

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Spatiotemporal variations in the distribution of round herring eggs in the East China and Japan Seas during 1997–2013



Kei K. Suzuki^{*}, Tohya Yasuda, Hiroyuki Kurota, Mari Yoda, Akira Hayashi, Soyoka Muko, Motomitsu Takahashi

Japan Fisheries Research and Education Agency, Seikai National Fisheries Research Institute, Nagasaki 851-2213, Japan

ARTICLE INFO	A B S T R A C T
A R T I C L E I N F O Keywords: Day length Small pelagic fish Spawning ground Spawning stock biomass Water temperature	Spawning stock biomass (SSB) and environmental factors, such as water temperature, can affect the size and location of spawning grounds of small pelagic fishes. We examined the effects of SSB, water temperature, and day length on the probability of egg presence of the round herring <i>Etrumeus teres</i> to clarify spatiotemporal variation in its spawning grounds in the Tsushima Warm Current region off the west coast of Japan. Egg presence probability (EPP) was estimated from monthly egg surveys and annual stock assessments from 1997 to 2013. Our results indicated that EPP was positively correlated with sea surface temperature (SST), and increased between 12 and approximately 17 °C, where it became constant, and then decreased when SST exceeded 24 °C. From February to June, locations of the main spawning grounds gradually shifted northeast from the waters off western Kyushu to the Japan Sea as the areas with water temperatures suitable for successful egg development (≥ 17 °C) expanded. However, few eggs were observed during the season when day length shortened daily, even when SST was suitable. The main spawning grounds expanded more towards northern waters in warmer years than in cooler years. In addition, EPP was positively correlated with SSB, which resulted in an expansion of the spawning grounds into coastal regions in years with high SSB. These results indicate that spawning of the round herring responds to seasonal changes in SST and day length, and interannual fluctuations in SST and SSB in the Tsushima Warm Current region.

1. Introduction

Small pelagic fishes respond plastically to changes in environmental factors by selecting adequate spawning grounds (Checkley Jr. et al., 2009; Giannoulaki et al., 2014). Especially, water temperature is an important factor in the formation of spawning grounds (e.g. Checkley Jr. et al., 2000; Coombs et al., 2006; Ibaibarriaga et al., 2007), and earlier studies showed that changes in the location and size of spawning grounds were possibly related to water temperature (Le Clus, 1990; Bellier et al., 2007). In addition, spawning stock biomass (SSB) is known to affect the size of spawning grounds of small pelagic fishes (Checkley Jr. et al., 2009). Therefore, to accurately evaluate the variability of spawning grounds, it is necessary to evaluate two factors simultaneously, and this means that long-term and large-scale data are required. However, the substantial effort required to collect spatio-temporal large-scale data for small pelagic fishes has made spawning ground analysis difficult.

The round herring *Etrumeus teres* is distributed in the temperate coastal waters of the northern and southern Pacific and is an important

commercial fish (Akel, 2009; Takasuka et al., 2017; Yasuda et al., 2017). There are two stocks of round herring in the coastal waters off Japan; the Pacific stock and the Tsushima Warm Current stock, and SSB in each stock has been estimated every year for stock assessments (Yasuda et al., 2017, Fig. 1). Stocks are separated based on differences in fisheries, spawning season and area, distribution, migration, growth, maturation, and/or survival (Fisheries Agency and Fisheries Research and Education Agency of Japan, 2017), although they are not necessarily genetically different. However, this source does not cover all aspect of round herring stocks, because of a lack of ecological information. The Tsushima Warm Current stock is distributed in the East China and Japan Seas, and SSB has been estimated since 1976 (Yasuda et al., 2017). While there are a few studies of egg collection for this stock, there are no accurate estimates of the spawning season. However, the limited information available indicates that the spawning seasons differ between the two seas. For example, the gonadosomatic index of the Tsushima Warm Current stock increased from December to the following June in the northern and western waters off Kyushu island in the East China Sea, which represents the southwestern part of the stock

E-mail address: pteromysuzuki@affrc.go.jp (K.K. Suzuki).

https://doi.org/10.1016/j.seares.2018.09.003

Received 30 January 2018; Received in revised form 31 August 2018; Accepted 7 September 2018 Available online 10 September 2018

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^{*} Corresponding author.

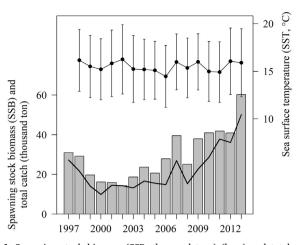


Fig. 1. Spawning stock biomass (SSB, thousand tons) (bars) and total catch (line) in the Tsushima warm current stock of *Etrumeus teres* and mean sea surface temperature (SST) (dots and line) from December to the following June. SSB and total catch data were taken from Yasuda et al. (2017). We identified locations where eggs were collected at least once, and SST at each location was averaged for each year. Error bars indicate standard deviations.

distribution (Ohshimo et al., 2011). In contrast, in the Japan Sea, which represents the north-eastern part of the distribution, round herring eggs were collected from April to July (Niwa et al., 1962). This disparity in spawning times between the two seas may be due to the different sea temperatures in these seas. Water temperature increase earlier in the East China Sea than the Japan Sea from winter to autumn. As the onset of round herring spawning in the Japan Sea is later than that in the East China Sea, it is likely that spawning season differs between the two seas based on temporal differences in water temperature. However, there are few studies showing the spawning grounds of round herring (Niwa et al., 1962; Kawano, 2008), and the factors that affect changes in their distribution remain unclear.

Intensive egg surveys of small pelagic fishes have been conducted in the Tsushima Warm Current region over a long-term period, and round herring eggs have been continuously collected in the East China and Japan Seas since 1997. Recent stock assessment analysis reported that SSB in this region decreased from 1997 to 2002 and then increased from 2003 (Fig. 1, Yasuda et al., 2017). These datasets may enable us to examine spatiotemporal patterns of egg distribution of round herring. Thus, the aims of this study were to clarify: 1) the effect of water temperature on round herring spawning; and 2) the spatiotemporal changes in the spawning grounds in relation to water temperature and the annual fluctuation in SSB.

2. Materials and methods

2.1. Egg collection survey

Egg collection surveys in Japanese coastal waters have been conducted since 1978. However, we used data from 1997 to 2013, as prior to 1996, sample sizes were small and geographically biased. These surveys were conducted using plankton nets a total of 25,880 times at 1318 sites (Fig. 2) in the East China and Japan Seas. The number of net tows per year varied from 1330 to 1771, and averaged 1522.4 (SD = 137.3). Historically, egg surveys have been conducted by 17 prefectural fisheries experimental stations and two national research institutes. This survey covered all seasons, but were more intensive from January to June.

The plankton nets (0.330 mm or 0.335-mm mesh aperture attached to a 45-cm ring flame) were towed from 150 m or just above the bottom when < 150 m depth to the surface. The depths of the net tows covered the vertical distribution of round herring eggs, which are usually 20 to

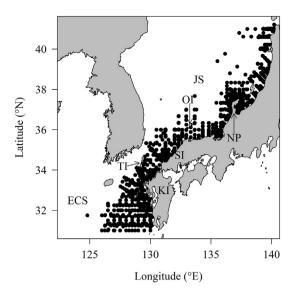


Fig. 2. Egg survey sites during the study period, 1997–2013. ECS: East China Sea, JS: Japan Sea, KI: Kyushu Island, TI: Tsushima Island, SI: San-In region, NP: Noto peninsula, and OI: Oki Island.

50 m from the surface (Uehara and Mitani, 2002). Collected eggs were identified to species level using a microscope. Sea surface temperature (SST, °C), location (°N and °E), and filtered volume were recorded simultaneously with the net tows.

2.2. Statistical analyses

To clarify the effects of SST and SSB on spawning and spatiotemporal changes in the spawning ground, we constructed a generalized additive mixed model (GAMM) with binomial distribution (Table 1). The presence or absence of round herring eggs in each net tow was used as the dependent variable. We used a smoothed term to represent SST, location, which was the tensor product of latitude and longitude, and the interaction between location and SST as fixed effect independent variables. Also, SSB, estimated using virtual population analysis (Yasuda et al., 2017), was added as the fixed effect. In addition, as the spawning season of many fish species is limited by the change in day length (Lam, 1983; Miranda et al., 2009), smoothed terms of the difference in day length between successive survey dates (ΔDL) was added as the fixed effect, to remove the effect of spawning season. We used stepwise backwards deletion to select a best model based on the lowest AICc. The influence of each fixed effect in the best model was evaluated using χ^2 test. Also, to avoid pseudo-replication of SSB and unclear effects of survey years (Bolker et al., 2009), we added the survey year to the model as a random effect. In addition, as water depth and the net type differed among sampling stations, the filtrated volume

Table 1

Effects of environmental factors on egg presence or absence by the generalized additive mixed model.

Fixed effect	χ^2	P value
s(SST)	250.0	< 0.001
te(latitude, longitude)	523.2	< 0.001
ti(latitude, longitude, by = SST)	98.8	< 0.001
SSB	12.2	< 0.001
s(ΔDL)	118.0	< 0.001

SST is sea surface temperature; SSB is spawning stock biomass; ΔDL is difference in day length between the survey day and the day before the survey day; s () are smoothed terms; te(latitude, longitude) is the tensor product of latitude and longitude; ti(latitude, longitude, by = SST) is the interaction between the tensor product of latitude and longitude and SST.

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