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Comparative larval growth and mortality of mesopelagic fishes and their predatory impact on zooplankton in the Kuroshio region

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ABSTRACT

Larvae of mesopelagic fishes usually dominate in oceanic larval fish assemblages, but detailed investigations of their ecology are limited and thus preclude full assessment of the ecosystem structure and dynamics in oceanic waters. Here, we examined the growth and mortality of six taxa of numerically dominant mesopelagic fish larvae and their predatory impact on zooplankton in the Kuroshio region off southern Japan during late winter. The weight-specific growth coefficient (G_w) ranged from 0.077 (*Sigmops gracilis*) to 0.156 d⁻¹ (*Vinciguerria nimbaria*), and the instantaneous daily mortality coefficient (M) from 0.067 (*S. gracilis*) to 0.143 d⁻¹ (*Myctophum asperum*). The ratio G_w/M , an index of stage-specific survival of the larvae, was from 0.90 (*Notoscopelus japonicus*) to 1.24 (*V. nimbaria*), without a significant difference from a value of 1 in all species. Based on the reported relationship between G_w and ingestion rate of the larval fishes, the daily ration of each species was calculated to be 32–57% of body dry weight d⁻¹. Mean and 95% confidence interval of food requirements of the six taxa of larvae was 1.41 ± 0.55 mg C m⁻² d⁻¹. Predatory impact of the mesopelagic fish larvae on the production rate of the available prey was estimated to be approximately 3.5–5.2%, implying that the larvae have a low level but consistent effect on zooplankton production in the oligotrophic Kuroshio region.

1. Introduction

Mesopelagic fishes are a key component of oceanic ecosystems. They numerically dominate in the fish assemblage and have a high biomass in the world's oceans (Gjøsæter and Kawaguchi, 1980) and are the main component of the deep scattering layer (Pakhomov and Yamamura, 2010). The global estimate of their biomass is in the order of 10 billion tons (Irigoién et al., 2014), that is about one hundred times the annual tonnage captured worldwide by fisheries (FAO, 2013). They act as an important link between secondary producers and upper trophic levels in the ecosystem of the world's oceans (Brodeur and Yamamura, 2005), and contribute to global carbon cycles through diel vertical migration, i.e. the biological pump (Davison et al., 2013). Mesopelagic fishes are composed of a variety of families, and the most diverse mesopelagic family, the myctophids (Myctophidae) includes about 33 genera with at least 248 species (Nelson et al., 2016).

Mesopelagic fishes spend their larval stages in the productive epipelagic layer of the upper 200 m depth and move to the mesopelagic layer (200–1000 m depth) when they begin the transformation from the larval to the juvenile stage (Badcock and Merrett, 1976; Loeb, 1979; Sassa et al., 2007; Bowlin, 2016). After that, most species begin diel vertical migrations to the epipelagic layer at night for feeding, although

there are also non-migrant species (Clarke, 1973; Percy et al., 1977; Watanabe et al., 1999). The dominance of mesopelagic fish larvae in the ichthyoplankton assemblage has been reported from various parts of the major oceans (Olivar and Fortuño, 1991; Moser, 1996; Richards, 2005; Okiyama, 2014). Therefore, they have been considered as potential competitors for prey with larvae of commercially valuable fishes (Ahlstrom, 1969; Sassa and Kawaguchi, 2005; Torres et al., 2011; Sassa and Konishi, 2015).

Extensive larval fish sampling has been conducted in the world's oceans to examine the recruitment processes of commercially valuable species (Lasker, 1981; Bailey and Houde, 1989; Cushing, 1990; Moser et al., 1993). Although the mesopelagic fish larvae are usually dominant in the samples, investigations on their ecology have been limited. Information on growth and mortality of the mesopelagic fish larvae as well as on abundance and distribution is fundamental for understanding the population dynamics of this group (Moser and Smith, 1993). Also, information on food requirements and predatory impact of the mesopelagic fish larvae on zooplankton is needed to quantitatively assess the competition for prey among the mesopelagic and the other fish larvae.

The Kuroshio region of the western North Pacific is an important spawning and nursery ground for various commercially valuable fish,

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such as Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), chub mackerel (*Scomber japonicus*), Pacific saury (*Cololabis saira*), and Japanese common squid (*Todarodes pacificus*) (Oozeki et al., 2007; Sugisaki et al., 2010). Recent studies show that various species of mesopelagic fishes including several subarctic and transitional water species also use this region as the spawning and nursery grounds (Balanov and Savinykh, 1999; Okamoto et al., 2004; Sassa et al., 2004). As a result, high abundances of mesopelagic fish larvae are always observed in the Kuroshio region (Sassa et al., 2002a; Sassa and Hirota, 2013; Sassa and Konishi, 2015); however, investigations on growth, mortality, and feeding of these larvae have been limited.

In this study, we examined the ecology of six taxa of numerically dominant mesopelagic fish larvae in the Kuroshio region during late winter off southwestern Kyushu Island, Japan: *Lipolagus ochotensis* (Microstomatidae), *Sigmops gracilis* (Gonostomatidae), *Vinciguerrina nimbaria* (Phosichthyidae), *Diaphus* spp. slender type, *Notoscopelus japonicus*, and *Myctophum asperum* (Myctophidae). Firstly, we described their larval distribution and abundance in relation to the Kuroshio axis and then we examined their growth and mortality. Finally, based on data for larval abundance, distribution, and growth, we estimated the food requirements of the larvae and their predatory impact on zooplankton production and discuss the limitations of this approach.

2. Materials and methods

2.1. Sample collection

Samples were collected using a regular sampling grid at 115 stations spaced 20 × 30 nautical miles apart off southwestern Kyushu Island from the shelf (< 200 m depth) through the slope, occasionally over 2000 m depth, during the cruise of the R/V ‘Wakatori-Mar’ (Tottori Prefecture; 516 t) from 28 January to 21 February 2010 (Fig. 1). Paired bongo nets with a 70 cm mouth diameter and 335 µm mesh were used for sampling with flowmeters and a depth meter attached to the nets for quantitative sampling. A double-oblique tow was conducted at each station from the surface down to 100 m depth or 10 m above the bottom at shallow stations. The net was towed regardless of day or night, with 51% of the towing carried out at night. A conductivity-temperature-depth profiler (CTD) cast was made at each sampling station down to 350 m depth, or close to the bottom at the shallow stations. Plankton samples were first fixed in 5% buffered formalin seawater for 6 h, formalin rinsed out with freshwater, and then transferred to 90% ethanol for preservation.

Mesopelagic fish show species-specific larval distribution depths in the epipelagic layer, although the habitat depth partly overlaps among species (Sassa et al., 2002a). Larvae of *D.* slender type mainly occur in the relatively shallow depths of 20–50 m, while *L. ochotensis* and *S. gracilis* are distributed in deeper layers, 30–100 and 60–100 m, respectively (Watanabe et al., 2010). The distributions of *V. nimbaria*, *N. japonicus*, and *M. asperum* show an intermediate pattern, with their centers of distribution at 25–75, 30–80, and 40–80 m, respectively (Loeb, 1979; Watanabe et al., 2010). Therefore, our sampling covered the depth range of the six taxa of larvae.

2.2. Hydrographic analysis

Based on Kawai (1972), the position of the Kuroshio axis was determined by the 16.5 °C isotherm at 200 m depth. A cluster analysis using sea surface temperature (SST) and salinity (SSS) was conducted to distinguish the water properties at each sampling station. During late winter, (1) the mixed layer depth is usually deeper than 100 m due to the strong northwest monsoon in the study area (Ichikawa and Beardsley, 2002; this study), and (2) the six numerically dominant taxa of mesopelagic fish larvae mainly occur in the upper 100 m layer (Loeb, 1979; Watanabe et al., 2010), so SST and SSS enabled us to characterize

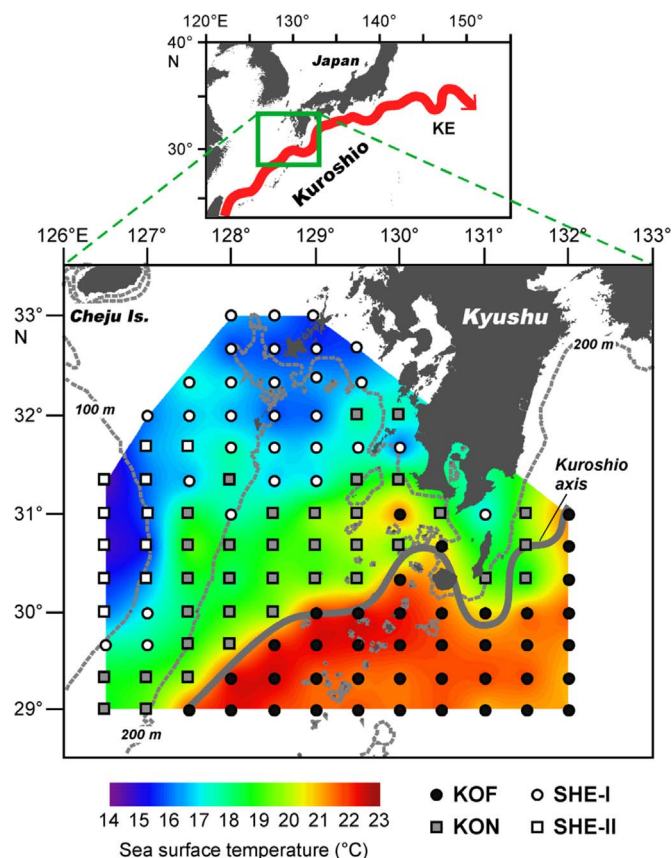


Fig. 1. Sampling localities off southwestern Kyushu Island, Japan, from 28 January to 21 February 2010, with the 100 and 200 m isobaths marked. The color contours indicate sea surface temperature (°C). The gray solid line denotes the position of the Kuroshio axis as defined by the 16.5 °C isotherm at 200 m depth following Kawai (1972). KE, Kuroshio extension. KOF, the Kuroshio offshore waters; KON, the Kuroshio onshore waters; SHE-I, the shelf waters-I; SHE-II, the shelf waters-II.

larval habitat conditions. Standardized Euclidean distance was used to evaluate the dissimilarity between water properties of each sampling station. Clustering by the farthest neighbor strategy was used to construct dissimilarity matrices for data of the total 115 sampling stations. Cluster analysis was performed with SYSTAT 11 (Systat Software, Inc.).

2.3. Analysis of distribution of larvae

All larval fish were sorted and counted from the samples and *L. ochotensis*, *S. gracilis*, *V. nimbaria*, *D.* slender type, *N. japonicus*, and *M. asperum* were identified according to Okiyama (2014). Larvae of *Diaphus* spp. were separated into slender- and stubby-body types: the slender type had numerous persistent postanal ventral melanophores, and the stubby type had fewer postanal melanophores (Moser, 1996). Within these two types, few characters are available for distinguishing species. Our preliminary mitochondrial DNA analysis verified that at least three species were included in *Diaphus* slender type larvae of our samples, of which *D. fulgens* was the most abundant (Sassa, unpublished data).

For all intact specimens of the six larval taxa, body lengths (BL) were measured to the nearest 0.1 mm using a measurement system that was composed of a stereomicroscope and video camera connected to a monitor and computer (Nikon Instech Co. Ltd., Tokyo, Japan). Notochord length (NL) was measured for preflexion larvae and standard length (SL) for flexion and postflexion larvae. As shrinkage due to the effect of preservation has not as yet been reported for most mesopelagic fish larvae, except for *D.* slender type (Moku et al., 2004), we present our data here as the unadjusted length. The number of larvae collected

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