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A retrospective study of ecosystem effects of the 1976/77 regime shift in the eastern Pacific warm pool

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A retrospective study of ecosystem effects of the 1976/77 regime shift in the eastern Pacific warm pool

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Oceanography

by

L. Ignacio Vilchis

Committee in charge:

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2010

The Dissertation of L. Ignacio Vilchis is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2010

DEDICATION

A mis padres,
Luis y Griselda Vilchis

EPIGRAPH

Todo lo arreglaremos
poco a poco:
te obligaremos, mar,
te obligaremos, tierra,
a hacer milagros,
porque en nosotros mismos,
en la lucha,
está el pez, está el pan,
está el milagro.

Oda al mar
Pablo Neruda

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Chapters 2 through 4 of this dissertation are composed of manuscripts that have been prepared for stand-alone publications in the peer-reviewed literature. Chapter 2 has been published in full under the same title in *Deep-Sea Research I* Vol. 56, pages 125–140, and was co-authored with Lisa Ballance and William Watson. I was the primary investigator and author. Chapter 3 is being prepared for submission to *Progress in Oceanography* and was co-authored with Lisa Ballance, with myself as the primary investigator and author. Chapter 4 is being submitted for publication to *Ecology* and was co-authored with Lisa Ballance, with myself as the primary investigator and author.

Completing a PhD is not an accomplishment achieved solely by individual efforts. This is particularly true in long-term ecological studies covering large ocean areas, like my dissertation, where success hinges on the collaborative efforts of several research programs and many individuals. As I write this, I realize just how many people I have drawn upon for support, guidance and assistance in the process of completing my dissertation. As a graduate student, I have had the good fortune of being mentored by both the scientific community of the Scripps Institution of Oceanography and the Southwest Fisheries Science Center. During this time I have met some of the most brilliant and wonderful people—people who have always opened their doors to my questions, offering friendship and advice. Simply saying thank you is not adequate representation of my appreciation for the mentoring I have received from the Scripps and Southwest Fisheries Science Center scientific communities. Nevertheless, in the following paragraphs I will try to thank them all.

"Nacho … Who the hell is Nacho?" Those were the first words I heard Mia Tegner say in her subtle voice, when Theresa Sinicrope told her I was waiting in the hallway to talk to her. Working with Mia and Paul Dayton prior to becoming a graduate student shaped me in a way that is hard to describe. Mia formally introduced me to marine conservation ecology and showed me that the best way to appreciate an ecosystem is to understand its history and document its present. Mia and Paul have both been exceptional role models and had a great hand in where I am now. Weekly diving trips to the Point Loma kelp beds and interactions with Pete Edwards, Ed Parnell, Kristin Riser and Theresa Sinicrope were a pleasure. While at the Dayton lab, I also had the pleasure of meeting and interacting with David Hyrenbach. Talking and sharing ideas with David influenced the path I took in my graduate studies.

My doctoral committee is composed of six brilliant scientists representing an amazing wealth and diversity of knowledge, besides being a top-notch group of people. They fostered my development through independence and treated me like a colleague, yet they were always available when needed. I am fortunate to have a committee co-chaired by two world-class open ocean ecologists, Lisa Ballance and Mike Landry. Both have greatly influenced my perspectives of ocean ecosystems, large and small.

Besides being a great ecologist, Lisa Ballance is a great person. She has an uncanny ability to manage an entire division of the Southwest Fisheries Science Center, lead research projects of her own and advise several graduate students. Conversations of seabird ecology with Lisa were invaluable in my development as a graduate student. Few parallel her knowledge of seabird and cetacean ecology in open ocean systems. I simply learned by osmosis while spending time on the flying bridge with her. Lisa facilitated my participation in scientific conferences and oceanographic cruises, always giving me the green light to explore and learn all that I could. Even when my research endeavors were unsuccessful, her faith in my ability to get the job done never appeared to waver. Lisa has provided wonderful and often needed advice and guidance, especially in editing my written work, which more often than not was filled with my Spanglish grammar. She has been an amazing teacher. I wholeheartedly appreciate all that she has done to make my graduate career at Scripps possible as well as a most enjoyable experience.

Mike Landry has an amazing ability to evaluate patterns in ocean processes and assess their ecological significance. The development of my dissertation greatly benefited from insights I gained from interacting with Mike during seminars and numerous lab meetings. Interactions in his lab covered a wide range of topics and were a great source of ideas. His critiques of my work were always constructive and productive. Above all, however, Mike is a true gentleman.

The remaining members of my committee, Dave Checkly, John McGowan, Dean Roemmich and Mark Thiemens, were always willing to give me feedback, advice and encouragement that improved my dissertation. Dave's thorough reviews of my manuscripts enhanced my dissertation tremendously. I have learned much from Dave. Having my office adjacent to John McGowan's allowed me to interact with him on nearly a daily basis. He always showed a genuine interest in my work. Talking with him over the years has been an invaluable source of ideas and inspiration. Dean Roemmich has been a great teacher and was always available to meet and talk about oceanography. His advice and suggestions were always a blessing. Because Mark Thiemens is the dean of the UCSD Chemistry department, I only interacted with him a few times, but he provided invaluable comments and feedback on my stable isotope work.

Retrospective studies like my dissertation rely on long-term ecological research projects, hinging on collaborative research with numerous programs and people. First, the invaluable source of marine environmental data from the National Oceanographic Data Center's World Ocean Database was indispensible. Second, the cooperative efforts of the EASTROPAC expeditions and the foresight of the Scripps Pelagic Invertebrates Collection to archive EASTROPAC samples for future research provided me with invaluable data. I am indebted to Mark Ohman, who graciously permitted me to use all of the EASTROPAC samples that I needed, and to Annie Townsend, who guided me through a formalin labyrinth while searching for samples. Third, thank you to the many members of the scientific and ship crew of the *David Starr Jordan, Endeavour* and *McArthur* for completing countless oceanographic and net-tow stations. In particular, I am indebted to the enthusiasm of the David Starr Jordan's then-Commanding Officer Keith Roberts and Chief Boatswain Chico Gomez, who were both indispensible in the collection of contemporary seabird specimens. Keith gave me all the trust in the world, giving me the liberty to drift far from the ship while searching for seabirds on the small boat. With Chico at the helm there was never a doubt of our safety or our success. Fourth, Bill Watson and the ichthyoplankton lab at the Southwest Fisheries Science Center shared an incredible amount of information with me and graciously allowed me to sort samples there. A large portion of the samples I used for my dissertation were sorted by Lucy Dunn, Jeanne Haddox, Barbara MacCall and Michael Yaguchi, who collectively spent hundreds of hours sorting under the scope. Elaine Acuña, Dimitry Abramenkoff, Noelle Bowlin, Sherri Charter, Richard Charter, Amy Hays, Bill Watson and Sarah Zao all shared their sorting and fish identification expertise with me. Bill Watson's and Barb MacCall's expertise on larval fish identification have been indispensible for my dissertation's success me. They both deserve an extra round of applause.

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I also want to express my gratitude to the awesome research and teaching staff at the Scripps Institution of Oceanography. I greatly appreciate the many professors who shared their knowledge and time with me. Talking science while surfing with Jerry Kooyman just does not happen anywhere else. Phil Hastings and HJ Walker were very helpful in answering any fish-related questions and lent me many fish specimens. I especially tip my hat to James J. Leichter. He has been a great teacher, running partner and friend. Learning from all of you both in the classroom and during TGs has been a pleasure.

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Vilchis, L.I., Ballance, L.T., Watson, W., 2009. Temporal variability of neustonic ichthyoplankton assemblages of the eastern Pacific warm pool: Can community structure be linked to climate variability? Deep-Sea Research I 56, 125–140.

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ABSTRACT OF THE DISSERTATION

A retrospective study of ecosystem effects of the 1976/77 regime shift in the eastern Pacific warm pool

by
L. Ignacio Vilchis

Doctor of Philosophy in Oceanography
University of California, San Diego

Professor Lisa T. Ballance, Chair
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Physical processes in surface ocean circulation are critical in shaping pelagic communities. On spatial scales that include entire ocean basins, climate oscillations drive changes in ocean physics that in turn shape biological production. The El Niño Southern Oscillation (ENSO), for example, persists for 6 to 18 months, spatially enveloping physical changes in the tropical and eastern Pacific. On the other hand, the Pacific Decadal Oscillation (PDO), while having a similar spatial fingerprint, has "regimes" lasting 20 to 30 years. Changes in these regimes, or regime shifts, can happen abruptly (within a year), affecting pelagic ecosystems by altering processes regulating nutrient supply that in turn drive biological production (bottom-up forcing). With the benefit of hindsight, we now recognize that regime shifts have impacted ecosystems in the eastern Pacific, particularly in extra-tropical regions. Despite covering the largest portion of the worlds oceans, few long-term ecological data sets exists for tropical oceanic ecosystems. Thus, there is a lack knowledge as to how tropical open ocean systems react to regime shifts. In this dissertation, I retrospectively built physical and biological data sets to test hypotheses linking the 1976/77 Pacific Ocean regime shift to bottom-up effects of ecosystem change in a tropical and oceanic system, the eastern Pacific warm pool.

I approached my research goals by analyzing three components of the eastern Pacific warm pool ecosystem during the 1960–2006 time period. First, I used historical hydrographic data from the World Ocean Database 2009 to characterize trends in thermocline depth and water column stratification in the upper 200 meters. Second, I tested hypotheses linking the 1976/77 Pacific Ocean regime shift to bottom-up control of ecosystem change in the eastern Pacific warm pool for mid-trophic-level organisms and apex predators. For the mid-trophic-level organisms I used ichthyoplankton samples collected during historical and contemporary expeditions to the eastern tropical Pacific. For the apex predators I used carbon and nitrogen stable isotope ratios measured from seabird feathers of a suite of ecologically and phylogenetically diverse seabird species collected in the eastern Pacific warm pool in 1960–2006 to gauge diet variability during this time period.

I found evidence suggesting that multidecadal changes occurred in the thermal structure of the upper 200 meters in the eastern Pacific warm pool. Furthermore, I found evidence suggesting that organisms from two trophic levels responded differently to these environmental changes. Temoral variability in species assemblages of mid-trophic organisms, ichthyoplankton, appeared to be higher in regions of the study area where upwelling is prevalent, while assemblages from oceanic regions with less or no upwelling were stable. In contrast to variability of mid trophic-level organisms, the carbon and nitrogen stable isotope proxy for diet of apex predators, seabirds, showed little variation over time. These results are in agreement with the notion that physical forcing shapes nutrient fluctuations driving biological production and that lower trophic levels are more likely to respond to these fluctuations than long-lived apex predators. However, stable isotope proxy data and biological survey of apex predators in the northeastern Pacific have shown fluctuations coherent with ocean warming and the 1976/77 regime shift.

The eastern tropical Pacific supports a unique multispecies community of apex predators comprised of around 50 resident seabird species and 30 cetacean species including several endemics and the world's largest yellowfin tuna fishery. The most recent regime shift is thought to have occurred in 1998/99. Future research should focus on more robust data sets that can further improve our knowledge of ecosystem effects of regime shifts in tropical systems.

CHAPTER 1

Introduction to the Dissertation

Pelagic ecosystems do not remain in constant states through time; instead they experience changes in the physical processes shaping biological production. In some cases, changes in physical regimes of ocean ecosystems occur within a few years and are relatively coherent with climate changes. Studying how ecosystems respond to these rapid shifts in physical regimes, or regime shifts, can give us insights into what drives ecosystem change in the open ocean. However, because most ecosystem effects only become apparent with the benefit of hindsight, most of what we know of ecosystem response to regimes shifts comes from retrospective studies analyzing long-term and historical data, data that are difficult to obtain especially in the open ocean. Retrospective studies using historical data of ecosystem response to regime shifts are of paramount importance, because knowledge of the past is indispensable for accurate assessment of current and future status of ecosystems.

This dissertation investigates ecosystem effects of the 1976/77 regime shift of the Pacific Ocean in the eastern Pacific warm pool. The objectives of this research are to quantify physical and biological changes in the ecosystem over the 1960–2006 period and gauge whether observed changes were large enough to substantially impact the ecosystem.

Regime shifts are abrupt and coherent changes in climatological conditions affecting entire ocean basins, causing sudden shifts in the structure and function of marine ecosystems (Cury and Shannon, 2004; McPhaden and Zhang, 2002). In the Pacific, regime shifts are thought to include low-frequency changes in ocean conditions that oscillate between the two phases of the Pacific Decadal Oscillation (Mantua and Hare, 2002). These phase changes, which occurred in 1925, 1947, and 1977, have been labeled as regime shifts (Mantua *et al.*, 1997; Minobe, 2000; Zhang *et al.*, 1997), with the most recent shift thought to have occurred in 1999 (Bidigare *et al.*, 2009; Bond *et al.*, 2003).

Robert Cushman Murphy was one of the first scientists to attribute ecosystem response to a regime shift (Murphy, 1926). After experiencing a strong El Niño in 1925 during an expedition to South America, Murphy (1926) used historical accounts of weather conditions accumulated by the International Petroleum Company in Talara, Peru, to deduce that such a strong event accompanied by ecosystem change had not occurred in 34 years. Later in California, (Hubbs and Shultz, 1929) also noticed deviations from "normal conditions" noting drastic changes in fish and invertebrate species compositions occurring along the West Coast of the United States in 1926. In 1948, after witnessing a second extreme event like the one in 1926 (Hubbs, 1948) concluded, that there had been long-term changes in sea surface temperatures with accompanying changes in the distribution of marine organisms.

Changes in ecosystem structure following a regime shift are thought to be a result of changes in physical factors affecting the supply of nutrients into the system, known as bottom-up forcing. Bottom-up forcing of ecosystem structure implies that the environment mediates the ecosystem structure of pelagic systems by regulating the supply of nutrients for primary production. This idea revolves around the association between vertical mixing (upwelling) in the upper water column and the mechanisms recharging the euphotic zone with inorganic nutrients (Cullen *et al.*, 2002). In general, in less stratified waters with a shallow thermocline, it is more likely that deep-water nitrate will be entrained into the euphotic zone (McGowan and Hayward, 1978). After the 1976/77 regime shift, sea surface temperatures in the eastern Pacific became anomalously warm, increasing stratification and affecting ecosystem structure at both the lower and upper trophic levels (Hayward, 1997). Effects of the 1976/77 regime shift in the eastern Pacific have been widely documented in polar and temperate ecosystems (Alheit and Ñiquen, 2004; Chavez *et al.*, 2003; Francis *et al.*, 1998), while relatively little is known about how tropical ecosystems have been affected.

Pelagic ecosystems respond to processes operating at multiple scales of space and time. Thus, in concert with asking an ecological question, one should identify the time and space scale at which that question is focused (Wiens, 1989). We know that organisms in the ocean aggregate in specific regions and are absent from others, with these patterns occurring at a variety of time and space scales. For example, at the largest spatial scales, biogeographic patterns extending over large parts of ocean basins are maintained by major oceanic circulation gyres (McGowan, 1971). Within biogeographic regions, smaller circulation features at spatial scales between 1,000 and 3,000 km also exist. These features differ from large-scale systems not only in size but also in having less variability in the species compositions found within them (Haury *et al.*, 1978). We also know that, depending on spatial scale, systems tend to have characteristic temporal variability (Levin, 1992). In pelagic ecosystems of the two spatial scales just described, climate cycles seem to have the greatest influence, since climate patterns determine annual cycles of water temperature and daylight, as well as properties in vertical mixing

(Haury *et al.*, 1978). The spatial and temporal scales addressed in this dissertation will be > 1,000 km, with and 10–30 years, respectively, to address changes in climate caused by regime shifts.

The eastern Pacific warm pool is a large (11.5 million km^2) ocean ecosystem within the eastern tropical Pacific. With relatively few islands, the eastern Pacific warm pool is mostly composed of pelagic habitat. I chose this subset of the eastern tropical Pacific to minimize spatial variation, since my dissertation's goals are to quantify temporal trends in the physical processes and biological response. With northern and southern boundaries at 5º and 20º N, it includes water masses carried eastward and westward by the North Equatorial Countercurrent and by the North Equatorial Current, respectively. Extending west from Central America and Mexico to 150º W, the eastern Pacific warm pool includes a range of pelagic habitats. From a zoogeographic perspective, two biogeographic regions, the Eastern Pacific Barrier and the Tropical Eastern Pacific (Hastings, 2000; Robertson and Allen, 1996), are included. In the eastern areas surrounding the Costa Rica Dome, higher productivity exists, along with peaks in zooplankton biomass(Fernández-Álamo and Färber-Lorda, 2006; Pennington *et al.*, 2006).

I approached the goals of this dissertation by retrospectively analyzing three components of the eastern Pacific warm pool ecosystem. First, I used historical hydrographic data from the World Ocean Database 2009 to characterize trends in thermocline depth and water column stratification in the upper 200 m. I then tested hypotheses linking bottom-up control of ecosystem change in the eastern Pacific warm pool for mid-trophic level organisms and apex predators. For the mid-trophic level organisms, I used ichthyoplankton samples collected during historical and contemporary expeditions to the eastern tropical Pacific. I assessed changes in species composition data of neustonic ichthyoplankton from 1,131 stations collected throughout the eastern Pacific warm pool between 1967 and 2006. Determining how neustonic ichthyoplankton species composition varied over time permitted me to then test the hypothesis of community structure change as result of increased stratification and a deeper thermocline depth. For the apex predators, I used stable isotope ratios measured from seabird feathers to quantify the variability in trophic level for the 1960–2006 period. I made this record by measuring stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes from feathers of specimens of a suite of ecologically and phylogenetically diverse seabirds I collected in the eastern Pacific warm pool. I combined this with measurements taken from historical specimens collected within the eastern Pacific warm pool during the 1960–2006 period that have been held in museum collections of the United States and Mexico. I then analyzed trends in the time series of stable isotope ratios to determine whether correlations existed with time and in response to the 1976/77 regime shift. These analyses and results are described in Chapters 2–4, and have been prepared for publication in the peer-reviewed literature. They are intended to be stand-alone documents; thus some material in each may be repetitive. To conclude, Chapter 5 summarizes the results of the dissertation and proposes possible avenues for future research.

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Chapter 2

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

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. On eight NOAA Fisheries cruises to the eastern Pacific warm pool (1987-1990, 1992, and 1998-2000), 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 multi-dimensional 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 thermo-

cline depth during the El Niños of 1987-1988, 1997-1998, and the extended warm period 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.

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 twelve 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). Though 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 alter species distributions of ichthyoplankton (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.

METHODS

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) (Figure 2.1). 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 and Hayward, 1978). Hence, the depth and strength (rate of temperature change as a function of depth) of the thermocline are strongly linked to primary productivity and zooplankton biomass in the ocean surface layer (Blackburn *et al.*, 1970; Fernandez-Alamo and Farber-Lorda, 2006; Ryther, 1969). Variations in thermocline depth and strength are also good indicators of what type of life may be found in the oceanographic habitat of the upper ocean (Ballance *et al.*, 1997; McGowan and Williams, 1973).

Oceanic upwelling and a basin-wide west-to-east shoaling thermocline create a west-to-east productivity gradient, and overall our study area can be divided based on thermocline depth into an upwelling region in the east, a coastal and oceanic region south of central Mexico, and an oceanic region in the west. In general, thermocline depth in our study area varies as a result of three factors: Pacific-wide shoaling from west to east due to the pile up of warm water in the west by the trade winds; a divergence between the NEC and NECC which stretches isotherms towards the surface, resulting in a thermocline ridge intersecting the warm pool at 9-10°N; and the proximity of the American continent which influences surface currents and oceanic upwelling.

With regards to this latter factor, a mountain range extending the length of southern Mexico and Central America forms a nearly perfect barrier between two distinct low level air masses, the lower pressure system in the eastern tropical Pacific and the slightly higher pressure systems in the Gulf of Mexico and Caribbean Sea (Chelton *et al.*, 2000). The resulting pressure causes winds to be funneled into the Pacific through three low-level gaps in the mountain barrier. These wind jets can reach as far as 600 km seaward, generating intense mixing and oceanic upwelling in the gulfs of Tehuantepec, Papagayo and Panama; the first two also are responsible for weakening the NECC as it nears Central America (Ballesteros and Coen, 2004; Kessler, 2002). Trade winds are also funneled through the Papagayo and Panama gaps, but not the Tehuantepec gap (Chelton *et al.*, 2000). The wind-jet-induced upwelling in the Gulf of Papagayo corresponds to the Costa Rica Dome, and is the surface expression of the countercurrent thermocline ridge. This ridge shoals gradually from 50 m depth at 110°W to around 25 m at 90°W, after which it deepens as it nears the coast. The Costa Rica Dome is at the peak of the countercurrent thermocline ridge. The synergistic effect of a shallow thermocline and wind-jet-induced Ekman upwelling creates a geostrophically balanced quasi-permanent cyclonic eddy. Similar upwelling exists in the Gulfs of Tehuantepec and Panama, but without a thermocline peak, quasi-permanent cyclonic eddies are not formed. The three wind-jet-generated upwelling regions in the eastern portion of our study area produce nutrient-rich environments that support highly productive oceanic ecosystems (Ayala-Duval *et al.*, 1996; Fiedler, 2003; Pennington *et al.*, 2006).

Sample collection

We sampled ichthyoplankton in the eastern tropical Pacific warm pool in the boreal fall periods of 1987-1990, 1992, and 1998-2000 during cruises conducted by NOAA Fisheries aboard the research vessels *David Starr Jordan* and *McArthur*. Eight survey years were completed, totaling 852 stations spanning a 13-year period (Figure 2.2).

We used a modified version of the Manta net originally described by Brown and Cheng (1981) to sample ichthyoplankton. Using a 333 μm nylon mesh and cod end, tows were conducted once daily during each cruise, approximately two hours after sunset. The net was towed in the dark from the ship's starboard side at a speed of 0.77 m sec^{-1} for 15 min. We used an asymmetrical tow bridle with a slightly shorter port side that towed the mouth of the net at a slight angle away from the ship. Volume of water filtered during each tow was estimated with a flow meter attached across the center of the net mouth. Samples from each tow were preserved in 5% formalin buffered with sodium borate. At the end of each cruise samples were transferred to the plankton sorting laboratory at the Southwest Fisheries Science Center. Sorting involved removal, identification and quantification of all ichthyoplankton from each sample. Except for damaged specimens, most fish larvae collected could be identified to species. In some cases, however, only genus or family or occasionally order-level identification was possible. The flow-meter data were used to covert the ichthyoplankton count data to numbers per volume of water strained.

Water column thermal and phytoplankton pigment structure were also determined at each manta tow station with a 12-bottle CTD cast to 1000 m. Seawater samples were collected with Niskin bottles tripped at 0, 20, 40, 60, 80, 100, 125, 150, 200, 350, 500 and 1000 m. Chlorophyll (down to 200 m) was determined by the fluorometric technique using Turner fluorometers calibrated before and after each cruise with commercial chlorophyll *a*.

Data analysis

Ichthyoplankton from the 852 stations was distributed among 227 taxa. Our data showed high diversity with only a few dominant taxa, a common phenomenon in biological survey data (McGill, 2003; Whittaker, 1965). Just over two thirds of all categories were encountered less than five times throughout the 852 stations. The majority of larval fish taxa are relatively rare in tropical oceanic samples resulting in a zero-inflated station-by-taxon matrix (i.e. large portion of the entries were zeros). To circumvent this zero-inflation, we transformed the data into percent dominance by determining, for each taxon, the proportion of individuals of the total number of larvae in the sample and multiplying by 100. An accepted practice that corrects for zero-inflation is to remove taxa/categories based on a threshold of rarity, commonly those that account for < 5% of the overall (all 852 stations) mean dominance (Field *et al.*, 1982; McGowan and Walker, 1988; Ward *et al.*, 2003). We used a lower threshold, 0.5%, for a more conservative dismissal of rare species. Taxa/categories ranked by the overall mean (all stations, all years) dominance are shown in Figure 2.3a; the 23 dominant taxa that were used for all further analyses are shown in Figure 2.3b and listed in Table 2.1.

Thermocline depth and integrated chlorophyll

Thermocline depth and integrated chlorophyll were derived from hydrocast data from each manta tow station. Thermocline depth was calculated as the midpoint of the depth interval with maximum temperature gradient (dT/dz, T=°C and z = m), where dT > 2. Chlorophyll *a* within the euphotic zone was integrated by fitting splines at 1-m intervals between bottle depths from the surface until the euphotic zone depth was reached. Euphotic zone depth was calculated from total pigment profiles according to Morel (1988).

Similarity measures

We used two community similarity indices to measure differences among stations, using the abundances of all 23 taxa per station instead of per individual taxon. The first measure was the Spearman's rank correlation coefficient. One pitfall of using rank correlations is their insensitivity to additive or proportional differences between samples (Krebs, 1999). For example, if sample A is identical to sample B but contains species' abundances that are one-half those in sample B, the rank correlation coefficient gives the same estimate of similarity as if the abundances were equal. We therefore applied a second similarity measure that accounts for these differences, the percent similarity index (PSI):

$$psi = 100 \sum \text{minimum} \, (p_{Ai} \, , p_{Bi} \,)$$

where *Ai* and *Bi* are the proportions of taxa *i* in samples *A* and *B*, respectively. PSI measures the extent to which two samples are alike in composition, while considering abundance, ranging from zero for samples with no taxa in common to 100 percent in identical samples. In spite of its simplicity the PSI is one of the best quantitative association coefficients available, since it is relatively unaffected by sample size and species diversity (Wolda, 1981), but is strongly affected by the most abundant taxa. Since most samples were dominated by only a few taxa, we considered an index that gives high importance to dominants appropriate. PSI has been commonly applied in analyses of zooplankton communities (Hayward and McGowan, 1979; Rebstock, 2001; Whittaker and Fairbanks, 1958).

Study area partitioning

Our goal was to measure the regional variability of species compositions over time and not space. We therefore excluded spatial variability from further analysis by dividing our study area into three sub-regions based on longitude: Eastern (75 to 95°W), Middle (95 to 110°W), and Western (110 to 160°W) (Figure 2.2). We analyzed temporal trends of species compositions within each region independently. We based this partitioning on three factors: first, the study area's thermocline and integrated chlorophyll longitudinal gradient (Figure 2.4); second, surface oceanographic patterns (e.g. tropical surface water mass, Costa Rica Dome, Gulfs of Tehuantepec and Panama); and third, results of pairwise PSI comparisons of all stations based on the longitudinal difference among stations (Figure 2.5). Sampling effort (number of stations) in each region varied among years (Table 2.2), with the greater part of the study area covered in all years except 1992, when sampling was limited primarily to the Eastern Region.

Temporal trends in PSI and Spearman rank correlations

To analyze temporal trends in species compositions of stations within each region, we pooled stations by region and year. We then made pairwise comparisons between all possible combinations of the eight cruise years within each region. This resulted in two measures of similarity (PSI and rank correlations) between comparisons of zero to 13 years apart within each of the three regions.

Cluster analysis and Multidimensional scaling

We identified specific groupings of taxa and stations using hierarchical clustering in conjunction with non-metric multi-dimensional scaling (MDS). Both methods are based on a triangular matrix of similarity coefficients computed between every pair of stations to measure the similarity of taxa among stations; we used the Bray-Curtis coefficient:

$$B_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{n}\left|X_{ij} - X_{ik}\right|}{\sum_{i=1}^{n}\left(X_{ij} + X_{ik}\right)}\right\}$$

where X_{ij} and X_{ik} are the abundance of taxon *i* in each sample (*j*, *k*), and *n* is the number of taxa. This coefficient provides an algebraic measure of similarities among stations for each of the ichthyoplankton taxa. From these, we created a hierarchical cluster tree of the taxa using the group-average algorithm. MDS then gave further insight into the grouping of taxa by transforming the multi-dimensional taxa-station data matrix into two dimensions. The distance measure used for the MDS ordination was the Bray-Curtis coefficient, completing 20 random restarts of the iteration in order to minimize the stress level, which measures the goodness-of-fit of the ordination. Hierarchical cluster analysis combined with MDS is a robust method for detecting important groups of stations with co-occurring taxa or groups of species/taxa within a community and identifying groups or assemblages (Clarke and Warwick, 1998; Field *et al.*, 1982).

RESULTS

Abundance and diversity patterns

A total of 19,247 fish larvae were sorted from the 852 manta tow stations. These were distributed among 227 categories that included 123 species, 61 genera, 39 families, two orders, and disintegrated and unidentified fish larvae. Fish abundance, species richness and diversity varied more with a deeper thermocline (>100m); however, as the thermocline shoaled from 100 to 10 m, all three community variables increased monotonically (Figure 2.6). Additionally, fish abundance, species richness and diversity showed a hump-shaped relationship with integrated chlorophyll, peaking near 20 mg chl *a* m^2 (Figure 2.6). Larger (>35 mg chl *a* m^2) values in Figure 2.6 correspond to extreme measurements in the gulfs of Chiriqui and Dulce, and Bahia de Coronado, and particularly in the Costa Rica Dome. Among the three regions of the study area, the Eastern Region contained 54.4% of all individuals sorted, and the Middle and Western Regions contained 34.5% and 11.1%, respectively.

Oxyporhamphus micropterus was clearly the most ubiquitous and dominant species, with the highest overall dominance and present at almost half of all stations (Table 2.1). A close second was *Vinciguerria lucetia,* with an overall dominance of 15.9% and occurring in 33.5% of all samples. *Coryphaena equiselis*, and bullet and frigate mackerels (*Auxis* spp.) ranked third and fourth in overall dominance, respectively, with flyingfish in the genus *Prognichthys* ranking fifth with 3.7%. Dominance tapered off quickly after *O. micropterus* and *V. lucetia*, and then gradually after *Prognichthys* spp (Figure 2.3).

The most abundant taxa (total number of individuals) were, in decreasing order, *Opisthomena* spp., *O. micropterus*, *V. lucetia*, *Auxis* spp., and *Cetengraulis mysticetus*

(Table 2.1). *Opisthonema* spp. occurred at only 5.0% of all stations and ranked tenth in overall dominance; nevertheless, it was the most abundant taxon in our study. *Cetengraulis mysticetus* also was abundant, ranking fifth, despite occurring at only 1.8 % of all stations and ranking 15th in overall dominance. This clearly reflects the dense patches of larvae in which these two near-shore clupeoids were occasionally found. Notably, even though ranking fourth after *C. equiselis* in overall dominance, *Auxis* spp. had more than twice the abundance of pompano dolphinfish larvae.

Temporal stability of ichthyoplankton assemblages

Over the 13 years of our study, ichthyoplankton assemblages in the Middle and Western Regions varied less than in the Eastern Region. Only in the Eastern Region did the least square fit of PSI comparisons between stations pooled by year show a significant decrease as a function of time between cruises (Figure. 2.7). In all other regions the fits were not significantly different from zero (95% confidence levels), indicating more change in assemblages in the Eastern Region over time compared with the more stable assemblages of the Middle and Western Regions. The proportion of variability explained for PSI as a function of time was highest in the Eastern Region, 21.7% compared to practically zero in the two western regions.

Cluster analysis and multiple dimensional scaling

Ordination and cluster analyses (Figure 2.8a) identified five larval assemblages corresponding to different oceanographic habitat and neustonic affiliation: true neuston, facultative neuston, or pseudoneuston (Hempel and Weikert, 1972). Larvae from the 23 dominant taxa all are planktonic, and as is common for tropical fishes, larval production is year-round and metamorphosis usually occurs within 30 days or less (Helfman *et al.*, 2005; Houde, 1989). All 23 taxa are oviparous with planktonic eggs and larvae (Nelson, 2006), except for most of the flyingfishes and *Canthidermis maculatus* which have attached eggs (Myers, 1999; Parin, 1995). We therefore propose that the 23 dominant taxa represent the neustonic ichthyoplankton assemblage of the eastern Pacific warm pool, and as a result, adult spawning location and/or oceanographic processes govern their placement within oceanographic habitats. We named each assemblage according to the known habitats of the taxa in the groups (Table 2.1).

Upwelling assemblage

Two engraulid taxa, the Pacific anchoveta, *Cetengraulis mysticetus,* and the genus *Anchoa*, made up the Upwelling assemblage. Anchovetas and other anchovies are largely restricted to nearshore productive areas where they can filter feed, primarily on diatoms and small crustaceans (Whitehead, 1985b). We consider larvae of *C. mysticetus* and *Anchoa* spp. taxa true-neustonic since they are rarely (< 2% occurrence) present in oblique bongo tow samples collected in the same region (Ambrose *et al.*, 2002a; Ambrose *et al.*, 2002b; Watson *et al.*, 2002).

Coastal assemblage

Seven phylogenetically diverse taxa consisting of a flyingfish genus *Prognichthys* (probably predominantly *P. tringa* in the Eastern Region), four perciform taxa: *Polydactylus approximans*, *Coryphanea hippurus*, the mojarra family Gerreidae, and the mullet genus *Mugil*, the clupeid genus *Opisthonema*, and a balistid, *Canthidermis maculatus,* formed part of the coastal assemblage. All of these larval taxa are rarely collected with oblique bongo tows (< 2%), except for *C. hippurus* (< 10%) collected in the same region (Ambrose *et al.*, 2002a; Ambrose *et al.*, 2002b; Watson *et al.*, 2002). Gerreids and *Opisthonema* spp. do not develop heavy pigment over the notochord until late in the larval stage. The remaining taxa of the group have rapid development of heavy dorsal melanistic pigmentation (Ditty *et al.*, 1994; Gibbs, 1959; Moser, 1996). Flyingfishes, in particular, hatch from relatively large eggs with well-developed and functional pectoral and caudal fins. This rapid larval development along with heavy dorsal melanistic pigmentation are adaptations to the neustonic habitat that is characterized by high solar radiation, wind stress, and predation (Moser, 1981). We therefore consider all species of this group true neustonic, with the exception of Gerreids and *Opisthonema* spp., which are facultative neuston.

Oceanic assemblages (a, b and c)

Three oceanic assemblages were identified. The largest (**a**) consisted of one mesopelagic and eight epipelagic taxa that included four of the most dominant taxa in our study. This assemblage included the highly abundant mesopelagic Panama lightfish *V. lucetia* and the epipelagic shortwing flyingfish *O. micropterus*; three other epipelagic flyingfish taxa: *C. xenopterus*, *H. marginatus*, and *Exocoetus* spp.; four epipelagic perciform taxa: a driftfish *Cubiceps pauciradiatus*, pompano dolphinfish *C. equiselis*; and two epipelagic scombrid genera: *Thunnus* and *Auxis*. With a prominent presence in oblique bongo tows collected in the same region (Ambrose *et al.*, 2002a; Ambrose *et al.*, 2002b;

Watson *et al.*, 2002), we consider *V. lucetia*, *C. pauciradiatus*, and *Auxis* spp. pseudoneustonic. *Thunnus* larvae occur predominantly in the upper 50 m and show some evidence of vertical migration within that stratum (predominantly below the surface during the day and at the surface at night); thus placing them in the facultative neuston, and the remainder of this assemblage in the true neuston. A smaller assemblage consisted of (**b**) two mesopelagic taxa: the lanternfish genus *Diaphus* and the barracudina genus *Lestidium*, both with pseudoneustonic larvae. The third oceanic assemblage (**c**) included two flyingfish genera *Cheilopogon* and *Hirundichthys*, and the pilotfish *Naucrates ductor*, all epipelagic (Leis and Miller, 1976; Moser, 1996; Watson, 1999) and true-neustonic.

MDS reduced the multidimensional taxa-by-station data matrix into the two axes of Figure 2.8 with low enough stress levels indicating good ordinations with no prospect of misleading interpretation of the 2-dimensional picture. Four of the five assemblages separated on Axis 2 and one separated on Axis 1 of Figure 2.8a. Assemblages containing oceanic taxa are to the left end of Axis 1 and the assemblage with upwelling taxa is towards the right, with the coastal assemblage in between. In addition, cluster and MDS analyses seemed to separate two of the three mesopelagic taxa from the neritic/epipelagic taxa, with *V. lucetia* not separating from the neritic/epipelagic group because it is more ubiquitous in the study area than *Diaphus* and *Lestidium* spp.

There was a gradient in community composition across regions and years. Region-year combinations of stations clustered into four groups with the gradient in community composition being traced along Axis 2 (Figure 2.8b). An oceanic group with all stations from the Western Region is farthest left on Axis 2. The largest group, in the middle of the Axis, includes Middle and Eastern Region stations. Two small groups of coastal and upwelling stations from the Eastern Region are farthest right of Axis 2, with stations from 1987 and 1998 grouped together and stations from 2000 occurring by themselves. Stations within the eastern region showed a greater degree of variability in community structure having marked changes during anomalously warm years (1987 and 1998), as well as during an anomalously cool year (2000). In contrast, community structure from western stations was steady with no differences between years.

DISCUSSION

Our analyses revealed a longitudinal gradient in community structure and temporal stability of neustonic ichthyoplankton taxonomic composition within the three regions we defined in the eastern Pacific warm pool. Among the oceanographic processes and types of forcing responsible for creating and maintaining this pattern, we hypothesize two to be the most likely principle contributors: a productivity gradient driven by thermocline topography and the variability induced by ENSO warm and cold water events.

Oceanographic habitat and species assemblages

Oceanographic habitat differed in each region, apparently structuring the ichthyoplankton community into a suite of assemblages that corresponded to specific habitat: oceanic in the Western Region, a combination of coastal and oceanic in the Middle Region, and coastal and upwelling in the Eastern Region. Our study area covers a variety of oceanographic habitats where adult spawning behavior combined with oceanographic processes aggregate neustonic ichthyoplankton assemblages that correspond to specific habitat. The majority of the dominant neustonic ichthyoplankton taxa within our study area spend most of their time at or near the surface, having short (30 days or less) larval stages common of tropical species (Helfman *et al.*, 2005; Houde, 1989). We therefore propose that adult spawning behavior, food availability and physical processes are mostly responsible for defining neustonic ichthyoplankton assemblages. These assemblages changed according to the oceanographic environment along a longitudinal productivity gradient, where species with ecological ties to specific environments (oceanic, coastal, or upwelling) clustered together (Figure 2.8a). For example, the two engraulids of the upwelling assemblage were tied to productive upwelling waters of the Eastern Region that serve as nursery areas for juveniles and larvae (Simpson, 1959; Whitehead, 1985b). In addition, the lack of islands in the study area makes fish larvae from the Western Region truly oceanic and distinct from the coastal and upwelling groups, as almost no taxa from the oceanic assemblages are tied to coastal or productive waters at any stage of their life cycle (Table 2.1). Ordination Axis 2 of Figure 2.8, which separated oceanic from upwelling assemblages and station groups, thus represents a productivity gradient, with higher values along the axis representing the more productive eastern longitudes (Figure 2.4).

Abundance, species richness and diversity

The more productive upwelling systems of the Eastern Region should support higher ichthyoplankton abundances than the other regions (Hempel and Weikert, 1972), and indeed the three wind-jet induced upwelling areas within the Eastern Region had the highest abundances of fish larvae. These oceanic upwelling regions have high productivity and are known to have high zooplankton standing stock (Blackburn *et al.*, 1970; Fernandez-Alamo and Farber-Lorda, 2006) with which ichthyoplankton abundance is generally positively correlated (Loeb, 1979). Similarly, the oligotrophic Western Region has lower abundances of zooplankton, productivity and fish larvae (Figure 2.6).

Ichthyoplankton abundances are determined primarily by the abundance and spawning behavior of adults, but are modified by advective processes, by larval survival and, at least in later development stages, by larval behavior. Egg and larval transport from spawning grounds to nursery areas that provide better larval survival may be critical if spawning is in a suboptimal habitat. On the other hand, if survival depends on local conditions, retention can be critical. Nursery areas offer successful feeding within a critical period; if newly hatched larvae pass this threshold without feeding, death will occur from starvation regardless of food availability (Cury and Roy, 1989; Hjort, 1926). Specifically in the tropics, larval fishes are more likely to die of starvation because of the high energetic demands of their rapid development (Houde, 1989). We therefore hypothesize that the relationship between abundance and productivity (only from 5 to 20 mg Chl *a* m^2) in the eastern Pacific warm pool is a result of a longitudinal productivity gradient, as upwelling areas in the Eastern Region can provide rich fish spawning grounds, higher food availability and better survival conditions for fish larvae.

Similarly, the more productive systems of the east with shallower thermoclines harbored higher species diversity and richness than the oligotrophic western regions. This relationship peaked at ≈ 20 mg chl *a* m^2 and decreased with higher values, although there were also some extreme values recorded (Figure 2.6). This ecological paradigm has been well studied and empirically proven (MacArthur, 1965, 1972), as ecological theory predicts that species richness and diversity increase as a hump-shaped function of productivity (Rosenzweig and Abramsky, 1993). Some studying zooplankton and phytoplankton have found higher species diversity in the oligotrophic central gyres of oceans (Hayward and McGowan, 1979; McGowan and Walker, 1988; Venrick, 1990). The relationship between primary productivity and species diversity on a regional scale is not simple, and opposite conclusions of the direction of this relationship are possibly reached as a result of the hump-shape relationship of diversity and productivity (Rosenzweig and Abramsky, 1993). We sampled a zonal gradient nearly 8,000 km in the eastern Pacific warm pool, and ichthyoplankton here represent only a small window of the complicated and mobile natural history of fishes. Studies covering this large zonal gradient in ichthyoplankton communities of the eastern Pacific are not as common as latitudinal gradients in other oceans, where high diversity in zooplankton and phytoplankton has been correlated with low productivity and high stability (McGowan and Walker, 1993). We believe that the acting mechanism with the neustonic ichthyoplankton of the eastern Pacific warm pool is that oligotrophic conditions in the western region provide inadequate resources to support a large species pool, while eutrophic conditions in the east support survival of more species and a more diverse and rich species pool. The oligotrophic Western Region simply has less ichthyoplankton to fluctuate over time while the productive and more diverse habitats of the Eastern Region support a larger, more abundant pool of species. Obviously, oceanic and atmospheric circulation patterns are more complex in the east as well, and this must have an influence.

Higher species diversity and richness in the Middle and Eastern Regions is also likely a result of nutrient and larval fish inputs from rivers and bays, as well as higher larval retention by oceanographic processes. The eastern portion of our study area includes nearshore ecosystems, and inflation of species richness and diversity by coastal species is a common feature (Franco-Gordo *et al.*, 2003). In addition, the cyclonic circulation surrounding the Costa Rica Dome could act like a hydrodynamic trap for larvae of nearshore species advected from the coast of Central America, preventing further advection to western oligotrophic waters. Evseenko and Shtaut (2005) found that larvae of nearshore fishes dominated waters of the Costa Rica Dome, and species diversity and abundance significantly decreased outside of it. Along with our results, this suggests that the trend of higher species diversity and richness as well as abundance towards the east in our study area could be a factor of higher larval retention in the Eastern Region.

Thermocline depth, productivity and ENSO effects

A shallow thermocline and wind-jet-induced oceanic upwelling make the Eastern Region the most productive area of the eastern Pacific warm pool and the end point of a zonal gradient in primary productivity and consequent ecology (Figure 2.4, Ballance *et al.*, 2006; Pennington *et al.*, 2006). Integrated chlorophyll is positively correlated with total primary production within the euphotic zone (Hayward and Venrick, 1982; Morel and Berthon, 1989); we therefore use the former as a proxy of productivity. We propose that ichthyoplankton communities of the eastern Pacific warm pool are structured along a longitudinal productivity gradient, with species assemblages, abundance, diversity and richness, as well as the temporal variability of these measures, being affected by thermocline depth and consequent productivity.

The effects of water column stratification and consequent deeper nutricline on eastern Pacific upwelling ecosystems have been well documented (Alheit and Niquen, 2004; Fiedler *et al.*, 1992; McGowan *et al.*, 1998; Wang and Fiedler, 2006). The upwelling ecosystem off southern California provides an excellent example. Here there was an incremental change of 1.5° C between 1951 and 1993, increasing stratification inhibiting upwelling and mixing of deep water and thus local productivity of the system, measured as a 70% decrease in macrozooplankton volume within the area (Roemmich and McGowan, 1995). In the eastern tropical Pacific during the 1986-87 El Niño, changes in thermocline depth and consequent nutrient availability resulted in a decrease of surface Chl *a*, with more pronounced changes along the countercurrent thermocline ridge and in coastal and upwelling regions (Fiedler *et al.*, 1992). In our study, productive wind-jet-induced upwelling systems of the Eastern Region harbored the highest variability in species composition, and the Eastern Region as a whole had more variable species composition than the other two regions. Our study suggests that wind-jet-induced upwelling systems like the Costa Rica Dome and the Gulfs of Tehuantepec and Panama are probably affected by a deepened thermocline in a similar fashion as temperate upwelling systems.

We hypothesize that a more variable productivity, driven by ENSO-scale climatic variability, is the reason for the higher variability in species composition in the eastern portion of our study area. The deeper thermocline during El Niño conditions generally results in more stratification and decreased likelihood of cold nutrient-rich seawater being upwelled (McGowan and Hayward, 1978). In addition, equatorial atmospheric circulation changes during El Niños, e.g. Walker and Hadley circulation (Wang, 2002), and the frequency and intensity of the mountain gap wind jets responsible for generating oceanic upwelling in the Eastern Region also change (Amador *et al.*, 2006). An El Niño could shift the abundances of resident species of an upwelling system in the direction of oceanic and mesopelagic species. In support of this idea, we saw more temporal variability in species composition within the Eastern Region. Stations pooled by region and year clustered as function of region and exhibited the higher variability of the Eastern system

(Figure 2.8b). Over the 13-year time span of our study, there have been two strong El Niños (1986-87 and 1997-98) and two strong La Niñas (1988 and 2000), with a period of rapid succession of El Niños from 1990 to 1994 (Figure 2.9, Trenberth and Hoar, 1996). Although we did not sample during the genesis of the two strong warm water events, the 1986-87 El Niño peaked during our sampling period of 1987 (Fiedler *et al.*, 1992; McPhaden and Hayes, 1990), and the 1997-98 El Niño was the strongest on record (McPhaden, 1999), leaving warm water anomalies in our study area throughout 1998 (Figure 2.9). Only during these two anomalously warm sampling years (1987 and 1998) did Eastern stations separate from all other years or regions (Figure 2.8b). Franco-Gordo *et al.* (2008) found similar results in their analyses of ichthyoplankton off the coast of central Mexico. In the Western Region, however, all years were grouped together, including warm and cold anomalous years. The two western regions also showed the most stability in PSI comparisons, while the eastern Region showed higher variability (Figure 2.7). Interannual variability of the eastern Pacific warm pool is related to El Niño events (Wang and Fiedler, 2006) and as is the case for temperate eastern Pacific ecosystems, we hypothesize that upwelling and coastal assemblages in our study area were affected by ENSO events.

CONCLUSION

Our results permit us to hypothesize that neustonic ichthyoplankton assemblages in the Western Region are more resilient to ENSO-driven environmental variability than assemblages in the Eastern Region. However, there could also be simply less physical variation in the Western Region (Wang and Fiedler, 2006). This underscores how long-term studies in the tropical Pacific are central to understanding ecosystem effects of increased climate variability. A tendency for more frequent and intense El Niño events and fewer La Niña events since the late 1970s has been linked to a climatic regime shift in the entire Pacific basin (Stephens *et al.*, 2001; Trenberth and Hoar, 1996). Physical evidence of this climatic shift in the eastern tropical Pacific is less obvious than in the North Pacific (Fiedler, 2002; Mestas-Nuñes and Miller, 2006). Nevertheless, our results suggest that variability in thermocline depth in the eastern Pacific warm pool related to El Niños corresponds with the more variable ichthyoplankton species assemblages that are tied to upwelling and coastal systems. Species in the tropics have most likely evolved to persist through quasi-regular warm water events by being resilient enough to rebound after strong El Niños. However, a global climate model forced by realistic future scenarios of increasing greenhouse gas concentrations forecasts that the frequency of El Niños will continue to increase in the near future (Timmermann *et al.*, 1999). What will the cumulative effect of more frequent El Niño events on tropical oceanic systems be? We need to establish historical baselines prior to the onset of more frequent El Niños by mining historical samples from cruises to the eastern tropical Pacific during the late sixties and early seventies (Ahlstrom, 1971, 1972). In this way we can see how variable the ichthyoplankton community was then, and if the variability changed significantly after the onset of more frequent El Niños after the late 1970s regime shift of the North Pacific.

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Table 2.1 Common taxa of fish larvae (mean dominance > 0.5%), their phylogenetic affiliation, known adult habitat and abbreviation used in figures.

Sapecies/Taxon	Family	Functional group	Common name	Habitat	Abbreviation
Oxyporhamphus micropterus	Exocoetidae	Flyingfishes	Shortwing flyingfish	Oceanic[1]	Omi
Vinciguerria lucetia	Phosichthydae	Lightfishes	Panama lightfish	Oceanic[2]	Vlu
Coryphaena equiselis	Coryphaenidae	Dolphinfishes	Pompano dolphinfish	Oceanic[3]	Ceq
Auxis spp.	Scombridae	Tunas and bonitos	Bullet tunas	Oceanic[4]	Aux
Prognichthys spp.	Exocoetidae	Flyingfishes		Coastal[5]	Pro
Cubiceps pauciradiatus	Nomeidae	Driftfishes	Longfin flathead	Coastal[6]	Cpa
Coryphaena hippurus	Coryphaenidae	Dolphinfishes	Dolphinfish	Coastal[3]	Chi
Cheilopogon xenopterus	Exocoetidae	Flyingfishes	Whitetip flyingfish	Oceanic[5]	Cxe
Hirundichthys marginatus	Exocoetidae	Flyingfishes	Banded flyingfish	Oceanic[5]	Hma
Opisthonema spp.	Clupeidae	Herrings and sardines	Thread herrings	Coastal[7]	Opi
Exocoetus spp.	Exocoetidae	Flyingfishes	Tropical flyingfishes	Oceanic[5]	Exo
Hirundichthys spp.	Exocoetidae	Flyingfishes		Oceanic[5]	Hir
Polydactylus approximans	Polynemidae	Threadfins	Blue bobo	Coastal[8]	Pap
Thunnus spp.	Scombridae	Tunas and bonitos	Tunas	Oceanic[4]	Thu
Cetengraulis mysticetus	Engraulidae	Anchovies	Pacific anchoveta	Upwelling[9]	Cmy
Lestidium spp.	Paralepidae	Barracudinas	Barracudinas	Oceanic[10]	Les
Cheilopogon spp.	Exocoetidae	Flyingfishes		Oceanic[5]	Che
Mugil spp.	Mugilidae	Mullets	Mullets	Coastal[11]	Mug
Anchoa spp.	Engraulidae	Anchovies	Anchovies	Upwelling[9]	Anc
Gerreidae	Gerridae	Mojarras	Mojarras	Coastal[12]	Ger
Naucrates ductor	Carangidae	Jacks and Pompanos	Pilotfish	Oceanic[10]	Ndu
Canthidermis maculatus	Balistidae	Triggerfishes	Oceanic triggerfish	Coastal[13]	Cma
Diaphus spp.	Myctophidae	Lanternfishes	Lanternfishes	Oceanic[10]	Dia

References for habitat associations: [1](Collette, 1999) ; [2](Cornejo and Koppelman, 2006; Leis and Miller, 1976; Teixeira Bonecker and Hubold, 1990); [3](Gibbs and Collette, 1959; Palko *et al.*, 1982); [4](Collette and Nauen, 1983; Leis and Miller, 1976); [5](Parin, 1995); [6](Haedrich, 1986); [7]; [8](Grove and Lavenberg, 1997; Whitehead, 1985a); [9](Chavez *et al.*, 2003; Whitehead, 1985b); [10](Leis and Miller, 1976); [11](Harrison, 1995; Leis and Miller, 1976); [12](Bussing, 1995); [13](Myers, 1999).

Table 2.2 Temporal and spatial distribution of numbers of stations within regions; for definitions of regions see Figure. 2.3.

		Year							
		1987	1998	1989	1990	1992	1998	1999	2000
Region	Eastern	24	21	16	20	67	46	31	31
	Middle	34	26	30	21	14	51	44	42
	Western	43	35	37	49	0	65	56	49

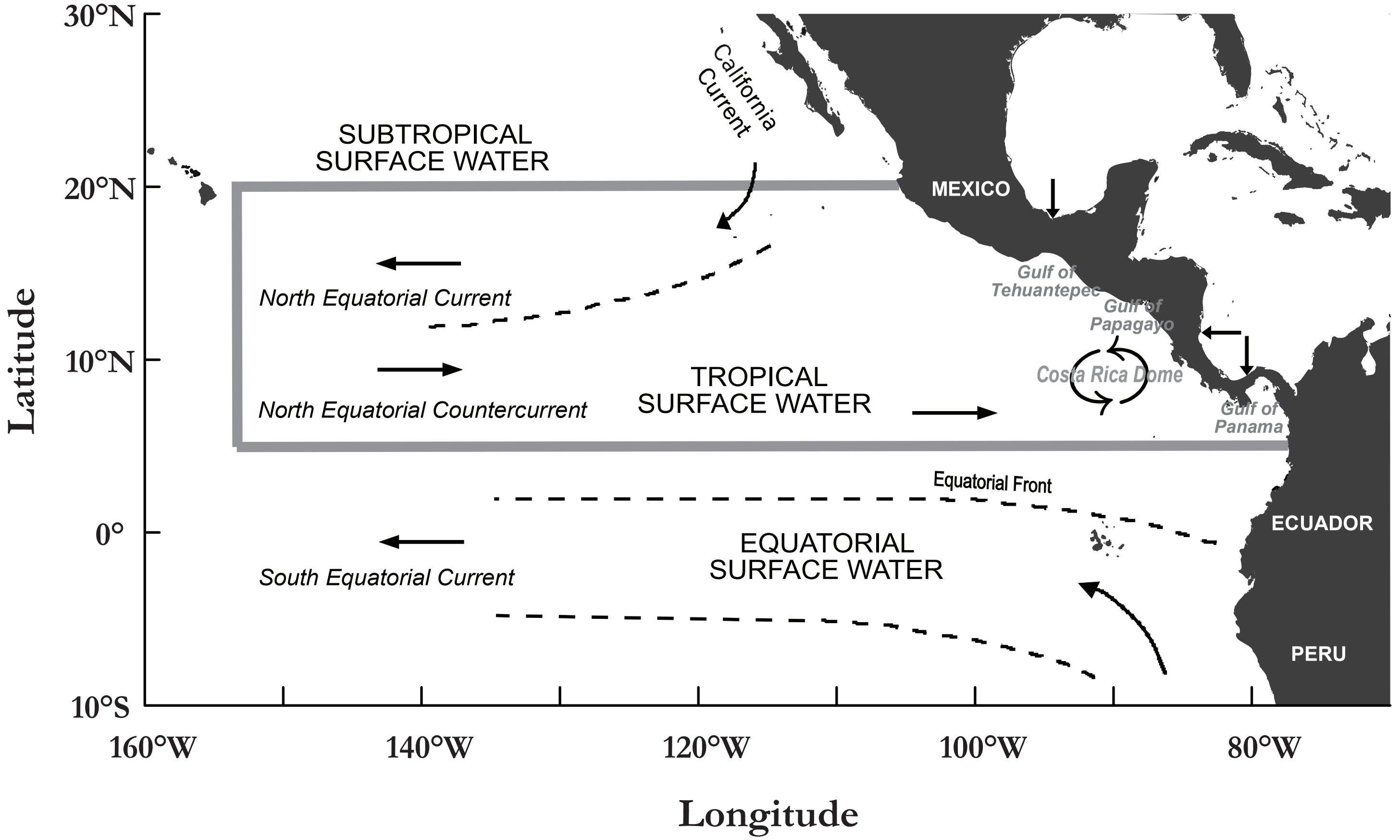

Figure 2.1 Schematic of the surface oceanography of the eastern tropical Pacific, adapted from (Fiedler, 1992). Red boundary delineates the eastern Pacific warm pool. Arrows on the Gulf of Mexico and Caribbean Sea indicate low-level mountain gaps in the Isthmus of Tehuantepec, Lake District of Nicaragua, and Lowlands of the Panama Canal.

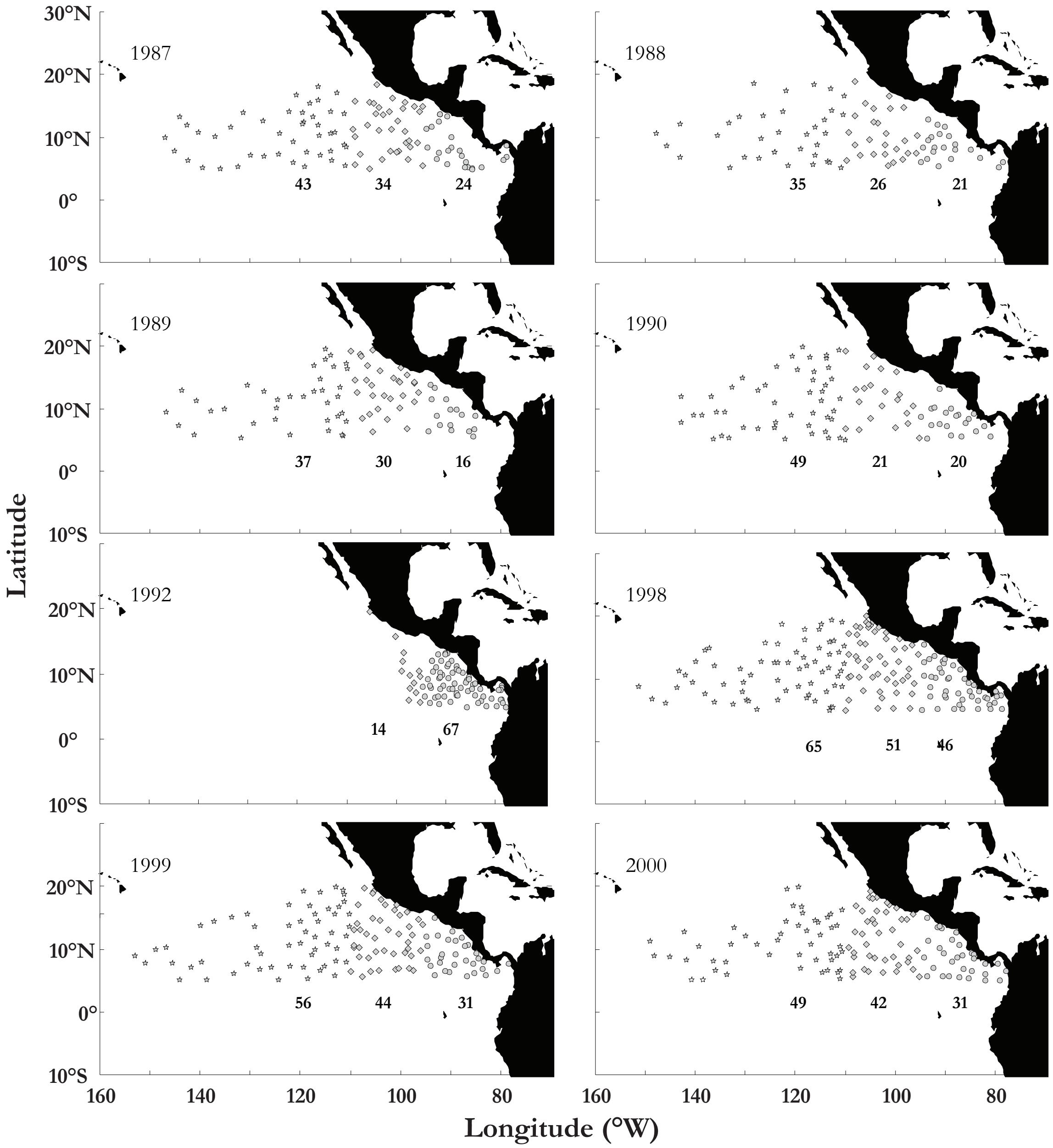

Figure 2.2 Geographical and temporal distribution of Manta tow stations. The survey year and total number of stations completed in that year are shown in each plot. Three regions defined within the study area: Western (☆), Middle (♢) and Eastern (○); based on surface oceanography, zonal productivity gradient and the longitudinal gradient depicted in Figure 5. Total number of stations within each region is shown under each region.

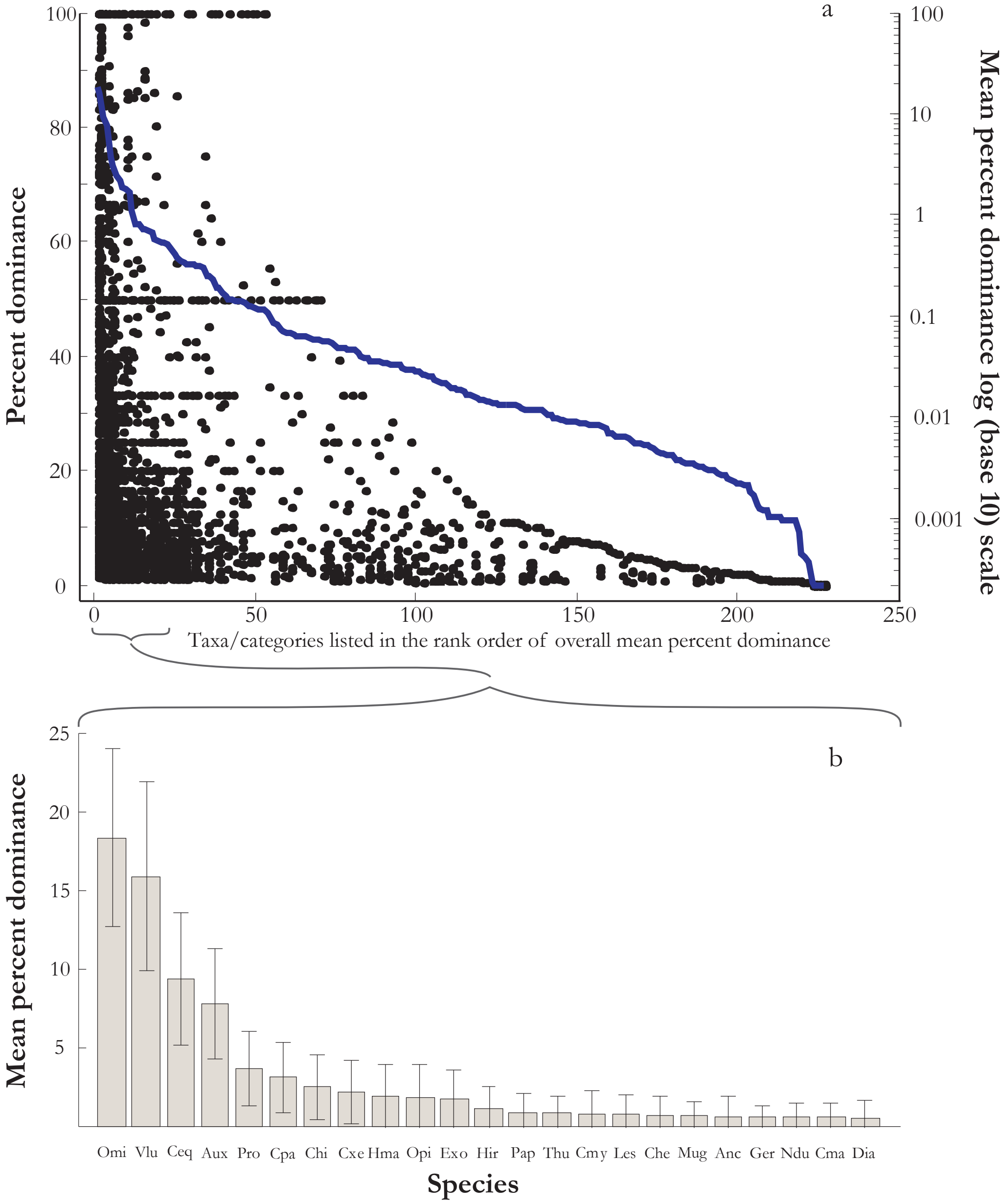

Figure 2.3 Rank order of dominance of ichthyoplankton taxa. **a**: percent dominance by taxon/category for all survey years sorted by the overall (all stations) mean percent dominance. Each dot represents the percent dominance of taxa at a specific station (n = 852 stations). Full names of all taxa/categories are listed in Table 2.1. On a logarithmic scale the blue line depicts the overall mean percent dominance. **b**: rank order dominance for the top (>0.05 overall % dominance) taxa; error bars represent the standard error of the mean.

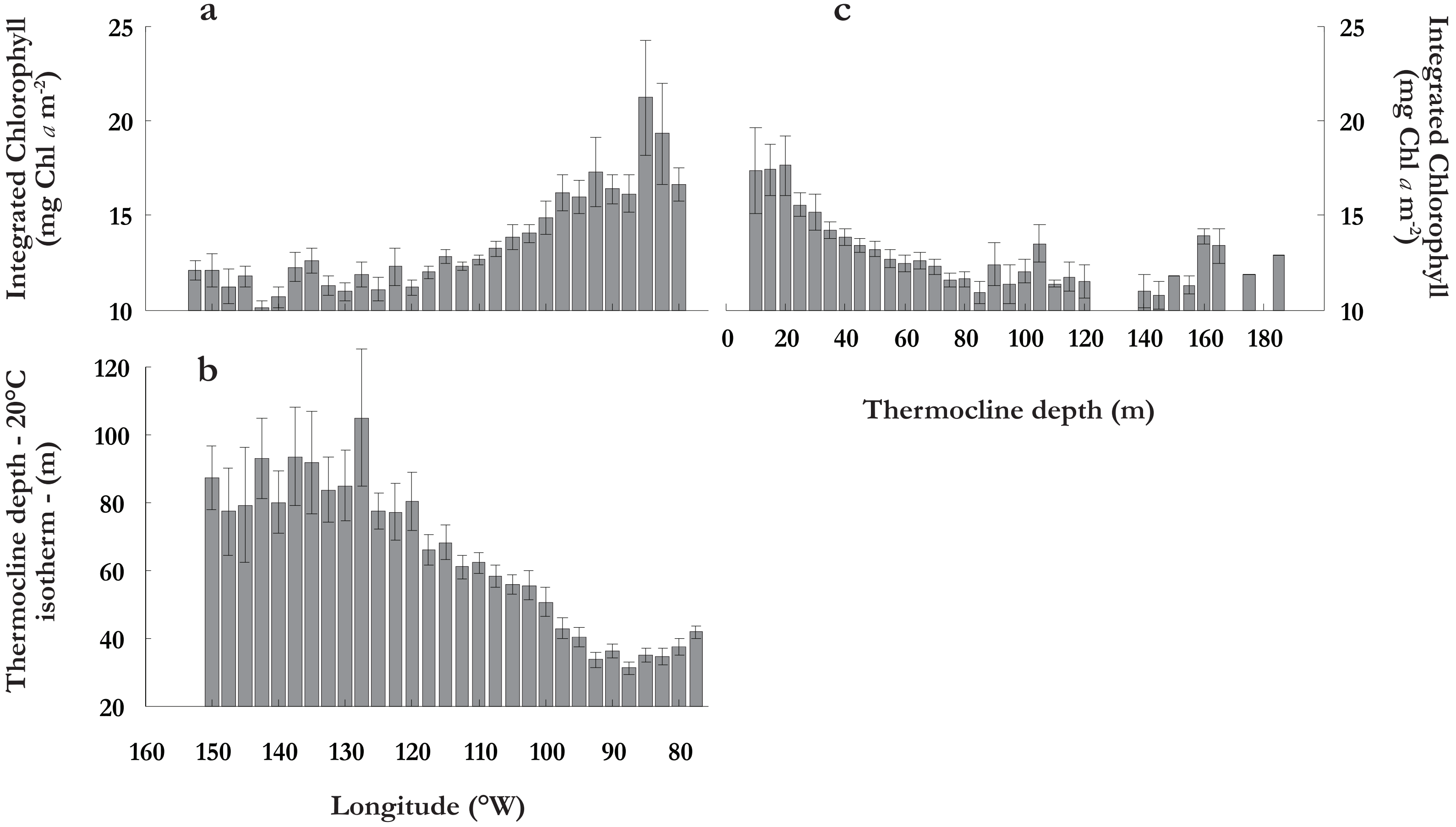

Figure 2.4 Integrated chlorophyll (**a**) and thermocline depth (**b**) as a function of longitude; histograms are of station means from all cruise years (± SE) binned at two and a half degrees of longitude. Integrated chlorophyll as a function of thermocline (**c**); histograms are of station means (± SE) from all cruise years binned at 5 m.

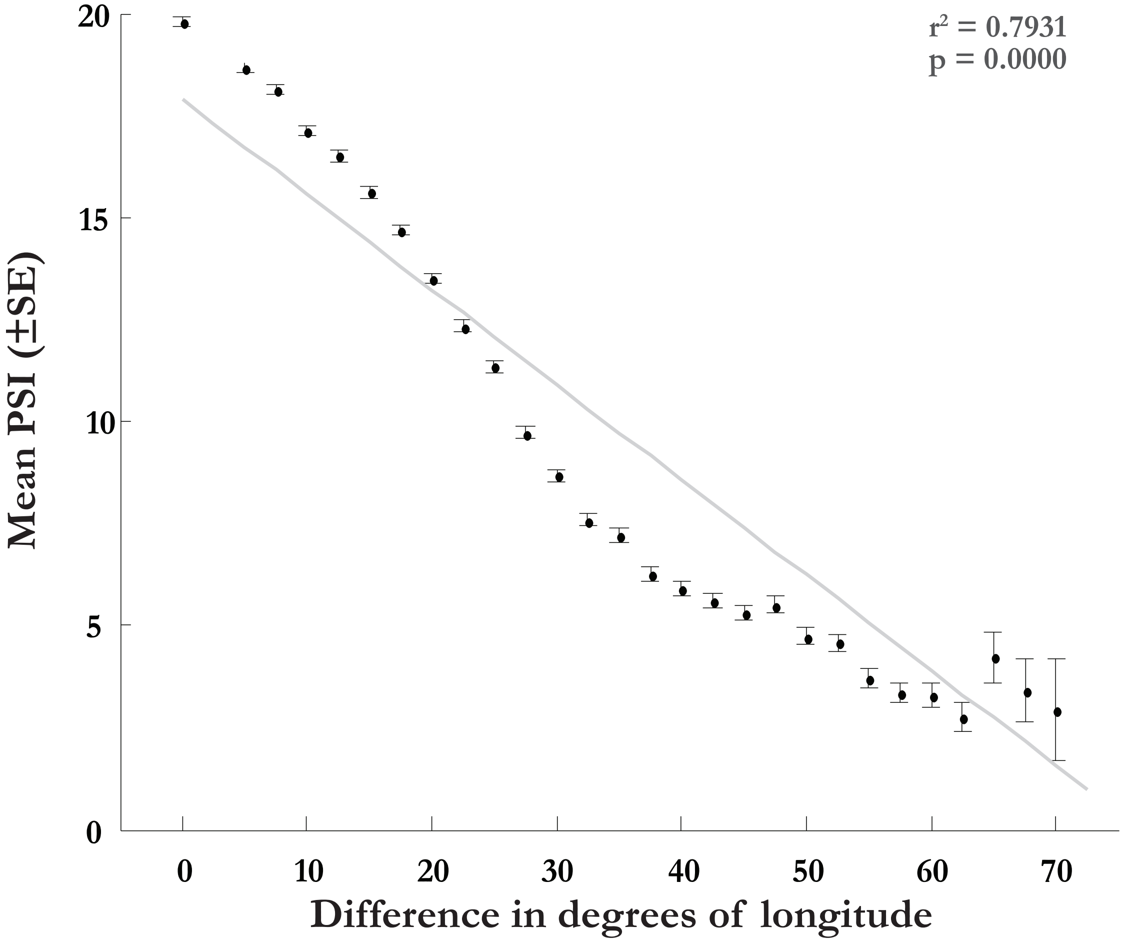

Figure 2.5 Mean percent Similarity Index as a function of longitudinal difference between stations. Pairwise comparisons, $n(n-1)/2$, among all stations totaled 344,865 comparisons along the 0 to 75 degree difference in longitude. For each of these comparisons we also calculated the PSI using the abundances of the 23 dominant species. Shown in the plot are means (± SE) of all stations binned at two and a half degrees. To test for trends in PSI over the longitudinal gradient, we fitted a least squares linear regression using the PSI estimates as the dependent variable and the longitudinal difference as the independent variable. The slope of the fitted line and the goodness of fit are shown in the top right corner.

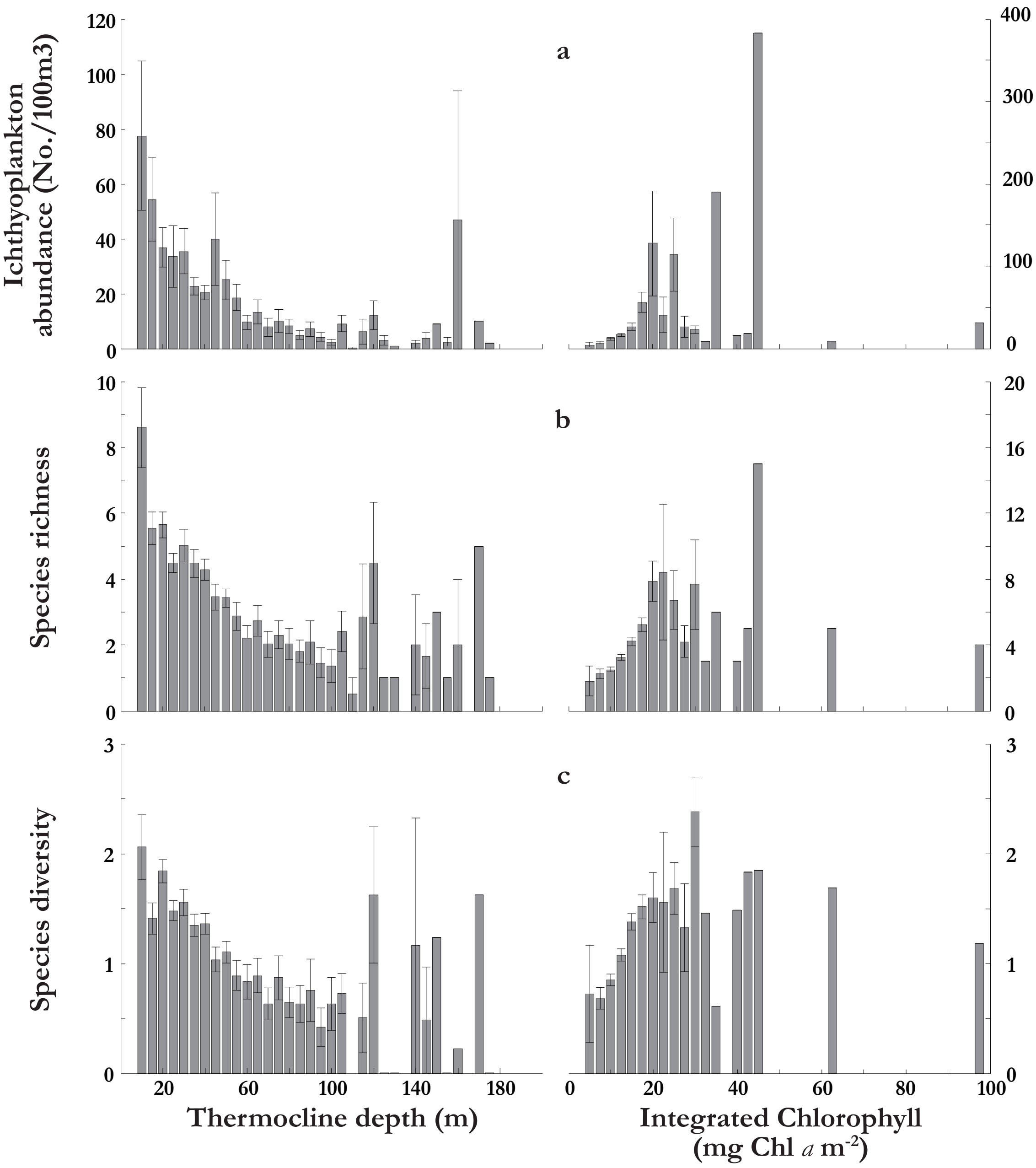

Figure 2.6 (**a**) Ichthyoplankton abundance: total number of larvae per sample, (**b**) species richness: number of different species in a sample, and (**c**) diversity: Shannon diversity index $H' = \sum_{i=1}^{S} (p_i)(\log_2 p_i)$ as a function of thermocline depth (left column) and integrated chlorophyll (right column). Histograms are of station means (± SE) from all cruise years binned at 5 m (thermocline depth) and 2.5 mg Chl *a* m^2 (integrated chlorophyll).

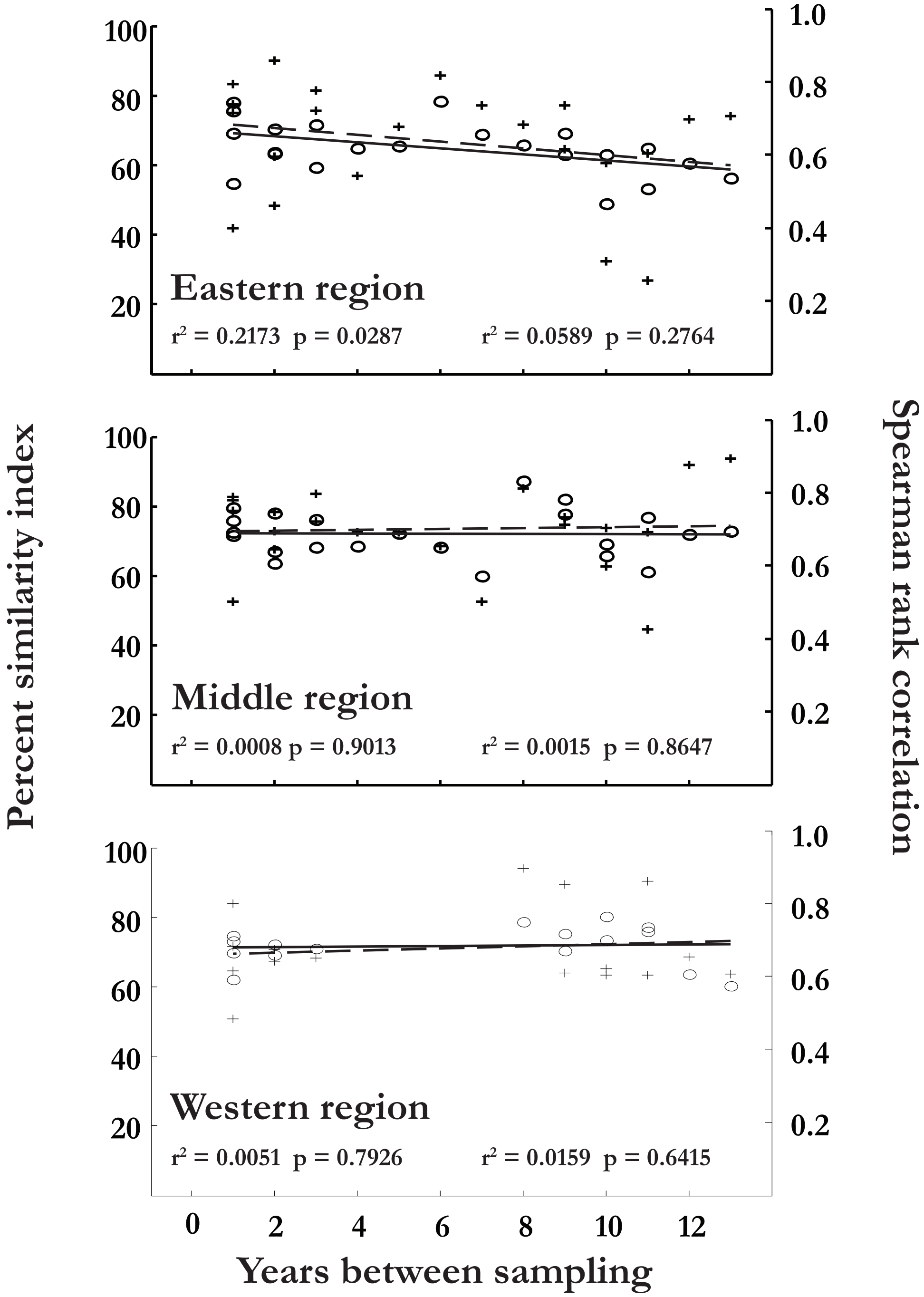

Figure 2.7 Percent Similarity Index (○ and solid line) and Spearman rank correlations (+ and dashed line) as a function of time between years.

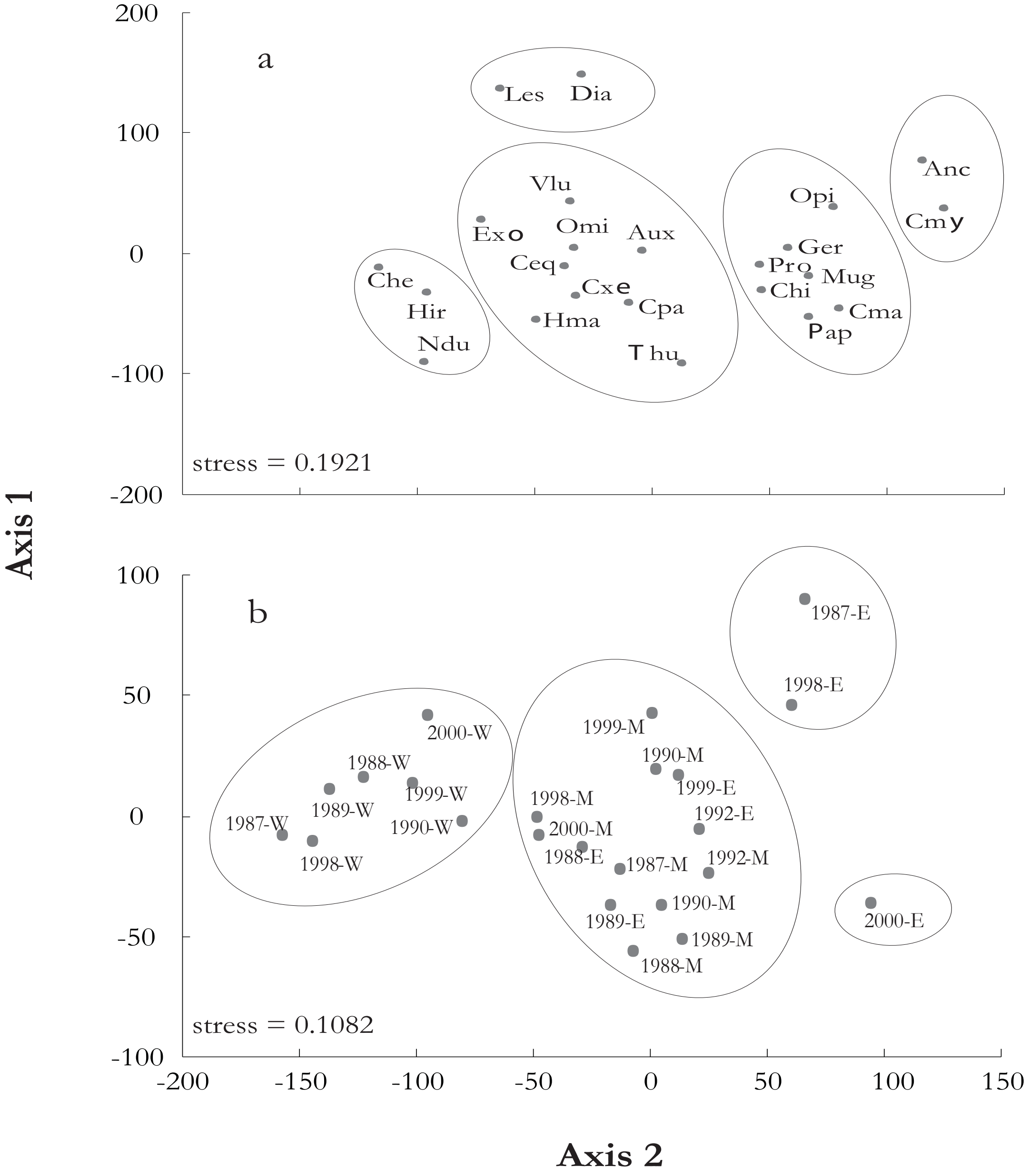

Figure 2.8 Results of clustering performed on the Bray Curtis similarity matrix created from ichthyoplankton taxa – station data; showing differences between (**a**) ichthyoplankton assemblages (abbreviations as in Table 1) and (**b**) pooled stations by region and year of collection. Superimposed clusters from a hierarchical cluster tree of taxa using the group-average algorithm at a similarity level of 25% are shown as circles. In the bottom left hand corner of each plot the stress level (goodness of fit) of the MDS is shown. Region-year combinations are denoted as the Year – and region – (E-Eastern), (M-Middle) and (W-Western).

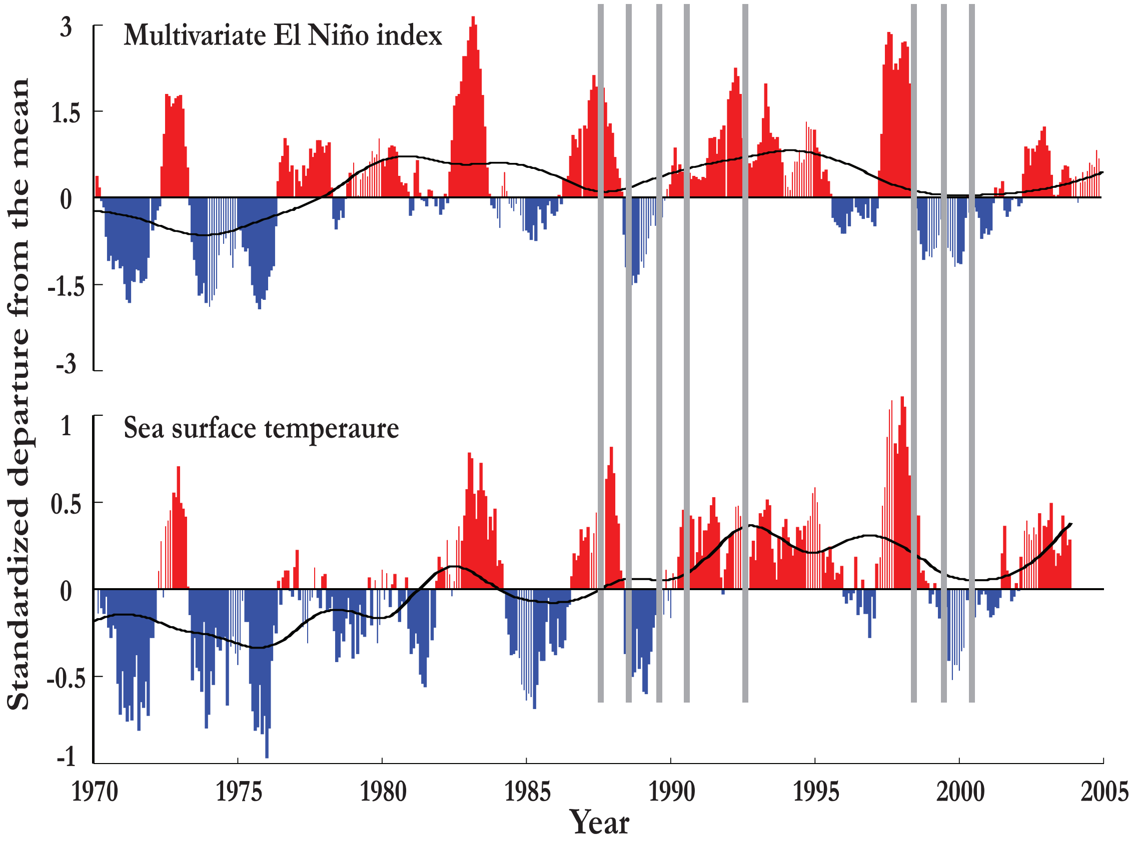

Figure 2.9 a: Time series of a multivariate El Niño Southern Oscillation (ENSO) index that combines sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky over the tropical Pacific. Positive values are shown in red, and negative in blue; indices > 1 and < -1 are considered strong El Niño and La Niña events, respectively. Monthly indices were acquired from the NOAA-CIRES Climate Diagnostic Center at the University of Colorado at Boulder (available online: http://www.cdc.noaa.gov). Black curve represents a smoothed regression (LOESS) running mean within a 20-yr span. b: Monthly time series of sea surface temperature (SST) anomalies (anomaly from 1971-2000 base period) from the eastern Pacific warm pool (5-20°N, 90-110°W). Values are monthly means from monthly 1° grids of sea surface temperature climatologies (HadISST SST, Version 1.1) and sea ice coverage (HadISST ICE, Version 1.1). Data were obtained from http://badc.nerc.ac.uk/data/hadisst/?source=dbrowser. Vertical bars represent sampling periods during survey years. Black line represents a smoothed regression (LOESS) running mean within a 20-yr span.

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CHAPTER 3

Bottom-up forcing of a tropical mid-trophic community: Ecosystem effects of the 1976/77 regime shift in the eastern Pacific warm pool

ABSTRACT

It is postulated that the upper ocean temperature structure of the Pacific basin changed after 1977. While ecosystem effects of this regime shift have been widely documented in temperate and polar ecosystems of the eastern Pacific, ecosystem effects in a tropical and pelagic setting are not as well understood. We do not know how the physical structure of the tropical eastern Pacific changed as a result of the 1976/77 regime shift or whether physical changes affected the ecosystem. Here we test hypotheses linking shifts in the physical structure of the water column to changes in the community structure of a mid-trophic community in the eastern Pacific warm pool for the 1960–2006 study period. Our approach to reach this goal was twofold. First, we used ocean temperature profiles from the World Ocean Database 2009 to characterize trends in thermocline depth and stratification in the upper 200 meters. Second, we used neuston tow samples taken during cruises to the eastern Pacific to determine whether observed trends have been large enough to affect a mid-trophic community. Thermocline depth of the eastern Pacific warm pool deepened 18.9 ± 5.7 m since 1960, with isotherms in the upper 100 meters deepening after the late seventies. We found community structure of neustonic ichthyoplankton to vary more through time in the eastern region of the study area, whereas communities from the western oceanic region displayed persistence in their species assemblages across the same time period. Furthermore, neustonic ichthyoplankton community structure during 1967 was extraordinarily different from all other years in the study. We suggest that ichthyoplankton in the upwelling areas of the eastern Pacific warm pool is more sensitive to stratification and thermocline trends as a result of bottom-up forcing of biological production in those regions.

INTRODUCTION

Accumulating evidence supports the conclusion that the Pacific basin underwent an abrupt and coherent change in physical processes that drive biological production in the late seventies. Collectively known as a regime shift, upper ocean temperatures restructured by warming in the eastern equatorial Pacific and cooling in the western equatorial Pacific (Stephens *et al.*, 2001), and the intensity and frequency of El Niño Southern Oscillation (ENSO) warm water events increased (Minobe, 1997; Zhang *et al.*, 1997). Regime shifts are thought to be attributed to abrupt phase changes in the Pacific Decadal Oscillation (PDO) from a cold phase to a warm phase (Mantua and Hare, 2002). These have occurred in 1925, 1947, and 1977, with another probably in 1998. It is thought that this climate-mediated ecological regime shift restructured entire ecosystems from primary producers to top predators as a result of changes in mixing processes in the upper ocean (Hayward, 1997).

Little doubt exists that ecosystems responded to the 1976/77 regime shift throughout the eastern Pacific. Changes in both phytoplankton and zooplankton were documented in the northeast Pacific. For example, Venrick *et al.* (1987) reported an increase in integrated chlorophyll *a* in the central North Pacific Ocean, which took place sometime in 1977. In the Gulf of Alaska, Anderson and Piatt (1999) found a decline in mid-trophics because of recruitment failure after 1977. And in the California Current, Roemmich and McGowan (1995) noted a 70% decrease in macro-zooplankton volume between 1951 and 1993 that began decreasing in the late seventies. Populations of upper apex predators, such as the Steller sea lion, *Eumetopias jubatus*, are also thought to have declined as a result of the changes associated with the 1976/77 regime shift (Trites *et al.*, 2006). In the southern hemisphere, ecological effects have been seen in the Humboldt Current off Peru (Alheit and Ñiquen, 2004). In the eastern tropical Pacific, however, the effects from this regime shift are less known. This is particularly interesting since it is now thought that the system may have shifted to conditions like those in the early 1970s (Bidigare *et al.*, 2009; Bond *et al.*, 2003).

We do not know exactly how the physical environment in the eastern tropical Pacific shifted in 1976/77. Lluch-Cota *et al*. (2003) reported that in the eastern Pacific coast, from the equator to about the Tropic of Cancer, sea-surface temperatures are mostly affected by the three to five year frequency of the El Niño Southern Oscillation, not showing any decadal trends related to the PDO. This is contrary to what Evans *et al.* (2001) concluded using proxy and instrumental evidence for robust PDO impacts within and around the Pacific Rim, both in the tropics and mid-latitudes of the northern and southern hemispheres. These authors support the idea that PDO variability reflects the entire Pacific, originating in the tropics. Long-term changes in physical shifts, as measured by thermal properties in the upper water column, are yet to be documented and should help shed light on this issue.

If the physical effects of the 1976/77 regime shift in the eastern Pacific have been significant, we have yet to determine if these changes were large enough to impact higher trophic communities. Variability in thermocline depth and water-column stratification, which we assume controls nutrient supply to low trophic levels, is known to modulate biological production and survival of upper trophic animals (Landry, 1977). Some of the very few biological data sets available to investigate low-frequency climate variability, which would include regime shifts (10–30 years) within tropical systems, come from neustonic ichthyoplankton collections. A unique collection exists from cruises assessing the oceanography and ecology of the eastern tropical Pacific, EASTROPAC Cruises (Wooster and Longhurst, 1964-69) and NOAA National Marine Fisheries Service (NMFS) ecosystem assessment cruises[1]. Analyzing long-term trends in species assemblages of a mid-trophic community of larval fishes can resolve patterns of ecological response to environmental variability (Hsieh *et al.*, 2009; Johnson and Barnett, 1975; Smith and Moser, 2003) and therefore give us insight into the environmental changes affecting the ecosystem.

Our goal for this study was to test hypotheses relating physical processes in the upper 200-meters water-column structure affecting the persistence of larval fish assemblages in the eastern Pacific warm pool within last 50 years. We approached our research goal by first gauging the magnitude of stratification in the eastern Pacific warm pool using temperature profile data from the World Ocean Database 2009 (Boyer *et al.*, 2009). We then tested whether a multi-decadal increase in the upper ocean stratification, if it occurred, would have been large enough to have a significant impact on the neustonic ichthyoplankton of the eastern Pacific warm pool.

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[1] Since the mid 1980s, an increased awareness of the incidental mortality of dolphins caused by the yellowfin tuna purse seine fishery in the eastern Pacific warm pool triggered NOAA NMFS to conduct ecosystem surveys to the ETP. These ecosystem surveys, known collectively as Monitoring of Porpoise Stocks (MOPS) and *Stenella* Abundance Research (STAR) project cruises (http://swfsc.nmfs.noaa.gov/prd/PROJECTS/star/), form part of a multi-year cetacean and ecosystem assessment study designed to assess the status of dolphin stocks that have been taken as incidental catch by the yellowfin tuna purse seine fishery in the ETP. The research program consists of a series of research vessel cruises that are repeated periodically. These include a five-year series from 1986 to 1990, a two-year series from 1992 to 1993, a three-year series from 1998 to 2000, and two cruises completed in 2003 and 2006. This research takes an ecosystem approach to surveying, which includes sampling the biological and physical habitat and collecting data on cetacean distribution, school size, and school composition, as well as data on prey fishes and squids, seabirds, and marine turtles.

METHODS

Study area

Our study area is the eastern Pacific warm pool, a large and productive body of water encompassing around 11.5 million km^2 in the eastern tropical Pacific. The eastern Pacific warm pool as we define it is a zonal slab of ocean extending west from Central America and Mexico to 150º W, between 5º and 20º N. Surface oceanography of the region is dominated by (*i*) two major surface currents: the westward-flowing North Equatorial Current (NEC) and the eastward-flowing North Equatorial Countercurrent (NECC); (*ii*) two major surface water masses: tropical surface water and subtropical surface water; and (*iii*) three different processes mediating nutrient supply into the euphotic zone: an eastward shoaling thermocline, a thermocline divergence between the NEC and the NECC, and localized wind-driven upwelling (Pennington *et al.*, 2006).

Most of the eastern Pacific warm pool is composed of tropical surface water (>27.5ºC) carried eastward by the NECC, while a smaller area is composed of subtropical surface water flowing southwest with the NEC. The NEC is the southern extension of the north Pacific subtropical gyre bounding the NECC to the north. The NECC carries tropical surface waters eastward and is bounded in the south by the relatively colder waters of the equatorial cold tongue. Heavy rainfall caused by the Intertropical Convergence Zone (ITCZ) lowers the salinity of surface waters of the NECC creating a strong and shallow pycnocline in much of the surface waters carried by this current.

Thermocline topography in the eastern Pacific warm pool mediates macronutrient supply into the euphotic zone in three ways. First, as a result of the trade winds piling up water in the western Pacific, mean thermocline depth decreases to the east across the entire tropical Pacific. In general the eastern Pacific warm pool thermocline shoals from depths of about 180 m in the west to 50 m in the east. Second, on a meridional perspective, thermocline topography consists of two troughs (along 5ºN and 14ºC) and a ridge along 9–10ºN, representing the boundary of geostrophic flow between the westward NEC and the eastward NECC (Kessler, 2006). And third, east of 90ºW, winds funneled through gaps in the mountain range extending the length of southern Mexico and Central America create positive and negative wind stress curl as far as 600 km offshore (Chelton *et al.*, 2000). In these areas, wind-forced upwelling and the quasi-permanent cyclonic Costa Rica Dome create areas of cool (<25 °C) nutrient-rich water within the less productive and warmer tropical surface water mass (Ballesteros and Coen, 2004; Kessler, 2002).

Historical temperature profiles

To test hypotheses regarding long-term changes in thermocline depth and water-column stratification over the time span of our study in the eastern Pacific warm pool, we obtained temperature profiles from the National Oceanographic Data Center's World Ocean Database 2009 (Boyer *et al.*, 2009) that were taken during 1960–2006 within our study area (Figure 3.1). We used profile data from five main instrument types: hydrographic bottles (Nansen and Rosette sample bottles), mechanical bathythermographs (MBT), expendable bathythermographs (XBT), conductivity-temperature-depth (CTD) recorders, and drifting profiling floats (mostly Argos). In order to use the most reliable profile temperature data, we excluded from further analyses profiles with the following criteria: (*i*) XBT profiles without sufficient fall-rate information, (*ii*) profiles beginning below 10 meters, (*iii*) profiles ending above 200 meters, and (*iv*) profiles with inversions in temperature gradients larger than 0.5º C per meter. This reduced the total number of profiles included to 51,583 (Table 3.1). XBT casts, which comprised 66% of all profiles, measure temperature with free-falling expendable probes and estimate depth by measuring the elapsed time since the probe entered the water using a fall-rate equation. Hanawa *et al*. (1995) have shown that in some cases small manufacturing changes in probes have altered fall rates. Thus, if using the original fall-rate equation provided by XBT manufacturers, systemic biases in depth and temperature measurements will occur. These casts have been flagged by the World Ocean Database (Johnson *et al.*, 2009), and we adjusted for documented time-dependent temperature biases as described by Levitus *et al.* (2009).

Because temperature profiles were not distributed evenly in space and time, we gridded profiles into 1º latitude by 2º longitude and seasonal bins (Figure 3.2). We chose this bin size for three reasons. First, seasonal time scales have been shown to be associated with vertical temperature gradients within our study area (Barnett and Patzert, 1980). Second, 1º of latitude has been found sufficient to resolve major meridional patterns of thermocline topography (Kessler and Taft, 1987). And third, using longitudinal bins of 2º allowed each 1º latitude by 2º longitude and seasonal bin to have at least 10–20 profiles for the length of the 1960–2006 study period.

Temporal distribution of sampling during our study period was not constant (Figure 3.3). An average of 845 profiles per year were obtained for the entire study period, with the lowest number during the 1960s and the highest during the 1970s, 1980s, and 1990s, increasing again in recent years mostly due to Argo float profiles (Boyer *et al.*, 2009). More than half of the profiles were generated from XBT casts (Table 3.1). Profiling floats, MBTs, and OSD data each had around 10% of the data, and CTD data had the fewest profiles, with 4%. Temporal and spatial locations of temperature profiles were not evenly spread throughout the study area (Figure 3.2). The highest sampling of the study area occurred during winter months (13,926 profiles) and the lowest during summer months (11,617 profiles). The most heavily sampled regions were along shipping lanes from the U.S. to the Panama Canal and to the South Pacific. Sampling frequency per spatial-temporal bins was 121, 21 per season. All but two of the spatial-temporal bins had more than 10–20 profiles per bin.

In the tropics a thermocline usually separates the upper warm layer of ocean from deeper waters, acting as a physical barrier to ocean mixing between the surface mixed layer and deeper water. Characterized as layers of water with a rapid change of temperature with depth, thermoclines in the tropical Pacific have been shown to lie near the 20ºC isotherm (Kessler, 2002). This isotherm can be considered to generally indicate thermocline depth, but recent work (Yang and Wang, 2009) suggests using the vertical gradient definition of thermocline and not the 20ºC isotherm when studying long-term changes in thermocline topography under the circumstances of a significant climate shift. In a changing climate the isotherm representing the thermocline could also change over time. We therefore characterized the depth of the thermocline of each profile by determining the midpoint of the depth interval with the maximum vertical temperature gradient ($\Delta T/\Delta z$, T=Temperature and z = depth), with $\Delta T > 2$ºC or $\Delta z > 10$ m.

Thermocline depths were then characterized as seasonal anomalies (observed minus long-term seasonal averages) through time to detect whether long-term trends in thermocline depth occurred during the 1960–2007 study period. We also measured stratification of the upper 200 meters using three proxies: temperature differences between the surface and 200 meters ($T_{z0\text{–}z200}$), surface and 100 meters ($T_{z0\text{–}z100}$), and 100 meters and 200 meters ($T_{z100\text{–}z200}$). These three indices were also characterized as seasonal anomalies to detect deviations from the long-term means. Salinity stratification in the eastern Pacific warm pool should be an important factor because of the heavy precipitation caused by the ITCZ. Additionally, Roemmich and McGowan (1995) argue that warming and deepening of the thermocline will lead to an increase in stratification of the water column.

Neuston samples

Neustonic ichthyoplankton samples were collected during two sets of cruises: NOAA NMFS ecosystem assessment cruises and EASTROPAC cruises. The NOAA NMFS cruises were completed during the northern hemisphere fall seasons of 1987–1990, 1992, 1998–2000, 2003, and 2006 aboard research vessels *David Starr Jordan*, *Endeavor*, *McArthur I,* and *McArthur II* (Table 3.2). Throughout these cruises, neuston was sampled using Manta tows (Brown and Cheng, 1981) with a 0.333-mm nylon mesh and cod end during daily night stations at approximately 2000–2300 local mean time (2 hrs post-sunset). Manta nets were towed in the dark from a starboard boom at approximately 0.77 m sec^{-1} for 15 min, and all samples were preserved in 5% formalin buffered with sodium borate. EASTROPAC cruises, part of a multinational effort directed toward understanding the oceanography of the eastern tropical Pacific, were completed during 1967–68. In these cruises, neuston samples were collected using a 1-m diameter mouth net with a 0.333-mm mesh and cod end towed half-submerged from the starboard boom for approximately 15 to 20 minutes at about 0.80 m sec^{-1}. Tows were completed during both day and night-time stations and all samples were preserved in buffered 5% formalin.

For net samples from all cruises, ichthyoplankton were removed, identified, and quantified. Except for damaged specimens, most fish larvae collected were identified to species, but in some cases, only genus or family was possible. NOAA NMFS cruise samples were sorted within two years of completion of the cruise. EASTROPAC cruise samples, which had been re-curated during 1990, were sorted in 2008. For purposes of comparison with NOAA NMFS cruises, we only used EASTROPAC samples collected between 2000–2300 during northern hemisphere fall cruises within the eastern Pacific warm pool.

Data analysis

Ichthyoplankton from the 1,131 neuston stations was distributed among 268 taxa. Because EASTROPAC cruises used a different neuston net, which was towed without a flow meter (Lanna Cheng, personal communication), we transformed all larval catch data to proportions of total larvae caught per tow for each sample and multiplied by 100 to use percentages. This standardized each station to a percent dominance for each taxon. As in most biological surveys covering large temporal and spatial scales, rare species comprised most of the 268 taxa; 222 taxa occurred in less than 10 stations and 95 in less than one. Including the 268 taxa in analyses to quantify changes in community structure will reduce the chance of generating an interpretable ecological picture (Stephenson and Cook, 1980). This is because of the randomness in occurrence of the rarer taxa across the stations. We therefore included only species that had an overall mean dominance higher than 0.5%, a procedure that allows both high diversity and dominance to be included in the data (Field *et al.*, 1982).

We measured changes in community structure of larval fishes (e.g., species composition) using two measures of similarity: (*i*) the Bray-Curtis similarity coefficient and (*ii*) percent similarity index. The Bray-Curtis similarity coefficient was introduced by Bray Curtis (1957) and is expressed as

$$B_{jk} = 1 - \frac{\sum_{i=1}^{n} \left| X_{ij} - X_{ik} \right|}{\sum_{i=1}^{n} \left(X_{ij} + X_{ik} \right)}$$

where B_{jk} is the similarity between the samples (*j* and *k*), X_{ij} and X_{ik} are the percent dominance of taxon *i* in sample *j* and *k*, and *n* is the total number of species in the combined species list of both samples. The quotient of the two summations is subtracted from 1 to give a measure of similarity between samples, giving a value of 0 for samples with no species in common and 1 when two samples are identical in percent dominance of species. Because the percent dominance of larval taxa was used instead of abundance, the change in tow types between EASTROPAC and NOAA NMFS cruises will not change the result of B_{jk}. Percent similarity index, which was first proposed by Whittaker (Whittaker, 1952), is calculated as

$$PSI = \sum_{i=j}^{n} \text{minimum}\left(p_{Ai}, p_{Bi} \right)$$

where *P* is the percent similarity between two communities (*A* and *B*), *n* is the total number of species in the combined list of taxa categories, and p_{Ai} and p_{Bi} are the percentages of taxa categories *i* of the compared communities. Percent similarity index is a simple measure indicating to what degree two communities are alike in their assemblages of species, ranging from zero for samples with no species in common to 100% in samples with identical dominance of species. In spite of its simplicity, the PSI is one of the best quantitative association coefficients available, since it is relatively unaffected by sample size and species diversity (Wolda, 1981).

When the number of stations across space and time is large, presenting data for every station and time period can be cumbersome. Thus, to control for spatial variability and present our data in a more interpretable fashion, we divided our study area into three regions based on longitude—Eastern (75 to 95°W), Middle (95 to 110°W), and Western (110 to 150°W)—and pooled stations according to their location and corresponding cruise year (Table 3.2). We pooled stations across cruise years and regions in the study area according to the following criteria: (*i*) Change in both Bray-Curtis similarity coefficients and percent similarity indices as a function of distance between stations, was larger based on longitude versus latitude. The maximum change between any two stations in Bray-Curtis similarity coefficients and percent similarity indices was 92.8 versus 93.5%, respectively, for differences in location as a function of longitude. The respective maximum changes for these same measures were 53.6 and 54.5% as a function of latitude. (*ii*) The eastern tropical Pacific biogeographic region is isolated by the Eastern Pacific Barrier near Clipperton Atoll (Robertson *et al.*, 2004). (*iii*) A well-known region-wide difference in productivity is mediated by thermocline depth and mountain-gap funneled winds from Central America and Mexico (Amador *et al.*, 2006; Pennington *et al.*, 2006). (*iv*) Our analysis goal was to test hypotheses regarding changes in community structure across time and not space. In all further analyses and results, we therefore use pooled year-region dominance patterns to analyze temporal trends of community structure of larval fishes within each region independently.

We applied cluster analyses to look for changes in community structure of larval fishes over the 39-year span of our study. A cluster analysis uses a triangular matrix of Bray-Curtis similarities between every pair of dominant taxa or pooled region-year stations (Figure 3.4). Using similarities between species addresses what groups of species tend to co-occur in a parallel manner across all stations and defines species assemblages. Using similarities between stations will show what stations have similar species compositions over space and time, defining geographic regions with similar community structure. We used both techniques to classify dominant species into assemblages and pooled year-region stations into groups by constructing two classification trees representing hierarchies of categories using the unweighted pair-group method with arithmetic averages (UPGMA).

In both cases, after the identification of species assemblages and station groups, we used an analysis of similarities (ANOSIM) (Clarke, 1993) to test the null hypotheses of no difference between observed groups. ANOSIM is an analogue of a one-factor analysis of variance test based on multivariate data, generating a test statistic (*R*) that is calculated as

$$R = \frac{\overline{r}_B - \overline{r}_W}{n(n-1)/4}$$

Where ($\overline{r}_B$) is the average of all rank Bray-Curtis similarities from replicates between different groups identified by the cluster analysis, ($\overline{r}_W$) is the average of all rank similarities among replicates within identified groups, and *n* is the total amount of samples (number of species or number of pooled stations). *R* statistics usually fall within 0 and 1, with the magnitude of *R* proportional to the separation of groups. A score of 1 indicates complete separation of identified groups, and a score of 0 indicates no separation. A permutation test then estimates the probability of the observed *R* statistic being randomly generated.

For further insights linking community structure to the environment, we applied multidimensional scaling ordination (MDS) to the pooled year-region stations data. Briefly, MDS reduces dimensionality of the data by placing the 32 pooled stations into an arbitrary two-dimensional space, such that relative similarities among pooled stations match in rank order, placing stations with similar community structure closer together. A stress level is generated for the ordination, ranging from 0 to 1, which gives a measure of how well the ordination fit the data. The closer a stress level is to 0, the better the MDS ordination represents the data.

Finally, we also analyzed temporal trends in species compositions within each region of the study area (Eastern, Middle, and Western) by relating the PSI of all pair-wise comparisons of pooled year-region stations as a function of time interval between cruises. This resulted in measures of similarity between stations from cruises completed between 1 and 39 years apart. We wanted to test whether PSI decreased significantly with increasing time between cruises and therefore used least squares to fit a trend line to the data. Least squares analysis, however, assumes that all time differences between cruises and corresponding PSI values were independent from each other. This was clearly not the case, since PSI between cruises greater than 20 years apart are all compared to the 1967 cruise. We therefore estimated the probability of generating the observed regression coefficient by comparing the observed value with the distribution of values obtained by randomizing cruise years and fitting a trend line 10,000 times. In this test, the null hypothesis is that PSI between stations taken at different years is not related to the difference between sampling years. Since all possible combinations of PSI versus time differences are equally likely to occur, this is an appropriate way to test the hypothesis (Manly, 2007).

RESULTS

Temporal trends in thermocline depth

Since profiles were not evenly distributed through all seasons of the year, a simple long-term average does not adequately estimate the true mean of thermocline depth in the eastern Pacific warm pool. We therefore averaged the thermocline from the four seasonal means so that that each season had equal weight in determining the long-term mean (Figure. 3.5). Thermocline depth in any meridional section of our study area was shallowest near 8–10º N, where the well-known 10º N countercurrent thermocline ridge marks the boundary between the geostrophic flow of the NEC and NECC (Fiedler and Talley, 2006). The position of this divergence, the countercurrent thermocline ridge, is similar to what is reported by Wyrtki (1966) and Kessler (2006). To the north and south of the countercurrent thermocline ridge are areas with deeper thermoclines. This trough-ridge-trough thermocline system extends zonally along the study area, except between 110 and 100º W, where the trough-ridge-trough thermocline topography is not as pronounced. The shallowest mean thermoclines (30 m) are at the eastern terminus of the shoaling ridge, near 90ºW, marking the position of the Costa Rica Dome (Fiedler, 2002; Kessler, 2002).

Seasonal and interannual variability in thermocline depth are shown in Figure 3.6. As mentioned above, we removed seasonal bias in estimating mean thermocline depth by using the average of the four long-term seasonal means. Seasonal variability is represented by the standard deviation of the four seasonal means, whereas interannual variability is represented by the standard deviation of the 47-year mean. Spatial patterns of seasonal variability were different than interannual variability. Seasonal variability in thermocline depth was largest along the countercurrent thermocline ridge (8–10º N), while the smallest variability was along thermocline troughs to the north and south of the ridge. In contrast, the largest interannual variability was along these same thermocline troughs to the north and south of the mean position of the countercurrent thermocline ridge. The largest seasonal variability was along the countercurrent thermocline ridge (along 8–10º N), and the smallest variability was along thermocline troughs to the north and south of the ridge. In contrast, the largest interannual variability was along these same thermocline troughs to the north and south of the mean position of the countercurrent thermocline ridge. Overall, seasonal variability accounted for 37.5% of the total variance, while interannual accounted for 62.5%.

For the entire eastern Pacific warm pool, seasonal anomalies of mean thermocline depth showed a deepening trend of 4.1 (±1.24) meters decade^{-1} (Figure 3.7) over the 1960–2006 period. Seasonal anomalies during the early 1960s were highly variable, being both deeper and shallower than the long-term mean. By 1965 mean thermocline depth was on average shallower than the long-term mean. After the late 1970s, however, mean thermocline depth seemed to be deeper than the long-term average. Figure 3.8 shows the spatial 46-year trend of change in thermocline depths across the study area. Thermocline depths seemed to be deepening more in the western region of the study area, particularly along the countercurrent thermocline ridge between 140º and 120ºW.

Thermal stratification of the stratification

Bulk stratification ($T_{z0\text{-}z200}$) in the eastern Pacific warm pool did not vary significantly from the long-term average, while the stratification proxies $T_{z0\text{-}z100}$ and $T_{z100\text{-}z200}$ had opposite long-term trends (Figure 3.9). The difference in temperature between the surface and 100 meters depth decreased at a rate of -0.36º C decade^{-1} (±0.16). Conversely, the temperature difference between 100 and 200 meters depth increased over time at a rate of 0.37º C decade^{-1} (±0.12º C). Both of the changes in stratification began after the 1970s. Figure 3.10 shows seasonal means and anomalies for the upper 200 meters integrated over latitude and longitude for the 1960–2006 period. After a large warm temperature anomaly in 1964–65, the upper 200 meters of the eastern Pacific warm pool were colder than the long-term average up to the late 1970s, after which warm water anomalies pulsating at a three-to-five-year frequency dominated the thermal structure. During this period, the 1982, 1987, 1991–1994, and 1997 El Niños are evident.

Overall dominance and temporal trends in fish larvae

We compiled a total of 1,131 neuston tow samples (Figure 3.11) taken over 39 years in the eastern tropical Pacific. From these, a total of 268 different taxa were identified: 140 to species, 76 to genus, and 52 to family. The 25 most dominant ichthyoplankton taxa are listed in Table 3.3, along with the bathymetric range of adult forms and the neustonic affiliation of larval forms (Hempel and Weikert, 1972; Miller and Kendall, 2009; Nelson, 2006; Parin, 1970). The five most dominant and common taxa categories were, in decreasing order, *Oxyporhamphus micropterus*, *Vinciguerria lucetia, Cory-*

phaena equiselis, and *Auxis* spp. and *Prognichthys* spp. At least one of these five taxa was found in 77% of all samples (876 stations). *O. micropterus* was the most ubiquitous and dominant species, with the highest overall dominance, and present at almost half of all stations. This species' degree of dominance varied between years, with lowest dominance in 1967 and highest during 1987–98, when it consistently stayed above 20%. After 1998, *O. micropterus* never surpassed 20% dominance again. The second most dominant species, *V. lucetia,* was found in one-third of all samples and also had a variable dominance pattern across years. *V. lucetia* dominance was consistently above 10% during most years, except for 1987, 1992, and 2006. *C. equiselis*, the third most dominant species, had overall dominance of 9.98% and was found in about one-third of all samples. This species had its highest dominance during 2006, 1992, and the 1980s, with lower dominance during 2000, 1990, and in 1967. The fourth most dominant taxa, *Auxis* spp., had its lowest dominance during the first three cruise years, with consistently higher dominances during cruise years in the 1990s and 2000s. *Prognichthys* spp. showed a similar pattern with its lowest dominances in 1967 and 1988 and highest dominance during 1992 and 2006 cruises.

Overall patterns of dominance for all 25 taxa varied from year to year (Figure 3.12). More taxa were absent during the first three cruises versus cruises during 1998, 1999, and 2000, when all 25 taxa were present. Most of the neritic-pelagic and reef-associated taxa were absent during 1988, including *Polydactylus approximans* and *Canthidermis maculates*, and, notably, all representatives of the Clupeiformes order. After 1988, *Cetengraulis mysticetus* was absent until 1992 and 1998–99 and then disappeared in 2003 and 2006. *Diplophos proximus,* after being present every year from 1967 to 2003, was absent in 2006. *Hirundichthys* spp. and *Mugil* spp. were both more common and dominant in later cruises than in stations from 1967 and 1980s. In contrast, *C. pauciradiatus* had its highest dominance in 1967, and subsequently declined until 2003.

Cluster analyses results of fish larvae

Cluster analyses of species identified four assemblages that had similar patterns with respect to co-occurring in similar habitat (oceanic, neritic-pelagic, mesopelagic, and upwelling) and similar dominance patterns: an oceanic assemblage (Figure 3.13). An ANOSIM test based on Bray-Curtis similarities (R=0.85 and P=0.0001, with 10,000 permutations) indicated that these groupings are significantly separable and not an artifact of chance. The oceanic assemblage was composed of all 10 taxa of oceanic fishes with epipelagic life histories and one mesopelagic species. This assemblage included the highly dominant *O. micropterus* and *V. Lucetia,* as well as *Auxis* spp., *C. equiselis,* and *hippurus*, and *Prognichthys* spp., *C. pauciradiatus,* and three genera of flying fishes: *Hirundichthys* spp., *Cheilopogon* spp.*,* and *Exocoetus* spp. The neritic-pelagic assemblage incorporated 8 taxa with both neritic and pelagic lifestyles as well as reef association. This group species included species in the *Engraulidae*, *Mugil*, *Bothus,* and *Opisthonema* genera; two carangids: *Caranx caballus* and *Naucrates* ductor; a threadfin: *Polydactylus approximans*; and a triggerfish: *Canthidermis maculatus*. With the exception of *Thunnus* spp., mesopelagic taxa composed the mesopelagic assemblage. These were: *Lestidium* spp, *Cyclothone* spp., and *Diplophus proximus*. Finally, two cupleids, species in the *Anchoa* genus and *C. mysticetus*, comprised the upwelling assemblage.

Cluster analysis of stations identified three groups of pooled year-region stations that had similar species compositions (Figure 3.13). These three groups were also found to be distinct by an ANOSIM test (*R*=0.93, *P*=0.0001 with 10,000 permutations). The first group consisted of all three pooled year-region stations from 1967, suggesting that during EASTROPAC community structure of the entire study area was more homogenous than in later years. This could be a result of *V. lucetia* having high dominances across the entire study area and the driftfish *C. pauciradiatus* also having its highest dominance during 1967. *O. micropterus*, *Auxis* spp., and *C. equiselis* all had lower dominances during 1967. *Hirundichthys* spp., *C. maculates, C. mysticetus,* and *Anchoa* spp. were all absent from EASTROPAC stations. The second group consisted of 20 pooled year-region stations and was the most variable in terms of the temporal and spatial origin of the pooled stations. This group included pooled year-region stations from the eastern and middle regions, excluding the 1967 cruise, with these two regions integrating most of the temporal variability in species composition seen in our study. It included cruises during El Niño and La Niña as well as years not classified as a major ENSO event. *O. micropterus* was the dominant species in this group, while *V. lucetia* was the least dominant. *C. equiselis*, *Hirundichthys* spp.*, Cheilopogon* spp.*, Exocoetus* spp., and *Opisthonema* spp. all had high dominance in this group. The last group consisted of nine pooled year-region stations from only the western region and all years except 1967. This group had high moderate dominances of *O. micropterus* and low dominances of *Auxis* spp., while *C. equiselis* and *V. lucetia* were high. There was an absence of all neritic or reef-associated species (*Opisthonema* spp., *Mugil* spp., *Polydactylus approximans,* and *C. maculatus*) in this group. The inclusion of stations from the western region from all years except 1967 suggests that the western region community structure of species assemblages had the least variability among all three regions.

Multivariate response patterns of cruise year were very similar to western region stations, while response pattern for stations from 1967 had a similar response pattern with respect to region. The response patterns for pooled year-region stations in the middle and eastern regions combined both region origin and cruise year. We saw minimal change across time in the community structure of larval fishes in the western region of our study. This was a marked contrast to the middle and eastern and upwelling regions, where station community structure from all cruise years (excluding 1967) was not segregated across time (Figure 3.13). Here, the community was composed of a strong dominance of the oceanic assemblage, except for *Prognichthys* spp. and *C. hippurus*, an almost complete absence of the neritic-pelagic assemblage (*C. maculatus* present in small dominances), an intermediate dominance of the mesopelagic assemblage, and an absence of the upwelling assemblage. This scenario, however, did not occur during 1967, when the oceanic and mesopelagic assemblages were more evenly distributed across regions. During 1967, there was less variability across space, while in other years in the western region, there was little variability across time. Clearly community structure was different in 1967 from all other cruise years.

Community similarity through time

Larval fish species assemblages within the eastern region varied more over time than those of the middle and western regions. Similarity in species composition decreased with increasing time between samples (Figure 3.14). This trend was only significant for the eastern region. Least square fits of PSI as a function of time difference between cruise years showed decreasing trends in all regions, but randomization tests confirmed that only the trend seen in the eastern region was significant (95% confidence levels). In all other regions, the fits were not significantly different from zero (95% confidence levels), indicating more change in assemblages in the eastern region over time compared with the more stable assemblages of the middle and western regions.

Discussion

This study provides insights into the long-term ecological dynamics of community structure of larval fishes in the eastern Pacific warm pool and their response to multidecadal changes in water-column stratification. We found patterns in our results suggesting deepening thermocline depth along with increased stratification in the upper 200 meters during the last 30 to 40 years. Seasonal anomalies of both thermocline depth and water-column stratification proxies showed changes in temporal trends during the late seventies. Multivariate analyses combining temporal and spatial variability in community structure of neustonic ichthyoplankton indicated a higher degree of temporal variability in the eastern region of the eastern Pacific warm pool and suggested more stability in the western region. Additionally, community structure in 1967 seemed to be different from all other years.

In the discussion to follow, we first interpret our results with respect to observed trends independent from our study and rationalize how our study allowed us to test hypotheses relating to environmental change and community response. We then argue that the multidecadal change in the upper-ocean thermal structure was large enough to have impacted a mid-trophic community of larval fishes.

Multidecadal increase in stratification

Changes in the pattern of ENSO variability have been proposed by several studies reporting an increase in the intensity, frequency, and duration of El Niño events after 1976 (Linsley *et al.*, 2000; Trenberth and Hurrell, 1994; Wang, 1995). During non-El Niño conditions, the thermocline across the Pacific has a seesaw structure, where thermocline depth is deep in the western Pacific and shallow in the east. During an El Niño, warm water in the western Pacific is displaced, changing the seesaw structure across the Pacific and causing anomalously deeper thermoclines and positive surface temperature anomalies in the eastern Pacific (Meinen and McPhaden, 2000). After 1976, sea surface temperatures in the eastern tropical Pacific increased (Mestas-Nuñez and Enfield, 2001; Zhang *et al.*, 1997). Could this change in ENSO frequency and sea surface temperature affect the mean depth of the thermocline and water-column stratification in the eastern Pacific warm pool? Guilderson and Schrag (1998) argue exactly that. They hypothesized that a persistent change in the subsurface waters in the eastern tropical Pacific occurred in 1976 and speculated that this change was responsible for the increased frequency of El Niño events in the Pacific after 1976. Our results, showing a deepening thermocline depth and increased stratification of the upper 200 meters after the late 1970s, offer support for this hypothesis.

A deepening trend in thermocline depth for the entire eastern Pacific warm pool began after the late 1970s. Between 1960 and 2006, mean thermocline depth in the eastern Pacific warm pool deepened 18.9 ± 5.7 meters. While seasonal means during the early 1960s were highly variable, thermocline depth began to show a deepening trend after 1979. Although 75% of the study area did show a deepening trend in thermocline depth, the trend was not consistent throughout the geographic extent of the study area. Thermocline shoaled along 5–6ºN for most of the eastern Pacific warm pool and deepened along the countercurrent thermocline ridge (8–10ºN) between 145–120ºW. The higher rate of change along the countercurrent thermocline ridge may reflect the variable position of the divergence separating the NEC and NECC. On the other hand, the NECC has been shown to have high interannual variability in its transport (Wang *et al.*, 2002). A period of increased El Niños should correspond to weaker trade winds and therefore a weaker NECC and NEC. Using observational and modeled data from a global climate model, Vecchi *et al*. (2006) reported that during the last part of the nineteenth century, the Walker circulation weakened along with surface equatorial winds. This, they suggest, has altered the thermocline structure and circulation of the tropical Pacific. Our results corroborate this idea.

While the index for bulk stratification proxy did not show a temporal trend, the two indices of the upper 100 meters and lower 100 meters showed temporal trends with opposite directions. T_{z0-100} decreased 1.64 ± 0.76 ºC over the study period, while $T_{z100-200}$ increased by 1.69 ± 0.54 ºC. Deepening of the isotherms near the thermocline could cause this difference. If the upper 100 meters were getting warmer overall along with a deeper thermocline, then the difference in temperature between the surface and 100 meters depth would decrease over time. On the other hand, since warming is less intense at depth, then the difference between temperatures at 100 and 200 meters should increase. The zonally and meriodonally integrated temperature anomalies for the upper 200 meters (Figure 3.10) support this idea. Temperature has been more variable at 100 meters than at the surface or at 200 meters. In this plot one can see the ENSO frequency in the temperature anomalies, but also the warming of the upper 200 meters after 1976. Overall, our results support the hypothesis that the thermal structure of the water column in the eastern tropical Pacific changed after the late 1970s.

Change in community structure of larval fishes across time

There appears to be a change over time in community structure in the neustonic ichthyoplankton of the eastern Pacific warm pool. Community structure in the Eastern region showed higher variability through the 11 cruises spanning 39 years. Conversely, communities from the Western oceanic region displayed persistence in their species assemblages across the same time period. Species assemblages from the Eastern region consistently decreased in similarity when compared to assemblages sampled farther apart in time. Although the type of tow used in 1967 cruises was different from all other years, the apparent difference in community structure between 1967 and other years is likely a result of 1967 having a starkly different community structure evenly distributed across all three regions of the study area. Maintenance in community structure of open-ocean ichthyoplankton can reflect behaviors of both adult and larval fishes, as well as oceanographic processes horizontally transporting larvae (Moser and Smith, 1993). Nevertheless, we hypothesize that differences in temporal variability of community structure among regions can be attributed to an increase in the variability of processes supplying subsurface nutrient-rich water to the euphotic zone. Alternatively, the variations in ichthyoplankton community observed through time in the eastern region could be entirely dependent upon community responses to changing environmental parameters.

Maintenance of community structure of tropical ichthyoplankton is driven by numerous mechanisms. A few well-known examples are: spawning over long or short periods of time, pelagic versus demersal eggs, egg hatching time and larval survival (Leggett and Deblois, 1994; Miller and Kendall, 2009). Our results suggest that the main mechanism driving variability of community structure in larval fishes in our study area involvesclimate-related changes in recruitment success. We hypothesize that during El Niño events certain thresholds of food availability are not reached as the environment is less productive, and consequently, larvae of the affected species will have lower survival rate and reduced dominance in the community. This mechanism would be more prevalent in the eastern region of our study area, because it is affected to a greater degree by a deeper thermocline than is the more oceanic western region.

In general, tropical fish species spawn intermittently throughout the year and have rapid embryonic development of eggs (Parin, 1970). As a result, fecundity is lower, but eggs are spawned intermittently over longer periods of time and are larger. The hypothesis is that larvae of larger size have a better chance of surviving in a low food environment, like in the tropics, where it is more likely for larvae to be food limited than to be eaten by larger animals (Johnson and Barnett, 1975; Winemiller and Rose, 1993). Larger larvae can search a larger area for food and eat a wider variety of prey. Higher temporal variability in dominance patterns of taxa from the eastern region in our study may reflect lower larval survival during less productive years caused by a suppressed thermoclines and higher stratification. In support of this hypothesis, seasonal thermocline anomalies were correlated more so in the eastern region than in the middle or western region (Figure 3.15), and the highest temporal variability in community structure and species assemblages over time was seen in the eastern region (Figure 3.13 and 3.14). During the time period of our study, El Niños occurred in 1965, 1972, 1976, 1982, 1987, 1997 and 2006, with prolonged El Niño conditions during 1991–1994. La Niñas occurred in 1964, 1970, 1973, 1975, 1988, 1998 and 1999 (Kiladis and Diaz, 1989; Larkin and Harrison, 2002; Trenberth and Hoar, 1996). *V. lucetia* consistently decreased in dominance during El Niño years; its lowest dominances were in 1987, 1992, and 2006, all El Niño years. During both 1997 and 2006, at least two species from the mesopelagic assemblage were absent. Maintenance of community structure of mesopelagic fishes is thought to be driven by food availability (Barnett, 1984), offering support for our results and hypothesis.

Alternatively, the variation in ichthyoplankton community observed through time in the eastern region could be entirely dependent upon community response to changing environmental parameters. Unlike commercially fished species in the tropical Pacific, which have shown changes in community structure coinciding with the commencement of fishing (Ward and Myers, 2005), abundances of most of the species in our study are not directly influenced by fishing mortality. Therefore, changes in dominance patterns may be interpreted as indicators of environmental change (Cushing, 1982). Even though *C. maculatus, C. mysticetus,* and species of *Hirundichthys* and *Anchoa* were completely absent during 1967, species richness (total number of species) in stations was two fold higher in 1967 versus all others years, except in 1992. This suggests that the community structure of larval fishes in our study area was different from that in later years. Supporting this idea is the observed change in similarity between species compositions through time in the eastern region. Lastly, changes in transport could cause a different dispersal pattern in the eastern portion of the study area.

Change in upper ocean stratification affecting a mid-trophic level community

The multidecadal change in stratification and thermocline structure in the upper 200 meters of the eastern Pacific warm pool has been strong enough to have impacted this area's larval fish community. In low- and mid-latitude oceans, where ecosystems are generally limited by nutrients (e.g., nitrate and phosphate) and not light (Longhurst and Pauly, 1987), changes in stratification and thermocline depth would likely affect biological production. Polovina *et al*. (2008) used this rationale to explain the recent expansion of oligotrophic waters in North Pacific, as did Behrenfeld *et al*. (2006), who report a ten-year (1996–2006) decrease in global ocean net primary productivity that they attribute mostly to stratified low-latitude oceans. It is known that changes in thermocline depth in our study area do result in a general decrease of surface Chl *a,* with more pronounced changes along the countercurrent thermocline ridge and upwelling regions (Fiedler *et al.*, 1992). As a result of the higher stratification and deeper thermoclines, the decrease in upward flux of deepwater nitrate could be causing decreasing biological production and consequent variability in larval fish communities in the eastern region of our study area. The MDS plot of pooled year-region stations (Figure 3.16) shown as both cruise years and corresponding El Niño, La Niña, or non-ENSO years suggests a different community structure during El Niño years versus non-ENSO and La Niña years. We hypothesize that changes in the upper water column thermal structure (Figure 3.17) are limiting nutrient influx more so now than before the late 1970s. These changes would be more prominent in the eastern region of the study area, where communities are structured around wind-driven upwelling productivity. Our hypothesis agrees well with what Saba *et al*. 2008 posit. These authors argued that leatherback turtles in the eastern Pacific have been resource limited as a result of the higher frequency of El Niño events since the regime shift of 1976/77.

CONCLUSION

Our study suggests that variation in community structure of neustonic ichthyoplankton in the eastern Pacific warm pool is linked to variability in the upper-ocean thermal structure. Our conclusions are supported by the minimal interannual variation in community structure from the oceanic region, while in the eastern upwelling region structure of species assemblages varied much more over time. Our data set is obviously weakened by the lack of cruises between 1967 and 1987. Nevertheless, studies quantifying interannual variability in community structure of larval fishes spanning several decades and covering large areas of tropical oceans are not common. In the eastern Pacific, most studies addressing long-term variability in ichthyoplankton species composition are from temperate ecosystems, e.g., Loeb and Rojas (Loeb and Rojas, 1988; Smith and Moser, 2003) and Smith and Moser (2003) or from smaller spatial scales and along the continental shelf (Franco-Gordo *et al.*, 2008). Vilchis *et al*. (2009) tested similar hypotheses using similar methods and data within a shorter time frame. In that study, Vilchis *et al*. hypothesized that the neustonic ichthyoplankton in the western oceanic region of the eastern Pacific warm pool are more resilient to ENSO-driven environmental variability than ichthyoplankton in the eastern region. Results from the present study support this hypothesis. We additionally find strong evidence suggesting that the larval fish community of the eastern Pacific warm pool was different prior to the 1976 than what it is today.

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Table 3.1 Description of instruments included in the data sets from the Word Ocean Database 2009 and the total number of profiles used from each data set.

Data Set	Description	Numer of profiles
OSD	Ocean station data: Nansen/Niskin bottle data and low-resolution expendable and non-expendable conductivity-temperature-depth recorders	4,253
MBT	Mechanical Bathythermographs	5,242
CTD	High-resolution expendable and non-expendable conductivity-temperature-depth recorders	2,060
XBT	Expendable Bathythermographs	33,823
PFL	Profiling floats	6,204

Table 3.2 Temporal distributions of cruises and oceanographic vessels, as well as the number of stations per year and region, see text for details.

Cruise	**Year**	**Ocenographic vessel**	**Number of stations**			
			Per Region			**Total per Year**
			Eastern	Middle	Western	
Eastropac 45	1967	*David Starr Jordan*	0	6	13	55
Eastropac 47	1967	*Rockaway*	12	2	0	
Eastropac 50	1967	*David Starr Jordan*	0	11	9	
Eastropac OP	1967	*Oceanographer*	2	0	0	
MOPS	1987	*David Starr Jordan* & *McArthur I*	24	34	43	101
MOPS	1988	*David Starr Jordan* & *McArthur I*	21	26	35	82
MOPS	1989	*David Starr Jordan* & *McArthur I*	16	30	37	83
MOPS	1990	*David Starr Jordan* & *McArthur I*	20	21	49	90
PODS	1992	*David Starr Jordan* & *McArthur I*	67	14	0	81
SPAM	1998	*David Starr Jordan*, *McArthur I* & *Endeavour*	46	51	65	162
STAR	1999	*David Starr Jordan* & *McArthur I*	31	44	56	131
STAR	2000	*David Starr Jordan* & *McArthur I*	31	42	49	122
STAR	2003	*David Starr Jordan* & *McArthur II*	27	32	49	108
STAR	2006	*David Starr Jordan* & *McArthur II*	27	48	41	116

Table 3.3 List of the 25 dominant species/taxa, their phylogenetic affiliation, common name, known habitat of adult forms and neustonic affiliation of larval forms as reported by Hempel and Weikert (1972), Miller and Kendall (2009), Nelson (2006) and Parin (1970).

Sapecies/Taxon	Percent		Family	Functional group	Common name	Habitat	Neustonic affiliation
	Dominance	*Occurrence*					
Oxyporhamphus micropterus	19.08	46.60	Exocoetidae	Flyingfishes	Shortwing flyingfish	Epipelagic	True-neuston
Vinciguerria lucetia	17.97	33.69	Phosichthydae	Lightfishes	Panama lightfish	Mesopelagic	Faculative-neuston
Coryphaena equiselis	10.98	32.80	Coryphaenidae	Dolphinfishes	Pompano dolphinfish	Epipelagic	True-neuston
Auxis spp.	9.38	31.39	Scombridae	Tunas and bonitos	Blullet tunas	Epipelagic	Faculative-neuston
Prognichthys spp.	4.70	19.10	Exocoetidae	Flyingfishes		Epipelagic	True-neuston
Cubiceps pauciradiatus	3.75	15.92	Nomeidae	Driftfishes	Bigeye cigarfish	Mesopelagic	Faculative-neuston
Hirundichthys spp.	3.40	13.26	Exocoetidae	Flyingfishes		Epipelagic	True-neuston
Coryphaena hippurus	3.00	17.06	Coryphaenidae	Dolphinfishes	Dolphinfish	Epipelagic	True-neuston
Cheilopogon spp.	2.83	13.70	Exocoetidae	Flyingfishes		Epipelagic	True-neuston
Opisthonema spp.	1.88	4.69	Clupeidae	Herrings and sardines	Thread herings	Neritic-pelagic	Faculative-neuston
Exocoetus spp.	1.70	8.13	Exocoetidae	Flyingfishes	Tropical flyingfishes	Epipelagic	True-neuston
Mugil spp.	0.93	6.90	Mugilidae	Mullets	Mullets	Neritic	True-neuston
Lestidium spp.	0.87	2.65	Paralepidae	Barracudinas	Barracudinas	Mesopelagic	Faculative-neuston
Polydactylus approximans	0.84	4.16	Polynemidae	Threadfins	Blue bobo	Neritic	True-neuston
Thunnus spp.	0.79	5.04	Scombridae	Tunas and bonitos	Tunas	Epipelagic	Faculative-neuston
Diplophos proximus	0.73	4.86	Gonostomatidae	Bristlemouths	Pacific portholefish	Mesopelagic	Faculative-neuston
Cetengraulis mysticetus	0.63	1.33	Engraulidae	Anchovies	Pacific anchoveta	Neritic-pelagic	True-neuston
Canthidermis maculatus	0.62	3.71	Balistidae	Triggerfishes	Oceanic triggerfish	Reef-associated	True-neuston
Cyclothone spp.	0.55	2.30	Gonostomatidae	Bristlemouths		Mesopelagic	Faculative-neuston
Engraulidae	0.54	1.95	Engraulidae	Anchovies		Neritic-pelagic	True-neuston
Naucrates ductor	0.53	3.45	Carangidae	Jacks and Pompanos	Pilotfish	Reef-associated	True-neuston
Diaphus spp.	0.53	1.95	Myctophidae	Lanternfishes		Mesopelagic	Faculative-neuston
Bothus spp.	0.51	3.63	Bothidae	Lefteye flounders		Demersal	True-neuston
Caranx caballus	0.51	4.69	Carangidae	Jacks and Pompanos	Green Jack	Neritic-pelagic	True-neuston
Anchoa spp.	0.50	1.15	Engraulidae	Anchovies		Neritic-pelagic	True-neuston

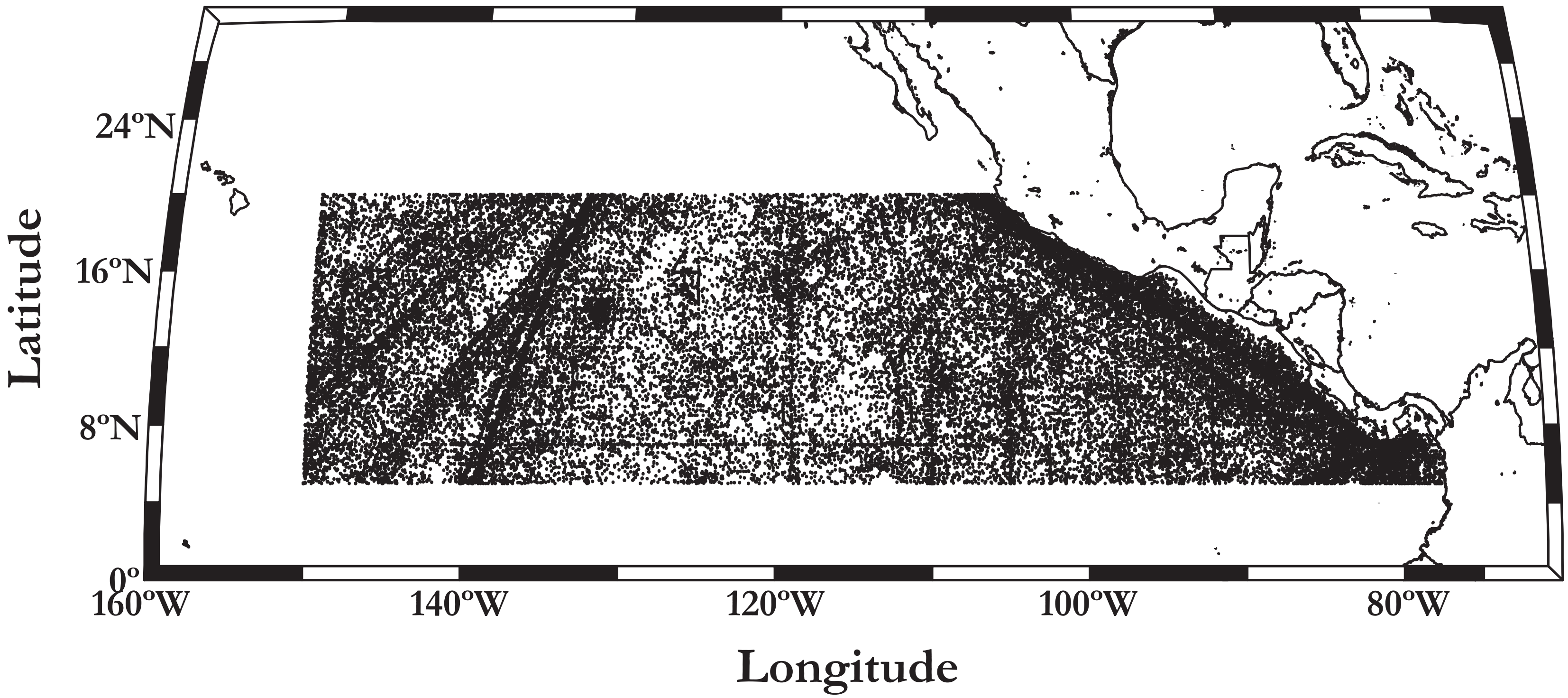


Figure 3.1 Geographical distribution of the 51,582 Word Ocean Database 2009 (Boyer *et al.*, 2009) hydrographic stations used in this study. All stations were completed during the 1960-2006 study period.

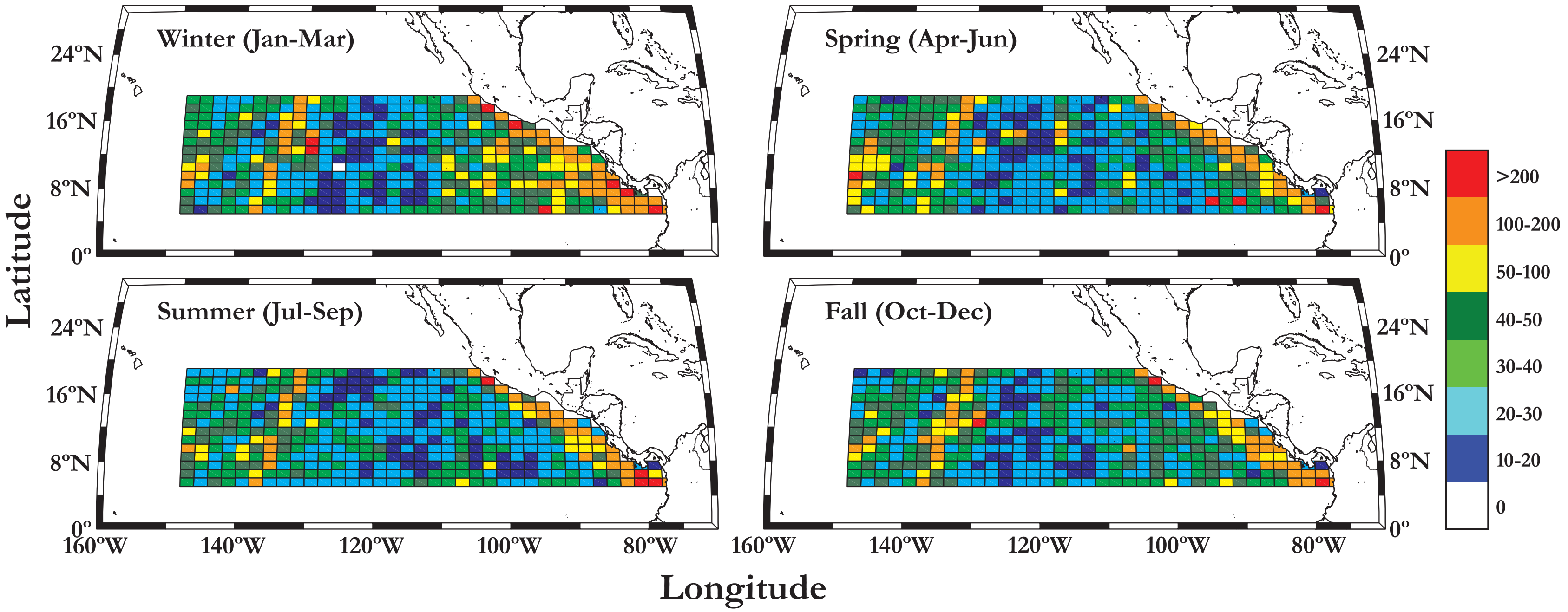


Figure 3.2 Number of World Ocean Database 2009 temperature profiles in each of the 1° latitude by 2° longitude and seasonal bins.

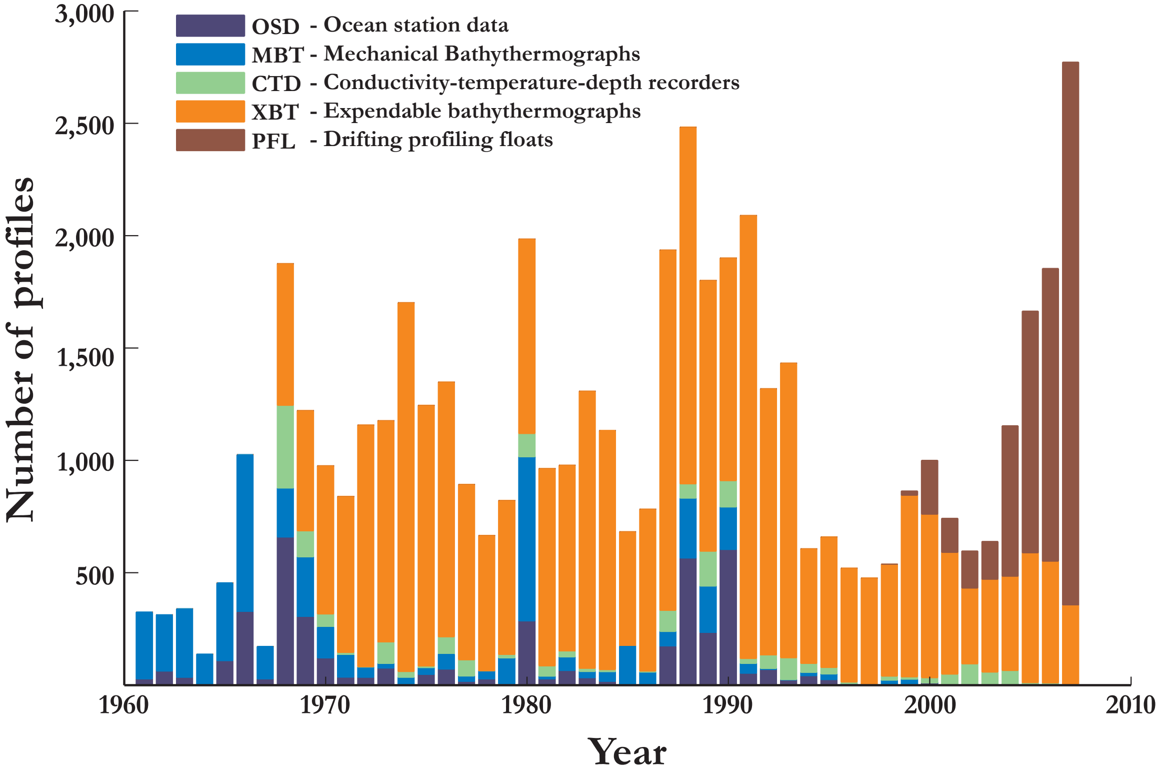
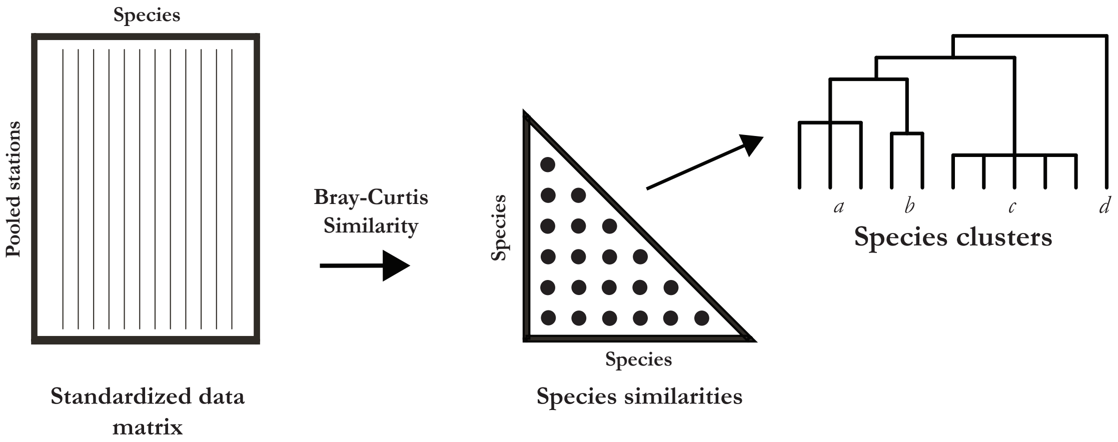


Figure 3.3 Frequency of profiles taken per year and main instrument type. Instrument type abbreviations as in Table 3.1.

a: *cluster analysis addressing species assemblages*



b: *cluster analysis addressing community structure*

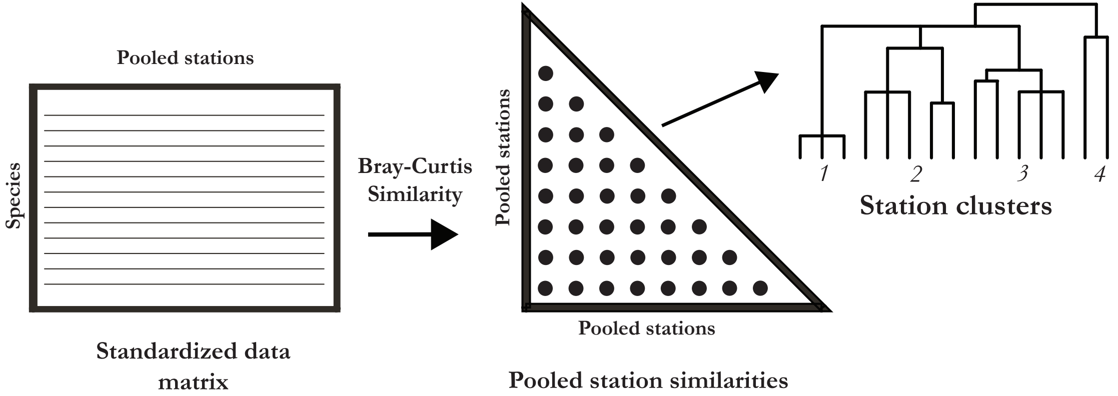


Figure 3.4 Flow diagram illustrating set up for cluster analyses addressing. (a) cluster of species to identify assemblages and (b) cluster of stations to indentify stations with similar community structure.

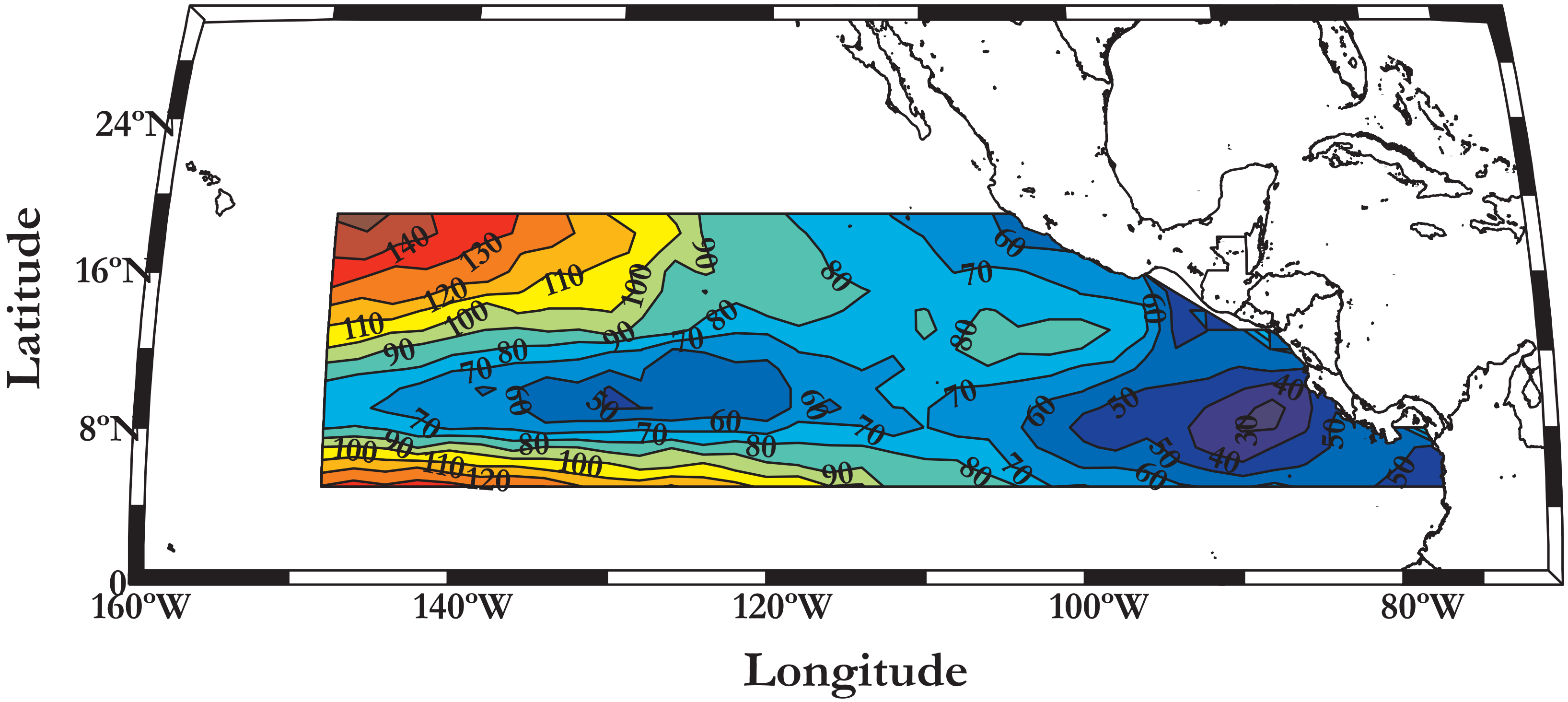


Figure 3.5 Mean depth (m) of the thermocline during 1960-2006. Seasonal sampling bias was removed by averaging the four long-term seasonal means so that each season had equal weight in determining the long-term mean. Contours are given every 10 m and were interpreted as heights with respect to the longitude-latitude projected Mollweide plane.

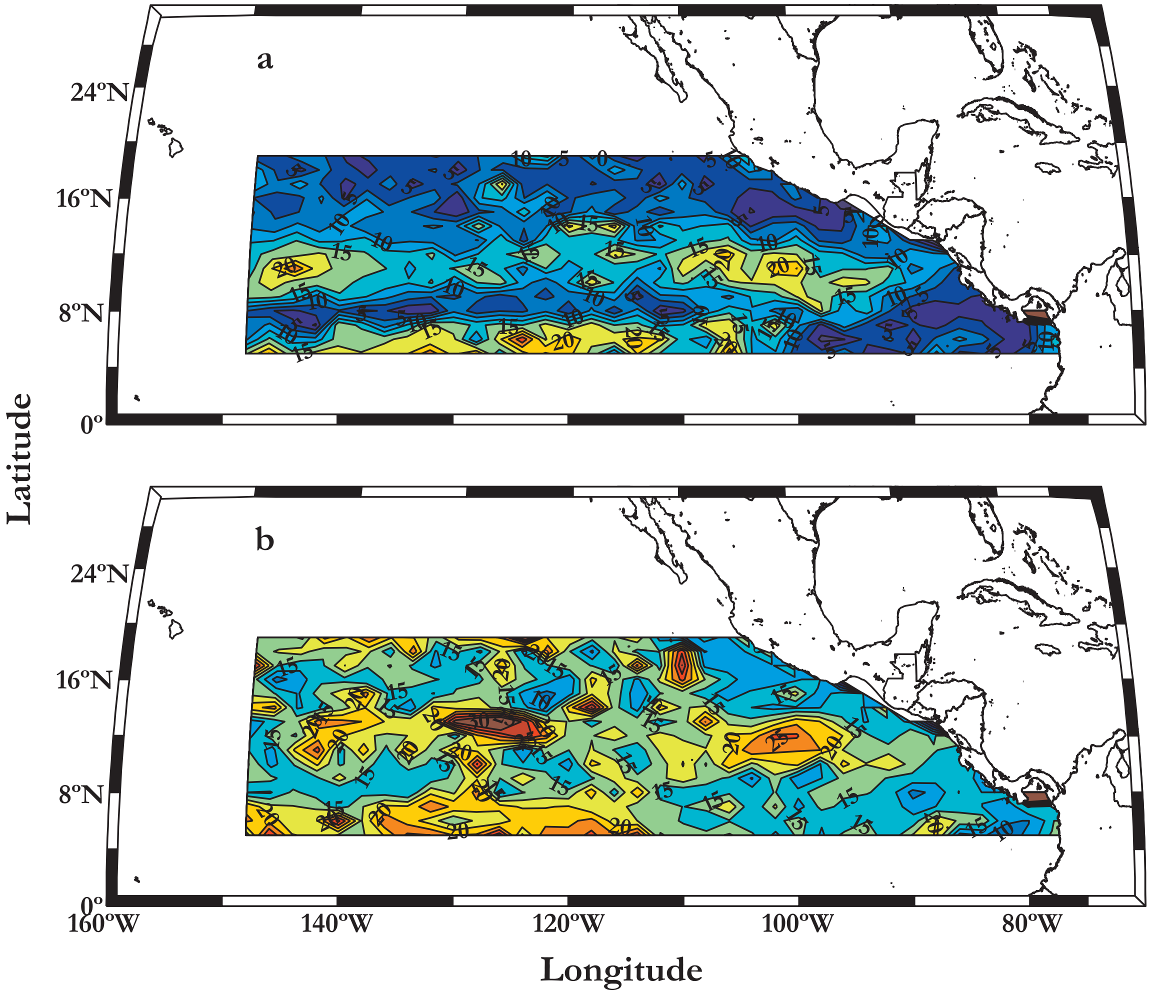


Figure 3.6 Seasonal (a) and interannual (b) standard deviation (m) of thermocline depth. Contours are given every 2.5 m and were interpreted as heights with respect to the longitude-latitude projected Mollweide plane.

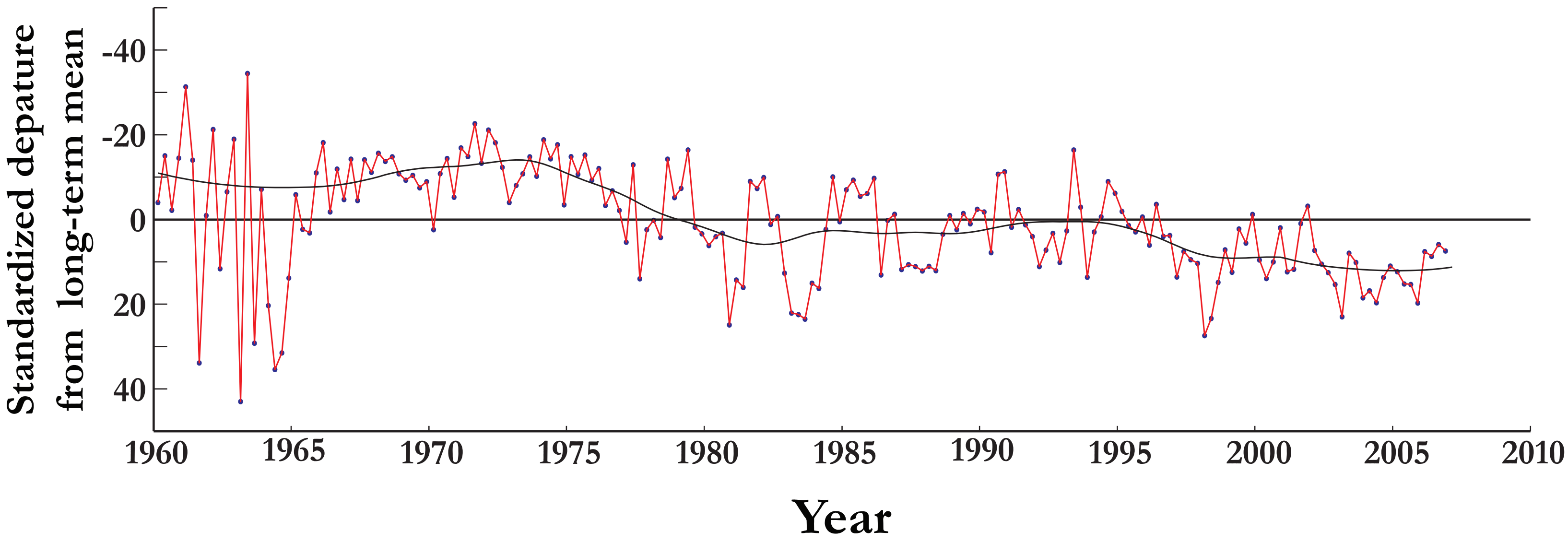


Figure 3.7 Mean seasonal anomalies of thermocline depth for each season in the 46-year study period in the entire eastern Pacific warm pool. The black line is a 10-year moving average using localized regression with weighted linear least squares and a 2^{nd} degree polynomial filter.

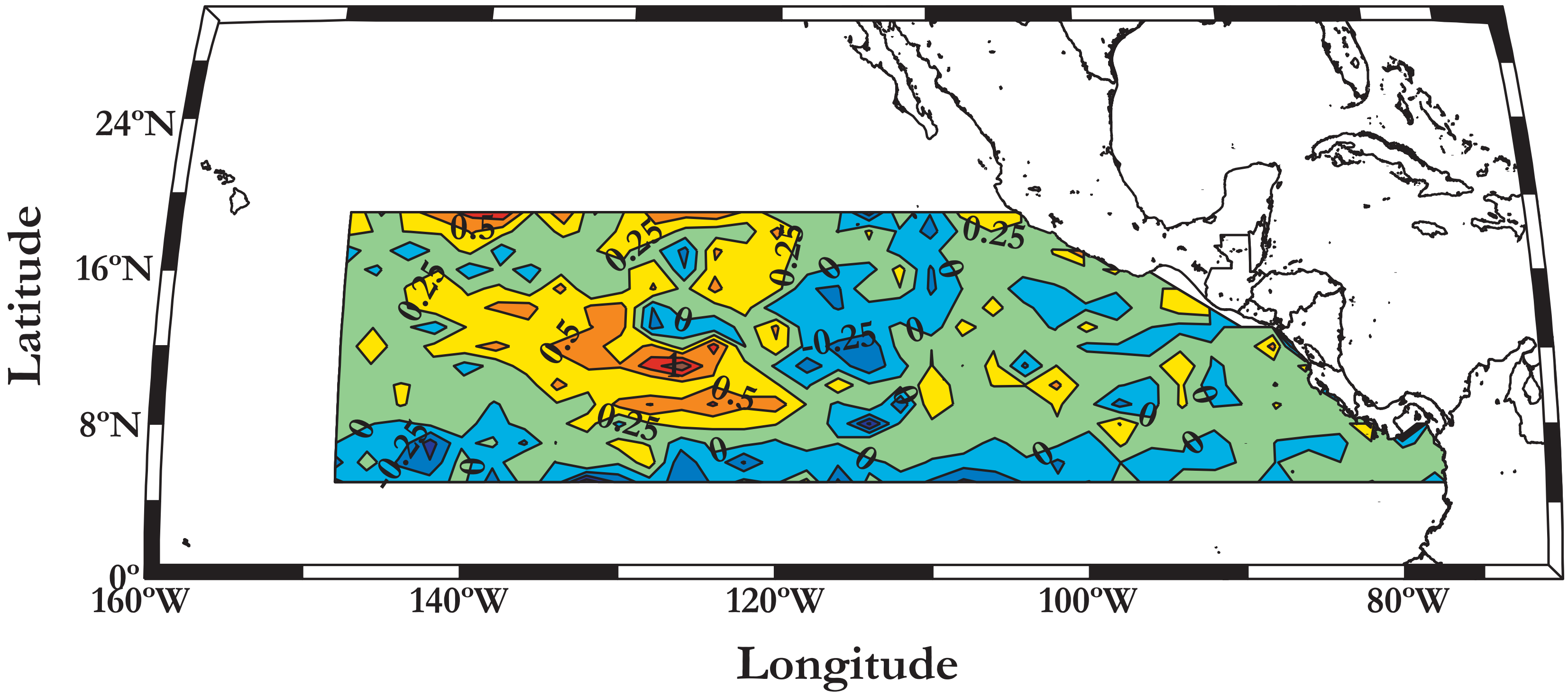


Figure 3.8 Spatial distribution of thermocline depth change (º C year^{-1}) for each 1º latitude by 2º longitude bin. Contours are given every 0.25 m and were interpreted as heights with respect to the longitude-latitude projected Mollweide plane.

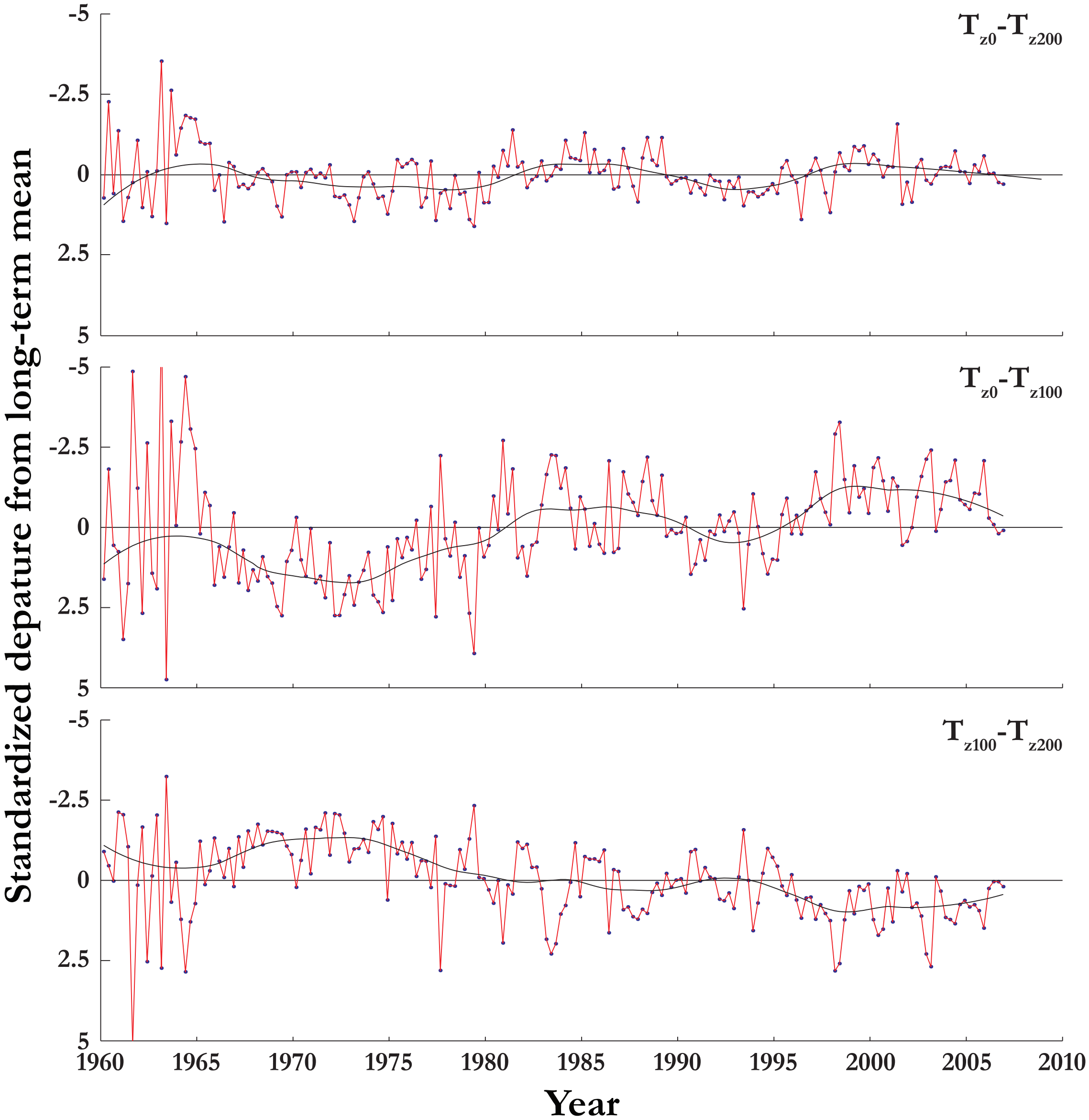


Figure 3.9 Mean seasonal anomalies of the three proxies for stratification: $T_{z0\text{-}z200}$, temperature difference between surface and 200 m; $T_{z0\text{-}z100}$, temperature difference between surface and 100 m; $T_{z100\text{-}z200}$, temperature difference between 100 and 200 m; for each season in the 46-year study period in the entire eastern Pacific warm pool. Black lines in each plot are 10-year moving averages using localized regression with weighted linear least squares and a 2nd degree polynomial filter.

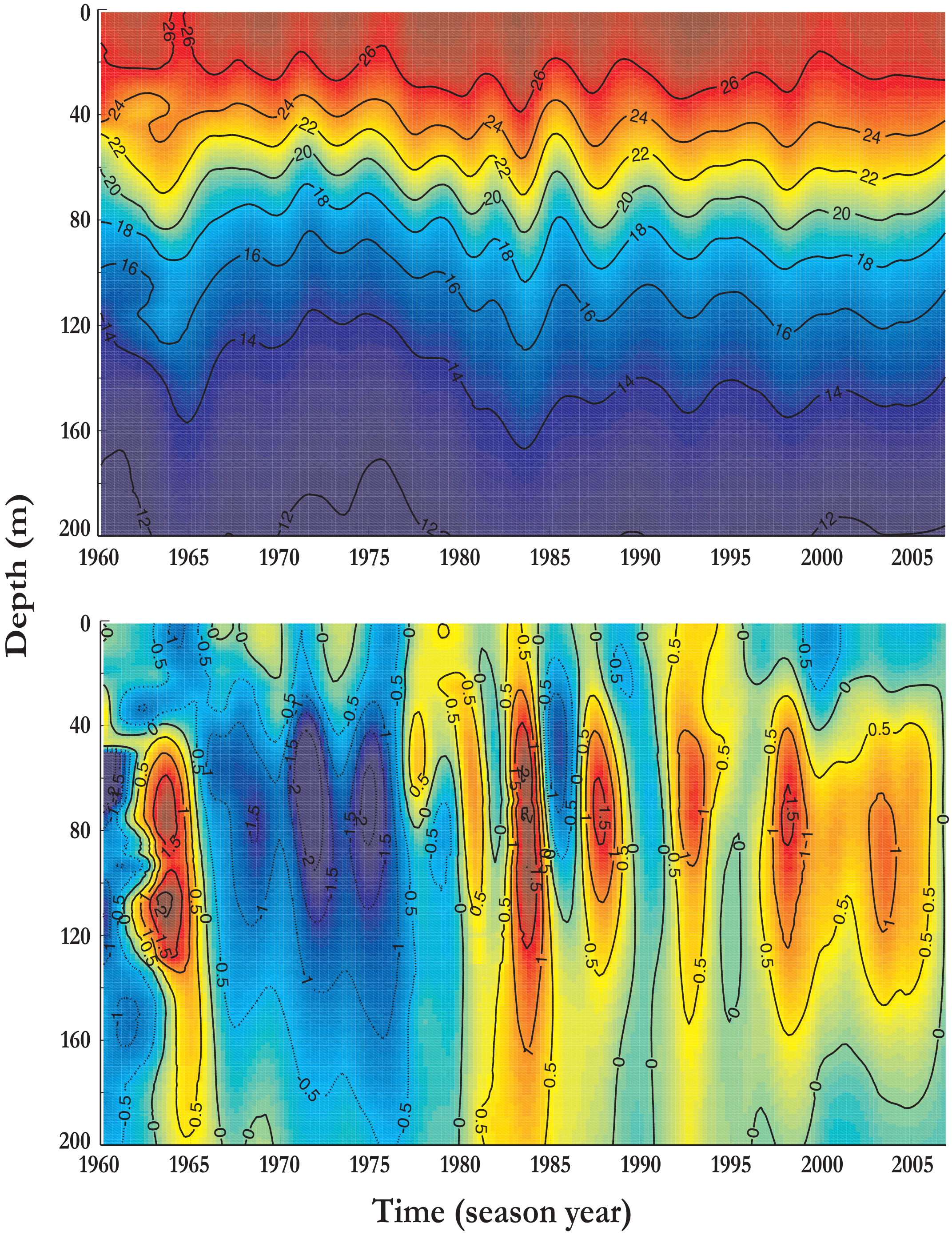


Figure 3.10 Time-depth plot of meridionally and zonally integrated seasonal means (upper figure) and anomalies (lower figure) of upper 200 meter temperatures in the eastern Pacific warm pool. Contours are given every 0.25º C and were interpreted as heights with respect to the time-depth plane, with negative anomalies shown as dashed lines. High frequency components in the data were attenuated with spatial filtration using a five-year window filter.

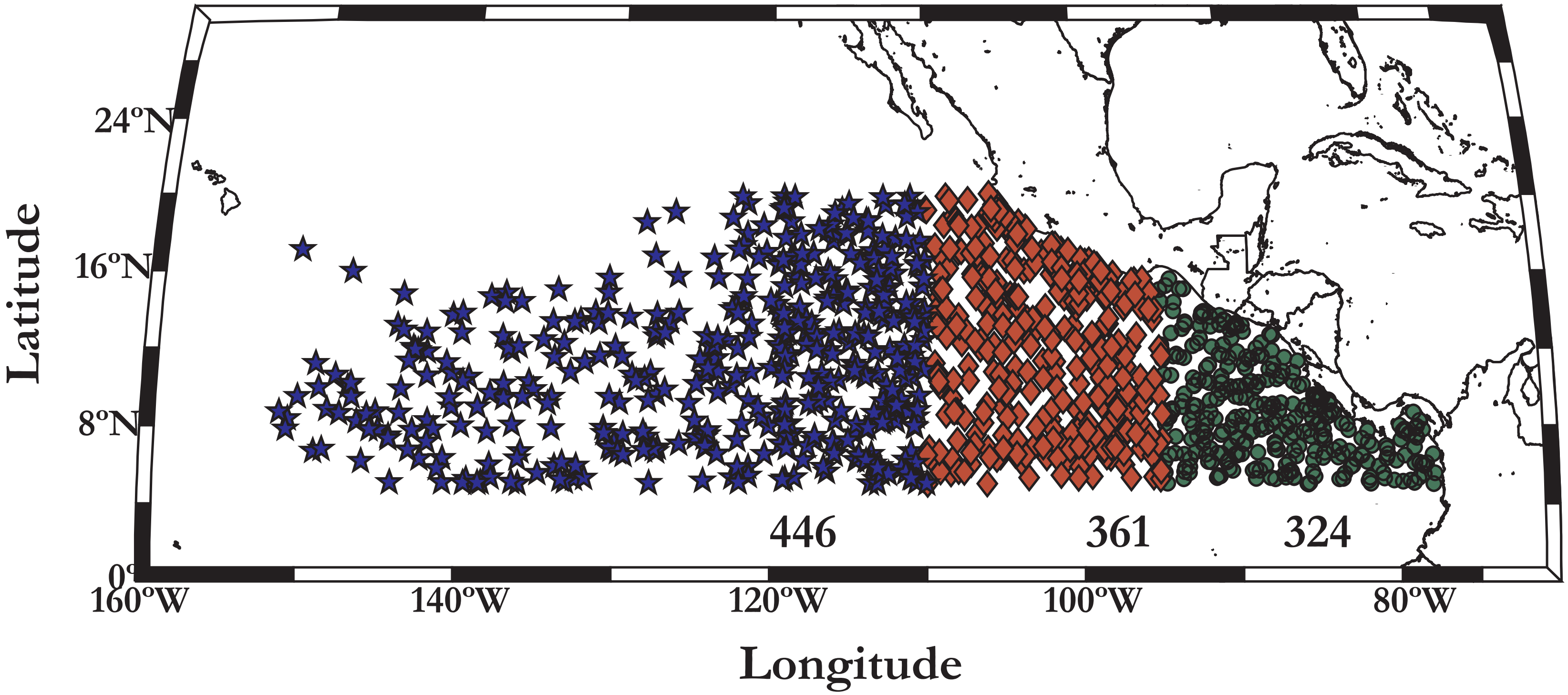


Figure 3.11 Geographical distribution of Manta tow stations within each of the three regions defined within the study area: Western (☆), Middle (◇) and Eastern (○); on the basis of surface oceanography, zonal productivity and biogeography. Total number of stations within each region is shown under each region.

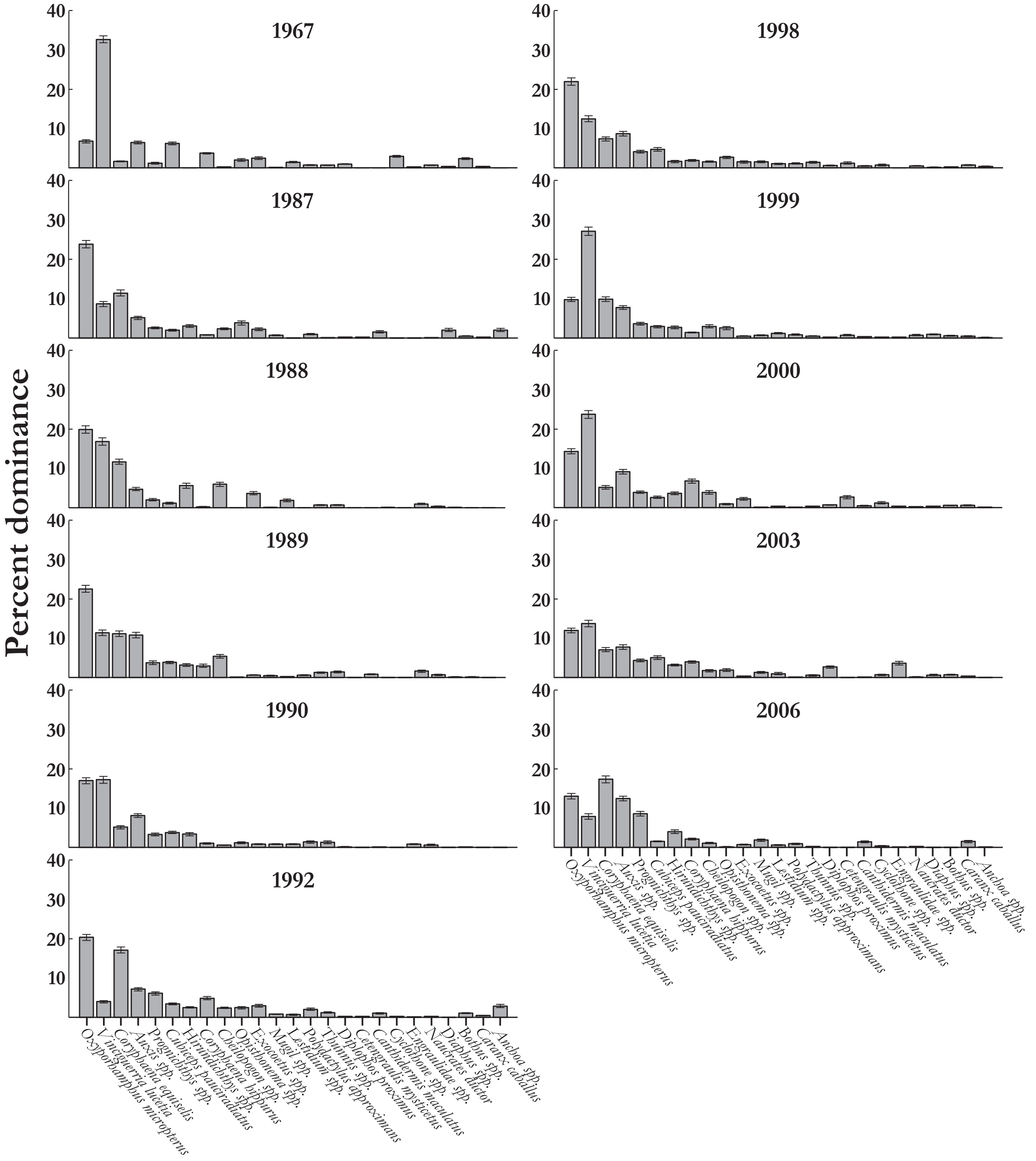


Figure 3.12 Annual mean dominance for the 25 top dominant taxa. Error bars are standard errors of the mean.

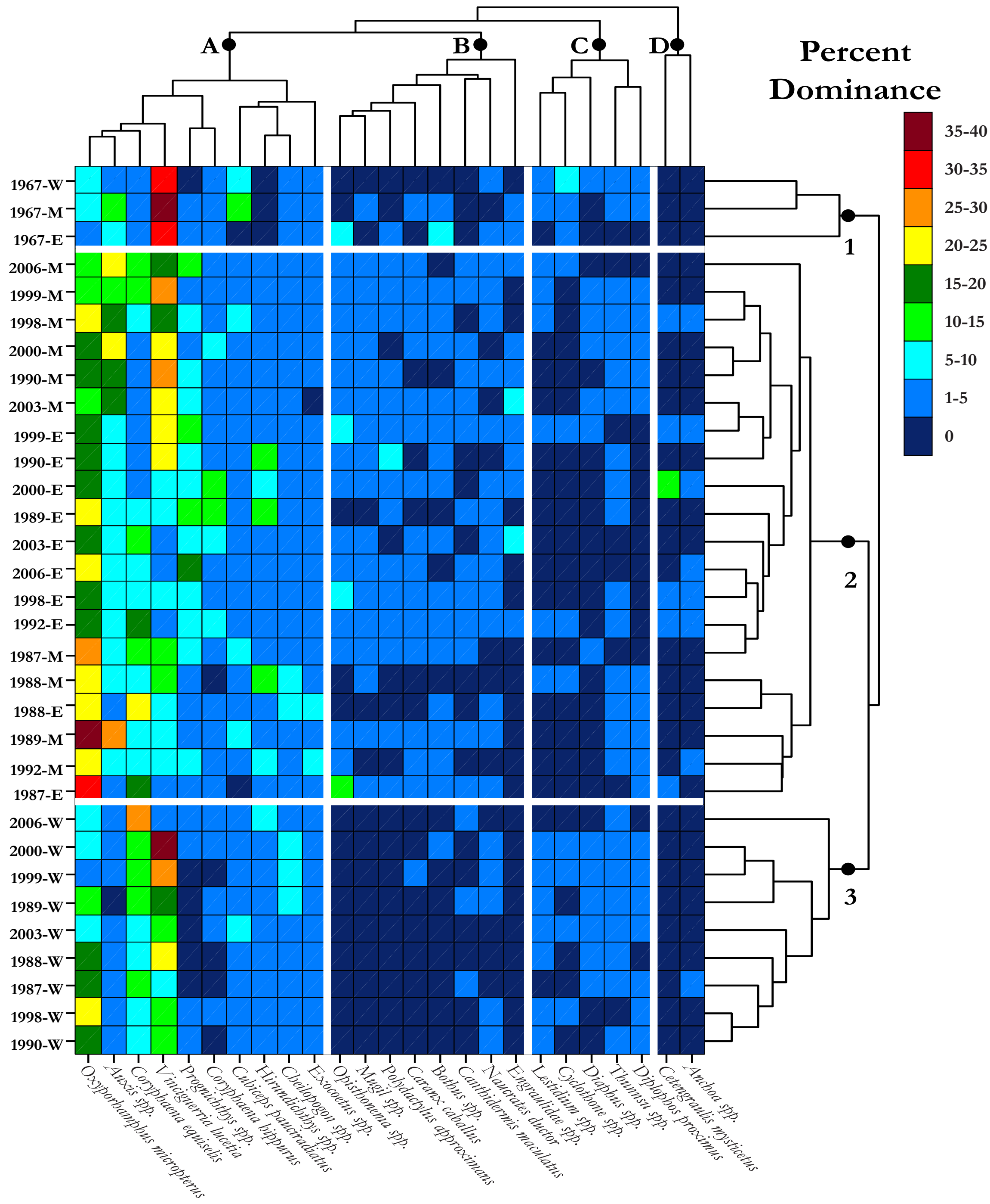


Figure 3.13 Species dominance patterns in a two-way table of species groups (species assemblages) in pooled year-region station groups (stations with similar community structure) from cluster analyses based on respective Bray-Curtis similarities of species and pooled region-year stations. ANOSIM tests using 10,000 permutations found species assemblage groups (R=0.85, P=0.0001) and pooled year-region groups (R=0.93, P=0.0001) to be significantly different and not likely generated by random chance.

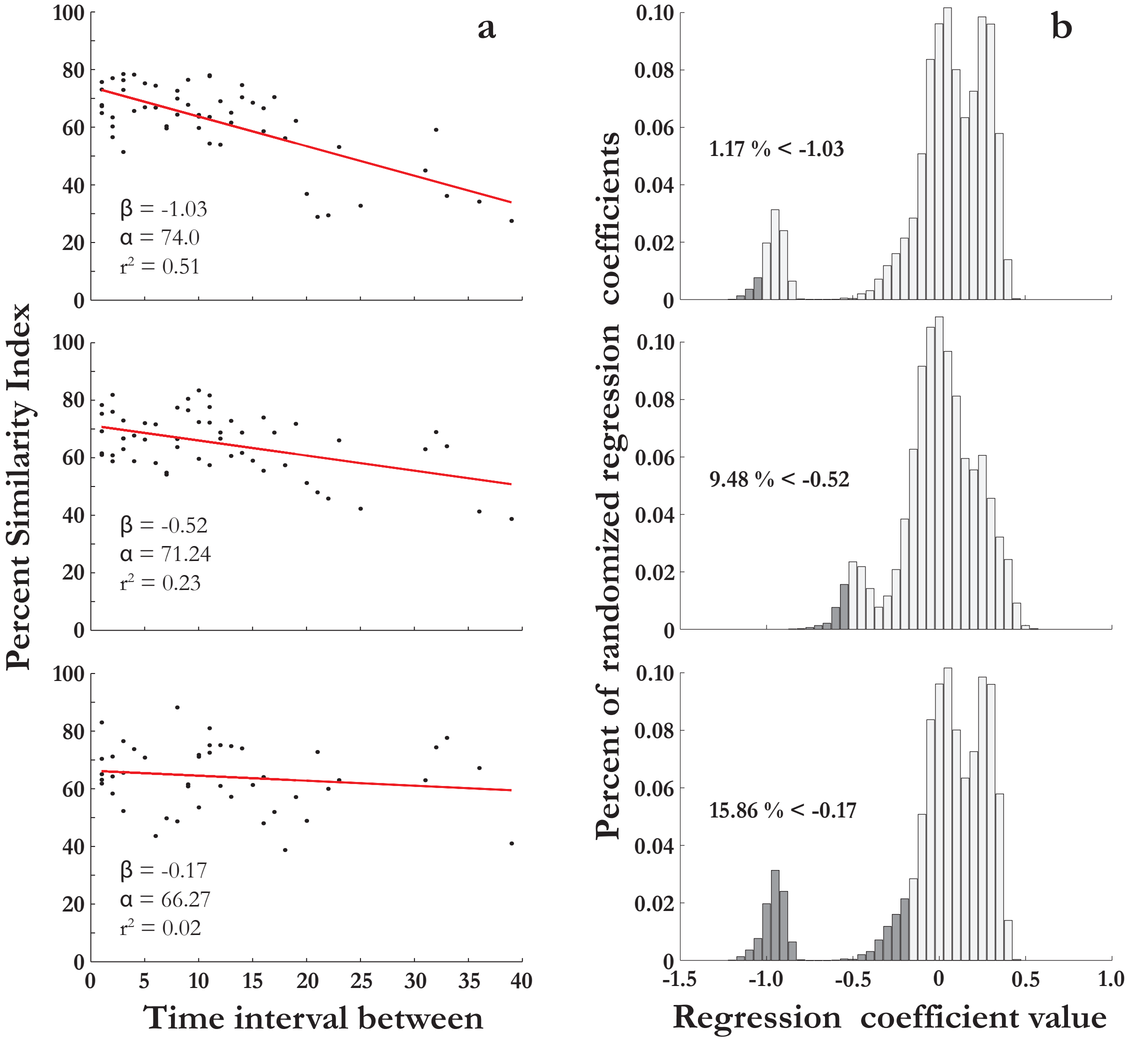


Figure 3.14 (a) Percent similarity index of larval fish assemblages plotted against time differences for each pair of cruises years in the three regions of the study area. Least-square fit lines are shown in red and the regression coefficient and r^2 in the bottom left of each plot. (b) Results of a randomization test gauging the one-tailed probability of obtaining the observed regression coefficient for each least-squares fit. Dark shaded bars represent frequency of instances when the randomized test produced a regression coefficient smaller than that observed.

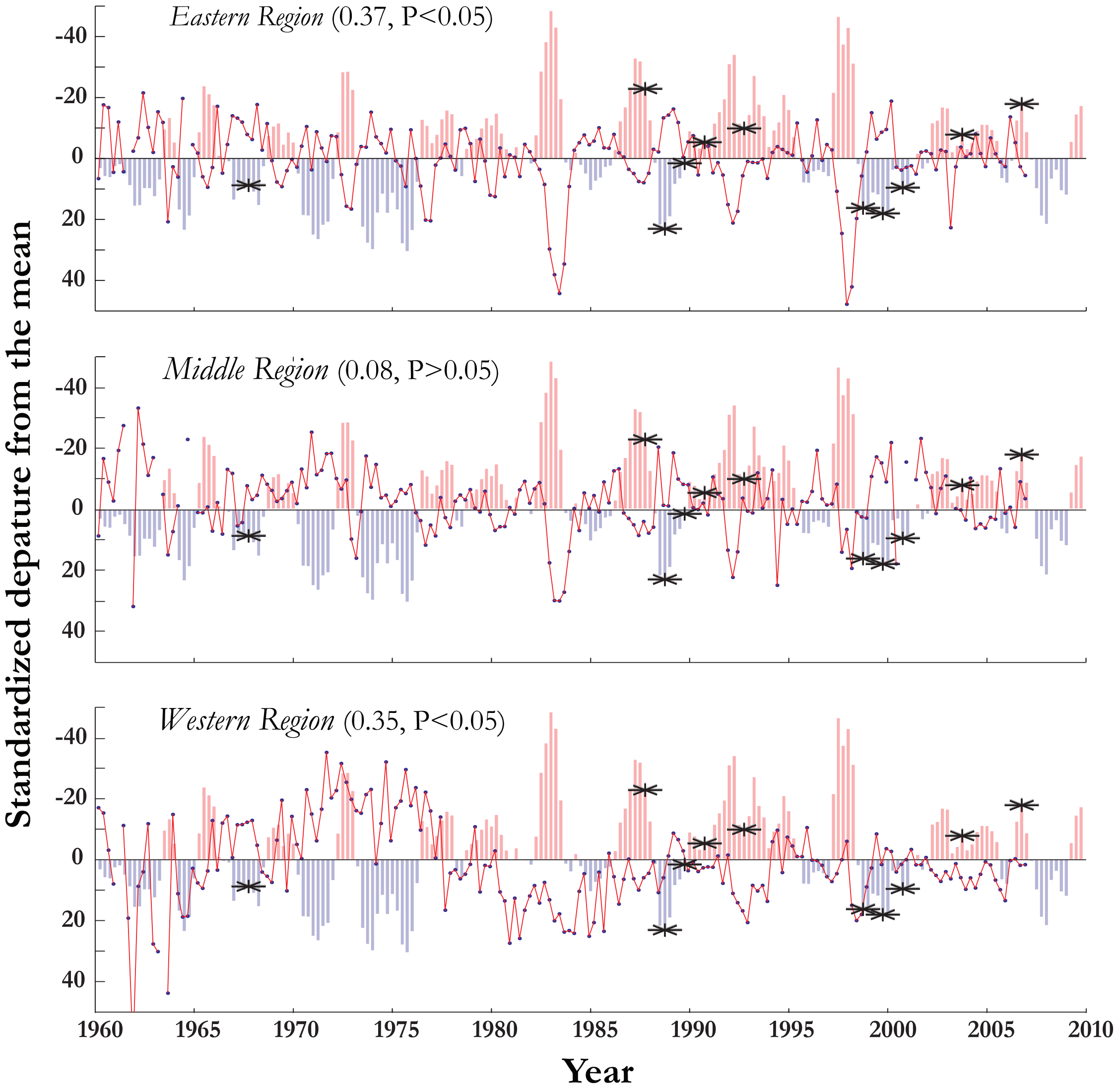


Figure 3.15 Mean seasonal thermocline depth anomalies for the 1960-2006 study period, in each of the regions of the study, superimposed on a time series of seasonal anomalies for a multivariate El Niño Southern Oscillation (ENSO) index that combines sea level pressure, zonal and meridional surface wind components, sea surface temperature, surface air temperature and total cloudiness over the tropical Pacific (NOAA-CIRES Climate Diagnostic Center at the University of Colorado at Boulder). Correlations for thermocline depth anomaly to the ENSO index are on top of each plot; black stars depict fall seasons when cruises took place.

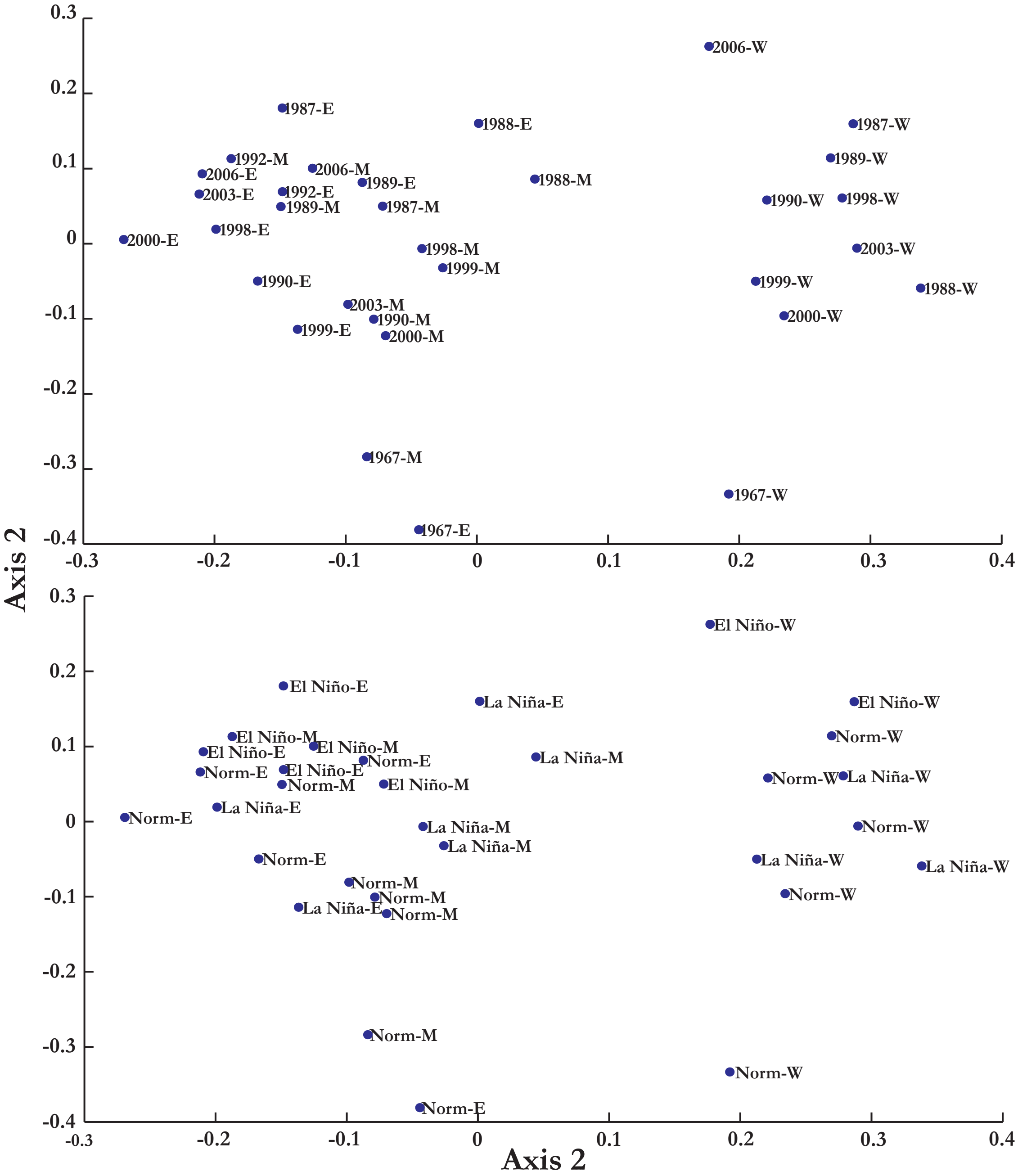


Figure 3.16 Multi-dimensional scaling ordination results for the pooled year-region stations shown as corresponding cruise year (top figure) and ENSO conditions (bottom figure). Stress value for the ordination was 0.1845.

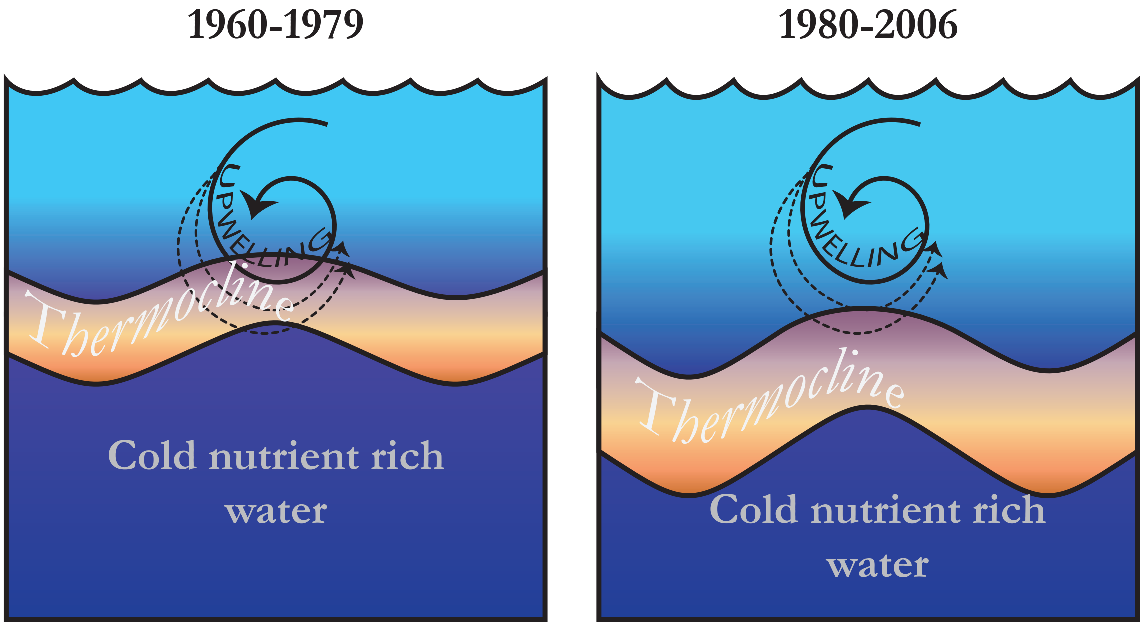


Figure 3.17 Hypothesized change in the state of stratification and thermocline depth for the eastern Pacific warm pool.

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CHAPTER 4

Analysis of long-term diet changes in tropical seabirds using naturally occurring stable isotopes

ABSTRACT

A clear understanding how ecosystems respond to past changes in the environment provides a more accurate interpretation of current ecosystem trends. With this mindset, we set out to investigate the effects of the 1976/77 regime shift in the Pacific Ocean on a tropical pelagic community of apex predators. Using study skins from museum collections from 1960 to 2006, we measured stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes for a suite of ecologically and phylogenetically diverse seabirds from the eastern Pacific warm pool. In this region, seabirds generally forage by depending on subsurface predators to drive prey to the surface or by associating with oceanographic features that increase productivity or aggregate prey in space and time. We found that annual $\delta^{15}N$ means from Sooty Terns' (*Onychoprion fuscatus*) feathers decreased by 2.98‰, while all other species did not show any significant trends over the study period. Annual $\delta^{13}C$ means from feathers of Sooty Terns, Wedge-tailed Shearwaters (*Puffinus pacificus*), Red-footed Boobies (*Sula sula*) and Juan Fernandez Petrels (*Petrodroma externa*) decreased by an average of 1.02‰, at rates between 0.01 and 0.02 $\delta^{13}C$‰ per year^{-1}. Our results do not suggest a response of the seabird community to the 1976/77 regime shift. Instead, they are consistent with a trophic shift and/or change in foraging area for Sooty Terns and a long-term decrease in feather $\delta^{13}C$ for the eastern Pacific warm pool seabird community. This long-term decrease in feather $\delta^{13}C$ is most likely due to the Suess effect and less likely due to a decline in primary productivity of the system. We hypothesize that a deepening trend in thermocline depth in the eastern Pacific warm pool affected Sooty Terns more than other species in the subsurface predator-dependent guild that depend less on smaller subsurface predators like skipjack tuna.

INTRODUCTION

Large marine ecosystems normally fluctuate around mean average climatological states, but on occasion they will change abruptly from one stable state to another. These decadal-scale or longer variations in ocean-atmosphere systems, known as regime shifts, occur in both Pacific and Atlantic Ocean ecosystems (Beaugrand, 2004; Chavez *et al.*, 2003; Mantua *et al.*, 1997). Understanding the ecological effects of past regime shifts on marine ecosystems is crucial to ecologists, since knowledge of past ecosystem response is required to assess the present and forecast future trends with more certainty.

In the eastern Pacific, a well-documented regime shift occurred in 1976/77, when the upper ocean temperature structure shifted from a relatively cool to a warm state (Stephens *et al.*, 2001), leading to an increase in the frequency and intensity of El Niño versus La Niña events (Trenberth and Hoar, 1996). The 1976/77 regime shift of the Pacific Ocean is known to have affected ecosystems across the eastern Pacific (Anderson and Piatt, 1999; Chavez *et al.*, 2003; McGowan *et al.*, 1998), impacting both lower trophic communities and apex predators. These impacts are attributed to bottom-up effects mediated by decreases in nutrient flux into the euphotic zone, resulting from a higher difference in density between the mixed layer and deeper water (Hayward, 1997). Ecosystem response to the regime shift of 1976/77, however, seems to differ with latitude; ecological effects of this shift have been less prominent in tropical ecosystems than in temperate and polar ecosystems of the eastern Pacific, particularly in the open ocean (Fiedler, 2002a). This is thought to be a result of tropical regions having a different frequency mode of temporal variability, one more closely related to the three to five year frequency of the El Niño Southern Oscillation (ENSO) (Lluch-Cota *et al.*, 2003). Interdecadal-scale trends in basin-wide sea surface temperatures in the Pacific have also been reported (Chao, 2000; Tourre *et al.*, 2001). These latter studies suggest that the Pacific-wide interdecadal variability is associated with abrupt regime shifts involving both tropical and extra tropical processes. Therefore, it is unclear whether the difference in documented response in temperate versus tropical systems is a result of a lack of research in what is a more remote and logistically less accessible system or a result of tropical ecosystems being more resilient to changes in climate variability.

Because of their life history and ecology (long-lived, pelagic predators) seabirds integrate information about large-scale oceanographic processes and offer insights into how ecosystems respond to physical change. For example, in the southern region of the California Current, Hyrenbach and Veit (2003) showed that seabird species assemblages changed in response to a ten-year decrease in productivity, from being dominated by cold-water species that dive in pursuit of their prey to warm-water species that predominately feed at the surface. In the northwest Atlantic Montevecchi and Myers (1997) documented how increases in populations of northern gannet, *Sula bassana*, corresponded to a warming trend in sea surface temperatures that they suggest allowed warm-water prey fish to move back into Newfoundland waters and support population growth of gannets. In the Antarctic, Barbraud and Weimerskirch (2001) showed how a 50% decline in emperor penguins, *Aptenodytes forsteri*, corresponded to an anomalously warm period during the late 1970s. All of these studies provide examples of how seabirds can respond to ecological change, yet such studies documenting long-term trends of tropical seabirds are less common. Interpretation of long-term trends for tropical seabirds is limited by a lack of observations and, more importantly, a lack of long-term ecosystem monitoring.

Historical specimens held in museums offer potential data sources for retrospective analyses of ecosystem baselines and considerably reduce uncertainty in determining what mechanisms have driven past ecosystem changes (Jackson *et al.*, 2001). Analyzing preserved specimens (teeth, scales, bones, or feathers) for variability in stable isotope ratios has proven to be a robust approach to retrospectively analyze ecosystem response to environmental change. In the Southern Ocean, for example, Hilton *et al*. (2006) analyzed feather carbon and nitrogen stable isotope ratios to reconstruct a 100-year-plus ecological history of Rockhopper Penguins, *Eudyptes chrysocome*. These authors proposed that long-term decreases in feather carbon isotopic ratios corresponded to decreases in primary productivity and hence carrying capacity of the Southern Ocean ecosystem. In the eastern Pacific, studies off central California (Becker and Beissinger, 2006) and British Columbia, Norris *et al*. (2007) used historical Marbled Murrelet, *Brachyramphus marmoratus*, specimens to show how this species shifted to lower trophic level prey over the past century and linked these shifts to declines in fisheries. And in the north Pacific, retrospective studies analyzing carbon and nitrogen isotopic ratios of pinnipeds (teeth and bone), whale baleen, and seabird feathers over the last 50 years have shown temporal variability, suggesting either anthropogenic effects or changes in diet and/or ecosystem productivity as probable causes (Hirons *et al.*, 2001; Hobson *et al.*, 2004; Newsome *et al.*, 2007; Schell, 2000).

Carbon and nitrogen isotope ratios of marine top predators can vary through time as a result of several factors. Changes in the isotopic composition of dissolved CO_2 and/or nitrogen sources (NO_3^- or N_2-fixation) in the euphotic zone can alter isotopic signatures of primary producers at the base of the food web and be carried up the food chain

(Cullen *et al.*, 2001; Dore *et al.*, 2002). The rate of nutrient (NH_4^+) recycling in oligotrophic waters can change the isotopic composition of source nitrogen (Checkley and Miller, 1989). Sea surface temperature and phytoplankton growth rates can alter carbon fractionation rates of phytoplankton (Laws *et al.*, 1995; Rau *et al.*, 1982), and hence the carbon isotopic composition at the base of the food web, leading some to also infer changes in primary productivity (O'Reilly *et al.*, 2003; Schell, 2000). In addition shifts in the trophic position of prey can cause C and N isotopic ratios of marine top predators to vary (Becker and Beissinger, 2006).

In this study, we test hypotheses regarding the response of an apex predator community in a tropical system to the 1976/77 regime shift of the Pacific Ocean. Our approach was to search for trends in trophic niche space in eight seabird species with diverse ecologies and phylogenies by measuring C and N isotope ratios from specimens collected in the eastern Pacific warm pool during a 46-year period, including 1976. We then investigated species-specific and community-wide changes in these ratios.

Methods

Study Area

Our area of study is the eastern Pacific warm pool. East of 150°W and flanked by the North Equatorial Current (NEC) and Mexico on the north and the equatorial cold tongue to the south (Figure 4.1), the eastern Pacific warm pool is the eastern extremity of a band of tropical surface water carried east by the North Equatorial Countercurrent (NECC). This region has sea surface temperatures greater than 27.5°C, with strong and shallow (< 100 m) thermoclines relative to the rest of the tropical Pacific (Kessler, 2002; Sverdrup *et al.*, 1942). As a result of its location in the zonal axis of the Intertropical Convergence Zone, high precipitation produces relatively low sea surface salinities within this region. Additionally, along 8-10°N, the countercurrent thermocline ridge is associated with a divergence between the NEC and the NECC. This countercurrent thermocline ridge shoals toward the east, breaking the surface near 90°W, where upwelling in the Costa Rica Dome creates an isolated patch of cool water (Fiedler, 2002b). Finally, a notable feature of the study area is the small number of islands in the region.

Focal species

Our sampling group included species from three orders: four Procellariiformes (Juan Fernandez Petrel, *Petrodroma externa*; Wedge-tailed Shearwater, *Puffinus pacificus*; Leach's Storm Petrel, *Oceanodroma leucorhoa*; and Wedge-rumped Storm Petrel, *O. tethys),* two Pelecaniformes (Great Frigatebird *Fregata minor* and Red-footed Booby *Sula sula)* and 2 Charadriiformes (Sooty Tern *Onychoprion fuscatus* and Brown Noddy *Anous stolidus*), and two foraging guilds. Six of the focal species (*P. externa*, *P. pacificus*, *F. minor*, *S. sula*, *O. fuscatus,* and *A. stolidus*) feed in multispecies flocks and form part of the subsurface predator-dependent community in the eastern tropical Pacific. Seabirds in this guild rely on underwater predators, mainly spinner and spotted dolphins (*Stenella longirostris* and *S. attenuata,* respectively), and yellowfin and skipjack tuna (*Thunnus albacares* and *Katsuwonus pelamis,* respectively), to drive prey to the surface (Ballance *et al.*, 1997). Species in the subsurface predator-dependent seabird community generally feed on exocoetids (flying fishes), hemirhamphids (half-beaks), and epipelagic cephalopods (e.g., ommastrephid squids) by surface seizing and plunging. The remaining two species (*O. leucorhoa* and *O. tethys*) feed in single species flocks or solitarily, by associating with oceanographic features that either increase productivity or aggregate prey in space and or time. These species generally feed on small mesopelagic fishes (e.g., phosichthyids and myctophids) and small planktonic prey (e.g. *Velella* sp., *Porpita* sp., and flying fish eggs) by pattering and surface seizing (Ashmole and Ashmole, 1967; Ballance and Pitman, 1998; Spear *et al.*, 2007). All species are residents (reside within the study area year-round) or seasonal residents (inhabit the study area as non-breeders) and are not central-place foragers as non-breeders. This is particularly true in the eastern Pacific warm pool because of the relative scarcity of islands.

Sample collection and stable isotope analysis

We sampled contour body feathers all taken from the belly of adult specimens collected within the eastern Pacific warm pool between 1960 and 2006, held in ornithological collections throughout the United States and Mexico (Figure 4.2). Feathers were thoroughly cleaned with a 2:1 methanol/chloroform solution and dried at 40° C for 48 hours. Stable isotope ratios measured from feathers will reflect diet during the period of feather growth (Hobson, 1999). Because our goals were to estimate the diet of seabirds wintering in the study area, we used only the most recent growth portion of the feather. We therefore sampled growing feathers when possible and only used the growing tip to determine isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) expressed relative to a known standard, Pee Dee Belemnite and atmospheric nitrogen for carbon and nitrogen, respectively. Approximately 1.2–1.5 mg of feather calamus was cut into small fragments, encapsulated into tin capsules, and analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility at the University of California, Davis. Isotope ratios are presented in standard δ notation and parts per thousand (‰), expressed relative to standards according to the following equation using nitrogen as an example:

$$\delta = \left(\frac{\frac{^{15}\mathrm{N}}{^{14}\mathrm{N}}\,sample}{\frac{^{15}\mathrm{N}}{^{14}\mathrm{N}}\,standard} - 1 \right) \times 1000$$

Data analysis

We tested our hypothesis of non-random change in annual mean feather δ^{13}C and δ^{15}N values through time for each species by fitting linear least squares regression to both isotope ratios as a function of time. To test more directly our hypotheses regarding species-specific and community-wide changes in trophic niche after the 1976/77 regime shift, we converted our data to polar coordinates and applied circular statistics (Batschelet, 1981) to examine the question of whether groups of samples separated in time pre- and post-regime change differed with respect to both δ^{13}C and δ^{15}N. To do this, we first calculated the δ^{13}C and δ^{15}N centroid of the entire seabird community by obtaining the mean δ^{13}C and δ^{15}N values for all species combined (Layman *et al.*, 2007). Second, we calculated the difference between this centroid and the δ^{13}C and δ^{15}N values for each species. Third, we transformed all data into polar coordinates, obtaining a direction and Euclidean distance from the centroid. This resulted in a mean magnitude and direction (0 to 360°) in trophic niche space for each species sampled over the 46-year period. We tested our hypotheses about species-specific and community-wide changes in trophic niche subsequent to the 1976/77 regime shift by applying a randomized intervention analysis (RIA) to each species' time series of mean annual directional angles in C-N food web space. RIA can detect step changes in manipulated ecosystems using time series data from before and after an ecosystem manipulation (Carpenter *et al.*, 1989). Here, we view the 1976/77 regime shift as the ecosystem manipulation, and the test statistic is the absolute value of the difference between the mean directional angles from before and after 1977 (Figure 4.3).

For each species, we calculated the probability of this statistic being more extreme than that observed under the null hypothesis (no change after 1977) with a Monte Carlo test. For this test, we randomly assigned directional angles to either before or after 1977, regardless of their position in the time series, and calculated the absolute values of the differences between mean directional angles before, $\overline{\mathrm{DA}}(pre)$, and after, $\overline{\mathrm{DA}}(post)$, for 10,000 iterations. The null model assumes that all possible differences of mean directional angles from before and after random sequences of the time series have an equal opportunity of being observed (Manly, 2007), and therefore a distribution of the test statistic can be determined. The proportion of $\left|\overline{\mathrm{DA}}(pre)-\overline{\mathrm{DA}}(post)\right|$ that exceeds the actual value is the approximate probability that the magnitude of change seen in the test statistic is random. A low probability suggests that a non-random change occurred following the hypothesized ecosystem manipulation. We replicated this procedure for annual mean feather δ^{13}C and δ^{15}N values as well.

RESULTS

Peach tree leaves and bovine liver standards run every 12 samples determined analytical precision (± standard deviation) of (± 0.05‰) for δ^{13}C and (± 0.16‰) for δ^{15}N. C to N ratios of all samples ranged between 2.6 to 3.7 (3.26 mean, SD 0.11) and were within the range characterizing unaltered pure feather keratin (Block, 1939), indicating feather decomposition did not occur during long-term storage. If feather keratin had undergone decomposition during long-term storage, measured C/N ratios would be larger than those of unaltered keratin (Kim *et al.*, 2001). It is likely that feathers retained their pristine C and N isotope composition as a result of museum archiving methods.

C-N food web space of all species and all years

We found patterns in directional angles in C-N food web space (Watson-William's Test, $F_{7,125}$=13.69, P<0.0001) and single δ^{13}C (ANOVA, $F_{7,125}$=5.58, P<0.0001) and δ^{15}N values (ANOVA, $F_{7,125}$=58.13, P<0.0001). Post hoc Tukey HSD multiple comparison tests indicated that both storm petrels had significantly lower δ^{13}C values than all other species. Moreover, Juan Fernandez petrels had significantly higher δ^{15}N values than all other species. Three groups of C-N combinations were evident: 1) two storm petrels with the lowest δ^{13}C values, 2) Juan Fernandez petrels alone with the highest δ^{15}N values, and 3) the five remaining species in one group with higher δ^{13}C values but lower δ^{15}N values (Figures 4.4 and 4.5).

Directional angles in C-N food web space of all species were also separated by feeding guild. As a group, storm petrels had directional angles between 270 and 300° (Figure 4.5), depicting trophic niches depleted in δ^{13}C and enriched with δ^{15}N. All other species had directional angles in the opposite direction, generally pointing toward 90°, suggesting enrichment in δ^{13}C, while only Juan Fernandez petrels and Brown Noddies had directional angles suggesting δ^{15}N enrichment or higher trophic level relative to the sampled community. All species belonging to the subsurface predator-dependent community had directional angles pointing toward 90° and all within 82° of each other, while both storm petrels pointed in the opposite direction and within 15° of each other.

Temporal trends in C-N food web space

Mean annual $\delta^{13}C$ declined over time more than expected by chance alone for four of the eight species in our study (Table 4.1 and Figure 4.6). Juan Fernandez Petrels, Wedge-tailed Shearwaters, Red-footed Boobies and Sooty Terns all had negative trends in mean annual $\delta^{13}C$ values since 1960. On average, feather $\delta^{13}C$ for these four species decreased by 1.13‰, at rates between 0.01 and 0.02 $\delta^{13}C$‰ year^{-1}. Red-footed Boobies decreased the most and Sooty Terns the least. Leach's and Galapagos Storm Petrels, Great Frigatebirds, and Brown Noddies did not show non-random changes in annual mean feather $\delta^{13}C$ values. Only Sooty Terns declined in annual mean feather $\delta^{15}N$ values more than expected by chance alone: 2.98 $\delta^{15}N$‰ in the 1960–2006 period at a rate of -0.06 $\delta^{15}N$‰ year^{-1} (Table 4.1 and Figure 4.6). All other species did not show significant long-term changes in annual mean feather $\delta^{15}N$ values.

Over the 46-year span of our study, all nine species varied interannually in their directional angles in C-N food web space (Table 4.2 and Figure 4.7). Brown Noddies and Great Frigatebirds varied the most interannually (angular deviation 62.1 and 53.3°, respectively), while Red-footed Boobies and both storm petrels varied the least (angular deviation 28.6 and ~35°, respectively). In this calculation, angular deviation ranges from a minimum of 0 to a maximum of 81.03° (Batschelet, 1981). Compared between feeding guilds, storm petrels varied less interannually than species belonging to the subsurface predator-dependent community. Particularly for Juan Fernandez Petrels and Wedge-tailed Shearwaters, angular deviation increased from the 1960s and 1970s to the 1980s and after (Table 4.2). All species, with the exception of Brown Noddies, had less angular dispersion during the 1960s when compared to later decades.

Effects of the 1976/77 regime shift

Effects of the 1976/77 regime shift in mean annual $\delta^{13}C$ and annual directional angles in C-N food web space were detected by the RIA at the 5% level, while no effects in mean annual $\delta^{15}N$ were found (Table 4.3). Juan Fernandez Petrels, Wedge-tailed Shearwaters, and Sooty Terns all had significant values (<5%) in the RIA of mean annual $\delta^{13}C$, while all other species did not. Wedge-tailed Shearwaters, Great Frigatebirds, Sooty Terns, and Brown Noddies all had significant P values from corresponding RIA of mean annual directional angles, suggesting a difference in C-N food web space before and after 1976 large enough to not occur by chance alone. However, for these four species, only Wedge-tailed Shearwaters and Sooty Terns also had significant P values for the RIA of mean annual $\delta^{13}C$. This is likely the result of the sample size of Great Frigatebirds and Brown Noddies in our data set, making their results less robust.

DISCUSSION

We found inconsistent indications of a step change in the seabird community as a result of the 1976/77 regime shift, as our analysis revealed long-term changes in species-specific mean annual feather $\delta^{15}N$ and $\delta^{13}C$ values only for Sooty Terns. Nevertheless, we found significant declines, an average of 1.02‰ year^{-1}, in species-specific annual mean feather $\delta^{13}C$ for four species: Sooty Terns, Wedge-tailed Shearwaters, Red-footed Boobies, and Juan Fernandez Petrels. These changes in $\delta^{13}C$ were more common in subsurface predator-dependent species than in species that do not rely on subsurface-predators for food availability. In contrast, both storm petrels showed little or no temporal variability in feather compositions for either isotope.

In the following discussion, we will first interpret $\delta^{13}C$ and $\delta^{15}N$ patterns in food web space for our suite of seabird species. Second, we will consider three processes that may account for temporal changes in stable isotope ratios of species in our study: (1) changes in prey abundance or availability affecting trophic position, (2) changes in foraging location, and (3) changes in the isotopic composition at the base of the food web.

Guild-specific isotopic niches

There was a clear separation in C-N trophic food web space of the two seabird feeding guilds (Figures 4.4 and 4.5), with the subsurface predator-dependent guild separating from the two storm petrels that generally feed solitarily on plankton and micronekton. C and N isotope ratios from resident and seasonal resident species within the same feeding guild were not significantly different, indicating that differences between isotopic niches of the two feeding guilds are reflect foraging behavior in the eastern Pacific warm pool. An assumption for this study was that no molt-breeding overlap occurred in all species, making the isotopic signal feathers reflect that of the non-breeding foraging grounds. We are aware that individual variation in the timing and extent of molt in our focal species is far from well understood and perhaps could account for some of the variability in our results. Most seabirds that travel long distances to winter in the tropics, however, molt primarily during their non-breeding period, because molting, breeding, and migrating are all energetically demanding (Bridge, 2006; Marshall and Serventy, 1956). Isotopic compositions of feathers should therefore reflect their diet during feather growth (Hobson and Clark, 1992) in their non-breeding period.

Separation of the two feeding guilds was more on the basis of $\delta^{13}C$ and to a lesser degree $\delta^{15}N$. As a group, both storm petrels overlapped in $\delta^{15}N$ values with species in the subsurface predator-dependent guild. This could be a result of storm petrels frequently feeding on mesopelagic fishes (Pitman and Ballance, 1990; Spear *et al.*, 2007) with high trophic status and $\delta^{15}N$ values. Storm petrels also frequently feed in convergence areas that concentrate their planktonic or micronektonic prey (reviewed in Ballance *et al.* 2006). These regions are most likely outside of the warm pool in the equatorial cold tongue, which is known to have lower $\delta^{13}C$ signatures because of upwelled dissolved inorganic carbon with low $\delta^{13}C$ (Gruber *et al.*, 1999). For these reasons, we propose that the isotopic information integrated by storm petrels may reflect factors outside of our study area. Additionally, species with the lowest temporal sampling frequency (Great Frigatebirds and Brown Noddies) did not show any temporal trends. We speculate this to be a result of low sample size for these two species. The following discussion will therefore only refer to four species in the subsurface predator-dependent guild: Juan Fernandez Petrels, Wedge-tailed Shearwaters, Red-footed Boobies, and Sooty Terns, which we propose adequately represent the eastern Pacific warm pool seabird community.

Diet changes

Changes in the seabird prey field of the eastern Pacific warm pool as a result of the 1976/77 regime shift may have caused the higher variability of feather isotopic signatures for Sooty Terns. An increase in $\delta^{15}N$ of 3 to 5‰ along with 1‰ in $\delta^{13}C$ indicate an increase of one trophic level (Peterson and Fry, 1987). If the mean decrease of 1.0‰ in $\delta^{13}C$ seen for Juan Fernandez Petrels, Wedge-tailed Shearwaters, Red-footed Boobies, and Sooty Terns (Figure 4.6) was due to prey switching, then it should have been accompanied by a decrease in $\delta^{15}N$. A lack of covariance in $\delta^{13}C$ and $\delta^{15}N$ decreases does not support a prey-switching hypothesis for all of these species except Sooty Terns. Sooty Terns did decrease in mean annual feather $\delta^{15}N$ values by 2.98‰ along with a decrease in $\delta^{13}C$ of 0.72‰. This supports a prey-switching hypothesis for Sooty Terns, as does the RIA results of Sooty Terns, which suggests that differences between directional angles in C-N food web space before and after 1976 are large enough to be considered non-random.

We propose two scenarios incorporating possible trophic shifts explaining the observed temporal changes in Sooty Terns $\delta^{13}C$ and $\delta^{15}N$ isotopic values. Of all species in the subsurface predator-dependent feeding guild, Sooty Terns rarely feed independently from tuna, since they are unable to capture prey deeper than a few centimeters below the surface (Au and Pitman, 1986; Gould, 1974). In addition, because of their smaller size, they have lower cost of flight and take smaller prey than the other species in the subsurface predator-dependent feeding guild. As a result, Sooty Terns venture farther westward in the study area in search for food associating with smaller tuna (i.e., skipjack and smaller yellowfin) than the larger yellowfin tuna of the middle and eastern portion of the study area (Ballance *et al.*, 1997).

The first scenario proposes that deeper thermoclines in the eastern Pacific as a result of the 1976/77 regime shift have caused skipjack tunas to spend less time near the surface searching for prey (Forsbergh, 1989) making fewer prey available for Sooty Terns. With the frequency of El Niño events increasing after 1977 (Trenberth and Hoar, 1996), it is possible that Sooty Terns have had to use other prey sources more so after 1977 than in prior years. If this explanation is valid, however, then similar isotope trends for the other species in the subsurface predator-dependent feeding guild should have resulted. In the eastern Pacific yellowfin tuna forage similarly to skipjack tuna (Alverson, 1963) and would likely react in the same way to the deeper thermoclines induced by El Niños. A second, more plausible scenario is that skipjack tuna biomass varied more from 1975 to 2003 than that of yellowfin tuna and altered the prey field of Sooty Terns more so than that of the other subsurface predator-dependent species (Maunder and Harley, 2005a; Maunder and Harley, 2005b).

Foraging location

Oceanic biogeographic patterns in C and N sources for the euphotic zone can create different isotopic ratios of prey and their predators. Such differences have been documented for seabirds in the North Pacific (Hobson *et al.*, 2004) and the southern coast of Africa (Jaquemet and McQuaid, 2008). In general marine phytoplankton $\delta^{13}C$ decreases poleward from equatorial waters as a result of water temperature and dissolved inorganic carbon availability (Goericke and Fry, 1994), while phytoplankton $\delta^{15}N$ varies according to the primary nitrogen source during photosynthesis: nitrate, ammonium, or N_2 fixation (Montoya, 2008; Wada and Hattori, 1991). Phytoplankton $\delta^{13}C$ in our study area would probably have little spatial variation because of the narrow latitudinal and temperature variation of the region. On the other hand, phytoplankton $\delta^{15}N$ would likely vary zonally with depth of the thermocline. Deeper thermoclines in the western portion of our study area (Fiedler and Talley, 2006) would decrease the upward flux of deep-water nitrate into the euphotic zone, changing the main nitrogen source from nitrate to regenerated ammonium or N_2 fixation (Dore *et al.*, 2002). Phytoplankton from nitrate-depleted waters where N_2 fixation or recycling is the primary nitrogen source are isotopically lighter (Wada and Hattori, 1991). It is therefore possible that the significant decrease in Sooty Tern feather $\delta^{15}N$ signatures is a result of this species consistently foraging farther west in the study area over time, where the phytoplankton community structure is thought to be changing to one dominated by N_2-fixing bacteria (Karl *et al.*, 2001) in an expanding oligotrophic system (Polovina *et al.*, 2008).

Baseline changes in carbon and nitrogen

A third explanation accounting for declines in feather $\delta^{13}C$ values is that the stable isotopic composition at the base of the food web has changed over time. Isotopic composition of phytoplankton reflects the isotopic signature of dissolved inorganic carbon, as well as carbon fractionation during cell growth. Recently, two hypotheses have been proposed to explain temporal declines in $\delta^{13}C$ of apex predators in ecosystems of the north Pacific. The first proposes that temporal decreases of $\delta^{13}C$ composition at the base of the food web in large bodies of water are related to declines in cell growth rates and hence primary productivity in the north Pacific (Hirons *et al.*, 2001; Schell, 2000). This hypothesized mechanism is based on experiments illustrating the relationship of phytoplankton growth rate and dissolved CO_2 concentration as a linear function of the carbon isotope fractionation associated with photosynthetic fixation (Bidigare *et al.*, 1997; Laws *et al.*, 1995). Because this linear relationship only holds when intracellular CO_2 transport is supplied by diffusion and not active transport, the above hypothesis assumes that species composition of the phytoplankton remained constant over time, since changes in species composition would change average cell size and therefore alter fluxes of CO_2 into and out of cells (Popp *et al.*, 1998). A second assumption is that dissolved CO_2 concentrations have also remained constant over time. If these two assumptions are valid, then the average 46-year decrease of 1.02‰ in seabird feather $\delta^{13}C$ in our study suggests a long-term decline in productivity in the eastern Pacific warm pool ranging from 10 to 15%.

The second hypothesis proposes that the invasion of isotopically light CO_2 from combustion of fossil fuels, the Suess effect, into ocean surface waters has changed phytoplankton $\delta^{13}C$ composition enough to penetrate top predators (Cullen *et al.*, 2001). Composition of $\delta^{13}C$ in dissolved inorganic carbon in surface waters of the Pacific basin is estimated to have decreased because of fossil fuel emissions at a rate of -0.018‰ per year between 1970 and 1990 (Quay *et al.*, 2003). Basin-wide patterns of ocean mixing and productivity will cause this rate of temporal change in $\delta^{13}C$ composition of dissolved inorganic carbon to vary spatially in the surface ocean, with the largest changes occurring in subtropical gyres and the smallest changes in equatorial upwelling areas and subpolar oceans (Gruber *et al.*, 1999). The decrease in dissolved inorganic carbon $\delta^{13}C$ in surface waters in the eastern Pacific warm pool would probably be near the -0.025‰ per year estimate measured near Hawaii by Gruber *et al.* (Gruber *et al.*, 1999). This implies that for our 46-year study, the Suess effect accounts for decreases in $\delta^{13}C$ from 0.8 to 1.2‰. Species-specific mean annual $\delta^{13}C$ feather values in our study declined from 0.72 to 1.25‰, well within the range of change that can be accounted for by the Suess effect.

CONCLUSION

In summary, we found changes in $\delta^{13}C$ and $\delta^{15}N$ for Sooty Terns suggesting changes in trophic level and foraging region, and changes in feather $\delta^{13}C$ signatures for Juan Fernandez Petrels, Wedge-tailed Shearwaters, Red-footed Boobies, and Sooty Terns. The latter are consistent with the Suess effect. Furthermore, while results from our study are consistent with other studies showing long-term decreases in $\delta^{13}C$ signatures of marine vertebrates in the Pacific (Hirons *et al.*, 2001; Hobson *et al.*, 1994; Newsome *et al.*, 2007; Schell, 2000), this is the first study to document such a decrease in a tropical pelagic ecosystem. We hypothesize that Sooty Terns have shifted their foraging grounds toward the western part of our study, where ecosystem primary productivity is increasingly based on ammonium recycling or N_2 fixation, and they are on average feeding less on prey being driven to the surface by subsurface predators. Devney *et al.* (2009) report a negative correlation between Sooty Tern breeding effort and thermocline depth in the western tropical Pacific. We propose that deepening thermoclines in the eastern Pacific warm pool are affecting Sooty Tern trophic structure and foraging areas, more so than other seabird species in its feeding guild, by forcing Sooty Terns to forage farther west. A possible test of our hypothesis could be to apply compound-specific stable isotope analyses to our feather samples and look for variations of baseline $\delta^{15}N$ from source amino acids that are not affected by trophic status (McClelland and Montoya, 2002). This could specifically test the prey-switching scenario our data suggests for Sooty Terns. Furthermore, preserved specimens from another apex predator in the region (e.g., teeth from dolphin by-catch in the yellowfin tuna fishery) could offer another avenue to see if the Suess effect has influenced isotopic ratios of yet another tropical marine vertebrate. Our results do not support the hypothesis of a community-wide response of top predators of the eastern Pacific warm pool to the 1976/77 regime shift.

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Table 4.1 Least square regression fits for mean annual $\delta^{13}C$ and $\delta^{15}N$ feather values as a function of time; n is the number of years sampled over the 46-year study period.

		$\delta^{13}C$ as a function of time			$\delta^{15}N$ as a functioin of time		
Species	n	r^2	F	P	r^2	F	P
Juan Fernandez Petrel	16	0.50	14.21	0.002	0.12	1.98	0.181
Wedge-tailed Shearwater	24	0.41	15.50	0.001	0.01	0.14	0.717
Leach's Storm Petrel	24	0.05	1.19	0.287	0.01	0.20	0.659
Galapagos Storm Petrel	18	0.02	0.36	0.559	0.01	0.09	0.773
Red-footed Booby	13	0.58	15.38	0.002	0.19	2.52	0.141
Great Frigatebird	9	0.14	1.14	0.321	0.32	3.24	0.115
Sooty Tern	19	0.28	6.47	0.021	0.22	4.76	0.043
Brown Noddy	10	0.17	1.62	0.239	0.18	1.74	0.223

Table 4.2 Mean directional angles in C-N food web space and angular deviations binned by decade; n is the number of years sampled per decade.

Species	1960-1969			1970-1979			1980-1989			1990-1999			2000-2010		
	n	Direction (μ)	Angular deviation	n	Direction (μ)	Angular deviation	n	Direction (μ)	Angular deviation	n	Direction (μ)	Angular deviation	n	Direction (μ)	Angular deviation
Juan Fernandez Petrel	6	31.0	16.3	1	92.7	-	6	56.4	36.9	2	93.7	70.4	1	362.2	-
Wedge-tailed Shearwater	9	95.1	34.8	5	111.1	49.2	5	161.5	44.3	3	157.1	60.9	2	52.4	71.9
Leach's Storm Petrel	5	307.0	24.2	9	256.1	42.9	6	260.9	29.9	3	266.3	5.2	1	267.5	-
Galapagos Storm Petrel	7	297.6	19.8	1	336.6	-	8	290.1	42.8	1	243.5	0.0	1	286.6	-
Red-footed Booby	4	127.9	18.7	4	93.3	31.0	3	131.4	16.8	-	-	-	2	88.3	11.1
Great Frigatebird	1	78.5	-	2	64.7	18.5	2	79.6	57.4	1	167.3	0.0	3	137.2	58.0
Sooty Tern	7	69.4	35.3	3	135.0	21.2	1	102.4	0.0	5	144.6	51.0	3	136.3	63.1
Brown Noddy	4	106.3	60.4	1	49.4	0.0	-	-	-	1	153.1	0.0	4	174.7	57.3

Table 4.3 *P* values from the Random Intervention Analyses (RIA) for mean annual $\delta^{13}C$ and $\delta^{15}N$ feather values, and mean annual directional angles in Carbon-Nitrogen food web space. Each column gives probabilities for the differences before and after the 1976-77 regime shift of each test statistic, being more extreme that what can be expected chance alone; n is the number of years sampled over the 46-year study period and an underline denotes $P < 0.05$.

		RIA procedure		
Species	n	$\left\lvert \overline{\delta^{13}C}(pre) - \overline{\delta^{13}C}(post) \right\rvert$	$\left\lvert \overline{\delta^{15}N}(pre) - \overline{\delta^{15}N}(post) \right\rvert$	$\left\lvert \overline{DA}(pre) - \overline{DA}(post) \right\rvert$
Juan Fernandez Petrel	16	$\underline{0.035}$	0.256	0.612
Wedge-tailed Shearwater	23	$\underline{0.004}$	0.777	$\underline{0.030}$
Leach's Storm Petrel	24	0.063	0.563	0.718
Galapagos Storm Petrel	18	0.926	0.607	0.332
Red-footed Booby	13	0.081	0.716	0.896
Great Frigatebird	9	0.660	0.267	$\underline{0.025}$
Sooty Tern	19	$\underline{0.047}$	0.125	$\underline{0.044}$
Brown Noddy	10	0.462	0.268	$\underline{0.020}$

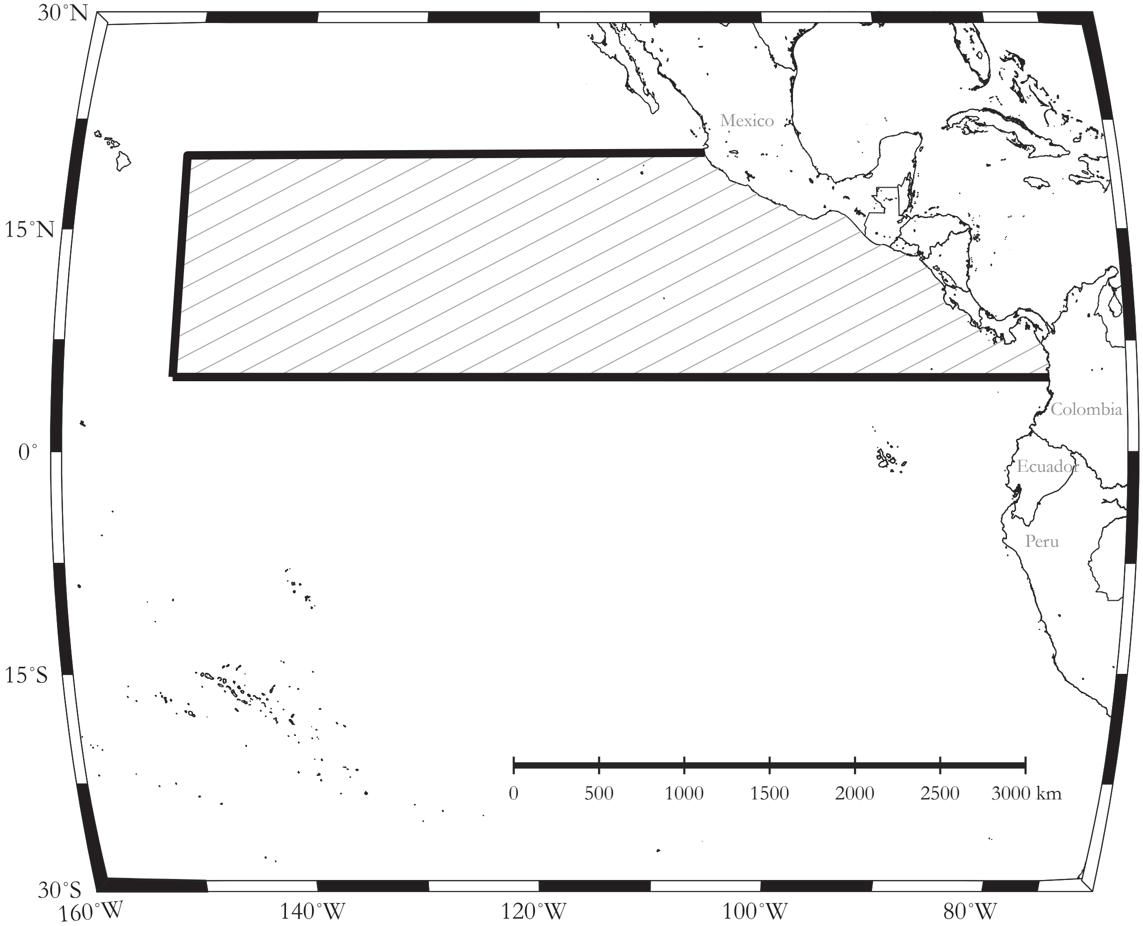


Figure 4.1 Geographical location of the study area, the eastern Pacific warm pool.

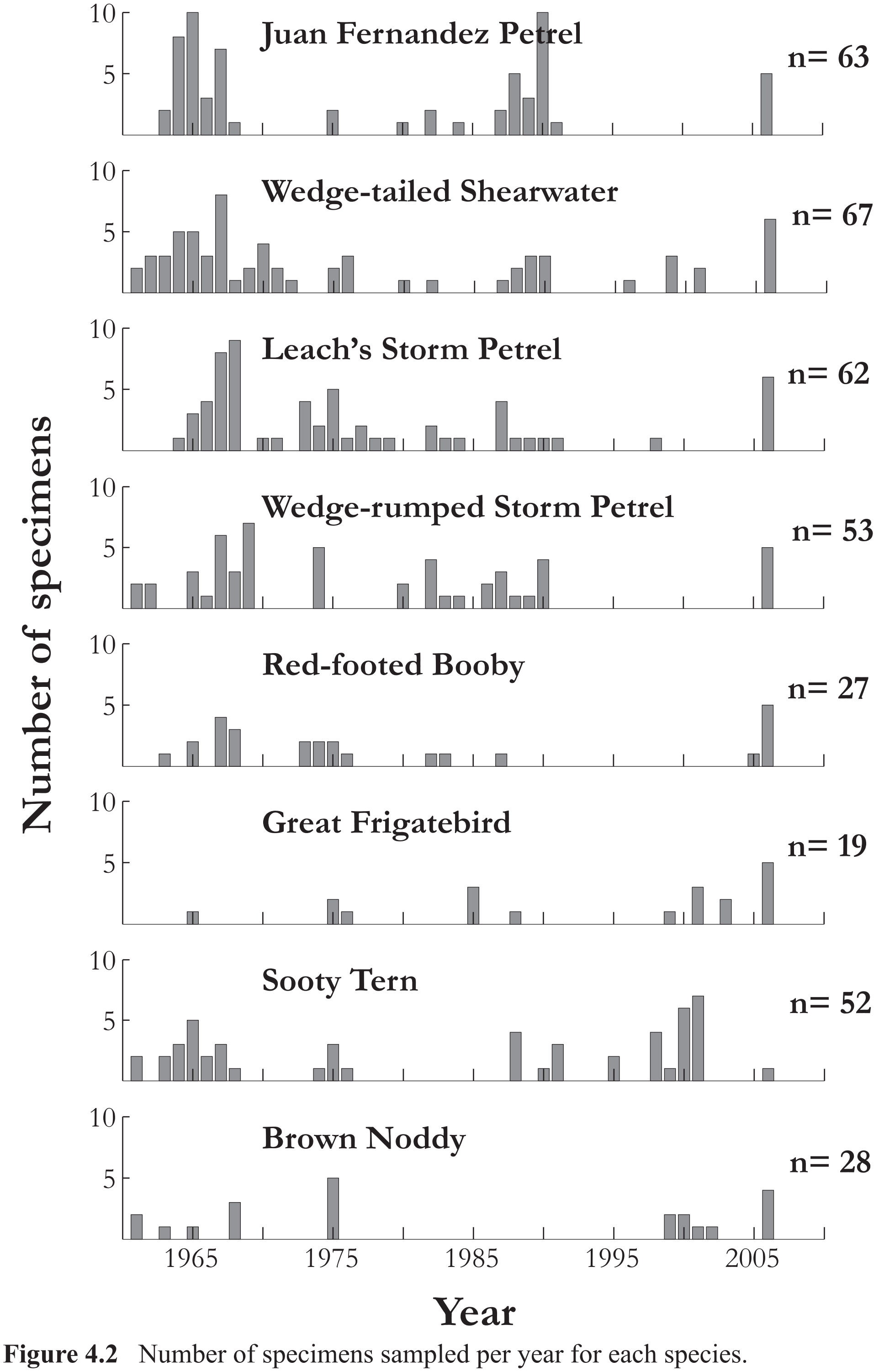


Figure 4.2 Number of specimens sampled per year for each species.

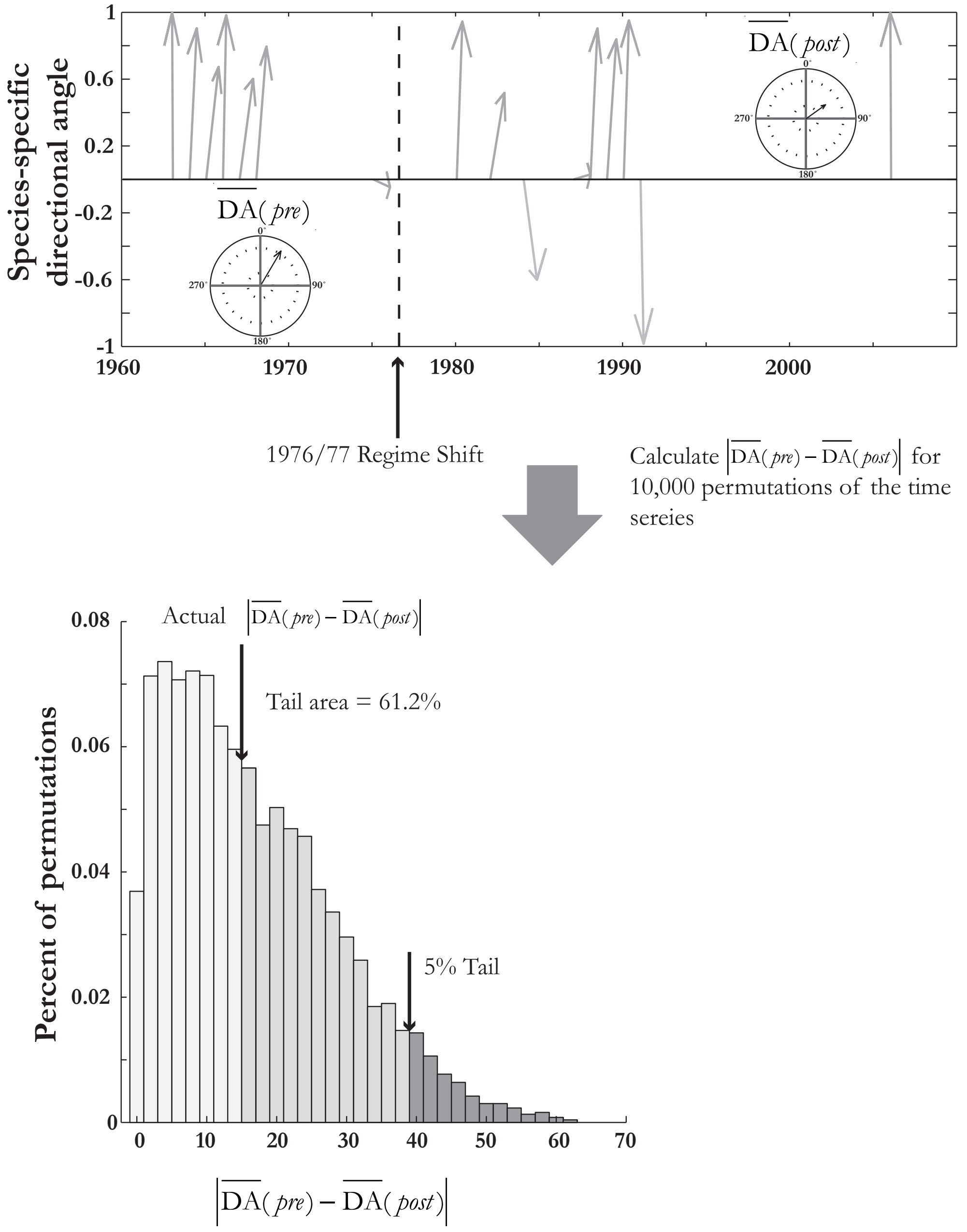


Figure 4.3 Flow chart of calculations for the Randomized Intervention Analysis. The test statistic is the actual difference between species-specific mean directional angles before and after the 1976/77 regime shift (shown as polar plots in the angle time series), and its distribution is produced by calculating absolute directional differences for all possible rearrangements of the time series. In this case the hypothesis stating species-specific changes in trophic niche after the 1976/77 regime shift is rejected because the proportion of randomized differences that exceeds the actual difference is 61.2%, much greater than 5% (using a 95% confidence level).

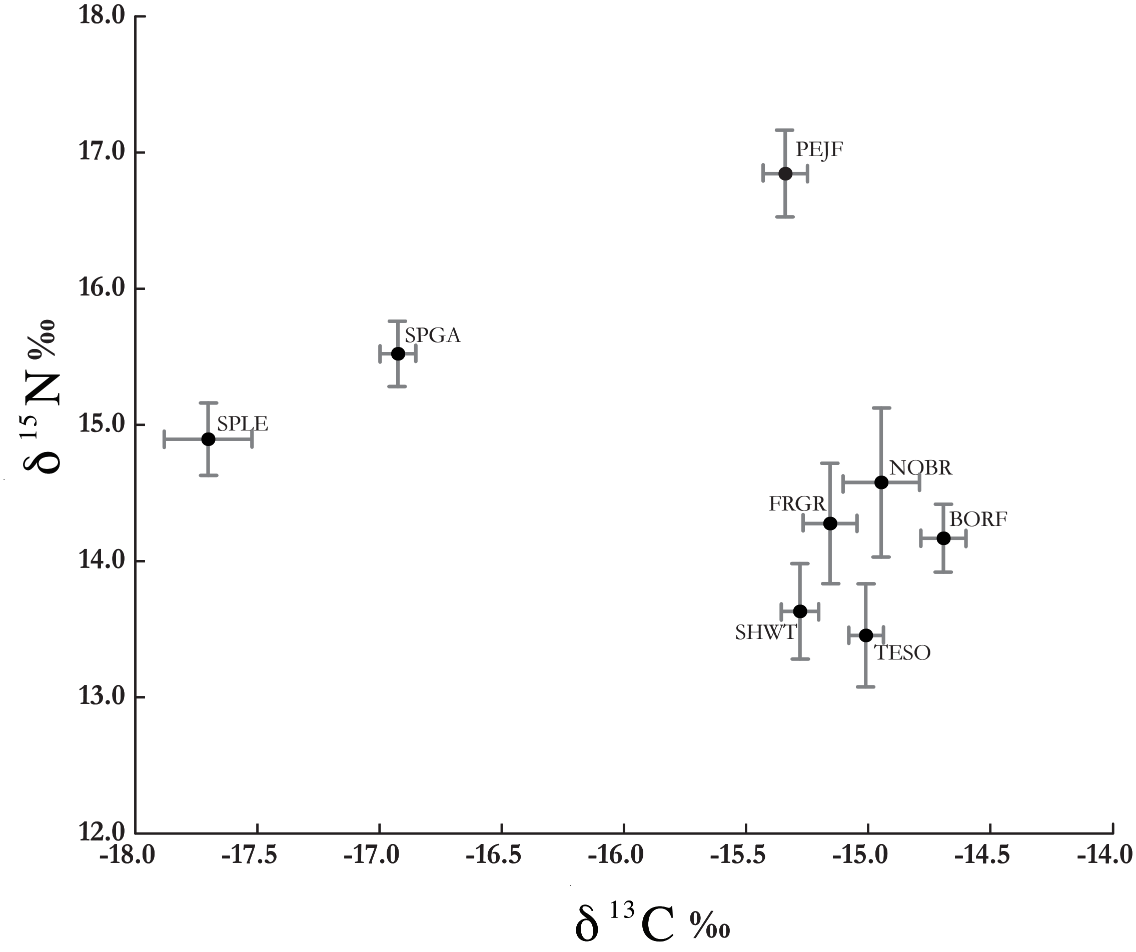


Figure 4.4 Trophic niches of all species in two-dimensional C-N food web space. Each point represents the mean δ13C and δ15N value (±SE from the mean) for a given species for all years. Species abbreviations: PEJF, Juan Fernandez petrel; SHWT, Wedge-tailed Shearwater; SPLE, Leach's Storm Petrel; SPGA, Galapagos Storm Petrel; BORF, Red-footed Booby; FRGR, Great Frigatebird; TESO, Sooty Tern; NOBR, Brown Noddy.

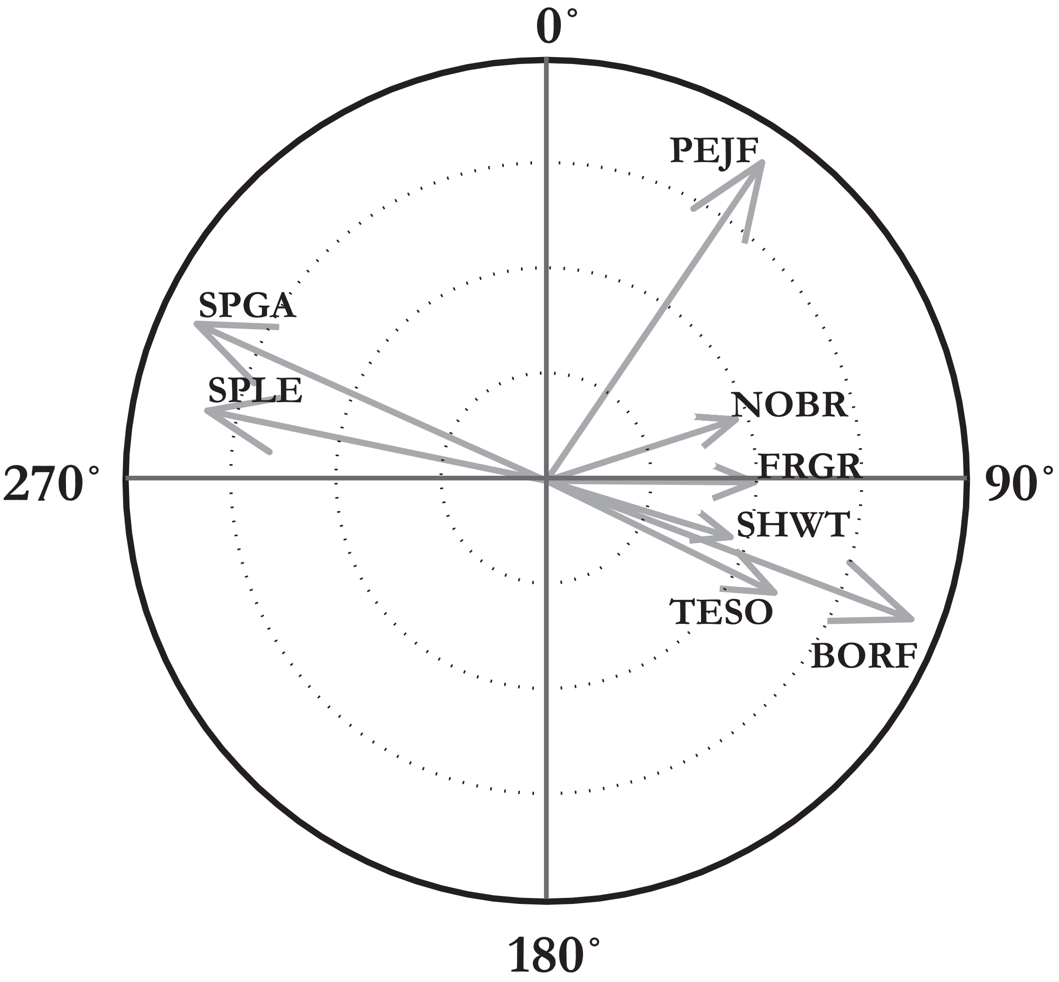


Figure 4.5 Species-specific mean annual directional angles in C-N food web relative to the community mean (all eight species). Species abbreviations as in Figure 4.4.

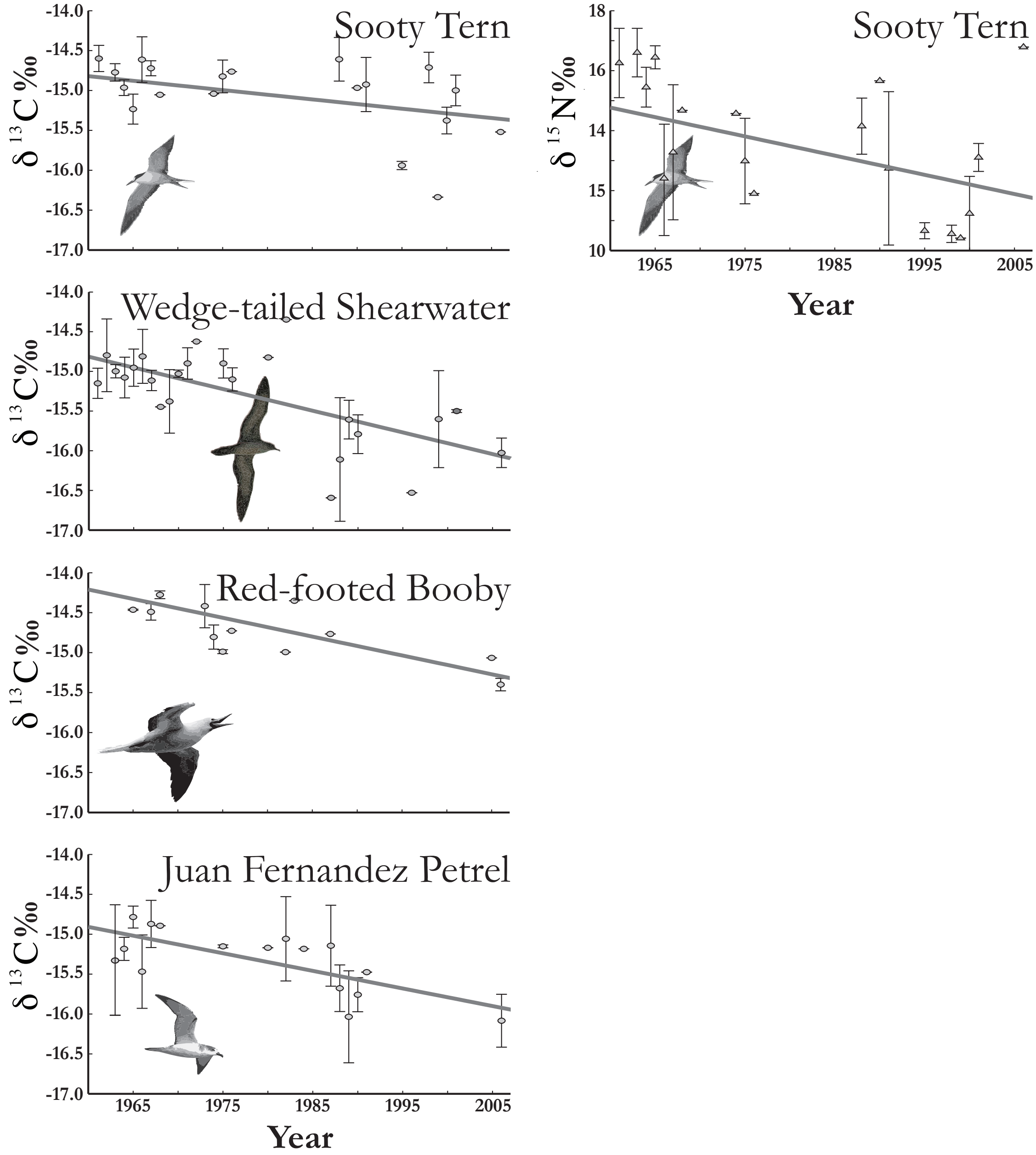
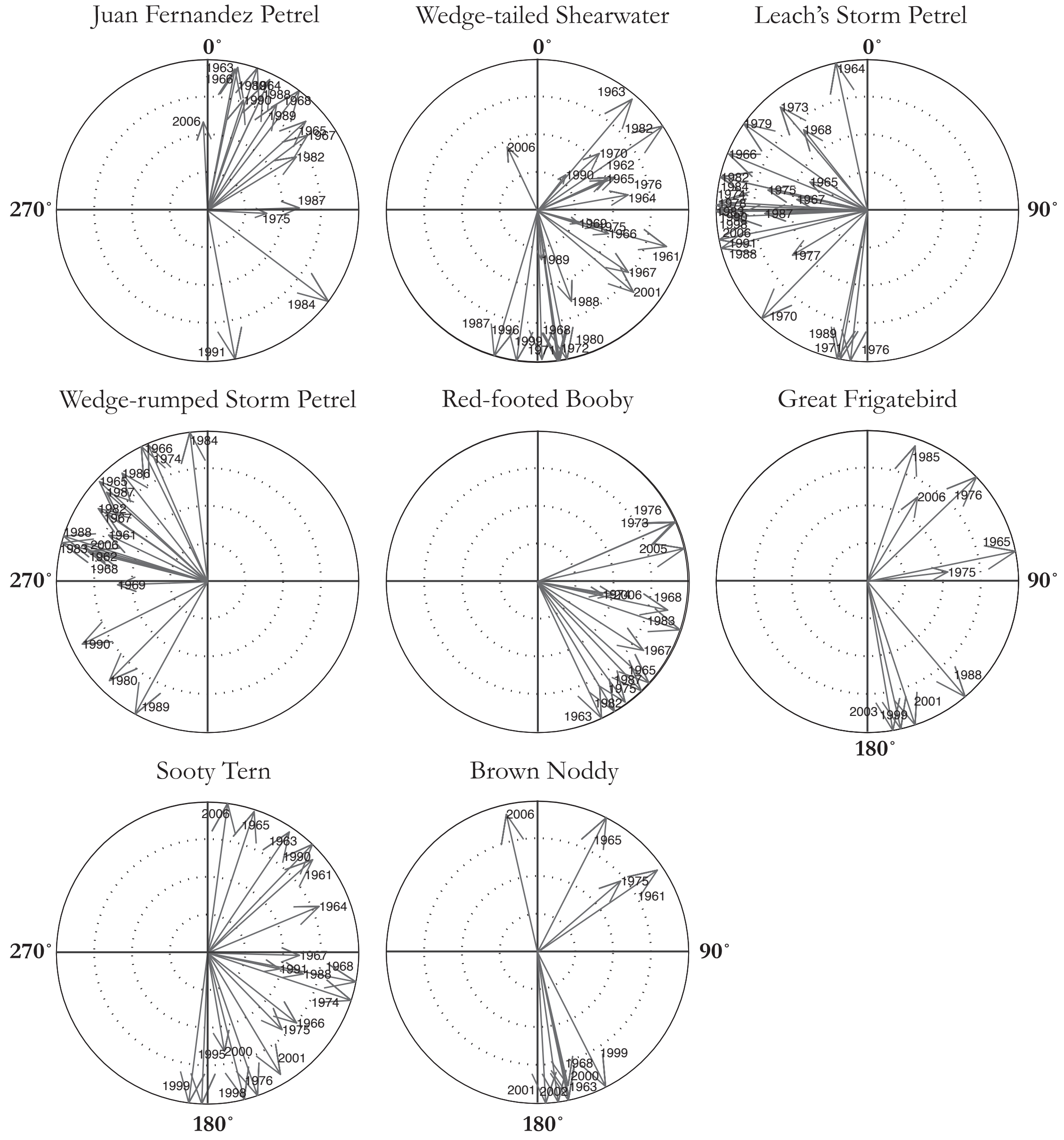


Figure 4.6 Mean annual $\delta^{13}C$ and $\delta^{15}N$ (±SE from the mean) feather values as a function of time for species having non-random changes in $\delta^{13}C$ and $\delta^{15}N$ values over time. Statistics for least square fits are in Table 4.1.



Juan Fernandez Petrel

Wedge-tailed Shearwater

Leach's Storm Petrel

Wedge-rumped Storm Petrel

Red-footed Booby

Great Frigatebird

Sooty Tern

Brown Noddy

Figure 4.7 Species-specific mean annual directional angles in C-N food web relative to the community mean (all eight species).

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Chapter 5

Conclusions to the Dissertation

Physical processes shaping biological production are the dominant drivers of ecosystem change in large-scale open ocean systems, while temporal variability in the form of low-frequency climate fluctuations is the main influence on physical processes in ocean basins (Chavez *et al.*, 2003; Cullen *et al.*, 2002; Francis *et al.*, 1998; Landry, 1977; McGowan *et al.*, 1998; Ware and Thomson, 2005) This dissertation documented ecosystem effects of the 1976/77 Pacific Ocean regime shift in the eastern Pacific warm pool, by linking changes in the upper-ocean temperature structure to community structure variability at two trophic levels: one mid-trophic and one of an apex predator. This dissertation is unique in the sense that it tests hypotheses relating ecosystem changes to a decadal scale ecosystem shift in a tropical oceanic setting, where the link between ecosystem effects and the 1976/77 regime shift has been vague. Tropical ecosystems cover the largest area of the world's oceans, but, due to logistic constraints and general remoteness, few long-term ecological data are available from such systems to test hypotheses linking physical and biological changes to regime shifts. There is a lack of research and thus a lack of knowledge as to whether tropical open-ocean ecosystems could have evolved enhanced buffering characteristics to this type of temporal variation. In the preceding chapters I attempted to build robust physical and biological data sets to investigate the effects of low-frequency climate variability affects tropical pelagic ecosystems and to test relevant hypothesis about direction and extent of responses.

The preceding chapters provide evidence that there have been multidecadal physical changes in the thermal structure of the upper 200 m in the eastern Pacific warm pool and that organisms from two trophic levels responded differently to these environmental changes. Temporal variability in the tropical Pacific is dominated by the three to five year frequency of the El Niño Southern Oscillation (ENSO) (Fiedler, 2002; Lluch-Cota *et al.*, 2003). Others, however, report that lower frequency variability or even abrupt changes in climate also influence the tropical Pacific (Deser *et al.*, 2004). The present research found that an abrupt change in upper ocean temperature structure also occurred in the eastern Pacific warm pool during the late 1970s. Variability in community structure of mid-trophic organisms, larval fishes, appeared to respond to an interdecadal scale change in the physical environment, while the proxy of diet we measured for apex predators did not. These results are in agreement with the notion that physical forcing shapes nutrient fluctuations driving biological production and that lower trophic levels are more likely to respond to these fluctuations than long-lived apex predators, like tropical seabirds.

Historical records from the eastern Pacific warm pool support the notion that past changes in water-column stratification have affected biological production. For example, on a much longer time scale (millions of years), Kamikuri *et al.* (2009) demonstrated how variability in radiolarian assemblages indicative of upwelling conditions reflected changes in the stratification regime in the area surrounding the Costa Rica Dome. On a time scale related to my dissertation, Linsley *et al.* (2000) found that records from Clipperton Atoll showed interdecadal scale variability associated with the Pacific Decadal Oscillation (PDO) in $\delta^{18}O$ measurements (a proxy for sea water temperature) for most of the last century. These authors postulated these fluctuations are caused by variability in the transport of the Northern Equatorial Current and Northern Equatorial Countercurrent. Results of this dissertation support this hypothesis.

In the pelagic ocean, multispecies larval fish associations are not randomly organized; instead, they are a result of adaptive responses from adult fishes (Frank and Leggett, 1983), larval transport, and life history characteristics of larvae (Miller and Kendall, 2009; Moser and Smith, 1993). Structure in these larval fish associations is linked to control of phytoplankton ecology by the physical motion and density structure of the water column (Barnett, 1984; Cullen *et al.*, 2002; Lasker, 1975; Margalef, 1978; Platt *et al.*, 2003). In Chapters 2 and 3, I linked changes in the thermal structure of the upper 200 m in the eastern Pacific warm pool to variability of species assemblages of larval fishes. These two chapters highlighted the importance of focusing on multispecies assemblages in linking the 1976/77 Pacific Ocean regime shift to bottom-up forcing of a mid-trophic community in a tropical oceanic system.

I found species assemblages of larval fishes to vary more through time in the eastern region of the study area, whereas oceanic assemblages in the west displayed stability. Specifically, I posit that a 14% decrease in thermocline depth along with warming in the upper 100 m of the water column affected productivity in the upwelling regions of the eastern Pacific warm pool, and this resulted in the higher temporal variability of larval fish species assemblages seen in that area. The notion that a lower trophic level community would be more responsive to low-frequency variations in climate is not unreasonable. In general, a mid-trophic community should have a faster population turnovers than higher trophic organisms, and thus be affected more from fluctuations in their environment. For example, Leatherback turtles, *Dermochelys coriacea*, which feed at low trophic levels, are thought to have decreased reproductive outputs in the eastern Pacific versus Atlantic and Indian Oceans, as a result of environmental variability derived from ENSO (Saba *et al.*, 2008).

Because of their natural history (long-lived, migratory apex predators), seabirds can be key indicators of marine ecosystem health and excellent indicators of change. Seabirds are known to respond to climate variability on multiple temporal (Hyrenbach and Veit, 2003) and spatial (Veit *et al.*, 2003) scales. On large scales within the eastern Pacific warm pool, they are also known to structure around open productivity gradients (Ballance *et al.*, 1997; Spear *et al.*, 2001). In general, changes in physical dynamics can reflect changes in the forage base of seabirds; thus seabirds should integrate ecosystem dynamics over a variety of time and space scales. In Chapter 4, I documented a time series of carbon and nitrogen stable isotopes, compiled from measurements taken from a suite of a phylogenetically diverse seabird species belonging to the two main foraging guilds in the eastern Pacific warm pool: a group that generally feeds in flocks that rely on underwater predators, like tunas and dolphins, to drive prey to the surface and a second group that feeds individually in single species flocks or solitarily by searching for oceanographic features that may aggregate their planktonic or micronektonic prey. I found decreases in annual feather values of δ^{13}C and δ^{15}N of 0.72‰ and 2.98‰, respectively, for sooty terns, *Onychoprion fuscatus,* which could suggest that this species is foraging further down the food web, or that it is foraging in more oligotrophic regains farther west in the study area. No other species had δ^{15}N annual feather variability that was correlated with time. I did find, however, a decrease in annual feather values of δ^{13}C accountable to the Suess Effect (a secular decrease in atmospheric δ^{13}C of CO_2 due to fossil fuel combustion) for most of the tuna- and dolphin-associated seabird species. This is the first time a decrease in δ^{13}C accountable to the Suess Effect has been shown for vertebrates in a tropical setting. Chapter 4 highlights the scientific value of long-term biological archives and suggests that seabird diet in the eastern Pacific warm pool has not shown a community-wide response to the 1976/77 Pacific Ocean regime shift. This supports the idea proposed by Veit and Montececchi (2006), who argued that seabird community structure in the north Pacific has been little affected by regime shifts. They proposed that seabird communities, because of advantageous longevity, can quickly recover from El Niño events and may have adaptations to withstand long-term decadal climate changes, since regime shifts have not resulted in major changes in the structure of these communities.

The approach taken in Chapter 4, however, did not quantify changes in the community structure of seabirds in the eastern tropical Pacific. Instead, I attempted to build a retrospective view of seabird diet changes or changes in baseline nutrients supporting their food webs. Finding a 46-year decrease in δ^{13}C of mean annual in feathers accountable by the Suess effect emphasizes this point. Long-term data sets of seabird community structure from the Pacific, including sampling effort before and after the 1976/77 regime shift, are rare. Studies based on the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program platform have shown changes in seabird community structure and abundance as a result of warming conditions in the California Current (Hyrenbach and Veit, 2003). Furthermore, other retrospective studies also using C and N stable isotopes have found susceptibility of marbled murrelets, *Brachyramphus marmoratus,* off Northern California to changing conditions in the California Current. Anderson and Piatt (1999) argued that a reorganization of forage fish in the Gulf of Alaska resulting from the 1976/77 regime shift, had negative effects on piscivorous seabirds and marine mammals. And Trites *et al.* (2006) hypothesized that a similar mechanism caused declines in Steller sea lions, *Eumetopias jubatus*, within the same region.

Clearly higher resolution data of seabird population dynamics from ship-board surveys extending time periods before and after regimes shifts is needed. Such data sets will shed light on the long-term effects of regime shifts on apex predators, such as seabirds. It has been proposed that a reversal to pre-1976 conditions in the Pacific Ocean occurred in 1998 (Batten and Welch, 2004; Bidigare *et al.*, 2009; Bond *et al.*, 2003; Lavaniegos and Ohman, 2003). This underscores the need to maintain long-term monitoring of at-sea seabird populations, such as CalCOFI's NOAA Fisheries ecosystem assessment cruises, as well as research programs monitoring long-term breeding success on islands (e.g. Velarde *et al.* 2004).

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