This article was downloaded by: [NOAA Seattle / NWFSC]
On: 27 August 2013, At: 10:55
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Marine Biology Research
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/smar20

Contrasting the maturation, growth, spatial distribution and vulnerability to environmental warming of Hippoglossoides robustus (Bering flounder) with H. elassodon (flathead sole) in the eastern Bering Sea

James W. Stark [a]

[a] Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, WA, Seattle, USA

Published online: 17 Oct 2011.

To cite this article: James W. Stark (2011) Contrasting the maturation, growth, spatial distribution and vulnerability to environmental warming of Hippoglossoides robustus (Bering flounder) with H. elassodon (flathead sole) in the eastern Bering Sea, Marine Biology Research, 7:8, 778-785, DOI: 10.1080/17451000.2011.569554

To link to this article: http://dx.doi.org/10.1080/17451000.2011.569554

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

Marine Biology Research, 2011; 7: 778–785

ORIGINAL ARTICLE

Contrasting the maturation, growth, spatial distribution and vulnerability to environmental warming of *Hippoglossoides robustus* (Bering flounder) with *H. elassodon* (flathead sole) in the eastern Bering Sea

JAMES W. STARK*

Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, WA, Seattle, USA

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

Abstract

Two similar appearing congeners, *Hippoglossoides robustus* (Bering flounder) and *H. elassodon* (flathead sole), inhabit the Bering Sea and are harvested together during the commercial fishery. In order to establish more precise overfishing limits, the annual spawning biomass must be estimated. Spawning biomass is modelled using the best estimate of the age and length at which 50% of the stock is expected to reach maturity (A_{50}, L_{50}). The major objective of this study was to establish the first maturity estimates for Bering flounder. Females matured at a similar age for Bering flounder (A_{50}, 9 years) and flathead sole (A_{50}, 10 years). However, the body length at which females matured was significantly smaller for Bering flounder (L_{50}, 238 mm) compared to flathead sole (L_{50}, 320 mm). The difference in the length-at-maturity was probably caused by growth differences, which significantly differed between species. The distribution and spawning locations of both species in the eastern Bering Sea survey area was related to the prevailing seawater temperatures and Bering flounder occurred in significantly colder water than flathead sole. The association between cold and the distribution of Bering flounder suggests that this species may be particularly vulnerable to periods of extended sea warming.

Key words: *Co-occurrence, distribution, growth, maturity, spawning*

Introduction

Bering flounder, *Hippoglossoides robustus* (Gill & Townsend, 1897) are distributed in the northern half of the Bering Sea, the Sea of Okhotsk, and the Chukchi Sea (Pertseva-Ostroumova 1961; Hart 1973; Minami 1995). Bering flounder also occur in the Beaufort Sea, based on unpublished results from the first demersal trawl survey conducted in this area by the Alaska Fisheries Science Center (AFSC) in 2008. The similar flathead sole, *H. elassodon* (Jordan & Gilbert, 1880) is distributed from the Sea of Okhotsk in the east through the southern half of the Bering Sea (generally south of Saint Matthew Island), across the Gulf of Alaska, and down the west coast of North America to California. The distribution of Bering flounder overlaps with the distribution of flathead sole only in the eastern Bering Sea (Grigorev & Fadeev 1995). There has been significant movement of Bering flounder and flathead sole distribution for many years in correlation with changing sea bottom water temperatures (Spencer 2008). These redistributions can impact where spawning occurs. During the warm period from 1980 to 2005, the centre of the eastern Bering Sea Bering flounder distribution retreated northward an average distance of 76 km, accompanied by a 57 km northerly advance of the flathead sole distribution (Mueter & Litzow 2008). Within that

*Correspondence: J.W. Stark, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA. E-mail: Jim.Stark@noaa.gov

Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

(Accepted 1 March 2011; Published online 17 October 2011; Printed 31 October 2011)

This work was authored as part of the author's official duties as an employee of the United States Government and is therefore a work of the United States Government. In accordance with 17 U.S.C. 105 no copyright protection is available for such works under U.S. law.

ISSN 1745-1000 print/ISSN 1745-1019 online
http://dx.doi.org/10.1080/17451000.2011.569554

time period, the northern extent of the area in which both species occurred (area of co-occurrence) was approximately 170 km north of St Matthew Island (62°N latitude), based on unpublished AFSC survey data. However, from 2006 to 2009, the northern boundary of the area of co-occurrence retreated approximately 110 km south to St Matthew Island (61°N latitude). This southward movement was correlated with the prevalence of cooler sea bottom water temperatures in the central Bering Sea (Stockhausen et al. 2009).

The primary objectives of this study were to establish baseline estimates of female Bering flounder length- and age-at-maturity, and other spawning-related parameters, for use in size- or age-structured stock assessment models. Other stock assessment-related objectives were to delineate aspects of the relationship between Bering flounder and its congener flathead sole, including reproductive biology, spawning, growth, and distribution.

Materials and methods

Sample site selection, collections and classifications

The Bering flounder collections were made during the annual AFSC eastern Bering Sea groundfish survey using standardized trawl survey gear at survey stations located northwest of Saint Matthew Island (Figure 1). The number of survey stations with Bering flounder collections was 20 during June and July 2006 and two during October 2007. This location was chosen because of the high abundance of Bering flounder. Specimen samples and data collected included ovaries, otoliths, measurements of body length, and seawater temperature profiles. Oocytes within each ovary were classified into six histological stages based on criteria used by Hunter et al. (1992) and Stark (2004). The six stages were perinucleus, cortical alveoli, early vitellogenesis, vitellogenesis, hydrated and post-ovulatory follicles. Individual ovaries were classified according to the

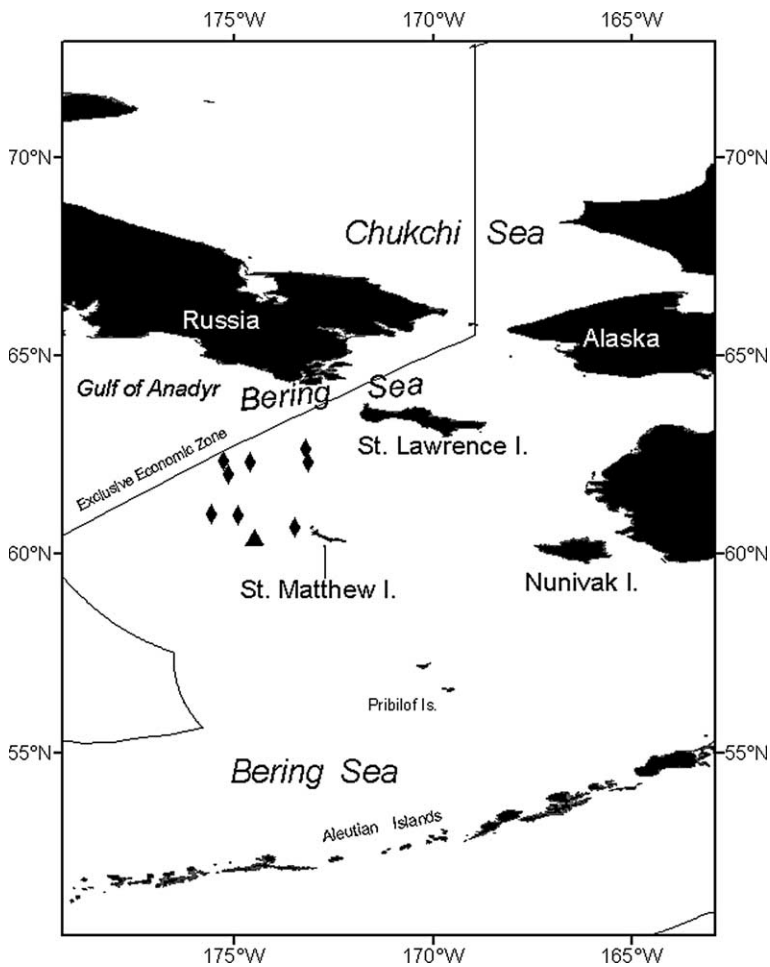

Figure 1. Station locations of the Bering flounder (*Hippoglossoides robustus*) maturity study by Alaska Fisheries Science Center, during June and July 2006 ($n = 20$, ◆) and October 2007 ($n = 2$, ▲). The station symbols do not total 22 because some symbols are merged together due to the scale of the map display.

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

most advanced stage of oocytes present in the histological sections. Individuals classified as spawners were those with ovaries containing either hydrated oocytes or post-ovulatory follicles. The methods used for sample collection, histological sample preparations, and ageing specimens are the same as those described in Stark (2004). Specimen collections were obtained during the summer (June and July, $n = 156$ specimens) and autumn (October, $n = 56$ specimens). Mature females were those classified with ovary maturities ranging from early vitellogenesis through post-ovulatory follicles. To evaluate the consistency of maturation within the ovaries, histological sections were made from the anterior, medial, and posterior areas of ovaries from 13 specimens. The posterior area was regarded as the standard sample section and was taken from every specimen collected. Each individual histological section received an independent maturity evaluation and classification.

Determination of length- and age-at-maturity

Statistical analyses were made using S-Plus software (vers. 2000 Professional release 3, MathSoft Inc., Cambridge, MA). Maturity was estimated as a function of total body length, L (mm), by fitting a logistic function to binary maturity data using generalized linear modelling (Venables 1997). The model was evaluated at 50% maturity, algebraically solving for length (L_{50}) for each month and all months combined. The variance of L_{50} was estimated using bootstrapping (Efron & Tibshirani 1993) based on 200 resamplings, with replacement, of the maturity and length data. Differences in the L_{50} by month, area, and species were tested with a Z-test (Sokal 1969). The same procedures were used to describe maturity as a function of age. The June, July, and October collections provided the means to test whether smaller and younger females matured later in the year than larger, older females using the statistical methods described. The June–July and October specimens were estimated to represent the same local stock of Bering flounder, based on the similar locations of specimen collections and similar maturity at age and length results. Based on these results the maturity data were pooled and reanalysed to obtain the most representative estimates of female Bering flounder age- and length-at-maturity. Differences in the estimated age and length at spawning between species were tested with a Z-test. Length and age were compared as predictors of maturity using generalized linear modeling of both total body length and age and modeling again without each component. The difference between models was tested using the Chi-square test. Differences in the estimated mean instantaneous growth coefficient, k, between sexes, areas, and species were tested with a Z-test. The flathead sole maturity and spawning data used in the comparisons with Bering flounder came from the Stark (2004) flathead sole maturity study.

Growth sampling methods and analysis

To investigate the basis for differences in maturity as a function of body length and age, the following procedures were used: Growth parameters were determined for Bering flounder and flathead sole using length- and geographic area-stratified otolith collections from the combined 2006, 2007, and 2008 annual AFSC area-wide groundfish assessment surveys of the eastern Bering Sea. Length-at-age was described by the von Bertalanffy growth function, using a nonlinear least-squares fit to length and age data (Venables 1997) with S-Plus software. Between-sex, between-area, and between-species differences in growth were tested by first fitting the von Bertalanffy model with a term distinguishing sex, area, and species, and repeating the procedures for combined sexes, areas, and species. The likelihood ratio of the two models was then determined for each category (Kimura 1980). Significance of the likelihood ratio was compared to determine if growth differed by sex, area, or species. To determine if differences in growth could be a factor in growth the energy acquisition was determined as $k \times L_\infty$ (van Walraven et al. 2010).

Growth study location

The geographic areas referenced in the analysis are located within the eastern Bering Sea and include

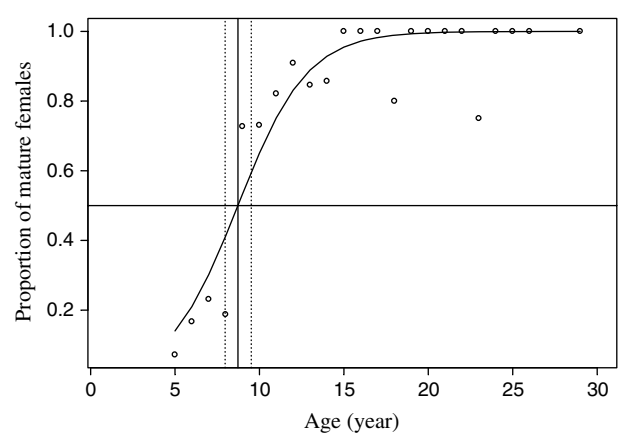

Figure 2. The proportion of mature female Bering flounder (*Hippoglossoides robustus*) by age, based on Alaska Fisheries Science Center maturity collections made during June and July 2006 ($n = 151$) and October 2007 ($n = 56$). The mean age at 50% maturity = 8.72 years; 95% confidence intervals are denoted by the parallel dotted lines. n: number.

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

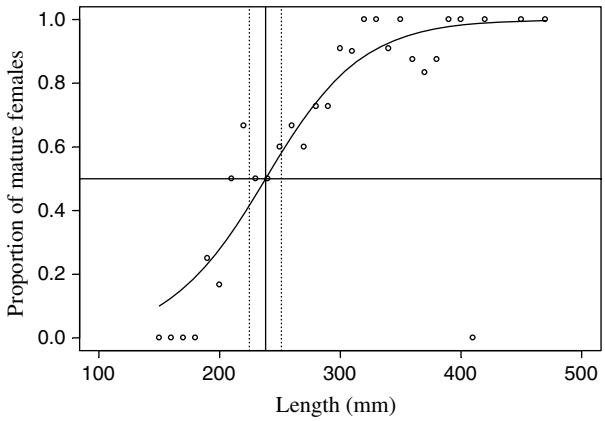

Figure 3. The proportion of mature female Bering flounder (*Hippoglossoides robustus*) by length, based on Alaska Fisheries Science Center maturity collections made during June and July 2006 ($n = 156$) and October 2007 ($n = 56$). The mean length at 50% maturity = 238.09 mm; 95% confidence intervals are denoted by the parallel dotted lines. *n*: number.

the area of co-occurrence, and an area of exclusive distribution, for each species based on the 2006, 2007 and 2008 annual AFSC groundfish surveys. The area of co-occurrence was that portion of the annual AFSC eastern Bering Sea survey area in which both Bering flounder and flathead sole occurred in the catch, which was in the vicinity of St Matthew Island. The exclusive Bering flounder area was located north of the area of co-occurrence. The area of exclusive flathead sole distribution was located south of the area of co-occurrence and west of Nunivak Island.

Seawater temperature assessment

Seawater temperatures were collected using calibrated, trawl-mounted microbathythermographs during the annual 2006 through 2009 AFSC eastern Bering Sea groundfish surveys. We tested for differences in the mean bottom water temperatures between years, areas, species, and species spawning periods using a *Z*-test. The flathead sole spawning results have not been presented before from the Stark (2004) study.

Results

Maturity relative to age and length

Ovaries from the 13 specimens examined in detail for consistency of maturation revealed that all sections (anterior, medial, and posterior) had the same maturity development as all other sections from the same ovary. Therefore, the standard sections from the posterior region provide samples that are representative of a female's maturity. The rate of maturation differed by body length, with larger Bering flounder females maturing earlier in the year than smaller females. During June and July, many of the larger females had completed spawning for that year and appeared immature, meaning that their ovaries most advanced oocytes were in the cortical alveoli maturity stage with no post-ovulatory follicles present. And during June and July the smallest mature females were 190 mm in length. In contrast, by October the smallest mature females were 240 mm in length. Consequently, the length at which 50% of females reached maturity (L_{50}) significantly differed between the two periods. During June and July females reached L_{50} at 222 mm, significantly ($P < 0.001$) smaller than the October collection which had an L_{50} of 277 mm. However the age at which females reached 50% maturity (A_{50}) did not significantly differ ($P = 0.17$) between June and July (9.4 years) and October (8.4 years). Consequently, the Bering flounder data collected in June and July (length data $n = 156$, age data $n = 151$) and in October (length and age data $n = 56$) were combined to obtain an estimate of L_{50} and A_{50} with the lowest variance. Based on the combined data, Bering flounder females were expected to reach A_{50} at 8.7 years (Figure 2, Table I) and L_{50} at 238 mm (Figure 3, Table II). As a predictor of female maturity age was slightly more significant ($P = 0.02$) than total body length ($P = 0.04$).

Growth, spawning and associated sea water temperatures

The models of length at age significantly ($P = 0$) differed between Bering flounder and flathead sole both within the area of co-occurrence and in areas not shared between the two species (Figures 4 and 5, Table III). Compared to flathead sole, the model of Bering flounder growth had a significantly ($P < 0.001$) lower slope (k) in every area for both

Table I. Female Bering flounder (*Hippoglossoides robustus*) age-at-maturity estimates based on ovary histology samples collected from the eastern Bering Sea during June and July 2006 and October 2007 (combined). The parameters of the logistic equation fit to the data are: B (slope of the line) and A (Y-intercept), while A_{50} is the age (years) at which 50% of females were expected to reach sexual maturity.

Sampling statistics	
n	207
B	0.48731
A	−4.25063
Variance (B)	0.00220
Variance (A)	0.97962
Covariance (B, A)	−0.00076
A_{50}	8.72272
Variance (A_{50})	0.16928

n: number.

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

Table II. Female Bering flounder (*Hippoglossoides robustus*) length-at-maturity results based on ovary histology samples collected from the eastern Bering Sea during June and July 2006 and October 2007 (combined). The parameters of the logistic equation fit to the data are: B (slope of the line) and A (*y*-intercept), while L_{50} is the length (mm) at which 50% of females were expected to reach sexual maturity.

Sampling statistics	
n	212
B	0.02487
A	−5.92212
Variance (B)	0.000003
Variance (A)	0.98461
Covariance (B, A)	0.00011
L_{50}	238.08999
Variance (L_{50})	55.33744

n: number.

males and females, including the area in which both species co-occurred. The length at maximum age (L_∞) did not differ significantly ($P > 0.20$) between areas for males or females of either species. Females of both species reached a larger length at maximum age than males. The energy acquisition ($k^\star L\infty$) results explain much of the differences in the growth models. Bering flounder energy acquisition was

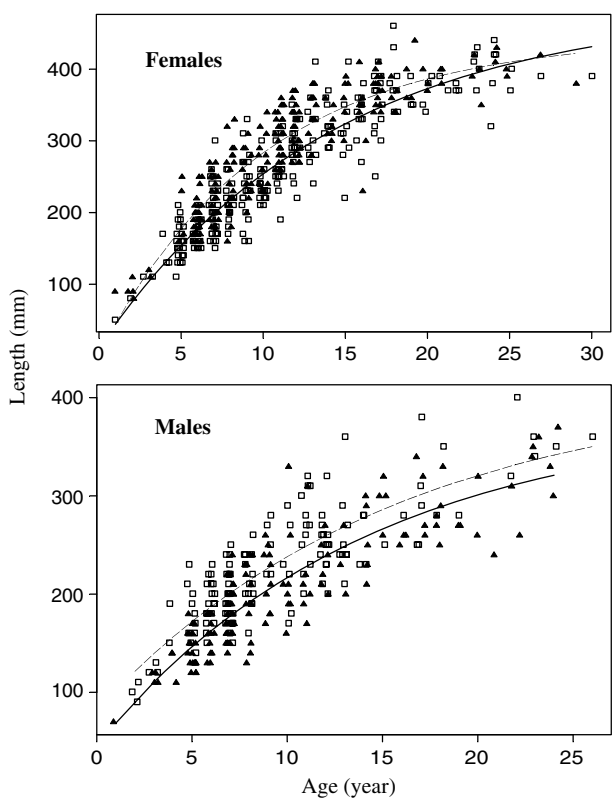

Figure 4. Total length-at-age of Bering flounder (*Hippoglossoides robustus*) females, and males within the area of co-occurrence with flathead sole (*H. elassodon*; ---, □) and within the area of exclusive distribution (—, ▲), based on annual Alaska Fisheries Science Center groundfish assessment surveys conducted in the eastern Bering Sea during 2006–2008.

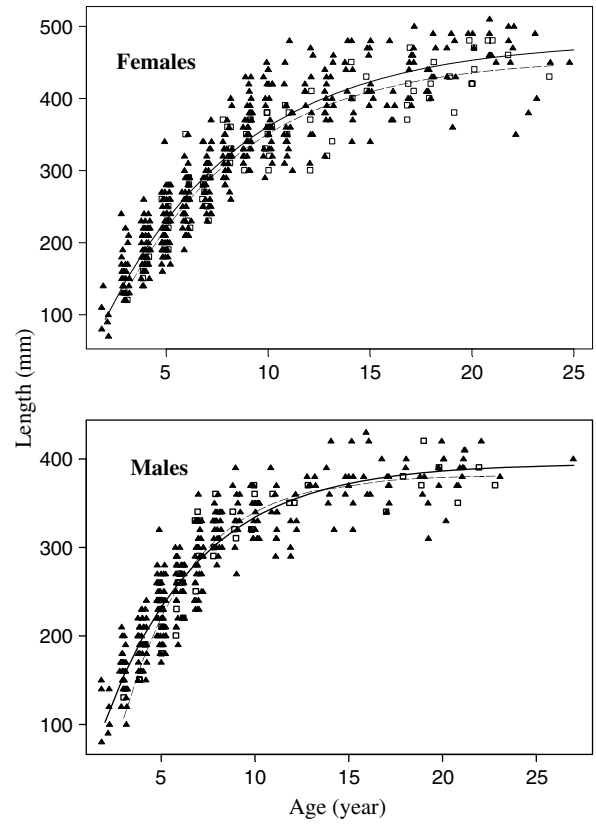

Figure 5. Total length-at-age of flathead sole (*Hippoglossoides elassodon*) females, and males within the area of co-occurrence with Bering flounder (*H. robustus*; ---, □) and within the area of exclusive distribution (—, ▲), based on annual Alaska Fisheries Science Center groundfish assessment surveys conducted in the eastern Bering Sea during 2006–2008.

significantly ($P < 0.001$) lower than flathead sole. Bering flounder energy acquisition ranged from approximately 2.7 for males to a maximum of 4.5 for females. Flathead sole energy acquisition was 7.0 for females and up to 10.0 for males.

Slower energy acquisition may be related to differences in ambient seawater temperatures. The sea water temperatures associated with the area of co-occurrence ranged from −1.5 to 2°C, while temperatures in the areas of exclusive distribution ranged from −1.7 to 2.3°C for Bering flounder ($n = 4172$) and −1.5 to 7.2°C for flathead sole ($n = 27{,}276$).

Seawater temperature did not have a significant ($P = 0.12$) relationship with Bering flounder spawning. During this study Bering flounder females spawned during June and July in bottom water temperatures ranging from −1.70 to 0.50°C, averaging −0.85°C with surface temperatures that averaged 6.5°C. Temperatures were similar during October. Bering flounder spawned actively during June and July, with spawners representing 40% of all females collected and occurring at over 90% of all stations where collections occurred. The female

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

Table III. Bering flounder (*Hippoglossoides robustus*, BF) and flathead sole (*H. elassodon*, FHS) length-at-age described by the von Bertalanffy growth equation for females and males residing within the shared area in the central eastern Bering Sea (area of co-occurrence), and in the eastern Bering Sea areas not shared by the two species (area of exclusive distribution). Sample size (n) and parameters L_∞, k, and t_0 are given. Results are based on the combined 2006, 2007, and 2008 annual Alaska Fisheries Science Center groundfish assessment surveys.

	Location			
	EBS area of co-occurrence		EBS area of exclusive distribution	
Sex	BF Females	FHS Females	BF Females	FHS Females
n	221	71	252	848
L_∞	445.7620	456.5638	487.3980	470.3836
var (L_∞)	255.7720	222.2080	794.5896	33.0114
k	0.1005	0.1614	0.0712	0.1495
var (k)	0.0001	0.0006	0.0001	0.0001
t_0	−0.0496	0.9157	−0.3327	0.0043
var (t_0)	0.1626	0.2834	0.2489	0.0210
cov (L_∞, k)	−0.1558	−0.3076	−0.2665	−0.0349
cov (L_∞, t_0)	−4.3472	−5.2041	−11.0289	−0.5370
cov (k, t_0)	0.0036	0.0112	0.0044	0.0009
$k^\star L_\infty$	44.7991	73.6894	34.7027	70.3223
	BF Males	FHS Males	BF Males	FHS Males
n	138	43	152	672
L_∞	413.1132	381.8928	382.3160	384.56
var (L_∞)	2565.6342	100.9958	1299.7964	13.3310
k	0.0639	0.2690	0.0710	0.2018
var (k)	0.0004	0.0013	0.0003	0.0001
t_0	−3.4409	1.7820	−1.7929	0.0353
var (t_0)	1.9088	0.1301	0.9339	0.0178
cov (L_∞, k)	−0.9478	−0.2692	−0.5920	−0.0255
cov (L_∞, t_0)	−58.8650	−1.6172	−29.1032	0.2625
cov (k, t_0)	0.0247	0.0112	0.0152	0.0011
$k^\star L_\infty$	26.3979	102.7292	27.1444	77.6042

L: length; k: mean instantaneous growth coefficient; var: variance; cov: covariance; t_0: theoretical age when length is 0; $k^\star L_\infty$ is a proxy of the rate of energy acquisition.

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

Bering flounder spawners ranged in age from 7 years up to the oldest female collected (29 years). However, results from the October collection maturity classifications indicated that the annual spawning cycle had concluded months earlier and females were developing oocyte stocks for the following year. During October over 60% of the females were classified in the vitellogenesis (yolk sequestering) stage of ovary development and the remaining females were less mature (38% cortical alveoli staged, and 2% perinucleus staged). Flathead sole spawners had a similar ($P = 0.33$) age range.

Discussion

Contrasting maturation and growth

Bering flounder females reached maturity at an L_{50} of 238 mm, which was significantly ($P < 0.001$) smaller than the 320 mm L_{50} reported for flathead sole females (Stark 2004). However, the average age at maturity (A_{50}) did not differ significantly ($P = 0.084$) between Bering flounder (8.7 years) and flathead sole (9.7 years). The difference in length-at-maturity between Bering flounder and flathead sole is attributable to the difference in their rate of growth. Compared to flathead sole, Bering flounder had significantly slower growth in every area, including the area in which both species co-occurred. Stockhausen et al. (2009) also found that Bering flounder grew slower than flathead sole. However, Bering flounder growth did not decline with age as much as flathead sole. Consequently, Bering flounder and flathead sole of both sexes reached a similar length at maximum age. The difference in growth between species was probably due to the differences in energy acquisition, which was substantially less for Bering flounder. It is not known what was responsible for the lower rate of energy acquisition. It may be due to differences in habitat and diet or sea water temperatures. It is well known that fish grow slower in colder temperatures.

Spawning

Within this area of co-occurrence, this study found primarily medium- and smaller-sized female Bering flounder spawning at a high rate during June (50%) and July (40%) 2006. Many of the large females from that collection were classified as immature and suggests that they had probably completed spawning for the year during April or May. Similarly, off the Kamchatka Peninsula Bering flounder spawned during May and June (Pertseva-Ostroumova 1961). Flathead sole had a similar spawning season in the eastern Bering Sea and Gulf of Alaska (Stark 2004). Because of similar spawning seasons, there is the potential for interspecies competition for available spawning grounds. Approximately 90% of Bering flounder catches contained some spawners during June and July. Therefore, spawning was probably occurring throughout the area, ranging to the Saint Lawrence Island area spawning grounds (Grigorev & Fadeev 1995), west to the Gulf of Anadyr in the western Bering Sea (Pertseva-Ostroumova 1961) and around the Kamchatka Peninsula to the Sea of Okhotsk. The Chukchi Sea may not be a significant spawning area for Bering flounder (Barber et al. 1997). This study found that the age of spawning female Bering flounder ranged from 7 years of age to 29 years (the oldest fish collected), and was similar to the range found for flathead sole. Consequently, the two species' potential reproductive life span is probably similar.

Distribution relative to seawater temperature

Bering flounder spawning occurred in waters that were highly stratified, as indicated by a seawater temperature profile gradient that averaged 6.5°C at the surface and −1.39°C at depth during June and July. No spawning was observed within the area during October, although seawater temperatures did not significantly differ from June and July, averaging 0.5°C at depth, and 5.9°C on the surface. Consequently, seawater temperature probably does not regulate the timing of spawning for Bering flounder. Bering flounder were not found in areas with bottom temperatures warmer than 2.3°C and averaged 0.9°C. Conversely, flathead sole occurred in eastern Bering Sea waters where temperatures averaged 2.2°C and ranged from −1.5 to 7.2°C during the same period. The difference in mean ambient temperatures associated with Bering flounder and flathead sole probably contributed to the significant difference in growth between the two species.

Potential response to environmental change

The correlation of Bering Sea bottom water temperatures with the extent of Bering flounder and flathead sole geographic distributions suggests that local abundance of these species would be directly impacted by changing environmental conditions. Future periods of extended warming will likely lead to a retreat of Bering flounder from some, but not all, established spawning grounds. The likelihood of flathead sole spawning on recently vacated Bering flounder spawning grounds is probably low because flathead sole spawn in significantly ($P<0.001$) warmer water (1.73 to 6.10°C, average 4.63°C) than Bering flounder (−1.70 to 0.50°C, average −0.85°C). However, if all Bering Sea bottom waters were to exceed 3°C for an extended period, Bering flounder would likely emigrate to cooler, more northerly waters and flathead sole would occupy the area. Such a retreat might substantially reduce the overall extent of Bering flounder feeding and spawning habitat because suitable habitat maybe limited in these waters, potentially leading to a substantial decline in overall abundance.

Acknowledgements

Thanks to the following AFSC personnel who made this study possible. Collections: E. Acuna, J. Clark, J. Conner, J. Hoff, S. Kotwicki, P. Logan, V. Lowe, D. Nichol, A. Whitehouse and M. Wilkins. Reviews: D. Somerton, W. Stockhausen, M. Wilkins, G. Duker, R. Nelson. Beaufort Sea data: L. Loggerwell, and K. Rand. Thanks to A. Rijnsdrop Institute for Marine Resources and Ecosystem Studies and the Aquaculture and Fisheries group Wageningen University Netherlands, and one anonymous reviewer for helpful suggestions. The findings and conclusions in the paper are those of the author and do not necessarily represent the views of the National Marine Fisheries Service, NOAA, and reference to trade names does not imply endorsement.

References

Barber WE, Smith RL, Vallarino M, Meyer RM. 1997. Demersal fish assemblages of the northeastern Chukchi Sea, Alaska. Fishery Bulletin 95:195–209.

Efron B, Tibshirani RJ. 1993. An Introduction to the Bootstrap. New York, NY: Chapman and Hall. 436 pages.

Grigorev SS, Fadeev NS. 1995. Distribution of Alaska plaice, flathead sole, and Bering flounder eggs in the eastern Bering Sea during April–July, 1988–1990. In Proceedings of the International Symposium on North Pacific Flatfish. Alaska Sea Grant College Program Report AK-SG-95-04, University Alaska Fairbanks, Alaska, p. 89–100.

Hart JL. 1973. Pacific Fishes of Canada. Fisheries Research Board of Canada Bulletin 180: 740 pages.

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013

Hunter JR, Macewicz BJ, Lo NHC, Kimbrell CA. 1992. Fecundity, spawning and maturity of female Dover sole, *Microstomus paciiticus*, with an evaluation of assumptions and precision. Fishery Bulletin 90:101–28.

Kimura DK. 1980. Likelihood methods for the von Bertalanffy growth curve. Fishery Bulletin 77:765–76.

Minami T. 1995. Spawning season of pleuronectid flatfishes in the coastal waters of Hokkaido, Japan (Review). Bulletin Hokkaido National Fisheries Research Institute 59:69–80.

Mueter FJ, Litzow MA. 2008. Warming climate alters the biogeography of the Bering Sea continental shelf. Ecological Applications 18:309–20.

Pertseva-Ostroumova TA. 1967. The reproduction and development of far eastern flounders. Akademiya Naunk SSSR, Institute Океанография. 484 pages (in Russian, 1961). English translation, Fisheries Research Board of Canada Translation Series 856:1–1003.

Sokal RR. 1969. Biometry. San Francisco, CA: W. H. Freeman and Company. 776 pages.

Spencer PD. 2008. Density-independent and density-dependent factors affecting temporalchanges in spatial distributions of eastern Bering Sea flatfish. Fisheries Oceanography 17:396–410.

Stark JW. 2004. A comparison of the maturation and growth of female flathead sole in the central Gulf of Alaska and southeastern Bering Sea. Journal of Fish Biology 64:876–89.

Stockhausen WT, Spencer PD, Nichol D. 2009. Flathead sole. In Stock Assessment and Fishery Evaluation Document for Groundfish Resources in the Bering Sea/Aleutian Islands Region as Projected for 2010. 605 W. 4th Ave. Anchorage AK 99510: North Pacific Fishery Management Council, p 821–908.

van Walraven LF, Mollet M, van Damme CJG, Rijnsdorp AD. 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). Journal of Sea Research 64:85–93.

Venables WN. 1997. Modern Applied Statistics with S-Plus. New York, NY: Springer-Verlag. 548 pages.

Editorial responsibility: Geir Ottersen

Downloaded by [NOAA Seattle / NWFSC] at 10:55 27 August 2013