensure that they qualitatively match the effect of that variable in a univariate model. The relationships between presence/density and single variables appear in Appendices A-J.

Capelin – surface zone. Capelin presence/absence in surface waters was best explained by the local Water Column hypothesis (w=0.986, $R^2=0.16$), although none of the hypotheses were good predictors of capelin presence, as shown by their low $R^2$ values (Table 3). The fitted values of the Water Column model predicted that capelin were more frequently present in cooler, less saline water. Capelin density was best explained by the local Depth hypothesis (w=0.999, $R^2=0.42$, with the fitted quadratic relationship predicting maximum capelin densities in the middle domain in water 72 m deep.

The average models for capelin presence and density were able to explain more of the deviance than the hypotheses alone ($R^2=0.34$ and 0.61, Table 4). The local variables, Depth, Depth$^2$, and TempAbove had similarly high variable importance weights in each model (Table 4). In addition, the SalAbove and JuneWind$^3$ variables were relatively important in the presence/absence model. The coefficients of both models predicted that capelin abundance would be highest in the middle domain (peaks at 64 for
Age-0 Pacific cod – surface zone. The presence/absence of age-0 Pacific cod in surface waters was best explained by the annual *Climate* hypothesis ($w=0.996$, $R^2=0.22$, Table 5). This model suggested that age-0 Pacific cod were more frequently found in the surface waters in years with low *MaySST*, with smaller effects of *SeaIce* and *Ice20%*. Age-0 Pacific cod density was best explained by the annual *Winds* hypothesis ($w=0.623$, $R^2=0.24$), followed by the *Depth* and *Climate* hypotheses ($w=0.293$ and $0.084$, $R^2=0.21$ and $0.21$). The annual *Winds* model predicted higher cod densities with increased winter upwelling (%*UpOctApr*), as well as higher densities with decreased June winds.

The average models for age-0 Pacific cod fit the data more closely than the best hypothesis models ($R^2=0.41$ and $0.39$ for presence/absence and density respectively). The local variable *TempAbove* was the most important variable for presence, followed closely by *MaySST*, *Depth*, and *Sealce* (Table 6). Age-0 Pacific cod were more likely to be present in the surface waters over deep bottom depths (middle and outer domains) with warmer August/September surface temperatures in years with higher sea ice extent and lower May temperatures. The most important variables for density were depth (*Depth* and *Depth$^3$*), *JuneWind$^3$*, and *SeaIce*. These variables predicted the highest densities in the outer domain (peak at 148 m bottom depth) in years with higher ice cover and lower storminess in June (Appendix C, Appendix D).

Age-0 pollock – surface zone. Presence/absence of age-0 pollock in the surface zone was best explained by the local *Depth* hypothesis ($w=1.000$, $R^2=0.15$, Table 7). The *Depth* hypothesis predicted the highest presence of surface age-0 pollock in the middle domain with a peak at 91 m bottom depth. Density of age-0 pollock in the surface zone was best explained by the annual *Winds* hypothesis followed by the annual *Climate* hypothesis ($w=0.531$ and $0.469$, $R^2=0.34$ and $0.34$, Table 7). The *Winds* hypothesis predicted that age-0 pollock densities were highest in years with decreased June winds.

Average models for age-0 pollock in the surface zone fit the data more closely than the best hypothesis models ($R^2=0.25$ and $0.54$ for presence and density respectively). The local variable *Depth* was the most important variable for presence/absence, followed by *Depth$^2$*, *LgChaeet*, *LgCope*, and *JuneWind$^3$* (Table 8). Based on the average model, presence of age-0 pollock in the surface zone was highest at sites in the middle domain (peak at 95 m bottom depth), higher chaetognath biomass, and lower large copepod biomass. Presence of age-0 pollock was also highest in years with low storminess in June (Table 8,
Appendix E). The most important variable for age-0 pollock density in the surface was Depth, followed by Depth$^2$ and JuneWind$^3$ (Table 8). Densities of age-0 pollock in surface waters were highest in the outer domain (peak at 103 m bottom depth) in years with lower storminess in June (Table 8, Appendix F).

Age-0 pollock – midwater zone. The local Water Column (w=0.71, $R^2=0.68$) hypothesis best described the probability of age-0 pollock occurrence in the midwater zone (Table 7). Depth, Predators, and Stability were also in the 90 or 99% confidence set. The Water Column hypothesis predicted that age-0 pollock were more often present in cooler water with higher salinities, which is was expected given they are primarily located below the pycnocline. The best density hypothesis for midwater age-0 pollock was the local hypothesis Comfort (w=0.973, $R^2=0.55$), followed by Water Column, and Prey Groups (w=0.011 and 0.008, $R^2=0.46$ and 0.50, Table 7). The Comfort hypothesis predicted higher deep age-0 densities when biomass of small zooplankton decreased and the bottom temperature increased.

Due to the analytic approach used to derive density estimates of midwater age-0 pollock (cf. Parker-Stetter et al., 2013), age-0 pollock were present in the midwater zone at all but one station. As a result, many models fit the data well as there was little variability in the data. The average model is therefore almost certainly overfit, and the variable importance weights are biased. For this reason, we do not feel that it is justified to report the average model for midwater age-0 pollock presence. Single variable relationships are presented in Appendix G.

The average model for midwater age-0 pollock density explained more deviance ($R^2=0.63$, Table 9) than any of the hypotheses. The best predictor of density was the local variable TempBelow, followed by SalBelow, Sealce, and SmCope. The average model predicted that midwater age-0 pollock densities were highest in warmer, more saline locations with lower small copepod biomass. Age-0 pollock densities were highest in years with lower sea ice anomalies (Table 9, Appendix H).

Age-0 pollock – water column zone. Presence of age-0 pollock in the water column was best explained by the local Depth hypothesis (w=1.000, $R^2=0.38$, Table 7). This hypothesis predicted that the presence of age-0 pollock increased with increasing bottom depth. Density of water column age-0 pollock was also best explained by the local Depth hypothesis (w=0.994, $R^2=0.43$, Table 7), which predicted maximum pollock density in the outer domain (peak at 139 m bottom depth).

The averaged models explained more of the variation in water column age-0 pollock presence and density than any of the hypotheses ($R^2=0.51$ and 0.72 for presence and density respectively, Table 10). For
presence/absence, the annual variable MaySST was the most important predictor, followed by Depth$^2$ and LgChaet. Water column age-0 pollock were more frequently present in years with higher May sea surface temperatures (SST) at locations with increasing bottom depth and higher chaetognath biomass (Table 10, Appendix I). The best predictor for density was the local variable Depth, followed by Depth$^2$, JuneWind$^3$, and Preflex (Table 10). Densities of water column age-0 pollock were predicted to be highest in the outer domain (peak at 155 m bottom depth), close to the location of preflexion pollock capture in late-spring and early-summer. Densities of water column age-0 pollock were highest in years with low storminess in June (Table 10, Appendix J).

**Model fits and diagnostics**

The average models for all species were able to fit the data reasonably well, without systematic biases geographically or with respect to the covariates (Fig. B, C, and D). Density model residuals were in all cases nearly symmetrical ($|\text{skewness}| < 0.35$), though four out of five were slightly leptokurtic (i.e., fat-tailed, kurtoses between -0.78 and -0.07). The averaged parameters should therefore be relatively unbiased, though the true distribution of fish densities includes more extreme values than the assumed lognormal distribution.

**Discussion**

Understanding how local, annual, and regional factors affect the presence/absence and density of forage fish is a basic research question with a complex answer. Hypotheses on how factors affect forage fish distributions are commonly proposed but rarely evaluated using a comprehensive suite of variables. Using 24 predictor variables, our results corroborated some of the previously tested or speculated hypotheses on capelin, age-0 Pacific cod, and age-0 pollock presence/density. Our findings also suggested that factors less commonly included in modeling exercises such as local variables based on zooplankton prey, and annual variables characterizing climate or wind conditions may influence the presence/absence and density of forage fish. In some cases, the overall presence/absence or density of forage fish may be more closely related to annual variables than to location-specific variables. Ultimately, the collective understanding of what factors affect forage fish distributions in the Bering Sea may not be as complete as previously thought.

**Capelin**

Our analysis of capelin presence/absence and density identified some of the same key factors as previous studies, but our analysis suggested that the nature of those relationships may be different than previously suggested and that additional factors may also be important. Our results were consistent with Brodeur et al. (1999) and Hollowed et al. (2012) in that bottom depth and temperature were important local variables
for presence/absence and density of capelin. But while both Brodeur et al. (1999) and Hollowed et al. (2012) found that capelin had a negative relationship with bottom depth (to a maximum of ~200 m), our results showed that both presence and density were highest within the 60-80 m bottom depth range in the middle domain. Hollowed et al. (2012) reported that capelin were observed over the entire range of sampled SST (~0-12°C), which contrasted with our analysis that suggested both capelin presence and density increased with decreasing SST. The local surface temperature variable in our analysis, TempAbove, was the common variable in all density hypotheses within the 99% confidence set.

Although salinity, a factor not evaluated in previous studies, had a negative relationship with capelin presence and a variable relative importance of >0.50, it can be correlated with temperature so may not be a novel result. In the model averaging of capelin presence, the variable LgOther, a category including larvaceans, had a negative coefficient. This result is consistent with Wilson’s (2009) speculation that capelin are avoiding larvaceans, but he also posited that mean daily current velocity may affect capelin distributions, which we did not test in our analysis. Of the annual climate variables, only JuneWind was an important predictor of capelin presence/absence, suggesting that more capelin were found in the surface water in years with high late-spring storminess. Only Ciannelli & Bailey (2005) have evaluated the effect of warm and cold years on capelin distributions and concluded that in cold years, such as those during this study, capelin were limited to the north side of the cold pool. While we did not include an index of cold pool distribution in our surface models, annual temperature or ice variables were not important in either capelin presence or density average models.

**Age-0 Pacific cod**

Both our hypothesis approach and model-averaging results suggested that annual climate and wind variables influenced age-0 Pacific cod presence/absence and density. To date, Hurst et al. (2012) is the only other study that has examined factors influencing offshore distributions of age-0 Pacific cod in the eastern Bering Sea. In their model selection, Hurst et al. (2012) determined that the best model fits for age-0 Pacific cod presence and density included all tested location (bottom depth, latitude, temperature deviation), annual variables (thermal regime, cohort size), and interaction terms. Although the form (i.e. categorical versus continuous) or calculation of tested variables varied, many of our results build on final models identified in Hurst et al. (2012). In our analysis, surface temperature was positively related to age-0 Pacific cod presence, consistent with the finding that age-0 Pacific cod catches were highest in the warmest waters of the survey area (deviation from the mean, Hurst et al. (2012)). Our analysis suggested that age-0 Pacific cod densities peaked at 148 m bottom depth in the outer domain, while Hurst et al. (2012) found that surface trawl catches of age-0 Pacific cod peaked at intermediate bottom depths of 50-80 m (categorical variable) in the middle domain. Among annual variables, May sea surface temperature
(negative coefficient for presence/absence) and sea ice extent (positive coefficient for presence/absence, negative coefficient for density), were important in our analysis and support the intent of Hurst et al.’s (2012) categorical thermal regime variable, although the signs of variable coefficients cannot be compared. Two differences in the two studies are that Hurst et al. (2012) did not include wind variables that were included in our analysis, and that the cohort size (categorical) variable to evaluate density dependence was included in Hurst et al. (2012) but not addressed in our analysis.

**Age-0 pollock**

There are few directly comparable studies evaluating biological and physical factors influencing the presence/absence or density of age-0 walleye pollock. Evaluations of age-0 pollock distributions have primarily examined factors influencing abundance, growth/bioenergetics, or interspecific competition. While sampling methods, statistical approaches, and explanatory variables differed from those used in the current study, it is worth comparing and contrasting factors reported to influence young pollock distributions.

In studies conducted near the Pribilof Islands and within walleye pollock nursery grounds, age-0 pollock distributions were related to euphausiid density (positive, Winter & Swartzman, 2006; Winter et al., 2007), aggregate prey density (positive, Swartzman et al., 1999), growth potential (positive and negative, Ciannelli, 2002; Ciannelli et al., 2002), and an index of predator abundance (positive and negative, Winter & Swartzman, 2006; Winter et al., 2007). Age-0 pollock distributions have also been reported as being independent of feeding habitat quality as inferred from body condition and stomach fullness (Schabetsberger et al., 2003).

Final regression models using surface trawl data to explain age-0 pollock presence/absence and density in Hollowed et al. (2012) contained bottom depth and surface temperature. Based on GAM derived surfaces, they concluded that in cold years age-0 pollock were most commonly found in the outer domain at bottom depths of 100-150 m. Densities of age-0 pollock were highest in the 50-150 m bottom depth range in surface temperatures >10°C. In our analysis, bottom depth was an important predictor for surface and water column models, with age-0 pollock most abundant in water 100-200 m deep, in the outer domain. Temperature above the pycnocline had a variable relative importance of 0.34 (presence/absence) and 0.06 (density) in our averaged models for age-0 pollock within the surface zone, suggesting that it was not as important as other variables in the models. Moss et al. (2009), using a subset of the surface trawl data used in Hollowed et al. (2012) speculated that water column stability may be important in explaining age-0 pollock distribution. In our analysis, the hypothesis containing the stability
variable was only included in a confidence set for water column age-0 pollock. Stability was not an important variable in any of the average models. This suggests that age-0 pollock are not more frequently found, nor occur at higher densities, at locations with high water column stability than at those with lower water column stabilities.

The importance of temperature on age-0 pollock distributions has been evaluated for both the Bering Sea and the Gulf of Alaska. Brodeur et al. (1999) concluded that water column age-0 pollock were associated with warmer bottom temperatures in the Bering Sea. In the Gulf of Alaska, Wilson et al. (1996) found no quantitative relationship between age-0 pollock densities and either surface or bottom temperatures, but qualitatively concluded that age-0 pollock densities were highest shoreward of the 7°C isotherm (measured at 50 m from the surface). Miyake et al. (1996) observed that no pollock were captured in bottom temperatures <6°C or >16°C along the coast of Japan. This result is consistent with the bioenergetics evaluation by Ciannelli et al. (1998) that reported 10°C was an optimal temperature for consumption by age-0 pollock, and that 13°C was optimal for respiration. In our analysis, temperature was only a significant variable in model averaging for midwater pollock densities. Age-0 pollock midwater densities increased with increasing bottom temperatures between -1.13 and 10.50°C.

Prey variables were important in our model averaging results for age-0 pollock presence/absence (surface and water column) and density (midwater). Positive chaetognath coefficients contrasted with negative relationships for large and small copepod biomass. Wilson (2009) reported that age-0 pollock were not closely associated with densities of zooplankton. From a bioenergetic perspective, Mazur et al. (2007) concluded that prey quality was more important to age-0 pollock growth than temperature. Our analysis suggested that prey energy density was negatively associated with four (surface presence/absence and density, water column presence/absence and density) of the five analyses, and that none of the variable relative importance weights were within 0.50 of the most important variable.

Our model average results for water column age-0 pollock indicate that age-0 pollock densities were highest close to the mean location of preflexion larvae in the late-spring and early-summer as reported by Smart et al. (2012). This infers that passive advection of eggs and larvae are consistent with patterns observed in other studies. Hinckley et al. (1991) found that the distribution of late larvae and post-flexion juvenile age-0 pollock in the Gulf of Alaska in June-July followed the same pattern as satellite drifters. This trend is also consistent with Brodeur & Wilson (1996) who speculated that age-0 pollock distribution could be explained by passive advection from spawning locations.
A large amount of research effort has focused on the influence of physical and/or biological factors on walleye pollock recruitment. While high densities of age-0 pollock do not guarantee high recruitment, growth and survival of early life history stages will maximize the probability of large year classes. We compare results of recruitment studies to those in our analyses.

Using data from age-2+ pollock, Mueter et al. (2006) evaluated the effect of bottom-up and top-down factors on recruitment success. The final combined model of age-0 pollock recruitment included five variables: final latitude of a 90 day drift trajectory, adult walleye pollock biomass, ice severity index, and spring bloom date. Of these, latitude and an earlier spring bloom date were the best predictors. Our analysis suggested that presence and density were generally highest when early summer (JuneWind^3, JulyWind^4) storminess was lowest, potentially due to the occurrence of an earlier spring bloom. Similarly, we did observe that the date at which sea ice had retreated to 20% of the area south of 60°N had a positive coefficient, meaning that the presence and/or density of age-0 pollock was highest when sea ice left the study area earlier, in three (surface presence/absence and density, midwater density) of the five models. In contrast, Bond & Overland (2005) observed that years with strong late-June to early-July wind mixing often had high pollock recruitment. They attributed this result to nutrient availability in the euphotic zone and subsequent increased production of young pollock prey.

Wespestad (2000) hypothesized that recruitment of walleye pollock was highest for years when winds transported larval pollock inshore and away from cannibalistic adult pollock. In the five averaged models, our %UpAprOct variable had a relative importance weight of ≤0.30. In four of the five average density models, the coefficient was positive, suggesting that presence and age-0 pollock densities were highest in years when October-April wind direction was more often oriented offshore.

Hunt et al. (2011) proposed that recruitment of walleye pollock from age-0 to age-1 is highest in years with late ice retreat and conditions that favor the production of lipid-rich, large copepods. Pollock recruitment was higher than average in four (2006, 2008, 2009, 2010) of our study years (Hunt et al., 2011; Ianelli et al., 2011), and higher abundances of lipid-rich, large copepods were present (2006-2009) as compared to previous years (2003-2005, Coyle et al., 2011). Our model averaging results suggested that sea ice retreat had a positive regression coefficient in three (surface presence/absence, surface density, midwater density) of the five averaged models, but that none had variable relative importance values within 0.50 of the best variable. Sea ice anomaly, as an indicator of sea ice extent, had a negative regression coefficient and only one model with a variable relative importance >0.50 (midwater density) in the five average models. This suggests that both the presence and densities of age-0 pollock increased as...
sea ice extent decreased. Similarly, our analysis suggested that large copepod biomass had a positive regression coefficient in two (surface density, midwater density) of the five average models for age-0 pollock, but only one negative coefficient (surface presence/absence) had a variable relative importance within 0.50 of the best predictor. These results do not negate the potential positive relationship between recruitment and copepod biomass as age-0 pollock grazing, or grazing by other large zooplankton such as chaetognaths, could reduce zooplankton biomass and mask the relationship at a station.

Comparing species

In spite of the extensive list of variables used in our analyses, many important factors from the model averaging exercises were common among species (Table 11). Bottom depth was a key variable in eight of the nine model averaging analyses, suggesting that the distribution of these species can be characterized by EBS domain in cold years. Capelin presence/absence and density peaked in the middle domain, surface age-0 pollock in the middle front, age-0 Pacific cod in the outer domain, and water column age-0 pollock in the outer domain (Table 11). These result quantify distributions observed by Parker-Stetter et al. (2013) and may reflect the spatial niche partitioning suggested by Hollowed et al. (2012). Local temperature and salinity were important factors in both presence/absence and density models, with capelin associated with colder, less-saline water, age-0 Pacific cod in warmer water, and midwater age-0 pollock in warm, more saline water (Table 11). Like bottom depth, annual variables were important in eight of nine model averaging analyses. Capelin probability of occurrence was highest in years with increased storminess in June, but age-0 Pacific cod and age-0 pollock presence/absence/densities were highest in years with low June storminess (Table 11).

Implications

Predicting how the Bering Sea will respond to changes in climate is complicated. Some aspects of the ecosystem, such as sea ice (Lee et al., 2012; Stabeno et al., 2012b; Wang et al., 2012), late-fall winds (Danielson et al., 2012), and transport of large zooplankton (Stabeno et al., 2012b) are predicted to change. Other attributes, such as annual cold-warm temperature anomalies (Overland et al., 2012; Stabeno et al., 2012b), mean annual wind direction (Danielson et al., 2012), and the presence of the deep cold pool (Stabeno et al., 2012b), are predicted to persist. How other aspects of the ecosystem will change, such as seasonal storminess, have not been fully explored. Further complicating climate predictions, recent work by Ladd & Stabeno (2012) found that a warm year did not guarantee the strongest water column stratification and Brown & Arrigo (2013) found that cold years had higher temperature stratification than warm years. This work suggests that our understanding of the influence of climate on water column structure and biological responses to environmental variability is not complete.
Mueter & Litzow (2008) suggested that species-specific responses to changes in climate are difficult to predict, and the breadth of our results supports that assertion. Looking only at signs of coefficients, and not the relative importance of variables, predicted decreases in sea ice extent (Wang et al., 2012; Lee et al., 2012; Stabeno et al., 2012b) may benefit age-0 pollock and potentially age-0 Pacific cod, but not capelin. In contrast, the predicted gradual increase in May SST (Wang et al., 2012) may benefit age-0 Pacific cod and age-0 pollock in the surface zone, but not midwater age-0 pollock, water column age-0 pollock, or capelin. The continued presence of the deep cold pool is predicted to limit the northern expansion of some pelagic and demersal species (Sigler et al., 2011; Stabeno et al., 2012b). As midwater age-0 pollock density increased with increasing bottom temperature, the range of midwater age-0 pollock is predicted to expand northward as the cold pool recedes, but ultimately be restricted by the continued presence of the cold pool. The final responses of forage fish to climate change will inevitably be an amalgam of preferences, tolerances, and the ability to adapt.

Analytic approach

The use of a priori hypotheses allowed us to test ideas about how local, annual, and regional factors potentially influence forage fish presence/absence and density. This approach led to the identification of multiple biologically-plausible hypotheses that were supported by the data, and contrasted the common goal of identifying a “best” model (cf. Burnham & Anderson, 2002). Our post hoc model averaging exercise evaluated whether any important combinations of variables were missed in our hypotheses. For all species and depth strata, the average models fit the data better than any single hypothesis. This result is not particularly surprising, since we tried to keep our a priori hypotheses relatively simple for the sake of interpretability. As a result, combinations of important variables were not included: for instance, average models and variable relative importance weights typically identified both local and annual variables as important, but these were not combined in any hypothesis. The exhaustive model comparisons, and the average models derived from them, were somewhat exploratory and should be interpreted cautiously due to the possibility of overfitting. However, the individual models being average were probably not overfit, since they were limited to five variables, and the gains in $R^2$ over the best hypothesis models were large. These facts suggest at least some of that improvement in fit is likely to be real, and the average models do contribute to an improved understanding.

As with any analysis, the representativeness of our results is contingent upon the underlying data. Analytic approaches used and/or potential biases identified for the distribution data, such as inadvertent classification of jellyfish as fish (cf. Parker-Stetter et al., 2013), could change hypothesis and full model results. The same may be said for the oceanographic data, that the accuracy and precision of variables...
used in our analysis could affect final results. In our selection of local, annual, and regional variables, we attempted to be as comprehensive as possible, building on the current understanding of important biophysical linkages in the SEBS. Ultimately our suite of variables was smaller than if we had supplemented our data with data from other sources or studies, but we chose to maintain spatial and/or temporal coherence between our data and the tested variables. These results represent the widest set of variables in a single study, but do not include all variables that have been used in previous studies (e.g. Mueter et al., 2006; Hurst et al., 2012)

Our modeling approach has several limitations. We did not test interactions between variables in the model averaging, due to lack of specific a priori expectations in the hypotheses and due to computational limitations. Also for computational reasons, models in the averaging exercise were limited to five variables. In theory this may have caused us to miss larger combinations of variables, but there were never more than five “important” (relative weight >0.5) variables in any of the average models. Many of the explanatory variables were correlated. Though steps were taken to eliminate the most redundant variables, these correlations may still confound our interpretations. The highest-correlated variables may not necessarily be the “true” causal ones, but simply representative of them.

More generally, regression models are static, while the processes we are trying to understand (e.g., dispersal, distribution, survival of forage fish in ocean environment) are dynamic. Our implicit assumptions were that the distribution measured by the survey was a representative snapshot (i.e. no directional change or bias between start and end), that there was no trend over time, and that environmental conditions at locations were representative of the conditions that caused fish to end up in that location. As our sampling was all during “cold” climate conditions (Stabeno et al., 2012a), our results may not represent the entire range or variability of all variables. Future work should incorporate data from “warm” climate conditions (Stabeno et al., 2012a). A logical next step for the modeling would be to evaluate the use of a dynamic simulation model and compare its output to the findings from this study.

**Concluding remarks**

Ultimately, fisheries scientists and managers want to understand what factors affect the distribution of forage fish given interannual variability in conditions (e.g. Stabeno et al., 2012a) and predicted changes in climate. Results from this study underscore that predicting distributions is nontrivial and that several competitive, supported variables and/or hypotheses may existed. This study identified potentially
important local, annual, and regional factors that influenced capelin, age-0 Pacific cod, and age-0 pollock
distributions that may be used to improve future distribution and recruitment modeling efforts.

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BSIERP Bering Sea Project publication number ###.

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Brodeur, R.D., Wilson, M.T., Walters, G.E. and Melnikov, I.V. (1999) Forage fishes in the Bering Sea:


Figure Legends

Fig. 1. Survey extent, CTD cast locations, and oceanographic Rossby radii by year. Shaded radii were used in water column analyses and denoted grey (surface and water column models) or black (surface, midwater, and water column models). Hollow symbols were used only in surface analyses.

Fig. 2. Observed capelin densities and predicted values from the average model. Open circles show observed densities where size is proportional to log(density), and “x” shows stations where no fish were observed. Filled circles show the predictions from the average model where shading shows the predicted probability of occurrence and the size of the circle shows the predicted log(density) given that fish are present. Observed and predicted densities use the same size scale.

Fig. 3. Observed age-0 Pacific cod densities and predicted values from the average model. Open circles show observed densities where size is proportional to log(density), and “x” shows stations where no fish were observed. Filled circles show the predictions from the average model where shading shows the predicted probability of occurrence and the size of the circle shows the predicted log(density) given that fish are present. Observed and predicted densities use the same size scale.

Fig. 4. Observed age-0 pollock densities and predicted values from the average model (A surface, B midwater, C water column). Open circles show observed densities where size is proportional to log(density), and “x” shows stations where no fish were observed. Filled circles show the predictions from the average model where shading shows the predicted probability of occurrence and the size of the circle shows the predicted log(density) given that fish are present. Observed and predicted densities use the same size scale.
Fig. 1. Survey extent, CTD locations, and Rossby radii by year.
Fig. 2. Observed capelin densities and predicted values from the average model.
Fig. 3. Observed age-0 Pacific cod densities and predicted values from the average model.
Fig. 4. Observed age-0 pollock densities and predicted values from the average model.
Table 1. Hypotheses used in analyses.

Hypotheses to evaluate Presence and Density (response variables, Factor) for age-0 pollock, age-0 Pacific cod, and capelin. For Temp and Sal variables, surface models used Above values, midwater models (age-0 pollock only) used Below values, and water column (age-0 pollock only) models used both Above and Below.

<table>
<thead>
<tr>
<th>Hypothesis Name</th>
<th>Model structure</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Local hypotheses</strong></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>Factor ~ Depth + Depth²</td>
</tr>
<tr>
<td>Water Column</td>
<td>Factor ~ TempAbove/Below + SalAbove/Below + Chlor-a</td>
</tr>
<tr>
<td>Stability</td>
<td>Factor ~ TempAbove/Below + WC-Stab</td>
</tr>
<tr>
<td>Total Prey</td>
<td>Factor ~ SmZoops + LgZoops</td>
</tr>
<tr>
<td>Prey Groups</td>
<td>Factor ~ SmCope+ LgCope + LgChaet + SmOther+ LgOther</td>
</tr>
<tr>
<td>Energetics</td>
<td>Factor ~ PreyEnergy</td>
</tr>
<tr>
<td>Predators</td>
<td>Factor ~ Preds</td>
</tr>
<tr>
<td>Comfort</td>
<td>Factor ~ TempAbove/Below + SmZoops + LgZoops + Pred</td>
</tr>
<tr>
<td><strong>Annual hypotheses</strong></td>
<td></td>
</tr>
<tr>
<td>Climate</td>
<td>Factor ~ SeaIce + MaySST + Ice20%</td>
</tr>
<tr>
<td>Winds</td>
<td>Factor ~ JuneWind³ + JulyWind³ + %UpOctApr</td>
</tr>
<tr>
<td><strong>Regional hypothesis</strong></td>
<td></td>
</tr>
<tr>
<td>Early Life Stage*</td>
<td>Factor ~ Preflex</td>
</tr>
</tbody>
</table>

*run only for age-0 pollock
Table 2. Data summary.

Data summary for surface, midwater, and water column analyses. # of CTD stations used in each analysis (# of 0.5 nmi acoustic bins within the Rossby radius of those CTD stations) for surface, midwater, and water column zones.

<table>
<thead>
<tr>
<th>Year</th>
<th>surface (# 0.5 nmi acoustic bins)</th>
<th>midwater (# 0.5 nmi acoustic bins)</th>
<th>water column (# 0.5 nmi acoustic bins)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>30 (122)</td>
<td>8 (43)</td>
<td>20 (83)</td>
</tr>
<tr>
<td>2007</td>
<td>61 (265)</td>
<td>3 (17)</td>
<td>37 (159)</td>
</tr>
<tr>
<td>2008</td>
<td>31 (183)</td>
<td>0 (0)</td>
<td>12 (48)</td>
</tr>
<tr>
<td>2009</td>
<td>86 (493)</td>
<td>40 (261)</td>
<td>86 (493)</td>
</tr>
<tr>
<td>2010</td>
<td>56 (293)</td>
<td>12 (80)</td>
<td>38 (169)</td>
</tr>
</tbody>
</table>
Table 3. Capelin hypothesis results.

Hypothesis model results for capelin presence and density in the surface zone. Hypothesis (details in Table 1), Delta AICc (AICc for the best model in the set), Akaike weight, and R-squared statistic are provided. The best hypothesis, 90% confidence set, 95% confidence set, and 99% confidence set are identified.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Presence</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Delta AICc</td>
<td>Akaike weight</td>
</tr>
<tr>
<td>Local hypotheses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>12.6</td>
<td>0.002</td>
</tr>
<tr>
<td>Water Column</td>
<td>0.0 (299.2)</td>
<td>0.986</td>
</tr>
<tr>
<td>Stability</td>
<td>8.8</td>
<td>0.012</td>
</tr>
<tr>
<td>Total Prey</td>
<td>50.8</td>
<td>0.000</td>
</tr>
<tr>
<td>Prey Groups</td>
<td>46.5</td>
<td>0.000</td>
</tr>
<tr>
<td>Energetics</td>
<td>51.0</td>
<td>0.000</td>
</tr>
<tr>
<td>Predators</td>
<td>50.6</td>
<td>0.000</td>
</tr>
<tr>
<td>Comfort</td>
<td>17.0</td>
<td>0.000</td>
</tr>
<tr>
<td>Annual hypotheses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Climate</td>
<td>25.1</td>
<td>0.000</td>
</tr>
<tr>
<td>Winds</td>
<td>25.4</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Table 4. Capelin model averaging results.

Model averaging results for capelin presence and density in the surface zone. Variable, the coefficient mean value, coefficient standard error value, and a measure of relative variable importance (Importance, calculated as $w_i/\max(w_\star)$) are provided. The $\max(w_\star)$ and variables with $w_i/\max(w_\star) \geq 0.50$ are shown.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Presence</th>
<th>Density</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Local variables</td>
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<td></td>
</tr>
<tr>
<td>Depth</td>
<td>0.24841</td>
<td>9.81E-06</td>
</tr>
<tr>
<td>Depth²</td>
<td>-0.00193</td>
<td>5.62E-10</td>
</tr>
<tr>
<td>TempAbove</td>
<td>-0.61107</td>
<td>4.69E-05</td>
</tr>
<tr>
<td>TempBelow</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>SalAbove</td>
<td>-1.05184</td>
<td>1.43E-04</td>
</tr>
<tr>
<td>SalBelow</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Chlor-a</td>
<td>-0.00034</td>
<td>2.47E-09</td>
</tr>
<tr>
<td>Stability</td>
<td>0.00000</td>
<td>7.56E-13</td>
</tr>
<tr>
<td>SmZoops</td>
<td>-0.00002</td>
<td>1.93E-08</td>
</tr>
<tr>
<td>LgZoops</td>
<td>-0.00001</td>
<td>3.02E-10</td>
</tr>
<tr>
<td>SmCope</td>
<td>0.00001</td>
<td>1.90E-08</td>
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<tr>
<td>LgCope</td>
<td>-0.00001</td>
<td>3.12E-10</td>
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<tr>
<td>LgChaet</td>
<td>0.00002</td>
<td>9.98E-10</td>
</tr>
<tr>
<td>SmOther</td>
<td>-0.00017</td>
<td>1.32E-08</td>
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<tr>
<td>LgOther</td>
<td>-0.00003</td>
<td>5.26E-10</td>
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<tr>
<td>PreyEnergy</td>
<td>-0.00001</td>
<td>5.25E-09</td>
</tr>
<tr>
<td>Preds</td>
<td>0.00000</td>
<td>6.41E-14</td>
</tr>
<tr>
<td>Annual variables</td>
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<td></td>
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<tr>
<td>SeaIce</td>
<td>0.06294</td>
<td>8.12E-07</td>
</tr>
<tr>
<td>MaySST</td>
<td>0.01409</td>
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</tr>
<tr>
<td>Ice20%</td>
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<td>1.85E-08</td>
</tr>
<tr>
<td>JuneWind³</td>
<td>0.01622</td>
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<tr>
<td>JulyWind³</td>
<td>0.00000</td>
<td>1.22E-13</td>
</tr>
<tr>
<td>%UpOctApr</td>
<td>0.00009</td>
<td>3.64E-10</td>
</tr>
<tr>
<td>Intercept</td>
<td>27.58842</td>
<td>2.06E-02</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.34</td>
<td></td>
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Table 5. Age-0 Pacific cod hypothesis results.

Hypothesis model results for age-0 Pacific cod presence and density in the surface zone. Hypothesis, Delta AICc (AICc for the best model in the set), Akaike weight, and R-squared statistic are provided. The best hypothesis, 90% confidence set, 95% confidence set, and 99% confidence set are identified.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Presence Delta AICc</th>
<th>Presence Akaike weight</th>
<th>Presence R-squared</th>
<th>Density Delta AICc</th>
<th>Density Akaike weight</th>
<th>Density R-squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local hypotheses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>35.1</td>
<td>0.000</td>
<td>0.12</td>
<td>1.5</td>
<td>0.293</td>
<td>0.21</td>
</tr>
<tr>
<td>Water Column</td>
<td>17.2</td>
<td>0.000</td>
<td>0.17</td>
<td>21.3</td>
<td>0.000</td>
<td>0.06</td>
</tr>
<tr>
<td>Stability</td>
<td>24.4</td>
<td>0.000</td>
<td>0.15</td>
<td>18.8</td>
<td>0.000</td>
<td>0.06</td>
</tr>
<tr>
<td>Total Prey</td>
<td>66.1</td>
<td>0.000</td>
<td>0.03</td>
<td>22.9</td>
<td>0.000</td>
<td>0.03</td>
</tr>
<tr>
<td>Prey Groups</td>
<td>66.3</td>
<td>0.000</td>
<td>0.05</td>
<td>22.3</td>
<td>0.000</td>
<td>0.10</td>
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<tr>
<td>Energetics</td>
<td>70.7</td>
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<td>0.01</td>
<td>22.3</td>
<td>0.000</td>
<td>0.01</td>
</tr>
<tr>
<td>Predators</td>
<td>66.8</td>
<td>0.000</td>
<td>0.02</td>
<td>19.0</td>
<td>0.000</td>
<td>0.04</td>
</tr>
<tr>
<td>Comfort</td>
<td>15.5</td>
<td>0.000</td>
<td>0.19</td>
<td>23.4</td>
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<tr>
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<td>0.004</td>
<td>0.19</td>
<td>0.0 (496.2)</td>
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### Table 6. Age-0 Pacific cod model averaging results.

Model averaging results for age-0 Pacific cod presence and density in the surface zone. Variable, the coefficient mean value, coefficient standard error value, and a measure of relative variable importance (Importance, calculated as \( w_s(i) / \max(w_s(i)) \)) are provided. The \( \max(w_s(i)) \) and variables with \( w_s(i) / \max(w_s(i)) \) ≥0.50 are shown.

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<tr>
<th>Variable</th>
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<th>Density</th>
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<td>NA</td>
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<td>0.30344</td>
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<td>Stability</td>
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<td>2.06E-10</td>
</tr>
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<td>SmZoops</td>
<td>0.00315</td>
<td>8.37E-06</td>
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<td>LgZoops</td>
<td>0.00026</td>
<td>9.26E-08</td>
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<td>0.00218</td>
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<td>MaySST</td>
<td>-0.43783</td>
<td>1.48E-04</td>
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<td>Ice20%</td>
<td>-0.04510</td>
<td>1.44E-07</td>
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<td>JuneWind(^3)</td>
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<td>1.64E-07</td>
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<td>JulyWind(^3)</td>
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<td>%UpOctApr</td>
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<td>R(^2)</td>
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Table 7. Age-0 pollock hypothesis results.

Hypothesis model results for age-0 pollock presence and density in the (A) surface zone, (B) midwater zone, and (C) water column. Hypothesis, Delta AICc (AICc for the best model in the set), Akaike weight, and R-squared statistic are provided. The best hypothesis, 90% confidence set, 95% confidence set, and 99% confidence set are identified.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Presence Delta AICc</th>
<th>Presence Akaike weight</th>
<th>Presence R-squared</th>
<th>Density Delta AICc</th>
<th>Density Akaike weight</th>
<th>Density R-squared</th>
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<td></td>
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<td></td>
<td></td>
<td></td>
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<td>0.15</td>
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<td>0.21</td>
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<tr>
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<td>0.01</td>
<td>52.9</td>
<td>0.000</td>
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<td>54.3</td>
<td>0.000</td>
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<td>0.00</td>
<td>52.5</td>
<td>0.000</td>
<td>0.01</td>
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<td>43.2</td>
<td>0.000</td>
<td>0.07</td>
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<tr>
<td>Comfort</td>
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<td>0.000</td>
<td>0.08</td>
<td>40.4</td>
<td>0.000</td>
<td>0.13</td>
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<tr>
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<tr>
<td>Early Life Stage</td>
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<td>0.05</td>
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(B) Midwater Local hypotheses

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<th>Presence Akaike weight</th>
<th>Presence R-squared</th>
<th>Density Delta AICc</th>
<th>Density Akaike weight</th>
<th>Density R-squared</th>
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<td>0.45</td>
<td>28.4</td>
<td>0.000</td>
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<td>10.4</td>
<td>0.005</td>
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<td>0.12</td>
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(C) Water column Local hypotheses

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<th>Presence Akaike weight</th>
<th>Presence R-squared</th>
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<th>Density Akaike weight</th>
<th>Density R-squared</th>
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<td><strong>0.0 (534.2)</strong></td>
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<td>0.01</td>
<td>49.9</td>
<td>0.000</td>
<td>0.08</td>
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<td>0.00</td>
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<td>0.07</td>
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<td>49.6</td>
<td>0.000</td>
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Table 8. Age-0 pollock surface zone model averaging results.

Model averaging results for presence and density of age-0 pollock in the surface zone. Variable, the coefficient mean value, coefficient standard error value, and a measure of relative variable importance (Importance, calculated as \( w_i / \max(w_i) \)) are provided. The \( \max(w_i) \) and variables with \( w_i / \max(w_i) >= 0.50 \) are shown.

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<td>NA</td>
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<td>NA</td>
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Table 9. Age-0 pollock midwater model averaging results.

Model averaging results for density of age-0 pollock in the midwater zone. Variable, the coefficient mean value, coefficient standard error value, and a measure of relative variable importance (Importance, calculated as $w_i / \max(w_i)$) are provided. The $\max(w_i)$ and variables with $w_i / \max(w_i) \geq 0.50$ are shown.

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<th>Variable</th>
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<td>Mean</td>
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<tr>
<td>Intercept</td>
<td>-38.19249</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.63</td>
</tr>
</tbody>
</table>
Table 10. Age-0 pollock water column model averaging results.
Model averaging results for presence and density of age-0 pollock in the water column.
Variable, the coefficient mean value, coefficient standard error value, and a measure of relative variable importance (Importance, calculated as $w_i / \max(w_i)$) are provided. The $\max(w_i)$ and variables with $w_i / \max(w_i) \geq 0.50$ are shown.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Presence</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td><strong>Local variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>0.02773</td>
<td>4.57E-08</td>
</tr>
<tr>
<td>Depth$^2$</td>
<td>0.00098</td>
<td>5.45E-11</td>
</tr>
<tr>
<td>TempAbove</td>
<td>-0.00039</td>
<td>1.92E-08</td>
</tr>
<tr>
<td>TempBelow</td>
<td>-0.00778</td>
<td>6.12E-08</td>
</tr>
<tr>
<td>SalAbove</td>
<td>0.11543</td>
<td>1.03E-05</td>
</tr>
<tr>
<td>SalBelow</td>
<td>-0.01919</td>
<td>2.39E-06</td>
</tr>
<tr>
<td>Chlor-a</td>
<td>-0.05002</td>
<td>2.76E-07</td>
</tr>
<tr>
<td>Stability</td>
<td>-0.00350</td>
<td>1.55E-09</td>
</tr>
<tr>
<td>SmZoops</td>
<td>0.01514</td>
<td>1.16E-06</td>
</tr>
<tr>
<td>LgZoops</td>
<td>0.01631</td>
<td>1.53E-07</td>
</tr>
<tr>
<td>SmCope</td>
<td>-0.00591</td>
<td>1.34E-06</td>
</tr>
<tr>
<td>LgCope</td>
<td>-0.14115</td>
<td>8.83E-07</td>
</tr>
<tr>
<td>LgChaet</td>
<td>0.31727</td>
<td>5.11E-06</td>
</tr>
<tr>
<td>SmOther</td>
<td>0.00701</td>
<td>3.34E-07</td>
</tr>
<tr>
<td>LgOther</td>
<td>0.00335</td>
<td>1.06E-07</td>
</tr>
<tr>
<td>PreyEnergy</td>
<td>-0.13170</td>
<td>3.83E-06</td>
</tr>
<tr>
<td>Preds</td>
<td>0.00019</td>
<td>7.61E-10</td>
</tr>
<tr>
<td><strong>Annual variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SeaIce</td>
<td>-0.00268</td>
<td>5.00E-06</td>
</tr>
<tr>
<td>MaySST</td>
<td>5.50063</td>
<td>4.04E-03</td>
</tr>
<tr>
<td>Ice20%</td>
<td>-0.04029</td>
<td>1.97E-07</td>
</tr>
<tr>
<td>JuneWind$^3$</td>
<td>0.00055</td>
<td>1.73E-09</td>
</tr>
<tr>
<td>JulyWind$^3$</td>
<td>-0.00202</td>
<td>4.97E-10</td>
</tr>
<tr>
<td>%UpOctApr</td>
<td>0.05641</td>
<td>6.46E-07</td>
</tr>
<tr>
<td><strong>Regional variable</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preflex</td>
<td>-0.00003</td>
<td>1.11E-11</td>
</tr>
<tr>
<td>Intercept</td>
<td>-10.59475</td>
<td>2.90E-02</td>
</tr>
</tbody>
</table>
Table 11. Comparison of model averaging results.

Summary of model averaging results for capelin, age-0 Pacific cod, and age-0 pollock. Variables with $w_i(i)/\max(w_i(i)) \geq 0.50$ from Tables 4, 6, 9-11 are shown. “—“ indicates a negative relationship with the factor and “+” indicates a positive relationship with the factor. “/” indicates that no variables from that category had $w_i(i)/\max(w_i(i)) \geq 0.50$. ND indicates that these model runs were not performed.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Local</th>
<th>Annual</th>
<th>Regional</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Capelin (surface)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence</td>
<td>64 m peak</td>
<td>+JuneWind</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>–TempAbove</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>–SalAbove</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>77 m peak</td>
<td>/</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>–TempAbove</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age-0 Pacific cod (surface)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence</td>
<td>Increases with depth</td>
<td>+SealIce</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>+TempAbove</td>
<td>–MaySST</td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>148 m peak</td>
<td>–SealIce</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>–JuneWind</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age-0 pollock (surface)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence</td>
<td>95 m peak</td>
<td>–JuneWind</td>
<td>/</td>
</tr>
<tr>
<td></td>
<td>–LgCope</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>+LgChaet</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>103 m peak</td>
<td>–JuneWind</td>
<td>/</td>
</tr>
<tr>
<td><strong>Age-0 pollock (midwater)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Density</td>
<td>+TempBelow</td>
<td>–SealIce</td>
<td>/</td>
</tr>
<tr>
<td></td>
<td>+SalBelow</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>–SmCope</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age-0 pollock (water column)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence</td>
<td>Increases with depth</td>
<td>+MaySST</td>
<td>/</td>
</tr>
<tr>
<td></td>
<td>+LgChaet</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>155 m peak</td>
<td>–JuneWind</td>
<td>–Preflex</td>
</tr>
</tbody>
</table>
Appendix 1. Variable relationships for capelin presence (surface).
Appendix 2. Variable relationships for capelin density (surface).
Appendix 3. Variable relationships for age-0 Pacific cod presence (surface).

![Graphs showing variable relationships for age-0 Pacific cod presence (surface).](image-url)
Appendix 4. Variable relationships for age-0 Pacific cod density (surface).
Appendix 5. Variable relationships for age-0 pollock presence (surface).
Appendix 6. Variable relationships for age-0 pollock density (surface).
Appendix 7. Variable relationships for age-0 pollock presence (midwater).
Appendix 8. Variable relationships for age-0 pollock density (midwater).
Appendix 9. Variable relationships for age-0 pollock presence (water column).
Appendix 10. Variable relationships for age-0 density (water column).
Conclusions

The distributions of forage fish varied both vertically and horizontally among study years. Capelin and age-0 Pacific cod were typically found in the surface zone (<35 m in depth), but capelin were present further offshore than previously reported. Age-0 pollock were frequently found in the surface zone, but high, previously unreported, biomass was observed in the midwater zone (>35 m below the surface). In 2009 and 2010, midwater fish dominated the water column biomass. These findings suggest that the use of bottom trawl or surface trawl data to quantify forage fish distributions may not be adequate in all years. A full water column survey is needed to evaluate the most appropriate gear, or combination of gears, needed to obtain representative samples of target species. The combination of an acoustic survey with supporting midwater and bottom trawling is the recommended, and international, standard for abundance estimates and distribution surveys of pelagic (i.e. water column) and semi-demersal (i.e. near bottom) fish species.

Our analyses underscored the need for additional, dedicated forage fish studies with emphasis on quantifying the potential effects of jellyfish on characterizations of densities or distributions. Data and conclusions from non-target surveys, such as those in this study, may be constrained compared to dedicated survey efforts, but can be used to provide baseline distributions, potential abundance indices, and insight for planning future research.

Many local, annual, and regional factors were useful in explaining the presence and density of forage fish. Using 24 predictor variables, our results corroborated some of the previously tested or speculated hypotheses on capelin, age-0 Pacific cod, and age-0 pollock presence/density. However, our findings also suggested that variables less commonly included in modeling exercises such as zooplankton prey, annual climate, or annual wind conditions may influence the presence and density of forage fish. In some cases, annual factors explained more variability in presence or density of forage fish than location-specific attributes. Support for single hypotheses was generally low as was, in some cases, support for the “best” averaged model. Ultimately, the collective understanding of how biological and physical factors affect forage fish distributions in the Bering Sea may not be as complete as previously thought. A natural next step for this work would be a spatially-explicit model that accounted for passive transport of larval forage fish in the spring and early-summer months.

Our project contributed data and expertise to the evaluation of how forage fish influence post-breeding seabird distributions in the Bering Sea, but the analyses are not complete. This analysis, which is ongoing and for which a draft manuscript is not yet complete, is part of BSIERP-B64. PIs from BSIERP-B59
continue to support this effort. When results are available, this analysis will provide an interesting look at seabirds during an understudied period of their lifecycle, and may provide insight into the spatial coherence of avian predators and their prey.

**BSIERP & Bering Sea Project connections**

Participation in the Bering Sea Integrated Ecosystem Research Program (BSIERP) provided context for the specifics and connections of our project with other Bering Sea research efforts. BSIERP PIs provided feedback on hunches, ideas, and data for analyses, and suggestions for hypotheses on the distributions of forage fish. Attendance at the BSIERP PI meetings, PI workshops at Alaska Marine Science Symposium (AMSS), and watching PI presentations at AMSS, provided insight into physical/biological oceanographic and climate-related processes that ultimately informed our second manuscript (Chapter 2).

Similarly, we were able to provide insight on forage fish distributions to PIs working on post-breeding (Kuletz) and nesting (Paredes) seabirds, age-0 Pacific cod (Hurst), and fish energetics (Heintz). Combined with data from our NPRB-1006 project, we also provided estimates of the vertical distribution of age-0 pollock for an energetic model (Siddon & Mueter). We also provided specimens for fish energetics (Heintz).

As our project involved 3 years of data collection prior to extensive analysis, our results mismatched the timing of some other projects. For instance, while our work is directly related to the Patch Dynamics group (particularly Benoit-Bird and Heppell’s work), their projects were completed prior to completion of our analyses. A combined effort examining distributions and dynamics of forage fish may have been more comprehensive and provided additional insight than through individual efforts. We were also unable to contribute data to some of the larger-scale analyses (e.g. predator distributions, species community compositions) that used existing data or trawl survey data that did not require extensive processing times.

**Management or policy implications**

Results from our BSIERP-B59 project have provided key information to managers on potential survey and analytic methods for evaluating forage fish for future reports, analyses, and ecosystem modeling. Our BSIERP-B59 study (with support from NPRB-1006) combined acoustic, midwater trawling, and BASIS surface trawling to address three critical needs; To compare abundances indices between surface trawl and acoustic estimates, to identify potential shifts in vertical distribution that may impact surface or...
bottom trawl survey results, and to evaluate factors affecting horizontal distribution of forage fish that
may influence survey or analytic decisions.

Forage fish catches from the BASIS surface trawl survey have been used and/or cited as measures of
relative abundance and for analyses on factors affecting their distribution (see Chapter 1 and Chapter 2, Ormseth, 2012). During 2009, the Science and Statistical Committee within the North Pacific Fishery Management Council requested that the Alaska Fisheries Science Center provide annual Stock Assessment and Fishery Evaluation (SAFE) reports on Bering Sea and Aleutian Islands (BSAI) forage fish to the Council for review. The preliminary assessment of forage fish in the BSAI (Ormseth, 2012) included CPUE of forage fish by region, distribution maps from surface and bottom trawls and NOAA acoustic surveys, and indices of abundance. Fish species included in the forage fish group are now classified within a federal Fishery Management Plan to prevent fishing-related impacts to the forage base in the BSAI as part of an ecosystem approach to management.

A preliminary comparison between age-0 walleye pollock surface trawl estimates of densities and surface acoustic density estimates suggested there was a relationship (linear model adjusted $R^2=0.45$, n=54 paired points from 2008-2010 within the 2008 study area only) between the two. However, surface trawl estimates were a median of 2.7% (min=0, max=1014, n=54) of the acoustic estimates, indicating that surface trawl substantially underestimated age-0 pollock densities at most locations.

Our analysis of the acoustic data also suggests that in the deep water of the middle and outer domains, age-0 walleye pollock densities were much greater below the depth of the surface trawl. For example, in 2009 and 2010, a large biomass of age-0 pollock was located below the footrope of the surface trawl and was not included in the CPUE data used to calculate the surface trawl abundance index. To the surface trawl, these were stations (and interpolated areas) of low abundance, but in the analysis using acoustic (i.e. whole water column) data, these regions often had some of the highest densities. Our analysis demonstrated that without a whole water column survey, characterizations of distribution based on the surface trawl and/or bottom trawl may be biased in some years or regions.

Predicting distributions of forage fish, and how distributions may change annually and/or in response to trends associated with climate change, could inform forage fish surveys, the recruitment of some commercially harvested species, and the management of upper trophic levels who rely on forage fish as prey. Although many studies have tested and/or speculated on what factors affect distributions of forage fish, the list of variables used in individual studies have been limited. Our analyses confirmed some
previous conclusions but also emphasized that the collective understanding of how local, annual, and regional factors affect forage fish distributions is much weaker than previously thought. This finding underscores the importance of dedicated forage fish biophysical studies if the ability to predict forage fish distributions and relative abundances are needed to support resource management and/or modeling efforts. While this study was restricted to the Bering Sea, we feel that the conclusions are equally applicable to the Gulf of Alaska and Arctic waters.

Publications

Published

In preparation

Poster & oral presentations at scientific conferences or seminars
Outreach
In concert with NPRB-1006 (which included Lisa Eisner as PI), we worked with the Oceanography 101 classes participating in the University of Washington’s ‘UW in the High School’ program. The three participating classes were Everett High School (Everett, WA), Ballard High School (Seattle, WA), and Winlock High School (Winlock, WA). This collaboration was facilitated by UW Professional & Continuing Education. Before the 2010 BASIS survey, we met with the teachers and provided them with an outline of the project and its objectives, list of specimens we could obtain, videos of the various gears being deployed, established criteria for making contact, and provided introductory videos by Parker-Stetter and Horne. While at sea, Parker-Stetter blogged the survey and answered questions from Ballard HS. Following the survey, specimens were distributed to all three classes and Horne did an in-class presentation summarizing the sampling and data from the 2010 survey to the Everett High School class.

In spite of numerous requests, none of the PIs were able to attend BSIERP-related outreach events or visit Alaskan coastal communities participating in the BSIERP program.

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NOAA-AFSC is gratefully acknowledged for its in-kind support of this project. The authors thank the Chief Scientists, scientific staff, Captains, and crews on the Epic Explorer, Northwest Explorer, Sea Storm, and the NOAA ship Oscar Dyson during 2006-2010 surveys. We also thank the NOAA-MACE program (Seattle, WA) for use of equipment and software during 2008-2010 and for providing calibration data for scientific echosounders. The NOAA-FEDZ Laboratory (Juneau, AK) is recognized for their assistance in species identification. We thank Jeff Napp (NOAA), Alex De Robertis (NOAA) and four anonymous reviewers for constructive comments that improved the final version of Chapter/Manuscript 1. The authors also thank Matt Baker (NOAA Alaska Fisheries Science Center, NOAA-AFSC), Seth Danielson (University of Alaska Fairbanks), Janet Duffy-Anderson (NOAA-AFSC), Sigrid Salo (NOAA-AFSC), and Tracey Smart (South Carolina Department of Natural Resources) for providing supplementary data that were used in the analysis for Chapter/Manuscript 2. We also thank Tim Essington (University of Washington), Ben Stewart-Koster (Griffith University), and Steve Barbeaux...
(NOAA-AFSC) for helpful model selection discussions that ultimately influenced our approach in
Chapter/Manuscript 2. The findings and conclusions in this paper are those of the authors and do not
necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade
names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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