

---

---

---

biogeochemical processes. As a result, habitats of organisms intolerant to low oxygen may be compressed into the shallow, near-surface oxygenated waters (Prince and Goodyear, 2006).

Members of the family Eucalanidae are dominant copepods in the ETNP, and include all four genera (*Eucalanus*, *Paracalanus*, *Diaptomus* and *Diaptomus*) (Chen, 1986; Longhurst, 1985; Saltzman and Wishner, 1997a; Sameoto, 1986). Like many other zooplankters in the region, these copepods display a variety of vertical distributions that are likely related to the oxygen environment (Chen, 1986; Saltzman and Wishner, 1997a; Sameoto, 1986; Vinogradov et al., 1991). *Eucalanus* (Giesbrecht, 1892), endemic to the ETNP, is found throughout the upper 1000 m, often with maximum concentrations in the chlorophyll maximum and the upper and lower edges of the OMZ core. *Paracalanus* (Giesbrecht, 1888), *Diaptomus* (Giesbrecht, 1888), and *Diaptomus* (Dana, 1849) are usually concentrated in the shallow euphotic zone. *Diaptomus* (Dana, 1849) [sometimes referred to as *Diaptomus* (Lang, 1965)] and *Diaptomus* (Giesbrecht, 1888), on the other hand, are often absent from the surface mixed layer, and instead are concentrated above and below the OMZ core. This suggests that a variety of ecological strategies occur within this family in the ETNP region.

Even though eucalanoid copepods are abundant in the ETNP, little is known about their ecology. As severe OMZ regions appear to be expanding (Stramma et al., 2008, 2010), understanding the strategies employed by zooplankton in current OMZ systems may help us to predict the effects of decreasing oxygen on marine ecosystems in other regions of the ocean. Eucalanidae is a relatively small family of copepods (24 described species) that are distributed throughout a majority of the world's oceans and occur in coastal and open water systems (Bradford-Grieve et al., 1999; Goetze, 2003; Grice, 1962; Lang, 1965). The abundance of eucalanoid copepods in the ETNP system, coupled with their broad distribution in other regions, make them a useful group for comparative studies within and between ecosystems. These copepods also have been the focus of several recent genetic studies, which aimed to further describe separate lineages within species (Goetze, 2003, 2005, 2006, 2010; Goetze and Ohman, 2010). Consequently, their phylogeny is fairly well described, which



lower values (13.9–18.0% of DW). . . again had intermediate ash content (22.7% of DW).

C content was lowest for . . . based on % WW and DW, and highest for . . . and . . . (Table 1). . . C content was significantly lower than . . . , . . . and . . . , based on WW and DW. However, when converted to % of ash-free dry weight (AFDW), . . . was more similar to . . . and . . . , and all three were lower than . . . c spp.

N content (% WW) was significantly different between . . . and . . . , which showed the highest and lowest values, respectively (Table 1). When converted to % of DW, . . . and . . . grouped together with high values, while . . . and . . . c spp. were lower and similar. When examining % of AFDW, . . . c spp. showed the lowest values, while . . . and . . . had about a factor of two higher. . . fell between the two.

H content per unit WW was significantly lower in . . . than . . . and . . . c spp. (Table 1). Per unit DW, three distinct

higher storage lipid mass than the other three species. . also had significantly more storage lipid than .

### 3.3. c – c

Comparisons between male and female . , as well as between shallow and deep-dwelling . females showed only a few differences in body composition ([Table 2](#)). Males had significantly higher C, N, protein content, and C:N ratios than females. Interannual



Although adult female . body contents were low based on WW relative to other eucalanoid species, comparing components on

2013). . stored primarily triacylglycerols (Cass et al., 2014), and their average storage lipid sac mass was higher per unit WW and DW than those of . and , but not nearly as high as c spp. These moderate lipid stores would supply them with energy during times of reduced feeding at depth. Relatively low metabolic demand and ability to use alternative metabolic pathways is another strategy that would allow . females to reside in low oxygen waters for periods of time.

Few differences were seen among the three groups of adult . examined in this study. It appeared that males had higher C, N and protein levels than females, possibly indicating greater muscle mass and organic matter. These males might have been more active than females, as they occurred almost exclusively in the upper 100 m of the water column (Fig. 3). Coupled with their smaller size (Table 2), increased mobility would aid in avoiding potential visual predation in the euphotic zone.

LDH levels also appe45(an(13(lsa0rg2g) 1og)e)-14u[(pp)-9(6.8u-12a) 16(te9o1tg)ewi-8(g)-5u1

e male(t)-297(h)-115(o)1g hed hädnaole



with our study, during which *C. affinis* spp. abundances were highest directly above the OMZ core, in the upper oxycline (Fig. 3). Like *C. affinis*, LDH activity was observed in *C. affinis* spp. All LDH values reported for *C. affinis* and *C. affinis* spp. are within ranges found for other copepod species (e.g., Geiger et al., 2001; Thuesen et al., 1998). However, based on activity per g protein, LDH activity levels in *C. affinis* spp. were only about one-half to one-third the levels found in *C. affinis*. This may point towards a lower anaerobic capacity, explaining their absence from the lowest oxygen regions. However, within taxa, trends have been found with size (Thuesen et al., 1998). The WW of *C. affinis* was approximately 5–10 times higher than WWs of *C. affinis* spp., indicating a large size gap. Differences in LDH activity might be due to such a relationship, and not necessarily represent differential adaptation to OMZs. Even though the metabolic rate of *C. affinis* was similar to that of *C. affinis* at 10 °C, its tolerance for low oxygen was superior. Survivorship at <20 M was more than 85% for *C. affinis* spp., compared to only 22% for *C. affinis*. Their swimming activity level also was much lower generally than *C. affinis*, and often little to no motion was observed in *C. affinis* spp. during sorting. Protein levels indicated that *C. affinis* had approximately twice as much muscle mass as *C. affinis* spp., providing further support for observations of large differences in activity levels.

One of the most distinctive features of *C. affinis* spp. was the large storage lipid sac that occupied a major portion of its body cavity. The percent of wet mass of storage lipids was more than 10 times that of *C. affinis*, *C. affinis* or *C. affinis*.

depletion (concentrations)

characteristics in the ETNP. *Uca* and *Libinia* were the only two species similar enough to classify together. *Uca* was able to tolerate exposure to low oxygen through adopting a physiological strategy more similar to gelatinous plankton than typical copepods. Adult females had high water content and low organic matter, resulting in a decreased metabolic demand. This species also had detectable levels of LDH, suggesting that it is metabolically poised to utilize anaerobic pathways to increase its tolerance for low oxygen conditions. *Uca* spp. were characterized by particularly high lipid content and low protein levels. LDH was present in moderate levels, leading to tolerance for low oxygen conditions when coupled with low general activity. *Uca* appeared to avoid the OMZ, as survivorship for this species was much lower than for *Uca* or *Libinia* spp. at  $<20 \text{ } \mu\text{M O}_2$ . *Uca* also had the highest protein and lowest lipid levels of the group.

