



Long-term change in reproductive condition and evaluation of maternal effects in Pacific bluefin tuna, *Thunnus orientalis*, in the Sea of Japan

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ABSTRACT

To evaluate long-term changes in reproductive characteristics and maternal effects in Pacific bluefin tuna in the Sea of Japan, we performed histological observations of the most advanced group of oocytes and measured batch fecundity and egg diameter. We sampled 6767 individuals from 1994 to 2015. The main spawning periods were from June to August, and the spawning intervals in June, July, and August were 1.34, 1.18, and 1.10 days, respectively. At higher sea surface temperatures, egg diameter might be smaller because the storage time of the yolk is limited due to the shorter spawning intervals at higher sea surface temperatures. Spawning periods were consistent throughout the survey years. There were significant positive correlations between batch fecundity and fork length and between batch fecundity and gutted body weight. The relative condition factor and relative batch fecundity were calculated. A generalized linear model showed that the relative batch fecundity was significantly correlated with year effects and fork length, and the egg diameter was significantly correlated with year effects and relative condition factor. Our results show that better nourished spawners have larger eggs, and larger eggs could positively affect the larval survival rate.

1. Introduction

Pacific bluefin tuna (PBT, *Thunnus orientalis*) is one of the most valuable fishes in the world and is exploited by many countries (Collette and Nauen, 1983). This species is distributed mainly in the North Pacific Ocean, but is also caught in small numbers in the southern hemisphere (Bayliff, 1994). The major spawning areas and seasons for PBT are from north of the Philippines north to around the Nansei Islands in the northwestern Pacific Ocean from April to June, and in the Sea of Japan from June to August (Yabe et al., 1966; Ueyanagi, 1969; Ashida et al., 2015; Okochi et al., 2016). Larvae hatched in the northwestern Pacific Ocean and Sea of Japan are carried to coastal areas in southwestern Japan by the Kuroshio and the Tsushima Warm Currents, respectively (Ohshimo et al., 2017). Juvenile PBT in the Pacific originate from the northwestern Pacific Ocean (Masujima et al., 2014; Suzuki et al., 2014; Furukawa et al., 2016), and juveniles in the Sea of Japan are a mixture from the two spawning grounds (Rooper et al., 2001; Tanaka et al., 2007; Itoh, 2009). Spawning adults in the both areas are also mixed from the natal origins (Uematsu et al., 2018). Age-

0 PBT migrate southward in the Sea of Japan in winter (Ichinokawa et al., 2014) and move to east to the offshore region in the Pacific (Fujioka et al., 2018). A portion of the PBT migrate to the eastern Pacific to coastal areas near the United States and Mexico (Madigan et al., 2012), stay several years (Madigan et al., 2017), and then return to the western Pacific for spawning (Madigan et al., 2017; Tawa et al., 2017).

Recently, the PBT spawning-stock biomass has been at a historically low level; this is important because the stock size dynamics of this species could depend on recruitment success, and the stock is overfished (ISC, 2016). Despite the low spawning-stock biomass, PBT recruitment does not show a clear declining trend as has been observed several times in the past (ISC, 2016), although a recent study suggested the existence of a weak stock-recruitment relationship (Nakatsuka et al., 2017). Key parameters for understanding the population dynamics are biological characteristics such as growth, mortality, and maturation. Reproductive characteristics in particular are very important because the quality and quantity of spawned eggs, along with biotic and abiotic environmental conditions, affect the survival of hatched larvae.

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Recruitment in fish is dependent on the spawning stock size and survival during early stages. Johnson et al. (2014) suggested that most early-stage mortality in fish is selective; the growth-dependent mortality hypothesis provides a theoretical framework for evaluating the importance of growth-related traits to larval survival (e.g., Meekan and Fortier, 1996; Robert et al., 2007; Sponaugle et al., 2011). Slower-growing individuals in the larval stage are more vulnerable to predation than the faster-growing individuals, even if they are the same size (Anderson, 1988; Takasuka et al., 2003); therefore, the mortality rates vary inversely with size and larger individuals will have a lower rate of mortality (Sponaugle et al., 2011). Growth-dependent mortality during the PBT larval stage indicated that higher growth rates during the larval period enhanced the survival to recruitment (Tanaka et al., 2006; Watai et al., 2017). The recruitment of bluefin tuna species (PBT; Atlantic bluefin tuna [ABT], *Thunnus thynnus*; and Southern bluefin tuna [SBT], *Thunnus maccoyii*) is affected by environmental factors such as sea surface temperature (SST; Harford et al., 2017; Muhling et al., 2018), and larval growth of SBT is density dependent (Jenkins et al., 1991).

In the black rockfish (*Sebastes melanops*), the growth rates of larvae from the oldest females are more than three times those of larvae from the youngest females, and these larvae survive starvation more than twice as long (Berkeley et al., 2004). In the Japanese anchovy (*Engraulis japonicus*), eggs from starved females have a significantly smaller volume than that of eggs from satiated females (Yoneda et al., 2014). Batch fecundity of Spanish flag snapper (*Lutjanus carponotatus*) increased with fork length (FL), and egg diameter increased with body size (Evans et al., 2008). These observations indicate that the condition of adult fish affects larval growth and survival. Greater batch fecundity and potentially greater larval survival due to larger egg size from bigger adults might significantly enhance growth of the population (Evans et al., 2008). The maternal effects seem to be an important factor for larval survival that cannot be ignored, although further studies are required to know how general this effect is among various fishes.

Goldstein et al. (2007) found no significant relationship between body condition and reproductive state of ABT in the Gulf of Mexico; however, they did not determine batch fecundity or egg diameter. Batch fecundity of PBT and ABT are positively correlated with body size, and batch fecundity or relative batch fecundity (RBF) vary widely by area (Medina et al., 2002; Chen et al., 2006; Aranda et al., 2013; Ashida et al., 2015; Okochi et al., 2016). The oocyte diameters of PBT in the Pacific region range from 0.75 to 1.1 mm (Ashida et al., 2015). Mean egg diameter of PBT in culture ranged from 0.90 to 1.06 mm; the minimum egg size was 0.83 mm and there was a strong inverse relationship between egg diameter and water temperature (Masuma et al., 2006). Egg diameter of yellowfin tuna (*Thunnus albacares*) has positive and negative relationships with body size and water temperature, respectively (Margulies et al., 2007). Therefore, batch fecundity and egg diameter in fish could be affected by body condition (Yoneda et al., 2014; Tanaka et al., 2017) and spawning region.

Whereas these reproductive characteristics of PBT and ABT were described on the basis of short-term observations (about 5 years or less), we have analyzed long-term observations (> 20 years) of PBT reproductive characteristics in the Sea of Japan, which is one of the major spawning grounds of this species (Okochi et al., 2016; Ohshimo et al., 2017). Our objectives in the present study are 1) to describe the long-term changes of RBF, such as spawning periods, relative batch fecundity and spawning interval, and 2) to evaluate the maternal effects using changes of egg diameter of PBT in the Sea of Japan.

2. Materials and methods

2.1. Sampling and measurements

All specimens in the present study were collected since 1994 at Sakai-Minato port in Tottori Prefecture, located in the southwestern Sea of Japan. Table 1 includes the sample sizes by year from 1994 to 2015.

At Sakai-Minato port, most of the PBT spawners were caught in the purse-seine fishery in the Sea of Japan (Fig. 1), and the catch quota of this fishery has been limited by self-management since 2011. The Fishery Agency of the Japanese government has controlled the catch quota of juvenile PBT since 2015. The fork length (FL, cm), gilled-and-gutted body weight (GBW, kg), and gonad weight (GW, g) were recorded for as many fish at the port as possible. Ovaries were removed from each fish and weighed to the nearest 0.1 g at the laboratory. The date-of-catch at the fishing grounds obtained from the ship's logbook was used for the analysis of the ovaries. The samples in 2011 and 2012 were already analyzed (Okochi et al., 2016), and these samples were included in the present study.

2.2. Histological treatment and maturity phase

A portion of the collected ovaries was preserved in 10% formalin. The tissues of fixed ovaries were dehydrated, embedded in paraffin wax, sectioned to 4- to 6-μm thickness, and stained with hematoxylin-eosin. The most advanced group of oocytes were classified as perinucleolus stage, lipid stage, early yolked stage, advanced yolked stage, migratory nucleus stage, or hydrated stage (Schaefer, 1996; Okochi et al., 2016), and the presence of postovulatory follicles (POFs) was also noted. Based on observations of the most advanced group of oocytes and the presence of POF, ovarian maturity phases were classified into five phases: immature phase, developing phase, spawning-capable phase (or regressing), spawning and regressed phase (Table 2).

There were two clear modes of FL observed in this study: 110–120 cm and 140–160 cm. The former group was considered to be age 3 and the latter age 4. The proportion of fish capable of spawning was high (nearly 100%) at age 4 and older, so we analyzed the differences in maturation rates between small (100–129 cm FL) and large (≥ 130 cm FL) fish.

2.3. Size at maturity

Annual proportion mature (PM) was calculated every 5 cm FL bins based on classification of the development of the oocyte (Table 2), and logistic function was estimated as follows,

$$PM = 1/(1 + \exp(a(FL + b))), \quad (1)$$

where a and b are coefficient. FL at 50% mature of this species were estimated after calculating the logistic function.

2.4. Spawning frequency and interval

In the present study, we followed the procedures of Okochi et al. (2016). Spawning frequency was estimated by the POF method in accordance with Hunter and Goldberg (1980) and Hunter and Macewicz (1985). Spawning frequency was calculated as the ratio of spawning females to mature females, and the mature females were shown maturity status in Table 2. The inverse of the spawning frequency was considered the spawning interval.

2.5. Relative condition factor and batch fecundity

The relative condition factor (K_n) was calculated based on a cube-law as

$$K_n = GBW/aFL^b, \quad (2)$$

where a and b are coefficients, and GBW and FL represent gutted body weight and fork length, respectively. The parameter K_n is a means of quantifying the deviation of an individual from the average weight for its body length (Le Cren, 1951).

Batch fecundities were estimated from ovaries with hydrated oocytes and without recent POFs (Hunter et al., 1985). A subsample of

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