Deep-Sea Research Part I (xxxx) xxxx–xxxx

Contents lists available at ScienceDirect

Deep–Sea Research I

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

Remarkable vertical shift in residence depth links pelagic larval and demersal adult jellynose fish

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ARTICLE INFO

Keywords:
Ateleopodidae
Otolith stable isotope
Ontogenetic vertical migration

ABSTRACT

Deep-sea fish show diverse migratory behaviors across depths at different life stages. The historical residence depths of jellynose fish *Ateleopus japonicus* and *Ijimaia dofleini* (Ateleopodidae) were reconstructed from otolith microstructures and isotopic compositions. $\delta^{18}O$ values in the otolith core areas ranged from −0.5 to −1.3‰ among individuals, suggesting that larval and post-larval stages lived in the mixed layer (50–200 m). Otolith growth increment widths surged for 10–30 rings around 300–600 µm from the core, indicating a fast-growth phase during the early post-larval stage. Fish then migrated downward to 350–800 m depth at about 2 months of age, possibly during the post-larval metamorphosis to the juvenile. Otolith growth increments became narrower and otolith $\delta^{13}C$ values increased from −5 to −1‰, suggesting a lower growth and metabolic rate when the fish experienced colder water during the downward migration. After arrival at the deepest waters, the fish then migrated upward to the continental margin or upper slopes where the adults persistently resided. A translucent otolith zone was formed after the residence depth shift from the deepest waters to shallower depths, indicating a transition from pelagic to bathydemersal life on the continental shelf or break. The down-and-up shift in residence depth of jellynose fish represents an indirect settlement process to the adult residence depth, which might be associated with a unique post-larval stage moving offshore before the downward migration. The results filled the gap of vertical distributions of jellynose fish from pelagic larvae near the sea surface to the bathydemersal adult dwelling on the continental shelf break.

1. Introduction

The sea floors below 200 m depth represent more than 60% of the Earth's surface area and the vast realm of the deep sea constitutes a large source of species diversity and richness on the Earth (Rameriz-Llodra et al., 2010). More than 1000 species of deep-sea fish living on the deep-sea floors have been identified (Marshall, 1971; Nelson, 2006). New species of deep-sea organisms are continuously identified via oceanic explorations and surveys (Snelgrove and Smith, 2003; Kaga, 2016). However, current knowledge on the life history of deep-sea fish and their adaptations to the deep-sea environment is still limited and deserves more investigations.

Diverse life strategies have evolved in various deep-sea fishes to cope with harsh environments characterized by low temperature, high pressure, darkness, and scarce foods. Planktons and organic debris are most abundant in the euphotic zone and limited in the deep sea (Buesseler et al., 2007). Therefore, many deep-sea fishes lay small and buoyant eggs which can float to upper depths where larvae hatch to feed and grow so as to avoid starvation and enhance larval survival (Marshall, 1973). For many deep-sea fish species, however, their habitat shifts along depths at different life stages are not fully understood. Otolith stable oxygen isotope ($\delta^{18}O_{oto}$) as a proxy of water temperature (Høie et al., 2004; Shiao et al., 2010) has been used to reconstruct the ontogenetic shift in residence depth of several deep-sea fishes. For example, post-larval orange roughy resided in the mesopelagic zone then moved to deeper waters as early juveniles based on the water temperature estimated by the $\delta^{18}O_{oto}$ values (Shephard et al., 2007). Grenadiers, Kaup's cutthroat eels and cusk eel had pelagic larval to juvenile stages in the upper oceans then the fish migrated to the deep-sea floor at later stages (Lin et al., 2012; Shiao et al., 2014; Chang et al., 2015). The upward migration of young alepocephalid fish was also revealed by their $\delta^{18}O_{oto}$ profiles (Shiao et al., 2016). The migratory behaviors of deep-sea fish across depths might be more diverse than our present understanding although most species tend to have their larval-to-young stages live in upper pelagic waters and their adult stage in the deep sea.

Among the numerous deep-sea fishes, the jellynose fish (or tadpole fish) of the small order Ateleopodiformes, which contains a single

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http://dx.doi.org/10.1016/j.dsr.2017.01.011
Received 25 September 2016; Received in revised form 22 January 2017; Accepted 23 January 2017

family (Ateleopodidae), four genera, and about ten species, is widely distributed in the Caribbean Sea, eastern Atlantic, the western and central Indo-Pacific Ocean and the eastern Pacific coast of Central America (Bussing and Lopez, 1977; Amaoka, 2003; Nelson, 2006). Jellynose fish are near-bottom dwellers living on the outer continental shelf and slopes down to more than 600 m (Mochizuki, 1988; Aizawa, 2002). Like the name indicates, jellynose fish are characterized by a compressed, elongated, and gelatinous body with soft muscles and a bulbous snout. The early larval form remains unknown for most species of jellynose fish (Amaoka, 2003) but the post-larvae (without the yolk sac) can grow to a large size (> 250 mm) with unique features of elongated dorsal and pelvic fin rays and many orange bands on the side of the translucent body (Amaoka and Kobayashi, 2003). Four nominal species of jellynose fish are known from Taiwanese waters (Shao, 2016). Kaga et al. (2015) regards *Ateleopus purpureus* and *A. tanabensis* as the synonyms of *A. japonicus*. Therefore, only two species of jellynose fish *A. japonicus* Bleeker, 1854 and *Ijimaia dofleini* Sauter, 1905 are distributed in Taiwanese waters and are occasionally caught by commercial trawl fisheries.

The biology, life history, and habitats of most jellynose fish species are poorly known. This study reports a novel down-and-up migratory life history for jellynose fish across pelagic and mesopelagic zones during the post-larval to juvenile stages. The unique ontogenetic shift in residence depth of jellynose fish was compared to other species and possible migratory routes are discussed.

2. Materials and methods

2.1. Fish collection and sampling areas

Four individuals of *Ateleopus japonicus* were collected from the fish landings at the fishing ports of Dashi, Ilan county in 2013. Another four otoliths of two *A. japonicus* and two *I. dofleini* were kindly provided by National Museum of Marine Biology and Aquarium. These four fish were collected in Nanfangao (Ilan county), and Donggong (Pingtung county) in 2010 (Table 1, Fig. 1). The exact depth and location of capture for the fish at catch was unknown but they are likely caught on the continental shelf to upper slop at 300–500 m depth which are the fishing grounds for most Taiwanese commercial fish trawlers. Hydrological data including salinity and temperature were measured in situ with a SeaBird Conductivity-Temperature-Depth recorder (SBE9/11 plus, SeaBird Inc., USA) offshore of northeastern (NET) and southeastern (SWT) Taiwan during the cruise of Ocean Research I (ORI) in 2011 (ORI Cr. 981) and 2012 (OR1 Cr. 1020), respectively. The data were provided by Ocean Data Bank, Institute of Oceanography, National Taiwan University.

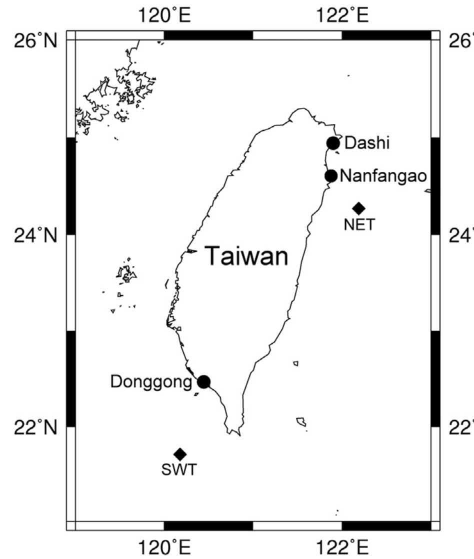

Fig. 1. Sampling sites for the jellynose fish (Ateleopodidae) around Taiwan. The solid circles represent the three fishing ports where fish were collected. The black diamonds represent the locations where sea water was measured by the Conductivity-Temperature-Depth recorder in the waters near northeastern (NET) and southwestern (SWT) Taiwan.

2.2. Otolith preparation

Sagittal otoliths were extracted from the fish under a stereo microscope, cleaned, dried, and embedded in Epofix resin (Struers, Denmark) after measuring the length and weight of the fish. The otoliths were ground and polished by a Buehler Metaserv grinder-polisher (Buehler, USA) along the sagittal plane. In order to collect enough powder from the core area, the otoliths were only ground until the core about 50–100 µm beneath the surface. Incomplete grinding and polishing made observations of microstructure near the core difficult. An otolith of *A. japonicus* (AJ131201-2) was ground and polished to expose the core in order to observe the growth increments. Both otoliths of *A. japonicus* AJ131201-1, AP131201-1 and AP110713-1 were used for the isotopic analysis. The initial 80–120 rings, depending on the readability of each otolith, were enumerated and the growth increment width was measured. Subsamples (about 40–50 µg) of otolith powders were collected sequentially from the core to the edge at intervals of about 130–200 µm by a micromill (ESI, USA). The tip of the drill was about 200 µm in diameter (H23RS, Comet, Germany) and the drilling depth was set at 50 µm.

2.3. Isotopic analysis

The milled powders were reacted with pure orthophosphoric acid at

Table 1
Biological and sampling information for the jellynose fish (Ateleopodidae) used in the analysis of otolith oxygen isotopic ratio.

Species	Code	Weight (g)	Length (cm)	Location	Date
Ateleopus japonicus	AJ131201-1	141	49.2[a]	DaShi	1 December 2013
	AJ131201-2	232	56.6[a]	DaShi	1 December 2013
	AJ#3320	–	65.5[a]	Nanfangao	6 September 2010
	AP131201-1	212	52.0[a]	DaShi	1 December 2013
	AP110713-1	440	66.2[a]	DaShi	13 November 2013
	AP#1910		70.8[a]	Nanfangao	26 July 2010
Ijimaia dofleini	ID#3070	–	118.5[b]	Donggong	19 May 2010
	ID#3071	–	124.0[b]	Donggong	19 May 2010

[a] Represents the total length.
[b] Represents the standard length.