
Zooplankton in the eastern tropical north Pacific: Boundary effects
of oxygen minimum zone expansion

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mesopelagic fish abundance (Koslow et al., 2011). “Dead zones” of low oxygen concentration and low biomass occur periodically

VERTEX cruises (Martin et al., 1987), while the CRD has been studied since the 1950s (Fiedler, 2002).

Day and night vertically-stratified samples to 1000 or 1200 m depth were obtained using a 1 m² MOCNESS (Multiple Opening-

the comparative differences between locations, provided a solid basis for logical interpretations about biomass boundary layers.

Biomass processing generally followed protocols from the Joint Global Ocean Flux Study (JGOFS) and Zooplankton Methodology Manual (Wishner et al., 1998; Postel et al., 2000). Cod ends were placed in buckets with plastic ice packs immediately upon retrieval to keep zooplankton cool in the tropical environment as an aid to preservation. Samples were rinsed from nets and cod ends with filtered seawater into 153 μm metal sieves and photographed. Samples were then split with a flat-bottomed Motoda splitter. Half the sample was preserved in 4% sodium-borate-buffered formalin for distributional studies, 1/4 was processed for size-fractionated biomass, and 1/4 was refrigerated for microscopical and stable isotope processing. For size-fractionated biomass, the sample split was poured through a stacked series of nitex mesh sieves (meshes of 5, 2, 1, 0.5, and 0.2 mm) using filtered seawater; then the contents of each sieve were poured onto pre-weighed 48 mm diameter circles of nitex mesh (200 μm) and rinsed with de-ionized water. In some cases with larger samples, the catch was split further or multiple filters were used for a single sample. At least two blanks (filters processed as above but with no sample) were prepared for each tow. Nitex circles were folded, wrapped in aluminum foil, and dried to 60 °C in a drying oven at sea for a minimum of 48 h, then stored in desiccators. After the cruise, samples were dried again to 60 °C in the lab and weighed on a Cahn ATI microbalance to obtain dry mass (mg). The term

"zooplankton" in this paper refers to animals 4 15 formalin44.6(01TD)00TJ/F11Tf.51980TD(m)-376.5(p80(n)-343.3(thie-frJ-20.5(us378.3088TD(on)ca)-4t58.2

transmissometer data, and this corresponded to the presence of a

OMZ core samples as those entirely within the lowest oxygen water, representing the most extreme habitat. Samples from depth strata that included any higher oxygen water were assigned to the oxyclines (or other) zones described below.

The Mixed Layer (ML), the epipelagic water column above the thermocline, was thin with oxygen approaching air saturation. The

A large gelatinous component occurred twice in 2007, in a TB night tow (609) and CRD day tow (614) (Table 3). Salps comprised

largest size class, dominated by fish and shrimp, showed a much broader water column biomass distribution and a large diel shift in dominant zone of occurrence. During the day, the majority of the largest size fraction water column biomass occurred in the 550 – 1000 m depth range (54% \pm 13, n=43) and in the OM to SO ecological zones (76% \pm 15, n=43). At night, much of this biomass moved into the UO and ML.

3.5. Diel vertical migration (DVM)

A strong signal of DVM, undertaken especially by larger size classes, was evident in comparisons of percent biomass change (night minus day) within each ecological and depth interval (Table 5). Large size classes moved from depth during the day into the upper 150 m, as shown by large positive values of % biomass change (357 \pm 28, range: 3–

community abundance peak occurred at 575–600 m at CRD both years and at 800–825 m at TB in 2008, at an oxygen concentration of $\sim 2 \mu\text{M}$ (0.045 mL/L) in all cases (Table 7). The precise oxygen value has some uncertainty (see methods) and covers the depth range of a net interval, but it was consistently slightly higher than the OM value. As discussed later, between-station spatial variability in LO layer depth in 2008 was used as a proxy for impacts of potential future OMZ expansion.

The ETNP LO community was a unique multispecies assemblage with characteristic copepods, shrimp, and fish, similar to that previously described from the Arabian Sea (Wishner et al., 2000, 2008). A key visually-prominent indicator species was the

extensive

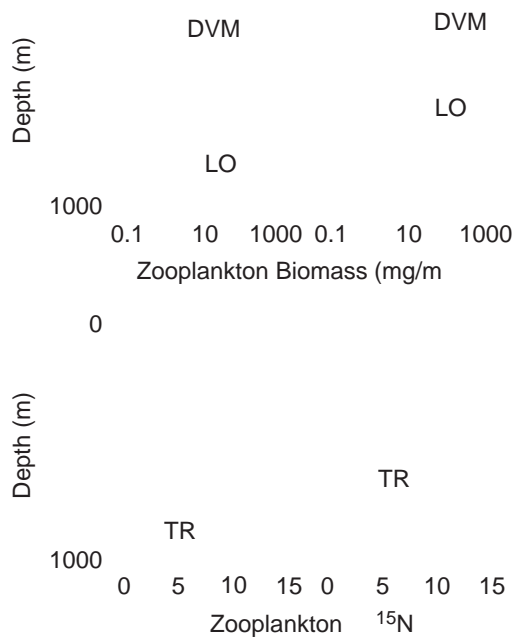
4.3. Zooplankton community structure and species distributions

Although many studies have documented distributions and adaptations of pelagic fauna in the California Current OMZ (e.g. Thuesen et al., 1998; Childress and Seibel, 1998; Seibel and Drazen, 2007; Robison et al., 2010), a key difference between that region

Although there is evidence for a variety of microbial production pathways (including chemoautotrophy) in strong oxyclines (e.g. Taylor et al., 2001; Voss et al., 2001; Lam et al., 2009; Molina and Farias, 2009; Kalvelage et al., 2011; Stewart F.J. et al., 2012; Wakeham et al., 2012), trophic transfer to zooplankton remains uncertain.

Stable isotopes (^{15}N of mixed zooplankton from these tows) showed virtually no change with depth through the OM but had an abrupt strong increase at the LO beginning at the depth of the zooplankton biomass peak (Fig. 11). An increasing gradient in ^{15}N is often used as an indicator of a feeding progression to higher trophic levels (Fry, 2006). The vertical juxtaposition of isotope and

compressed into narrower vertical zonation as the UO thins, with potentially more encounters with competitors and predators. Confirmation of this habitat compression effect in 2008 was the occurrence within the upper 150 m of 82% of zooplankton biomass at TB with its thick OMZ, compared to only 54% at CRD (0–550 m biomass, [Table 3](#), [Fig. 6](#)). On the short term, this forced aggregation could benefit large epipelagic predators, making it easier for them to find food and possibly enhancing fisheries, but over time, with no physical refuge, zooplankton populations and the predators that depend on them would likely decline.



food sources for suspension-feeding benthos and demersal fish. Thus, changes in zooplankton layer depths in OMZs could affect food availability and alter benthic zonation (Wishner et al., 1990; 1995; Levin et al., 2003, 2009; Gallardo et al., 2004; De Leo et al., 2012).

proved to be a useful proxy for possible future temporal change and revealed how variability in oxycline depth at the upper and lower OMZ boundaries could have broad consequences for biological distributions and ecosystem function (Fig. 12). The same biomass and distributional features, present at both locations, responded differently to changes in OMZ thickness and boundary depths. Peak zooplankton biomass occurred at the thermocline regardless of OMZ core depth, but two secondary mesopelagic biomass and abundance peaks showed very different responses to changes in oxygen vertical profiles between locations. The impact of habitat compression was quantified by the change in proportion of zooplankton biomass in the upper water column. Key findings include:

1. At the lower oxycline, a unique zooplankton assemblage and secondary biomass peak (sharp order of magnitude jump from OMZ biomass levels) occurred at an oxygen concentration of $\sim 2 \mu\text{M}$. The LO layer, strongly locked into position by oxygen concentration, changed depth by over 200 m between the two locations (775–800 m vs. 525–550 m, respectively) while remaining at the same oxygen level (but different temperature). The sharpness of the boundary between the OMZ core and LO layer, definition of its structure as a mesopelagic biomass peak rather than a continuous biomass increase with depth, and its precise association with a specific extremely low oxygen value, were important new findings from this work.
2. Quantification of the dense monospecific layer of the copepod *Paracalanus crassirostris*, sometimes present just above the regular LO assemblage, filled a gap in knowledge of this important species. While its general distribution and ontogenetic migration was previously known, its precise positioning relative to oxygen concentration and the LO community was a new discovery.
3. In contrast, the other secondary biomass peak, corresponding to the daytime depth of diel vertical migration and occurring within the upper oxycline or OMZ core, was present at the same depth (200–300 m) at both locations, despite different oxygen concentrations. If migrators must descend to this depth (to avoid predators, for example) through an expanded OMZ with an increased depth range of low oxygen, their longterm existence in the changing ocean of the ETNP might be compromised.

In summary, the vertical re-positioning of biomass layers at the thermocline and lower OMZ boundaries, and the increased depth range of low oxygen water that diel vertical migrators and sinking particles must transit in an expanded OMZ, could have widespread effects on species distributions, particle fluxes, the biological pump, and benthic–pelagic coupling.

The spatial comparison between the two stations (Tehuantepec Bowl and Costa Rica Dome), with different OMZ thicknesses,

Levin, L.A., Whitcraft, C.R., Mendoza, G.F., Gonzalez, J.P., Cowie, G., 2009. Oxygen and organic matter thresholds for benthic faunal activity on the Pakistan