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Availability of yellowfin sole *Limanda aspera* to the eastern Bering Sea trawl survey and its effect on estimates of survey biomass

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ABSTRACT

Availability of yellowfin sole *Limanda aspera* to the National Marine Fisheries Service eastern Bering Sea trawl survey, rather than trawl sampling efficiency, is proposed as the primary reason for relatively high annual variability of biomass estimates in this region, including most recently, a 48% increase from 2015 to 2016. The main hypothesis presented here is that temperature-mediated differences in the timing of spring-summer spawning migrations to unavailable nearshore spawning grounds, affect survey biomass estimates. Colder bottom temperatures delay both migrations and spawning, causing higher proportions of mature individuals to reside in the unavailable nearshore grounds at the time of annual survey (June–July). Indicators of this scenario include decreases of mature fish proportions and decreases in mean overall fish lengths during colder years when biomass was less than expected. Further evidence includes differences in spatial distribution between warm and cold years, and spatial shifts away from nearshore areas between early June and July–August sampling during which catch per unit effort (CPUE) increased and proportion of females increased. That neither of these spatial shifts nor temperature-CPUE relationships occurred for northern rock sole *Lepidopsetta polyxystra*, a species of similar morphology and abundance, and overlapping spatial distribution, suggests that temperature-mediated trawl sampling efficiency was not a major contributing factor for yellowfin sole. We have also found a positive relationship between survey biomass estimates and survey start times, reinforcing that availability is a function of timing. The addition of survey start time to the catchability (q) parameter within the current stock assessment model significantly improved model fits to abundance data.

1. Introduction

This study investigates mechanisms responsible for large shifts in annual biomass estimates of yellowfin sole (*Limanda apera*) in the eastern Bering Sea (EBS) and provides evidence that temperature-mediated changes in availability (i.e., to the bottom trawl survey) is a major contributor. The distribution of yellowfin sole in the EBS extends into nearshore waters not currently accessed by the bottom trawl assessment survey (Fig. 1), and potentially large portions of the biomass are unavailable to sampling due to high concentrations of adult fish that are spawning in nearshore waters at the time of the survey (June–July) (Nichol, 1995). Tagging studies have shown that adult yellowfin sole undergo long seasonal migrations (Wakabayashi, 1989) from wintering areas south and north of the Pribilof Islands (depths ~ 200 m) to nearshore spawning grounds of Bristol and Kuskokwim bays. Such migrations are thought to follow the ice-edge as it retreats during early spring and may be delayed when ice cover is more extensive or when winter bottom temperatures are colder (Bakkala, 1981). If this is true, then it is reasonable to assume, during warmer years when the ice retreats earlier or is more limited in extent, that yellowfin sole migrate inshore earlier. With earlier migrations, spawning is likely more complete at the time of the survey, and theoretically larger portions of spent individuals would have migrated out of the unsurveyed nearshore spawning grounds into the survey area.

Survey-derived estimates of annual yellowfin sole abundance (e.g., biomass) increase linearly with mean annual survey bottom temperatures (Nichol, 1998). While stock assessment models have incorporated this temperature effect (Wilderbuer et al., 2017), the exact mechanism is unclear. Two potential mechanisms have been suggested: 1) a change in fish availability due to annual variability in timing of the yellowfin

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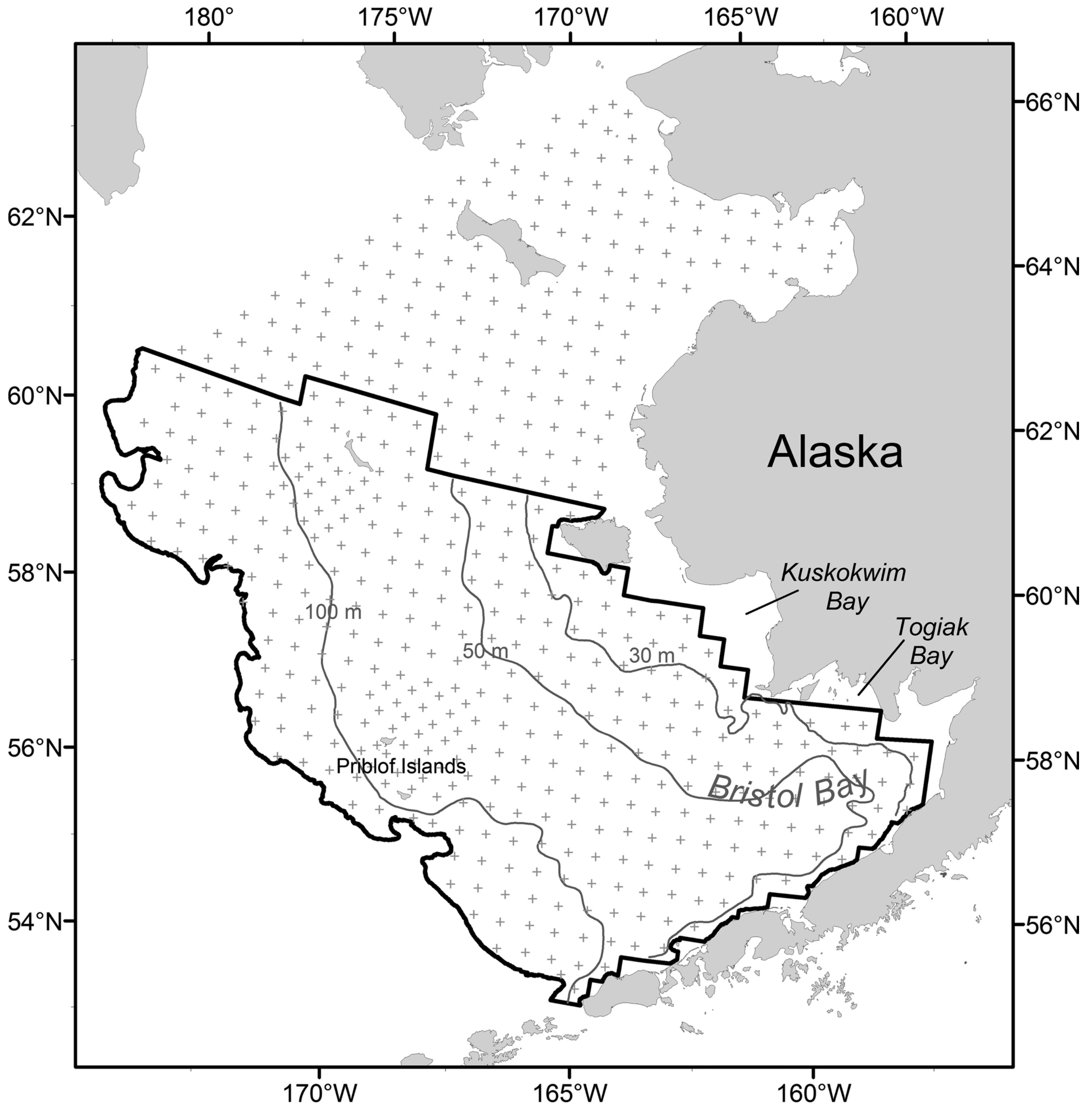

Fig. 1. Eastern Bering Sea bottom trawl survey station locations. Stations within the standard survey area (outlined in black) have been conducted annually since 1982. Stations north of the standard area were conducted in both 2010 and 2017.

sole spawning migration, as described above, and 2) a temperature-mediated change in trawl sampling efficiency where, under colder conditions, the catch per unit effort decreases due to a slower response of yellowfin sole to the approaching survey trawl, resulting in less herding by the trawl bridles and/or greater escapement under the trawl footrope. Somerton and Munro (2001) demonstrated that yellowfin sole catch rates increase significantly with increased bridle lengths and Munro and Somerton (2002) demonstrated that a significant portion of adult yellowfin sole (23%) can escape under the footrope, more so than other EBS flatfishes such as northern rock sole (6%), flathead sole (5%), and Pacific halibut (2%). However, it is unclear whether these behaviors are affected by temperature.

In this investigation, we test the hypothesis that high annual variability in yellowfin sole biomass is due to temperature effects on the migration of inshore spawning fish, rather than temperature effects on the efficiency of the survey trawl gear. This was done with five different analyses. First, we used the 36 year EBS bottom trawl survey time series conducted by the Alaska Fisheries Science Center (Lauth and Nichol, 2013) to plot the summer spatial distributions of yellowfin sole during representative “warm” and “cold” years, doing so separately for immature and mature males and females. Overall distributions were expected to shift farther offshore during warmer years. Second, we examined 8 years of trawl survey catch per unit effort (CPUE) data during which common stations (19–34) in Bristol Bay were sampled twice within the same year, once in early June and again between late July and early August. The logic here is that if the timing of spawning affects yellowfin sole availability to the survey, with greater availability when spawning is more complete, then we should observe increases in abundance when stations are sampled later in the season. Furthermore, if males remain on the spawning grounds longer than females, as for other flatfishes (Rijnsdorp, 1989; Arnold and Metcalf, 1996; Solmundsson et al., 2003; Hirose and Minami, 2007), we should observe increased numbers of mature females relative to mature males (i.e., sex-ratio) during the later sampling, owing to higher percentages of spent females that have migrated out of the spawning grounds. Third, we tested for a relationship between annual survey biomass estimates and survey start dates, which have ranged from May 23rd to June 11th, averaging June 4th. Fourth, we examined the relationship of annual survey biomass estimates with the proportion of mature fish and mean fish lengths observed during each survey, which should both increase if spawning is more progressed (i.e., during warmer years). Fifth, we examined various measures of climate (e.g., surface temperature, bottom temperature, cold pool area, spring ice extent) to determine which measures explain variability in annual survey biomass estimates. This variability included a 48% increase in estimated survey biomass from 2015 to 2016, an increase that, within the stock assessment model, cannot be explained by population growth, age composition or recruitment (Wilderbuer et al., 2017).

Additionally, in an effort to resolve whether some of the temperature effect on estimated survey biomass could be explained by temperature-mediated trawl sampling efficiency, some of the same analyses were conducted for northern rock sole (*Lepidopsetta polyxystra*), a species that is morphologically similar to yellowfin sole, is similarly abundant in the Bristol Bay region during summer, and is similarly herded by survey trawl bridles (Somerton and Munro, 2001), but does not spawn or aggregate in the nearshore areas at the time of the survey. If only yellowfin sole undergo distributional shifts due to spawning, but the CPUE of both yellowfin sole and northern rock sole increases with increasing temperatures or as summer progresses (during which temperatures increase), then temperature-mediated trawl sampling efficiency must also be considered to have a significant impact on yellowfin sole biomass estimates.

Trawl survey catchability (q), can be defined as having three components: vulnerability to the trawl (i.e., sampling efficiency), vertical availability, and areal availability (Francis et al., 2003), all of which should be considered when calculating individual species abundance for stock assessment. Most of the research for species in the EBS has focused on the first component, with examinations of escapement under the trawl footrope (Munro and Somerton, 2002; Weinberg et al., 2002), bridal herding (Somerton and Munro, 2001; Somerton, 2003), and influence of sea-state (Somerton et al., 2018). The second component, vertical availability has also been examined to some extent, but the focus has been on more semi-demersal species such as walleye pollock (Kotwicki et al., 2009, 2015) and Pacific cod (Nichol et al., 2007), and is likely not a factor for most flatfishes. The last component, areal availability (hereafter referred to as "availability"), has not been addressed at any level for EBS species, despite the knowledge that distributions for many species extend beyond the survey boundaries, particularly for yellowfin sole. The current stock assessment for yellowfin sole (Wilderbuer et al., 2017) includes a q parameter with a survey bottom temperature correlate ($q = e^{-\alpha+\beta T}$) that significantly improves model fits to the survey biomass estimates, but it has not been clear whether this temperature effect is due to survey availability or survey trawl sampling efficiency. This research provides evidence for how yellowfin sole survey biomass estimates change with their availability to the bottom trawl survey due mostly to temperature-mediated changes in the timing of spawning. This research also explores the correlations of variables in addition to bottom temperature that might help explain additional annual variability of survey biomass estimates due to yellowfin sole availability, and improve the stock assessment quantification of q.

2. Methods

2.1. Eastern Bering Sea bottom trawl survey

The EBS bottom trawl survey is a dedicated multi-species research survey conducted by the Alaska Fisheries Science Center to provide fishery-independent estimates of abundance for stock assessment and management (Lauth and Nichol, 2013). This survey has been conducted annually since 1982 using the same trawl gear and sampling protocols (Stauffer, 2004), and consists of 356 standard stations (Fig. 1). Annual biomass for individual species were estimated for each of 10 strata areas as the mean stratum CPUE multiplied by the stratum area, where CPUE (per station) was calculated as the total catch weight (kg) divided by the trawl area swept (distance-fished × mean net width). Overall survey biomass estimates were then calculated as the summation of the strata estimates (Lauth and Nichol, 2013).

2.2. Apportioning by sexes and maturation

Male and female station CPUE (no/ha) were apportioned into immature and mature categories by first apportioning CPUE among each fish length (cm) for each year (1982–2017), station (n = 356), and sex using length composition proportions from randomly-collected length-composition data available for each year, station, and sex (Lauth and Nichol, 2013). The mature portion of CPUE at length (CPUE_{L}) for each year, station and sex was then calculated as $P_{L*}\text{CPUE}_L$ where $\text{P}_L = 1/(1+\text{e}^{AL+B})$, and $L =$ length in centimeters. For males, parameters A and B were estimated as -0.48 and 10.34 (see Appendix), respectively, and for females as -0.78 and 22.94, respectively (Nichol, 1995). Immature portions were calculated as 1-P_L. For each year, station, sex, and length, CPUE by weight (kg/ha) was then calculated for mature fish as $P_{L*}\text{CPUE}_L{*}W$ and for immature fish as CPUE as $(1\text{-}\ P_L)_*\text{CPUE}_L{*}W$ where $W = aL^b$ and $W =$ fish weight in kg, a = 0.007441, and b = 3.13, as estimated for combined sexes from survey length/weight collections (Lauth and Nichol, 2013).

2.3. Warm versus cold year CPUE comparison

Representative warm year data sets were chosen by selecting years in which the average annual bottom temperature at depths ≤100 m was greater than the overall mean plus 0.5 SD. Cold years were defined as those where the annual temperature was less than the overall mean minus 0.5 SD. Mean station CPUE values (kg/ha), spaced 20 nautical miles apart (Lauth and Nichol, 2013), were then plotted geographically using inverse distance weighting interpolation (ArcMap version 10.5.1; www.esri.com). Values at each station were averaged across the 11 most recent warm years and the 11 most recent cold years, by sex (males, females), and by maturity (immature, mature).

2.4. Comparison of early June sampling to July–August sampling

Geographic CPUE (kg/ha) plots comparing early June sampling with late July to early August sampling for 9 years (1999, 2006, 2007–2012, 2017) were created as above using ArcMap inverse distance weighting interpolation. Common trawl locations within each year varied from 19 to 34 stations (again, spaced 20 nautical miles apart), encompassing areas of 41,000 to 46,000 km^2 within Bristol Bay where yellowfin sole are commonly distributed during summer.

The percentage of change in yellowfin sole CPUE (numbers/ha), from early to late sampling, was calculated separately for immature and mature males and females. Relationships between mean station bottom temperature, CPUE (numbers/ha), and the proportion of mature females were also examined for both early and late samplings. This was done for both yellowfin sole and northern rock sole in an effort to distinguish between effects resulting from temperature-mediated spawning dynamics (i.e., as for yellowfin sole only) and those resulting

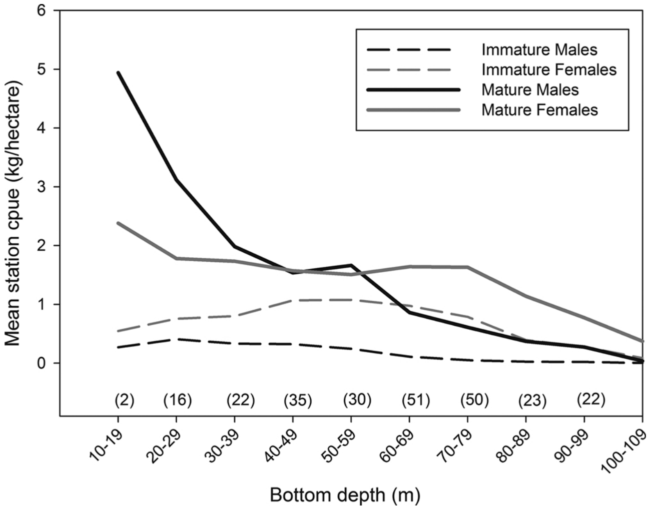

Fig. 2. Distribution by depth of immature and mature male and female yellowfin sole, averaged across years 1982–2017. Numbers in parentheses indicate the average number of stations sampled each year at the specified depth interval.

from temperature-mediated trawl sampling efficiency (potentially both species).

2.5. Correlates to estimated survey biomass

Annual bottom trawl survey estimates of yellowfin sole biomass were linearly regressed against previously known correlates such as mean annual survey bottom temperatures (stations < 50 m and < 100 m depth), in addition to other factors that were consistent with the scenario of increased availability during years when spawning is more progressed at the time of the survey. Such factors included the annual start date of the survey (i.e., deviation in days from mean survey start date), mean annual yellowfin sole length, and the proportion of mature individuals calculated as the CPUE (no/ha) of mature fish divided by the CPUE of all fish. Years 1982 through 1984 were excluded from these regressions because of the vastly different age-structures present during these years that differentially affected yellowfin sole availability (see Discussion, Section 4.5; Nichol, 1998).

2.6. Testing for climate-related changes in estimated survey biomass

Different measures of climate were examined in an effort to determine which ones explained the most year-to-year variability in the estimated survey yellowfin sole biomass, and to determine whether the survey bottom temperature (< 100 m) variable, which is currently used within the q parameter calculation of the yellowfin sole stock assessment model, is the most appropriate. This was done by regressing the change in estimated biomass from one year to the next ($B_{yr+1} - B_{yr}$) against the annual change of different climate measures ($C_{yr+1} - C_{yr}$), where C included: mean annual survey bottom temperatures (< 100 m), mean annual survey surface temperatures, the area of cold pool in the EBS (Kotwicki and Lauth, 2013), air temperatures at different months in the EBS (Bond and Adams, 2002), and the number of days after March 15 in which ice extended past latitude 56.9 °N, longitude 164.1 °W (location of M2 mooring buoy; Stabeno et al., 2017). Simple linear regressions were run and r^2 values calculated for each of the climate variables (independent) to determine which one best explained the annual changes in estimated biomass (dependent variable). An advantage of examining $B_{yr+1} - B_{yr}$ as opposed to just B_{yr} is that we eliminate the effects of multi-year trends, and we reduce the effects of availability caused by changes in population age structure (i.e., due to variable fractions of mature and immature individuals), thereby focusing on the effect of climate on estimated survey biomass.

2.7. Effect of survey start date to catchability (q) in stock assessment model

In addition to survey bottom temperature (T), currently used as a variable within the stock-assessment model catchability parameter ($q = e^{-\alpha+\beta T}$), we explored whether or not the addition of survey start date (S) could explain additional annual variability within survey biomass estimates, and whether this addition could improve overall model fits to the survey biomass data. Other potential variables such as proportion mature and mean fish length were not considered here because their correlations to survey biomass estimates were essentially the same as for survey bottom temperature (i.e., both were highly correlated to annual survey bottom temperature).

First, annual survey biomass estimates (dependent variable) were linearly regressed against independent variables bottom temperature (T), survey start date (S), and the interaction of T and S (T:S) using generalized linear modeling (glm; R Core Team, 2017). Again, start date was expressed as deviation in days (- and +) from the average survey start date of June 4th. Regressions were run first with T only, then $T+S$, then $T+S+T{:}S$, and Akaike Information Criterion (AIC) used to determine whether the additional variables (S and $T{:}S$) improved the regression fit. If S and $T{:}S$ significantly improved the fit, they were then added to the catchability parameter q within the current stock assessment model (i.e., $q = e^{-\alpha+\beta T+\gamma S+\mu T:S}$). As with the glm, stock assessment models were run with and without the additional significant variables, to determine if the model fit to survey biomass estimates improved, and was evaluated as above using AIC.

3. Results

3.1. Distribution of mature and immature males and females

On average, over all years (1982–2017), mature individuals accounted for approximately 74% of the yellowfin sole biomass in the EBS, although this varied from a low of 50% in 1982 to a high of 87% in 2016. Mature males dominated the shallowest survey depths (< 30 m), with twice the CPUE (kg/ha) compared to mature females at these depths (Fig. 2). This result was expected given that males mature 3 to 4 years earlier than females (thus, there are always more male spawners than female spawners), and given the tendency for male flatfishes to remain on the spawning grounds longer than females (see Introduction). Mature females were more abundant (by weight) than males at bottom depths > 60 m. Among immature yellowfin sole, females were more abundant than males at all survey depths due to later female maturation. Summing across the entire survey area, females (immature + mature) were more abundant than males in all survey years in terms of both weight (57–65%) and number (51–57%).

3.2. Warm versus cold year CPUE comparison

In comparing yellowfin sole mean distributions between warm and cold years, the most significant shift was among mature females, with concentrations much deeper (> 50 m) during warmer years (Fig. 3A, B). Mature males, contrarily, were distributed similarly between warm and cold years with largest concentrations at the nearshore survey edge during both phases (Fig. 3C, D). Immature females (Fig. 3E, F) and males (Fig. 3G, H) were also similarly distributed between warm and cold years. Distributions of immature males were always centered closer to shore (shallower) than immature females due to their younger age at maturation and consequently smaller sizes, and positioning along a size-depth continuum (i.e., smaller sizes at shallower depths).

3.3. Comparison of early June sampling to July-August sampling

Yellowfin sole were more concentrated by weight (kg/ha) during

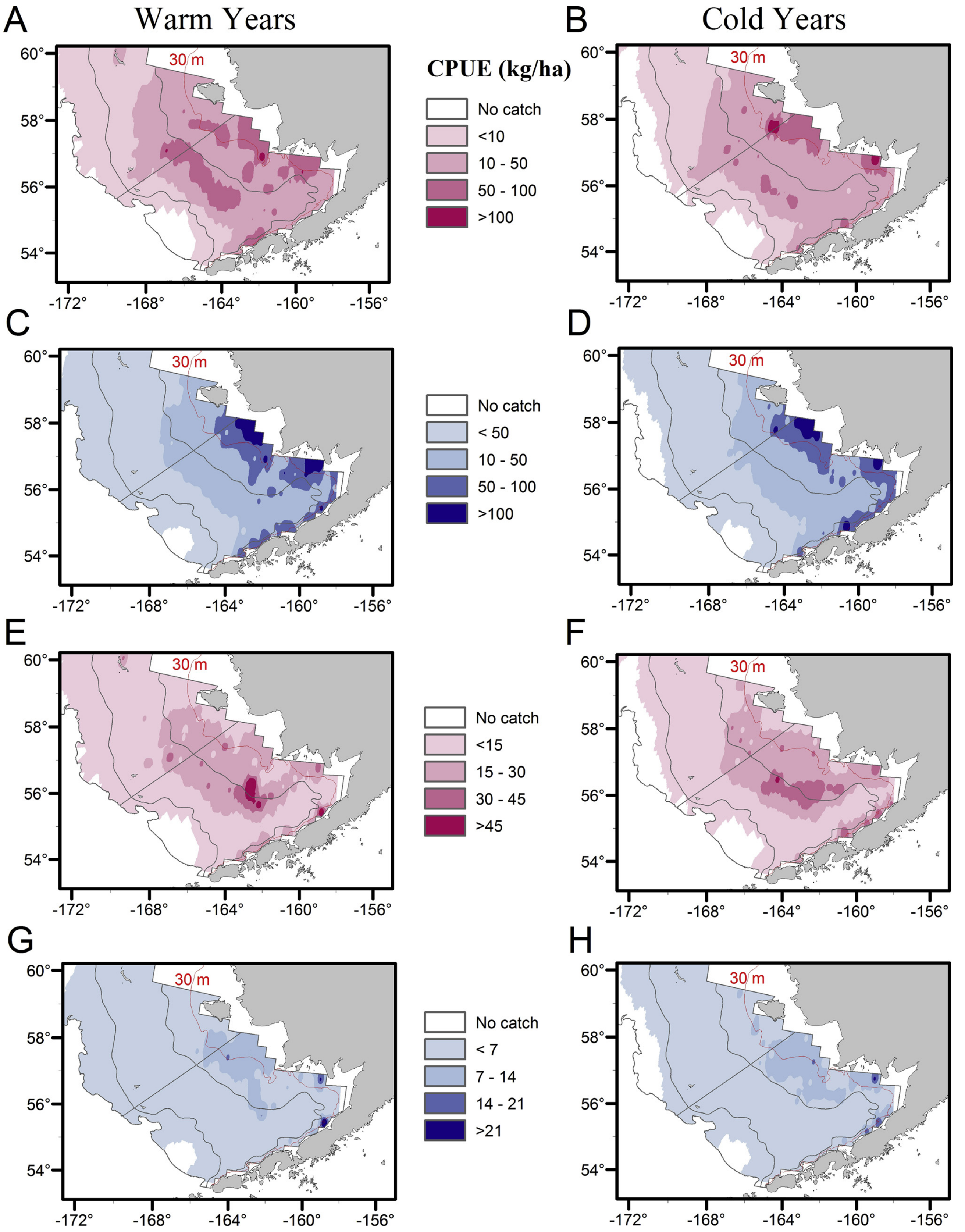

Fig. 3. Mean CPUE (kg/ha) distributions of yellowfin sole mature females (A, B), mature males (C, D), immature females (E, F), and immature males (G,H), averaged separately for 11 warm years (1989, 1993, 1996, 1998, 2002, 2003, 2004, 2005, 2014, 2015, 2016) and 11 cold years (1992, 1994, 1995, 1999, 2006, 2007, 2008, 2009, 2010, 2012, 2013).

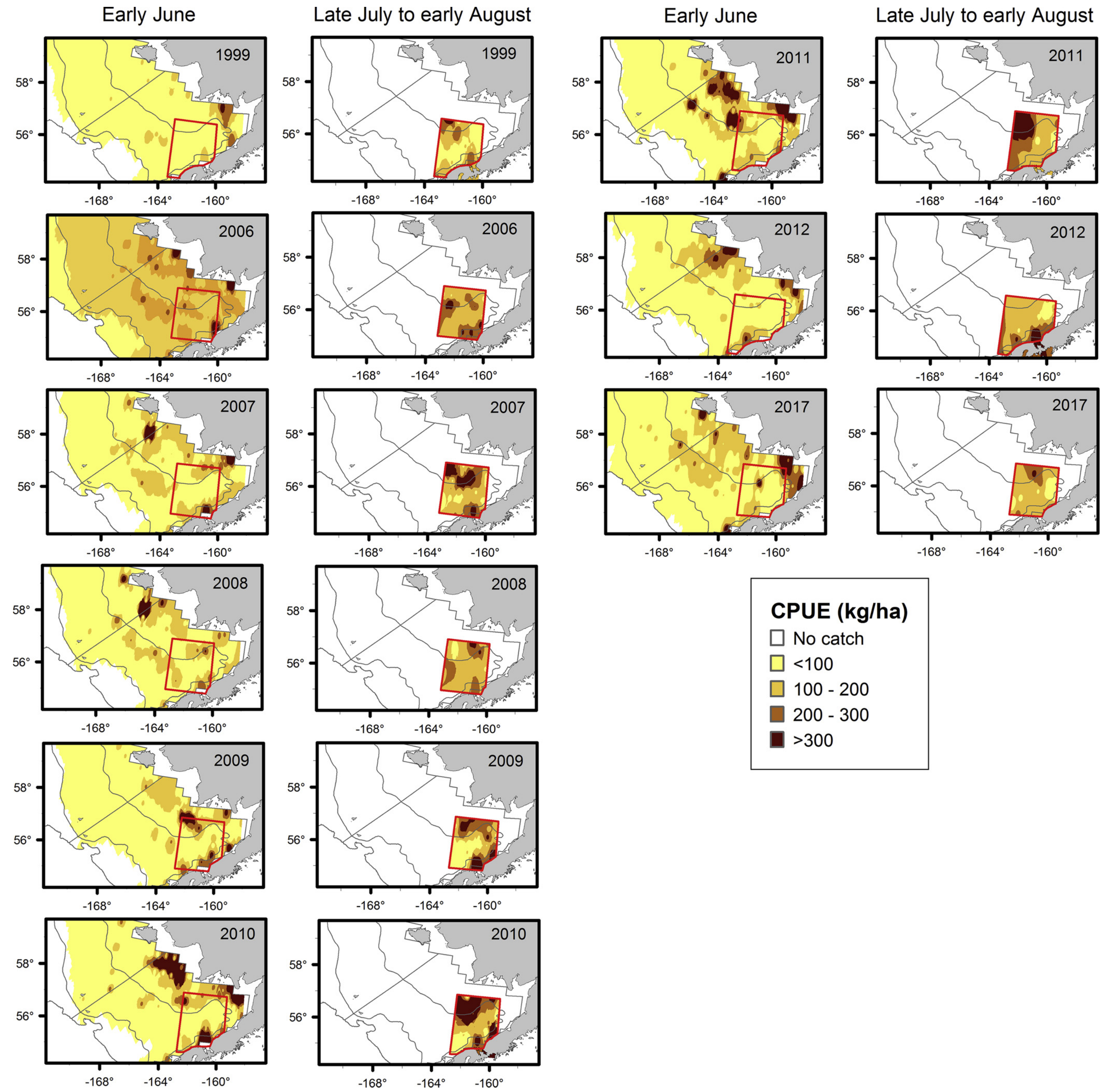

Fig. 4. Comparisons of yellowfin sole CPUE (kg/ha) between early June sampling and late July-August sampling, for years 1999, 2006, 2007, 2008, 2009, 2010, 2011, and 2012. The red outline identifies the areas commonly sampled each year during both early June and late July (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

the later sampling period in all 9 years sampled (Fig. 4). These increases were accompanied by increases in numbers of both mature and immature females, as well as mature and immature males, although the largest percentage increase (110%) occurred for mature females (Fig. 5).

Both the CPUE (number/ha) and the proportion of mature yellowfin sole females among all yellowfin sole (immature and mature sexes) increased from early to late sampling in all 9 years of sampling, and also increased linearly with increasing mean station bottom temperatures (Fig. 6A, B). By comparison, for northern rock sole, the CPUE actually decreased slightly from early to late sampling and the proportion of mature females essentially did not change (Fig. 6C, D).

3.4. *Correlates to estimated survey biomass*

In addition to the known increase in the estimated survey biomass with increasing annual bottom temperatures (Fig. 7A), estimated biomass also increased with increasing (i.e., later) survey start date (Fig. 7B), with increasing mean fish lengths (Fig. 7C) and with increasing proportion of mature fish (Fig. 7D). Together, bottom temperature and survey start date, accounted for 50% of the annual survey biomass variability, as indicated with multiple linear regression (Tables 1 and 2). Although both mean fish length and the proportion of mature fish were highly correlated with estimated biomass ($r > 0.5$), neither was determined to be causal, but rather an outcome resulting from the state of spawning progression. This was clear considering how similar

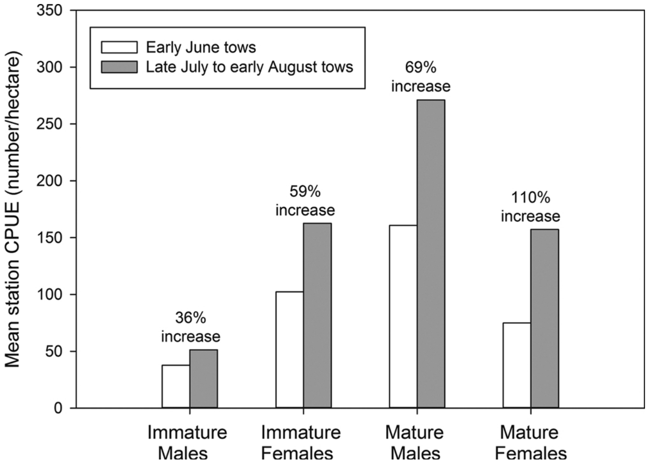

Fig. 5. Comparison of yellowfin sole mean station CPUE (number/ha) between stations conducted in early June and the same stations conducted from late July to early August; for immature males, immature females, mature males, and mature females. CPUE by weight (i.e., kg/ha) was not used here due to the possibility that growth of individuals between early June and later sampling might bias the result.

each of these factors was related to annual survey biomass (Fig. 7A, B) and that each was positively linearly correlated with annual bottom temperatures, explaining the same amount of variance ($r^2 = 0.35$).

3.5. Climate-related changes in estimated survey biomass

Among the various climate indicators that were regressed with the annual change in EBS survey biomass estimates (Table 1), the annual change of the cold pool area (bottom temperature ≤ 2 °C) explained the most variability ($r^2 = 0.41$), although the annual change in survey bottom temperatures at < 100 m depth explained almost as much ($r^2 = 0.39$). All were linearly correlated ($r \geq 0.30$) with the change in estimated biomass, likely because all are either measures of temperature (bottom, surface) or results of temperature (e.g., ice extent) and thus are correlated to each other. While this climate relationship was clear for yellowfin sole (Fig. 8A), the year-to-year increase in biomass with year-to-year increases in mean annual survey temperature (< 100 m), was nonexistent for northern rock sole (Fig. 8B).

3.6. Effect of survey start date to catchability (q) in stock assessment model

The average annual survey start date (i.e., actual sampling) over the 1985–2017 time-series was June 4th, with deviations of up to 12 days earlier and 7 days later. The addition of survey start date (S) as an independent variable along with mean annual survey bottom temperature (T), and the addition of an interaction term between the 2 variables ($T{:}S$), helped explain more of the variability among annual survey biomass estimates, from $r^2 = 0.27$ to $r^2 = 0.51$ (Table 2). Despite no linear correlation between bottom temperatures and survey start date ($r = 0.10$), inclusion of an interaction term improved both the r^2 (from 0.44 to 0.51) as well as the AIC.

The introduction of survey start date as a variable within the q

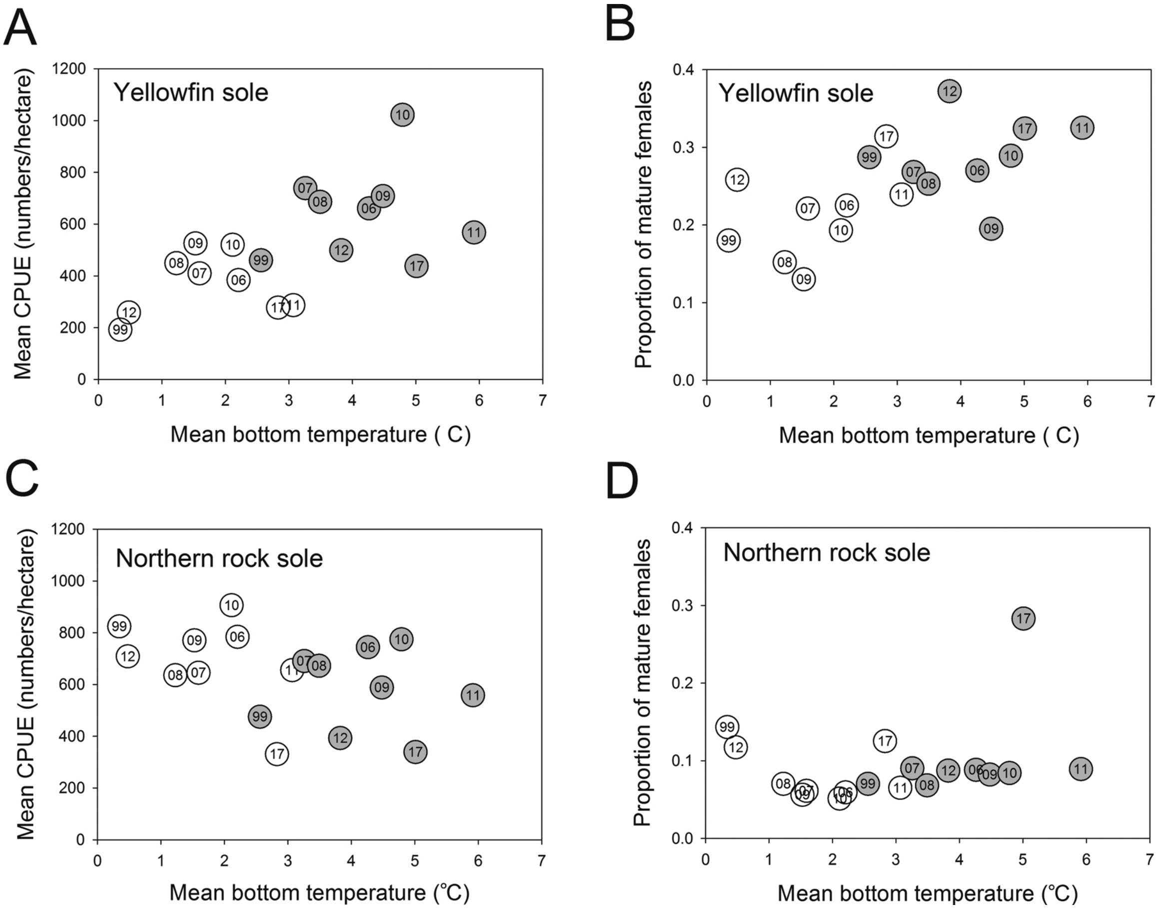

Fig. 6. Mean catch per unit effort (CPUE; number/ha) and the proportion of mature female yellowfin sole (A, B) and northern rock sole (C, D) plotted against the mean bottom temperatures at stations (n = 19–34) that were sampled in early June (white circles) and 43–69 days later in late July (gray circles) during years 1999, 2006, 2007, 2008, 2009, 2010, 2011, 2012, and 2017. Years are labeled within circles. Proportions were calculated as the CPUE (numbers/hectare) of mature females divided by the CPUE of all males and females (mature and immature).

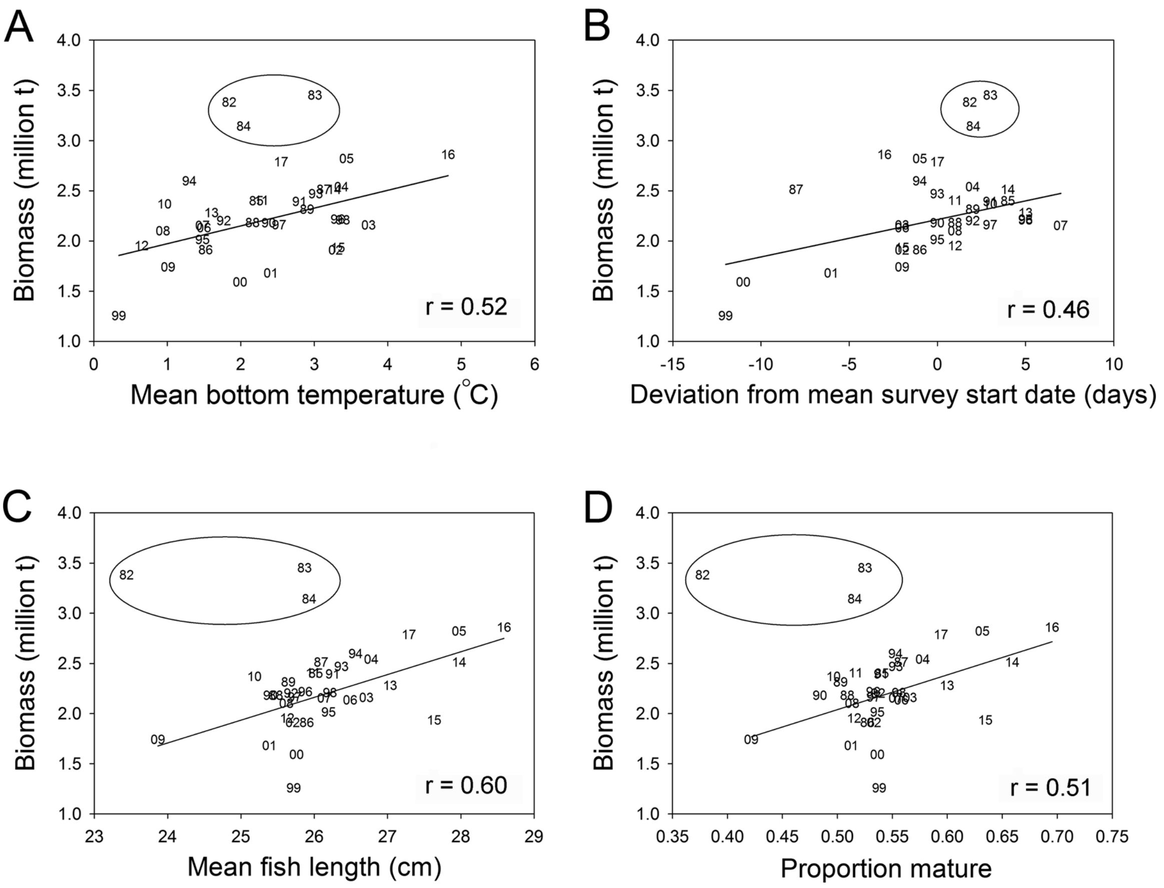

Fig. 7. Estimated annual survey biomass of yellowfin sole as related to mean annual bottom temperatures at bottom depths less than 100 m (A), the deviation of the survey start date from the mean, June 4th (B), mean survey fish length (C), and the proportional CPUE (numbers/hectare) of mature individuals (D). Numbers within graphs indicate the years. Regression lines and correlation coefficients (r) were calculated using years 1985 to 2016. Years 1982 to 1984 (circled) were excluded from regressions due to the vastly different age structure of the yellowfin sole population, which differentially affected the fish's availability to the survey (Nichol, 1998).

Table 1
Amount of variability of the annual change [(year + 1) – year] in estimated yellowfin sole survey biomass (t) explained by the annual change of different measures of climate, 1982–2017 (n = 36). Units for temperatures are °C and cold pool areas are km^2.

Climate variable (x-axis)	Slope	y-intercept	r^2
Bottom temperature, < 100 m	213,528	−21,280	0.393
Bottom temperature, < 50 m	171,837	−27,492	0.317
Bottom temperature, 50-100 m	200,858	−16,380	0.369
Surface temperature, 50-100 m	170,936	−29,168	0.395
Surface temperature, < 100 m	165,688	−28,024	0.377
Surface temperature, < 50 m	143,964	−25,388	0.317
Cold pool area, ≤ 2 °C	−2.469	−20,412	0.408
Cold pool area, ≤ 1 °C	−2.469	−17,332	0.366
Cold pool area, ≤ 0 °C	−3.933	−15,325	0.356
Air temperature, April	83,407	−23,685	0.184
Air temperature, May	124,914	−26,112	0.158
Air temperature, June	124,912	−23,917	0.149
Air temperature, July	121,344	−23,019	0.120
Air temperature, August	148,922	−22,594	0.231
Air temperature, September	96,044	−19,860	0.089
Days of ice past March 15	−10,127	−21,884	0.271

Table 2
Multiple linear regression (R, lm and glm functions), of yellowfin sole survey biomass (dependent variable) and mean annual bottom temperatures (< 100 m depth) and the annual start date of the survey for years 1985–2017. Survey start date values were calculated as the deviation in days (– and +) from the mean survey start date of June 4th. *T:S* denotes the interaction between bottom temperature (*T*) and survey start date (*S*).

Regression model comparisons:

Independent variables	r^2	AIC
Survey start date (*S*)	0.21	933.9
Bottom temperature (*T*)	0.27	931.2
T + *S*	0.44	924.3
T + *S* + *T:S*	0.51	922.3

Full model (*T* + *S* + *T:S*):

Independent variables	Estimate	*P*-value
Intercept	1,897,327	< 0.001
Survey start date (*S*)	71,532	0.003
Bottom temperature (*T*)	138,512	0.006
T:S	−19,341	0.061

parameter calculation of the stock assessment model, similarly improved overall model fits to the survey biomass data (Fig. 9), with the full model ($q = e^{-\alpha+\beta T+\gamma S+\mu T:S}$) providing a better fit (AIC = 2337) to the survey biomass data compared to models in which neither annual bottom temperature nor start date variable were included (i.e., constant q across years; AIC = 2370), or models with only a bottom temperature variable ($q = e^{-\alpha+\beta T}$; AIC = 2359). In particular, inclusion of the start date in the model improved model fits for years 1999 to 2003, years for which the reduced models (Fig. 9A, B) clearly overestimated survey biomass. Full model estimates of q ranged from 0.506 in 1999 to 1.087 in 2016, averaging 0.821 (SD = 0.0875).

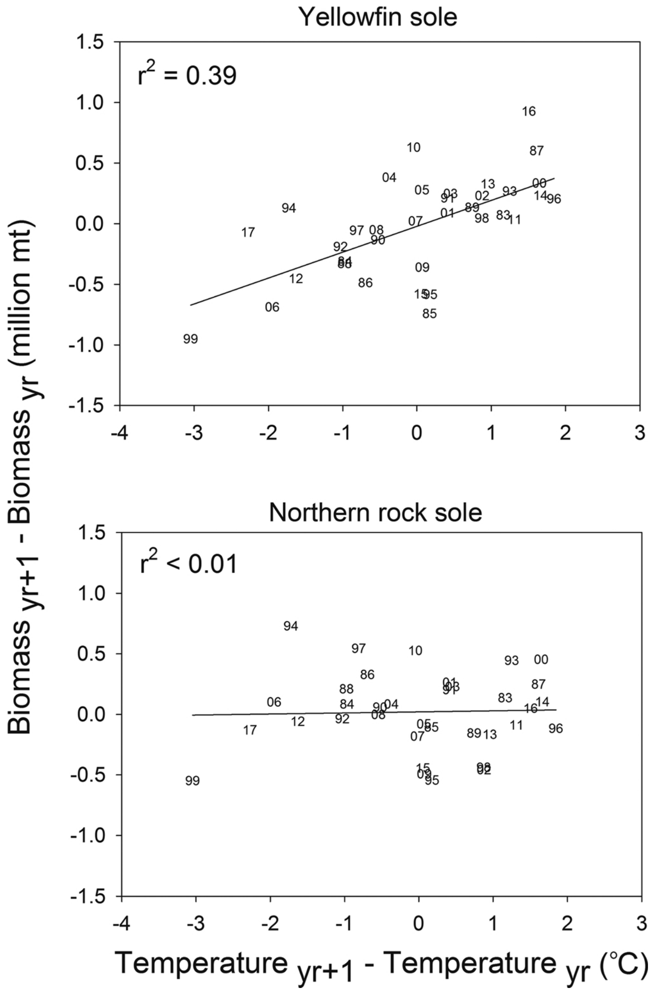

Fig. 8. Difference in the estimated yellowfin sole biomass between consecutive years as related to the difference in mean annual bottom temperatures (< 100 m) between consecutive years, during the eastern Bering Sea bottom trawl survey, 1982–2017. Symbol labels are year + 1 (e.g., 99 = the change in biomass versus the change in temperature from 1998 to 1999). The temperature effect on yellowfin sole biomass was highly significant (p < 0.001).

4. Discussion

4.1. General conclusions

This study supports the hypothesis that the spatial availability of yellowfin sole to the EBS bottom trawl survey is affected by the timing and progression of spawning, and the progression of spawning is dependent on mean annual bottom temperatures. Evidence included the positive correlations of two indicators with annual estimated survey biomass: mean fish length and the proportion of females relative to males. Mean fish lengths (and estimated biomass) were greater during years in which spawning was more progressed (e.g., in warmer years) because a larger proportion of mature individuals, mostly spent females, had migrated out of the unavailable nearshore areas. Higher proportions of females in the survey reflected more progressed spawning because males remained on the spawning grounds longer than females. This scenario was evident for two reasons. First, only mature females, not mature males, were distributed deeper during the warmer years compared to colder years. Second, the proportion of females, in addition to overall CPUE, increased between early (June) and late (July-August) samplings for all 9 years when repeated sampling was conducted. Positive correlations of bottom temperature with the above indicators, with annual survey biomass, and with the year-to-year changes in survey biomass providing evidence linking annual temperatures with the progression of spawning, subsequent availability to the survey, and resulting survey-derived estimates of biomass.

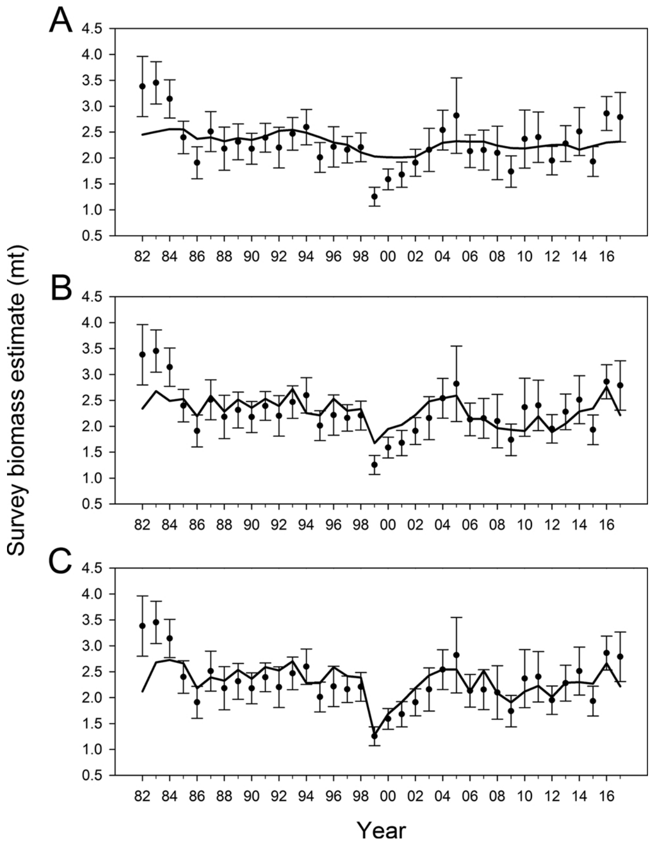

Fig. 9. Stock assessment model fits (bold line) to yellowfin sole survey biomass estimates (circles and 95% CI), with catchability (q) held constant (A), with $q = e^{-\alpha+\beta T}$ as used in the current stock assessment (B), and with $q = e^{-\alpha+\beta T+\gamma S+\mu T:S}$ (C), where T = mean annual survey bottom temperatures (< 100 m), S = survey start date, and $T{:}S$ = interaction of T and S.

Biomass estimates for yellowfin sole decreased when the surveys were conducted earlier in the year, which reinforces the timing aspect of the spawning scenario, but it was unexpected that survey start dates were then not correlated to mean survey bottom temperatures (< 100 m). One possibility is that the 19-day range of survey start dates was sufficiently long to capture the timing effect of availability, but the correlation between availability and temperature occurred over a longer time scale. It is also possible that, in addition to the temperature-mediated timing of yellowfin sole spawning and subsequent movement away from nearshore spawning areas, within-summer offshore movements may occur for other reasons (e.g., foraging, light, etc.).

4.2. Warm verses cold years

Earlier inshore migrations, earlier annual spawning, and consequently increased summer survey availability during warmer years are likely to occur for a variety of reasons. First, warmer temperatures preceding spawning, that is, cumulative temperatures from winter to spring, could promote earlier seasonal gonadal development, and/or increase the rate of gonadal development, as for *Limanda limanda* (Lang and Greve, 1997), thus prompting earlier spawning migrations. Second, earlier migrations may be dependent on earlier ice-edge retreat or preferred bottom temperatures above a certain threshold. Our comparison of catch distributions between warm and cold years were consistent with results of Bakkala (1981) who cited a delayed spring inshore migration for yellowfin sole during a particularly cold year

(1976) when the seasonal ice coverage across the shelf was particularly extensive. He also reported more northerly Bristol Bay summer distributions during warmer years (i.e., 1978) compared to colder years (1975, 1976), again suggesting seasonal migrations were delayed in colder years. Finally, it is possible that the migration is influenced by the nearshore arrival of Pacific herring (*Clupea pallasii*), a species whose eggs yellowfin sole are known to feed on in nearshore areas of Bristol Bay immediately after the herring spawn (Funk, 1988; Wespestad, 1981). Given that different temperature measures (e.g., surface, bottom, air, cold pool area) and ice measures were all positively correlated with the change in estimated survey biomass, no one measure could be identified as the sole reason for early or late spawning migrations, but more than likely, multiple temperature-related factors act to affect the timing and subsequent availability of yellowfin sole to the survey.

4.3. Availability or trawl sampling efficiency?

Our results suggest the positive correlation between survey biomass and mean annual bottom temperature is more likely due to changes in availability than temperature-mediated survey trawl sampling efficiency. For northern rock sole, the lack of any increase in annual biomass with annual temperature, or lack of increase in catch rate from early to late sampling when temperatures increased, suggests that trawl sampling efficiency did not significantly influence catch rates and resulting survey biomass estimates. If trawl sampling efficiency significantly affects overall catchability, then we would expect survey biomass estimates (or CPUE) for both yellowfin sole and northern rock sole to increase with warmer temperatures. The simplest explanation for the species difference is that only yellowfin sole spawn at the time of the survey, with a migration, distribution, and subsequently availability that is influenced by temperature.

It is possible that trawl sampling efficiency is only affected when temperatures are below an extreme threshold. There was only one year, 1999, the coldest in the time-series (bottom temperature = 0.34 °C at < 100 m depth), during which the survey biomass for nearly all the major flatfish species in the EBS decreased from the previous year. In addition to a 43% decrease in yellowfin sole survey biomass from 1998 to 1999, decreases also occurred for northern rock sole (25%), flathead sole (42%), Pacific halibut (21%), arrowtooth flounder (31%) and Greenland turbot (27%). A notable exception was for Alaska plaice, which increased by 6% from 1998 to 1999; however, Alaska plaice is a cold tolerant species (Knight et al., 1991; Wilderbuer et al., 2017). It is also possible, however, that the low temperatures in 1999 could have affected the survey availability of these species. The cold pool was at its greatest spatial extent in 1999, and the annual changes in the summer cold pool area are known to affect the summer spatial distributions of many of the fish species in the EBS (Stevenson and Lauth, 2012; Kotwicki and Lauth, 2013). Compounding the availability effect in 1999, as observed for yellowfin sole, was the early survey start date (12 days earlier than the mean). Further research is needed to determine the extent to which other species are affected by annual changes in availability to the bottom trawl survey.

4.4. What portion of the actual biomass is lost to nearshore waters?

The annual variability of stock assessment model estimates of q (catchability) for yellowfin sole can provide a relative measure of the availability of yellowfin sole within the survey area, and hence corrects the assumption that the survey covers the effective range of the stock. The integrated assessment models incorporate these survey biomass estimates and their standard errors, but they also incorporate estimates of fishing mortality, age-structure, recruitment, and somatic growth, all of which can affect annual changes in biomass (Wilderbuer et al., 2017). These combined effects are thought to provide more realistic estimates of the population biomass and trends compared to survey estimates alone. With both bottom temperature and survey start data incorporated into q, some of the annual variability in biomass caused by population shifts in the spatial distributions is explained. We have demonstrated this variability results mostly from availability rather than trawl efficiency, therefore, the annual variability of q provides an indication of the fraction of fish unavailable to the survey. With both bottom temperature and survey start date incorporated, q was highest in 2016 (1.087) and lowest in 1999 (0.551). If we assume, conservatively, that survey availability was 100% (i.e., $q = 1$) in 2016, when other indicators of availability (mean length and proportion mature) were also at a maximum, then in 1999 only half ($q = 0.506$) of the yellowfin sole were available to the survey. While this estimate ignores sampling variability, the sampling CVs are generally low (annual mean = 8%) and adding in this source of uncertainty would have little effect on the relative magnitude of the process errors (i.e., date and temperature) affecting the stock's availability to the survey.

4.5. Other factors that affect availability

Two other factors that can affect yellowfin sole availability, but were not directly addressed by this research, include distributional shifts due to recruitment and shifting of the population across the northern border of the standard annual survey. First, recruitment events that introduce a younger age structure with a high proportion of immature fish, as occurred from 1982 to 1984, can cause a disproportionate increase in abundance within the survey area because the immature fish do not migrate inshore for spawning (Nichol, 1998). This has not been an issue for more than 30 years because the population age structure has been relatively consistent since 1985 (Wilderbuer et al., 2017), but stock assessors should be aware of this effect in the event of strong recruitment in future years. Second, availability also may be dependent on shifts of the population across the northern border of the standard bottom trawl survey (Fig. 1), given that some yellowfin sole were observed well north of the standard survey area in both 2010 and 2017 when survey sampling was extended north to latitude 65 °N (Lauth, 2011; Siddon and Zador, 2017). Based on survey biomass estimates in 2010 and 2017, 16% and 14% of the biomass, respectively, inhabited areas north of the standard survey area. Northern portions of the yellowfin sole population may constitute a different spawning stock and may be independent from southern concentrations, but depictions of seasonal migrations based on tagging research (Wakabayashi, 1989; see Fig. 4 in Wilderbuer et al., 1992), indicate that some yellowfin sole do migrate from south to north and back across the northern border of the survey between spring and summer. Temperatures in southeastern Bering Sea are predicted to increase and ice extent decrease over the next several decades (Hermann, et al., 2016), thus, there is potential for increased northward movement of yellowfin sole beyond the current survey boundaries. More extensive and frequent monitoring of yellowfin sole outside current survey boundaries, both nearshore and farther north, may be necessary.

One unexpected result in this analysis was that immature males and females increased in abundance between early June and July-August sampling (Fig. 5), despite no clear spatial differences in their distribution between warm and cold years (Fig. 3). Increases of mature individuals from early to late season samplings can be explained by the progression of spawning, but for immature yellowfin sole, most of which were females due to their later age at maturity, reasons for the increased numbers are less clear. Among immature yellowfin sole, larger individuals inhabit deeper depths than smaller ones (Nichol, 1997), and are thought not to undergo the long seasonal migrations that mature fish do (Bakkala, 1981; Fadeev, 1970), but clearly they are not stationary. Yellowfin sole availability, therefore, also may be affected by seasonal distributional changes of immature individuals, although not nearly as great as for mature individuals.

4.6. Stock assessment implications

One of the goals of this research was to determine what measures of temperature would most accurately reflect the annual change in survey biomass estimates, regardless of whether such changes were due to temperature-mediated availability or trawl sampling efficiency. Accounting for these changes may be especially important given the projected increase in overall arctic temperatures in the coming years (Hermann et al., 2016). Current stock assessment models for yellowfin sole (Wilderbuer et al., 2017) incorporate a survey catchability parameter ($q = e^{-\alpha+\beta T}$) with a temperature variable (T) meant to account for the observed increases in survey biomass estimates with increased bottom temperature. This relationship is important because it is used to essentially scale survey biomass to actual biomass, and it significantly improves the model fit to survey biomass estimates (Wilderbuer et al., 2017). Among the different temperature-related measures, the cold pool areal extent ($\leq$ 2 °C) explained the most year-to-year variability ($r^2 = 0.41$), and thus could be used as an alternative to the mean annual survey bottom temperatures (< 100 m) currently used. However, the mean bottom temperatures explained nearly as much variability ($r^2 = 0.39$), so it may be inconsequential to modify the current relationship. Inclusion of either mean fish length or the proportion mature would also not improve model accuracy, as these factors largely result from the temperature effect on spawn timing, and they would not account for the effects of trawl sampling efficiency, if they exist.

One factor that can improve agreement between survey and assessment biomass, as an addition to the q parameter, is survey start date. Survey start date, along with survey bottom temperatures, significantly improved the model fit to survey biomass estimates, reinforcing that significant annual change in estimates of yellowfin sole biomass result from changes in yellowfin sole availability to the survey. As argued, yellowfin sole availability is a function of the timing of spawning, but this is relative to the timing of the survey. Surveys with the earliest start dates capture yellowfin sole at an earlier period of their spawning and migration cycle, and thus introduces an additional (e.g., to temperature) and independent effect on estimates of survey biomass. The combined effects of temperature and survey start date were most apparent in 1999, during which temperatures were the lowest and survey start dates were the earliest within the time series (1982-present). The inclusion of both variables in the model explained much of this annual variability, as indicated by a significantly improved fit through the 1999 survey biomass estimate. In addition to improving the stock assessment model fit to survey biomass, knowledge of the survey start date effect provides incentive to adhere to a consistent annual start date, when practicable.

4.7. Future research

This research provides evidence that annual yellowfin sole survey biomass estimates vary with the fish's availability to the survey, and that the incorporation of both bottom temperature and survey start date into the catchability parameter (q) can explain a large portion of this variability. However, this research does not clearly define the estimated portion of the population that the survey misses due to the species' availability. Future research currently proposed by the Alaska Fisheries Science Center (North Pacific Research Board proposal, https://www.nprb.org; Investigators: Hoff, G.R., Thorson, J.T., Punt, A.E.) includes the use of spatio-temporal modeling (Thorson and Barnett, 2017) of the bottom trawl survey data to extend abundance estimations of various species in EBS beyond survey boundaries by incorporating auxiliary species abundance data collected in traditionally unavailable areas. For yellowfin sole, auxiliary data includes standardized survey sampling in nearshore areas of Togiak and Kuskokwim bays, with a total of 126 trawls conducted between 1988–1991 (Nichol, 1998) and 2000–2004, as well as sampling north of the standard eastern Bering Sea survey in 2010 and 2017 (Lauth, 2011; Siddon and Zador, 2017). With spatio-temporal modeling, we hope to more clearly define annual survey availability, the variance associated with this availability, and to provide more accurate (i.e., absolute) and precise measures of yellowfin sole abundance.

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Appendix A

The proportion of mature male yellowfin sole (P) at fish length (L; cm) was calculated using maturity data (0 = immature; 1 = mature) collected during 1992 through 1995 eastern Bering Sea bottom trawl surveys (n = 1784). Immature testes were identified as those with clear color; and mature testes as those that were opaque, white, running with sperm, or deflated (i.e., spent). The mature proportion at length was modeled as $PL = 1/(1 + e^{AL+B})$ where parameters A and B were estimated by fitting this logistic curve to the data using generalized linear modeling (glm; family = binomial (logit); R Core Team, 2017). Results of the glm are as follows:

Independent variables	Estimate	P-value
Intercept	10.34126	< 0.001
Fish length in cm (L)	−0.47762	< 0.001

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