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Determining the age of tropical tunas in the Indian Ocean from otolith microstructures

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ABSTRACT

The Indian Ocean Tuna Tagging Program (IOTTP) provided a unique opportunity to assess the viability of estimating the age of tropical tunas from the micro-structural features of otoliths. Here, we analyzed the length measurements and micro-increment counts collected for 506 sagittal otoliths, of which 343 were chemically marked with oxytetracycline, for bigeye (*Thunnus obesus*), skipjack (*Katsuwonus pelamis*), and yellowfin tuna (*Thunnus albacares*). Our results show that the otoliths of tropical tunas grow more slowly than the rest of the body. Our findings confirm that both yellowfin and juvenile bigeye deposit daily increments in their otoliths, though ages are underestimated for large bigeye (>100 cm) when derived from micro-increment counts. Our results also indicate that skipjack otoliths are not suitable for age estimations during the adult phase, as evidenced by the poor agreement between micro-increment counts and days-at-liberty. We hypothesize that the income breeding strategy of skipjack could explain the variability observed in the deposition rates. Due to their complex micro-structural patterns, the reading of tropical tuna otoliths requires a degree of interpretation that can result in poor count precision and large variability in micro-increment counts, both among and within teams of readers. Age estimates were found to vary between readers, a factor which can eventually affect growth estimates and ultimately, impact on fisheries management decisions and outcomes. To address this, we recommend that reference collections of otoliths are developed, with a view to standardizing the reading process. Further, alternative methods, such as annual age estimations (as opposed to daily), and alternative structures, such as dorsal spines for skipjack, should be used to improve the accuracy of age estimations and the speed with which they can be made.

1. Introduction

Information from age structures plays a significant role in fisheries science, with fish population models largely based on age-dependent demographic features. Worldwide, millions of otoliths are read annually to estimate fish age and provide essential information to improve the stock assessment models which underpin fisheries management (Campana and Thorrold, 2001). Otoliths are commonly used because uniquely, they do not absorb calcium. However, other calcified structures, such as dorsal spines, scales, and vertebrae have also been widely used to provide annual age estimates (Panfili et al., 2002). The chronological properties of otoliths have been known since the 19th century, but gained wider recognition with the seminal article by Pannella (1971). Since then, the growing demand for fish age estimates have led scientists to conduct further research in the field of sclerochronology, focusing in particular on improving the preparation, conservation, and reading of otoliths (Secor et al., 1995; Panfili et al., 2002; Begg et al., 2005).

In tropical environments, it is particularly difficult to estimate fish age using otolith increments (annual or seasonal) because growth cycles are not related to environmental conditions (e.g., there is less seasonal contrast in tropical waters as compared with temperate waters; Green et al., 2009). In the 1970s, the sub-seasonal patterns in the micro-structural features (i.e., micro-increments) of otoliths were investigated in several tropical fish

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Table 1
Summary of studies that have used otolith micro-structures to estimate the age and growth of tropical tunas in the eastern Pacific Ocean (EPO), western central Pacific Ocean (WCPO), Atlantic Ocean (AO), and Indian Ocean (IO) outlining the otolith section that was read (Whole otolith (WO); External surface (ES); Frontal section (FS); Transverse section (TS)) and which experiment type was used to source the otoliths (mark-recapture experiments using oxytetracycline (MR) or captive experiments (CE)), where the number of tunas considered (N) are given for yellowfin (YFT), skipjack (SKJ), and bigeye (BET).

Basin	Species	Size range (cm)	*N*	Otolith reading method	Validation method	Validation size range (cm)	Deposition rate ($m\,d^{-1}$)	Reference
EPO	YFT	40–110	53	ES	MR	40–110	0.985	Wild and Foreman (1980)
		30–168	196	ES	–	–	–	Wild (1986)
		40–148	103	ES	MR	40–148	1.014	Wild et al. (1995)
	SKJ	42–64	26	ES	MR	42–64	0.761	Wild and Foreman (1980)
		38–65	25	WO	CE	45–49.3	Qualitative	Uchiyama and Struhsaker (1981)
		42–64	42	ES	MR	42–64	0.744	Wild et al. (1995)
	BET	30–149	254	FS	MR	38–135	0.999	Schaefer and Fuller (2006)
WCPO	YFT	7–93	14	WO	CE	52	Qualitative	Uchiyama and Struhsaker (1981)
		15–28	68	WO	CE	25–40	~1	Yamanaka (1990)
		16–79	139	FS				
		20–145	180	TS	MR	39–90	Qualitative	Lehodey and Leroy (1999)
	SKJ	3–80	51	WO	CE	42–64	Qualitative	Uchiyama and Struhsaker (1981)
		30–68	61	TS	–	–	–	Leroy (2000)
		1.3–4.0	72	WO	–	–	–	Tanabe et al. (2003a)
		18–71	453	ES	CE	21–52	0.99	Tanabe et al. (2003b)
		24–34	54	ES	CE	24–34	0.996	Kayama et al. (2007)
	BET	33–58	9	WO	–	–	–	Matsumoto (1998)
		25–157	149	TS	–	–	–	Lehodey et al. (1999)
AO	YFT	0.3–0.8	768	ES	–	–	–	Lang et al. (1994)
		53–113	65	TS	–	–	–	Driggers et al. (1999)
		5–179	132	TS	–	–	–	Shuford et al. (2007)
	BET	29–190	255	TS	MR	44–95	0.97	Hallier et al. (2005)
IO	YFT	30–140	151	TS	–	–	–	Stéquert et al. (1996)
	SKJ	48–57	8	TS	MR	48–57	0.245	Adam et al. (1996)
		42–66	25	ES	–	–	–	Kayama et al. (2004)
	BET	NA	154	TS	–	–	–	Stéquert and Conand (2000)
		30–165	164	TS	–	–	–	Stéquert and Conand (2004)

species. This research revealed that these micro-increments followed a circadian rhythm which was physiologically controlled and influenced by environmental conditions (Pannella, 1971, 1974). Each micro-increment corresponds to a bipartite structure which is composed of two alternating zones, an incremental (or accretion) zone and a discontinuous zone. Each zone is characterized by a distinct composition of organic and mineral fractions (Campana and Neilson, 1985; Campana, 1999). These early findings prompted the significant growth in studies that used optical microscopes to investigate otolith micro-structures as a way of estimating the age and growth of tropical tunas worldwide (Table 1**)**. Counts of micro-increments in sagittal otoliths were first used to estimate ages of yellowfin (*Thunnus albacares*; YFT) and skipjack tuna (*Katsuwonus pelamis*; SKJ) in the Eastern Pacific Ocean (Wild and Foreman, 1980). This study validated the presence of a daily deposition rate in the otoliths of YFT (size range: 40 cm–110 cm fork length; F_L; i.e., the length measurement taken from the tip of the snout of a fish to the fork of its tail) collected from oxytetracycline (OTC) mark-recapture experiments. SKJ, however, was found to exhibit a non-daily deposition rate. Subsequent studies conducted in the Pacific Ocean increased the number and extended the size range of fishes sampled and confirmed a daily micro-increment deposition rate for YFT between 40 cm and 148 cm F_L (Yamanaka, 1990; Uchiyama and Struhsaker, 1981; Wild et al., 1995; Lehodey and Leroy, 1999). More recently, Hallier et al. (2005) and Schaefer and Fuller (2006) validated a daily deposition rate for bigeye (*Thunnus obesus*; BET) sized between 44 cm and 95 cm F_L in the Atlantic Ocean and between 38 cm and 135 cm F_L in the Eastern Pacific Ocean (Table 1). For SKJ, although further research (e.g., mark-recapture and captivity experiments) were conducted, none of the results pointed to a link between days-at-liberty and micro-increment counts (Table 1). There is also a growing body of literature investigating the use of annual (as opposed to daily) age structures to provide age estimates in tunas including vertebrae (Prince et al., 1985; Rodriguez-Marin et al., 2006), dorsal spines (Sun et al., 2001; Lessa and Duarte-Neto, 2004), and more recently, otoliths (Farley et al., 2003; Griffiths et al., 2010; Chen et al., 2012; Shih et al., 2014; Williams et al., 2013).

In the Western Indian Ocean, the few studies that have dealt with age estimates of tropical tunas have had contradictory results and none have investigated the micro-increment deposition rates for YFT and BET (Table 1). Stéquert et al. (1996) was the first to establish a Von Bertalanffy (1938) growth curve for YFT based on otolith micro-structures. However, it resulted in an asymptotic length estimate that was inconsistent with YFT biology (i.e., $F_L > 270$ cm). In addition, the growth pattern estimated for juvenile YFT ($F_L < 60$ cm) differed considerably from the results of an extensive analysis of length-frequency distributions which were based on purse-seine, gillnet, and longline fisheries landings (IOTC, 2005; Viera, 2005). For BET, age and growth estimates were made from micro-increment counts obtained using both an optical microscope and scanning electron microscope, particularly for large fish ($F_L > 120$ cm) (Stéquert and Conand, 2000, 2004). Finally, micro-increment deposition rates for SKJ derived from mark-recapture experiments were found to vary greatly among individuals, suggesting that micro-increment counts are not suitable for estimating the age of this species. However, this study was only based on a small, localized sample of fish ($n = 8$) collected from Maldivian waters.

The Indian Ocean Tuna Tagging Program (IOTTP), which began in 2004, provided a unique opportunity to improve research efforts into understanding the age and growth rates of tropical tuna. An area of particular interest was the hypothesis that micro-increment deposition occurs at a rate of one per day in the otoliths of YFT, BET, and SKJ in the Indian Ocean. More than 200,000 tunas were tagged with conventional dart tags through the IOTTP and about 3% of these were also injected with a fluorescent marker that is rapidly incorporated into the otoliths (Hallier, 2008). Using recovered otoliths, the main objectives of this study were to (i) estimate the frequency and consistency of micro-increment deposition in otoliths for the