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Spatiotemporal variability in the reproductive dynamics of Skipjack Tuna (*Katsuwonus pelamis*) in the eastern Pacific Ocean

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ABSTRACT

The reproductive dynamics of skipjack tuna (*Katsuwonus pelamis*) were investigated by sampling 8136 fish caught by purse-seine vessels in the eastern Pacific Ocean from January 1996 to January 1998. The overall sex ratio deviated significantly from the expected 1:1 ratio, with a greater number of males. Histological evaluations of ovaries from 3732 females provided the foundation for the estimates of length-specific reproductive characteristics. Spawning was widespread from about 19 °N to 12 °S and from 79 °W to 136 °W, and continuous throughout the year between about 15 °N and 10 °S. Spawning was observed for fish captured in unassociated sets, floating-object sets, and dolphin sets. Although spawning occurred from 24 °C to 30 °C, 76.9% took place between 26 °C and 29 °C. Results of fitting a general additive model to the maturity-at-length data indicated significant spatial variation in maturity, with estimated lengths at 50% maturity of 56 cm north of 15 °N, 53 cm between 15 °N and 5 °S, and 47 cm south of 5 °S. The significant spatial variation in estimates of relative fecundity (oocytes per gram of body weight) is attributed to the differences between relative fecundities north of 15 °N and between 15 °N and 5 °S. The estimated average batch fecundity, based on counts of late-stage migratory-nucleus or hydrated stages of oocytes from 129 fish, was 296,475 oocytes, and the estimated mean relative fecundity was 54.9 oocytes per gram of body weight. The estimated fraction of mature females in the population spawning per day was 0.21, equivalent to a spawning frequency of 4.76 d, whereas for actively spawning females, the fraction spawning per day was 0.85, equivalent to a mean spawning interval of 1.18 d.

1. Introduction

Skipjack tuna (*Katsuwonus pelamis*), family Scombridae, is an epipelagic oceanic species with a worldwide distribution in tropical and subtropical waters (Collette and Nauen, 1983). It is the principal species of tropical tuna exploited by large-scale international purse-seine fisheries for sale to canneries (Miyake et al., 2010). The 2015 catch of skipjack tuna in the Pacific Ocean, for all gear types combined, was about 2.16 million metric tons (t), of which about 334 thousand t, or 16%, came from the eastern Pacific Ocean (EPO), defined as east of 150 °W (Anonymous, 2017). Estimated annual catches of skipjack tuna in the EPO during 1985–1994 averaged about 79 thousand t (range: 52.0–100.4 thousand t), whereas during 1995–2004 they increased substantially to about 200 thousand t (range: 132.3–300.5 thousand t). Since 1995, catches of skipjack tuna in the EPO have increased significantly as a result of purse-seine vessels targeting multi-species tuna aggregations associated with drifting fish-aggregating devices (FADs) between about 10 °N and 20 °S, along with substantial increases in fleet capacity and fishing power (Anonymous, 2017).

The Inter-American Tropical Tuna Commission (IATTC) is responsible for the conservation and management of skipjack tuna in the EPO (Bayliff, 2001). Because there is uncertainty about stock structure, estimates of natural mortality, growth, and maturity rates, and no reliable index of catch-per-unit-of-effort, traditional reference points are not available for conducting a formal stock assessment of skipjack tuna in the EPO. The IATTC staff has instead used a suite of eight different data and model-based indicators, along with their respective reference levels, to evaluate the status of the stock (Maunder and Deriso, 2007). There is uncertainty in the most recent evaluation of the status of skipjack tuna in the EPO, including the exploitation rate. The average weight of skipjack tuna in the catch has been steadily declining over the past decade in the EPO, and was below its lower reference level in 2015 and 2016. This can be a consequence of overexploitation, but it can also be caused by recent recruitments being greater than past recruitments (Maunder, 2017).

Early research on the reproductive biology of skipjack tuna in the EPO indicated spawning off Central America and in the vicinity of southern Baja California, Mexico, and also smaller sizes at maturity off

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Central America compared to off southern Baja California (Schaefer and Orange, 1956; Orange, 1961). Larval surveys also indicated spawning in offshore waters and, to a lesser extent, in coastal waters of the EPO (Matsumoto, 1975; Matsumoto et al., 1984; Nishikawa et al., 1985). Results of a more recent investigation of skipjack tuna spawning activity indicated that significant spawning of fish 50 cm or more in length occurs in areas of the EPO with sea-surface temperatures of 24 °C or more (Schaefer, 2001a). However, accurate estimates of the important reproductive parameters for skipjack tuna from throughout the EPO, based on histological techniques and valid ovarian classification criteria, have been lacking (Schaefer, 2001b).

A comprehensive understanding of the reproductive dynamics of skipjack tuna in the EPO is fundamental to an understanding of its population dynamics and for predicting the effects of fishing on the reproductive potential of the stock (Marshall et al., 2009). The important reproductive parameters for skipjack tuna have not been determined for stocks across the Pacific, but, considering their probable plasticity, they should be routinely monitored in order to appropriately estimate population productivity and resilience to increasing rates of exploitation and habitat variability (Palumbi, 2004; Beamish et al., 2006; Young et al., 2006). Knowledge of the spatial and temporal variability in spawning distributions and reproductive parameters for skipjack tuna throughout the Pacific, coupled with information on movements derived from tagging studies, would also be useful for elucidating putative stock structure (Begg, 2005; Begg and Cadrin, 2009). In addition, spatially-explicit reproductive parameters for skipjack tuna from throughout the Pacific would be beneficial in future Pacific-wide environmentally-driven population dynamics models for skipjack tuna (Senina et al., 2008; Lehodey et al., 2013).

The objective of this investigation is to estimate the essential reproductive parameters and elucidate the reproductive dynamics of skipjack tuna from throughout the EPO, based on a large-scale sampling program undertaken during two consecutive years (January 1996 to January 1998), so that such information will be available for inclusion in stock assessments. It provides information on the reproductive biology of skipjack tuna, including sex ratios, length at maturity, spatiotemporal spawning distributions, batch fecundity, and spawning periodicity and frequency.

2. Materials and methods

2.1. Collection of samples

Skipjack tuna gonads were collected by observers working for the IATTC during 62 trips aboard purse-seine vessels in the EPO from January 1996 to January 1998. Gonads were sampled from 8136 fish captured in 64 sets on unassociated schools, 123 sets on schools associated with dolphins, and 273 sets on schools associated with floating objects, for a total of 460 sets (Fig. 1).

The at-sea sampling program involved two trained and experienced observers from each of four IATTC field offices in Latin America aboard purse-seine vessels from the fleets of four different countries per quarter. Gonads were sampled from skipjack tuna caught in all set types, across eight 5-cm length classes between 40 and 80 cm fork length (FL). The observer was to sample 12 female skipjack within each of the eight length intervals during a trip, if available. When possible, 20 fish were to be sampled from individual sets. The FL of each fish was measured with calipers to the nearest centimeter. The body cavity was cut open with a knife, the gonads removed, and the sex determined. The reproductive status of testes from males was not assessed. From each female, a central section approximately 1 cm in length was cut from the right or left ovary and placed in a jar with 10% neutral buffered formalin, together with a Nalgene Polypaper label with the capture information and length of the fish. The ovaries were placed in a plastic bag with a duplicate label and frozen. For each set in which gonad samples were collected, position, date, time, set type, and sea-surface temperature (SSTs) were recorded.

Length distributions of females and males sampled are shown in Fig. 2.

2.2. Sex ratio

Sex ratio analyses were based on the macroscopic identifications of ovaries and testes by observers at sea. These identifications were confirmed when conducting histological evaluations of ovarian tissues, with just 6 males misidentified as females. Sex ratios within samples from single sets were based on those sets in which a minimum of 10 skipjack tunas were sampled.

2.3. Histological methods

A portion of each of the 3732 samples of preserved ovarian tissue was embedded in paraffin, sectioned at approximately 5 μm, and stained with Harris hematoxylin, followed by eosin counterstain. Slides prepared from these ovarian tissues, containing multiple serial sections, were examined with an Olympus Vanox light microscope.

2.4. Classification of females

Histological analyses of ovarian tissue were used to estimate the maturity and reproductive activity stages for individual females (Table 1). The histological classification of the ovaries was primarily based on the system of Schaefer (1998, 2001). The ovary in skipjack tuna is considered asynchronous (Wallace and Selman, 1981; DeVlaming, 1983) because oocytes in various developmental stages are present in the ovary simultaneously. For each ovary, the oocytes in the most-developed mode were classified as (1) unyolked, (2) early yolked, (3) advanced yolked, (4) migratory-nucleus stage, or (5) hydrated. Postovulatory follicles (POFs) identified in ovaries were classified into one of three age groups (0 h, < 12 h, or > 12 h old). Identification of alpha (α) atresia was restricted to advanced-yolked oocytes. Ovaries were classified into one of three categories of α atresia (none, minor (< 50%), and major (> 50%)), and presence or absence of beta (β), gamma (γ), and delta (δ) atresia (Hunter and Macewicz, 1985a). The relative thickness of the ovarian wall was also included as a maturity marker (Morrison, 1990; McMillan, 2007), as it is informative when the later γ and δ atretic stages are no longer present in ovaries of inactive mature females.

Females were classified as reproductively active if the ovary contained advanced-yolked oocytes, and there was no atresia or only minor α atresia present. Active females were then further classified, using additional histological criteria, into spawning and non-spawning groups. Females whose ovaries showed evidence of past spawning (POFs present) or imminent spawning (hydrated or migratory-nucleus oocytes present), were classified as spawning, whereas those whose ovaries showed no such evidence were classified as non-spawning. A spawning-rate index was estimated from the proportion of active females classified as spawning. Spawning performance was also assessed by evaluating the number of females whose ovaries showed more than one spawning state, *e.g.* migratory nucleus or hydrated-stage oocytes and also POFs present (Hunter and Macewicz, 1985b).

Females with ovaries classified as inactive can be either immature or mature, since an active mature female can resorb the ovary and regress to an inactive state. The classification used for inactive ovaries provides the best method to distinguish between mature and immature states. The inactive-mature class included ovaries with evidence of previous reproductive activity. Ovaries with oocytes in either unyolked or early-yolked developmental stages also contained α atresia of advanced-yolked oocytes, and/or β, γ, or δ atresia, or a distinctly thick ovarian wall. Also included in this class were ovaries with major atresia, *i.e.* containing advanced-yolked oocytes, of which more than 50% were atretic. The immature class consists of females whose ovaries contained