Delineating yellowfin sole (*Limanda aspera*) reproduction in the northern Bering Sea provides information across the eastern Bering Sea continental shelf

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Abstract

Yellowfin sole (*Limanda aspera*) is an abundant, commercially harvested flatfish that ranges across the northern and southeastern Bering Sea continental shelf. In recent years, the summer bottom trawl survey of the southeastern Bering Sea (SEBS) conducted by the National Marine Fisheries Service's Alaska Fisheries Science Center (AFSC) extended into the northern Bering Sea (NBS) in August. This opportunity allowed for describing yellowfin sole reproductive parameters in the NBS, such as female length and age at maturation, reproductive status, and sex ratio distribution. Estimates of 50% female sexual maturity were 10.11 years (A_{50}; 95% CI: 9.47 - 10.76 years; n = 209) and 28.47 cm (L_{50}; 95% CI: 27.16 - 29.68 cm; n = 212). Histology indicated much of the mature population was approaching the end of spawning. Yellowfin sole spawning timing (summer) appears to be synchronous across the NBS and SEBS. There is evidence that part of the yellowfin sole spawning population in the NBS is connected to a recognized spawning migratory group from the SEBS. A higher proportion of females than males was observed, which varied by year and stratum. This was negatively related to warmer bottom temperature and positively related to location (western longitudes and northern latitudes). Yellowfin sole females in the NBS exhibit a similar size and age of maturation, depth of spawning, and sex ratio proportions with those females inhabiting the SEBS. These results provide further information for fisheries managers on the yellowfin sole stock throughout this region. Spatial and temporal aspects of reproduction, however, should be more thoroughly investigated.

Keywords: Yellowfin sole, northern Bering Sea, reproductive status, population structure, maturity, sex ratio

1. Introduction

The eastern Bering Sea (EBS) continental shelf is broad with two major cross-shelf domains, the southeastern Bering Sea (SEBS) and the northern Bering Sea (NBS; Sigler et al., 2015), each exhibiting unique biological and oceanographic processes. The SEBS consists of three main oceanographic domains (inner, 0−50 m; middle, 50−100 m; and outer, 100−200 m), with distinct oceanic and biological patterns (Stabeno et al., 2001). An important hydrographic feature is a subsurface cold pool of water (<2°C), formed by melting of the previous winter's sea ice, that can extend southward through the middle domain during the summer. This cold pool is a dominant factor influencing fish distributions (Mueter and Litzow, 2008; Kotwicki and Lauth, 2013). This area has recently shifted towards a pattern of multi-year temperature stanzas with warm periods (2002–2005, 2014–2019) separated by a cold period (2006–2013; Stabeno et al., 2012a, 2012b, 2017). However, in the NBS warmer surface and bottom water temperatures occur, especially along the broad inner shelf that dominates this area (Lauth, 2011; Lauth et al., 2019). Much of the trawl survey area of the NBS has a bottom depth of ≤50 m, shallower than the SEBS. Conditions are less variable in the NBS, with sea ice covering this area for longer periods (Stabeno et al., 2012a; Stabeno et al., 2018). In recent years, there have been observations of a northward shift in the pelagic-dominated ecosystem in the NBS (Grebmeier et al., 2006).

To address concerns about climate change and its impacts on the EBS continental shelf ecosystem, the Alaska Fisheries Science Center (AFSC) developed a Loss of Sea Ice (LOSI) Research Plan (Hollowed et al., 2007). Its primary objective is to conduct a series of bottom trawl surveys of the NBS to collect baseline biological and distribution data for many ecologically and commercially important species (Lauth, 2011). The AFSC conducted a LOSI survey of the NBS in 2010, and 2017–2019 (Sigler et al., 2015). The approximate coverage of the NBS surveys is from St. Matthew and Nunivak Islands to the south, the U.S.-Russian Maritime Boundary to the west, and north to the Bering Strait (Lauth, 2011).

The flatfish (Pleuronectidae) fauna of the EBS continental shelf is comprised of several species. A few species are particularly abundant, commercially important, and represent vital components of the benthic fish community. Yellowfin sole (*Limanda aspera*) is an abundant flatfish in the EBS, accounting for roughly a third of the total flatfish biomass (Lauth et al., 2019). This species is the target of the largest flatfish fishery in the world, with annual catches exceeding 100,000 metric tons on average since 1991 (Spies et al., 2019). In 2020, the fishery catch totaled 290.5 million pounds with a value of $60 million (Retrieved January 2022 from https://www.fisheries.noaa.gov/species/yellowfin-sole#overview). Yellowfin sole stock structure has not been clearly defined but the species is currently considered a single stock throughout the U.S. Bering Sea management area (Grant et al., 1983; Wilderbuer et al., 1992; Spies et al., 2019).

Reproductive biology is integral to population dynamics and therefore an essential component of fisheries management (Lowerre-Barbieri et al., 2011). Reproductive traits such as size and age at maturation are used as indices to measure productivity, and are key to estimating spawning stock biomass (Hilborn and Walters, 1992; Morgan, 2008). As we move towards ecosystem-based fisheries management, knowledge of spatial and seasonal spawning dynamics is increasingly important for improving management (Marshall et al., 2019). Spatial understanding of sex ratio provides information on population dynamics and productivity

(Kraus et al., 2002; Young et al., 2003). Identifying varying scales of temporal and spatial distribution, changes in the demographics of a spawning stock, and movement patterns contributes to more informed management strategies. Spatial segregation on size or sex, determines population structure, and these relationships may be variable under different environmental regimes (e.g., Maxwell et al., 2019).

Key parameters of the reproductive biology of yellowfin sole have been broadly studied in the SEBS due to the ecological and commercial importance of this abundant species. Yellowfin sole exhibit sexual dimorphism in body size, which is typical of many pleuronectids, with females larger than males. Yellowfin sole are group-synchronous batch spawners, as evidenced by a separate distribution of completely yolked oocytes in more advanced ovaries (Nichol and Acuna, 2001). In the SEBS, yellowfin sole exhibit peak spawning during the months of June and July. The spawning season has been observed to start as early as March and ending in August (Nichol, 1995; Nichol and Acuna, 2001; TenBrink and Wilderbuer, 2015) or ending as late as September for a fraction of the population (Waldron, 1981). Timing of the spawning cycle may be related to bottom temperature (Nichol et al., 2019) and vary annually (Wilderbuer et al., 1992; Nichol, 1998; Nichol et al., 2019). Spawning distributions of yellowfin sole may shift due to variable warm and cold years (Porter, 2021). Tagging studies have shown that distinct population groups in the SEBS migrate from wintering areas off the continental shelf-slope break to nearshore waters to spawn, with one group believed to spawn north of Nunivak Island within the NBS survey area (Wakabayashi, 1989). This annual adult migration is thought to be timed with the receding ice edge (Bakkala, 1981). Yellowfin sole are known to spawn in depths of less than 25 m, although they have been observed spawning as deep as 50–60 m (Wilderbuer et al., 1992; Nichol, 1995), with females moving off into deeper waters after spawning (Nichol and Acuna, 2001). Proportions of females have been shown to increase with depth during warmer years, where spawning has shown to occur earlier with subsequent migration to deeper waters (Nichol et al., 2019). TenBrink and Wilderbuer (2015) published an updated estimate of age at 50% maturity (A_{50}) twenty years after Nichol's (1995) study and found similar results (10.1 vs. 10.5 years). Current calculations of spawning stock biomass for fisheries management uses a maturity schedule derived from both of these studies (Spies et al., 2019).

Recent surveys of the NBS provided an opportunity to collect data on the reproductive biology of yellowfin sole and to compare key parameters with our existing knowledge from the SEBS. Reproductive patterns for yellowfin sole, including trends in the structure of the population during warm and cold years, are currently unknown in the NBS. For this study, I examined three key reproductive parameters: 1) length at 50% maturity (L_{50}) and A_{50}; 2) assess female reproductive status from late summer collections; and 3) population structure through sex ratio modeling.

2. Material and methods

2.1 Field collections and study area

Yellowfin sole specimens were obtained during bottom trawl surveys of the NBS conducted by the AFSC during August 2010, 2017, and 2019. These three surveys represent the full spatial coverage years of this area (note: 2018 was excluded due to only partial spatial coverage). These surveys were extensions of the annual SEBS survey with a coverage area bounded by the U.S.-Russian Maritime Boundary, the Bering Strait and Norton Sound, south to

Nunivak Island (Fig. 1; Lauth et al., 2019). The NBS survey is divided into three strata: an area north of St. Lawrence Island (71) including Norton Sound, and two strata south of St. Lawrence Island separated by the 50-m isobath (70 and 81; Fig. 1). Standardization of bottom trawl gear and survey design methodologies followed the protocols in Stauffer (2004). The survey design consisted of a transect of stations approximately 20 nautical miles apart along a fixed sampling grid. Each station tow was centered within a grid and performed for 30 min, totaling 144 stations. Bottom temperatures (°C) and bottom depth (m) were measured at each station. Catches estimated to be ≤ 1150 kg (2500 lbs) were individually sorted and tallied, while larger catches were weighed and subsampled prior to sorting (Lauth et al., 2019). When yellowfin sole were present, sex and fork length (cm) were recorded from a random subsample of up to approximately 300 specimens per station.

In 2017, otoliths were extracted for age determination and whole ovaries collected to investigate aspects of reproductive biology using a length-stratified sampling scheme. After the random subsample of yellowfin sole for sex and length measurements, otoliths and ovaries were then taken with a target number of 5 per 1 cm length bin. Every attempt was made to distribute the collections across the survey area. Station location information for each sample was recorded. Macroscopic assessments using visual keys to describe ovary condition were not conducted. Ovaries were fixed in 10% formalin for storage, while otoliths were stored in vials of a 50% glycerol thymol solution prior to laboratory processing (see Lauth, 2011).

2.2 Histology staging and maturity

Histological analysis of one ovarian lobe was conducted, from slides stained with hematoxylin and eosin (H&E) using 40× to 100× magnification. Ovaries were assigned a maturity status (0 = immature; 1 = mature) based on histological features from Nichol (1995) and TenBrink and Wilderbuer (2015; Table 1). Quality control of histological analysis included blind double reads by the same reader (TTT) on all samples from the original analysis to measure the precision of the author's descriptions and variability in assignments (Cohen's Kappa coefficient; Fallisard, 2015). A minimum value of 0.80 was the accepted level of performance, defined as 'near perfect agreement' by Landis and Koch (1977). Histological features were categorized into reproductive phases using the standardized terminology of Brown-Peterson et al. (2011). Observations of atretic stages (i.e., resorption of oocytes that are not released; early-stage [alpha, α] and late-stage atresia [beta β, gamma γ and delta δ]) were recorded and based on histological characteristics following Hunter and Macewicz (1985). Females exhibiting abortive maturation were mainly characterized by mass atresia of primary vitellogenic (Vtg1) oocytes, identified by the presence of extensive α-atresia, with no evidence of late-stage atresia or prior spawning (Table 1, phase 1). Abortive maturation attempts by first-time spawners were recorded. Females that exhibited abortive maturation were considered to be in a non-reproductive phase and categorized as 'immature'. Ovaries from skip spawning females, exhibited by the resorption of oocytes before the completion of vitellogenesis, presence of post ovulatory follicles (POFs) and a high percentage of late-stage atresia (Rideout et al., 2005), were not observed in this study. A fish was defined as mature if there was evidence that spawning would occur during the current reproductive year or if evidence suggested that the fish had spawned in the current or recent reproductive cycle (Brown-Peterson et al., 2011; Table 1, phase 2-5).

Maturity data were fitted with logistic regression to estimate L_{50} and A_{50} at 50% maturity with generalized linear modeling (GLM) based on binomial data (0 = immature; 1 = mature) using a *logit* transformation. The equation for the proportion of mature females (M) was:

$$M = \frac{1}{(1 + e^{-\delta(x - x_{50\%})})}$$

where M is the estimate of the proportion mature at length or age, δ is the parameter that describes the slope of the logistic curve and $x_{50\%}$ is the length or age at which 50% of the fish are mature. A weighted GLM for the proportion mature at age was incorporated due to the length-stratified sampling; observations were weighted by the abundances of the size groups (Morgan and Hoenig, 1997). Confidence intervals (CIs) for the maturity ogives were estimated through bootstrapping methods by resampling cases 10,000 times (Ogle et al., 2018). Regression diagnostics included plots with Cook's distance measures that were used to identify GLM model influential data points ≥ 1 (Fox and Weisberg, 2019). An analysis of deviance was used to evaluate logistic regression model fits and measure the difference between models with the full model maximizing the log-likelihood function. Maturity-at-age estimates were based on age determinations and criteria following quality control protocols in Matta and Kimura (2012).

2.3 Reproductive status

Reproductive status of the population of NBS yellowfin sole captured in August was assessed. Due to the limited temporal resolution from the collections, a general evaluation of yellowfin sole reproduction was provided for this study (Table 1). In the NBS, spawning females were identified by a number of histological characters, including the presence of POFs, oocytes exhibiting tertiary vitellogenesis (Vtg3) , germinal vesicle migration, and those females exhibiting hydration (HY) or ovulation (Table 1, phase 3a, 3b). Females that exhibited a leading cohort of non-atretic oocytes (oocytes with yolk coalescence or HY) with no trailing Vtg3 or germinal vesicle migration cohort were considered to be in their final batches. Based on observations in this study and our current knowledge of yellowfin sole reproduction in the SEBS, a spatial map of yellowfin sole reproduction in the NBS was constructed. This map also incorporated recent information on larval transport modeling (Laman et al., 2017) and observations of the occurrence of eggs and early-stage larvae (Busby et al., 2015; Busby et al., 2017; Logerwell et al., 2020; Porter, 2021).

2.4 Sex ratio modeling

Sex ratio distribution was investigated as a means to assess yellowfin sole population dynamics in the NBS. After initial examination of the data, generalized linear mixed effects models (GLMMs; Bates et al., 2015) were used to describe possible variation in sex ratio. GLMMs are an extension of generalized linear models (GLMs) that include both fixed and random effects and allow testing for trends from repeated measurements, such as those found in fishery surveys. These models have been widely used in fisheries research and the analysis of biological data (Bolker et al., 2009).

Sex ratio models evaluated female presence from the total number of fish caught using a binomial response variable (presence [female] = 1; absence [male] = 0) and a logit link function. Stations that had at least 10 total fish caught, regardless of sex, were included in the GLMM analysis. Observations were weighted based on the total number per station to overcome any spatial heterogeneity from sampling. For each model, station was assigned as the random effect to control for the non-independence of fish caught from a single location.

I evaluated two GLMMS: 1) broad-scale spatio-temporal variation, and 2) environmental predictors to assess variable warm and cold years on sex ratio. For the first GLMM, categorical variables year and stratum with three levels were treated as fixed effects. Additional fixed effects included continuous variables of latitude and longitude. To address collinearity, fixed effects were examined using Pearson's correlation coefficient, with maximum scores of 0.7 being the limit for model incorporation (Dormann et al., 2013). All values were below this maximum so all variables were retained in the models. Models with different combinations of fixed effects were compared with Akaike's Information Criterion (AIC) with the lowest AIC being considered the optimal model. The second GLMM was evaluated as a single model, with year added as a predictor to assess sex ratio differences among survey years with variables, bottom and sea surface temperatures. Bottom and sea surface temperatures were moderately correlated (0.55), but a likelihood ratio test suggested model improvement with the addition of sea surface temperature. Bottom depth had a strong negative correlation with bottom temperature (-0.76), so it was excluded from the second model. Model performance was controlled using a bound optimization by quadratic approximation (BOBYQA, nAGQ = 0) rather than Laplace approximation. No interactions were included with the fixed effects. Full models followed these general matrix notations:

$$Y_{ij} = \beta_0 + \beta_1 Year_{ij} + \beta_2 Stratum_{ij} + \beta_3\, Latitude_{ij} + \beta_4 Longitude_{ij} + \mu_1 Station_j$$

$$Y_{ij} = \beta_0 + \beta_1 Year_{ij} + \beta_2 Bottom\ Temperature_{ij} + \beta_3 Surface\ Temperature_{ij} + \mu_1 Station_j$$

where *Y* is the proportion of females from *i*-th fish at station *j*, β_0 was the intercept, β_{ij} denotes model fixed effects, and μ_1 is the random effects intercept at station *j*. The GLMMs used here and all other data analyses were conducted from various packages in R v. 3.6.3 (R Core Team, 2020).

3. Results

3.1 Field collections

Of the total yellowfin sole specimens measured during the three survey years, 19,094 were females and 13,835 were males, indicating an overall 1.37:1 sex ratio of females to males (Table 2). Yellowfin sole distribution by year was variable with specimens exhibiting a more westerly distribution during the most recent surveys in 2017 and 2019 (Supplementary Fig. S1). A total of 212 ovaries from yellowfin sole females were collected in 2017 (Table 2). Sizes of these females ranged from 16 to 47 cm and were captured across the depth range (12-60 m) of the NBS survey area (Fig. 2). Both mature (15-55 m) and immature fish (12-60 m) occupied similar depths. Mature females were generally equally distributed across the depth range, with a few of the larger, older mature females remaining in shallower depths (Fig. 2). Larger immature females (25-35 cm) were generally found in deeper waters (Fig. 2).

3.2 Maturity

A total of 91 females were classified as 'immature' and 121 females were classified as 'mature'. Precision from maturity assignments was calculated at 0.90 (95% bootstrapped CIs: 0.83, 0.95). Logistic regression models were compared between the original and blind histological analysis and indicated there was no significant differences in model fits for either length or age (Analysis of deviance, $P > 0.05$). The GLM results indicated that the percent deviance accounted for by the combined NBS models was 52% for the length at maturity analysis and 44% for the age at maturity analysis. The NBS model resulted in a L_{50} of 28.47 cm (95% CIs: 27.16, 29.68; Table 3; Fig. 3) and an A_{50} estimate of and 10.11 (95% CIs: 9.47, 10.76 years; Table 3; Fig. 3), with 90% of the population mature at a length of 35.15 cm (95% CIs: 33.25, 36.98 cm) and age of 13.30 years (95% CIs: 11.86, 14.76 years). The length data was more variable than the age data with some small mature (< 20 cm) and larger immature fish present (≥ 30 cm; Fig. 3).

3.3 Reproductive status

The 212 females used to describe reproductive status were collected from 39 different stations spread throughout the survey area (Table 4). Immature and regressing females were distributed across the NBS survey area (Fig. 4) while nearly all females that were actively spawning were clustered in the southeastern portion of the survey area, with the exception of a single spawning female captured at a location south of St. Lawrence Island (Fig. 4). Spawning females were observed throughout the sampling month of August. Active spawning females represented 14% of the total mature females collected and were generally older and larger females (17 of 121; Table 4). Five females were observed undergoing a reproductively inactive or regeneration phase prior to beginning the initial developing period for the next reproductive cycle. Depth occurrence by reproductive phase indicated spawning females in nearshore or shallow areas (20-55 m; mean = 25.5 m; Table 4), and regressing females in deeper waters after spawning (15-60 m; mean = 35.5 m; Table 4). Females exhibiting abortive maturation characteristics were found to occupy similar depths as spawning females (15-36 m; mean = 26.5; Table 4).

A general map of the spawning distribution of yellowfin sole in the NBS was constructed, indicating connectivity between the SEBS and NBS (Fig. 5). Actively spawning females observed in this study likely represent the adult migration group that is present north of Nunivak Island in the southern area of the NBS (Fig. 5). Females are likely to occupy the shallower waters for spawning in the NBS prior to any migration into deeper waters, as indicated by the mean depth of spawning from this study (25.5 m; Table 4; Fig. 5).

Histological examination of ovary condition showed that female yellowfin sole were entering a largely post-spawning period in August (Table 4; Fig. 6A-D). Ovaries from spawning females exhibited a fairly distinct “clutch” of advanced oocytes, group-synchronous batch spawning: Vtg3, HY, and POFs (Fig. 6B). For the active spawning female population, the presence of at least α and β-stage atresia was noted in all 17 females exhibiting atresia, including POFs, indicating that these females had already released previous batches. Of the active spawning females, a total of three were observed spawning a final batch, primarily identified by an ovary exhibiting a leading advanced oocyte cohort (Vtg3 or nucleus migration) with no evidence of a recruiting cohort to be spawned. Ovaries of regressing females exhibited characteristics such as atretic Vtg3 oocytes, remnant HY oocytes, areas of ovarian lumen (L), and POFs (Fig 6C, D).

3.4 Sex ratio modeling

Observations of yellowfin sole per station ranged from 10 to 323 fish. The proportion of female yellowfin sole exhibited variability across the NBS. The full GLMM model of spatio-temporal variables was the best performing model, which accounted for 98% of the AIC weight (Table 5). Proportions of females were variable across years and strata (Fig. 7; Table 6). Patterns emerged across the NBS, where proportions of females throughout the study period were greater at higher latitudes and further west (> 70%). Females were in greater proportion at higher latitudes during the cold year of 2010 by > 5%, but were similar in proportion for all years across the survey area, increasing from east to west (Fig. 7). There was a negative correlation between higher female proportions and bottom temperature for each year (Fig. 8). During the cold year of 2010, a greater proportion of females were observed, by approximately 10%, where the highest bottom and surface temperatures were recorded, corresponding to shallower depths where spawning might be occurring. During the warm years of 2017 and 2019, females were in smaller proportions relative to 2010, indicating that spawning (and migration away from nearshore areas) was more progressed.

4. Discussion

Results from this study suggest that yellowfin sole exhibits similar spawning timing and bathymetric distribution patterns across the EBS continental shelf. In the NBS, only a small percentage of yellowfin sole females were actively spawning or spawning final batches in August, while much of the mature population had completed spawning. This observation is consistent with previous studies from the SEBS that suggested spawning likely ends during this late summer period (Wilderbuer et al., 1992; Nichol, 1995; Nichol and Acuna, 2001; TenBrink and Wilderbuer, 2015). The bathymetric distribution of females in the NBS followed a size-depth relationship similar to what is observed in the SEBS (Nichol, 1997), including the relationship with reproductive phase and depth of occurrence (Nichol, 1995). Given the relatively shallow bathymetry of the NBS compared with the SEBS ecosystem, much of the area might be favorable as a spawning ground north and south of St. Lawrence Island and into Norton Sound, but it is likely females migrate to shallower areas for spawning (Nichol, 1995).

Climatic changes such as a rise in bottom temperature have been known to create shifts in spawning phenology and distribution (e.g., McQueen and Marshall, 2017; Rogers and Dougherty, 2018). For yellowfin sole, spawning is generally followed by feeding during late summer and fall migrations to deeper waters (Wakabayashi, 1989). Temporal shifts in spawning migrations and peak spawning events have the potential to disrupt migration timing to offshore feeding grounds. It was not possible to determine a seasonal shift in spawning phenology of NBS yellowfin sole from this study, but annual shifts in peak spawning are apparent between warm and cold years in the SEBS, where progression of spawning is dependent on mean annual bottom temperatures (Nichol et al., 2019). Our results suggest that there is a temperature effect on spawning distribution in the NBS between cold and warm years, with a relatively higher proportion of females present along the spawning grounds in the cold year of 2010 during the end of spawning (August), where a delay in spawning might have occurred. Under warmer conditions, the distribution of spawning areas may expand because of favorable temperatures extending offshore and northward (Bartolino et al., 2011; Porter, 2021). It is possible that yellowfin sole oogenesis is temperature-dependent, and oocyte development occurs earlier in warmer temperatures, as seen in the congeneric species common dab *Limanda limanda* (Lange and Greve, 1997). Increased warming may decrease the annual sea ice period in the EBS, potentially leading to more variable conditions that could alter spawning timing (e.g. Smart et al., 2012; Neidetcher et al., 2014).

With the NBS likely becoming a more frequent area for monitoring by trawl surveys, knowledge of the spatial structure and distribution of the stock will be critical for management (e.g., Punt, 2019; Cadrin, 2020). In this study, locations of active spawning females in the NBS suggests spatial connectivity with the SEBS. A large percentage of spawning females were observed in the southeastern portion of the NBS survey area north of Nunivak Island in approximate locations that appear to form part of the Pribilof-West migratory population group (Wakabayashi, 1989; Wilderbuer et al., 1992). Spawning females from this group are known to migrate southwest offshore to deeper waters into the SEBS. Observations of these larger-scale spatial movements of the yellowfin sole is not unique to *Limanda* spp. Rijnsdorp et al. (1992) showed from tagging experiments with dab (*Limanda limanda*) in the North Sea that movement to offshore waters occurred after aggregating in shallow coastal areas. Such movement is also seen in the yellowtail flounder (*Limanda ferruginea*) in the western North Atlantic (Wood and Cadrin, 2013).

Aside from the presence of spawning females observed in this study, documented egg and larval presence further suggests connectivity between the SEBS and NBS. Field collections of ichthyoplankton samples accompanied by modeled drift patterns of larval distribution have identified potential spawning grounds. Wilderbuer et al. (1992) reported on the presence of eggs found north of Nunivak Island. Yellowfin sole early-stage larvae (< 4 mm) were present during the months of July through September in the NBS between Nunivak Island and Norton Sound at bottom depths of ≤ 30 m (Porter, 2021), with large larval catches north of St. Lawrence Island (Busby et al., 2017). Yellowfin sole larvae and egg presence in the NBS are the result of northward transport from the Alaska Coastal Current from the SEBS (Laman et al., 2017; Logerwell et al., 2020). Further north, Busby et al. (2015) found that yellowfin sole larvae were the dominant component of a southern, nearshore assemblage in the Chukchi Sea, strongly associated with the northward flowing Alaska Coastal Current. Eggs and early-stage larvae are likely to be transported into the Chukchi Sea from the NBS; however, recent collections of very early stage eggs of yellowfin sole that had been recently fertilized almost certainly would mean a resident population in the Chukchi Sea (Pers. Comm., Morgan S. Busby, Alaska Fisheries Science Center. 16 October 2020). Population-level genetic analysis would help resolve this, but if the divergence was very recent, it might not be detectable (Pers. Comm. Morgan S. Busby, Alaska Fisheries Science Center. 16 October 2020).

Some yellowfin sole females may be capable of spawning more than a single series of batches in the SEBS (Nichol and Acuna, 2001). While multiple groups of advancing oocytes were not observed in this study, typical of fishes that exhibit indeterminate fecundity, a small percentage of spawning females (6%) examined by Nichol and Acuna (2001) appeared to have the potential to recover spent ovaries and spawn another series of batches (Nichol and Acuna, 2001). The presence of residual chorion tissue (egg envelope) from unspawned ova in females appeared to be the marker that indicated females had spawn at least another series of batches. The presence of these characteristics, however, was inconclusive for NBS females, perhaps due to sampling an end-of-spawning population where presence of this tissue would be less visible. Additional studies throughout the EBS, however, are needed to corroborate evidence that females are capable of releasing more than a single series of batches. For yellowfin sole, a highly fecund species, the ability to release a second batch would have a potentially large effect on estimates of stock reproductive potential for management. This is especially true if total egg production is to be considered as the method for estimating stock reproductive potential rather than spawning stock biomass (e.g., Kell et al., 2016).

Bias in estimates of length and age at maturity can arise when spatial distributions of mature or immature fish within a population are not accounted for in the analysis (e.g., Williams et al., 2016). Biased maturity ogives can affect calculations of spawning stock biomass and fisheries management reference points. Bottom trawl research surveys in the SEBS have not typically covered the shallowest nearshore areas of yellowfin sole distribution during June and July each year, when peak spawning may be occurring. For this reason, Nichol (1997) suggested that previous estimates of yellowfin sole L_{50} (30.7 cm) and A_{50} (10.5 yrs; Nichol, 1995) might be biased high as larger, older immature fish were more abundant in the deeper waters sampled by the survey. Wilderbuer et al. (1992) calculated a similar length estimate of 28.8 cm from summer survey collections where depth-sampling issues might also occur. TenBrink and Wilderbuer (2015) calculated similar estimates of L_{50} (29.6 cm) and A_{50} (10.1 yrs) from collections in March and April in the SEBS, prior to any large-scale ontogenetic distribution shifts to nearshore waters. Proportions of mature females within each age class were relatively consistent between Nichol's (1995) and TenBrink and Wilderbuer's (2015) estimates (Spies et al., 2019). The survey area of the NBS includes sampling stations as shallow as 11 m, likely shallow enough to capture many active spawning females or those that had spawned. In this study, estimates of L_{50} (28.5 cm) and A_{50} (10.1 yrs) showed little deviation from known estimates of maturation across the EBS continental shelf. From a management perspective, these results indicate that calculations of spawning stock biomass from maturity-at-age estimates should continue to be represented by a single calculation derived from both the SEBS and NBS.

Despite similar estimates across the EBS continental shelf, maturity is not fixed, but time variant. Variability in maturity and other life history parameters (such as growth) is likely to occur, especially given the unique and often cyclical oceanographic characteristics of the SEBS and NBS. Maturity has often been correlated with growth (e.g., Stearns and Crandall, 1983; Froese and Binohlan, 2000). Yellowfin sole growth is strongly influenced by bottom temperature of the SEBS (Matta et al., 2010), and a south to north pattern has been observed with reported age-length relationships, with fish growing slower to greater lengths at higher latitudes (Matta et al., 2016). Additionally, the yellowfin sole stock is currently managed with growth modeling varying year to year, given the age and year effect on growth (Matta et al., 2010; Wilderbuer et al., 2014; Spies et al., 2019). Yellowfin sole weight at age exhibits variability and is highly correlated with summer bottom water temperature with a lag of 2-3 years. Determining a year effect on estimates of maturity was not possible in this study, but given that growth can be affected by a variety of biotic and abiotic factors such as prey availability and bottom temperature, it is likely that maturity will also vary in response to these factors. Changes of this nature need to be adequately modelled in assessments if their effects are large. For the yellowfin sole analyzed in this study, responses in reproductive processes (e.g., sex ratio distribution) were evident between varying spatial and temporal temperature regimes among years. The need to monitor how length and age at maturity varies is also clearly important.

Understanding variability in life history parameters are essential for sustainable management of marine species. Results from this study are important for yellowfin sole stock management across the EBS continental shelf. Poleward shifts in the distributions of many species have occurred with warming in the northern hemisphere (Nye et al., 2009; Stevenson and Lauth, 2019). Shifts in distributions may include a northward migration to the NBS where likely a commercially exploitable abundance of yellowfin sole already resides. Aside from estimates of their abundance and general distribution, little has been known about the life history of yellowfin sole on larger spatial scales. This information is critical if two separate reproductive stocks were to be discovered, leading to possibly separate management reference points. The yellowfin sole population in the EBS is currently managed as a single stock (Spies et al., 2019). Based on previously published information and the results of this study, there appears to be mixing across the EBS continental shelf to continue to support current management practices of a single spawning stock. Additional work is needed to fully evaluate yellowfin sole reproduction and productivity in the NBS, including multi-year sampling that would corroborate results here and determine the level of variability during different environmental conditions. Other tools, such as tagging, otolith chemistry and morphology, and genetics should also be explored as a multidisciplinary approach to evaluate stock structure (e.g., Begg and Waldman, 1999).

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Table 1. Reproductive phase, maturity status and histological description of the ovarian condition and oocyte stages of female yellowfin sole (*Limanda aspera*) from the northern Bering Sea (NBS), modified from Nichol (1995) and TenBrink and Wilderbuer (2015). MAGO = most advanced group of oocytes. Phase terminology from Brown-Peterson et al. (2011).

Phase	Maturity Status	Main Histological Description
1. Immature	Immature	Primary growth oocytes (PG), including oogonia, early and late perinuclear stages; cortical alveoli (CA) also present. These stages often dominant. Thin ovarian wall (OW). Lamellar structure generally organized. No indication of previous spawning. Females with primary vitellogenesis (Vtg1) as the MAGO late in the spawning season with no visible signs of spawning in the current cycle are assigned here. Abortive mature females with mass α-atresia of Vtg1 oocytes, no late-stage atresia or post-ovulatory follicles (POFs). Atresia generally absent or minimal if no abortive attempt was made.
2. Developing	Mature	Vtg1 and/or secondary vitellogenesis; small yolk globules or drops begin to form along the periphery of oocytes, with a stronger globule presence as oocytes enlarge, with the larger globules moving inward towards the nucleus. Atresia may be present. No POFs.
3a. Spawning-Capable 3b. **Active Spawning*	Mature	Tertiary vitellogenesis (Vtg3): yolk globules cover large majority of oocyte cytoplasm; some oocytes exhibiting nucleus or germinal vesicle migration; oocytes are becoming larger, with a noticeable size difference compared with primary growth oocytes. Atresia of advanced-stage oocytes may be present. Thick ovarian wall. *Hydrated oocytes (HY) and ovulation present in spawning females. POFs may be present. Distinct batches may be present. Leading MAGO oocyte cohorts with large size discrepancies from primary growth stages.
4. Regressing	Mature	POFs present. Thick OW. All stages of atresia may be present. Residual and/or atretic late-stage oocytes present, including HY. Muscle bundling, lamellar disorganization, and intermittent areas of blood vessel presence. Large areas of ovarian lumen (L). PG, CA, primary and secondary vitellogenesis observed, but no leading advanced-stages that would constitute an upcoming batch.
5. Regenerating	Mature	PG oocytes and/or CA present. No vitellogenesis. Thick OW. Late-stage atresia and muscle bundling may be present. POFs largely absorbed and not observed. Large areas of L present.

Table 2. Number of yellowfin sole (*Limanda aspera*) specimens measured and identified to sex in the northern Bering Sea (NBS) in 2010, 2017, and 2019. Numbers in parentheses from 2017 indicate those females collected to investigate length and age at maturation and to describe reproductive status.

Year	Stratum	Males	Females
2010	70	3,166	4,564
	71	1,161	1,673
	81	139	750
2017	70	3,043	3,579 (118)
	71	1,095	1,584 (82)
	81	92	752 (12)
2019	70	3,134	2,869
	71	1,696	2,254
	81	310	1,069
	Total	13,835	19,094

Table 3. Estimates for parameters, length (L_{50}) and age (A_{50}), from binomial logistic regression models predicting proportion mature for yellowfin sole (*Limanda aspera*) females from the northern Bering Sea (NBS). Logistic model includes strata 70, 71, and 81. 95% CI = lower and upper confidence intervals of the parameter estimates. Coefficients, α and β, represent, the model intercepts and slopes, respectively. The formula for computing the parameters, where *Y* represents L_{50} and A_{50}: $Y = -\frac{\alpha}{\beta}$.

Parameter	*N*	α	β	Estimate	95% *CIs*
Length (L_{50})	212	-9.3697	0.3291	28.47	27.16, 29.68
Age (A_{50})	209	-6.9787	0.6902	10.11	9.47, 10.76

Table 4. Summary measurements describing northern Bering Sea (NBS) yellowfin sole (*Limanda aspera*) females by reproductive phase (Brown-Peterson et al., 2011). Females from the southeastern Bering Sea (SEBS) are listed for comparison from Nichol (1995). Metrics length (cm), age, and depth (m) are the respective mean values (± SD or range). Females from the NBS exhibiting abortive maturation were part of the 'immature' phase total. No ages were associated with collections from the SEBS.

Area	Month	Phase	*N*	Length	Age	Depth (range)
SEBS	June	Immature	116	28.78 ± 2.51	–	37.4 (18-79)
		Spawning-capable	447	34.39 ± 3.26	–	36.8 (16-79)
		Spawning	62	34.34 ± 3.54	–	21.6 (16-60)
		Regressing	135	35.41 ± 3.08	–	36.7 (16-68)
NBS	August	Immature	91	23.69 ± 4.26	7.77 ± 1.54	36.6 (12-60)
		Abortive maturation	4	22.25 ± 2.75	7.25 ± 1.50	26.5 (18-36)
		Spawning	17	37.18 ± 4.59	18.29 ± 5.64	25.5 (20-55)
		Regressing	99	35.96 ± 7.08	16.29 ± 6.77	35.5 (15-60)
		Regenerating	5	37.40 ± 3.44	17.80 ± 2.77	50.0 (30-55)

Table 5. Akaike's information criterion (AIC) comparing generalized linear mixed models (GLMMs) assessing the influence of spatio-temporal variables on female proportions of yellowfin sole (*Limanda aspera*) in the northern Bering Sea (NBS). Year and stratum were modeled as factor variables.

Model	df	Δ AIC	AIC Wt
Year + Stratum + Latitude + Longitude	8	0	0.98
Year + Latitude + Longitude	6	8	0.02
Year + Stratum	6	67	0
Stratum + Latitude + Longitude	6	15,929	0
Latitude + Longitude	4	16,092	0
Latitude	3	16,123	0

Table 6. Results of the binomial generalized mixed effects models (GLMMs) for predicting proportion of yellowfin sole (*Limanda aspera*) females in the northern Bering Sea (NBS). Model 1: Proportion = Year + Stratum + Latitude + Longitude; Model 2: Proportion = Year + Bottom temperature + Surface temperature. SE = standard error; SD = standard deviation. Random effect was station.

Model	Fixed Effects	Estimate	SE	z-value	*p*-value
1	Intercept	-55.591	5.726	-9.708	0.000
	Year 2017	-0.254	0.003	-90.900	0.000
	Year 2019	-0.334	0.003	-119.462	0.000
	Stratum 71	0.594	0.215	2.767	0.006
	Stratum 81	0.447	0.192	2.328	0.012
	Longitude	-0.246	0.028	-8.704	0.000
	Latitude	0.235	0.068	3.484	0.000
2	Intercept	0.644	0.091	7.083	0.000
	Year 2017	-0.189	0.004	-43.474	0.000
	Year 2019	-0.277	0.005	-50.831	0.000
	Bottom temperature	-0.023	0.001	-28.080	0.000
	Surface temperature	0.037	0.001	36.359	0.000

Figure captions

Fig. 1. Sampling coverage for Alaska Fisheries Science Center's (AFSC) bottom trawl surveys of the Bering Sea, separated by the northern Bering Sea (NBS; white) and the southeastern Bering Sea (SEBS; gray). Zoomed image is the NBS survey area separated by the three strata (70, 71, and 81). Stratum 81 is partially separated by the 50 m isobath.

Fig. 2. Maturity status of yellowfin sole (*Limanda aspera*) females (immature; mature) caught by depth in the northern Bering Sea (NBS).

Fig. 3. Proportion mature of length and age at maturity for yellowfin sole (*Limanda aspera*) in the northern Bering Sea (NBS).

Fig. 4. Spatial plots of selected reproductive phases observed for yellowfin sole (*Limanda aspera*) females. Blue dots represent stations where these observations occurred.

Fig. 5. A map of spawning for yellowfin sole (*Limanda aspera*) females constructed across the northern Bering Sea (NBS). Notes: Black arrow represents the spring migration route from deeper feeding and overwintering areas from the southeastern Bering Sea (SEBS). Gray arrow represents the late summer and fall migration route back to deeper waters in the SEBS. It is hypothesized that the presence of yellowfin sole eggs and larvae in the Chukchi Sea (red) represents resident fish, separate from the NBS. Larval and eggs from spawning fish north of Nunivak Island are transported by the ACC into waters north and south of St. Lawrence Island

and into Norton Sound. Light purple areas indicate potential spawning areas, with the likelihood of female spawners occupying shallower depths within these areas, and moving away to deeper waters after spawning (this includes Norton Sound). Spawning fish collected in the southeastern portion of the NBS survey area likely represent migratory fish from SEBS (blue). Results suggest NBS spawning timing overlaps with the SEBS (blue in panel). Samples from August collections suggest a largely regressing population which partially spawned in July (light blue in panel); spawning individuals were observed in late August, suggesting a continuation of some spawners into September (light blue in panel). ACC = Alaska Coastal Current; BSW = Bering Shelf Water mass.

Fig. 6. Representative images of histology from ovaries of female yellowfin sole (*Limanda aspera*) from the northern Bering Sea (NBS): A) an immature female exhibiting primary growth (PG) oocytes at the perinuclear stages with thin ovary wall (OW; scale bar = 0.250 mm); B) an active spawning female exhibiting tertiary vitellogenic oocytes (Vtg3) with scattered early post-ovulatory follicles (POFs; scale bar = 0.250 mm); C) regressing female exhibiting atresia (early-stage α-atresia (α), late-stage α-atresia α_L, beta β), tertiary vitellogenic and remnant hydrated oocytes (HY; scale bar = 0.250 mm); and D) a regressing female exhibiting remnant HY oocytes, surrounded by PG and cortical alveoli (CA) oocytes, thick OW, general lamellar disorganization and larges areas of ovarian lumen (L; scale bar = 0.250 mm).

Fig. 7. Predictions from the best performing generalized linear mixed model (GLMM) assessing spatio-temporal effects on yellowfin sole (*Limanda aspera*) sex ratio.

Fig. 8. Predictions assessing the effects of bottom and sea surface temperature on yellowfin sole (*Limanda aspera*) sex ratio by survey year from generalized linear mixed models (GLMMs).

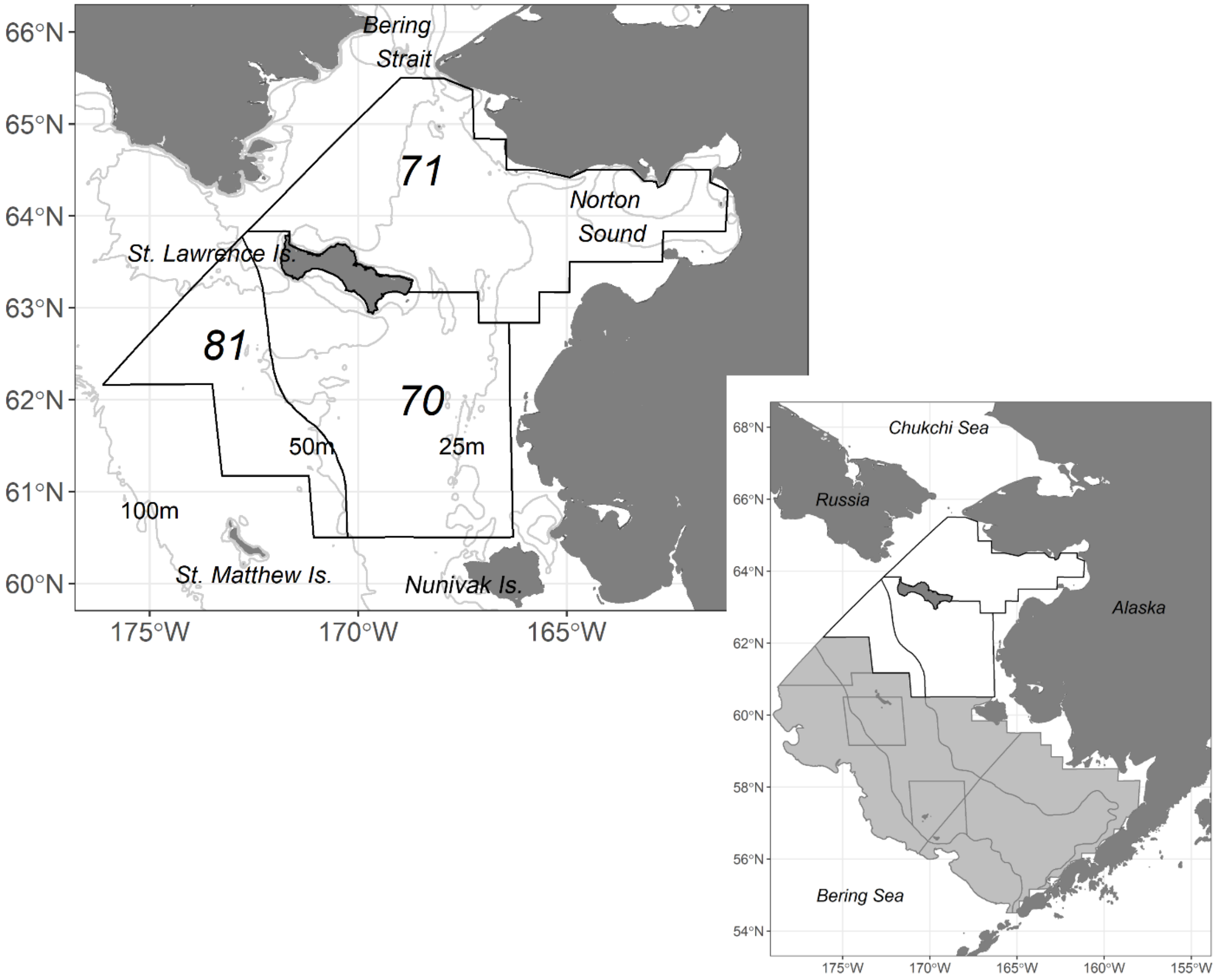

66°N
65°N
64°N
63°N
62°N
61°N
60°N
175°W
170°W
165°W
Bering
Strait
71
Norton
Sound
St. Lawrence Is.
81
70
50m
25m
100m
St. Matthew Is.
Nunivak Is.
68°N
66°N
64°N
62°N
60°N
58°N
56°N
54°N
Chukchi Sea
Russia
Alaska
Bering Sea
175°W
170°W
165°W
160°W
155°W

Fig. 1.

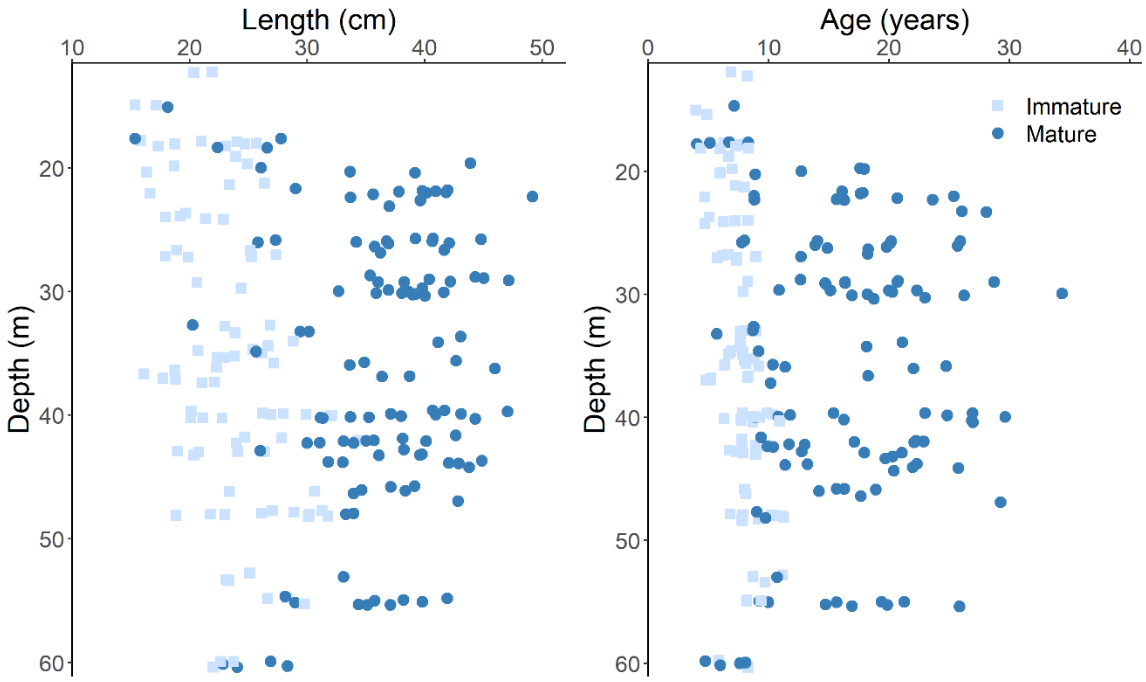

Length (cm)
10
20
30
40
50
Depth (m)
20
30
40
50
60
Age (years)
0
10
20
30
40
Depth (m)
20
30
40
50
60
Immature
Mature

Fig. 2.

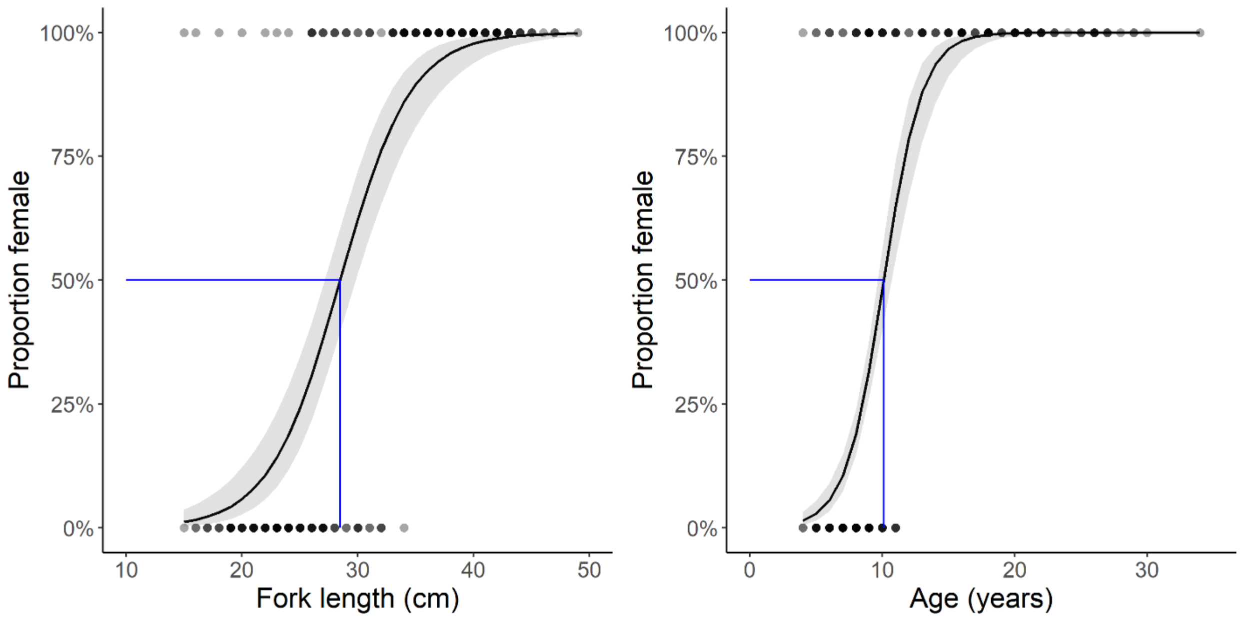

Proportion female
100%
75%
50%
25%
0%
10
20
30
40
50
Fork length (cm)
Proportion female
100%
75%
50%
25%
0%
0
10
20
30
Age (years)

Fig. 3.

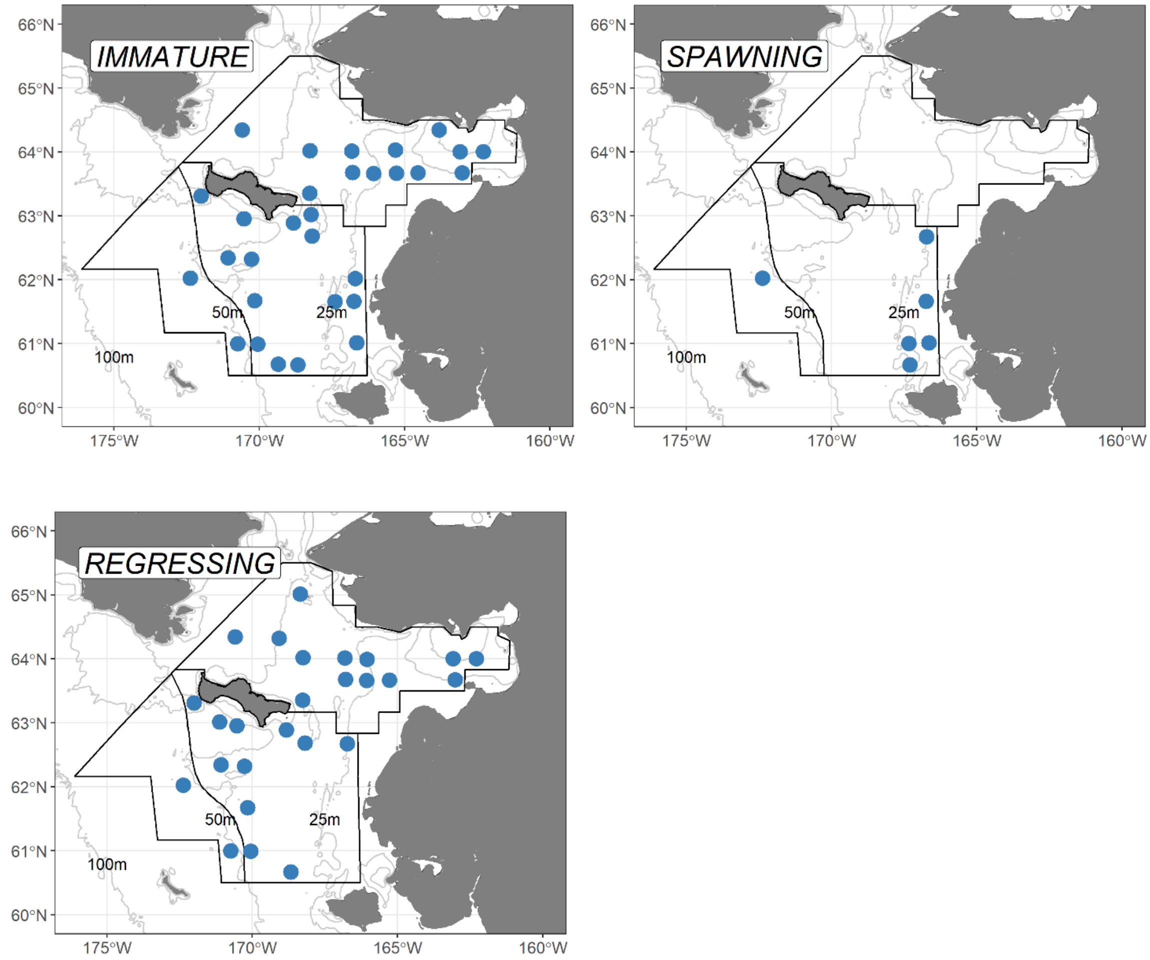

IMMATURE
SPAWNING
REGRESSING
66°N
65°N
64°N
63°N
62°N
61°N
60°N
175°W
170°W
165°W
160°W
50m
25m
100m

Fig. 4.

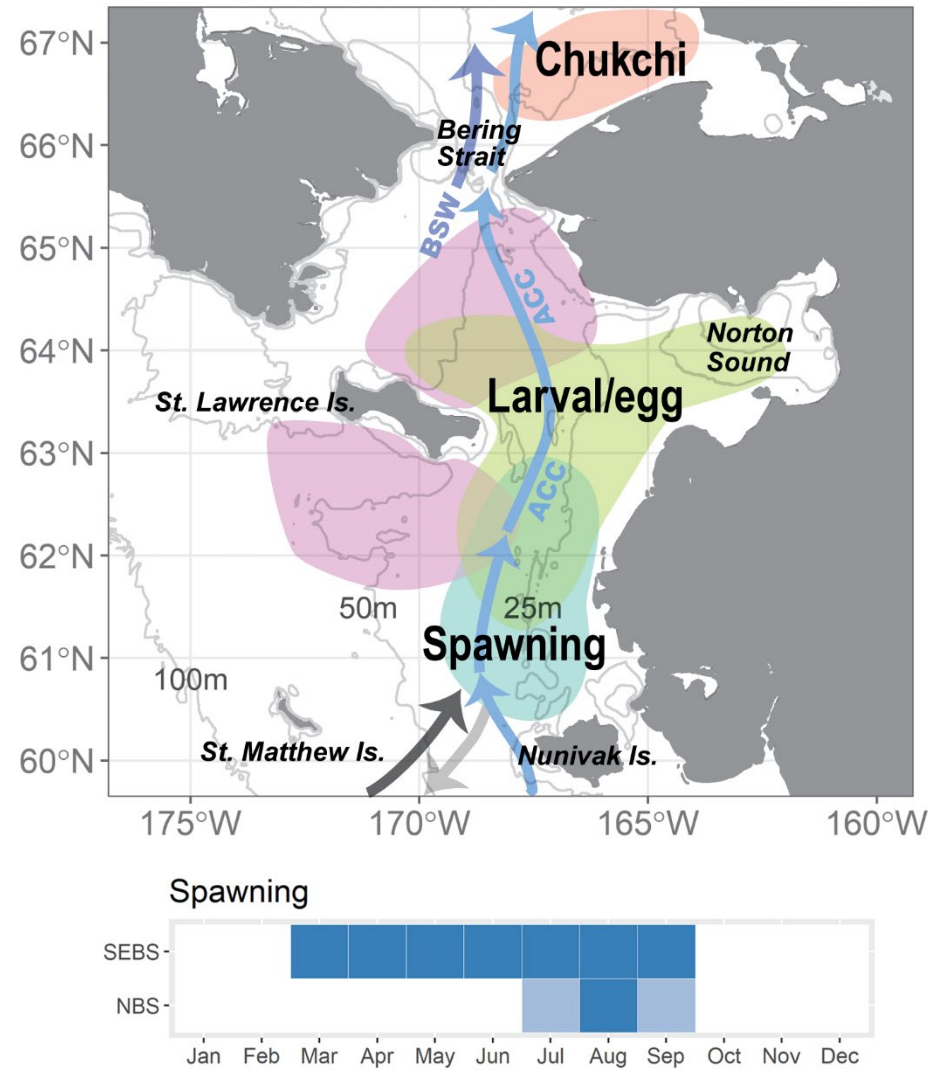

67°N
66°N
65°N
64°N
63°N
62°N
61°N
60°N
175°W
170°W
165°W
160°W
Chukchi
Bering Strait
BSW
ACC
ACC
Norton Sound
St. Lawrence Is.
Larval/egg
50m
25m
Spawning
100m
St. Matthew Is.
Nunivak Is.
Spawning
SEBS
NBS
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig. 5.

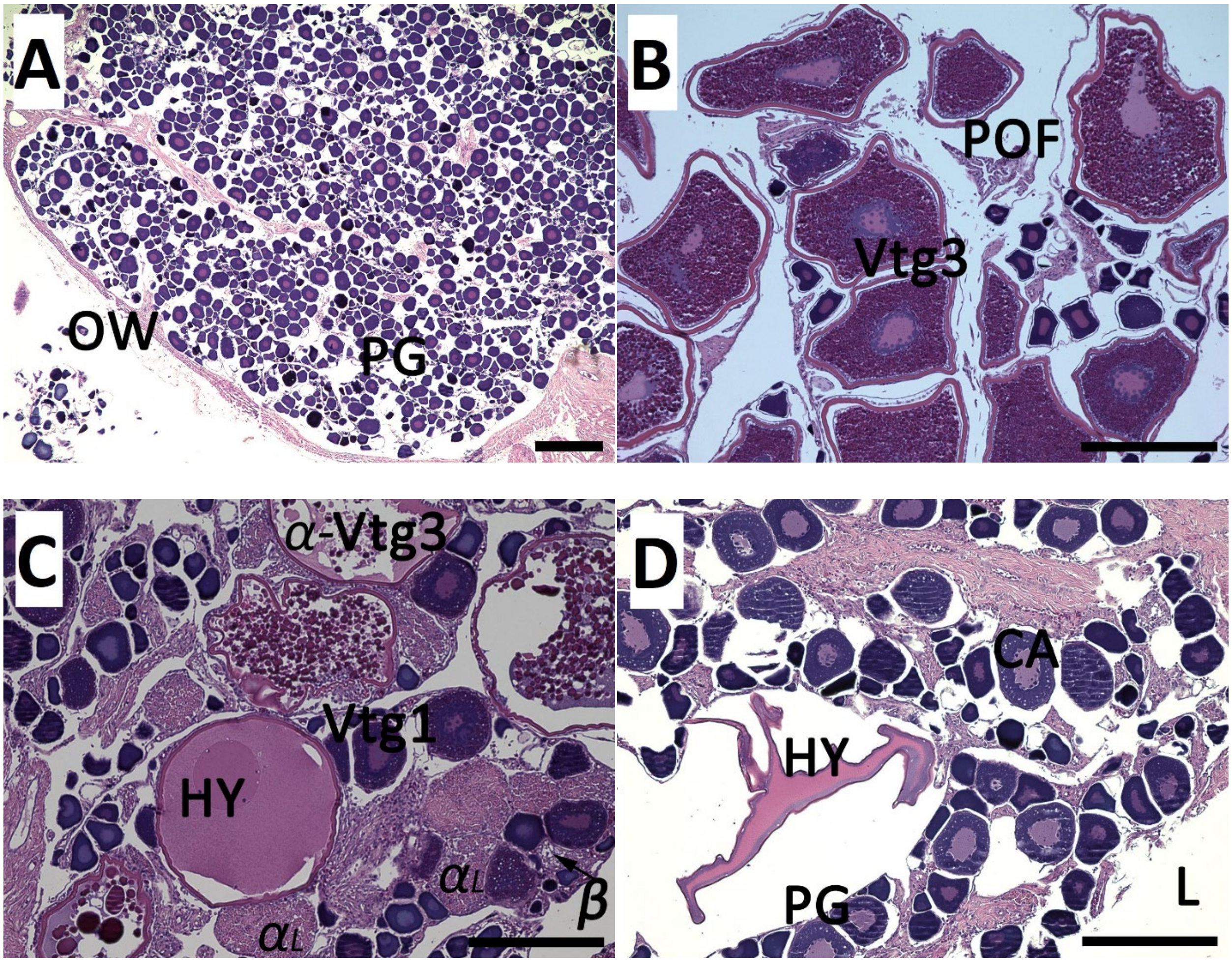


Fig. 6.

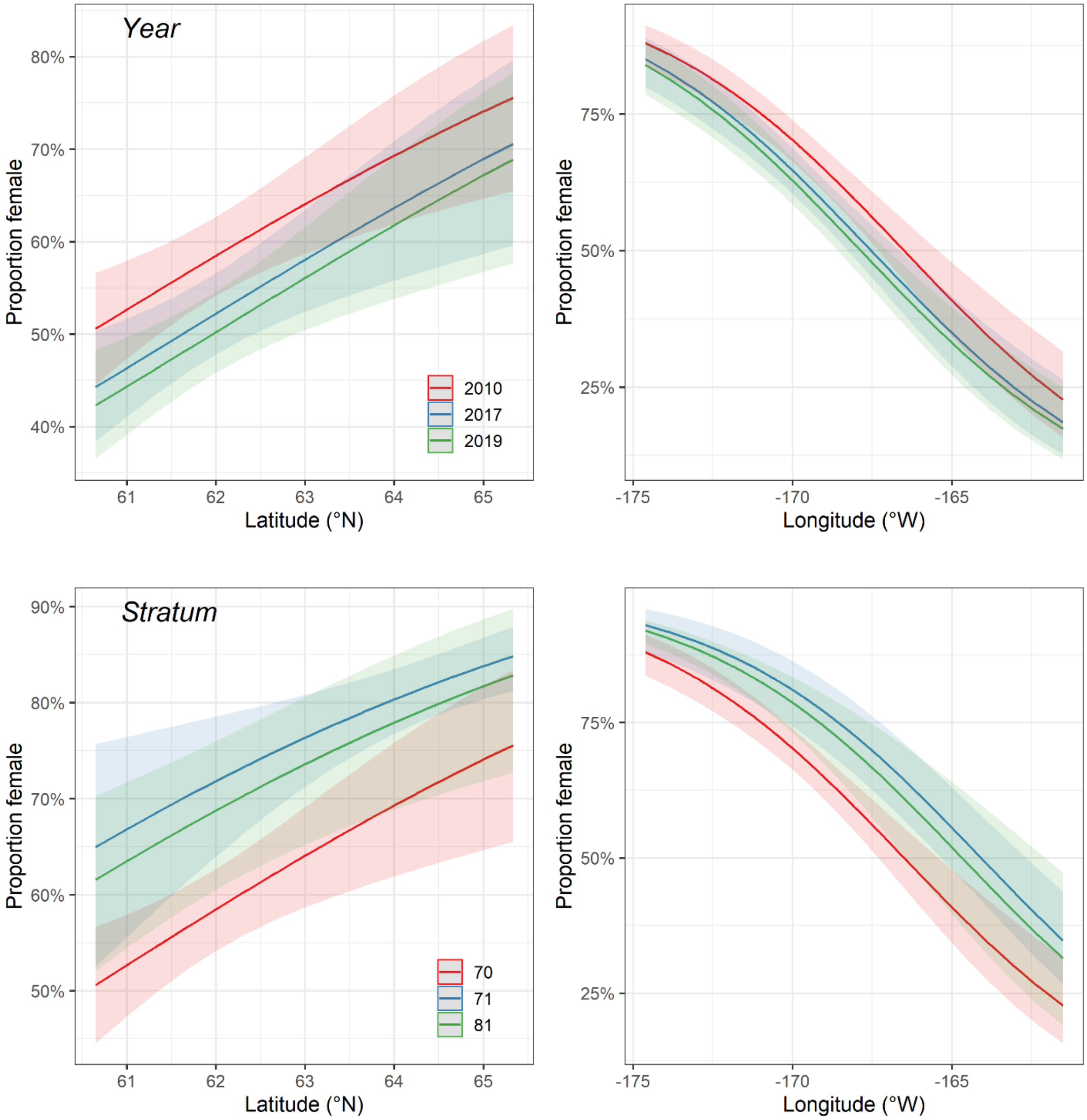
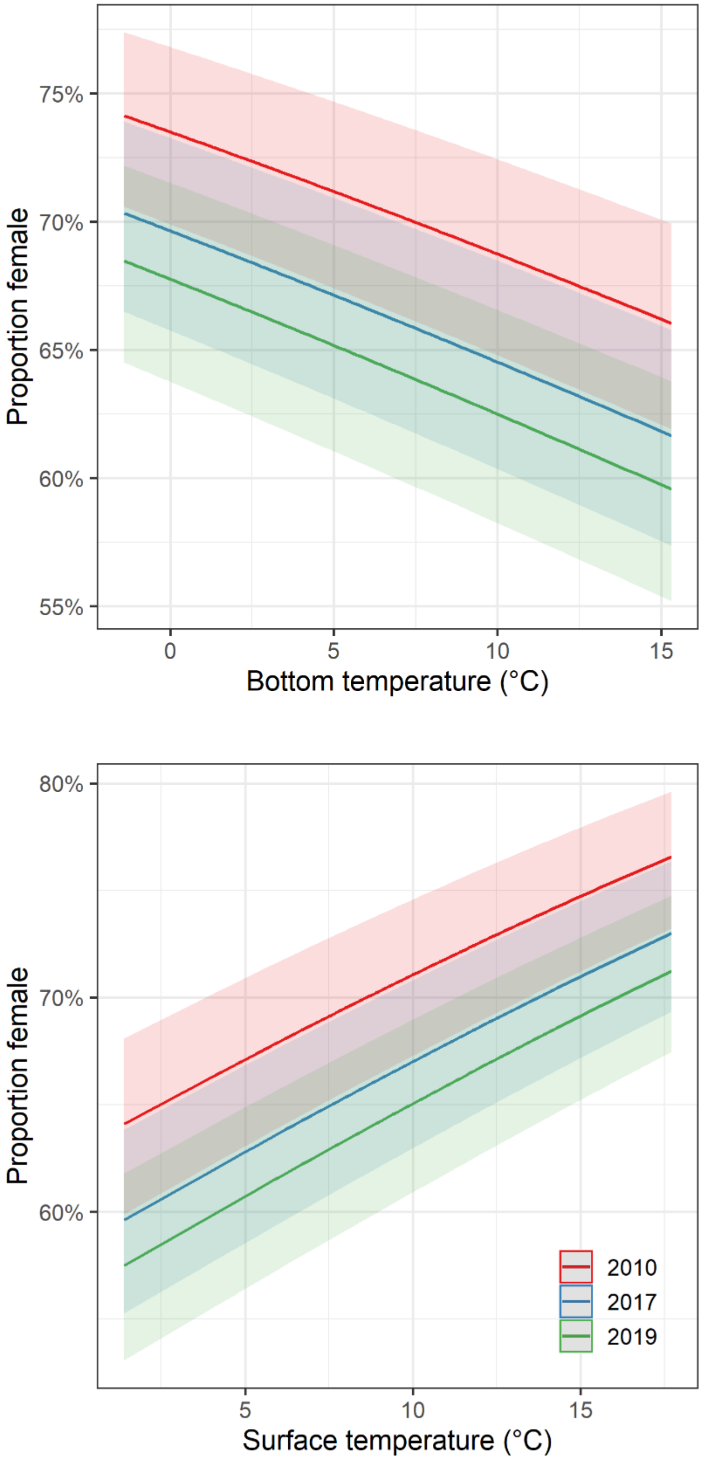

Year
80%
70%
60%
50%
40%
Proportion female
61
62
63
64
65
Latitude (°N)
2010
2017
2019
75%
50%
25%
Proportion female
-175
-170
-165
Longitude (°W)
Stratum
90%
80%
70%
60%
50%
Proportion female
61
62
63
64
65
Latitude (°N)
70
71
81
75%
50%
25%
Proportion female
-175
-170
-165
Longitude (°W)

Fig. 7.



75%
70%
65%
60%
55%
Proportion female
0
5
10
15
Bottom temperature (°C)
80%
70%
60%
Proportion female
5
10
15
Surface temperature (°C)
2010
2017
2019

Fig. 8.

Supplementary Information

Fig. S1

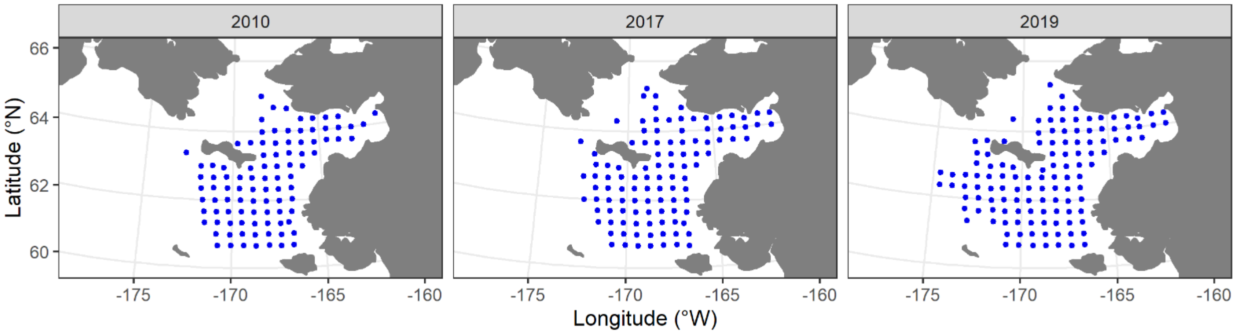


Fig. S1. Station locations where yellowfin sole (*Limanda aspera*) specimens were caught by year during the northern Bering Sea (NBS) bottom trawl survey. Note: Of the survey years, 2010 represented a "cold" year for the southeastern (SEBS) and NBS ecosystems, while both 2017 and 2019 represented "warm" years.