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Temporal variability of neustonic ichthyoplankton assemblages of the eastern Pacific warm pool: Can community structure be linked to climate variability?

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ABSTRACT

Considerable evidence exists, showing an accelerated warming trend on earth during the past 40–50 years, attributed mainly to anthropogenic factors. Much of this excess heat is stored in the world's oceans, likely resulting in increased environmental variability felt by marine ecosystems. The long-term effects of this phenomenon on oceanic tropical ecosystems are largely unknown, and our understanding of its effects could be facilitated by long-term studies of how species compositions change with time. Ichthyoplankton, in particular, can integrate physical, environmental and ecological factors making them excellent model taxa to address this question. While on eight (1987–1990, 1992 and 1998–2000) NOAA Fisheries cruises to the eastern Pacific warm pool, we characterized the thermal and phytoplankton pigment structure of the water column, as well as the neustonic ichthyoplankton community using CTD casts and Manta (surface) net tows. Over the 13-year period, 852 CTD and Manta tow stations were completed. We divided the study area into three regions based on regional oceanography, thermocline depth and productivity, as well as a longitudinal gradient in species composition among stations. We then analyzed temporal trends of ichthyoplankton species composition within each region by pooling stations by region and year and making pairwise comparisons of community similarity between all combinations of the eight cruises within each region. We also identified environment-specific species assemblages and station groupings using hierarchical clustering and non-metric multidimensional scaling (MDS). Our analyses revealed a longitudinal gradient in community structure and temporal stability of ichthyoplankton species composition. Over the 13 years ichthyoplankton assemblages in the two westernmost regions varied less than in the eastern region. MDS and cluster analyses identified five ichthyoplankton assemblages that corresponded to oceanographic habitats and a gradient in community composition. We hypothesize that the changes in thermocline depth during the El Niños of 1987–1988, 1997–1998 and the extended period of warmth during 1990–1994 altered productivity sufficiently to cause a shift in the abundances of foundation species of the upwelling systems of the eastern Pacific warm pool. Our study suggests that ichthyoplankton assemblages in oligotrophic waters are more resilient to changes in the thermocline than assemblages in upwelling regions; or that oligotrophic regions simply have less physical variation compared to upwelling regions.

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1. Introduction

Predicting and assessing the ecological consequences of climatic variability caused by current global warming trends are major challenges for ecologists. In the 150-year-long global instrumental temperature record, all but one of the past 12 years have ranked among the warmest on record, and it is likely that Northern Hemisphere temperatures of the last 50 years have been higher than those of any other comparable period within the last 500 years (Solomon et al., 2007). Due to its large heat capacity (Curry and Webster, 1999; Willis et al., 2005), much of this excess heat is stored in the oceans (Barnett et al., 2005; Levitus et al., 2005). And although not monotonic, the Pacific Ocean has undergone a net warming since the 1950s (Levitus et al., 2000). Long-term ecological research also suggests that the climate of the past few decades is anomalous compared with earlier climate variation and that ecosystems have and are responding to these changes (Hughes, 2000; Parmesan and Yohe, 2003; Root et al., 2003; Walther et al., 2002).

Awareness of ecosystem effects at the onset of higher climate variability underscores the value of long-term ecological research and the time series constructed from such studies. It often takes hindsight to notice shifts in ecosystems; hence, most ecological research pertaining to climate change takes place after a shift has occurred. Analyses of long-term research have revealed decadal-scale variation in the ocean–atmosphere system and consequential marine ecosystem response (Mantua et al., 1997; Satterfield and Finney, 2002). Most ecosystems can withstand stochastic changes in environmental conditions, with the persistence of long-lived species and the explosive reproduction of short-lived species. Cumulative effects of more frequent and intense fluctuations in environmental conditions can however affect whether, how and at what rate an ecosystem will return to normal conditions. For example, the more frequent and stronger El Niño events and fewer La Niña events in the eastern Pacific that have occurred since the late 1970s (Miller and Cayan, 1994; Stephens et al., 2001) could alter the rate of species exchange between environmental conditions and create opportunities for the establishment of new resident species.

Long-term studies in oceanic tropical systems lag behind those from other regions. The few long-term marine data sets that do exist are in coastal, benthic or nearshore ecosystems, and are mostly from temperate and polar systems (e.g. Alheit and Niquen, 2004; Anderson and Piatt, 1999; Barry et al., 1995; McGowan et al., 1998; Napp et al., 2002; Roemmich and McGowan, 1995; Spies, 2007). Even though tropical oceans cover the largest area of the world's oceans, because of logistic constraints few studies exist concerning ecological impacts in tropical oceanic ecosystems of the recent increase in environmental variability, in particular the increased frequency and intensity of El Niño events of the past 30 years. Long-term ecological effects in open tropical oceans as profound as those in higher latitude systems are less common; could the tropics be buffered to this increase in climate variability, or has there been a lack of research effort?

It has been hypothesized that marine fish spawning strategies have evolved in synchrony with oceanographic conditions, creating persistent multi-species assemblages of fish larvae in specific oceanographic habitats (Frank and Leggett, 1983). Additionally studies of larval fish ecology have played a key role in understanding of how marine ecosystems function (Moser and Smith, 1993) and respond to interannual climate variability (Doyle, 1995; Loeb and Rojas, 1988). Variations in entire ecosystems reflect environmental fluctuations and consequent changes in oceanographic conditions, since these could alter the foundations structuring species assemblages. For example, water mass distributions shift with changes in the thermal structure of the water column during El Niño Southern Oscillation (ENSO) events (McPhaden, 1999), and these types of environmental fluctuations can change ichthyoplankton species distributions (Doyle, 1995; Evseenko et al., 1990; Loeb and Rojas, 1988). Therefore tracking changes in ichthyoplankton assemblages through time can provide excellent insight regarding questions of ecosystem change and environmental variability in the eastern tropical Pacific.

Our research objective was to investigate temporal and spatial trends of ichthyoplankton species assemblages in the eastern tropical Pacific. We approached this goal by investigating spatial trends of species abundance, richness and diversity, and temporal trends of species dominance and abundance. In doing so, we investigated patterns regarding the effects of the ENSO-scale climate variability on neustonic ichthyoplankton assemblages of the eastern Pacific warm pool, in an attempt to learn the magnitude and direction of ecosystem change (if any) in the tropics as compared with higher latitudes.

2. Methods

2.1. Study area

Our region of study is the eastern Pacific warm pool—an area covering roughly 11.5 million km^2 between 20° and 5°N latitude, and from 150°W longitude to the coast of Mexico and Central America. Here, surface oceanography is dominated by the zonal circulation of the northern trade wind current system: the westward North Equatorial Current (NEC) and the eastward North Equatorial Countercurrent (NECC) (Fig. 1). The NEC is the southern extension of the California Current carrying subtropical surface water into the tropics and westward to the central Pacific, whereas the NECC carries warmer tropical surface water from the western Pacific into the eastern Pacific warm pool.

In the tropics, the 20 °C isotherm, at about the middle of the thermocline, generally separates the mixed layer from the rest of the water column (Fiedler, 1992; Kessler, 1990). Water below the thermocline is more likely to breach the mixed layer the shallower the thermocline. Therefore, thermocline topography affects nutrient flux into the upper euphotic zone and hence the system's productivity: a thermocline that is closer to the surface leads to higher rates of primary productivity (McGowan