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Influence of Central Pacific Oceanographic Conditions on the Potential Vertical Habitat of Four Tropical Tuna Species¹

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Abstract: Climate change has resulted in the geographic and vertical expansion of oxygen minimum zones but their impact on the vertical distribution of commercially important species, such as tunas, is not well understood. Although La Niña events are characterized by increased upwelling along the equator, the increased primary productivity and bacterial proliferation drive the expansion of oxygen minimum zones. Vertical habitat of four tropical tuna species were characterized using direct observations of the oceanographic conditions of the Central Pacific Ocean during the 2008 La Niña event and existing primary literature on temperature and dissolved oxygen physiological tolerances for these tunas. Concentrations of potential prey were estimated using Acoustic Doppler Current Profiler raw backscatter and surface zooplankton tows. Based on the oceanographic conditions observed from February to June, low dissolved oxygen levels, more so than low temperatures, were inferred to restrict the predicted vertical habitat of four commercially important tuna species (bigeye, yellowfin, skipjack, and albacore). During peak La Niña conditions, temperature and dissolved oxygen tolerance limits of all four tuna species were reached at approximately 200 m. Zooplankton and myctophid fish densities peaked in the upper 200 m between 0° N and 5° N, which corresponded to a region with a shallow thermocline (150 m). Our findings suggest the possibility that competition and susceptibility to surface fishing gears may be increased for tropical tunas during a strong La Niña event due to vertical habitat restrictions.

OXYGEN MINIMUM ZONES (OMZs) are persistent, mid-water layers with oxygen concentrations <23.3 μmol/kg (Levin 2003). In the tropical Equatorial Pacific Ocean, OMZs

have been expanding and intensifying over the past 50 years due to anthropogenic influences, such as increasing industrial emissions, which are increasing global water temperatures and stratification (Stramma et al. 2008, Bertrand et al. 2010). Some of the largest OMZs are sustained in upwelling regions because upwelling introduces nutrients to surface waters, which support high levels of primary productivity and bacterial decomposition on sinking material that can induce hypoxia to form an OMZ (Levin 2003, Prince and Goodyear 2006, Bertrand et al. 2010). Other possible mechanisms leading to increased deoxygenation of oceanic water masses include surface layer warming, reduced oceanic mixing, and higher metabolic rates of organisms (Stramma et al. 2010).

The study of El Niño–Southern Oscillation (ENSO) phenomena has resulted in large-scale studies of the Central Pacific Ocean to characterize the long-term variability of

¹ This work was funded by a National Science Foundation GK-12 PERFECT grant and a National Oceanic and Atmospheric Administration Hollings Scholarship. Manuscript accepted 15 February 2015.

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surface oceanographic conditions using an array of moored instruments (Lu et al. 2001, Trenberth and Smith 2006, Kao and Yu 2009). In general, La Niña events in the Central Pacific Ocean result in temperatures in the upper 150 m being 0.8°C cooler than in a normal year due to increased upwelling (Kao and Yu 2009). Due to perturbations in the marine environment associated with climate change, the upper limit of the Equatorial Pacific Ocean OMZ is becoming shallower (Bertrand et al. 2010, Stramma et al. 2010). This expansion of the OMZ may constrict the potential vertical habitat of organisms, which may result in a barrier to fishes and potential prey intolerant of hypoxic conditions (Bertrand et al. 2010). The reduction of available, well-oxygenated vertical habitats in the water column to the upper epipelagic zone can increase the vulnerability of pelagic fish populations to surface fishing gears, interspecific competition, habitat overlap with prey, and energetic costs related to foraging (Prince and Goodyear 2006; Zhang et al. 2009). In the Western and Central Pacific Ocean, there was an increase in the annual catches of yellowfin, bigeye, and Southern hemisphere albacore tuna by all gear types during the 2008 La Niña event (Inter-American Tropical Tuna Commission 2013). One possible explanation for these increases in catches is the reduction of suitable vertical habitat available to these tunas during the La Niña event, though changes in horizontal distribution could have also occurred.

Tropical tunas (Family: Scombridae) are fast, continuously swimming teleosts that are also apex predators vital to the commercial long line and purse seine fishing industries of many nations in the Pacific Ocean, and they are at risk of vertical habitat compression events (Lu et al. 2001, Wegner et al. 2010). The four most abundant and commercially important tuna species in the tropical Pacific Ocean are bigeye tuna (*Thunnus obesus*), skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*T. albacares*), and albacore tuna (*T. alalunga*). These tunas exhibit systemic endothermy, a unique adaptation that allows them to regulate a body temperature higher than the ambient water temperature, although there are

species-specific differences in the structure and efficiency of their endothermic systems (Brill 1994, Lu et al. 2001). However, endothermy, as well as high somatic and gonadal growth rates, elevates the metabolic demands of tunas, which increases their oxygen demand relative to other fishes (Wegner et al. 2010) and their potential sensitivity to OMZs.

Of the examined tuna species, adult bigeye tuna are able to tolerate the deepest and coldest waters because they are more efficient at retaining heat and oxygen (Brill 1994, Lowe et al. 2000, Graham and Dickson 2004) (Table 1). Adult albacore tuna (a subtropical tuna species) can tolerate colder water temperatures than yellowfin and skipjack tunas (Bernal et al. 2001, Graham and Dickson 2004, Chen et al. 2005); however, adult albacore tuna are less tolerant of hypoxic conditions than adult bigeye and yellowfin tunas (Bertrand, Josse et al. 2002).

In addition to their physiological tolerances, a tuna species' diving behavior is associated with the vertical distribution of their primary prey (Allain 2005). For example, albacore and bigeye tunas are deep-diving tunas due to their tolerances to low temperature and dissolved oxygen (DO) conditions and their diets are dominated by mesopelagic and bathypelagic prey. Skipjack tuna are not tolerant of low temperatures or DO levels, spending approximately 60% to 80% of their time within the surface mixed layer (upper 200 m) and rarely diving below the thermocline (Schaefer and Fuller 2007; although

TABLE 1

Physiological and Comfort Values for Temperature and Dissolved Oxygen Used to Define the Potential Vertical Habitat of the Four Examined Tuna Species in the Central Pacific Ocean

| Species | T _{Phy} (°C) | T _{Comfort} (°C) | DO _{Phy} (μmol/kg) | DO _{Comfort} (μmol/kg) |
|-----------|--------------------------|------------------------------|--------------------------------|------------------------------------|
| Bigeye | 8.0 | 12.0 | 26.1 | 139.5 |
| Skipjack | 11.0 | 22.0 | 89.3 | 176.0 |
| Yellowfin | 10.5 | 17.5 | 43.6 | 107.4 |
| Albacore | 10.0 | 18.0 | 65.4 | 162.8 |

Note: DO = dissolved oxygen; Phy = physiological; T = temperature.

these observations are only based on five tagged specimens). As expected, skipjack tuna feed almost exclusively in the epipelagic zone (Bertrand, Bard, and Josse 2002, Allain 2005). Similar to skipjack tuna, yellowfin tuna spend the majority of their time in the surface mixed layer with uniform temperatures and DO concentrations at or near saturation (Block et al. 1997, Swimmer et al. 2004). Although yellowfin are not able to physiologically thermoregulate as efficiently as bigeye tuna can, their behavior remains unaffected by low DO even after skipjack tuna behavior has been significantly altered (Brill 1994). Foraging on mesopelagic fishes and bathypelagic organisms has been observed in yellowfin tuna in addition to their typical diet dominated by epipelagic prey (Brill 1994, Bertrand, Bard, and Josse 2002, Allain 2005, Brill et al. 2005, Potier et al. 2007).

Few studies have associated vertical changes in temperature and DO, due to ENSO cycles, with the impacts that these oceanographic conditions may have on the potential vertical habitat of commercially important tuna species in the Central Pacific Ocean (Prince and Goodyear 2006, Bertrand et al. 2010). In addition, the effects of subsurface DO and temperature features on zooplankton and nekton distribution in the Central Pacific Ocean have rarely been examined in detail (Bertrand, Josse et al. 2002, Dagorn et al. 2006, Schaefer and Fuller 2007). In this study, we characterized vertical temperature and DO conditions in the Central Equatorial Pacific Ocean during the La Niña event in 2008, identified the geographic and vertical extent of OMZs, and assessed the potential vertical habitat of four commercially important tuna species in the Central Equatorial Pacific Ocean in relation to our oceanographic observations.

MATERIALS AND METHODS

Oceanographic Data

Observations of the physical marine environment for this study were collected aboard the SSV *Robert C. Seamans*, a sailing school vessel with deep deployment capabilities and a suite

of remote sensing equipment that is owned and operated by the Sea Education Association (Woods Hole, MA). In 2008, data were collected during three cruises between Papeete, Tahiti (French Polynesia), and Honolulu, Hawai'i. Exact cruise tracks were determined by meteorological conditions present during each cruise transect. The S215 cruise sailed from Tahiti to Hawai'i between 16 February and 16 March; the S216 cruise returned from Hawai'i to Tahiti between 30 March and 2 May; and the S217 cruise leg sailed from Tahiti to Hawai'i between 11 May and 12 June (Figure 1).

To examine temporal changes to temperature and DO, vertical profiles of temperature and DO were measured on each cruise by a Seabird SBE 19plus V2 Conductivity Temperature Depth (CTD) device equipped with a SBE 43 DO sensor. The CTD was deployed twice a day (approximately at noon and midnight), roughly 121 km apart, to a depth of 500 m. Final temperature and DO data were postprocessed at 1 m intervals for S216 and 5 m intervals for S215 and S217.

Acoustic Doppler Current Profiler (ADCP) raw backscatter data and surface zooplankton density data were used to indicate areas with higher concentrations of potential tuna prey (Lara-Lopez and Neira 2008, Burd and Thomson 2012). Acoustic samples were collected with a hull-mounted RDI Ocean Surveyor ADCP (75 kHz) and these data were averaged every 20 min with a bin length of 10 m to a depth of approximately 600 m. The acoustic reflectance data were used to describe the deep scattering layer and other areas of high backscatter, which can correlate with high planktonic biomass (Fielding et al. 2004, Burd and Thomson 2012). To account for day and night differences of the deep scattering layer, day and night ADCP data were examined separately. Daytime was defined as the hours between 0800 and 1700 and nighttime was defined as the hours between 2000 and 0500 in order to remove the effects of transitional periods (Domokos et al. 2007). To characterize the planktonic community, planktonic organisms were sampled twice a day (at noon and midnight) with a neuston net (1 × 0.5 m wide opening; 335 µm mesh) towed

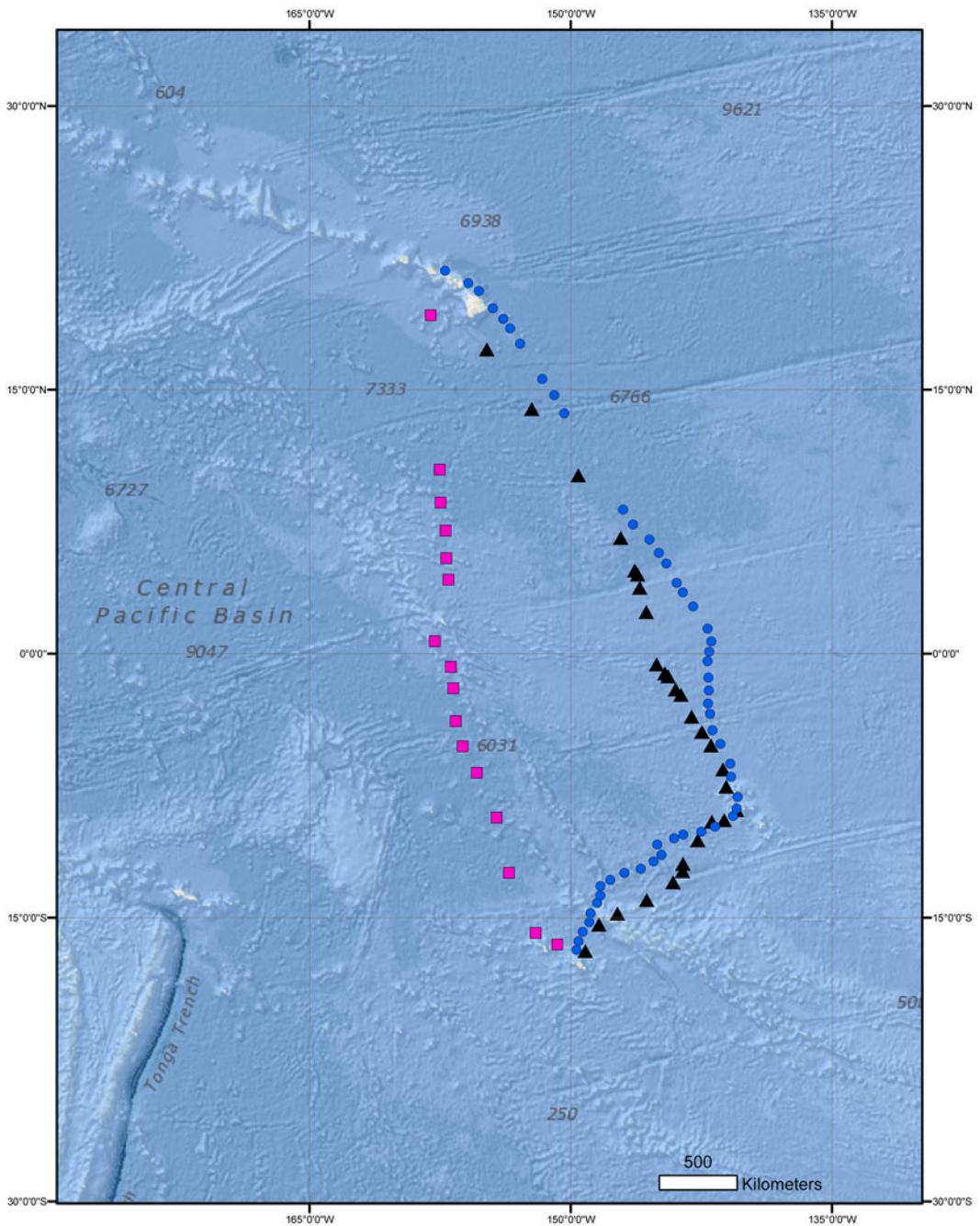


FIGURE 1. Map of the three 2008 Sea Education Association cruise transects between Hawai'i and Tahiti. Symbols indicate zooplankton and CTD sampling stations corresponding to the February–March (triangles), March–May (squares), and May–June (circles) transects.

at the air-sea interface for approximately 1 nautical mile (1.85 km) for all three cruises. GPS locations were used to determine the tow volume and tow distance for the neuston net. Myctophid fishes were sorted from the zooplankton samples and counted. Myctophid fishes were separated from the samples because they are a common mesopelagic fish family and are consistently found in the diets of yellowfin, bigeye, and albacore tunas (Bertrand, Bard, and Josse 2002, Allain 2005, Potier et al. 2007). Zooplankton density was determined by dividing volumetrically displaced mass by tow distance, and myctophid fish densities were calculated separately by dividing myctophid counts by tow distance.

Hydrographic Preferences of Tunas

Temperature and DO limit estimations for the four examined tuna species were based on adult and juvenile specimens from the work of Bertrand, Josse et al. (2002) and Brill (1994) (Table 1). The specific physiological vertical habitat (PVH) was defined as the depth at the lower limits of the temperature or DO tolerances reported for the adults from each species of tuna. For bigeye, yellowfin, and albacore tunas, the temperature and DO conditions used to predict PVH was estimated based on where <2.5% of longline catches occurred in Bertrand, Josse et al. (2002) (Table 1). Their study had large sample sizes (≥ 100 individuals) of albacore, bigeye, and yellowfin tunas but collected no skipjack (Bertrand, Josse et al. 2002). Brill (1994) experimentally estimated physiological DO limits for bigeye, yellowfin, and albacore that were approximately twice the limits defined by Bertrand, Josse et al.'s (2002) in-situ catch data (Table 1), which suggest a possible disconnect between distribution of longline tuna catches and tuna distribution. Given the consistent DO limit relationship found between the Brill (1994) and Bertrand, Josse et al. (2002) studies for albacore, bigeye, and yellowfin, we estimated the DO PVH limit for skipjack tuna to be half of the DO limit measured by Brill (1994). The temperature PVH limit for skipjack tuna was obtained from two tagging

studies (Ogura 2003, Schaefer et al. 2009) (Table 1).

The comfort vertical habitat (CVH) of a tuna species was defined as the portion of the water column where a tuna spends >50% of its time and is within the preferred temperature and DO ranges of that species based on previous studies. Therefore, CVH is an approximation of the preferred habitat conditions for each tuna species and attempts to describe the habitat where tunas spend the majority of their time. The CVH was defined for bigeye as the temperature and DO conditions most frequently observed in tagged and longline bigeye captures (Dagorn et al. 2000, Bach et al. 2003, Evans et al. 2008) (Table 1). Lower limits of the CVH for yellowfin tuna were defined as temperature and DO concentrations corresponding to highest observed longline catch rates, which may indicate the lower limit of oceanographic conditions within the preferred conditions (Song et al. 2008). The temperature CVH was also corroborated by tagging study that recorded a similar temperature range (Block et al. 1997) (Table 1). For albacore tuna, the DO where swimming behavior was observed to be negatively impacted under controlled conditions was selected as the DO CVH limit (Brill 1994), whereas the temperature CVH limit was determined from observations collected via electronic tag deployments (Williams et al. 2015). The DO CVH limit for skipjack tuna was estimated from the DO level at which venous oxygen content significantly decreased in skipjack individuals under laboratory conditions (Brill 1994) and the temperature CVH limit was estimated from a tagging study (Schaefer and Fuller 2007) (Table 1).

RESULTS

Oceanographic Data

All three cruises occurred during a La Niña period, although February had the highest Southern Oscillation Index value at 21.3 (Bureau of Meteorology 2012) (Figure 2). Water temperatures in the upper 100 m were approximately 30°C in the Southern hemisphere stations relative to 25°C in the Northern

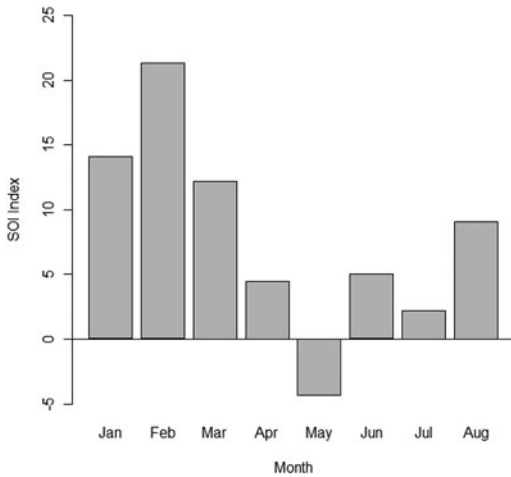


FIGURE 2. Southern Oscillation Index (SOI) by month over the study period in 2008. Positive numbers indicate La Niña conditions and negative numbers indicate El Niño conditions with the value corresponding to the strength of the conditions. Data from Bureau of Meteorology (2012).

hemisphere stations for all three transects (Figure S1 [available online from www.BioOne.org]). The thermocline shoaled to approximately 150 m between 5° S to 15° N during February to March and May to June, but between March and May, the shallowest thermocline was observed at 100 m near 10° N (Figure S1).

Generally, DO concentrations were greater in the Southern hemisphere stations relative to the Northern hemisphere stations (Figure S1). There was an OMZ (<23.3 $\mu\text{mol/kg}$) present between 5° N and 15° N between February and March, extending approximately 1,280 km in width and with an upper boundary at 175 m. In the Southern hemisphere, a small OMZ was present (282 km wide; extending 250–425 m deep) with subsurface DO concentrations of approximately 50 $\mu\text{mol/kg}$ between 10° S and the equator below 150 m (Figure S1). Between March and May, subsurface DO concentrations were >100 $\mu\text{mol/kg}$ between 10° S and 4° S throughout the water column, and the Northern hemisphere OMZ was not as extensive,

ranging between 2° N and 15° N (787 km wide; upper limit of 150 m). From May to June, a Southern and a Northern hemisphere OMZ was observed between 10° S and 4° S (692 km wide; upper limit of 175 m) and between 5° N and 20° N (1,812 km wide; upper limit of 100 m), respectively (Figure S1).

Projected Vertical Tuna Habitat

Potential vertical habitat of the four examined tuna species in the Central Pacific Ocean was mainly limited by DO (Figure 3), though temperature also limited potential vertical habitat, especially for yellowfin tuna CVH. Following the patterns observed in the oceanographic data, the predicted vertical tuna CVH and PVH were more restricted in the Northern hemisphere stations than in the Southern hemisphere stations for all tuna species. The DO CVH was restricted to the upper 150 m between 5° S and 10° N from February to March, to the upper 200 m between 5° S and 10° N from March to May and to the upper 125 m between 2° S and 6° N from May to June for all species except for yellowfin tuna near the equator (200 m, 300 m, 250 m, respectively) (Figure 3). Unlike the CVH, PVH for all tuna species was most restricted during February and March between 5° S and 1° N and between 4° N and 10° N. During all three cruises, there was a deepening of PVH between 1° S and 1° N.

Yellowfin tuna potential vertical habitat was limited primarily by temperature with some exceptions in the latitudes on either side of the equator for all three cruises (Figures 3–5). Bigeye tuna had a more extensive PVH that could be limited by either temperature or DO depending on the hydrographic conditions (Figures 3 and 4). Albacore tuna had a deeper predicted temperature PVH relative to yellowfin and skipjack but due to their DO sensitivities, their vertical habitat was restricted to a shallower depth by DO (Figures 3–5). Of the examined tuna species, skipjack tuna had the most restricted temperature and DO potential vertical habitat based on the observed oceanographic conditions in the Central Pacific Ocean.

CVH (DO)

PVH (DO)

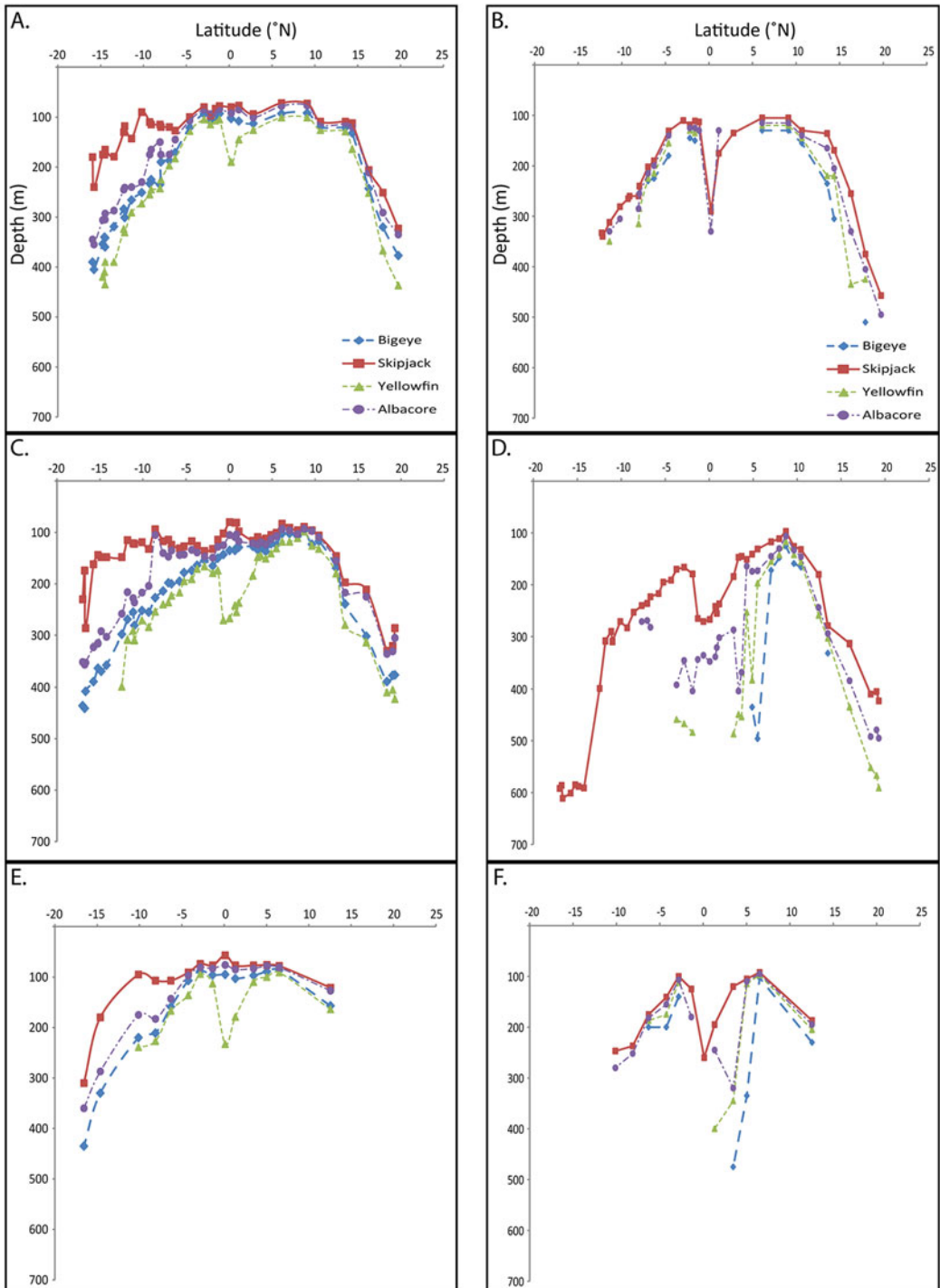


FIGURE 3. Potential lower boundary of vertical habitat of bigeye (diamond; dashed), skipjack (square; solid), yellowfin (triangle; dashed), and albacore (circle; dot-dash) tunas based on dissolved oxygen (DO) tolerances during the February–March (A,B), March–May (C,D), and May–June (E,F) transects. Comfort vertical habitat (CVH) is on the left and the physiological vertical habitat (PVH) is on the right.

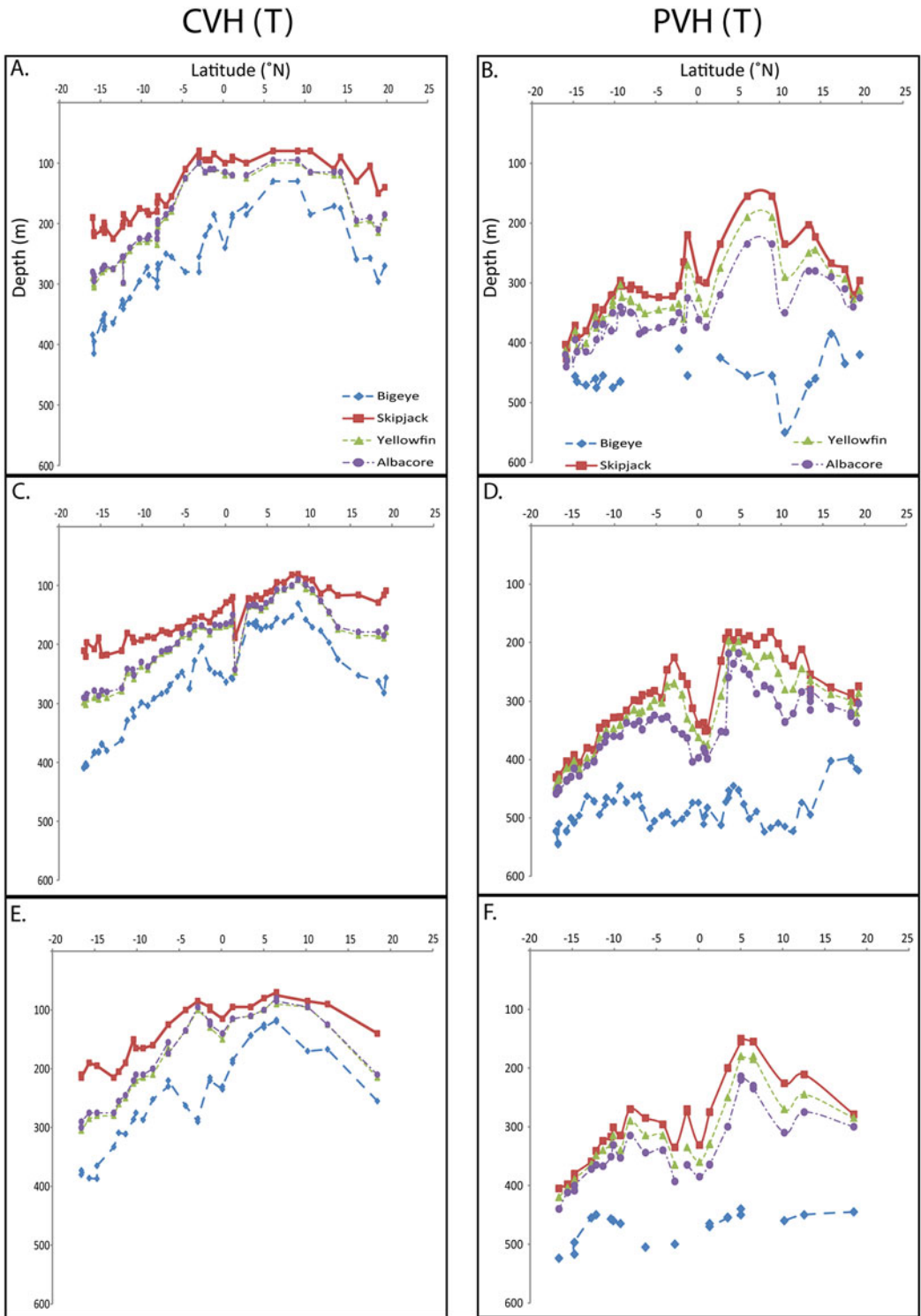


FIGURE 4. Potential lower boundary of vertical habitat of bigeye (diamond; dashed), skipjack (square; solid), yellowfin (triangle; dashed), and albacore (circle; dot-dash) tunas based on temperature (T) tolerances during the February–March (A,B), March–May (C,D), and May–June (E,F) transects. Comfort vertical habitat (CVH) is on the left and the physiological vertical habitat (PVH) is on the right.

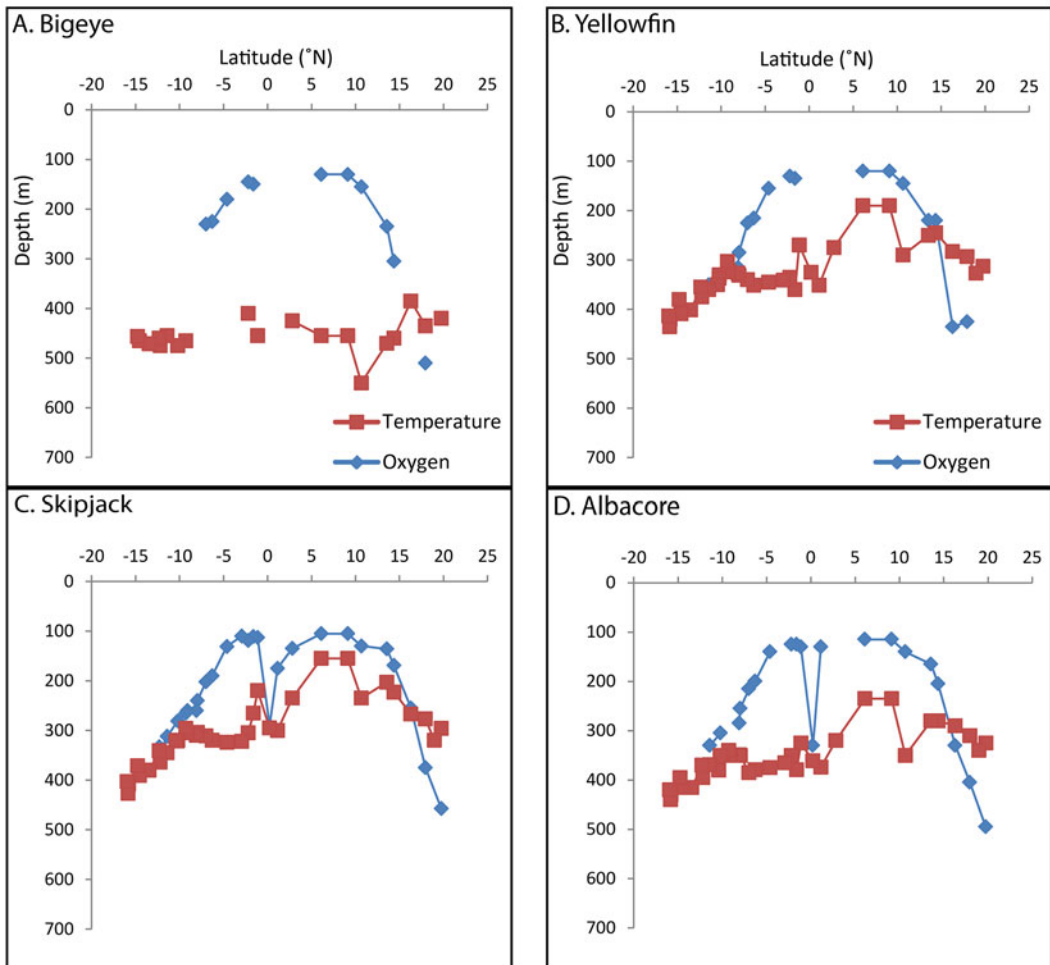
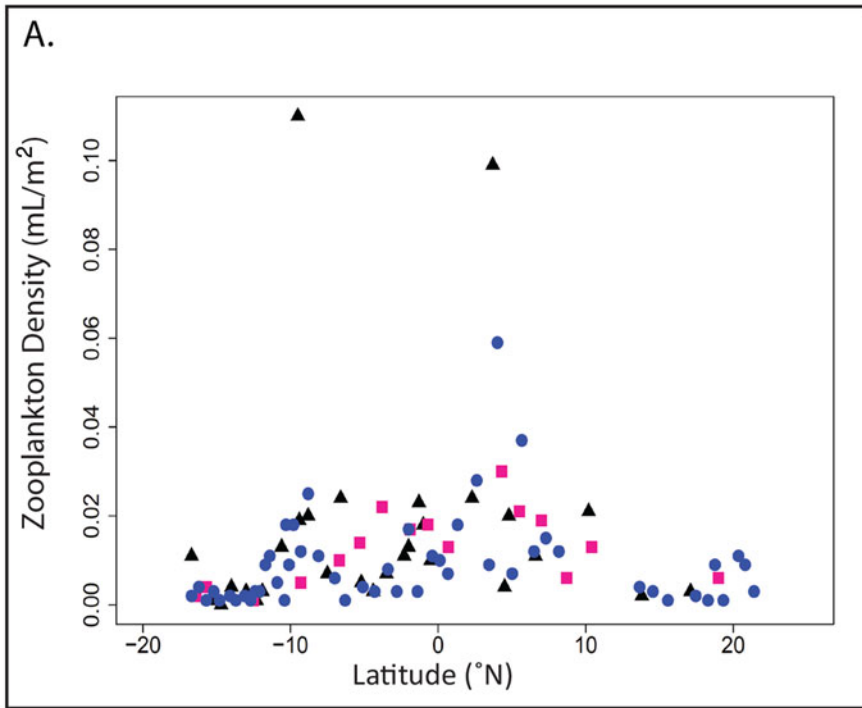


FIGURE 5. Comparison of physiological vertical habitat as delimited by dissolved oxygen (diamonds) and temperature (squares) for bigeye (A), yellowfin (B), skipjack (C), and albacore (D) tunas between February and March.

Potential Prey

ADCP backscatter echo counts were highest during both the day and night between 3° S and 7° N (175–200 counts) in the upper 50 m from February to May (Figure S2 [available online from www.BioOne.org]). However, between May and June, echo counts (175–200 counts) were more restricted vertically and horizontally, with the highest counts found between 3° S and 5° N in the upper 25 m (Figure S2). Echo counts were also higher in the Southern hemisphere relative to the

Northern hemisphere during all three cruises, especially between 150 and 225 m in depth. In this depth range, the echo counts in the Northern hemisphere were lower (approximately 50 counts) compared with those in the Southern hemisphere (75–80 counts) for all three cruises. In addition, zooplankton densities from net tows were highest between 10° S and 7° N in all three cruises, paralleling backscatter data (Figure 6). The density of myctophid fishes was greatest between 3° S and 7° N, similar to what was observed in the ADCP data.



▲ February-March ■ March-May ● May-June

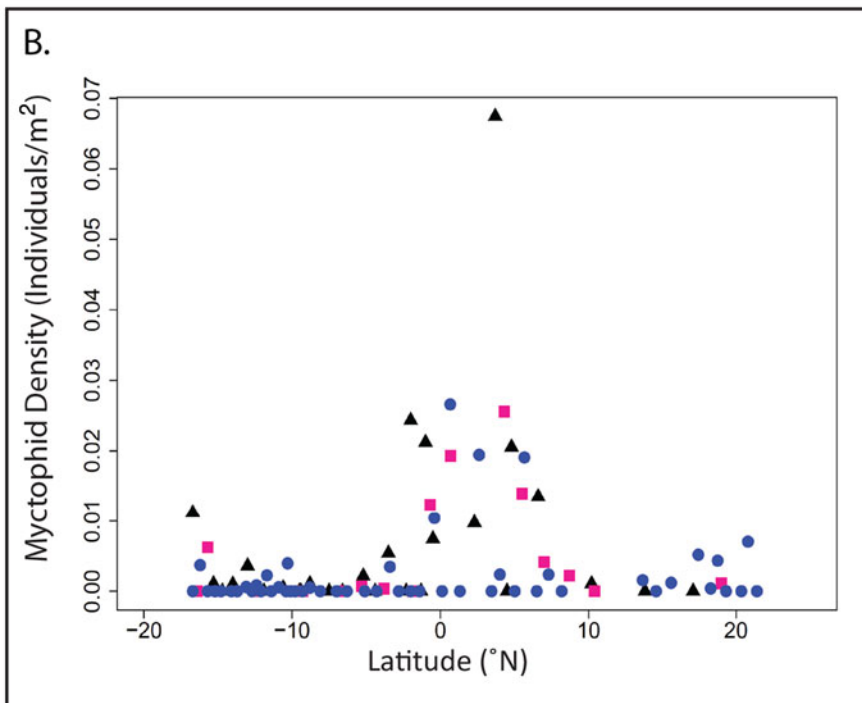


FIGURE 6. Zooplankton density (*A*) and myctophid density (*B*) during three transects in the Central Pacific Ocean in 2008: February–March (triangles); March–May (squares); May–June (circles).

DISCUSSION

The primary goal of this study was to use observations of oceanographic conditions to infer the potential vertical habitat of four commercially important tropical tuna species in the Central Pacific Ocean. Both subsurface DO and temperature are important variables when predicting regions of suitable vertical habitat for these four tuna species. The examined tuna species are able to conserve heat produced during metabolism, but there are species-specific differences in the overall efficiency of the heat exchangers and an overall cost of systemic endothermy is elevated oxygen demands (Graham and Dickson 2004). Our understanding of the physiological tolerances of these four tuna species is incomplete, so our assessments of potential tuna distributions are rough predictions based on current knowledge.

In the Central Pacific, the estimated values of PVH and CVH suggest that DO restricts the potential vertical habitat distribution of tuna more than temperature. However, temperature is the most commonly used oceanographic variable to forecast tuna distribution (Andrade 2003). Yellowfin tuna are sensitive to low temperatures that accompany upwelling events, such as the 2008 La Niña, and their estimated CVH was limited primarily by temperature, suggesting that thermoregulation may not be as efficient in yellowfin as it is in bigeye and albacore (Brill 1994, Graham and Dickson 2004). However, yellowfin tuna are tolerant to low DO levels (Brill 1994, Bertrand, Josse *et al.* 2002, Song *et al.* 2008) and had a DO CVH deeper than bigeye tuna, with the caveat that this difference may also be attributed to how the CVH was estimated for the four tuna species in this study. Bigeye tuna are the most tolerant of all the examined species to low temperatures, resulting in a more extensive predicted PVH limited by temperature or DO depending on the oceanographic conditions. Albacore tuna are more tolerant of low temperatures relative to yellowfin and skipjack tunas and had a deeper PVH estimated by temperature. However, albacore tuna are not as tolerant to low DO levels and their potential vertical habitat was

limited by DO. Skipjack tuna are the least tolerant to low temperatures and DO levels, and therefore were predicted to have the most restricted vertical habitat between February and June in the Central Pacific Ocean. The PVH determined by temperature and DO profiles is always deeper than the CVH. However, between 5° and 10° N, the OMZ reached a minimum in the upper 200 m, creating a significant barrier to the four tunas and resulting in the overlap of PVH and CVH in all three transects.

As the Southern Oscillation Index value decreased from February to March (Bureau of Meteorology 2012), the OMZ decreased both horizontally and vertically in size while the thermocline increased in depth. During these months, the estimated PVH of all four tuna species were less restrictive and expanded vertically and horizontally. Between May and June, an OMZ in the Southern hemisphere was observed, but it did not extend as deep or wide as the more homogeneous Northern hemisphere OMZ. On the basis of the estimated PVH and CVH, the Northern hemisphere OMZ likely constituted a significant barrier to even the more hypoxia-tolerant tuna species such as yellowfin and bigeye. Between 0° and 5° N, the estimated PVH deepened for all the examined tunas due to an increase in DO. Based on their specific physiological capabilities, this may have allowed yellowfin and bigeye to dive deeper and exploit deeper vertical habitats than skipjack and albacore. It should be recognized that although the estimated vertical habitat was expanded due to increased DO concentrations between 0° and 5° N, the thermocline remained shallow and the physiological thermal minimum of yellowfin, skipjack, and albacore was reached at 300–350 m between February and March, 375 m from March to May, and 350–400 m between May and June (Figure 4). Under these oceanographic conditions, the predicted vertical habitat of yellowfin, skipjack, and albacore were not exclusively limited by DO, but also by temperature between 0° and 5° N (Figure 5).

ADCP echo counts were high in the upper 50 m during all three cruises between 3° S and 5° N regardless of time of day, which also

corresponded to the region where relative zooplankton and myctophid densities collected from net tows peaked in the upper 200 m. This suggests that upwelling related to the La Niña event increased secondary productivity (echo counts >175) and potential prey in the upper 200 m (Bertrand, Bard, and Josse 2002, Allain 2005, Scholz et al. 2011), which coincided with the predicted CVH and PVH of all four tuna species. Upwelling was directly observed during all three cruises and is reflected in the temperature profiles. Between March and June, the 2008 La Niña event brought cold (10°C–15°C), deep water to the upper 200 m of the ocean around the equator and surrounding areas (10° S to 10° N). These latitudes also correspond to the region with the most severe projected vertical habitat restriction for the examined tuna species.

The colder, upwelled water induces OMZs below the thermocline due to the bacterial decay of large amounts of sinking biological material (Prince and Goodyear 2006). During an El Niño year, upwelling is minimal, resulting in increased stratification, a deeper thermocline, and reduced nutrient input into the upper layers (Levin 2003, Scholz et al. 2011) of the Central Pacific Ocean between 10° S and 10° N. Based on the physiological tolerances of the examined tunas, it is expected that the potential vertical habitat restrictions during El Niño conditions would be reduced due to smaller and deeper OMZs and a deeper thermocline, therefore allowing tuna to vertically partition their habitat. It is expected that in an El Niño year, skipjack would possess the shallowest CVH due to their low temperature and DO tolerances, followed by yellowfin, albacore, and bigeye based on their physiological capabilities (Brill 1994, Bertrand, Josse et al. 2002, Schaefer and Fuller 2007). However, during La Niña years when the potential vertical habitat is restricted and there are expected overlaps between the vertical habitat ranges of these tuna species, increased competition for prey could be balanced by the associated increase in secondary production, especially in the upper 200 m. Another possible consequence of tunas encountering unsuitable oceanographic conditions at depth is that they may undergo

horizontal migrations to escape these conditions (Lehodey et al. 1997, Lu et al. 2001, Ganachaud et al. 2013).

Based on the oceanographic conditions observed during the 2008 La Niña, the predicted vertical habitat was expected to be vertically restricted for the four tunas, especially in the latitudes adjacent to the equator in the Northern and Southern hemispheres. If tunas do not horizontally migrate from these areas with unsuitable oceanographic conditions, habitat compression due to expanding OMZs and a shallower thermocline could result in tunas possibly not being able to avoid longline and purse seine fishing gears (Andrade 2003, Prince and Goodyear 2006, Zhang et al. 2009). Therefore, during La Niña conditions, all four tuna species are potentially more vulnerable to capture by surface fishing gears, even if depth selective gear deployment schemes are employed to reduce tuna bycatch in the region between 5° S and 10° N (Bigelow et al. 2006, Beverly et al. 2008). Local extirpation is another potential impact of low temperature and DO conditions related to La Niña events due to the highly migratory nature of these tuna species (Graham and Dickson 2004). Further understanding of the relationship between oceanographic conditions, particularly DO and temperature during different ENSO cycles may allow us to make better predictions regarding suitable vertical habitat usage of target species.

ACKNOWLEDGMENTS

We are grateful for the work of the Sea Education Association (www.sea.edu), especially the crew of the SSV *Robert C. Seamans*, for tirelessly collecting oceanographic data and providing unique research opportunities to undergraduate students.

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