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Temporal and spatial changes in the copepod community during the 1974–1998 spring seasons in the Kuroshio region; a time period of profound changes in pelagic fish populations

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ABSTRACT

The long-term change (1974–1998) of the pelagic copepod community in the Kuroshio region, western Pacific was examined in archival samples collected both day and night in April/May in a time period of profound changes in the pelagic fish populations. A total of 162 adult copepod species was found. The community analysis based on species composition and abundance of adult copepods identified five assemblages (A–E) by cluster analysis. These assemblages were distributed in the north-frontal area of the Kuroshio Current within the slope area (A), the Kuroshio axis area (B), the subtropical area (C, D), and the coastal area within the slope area (E), indicating that such diverse communities were formed to correspond with the gradual change in the oceanic environment across the Kuroshio Current. The abundance of copepods in the north-frontal area of the Kuroshio Current (A) was 1.6 times greater than that of the other assemblages. Kuroshio/subtropical species were abundant in the assemblage, suggesting that these species that were transported from the Kuroshio and/or subtropical regions increased in the slope region. Abundance and species richness of two assemblages (C, D), which were found in the subtropical areas were higher at night (C) than during the day (D), suggesting that diel vertical migration of copepods is one of the most important factors affecting changes in the community. Furthermore, a generalized additive model revealed that the most dominant subtropical/Kuroshio species increased in years in which the Kuroshio Current flowed further south, with the Kuroshio axis located far from the Japanese coast. In contrast, the model showed that the lower latitude of the Kuroshio axis positioned negatively affected coastal-dominant species, such as *Paracalanus parvus* sensu lato (s.l.). These results indicate that onshore-offshore shifts of the Kuroshio axis caused by Kuroshio meandering was an important factor involved in the inter-annual change in the copepod community during April–May in the Kuroshio region, suggesting that the inter-annual change of copepod communities might affect survival and growth rates of larvae in pelagic migratory fish which utilize the Kuroshio region as spawning and nursery grounds.

1. Introduction

Copepods account for about 90% of the total zooplankton biomass in all pelagic ecoregions and play a key role in oceanic ecosystems and biochemical cycles linking primary production to upper trophic organisms as secondary consumers (Ohman and Hirche, 2001). Because their abundance and distribution are influenced by hydrographical conditions, copepods and their communities are regarded as an indicator of the oceanic environment (Ashjian and Wishner, 1993; Beaugrand and Ibanez, 2004; Tseng et al., 2008). Several studies have reported that the abundance and distribution of copepods have been altered by multi-decadal temperature change due to climate change (Beaugrand et al., 2002; Chiba et al., 2006). Understanding the relationship between the environment and the copepod community, such as species composition and population dynamics, based on long-term observations is fundamental to precisely grasp the influence of climate change not only on the copepod community but also marine ecosystems.

The Kuroshio Current is a western boundary current that flows along the southeastern coasts of Taiwan and Japan. Kuroshio and the

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adjacent waters (hereafter the Kuroshio region) in the southern area of the main Island of Japan (Honshu) are major spawning and nursery grounds for various migratory fishes, such as Pacific sardine and Pacific saury (Heath et al., 1998; Yatsu et al., 2005; Takasuka et al., 2008). Larvae of these fishes feed on copepods in the region (Nakata, 1995; Watanabe and Saito, 1998). Thus, the dynamics of the physical environment and associated prey distribution and abundance in the Kuroshio region affect fish larval recruitment (Nakata, 1995; Nishikawa et al., 2013).

Because copepods are important in food webs, several studies have focused on the distribution and abundance of copepods in the Kuroshio region of southern Honshu (e.g., Tanaka, 1953; Honjo, 1951; Honjo et al., 1957; Hirota, 1995). The oceanic environment in the Kuroshio region differs between the eutrophic slope area and the oligotrophic subtropical area across the Kuroshio Current. The abundance of all copepods is generally higher in the slope area than that in the subtropical area (Furuhashi, 1961). In addition, the species and communities are different between the slope and subtropical areas (Furuhashi, 1961; Kidachi and Ito, 1979).

Furthermore, some studies have reported long-term variations in the abundance of coastal species. Nakata (1997) suggested that inter-annual changes in *Paracalanus* sp. abundance are related to the meandering pattern. On the other hand, the abundance of large copepods (prosomal length > 1 mm), such as *Calanus sinicus*, during the spring bloom season has been suggested to be affected by the strength of winter winds, which indirectly influence the inter-annual fluctuations in primary production during spring (Nakata and Hidaka, 2003). Thus, the spatiotemporal fluctuations in coastal calanoid copepods, such as *Paracalanus parvus* s.l. and *Calanus sinicus*, is also influenced by the meandering of the Kuroshio and winter wind. However, an investigation of the copepod community structure including the non-calanoid copepods (i.e. cyclopoid and poecilostomatoid copepods), which are important prey for fish larvae across the Kuroshio Current, is lacking. The non-calanoid copepods dominate the copepod community in the Kuroshio region around Taiwan (Hwang et al., 2007; Tseng et al., 2008; Hsiao et al., 2011). Because the prey and behavior of the non-calanoid copepods differ from those of the calanoid copepods (e.g., Landry et al., 1985; Nishibe et al., 2015), the response to environmental change (e.g., environmental gradients across the Kuroshio, such as phytoplankton abundance and sea surface temperature, meandering, and winter wind) of subtropical copepods might be different from that of the coastal calanoid copepods.

The area investigated off Boso Peninsula is the most downstream area of the Kuroshio Current (Fig. 1). The distance between the axis and the Japanese coast increases when meandering occurs off the Boso Peninsula (Types B and C defined by Yoshida et al., 2014). The main spawning grounds of chub mackerel, Pacific sardine, and Pacific saury form in April and May around this area (Kuroda, 1991; Kosaka, 2000; Watanabe, 2010). It is known that species replacement of these small pelagic fishes occurred from the 1960s to the 1990s (Yatsu et al., 2005). For example, Japanese catch of mackerel which reached 1.63 million ton at 1978 decreased in 1980s. Conversely, the catch of Pacific sardine increased drastically in 1980s. In the 1990s, standing stock of Pacific sardine decreased suddenly. Thus, the long-term change of prey copepod communities in the nursery ground of the Boso area from the 1970s to the 1990s is suggested to be related to drastic changes in standing stock and recruitment of these small pelagic fishes. The Japan Meteorological Agency (JMA) has conducted oceanic observations and zooplankton sampling at several stations in April and May along a transect line (Pollution Tokyo Line; hereafter PT-Line) crossing the Kuroshio axis from 1974 to 1998. These environment datasets and zooplankton samples are effective tools to reveal the long-term changes of copepod communities in this region. Our objectives in this study using the JMA zooplankton samples were to: (1) reveal the copepod community structure in the Kuroshio region in April and May from 1974 to 1998 and (2) identify the environmental factors that influence spatial and temporal (inter-annual) variations in copepod abundance using multivariate statistical analyses, such as cluster analysis, and a generalized additive model (GAM).

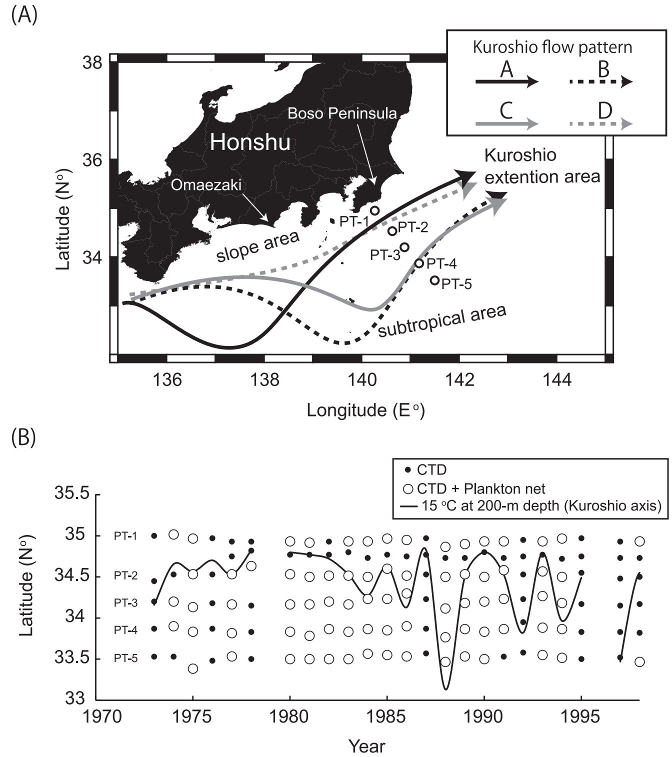

Fig. 1. Position of the observation stations (PT-1 to -5) (A). Arrows represents typical flow pattern (A–D) of the Kuroshio Current defined by Yoshida et al. (2014). Slope area represents area between coast and Kuroshio axis, while subtropical area is southern area of Kuroshio axis. (B) Latitudes (°N) of the observation stations for each year. Circles and dots represent the plankton net tow and CTD observation stations and only the CTD observation stations, respectively. Line indicates 15 °C at 200-m depth, which is an index of the Kuroshio axis position.

2. Materials and methods

2.1. Collection and analysis of zooplankton samples

The zooplankton samples were collected from April 22 to May 16 at five stations along the PT-Line during 1974–1998 using vertical tows (from 150-m depth to the surface) of a NORPAC net (Motoda, 1957: mouth diameter, 45 cm; mesh opening, 0.33 mm) (Fig. 1). Net sampling was conducted both at day and night. After towing, the samples were fixed immediately and preserved in ~5% formaldehyde/seawater solution buffered with sodium tetraborate.

All zooplankton samples were split by pipette or plankton splitter in the laboratory to obtain at least 250 specimens to identify and count. Adults and immature copepodids were identified under a stereomicroscope to species and order levels, respectively. In the present study, three forms (small, medium, and large) of *Oncaea venusta* were classified by body length, shape of the second thoracic somite, and morphology of the genital double-somite (see Böttger-Schnack and Huys, 2004, Itoh et al., 2014). Also, *Paracalanus aculeatus* was identified to subspecies levels. They were treated as equivalent to species in the present statistical analysis. The present study identified as *Paracalanus parvus* sensu lato (s.l.) in accordance with the criterion of Chihara and Murano (1997), because some confusions still remain in the taxonomy of this species (Hidaka et al., 2016). The count data were converted to abundance per unit area (inds m^{-2}) assuming 100% filtration efficiency. Species richness [*SR* (the number of species per tow)] and the Shannon diversity index (*H′*, $\log_e$-base; Shannon, 1948) of adult copepods were calculated for each tow.