



J. Plankton Res. (2014) 0(0): 1–19. doi:10.1093/plankt/fbu077

Fine-scale vertical distribution of macroplankton and micronekton in the Eastern Tropical North Pacific in association with an oxygen minimum zone

AMY E. MAAS^{1†*}, SARAH L. FRAZAR², DAWN M. OUTRAM², BRAD A. SEIBEL¹ AND KAREN F. WISHNER²

¹DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF RHODE ISLAND, KINGSTON, RI 02881, USA AND ²GRADUATE SCHOOL OF OCEANOGRAPHY, UNIVERSITY OF RHODE ISLAND, NARRAGANSETT, RI 02882, USA

[†]PRESENT ADDRESS: DEPARTMENT OF BIOLOGY, WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MA 02543, USA.

*CORRESPONDING AUTHOR: amaas@whoi.edu

Received May 6, 2014; accepted July 31, 2014

Corresponding editor: Roger Harris

The 0- to 1000-m vertical distribution patterns of micronekton and macrozooplankton were determined in the Costa Rica Dome region (9° N; 90° W) of the Eastern Tropical North Pacific in October–November 2007 and December 2008–January 2009. The area has a pronounced oxygen minimum zone (OMZ) that impacts the distribution of both migrating and mesopelagic species. Sampling was conducted at a relatively fine scale (mesopelagic depth intervals as small as 25 m) within ecologically relevant strata to assess how this hydrographic environment influenced the structure of these groups. Zooplankton were collected in vertically stratified Multiple Opening/Closing Net and Environmental Sensing System tows during the day and the night, and abundances were analyzed in association with variations in oxygen concentration, temperature and depth. Each vertical stratum of the water column was a unique ecological zone with a specific community makeup. The upper and midwater column (0–550 m) was strongly influenced by diel vertical migration patterns, particularly the daytime descent of euphausiids and myctophid fish into the core of the OMZ. Distinctly different communities occurred below the OMZ core. The lower oxycline (LO) (~500–700 m depth range) was dominated by *Cyclothone* spp. fish as well as a diverse population of other taxa, often aggregated into a discrete layer (25 m thick), particularly in 2008. In the suboxycline (> 700 m depth range), the community shifted to

typical bathypelagic taxa. These finer scale vertical patterns provided new insight into the ecological structure of OMZs, revealing the unique layering at the LO and differential impacts on diel vertical migrators.

KEYWORDS: zooplankton; micronekton; diel vertical migration; oxygen minimum zone; Eastern Tropical North Pacific; vertical distribution; Costa Rica Dome

INTRODUCTION

Oxygen minimum zones (OMZs), defined as regions where a subsurface minimum oxygen level occurs (Seibel, 2011), are large, stable oceanic features that are most pronounced in highly productive regions such as the Arabian Sea, the eastern tropical Pacific and off the coast of northwest Africa (Kamykowski and Zentara, 1990). Local hydrography and wind patterns create surface conditions where warm, stable, nutrient rich waters stimulate phytoplankton populations (Wyrski, 1962; Fiedler and Talley, 2006; Karstensen *et al.*, 2008). In these regions, the primary productivity is so great that it is not all consumed in the upper water column and thus directly supports a zooplankton and bacterial population below the mixed layer (ML) (i.e. Saltzman and Wishner, 1997a; Morrison *et al.*, 1999; Escribano *et al.*, 2009). At midwater depths, where oxygen is often already depleted as a consequence of the long residence time of deep open ocean waters, high biological oxygen demand results in pronounced oxygen depletion and carbon dioxide production, which outpaces diffusive and convective replenishment provided by the generally slow horizontal deep ocean mixing (Wyrski, 1962; Karstensen *et al.*, 2008). Pronounced OMZs, where oxygen drops $<20 \mu\text{M}$, make up $\sim 8\%$ of the ocean by volume (Paulmier and Ruiz-Pino, 2009) and are thought to be expanding as a result of human induced increase in surface ocean temperatures, which in turn drives increased stratification and decreased vertical mixing (Oschlies *et al.*, 2008; Stramma *et al.*, 2008, 2010; Keeling *et al.*, 2010).

Regions of persistent hypoxia have a profound influence on the vertical distribution of animals. In general, there is a sharp decrease in biomass as oxygen levels drop, persisting until the lower interface of that zone is reached. There, an increase in oxygen and zooplankton numbers occurs, sometimes focused in a sharply defined layer (Vinogradov and Voronina, 1961; Wishner *et al.*, 1995, 1998, 2008, 2013; Saltzman and Wishner, 1997b; Rapien, 2004; Smith and Madhupratap, 2005; Escribano *et al.*, 2009). The cores of OMZs, however, serve as habitat for both permanent and migratory populations of specialized hypoxia-tolerant species, creating a unique zooplankton ecological zone. These animals are able to survive in severe hypoxia as a result of adaptations for

increased capacity for oxygen extraction, anaerobic metabolism and/or an ability to reduce energy demand through lifestyle or diel periods of metabolic suppression (Childress and Seibel, 1998; Rosa and Seibel, 2008; Seibel, 2011; Maas *et al.*, 2012b).

The ecological cost of oxygen limitation must in some way be outweighed by the benefits of OMZ habitation. Regions of hypoxia may provide refuge from predators unable to penetrate the OMZ core and a possible food source of particles and bacterial colonies that occur at the low oxygen boundaries (Gowing and Wishner, 1998; Wishner *et al.*, 2000, 2008, 2013; Steinberg *et al.*, 2008a; Podlaska *et al.*, 2012). Many species inhabit the OMZ only during the daytime. These transient species consume food in the warm oxygenated photic zone during the night and then migrate into colder, hypoxic water during the day. This diel vertical migration (DVM) is believed to provide a number of advantages including niche partitioning, metabolic advantage, avoidance of light or high temperatures, and, most importantly, predator avoidance (Hays, 2003; Antezana, 2009).

Both resident and migratory species that inhabit OMZ waters have a profound impact on midwater nutrient and carbon transport. Migrators release surface derived carbon (CO_2 from respiration) and other waste products (urea, NH_3 , fecal matter, DOC etc.) below the thermocline where they, and the permanent fauna, likely consume particles, one another, and local bacterial aggregates, significantly modifying the export of nutrients and carbon from the ML (Longhurst and Harrison, 1989; Dam *et al.*, 1995; Hays *et al.*, 1997; Steinberg *et al.*, 2000; Rapien, 2004; Honjo *et al.*, 2008; Robinson *et al.*, 2010). Therefore, understanding the distribution of meso- and bathypelagic zooplankton is important for parameterizing the pelagic carbon and nitrogen budgets (Wishner and Gowing, 1992; Steinberg *et al.*, 2008b). However, we lack a strong understanding of food web dynamics in this oceanic “twilight zone”, which contributes to the large uncertainties in carbon export models in the ocean (Burd *et al.*, 2010). These poorly understood biogeochemical processes are expected to be impacted by expanding OMZs with profound implications for food webs, fisheries and carbon export (Stramma *et al.*, 2010; Cheung *et al.*, 2011; Seibel, 2011; Bianchi *et al.*, 2013).

Our lack of knowledge is in part an effect of the rarity of analyses that closely correlate distributions with the

pertinent ecological boundaries such as the upper and lower oxygen gradients (oxyclines) of the OMZ. This study expands our knowledge of the vertical resolution of taxon distribution in relation to regions of low oxygen. In the Eastern Tropical North Pacific (ETNP), there is a significant and persistent OMZ where oxygen drops to $<5 \mu\text{M}$ ($<0.08 \text{ kPa}$) just below the thermocline. This OMZ water vertically spans hundreds of meters and horizontally hundreds of kilometers and can reach levels as low as $1 \mu\text{M}$ in its core. Despite these pronounced hypoxic conditions, the OMZ in the ETNP supports both a population of resident and diel migratory species (Longhurst, 1967; Fernández-Álamo and Färber-Lorda, 2006; Rosa and Seibel, 2010; Maas *et al.*, 2012a; Wishner *et al.*, 2013). This paper is part of a wider multidisciplinary study (the Eastern Tropical Pacific project), whose focus was to investigate the ecological and physiological impact of the OMZ of the ETNP. Previous work from this project described vertical patterns of zooplankton biomass size fractions, including DVM and the occurrence of a biomass peak at the lower oxycline (LO) (Wishner *et al.*, 2013). Here, we report the abundances and distribution of the large sized macrozooplankton and micronekton taxa found in the ETNP in 2007 and 2008. The relatively fine-scale vertical resolution sampling scheme (with strata as narrow as 10 m near the surface and 25 m at mesopelagic depths) was adaptively designed to characterize ecologically relevant patterns in temperature and oxygen.

METHOD

Study area and sampling

Specimens were collected in the Costa Rica Dome region (9° N ; 90° W) on two research expeditions to the ETNP

that took place 18 October to 17 November 2007 aboard the *R/V Seward Johnson*, and 7 December 2008 to 6 January 2009 aboard the *R/V Knorr*. Mesozooplankton were sampled at 10–150-m vertical intervals using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) equipped with 153- μm mesh nets and electronic sensors for temperature (SBE 3P-1), conductivity (SBE 4C-1), fluorescence (Seapoint chlorophyll fluorometer), light transmission (Wetlabs CST-667DR 25 cm beam transmissometer), oxygen (SBE 43-1), pressure (depth) and volume filtered (Wiebe *et al.*, 1976, 1985; detailed in Wishner *et al.*, 2013).

In both cruises, three independent oblique tows (surface, mid and deep), each consisting of up to eight depth intervals, were conducted during the day (10 a.m. to 2 p.m.) and the night (10 p.m. to 4 a.m.). Occasionally, a fourth tow was made to fill in gaps in sampling and to provide finer vertical resolution at the LO. All tows were conducted over a period of 5 days during both years (Table I). Surface samples (0–150 m) were taken in 10–50-m intervals, mid-depth tows (150–550 m) were taken in 25–50 m intervals and the deepest samples (550–1000 m) generally spanned 25–200 m intervals (Table I). During the daytime of 2007, however, the maximum depth was 1200 m, with a depth interval of 300 m for the deepest net. The three independent profiles were assembled to obtain a water column profile from 0 to 1000 m day and night (Table I). Zooplankton were sampled on the upcast portion of the tows.

Immediately upon collection, each net was washed down with filtered seawater. Samples were poured into a 153 μm sieve and then split using a flat-bottomed Motoda splitter (Motoda, 1959). Half of each sample was preserved in 4% sodium borate-buffered formalin and filtered sea water for abundance estimates and the remainder of the sample was processed for size-fractionated

Table I: Tow and net data from sampling in 2007 and 2008.

Year/time	Tow ID	Date	Depths (m)	Net intervals (m)
2007 Day	614	November 7	750–1200	1200–900–750
	623	November 12	550–775	775–725–700–675–650–625–600–575–550
	616	November 8	150–550	550–500–450–400–350–300–250–200–150
	618	November 9	0–150	150–100–80–60–50–40–30–20–0
2007 Night	619	November 10	750–1000	1000–950–900–850–800–750
	617	November 9	550–750	750–550
	615	November 8	150–550	550–500–450–400–350–300–250–200–150
	621	November 11	0–150	150–100–80–60–50–40–30–20–0
2008 Day	639	December 30	550–1000	1000–900–750–650–625–600–575–550
	637	December 29	150–550	550–500–450–400–350–300–250–200–150
	635	December 28	0–150	150–100–80–60–50–40–30–20–0
2008 Night	636	December 29	525–1000	1000–900–750–650–625–600–575–550
	641	January 1	200–500	500–450–400–350–300–250–200
	638	December 30	0–150	150–100–80–60–50–40–30–20–0

Profiles from 0 to 1000 m were assembled from three or four discrete tows which were conducted on different dates. Zooplankton samples were collected on the upcasts from deep to shallow depths. Note the gap in sampling between Tows 636, 641 and 638 as well as the greater depth sampled during Tow 614 during the day in 2007.

biomass or reserved for microscopic, physiological or isotopic analysis. Back in the laboratory, the entire preserved sample was poured onto a 64-µm mesh sieve and rinsed with filtered seawater into a large Pyrex dish. Large non-copepod taxa (generally, those >3 mm in size; Table II) were removed by hand. Copepods were analyzed separately by Wishner *et al.* (Wishner *et al.*, 2013). Organisms were sorted to broad taxonomic groups and enumerated using a dissecting microscope (Table III; volume filtered, raw counts and abundances in Supplementary data, Table SI). Many groups contained multiple species. Funding and

time constraints precluded species identifications for most taxa. Unidentified or rare fish (typically Melamphaidae) were classified as “misc. fish”, while unidentified or rare invertebrates (i.e. isopods, stomatopods, pycnogonids, pyrosomes) were grouped as “other”.

Euphausiids were classified into four subclassifications based on eye morphology (*Stylocheiron* spp., *Bentheuphausia amblyops*, type 1 euphausiids = bilobed-eyed, type- 2 euphausiids = round-eyed). Myctophid fish were separated into three categories based on size and developmental status. Individuals which were pre-tail flexion (larval) were

Table II: Taxonomic groups.

Taxonomic groups				
Phylum	Class	Order	Group name	Size
Chaetognatha			Chaetognaths*	>20 mm
Annelida	Polychaeta		Polychaetes*	>5 mm
Mollusca	Gastropoda		Gastropods*	>3 mm
Arthropoda	Ostracoda		Ostracods*	>3 mm
Arthropoda	Malacostraca	Decapoda	Decapods	All
Arthropoda	Malacostraca	Euphausiacea	Euphausiids	All
Arthropoda	Malacostraca	Lophogastrida	Lophogastrids	All
Arthropoda	Malacostraca	Mysida	Mysids	All
Arthropoda	Malacostraca	Amphipoda	Amphipods*	>3 mm
Chordata	Thaliacea	Salpida	Salps	All
Chordata	Thaliacea	Doliolida	Doliolids	All
Chordata	Actinopterygii	Myctophiformes	Myctophids	All
Chordata	Actinopterygii	Stomiiformes	Stomiiformes	All
Chordata	Actinopterygii		Misc. fish	All
Other			Other	>5 mm

Taxa were lumped by groups (Group name) for the quantification of abundance based on phylogenetic relationships. Note that the Stomiiformes group was comprised of cyclothone, hatchetfish, dragonfish and viperfish. There were some taxa that were also abundant in the small-size fraction and were sorted separately (*). Abundances of only the large size fraction were used in the statistical analyses in this paper. The size cutoff (size) for inclusion in this dataset varied among phyla and is the length of the individual specimen.

Table III: The depth integrated abundance of individuals (no. of individuals per square meter for 0–1000 m) for each group.

Groups	Total abundance (no. of individuals per square meter, 0–1000 m)				Rank				
	07 D	07 N	08 D	08 N	Total	07	08	D	N
Chaetognaths*	14 944	12 061	37 220	55 910	10	10	9	10	10
Polychaetes*	63 273	123 550	198 720	128 442	6	4	5	6	6
Gastropods*	125 277	270 421	197 353	76 044	5	2	6	4	5
Ostracods*	6288	7791	15 205	3200	12	11	12	12	12
Decapods	70 450	100 853	489 777	267 203	3	5	3	2	4
Euphausiids	333 701	948 970	963 858	899 096	1	1	1	1	1
Lophogastrids	676	536	909	1278	15	15	15	15	14
Mysids	2995	6403	11 106	2925	13	13	13	13	13
Amphipods*	55 410	91 085	502 722	382 001	2	6	2	3	3
Salps	76 710	303 203	244 758	250 444	4	3	4	5	2
Doliolids	33 852	65 290	51 638	34 767	8	8	11	8	8
Myctophids	68 493	47 489	39 246	82 689	7	7	7	7	7
Stomiiformes	16 523	19 372	65 594	27 515	9	9	10	9	11
Misc. fish	1393	705	42 049	70 826	11	14	8	11	9
Other	10 054	882	3389	846	14	12	14	14	15
Total	880 041	1 998 609	2 863 545	2 283 185					

The group rank, from most to least abundant, is reported for the total study (total) for each year (07, 08) and for the day (D) and the night (N). See Table II for explanation of asterisk.

one group and were counted separately; all post-flexion through adult myctophids were separated into two groups based on an inherent break in the size classes (<22 and >25 mm in length, respectively). Due to their fragility and poor preservation in formalin, cnidarians and ctenophores were reported only as present or absent and were excluded from our analyses. Some taxa were also common in the separately sorted small-size fraction (Table II), but the analyses in this paper were done only with the large individuals.

Vertical structure

To understand the vertical structure of the plankton distribution, the nets were clustered based on the depth zones of upper (0–150 m), middle (150–550 m) and deep (550–1000 m). The importance of the OMZ for the vertical structure of the macrozooplankton and micronekton abundances was also explored by splitting the water column into ecological zones based on depth, temperature and oxygen profiles. In this region, the 0–1000-m water column was divided into six ecological zones, as described in Wishner *et al.* (Wishner *et al.*, 2013). These zones are termed the ML, upper oxycline A (UO-A), upper oxycline B (UO-B), OMZ core (OM; bounded by 1.8 $\mu\text{M O}_2$), LO and suboxycline (SO).

Direct comparisons of discrete nets require analysis using abundances within each net (no. of individuals per cubic meter), while comparisons between zones require the use of depth integrated abundance (no. of individuals per square meter for a particular depth range). This is calculated by multiplying the concentration of individuals within a net by the depth range of that net and then summing multiple values over a total depth range. To adjust for the greater depth of sampling during the day in 2007, the concentration in the deepest net was multiplied by a depth interval of 100 rather than 300 to obtain a depth integrated abundance to 1000, consistent with the other profiles (Table I, Tow 614). The gaps in sampling from the night of 2008 between tows (25 m between Tows 636 and 641 and 50 m between 641 and 638; Table I) were estimated as:

$$z \times \frac{(m_a^{-2} + m_b^{-2})}{(a + b)}$$

where m_a^{-2} is the depth integrated abundance for the net above, m_b^{-2} is the depth integrated abundance for the net below, a and b are the intervals for the net above and below, respectively, and z is the missing depth interval. The resulting total depth integrated abundance (no. of individuals per square meter) from 0 to 1000 m was used to assess the comparative abundance of the taxonomic groups, ranking them from most to least abundant

overall, within each year, and during either the day or night (Table III).

To investigate the vertical structure and DVM behavior of taxonomic groups, we compared the depth of 50% cumulative abundance during the day and night at each site following Wiebe *et al.* (Wiebe *et al.*, 2011). This was done by cumulatively adding the depth integrated abundances (no. of individuals per square meter) from the deepest net to the surface, then interpolating the depth at which 25, 50 and 75% of the populations were found using the MATLAB algorithm `interp1q`. A number of taxa demonstrated bimodal distributions, and we investigated these populations by calculating the depth interval of maximal abundance (DMA). The DMA is the net interval in which the macroplankton and micronekton abundance (no. of individuals per cubic meter) was highest for a taxonomic group.

Environmental data

Oxygen and temperature profiles were taken from the upcast of the MOCNESS to provide simultaneous hydrographic profiling. Calibration and processing of the MOCNESS hydrographic data are described in Wishner *et al.* (Wishner *et al.*, 2013). Oxygen concentration data were unavailable from the MOCNESS sensor for the top 40 m in 2007, so measurements were used from CTD casts made at the same station and year (processed by C. Flagg, Stony Brook University). Electronic failures during some tows for some sensors prevented a full analysis of all environmental parameters.

Analysis

Statistical analyses were conducted using the PRIMER version 6 statistical package (Clarke and Warwick, 2001; Clarke and Gorley, 2006). Standardized square-root abundance data using taxonomic groups (individuals per cubic meter in each net) were used to compare micronekton assemblages using multi-dimensional scaling (MDS) plots and cluster analyses of Bray–Curtis similarity matrices. A Pearson correlation, which produces a vector by calculating the covariance of the normalized physical data and dividing it by the product of their standard deviations, was superimposed on the MDS plots to distinguish which hydrographic parameters most contributed to the groups. *A priori* factors, including ecological zone, depth zone, station, year and day–night status, were tested using ANOSIM and SIMPER. Finally, the BIO-ENV test was applied to the normalized physical data and the normalized transformed abundance data using Spearman's coefficients. Nonparametric sign tests were conducted to compare broad patterns of abundance between years and diel cycle using the SPSS statistical package.

RESULTS

Hydrography

The OMZ varied only slightly in depth and thickness between years at this station, with a somewhat larger LO and smaller UO in 2008 compared with 2007 (Fig. 1). The thermocline was near 20 m for both years, while below the thermocline, temperature decreased steadily to $\sim 4.5^\circ\text{C}$ at 1000 m. Oxygen concentration decreased to $\sim 1\ \mu\text{M}$ within the OM, then at $\sim 600\ \text{m}$ increased with depth to $>20\ \mu\text{M}$ by 1000 m. These patterns were consistent between years and during both the day and night.

Distribution

Overview

Each of the six ecological zones of the water column was dominated by different taxonomic groups and had a distinct community makeup independent of abundance

(Fig. 2). Crustaceans dominated the ecosystem, with the top three taxonomic groups generally being euphausiids, amphipods and decapods in order of abundance (Table III), with salps and gastropods occasionally outnumbering the amphipods and/or decapods. In both 2007 and 2008, the depth integrated abundances within a group (0–1000 m, no. of individuals per square meter) were not significantly different during the daytime and nighttime (sign test $P = 0.302$; Table III). There were, however, significantly higher combined day and night abundances in 2008 (sign test $P = 0.035$) as compared with 2007 as a consequence of differences in daytime abundances (sign test $P = 0.007$ for daytime, sign test $P = 1.0$ for nighttime). This difference appears to be driven, primarily, by the low daytime abundances in 2007 from 0 to 550 m. The upper water column (0–150 m) had the highest abundances of animals, containing 68% of the individuals (no. of individuals per square meter) during the daytime and $>90\%$ of the individuals during the night

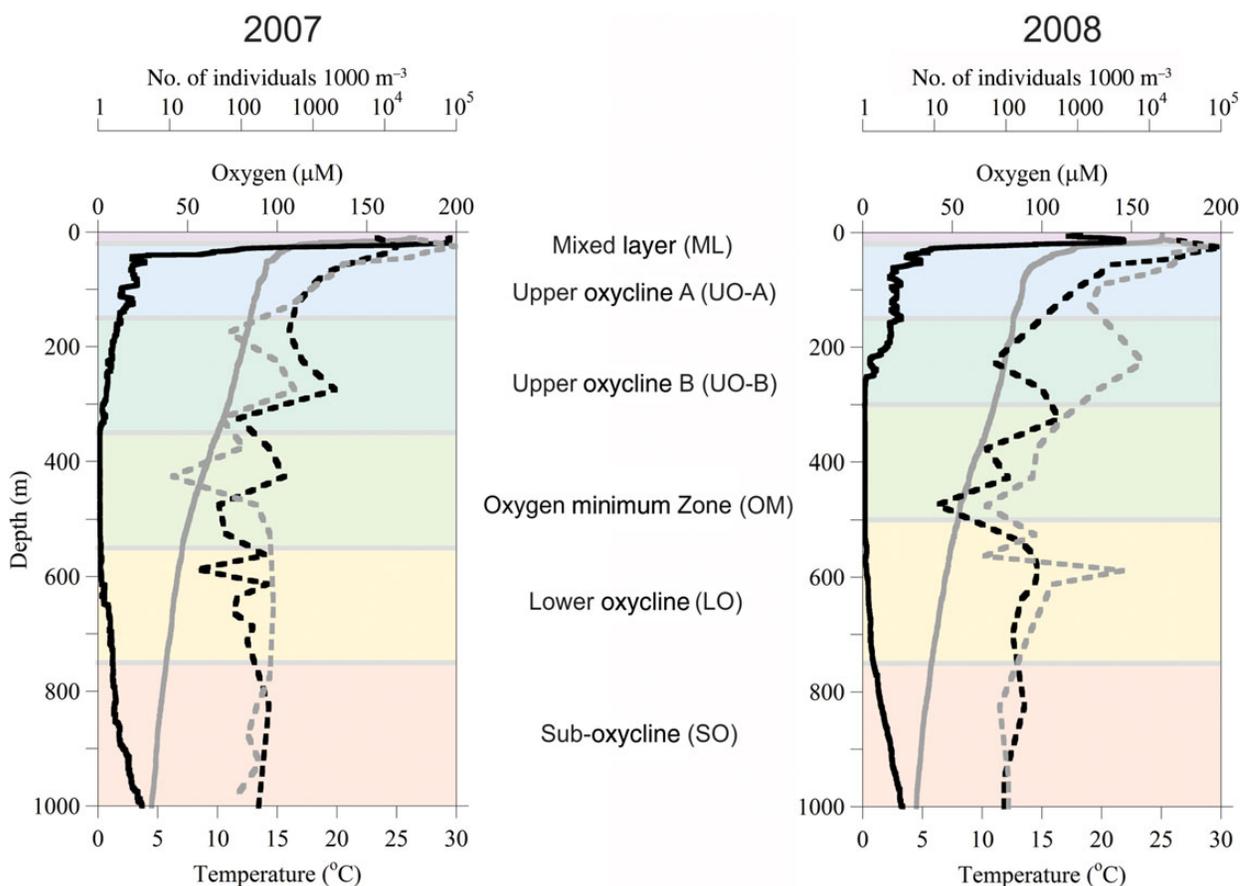


Fig. 1. Temperature ($^\circ\text{C}$, solid grey) and oxygen concentration (μM , solid black) profiles for the Costa Rica Dome for 2007 (MOCNESS Tow #619) and 2008 (MOCNESS Tow #636). Depth and oxygen concentration were used to establish the ecological zones of the ML, UO-A, UO-B, OMZ core, LO and SO. Total daytime (dashed grey) and nighttime (dashed black) abundances (sum of all taxa) are reported on a log scale. Abundances are plotted at the midpoint of each net depth interval as the number of individuals $1000\ \text{m}^{-3}$. Note that the abundance profiles were relatively similar between years with the exception of a reduced abundance above 100 m during the nighttime of 2007.

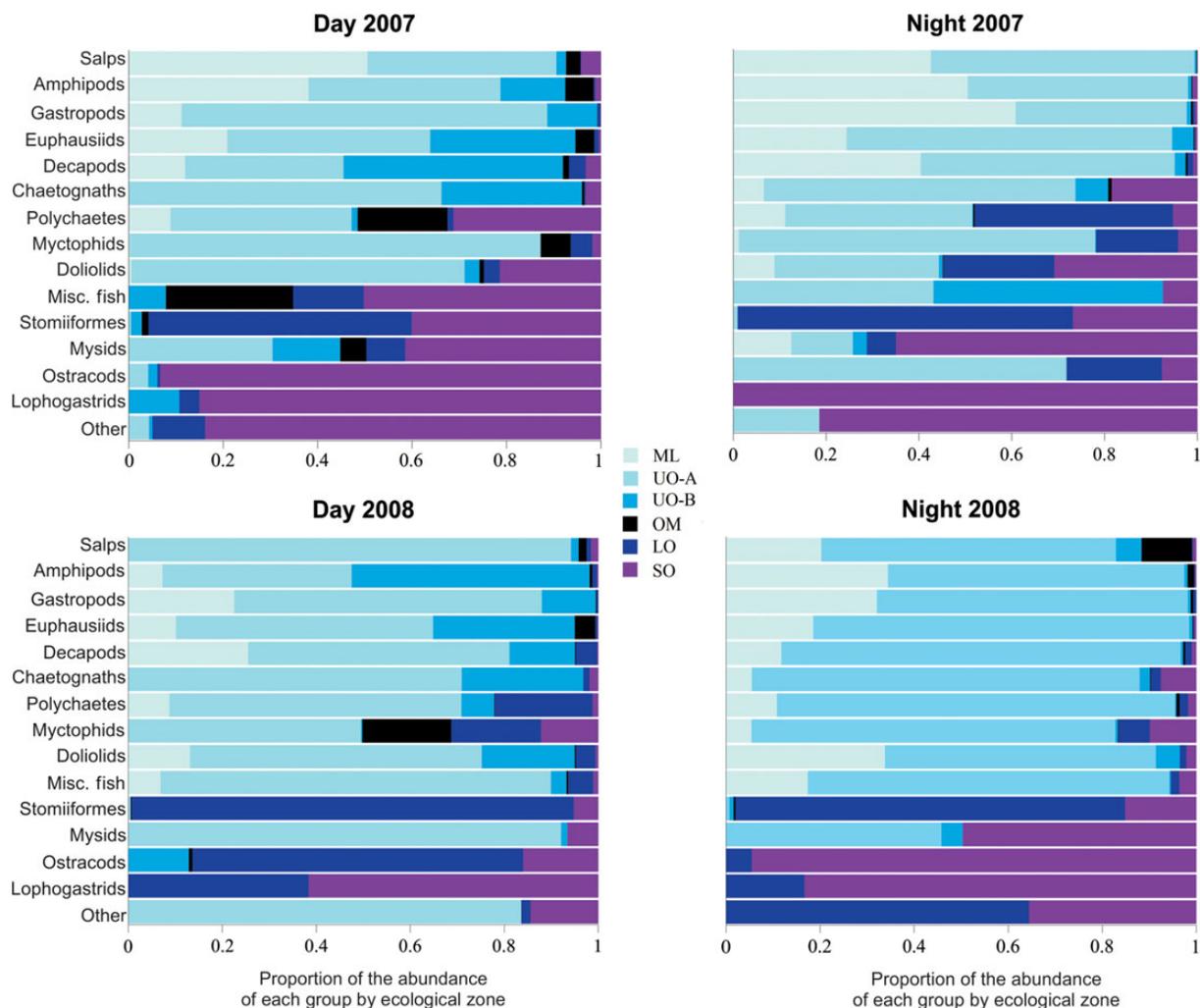


Fig. 2. Proportion of each taxonomic group (based on the no. of individuals per square meter) within each ecological zone during the day and night of 2007 and 2008. A higher proportion of animals occurred in the oxyclines and OMZ core during the day compared with the night during both years for many taxa (representation by depth zone is available in Supplementary data, Fig. S2).

during both years (Fig. 1; Supplementary data, Table SI). Although the lower water column (150–1000 m) had less total abundance, it was the habitat for a diverse and structured population of macroplankton and micronekton and was the daytime location of a number of diel vertical migrators. Despite differences in total abundance, the taxonomic composition of the upper and middle water column (0–550 m) was similar day and night and between years (Supplementary data, Fig. S1). However, the lower water column (550–1000 m) was comprised of a distinctly different and more diverse set of taxa compared with shallower depths, with a greater evenness among groups.

Upper water column

The thermocline (20–30 m) was the region with the greatest abundance of animals in both years. As such, a

large proportion of the total depth integrated abundance for all taxa in the upper water column (0–150 m, no. of individuals per square meter) was aggregated in the top 30 m during both the day (~50% in both years) and night (~65% in both years; Table IV; Fig. 3A). This depth region was usually the DMA for all groups during the night except Stomiiformes fish and lophogastrids.

DVM in the UO

In spite of the pronounced OMZ, there was observable DVM during both years into the UO and the OM during the day. In 2007, the daytime DVM layer was less pronounced, with only ~3.5 times as many individuals at midwater depth (150–550 m) during the day as during the night (Fig. 3B). Most of these individuals (~80%) were found between 150 and 350 m. Euphausiids were

Table IV: Depth interval of maximum abundance (DMA; no. of individuals per cubic meter) and quartile depth of cumulative abundance from deep to shallow 1000–0 m (no. of individuals per square meter).

	DMA		07 Day				07 Night				08 Day				08 Night			
	07 D	07 N	08 D	08 N	25	50	75	25	50	75	25	50	75	25	50	75		
Chaetognaths	20–30	20–30	50–60	20–30	143	94	26	177	34	24	159	92	58	59	34	26		
Polychaetes	20–30	20–30	20–30	20–30	767	360	32	657	101	25	181	61	27	28	25	22		
Gastropods	20–30	20–30	20–30	20–30	57	24	15	24	16	8	36	26	21	27	23	16		
Ostracods	900–1200	20–30	575–600	750–900	–	816	775	581	127	100	651	595	581	878	832	786		
Decapods	20–30	20–30	20–30	20–30	220	179	18	29	22	12	39	26	20	29	26	22		
Euphausiids	30–40	20–30	20–30	20–30	240	43	26	94	42	20	218	61	28	38	28	22		
Lophogastrids	725–775	900–950	650–750	900–1000	–	740	724	950	917	823	–	804	715	–	–	859		
Mysids	20–30	800–850	20–30	20–30	813	426	105	839	811	146	34	27	24	824	296	25		
Amphipods	0–20	20–30	20–30	20–30	89	21	7	27	20	10	210	156	29	40	27	15		
Salps	20–30	20–30	40–50	20–30	24	10	5	27	22	12	51	47	43	36	26	21		
Doliolids	20–30	20–30	50–60	30–40	451	26	18	825	589	26	148	61	51	44	30	15		
Myctophids	40–50	20–30	50–60	20–30	57	43	34	55	42	26	662	301	57	38	29	24		
Stomiiformes	600–625	550–750	575–600	550–575	763	668	601	762	686	616	600	591	582	679	599	565		
Misc. fish	900–1200	50–60	50–60	20–30	–	719	477	285	168	117	69	55	41	43	31	23		
Other	900–1200	80–100	40–50	525–550	–	–	793	886	793	759	109	85	49	791	548	532		

Blanks (–) represent quartiles which cannot be calculated for a species due to the narrow depth interval of abundance.

the most abundant with a large peak in numbers between 250 and 300 m (Fig. 3B). Decapods contributed substantially between 200 and 300 m while other smaller aggregations of mysids (200–300 m), ostracods (200–250 m), gastropods (150–250 m), lophogastrids, polychaetes and chaetognaths (150–200 m) also contributed to the daytime DVM layer in 2007.

In 2008, DVM was much greater, with ~10 times as many individuals at 150–350 m during the day versus the night. Groups that had been abundant migrators in 2007 were found at similar depths in 2008, with decapods, gastropods and ostracods in high abundance during the day between 200 and 250 m, and chaetognaths at 150–200 m. In 2008, however, there were also substantial numbers of doliolids and polychaetes peaking from 150 to 200 m, while mysids had a subsurface daytime maximum between 150 and 200 m along with the misc. fish. Amphipods and euphausiids, which were numerically the most abundant diel vertical migrators, had broader depth ranges, with daytime peaks from 150 to 250 m for amphipods and 150 to 300 m for euphausiids.

This pattern of distinct vertical zonation patterns for DVM was further borne out by abundance analyses at a higher taxonomic resolution, especially for euphausiids. When euphausiids were grouped by eye morphology, only two of the four types contributed to the strong DVM patterns (Fig. 4). At the surface, there was a nonmigratory group comprised of *Stylocheiron* spp. that maintained a numerically dominant epipelagic presence. Although type-1 and type-2 euphausiids were frequently found in this ML during both day and night, individuals from these two groups were responsible for the euphausiid patterns of DVM to depth during the daytime. Type-1 (bilobed-eyed) euphausiids contributed significantly to the 2008 daytime peak between 150 and 250 m with a further deep peak between 350 and 450 m, although type-2 (round-eyed) were numerically dominant and found at a daytime depth range from 200 to 250 m. In 2007, a similar pattern was present, with the type-1 euphausiids having two daytime abundance peaks in midwater; this time in the same depth strata as the greater abundance peak of the type-2 euphausiids (250–300 m) and another from 350 to 450 m. Some of the type-2 (round-eyed) euphausiids were found below the OM, but one distinctive species, *B. amblyops*, was consistently found only in the LO and SO waters.

Other complex distribution patterns were observed in the myctophid fish based on their developmental stage and size (Fig. 5). Pre-flexion individuals, found only in 2007, were observed exclusively in the upper water column. Small post-flexion myctophids (<22 mm in length) were found in each depth zone during the day, but were almost completely absent at midwater (150–550 m) at night during both years. The largest individuals

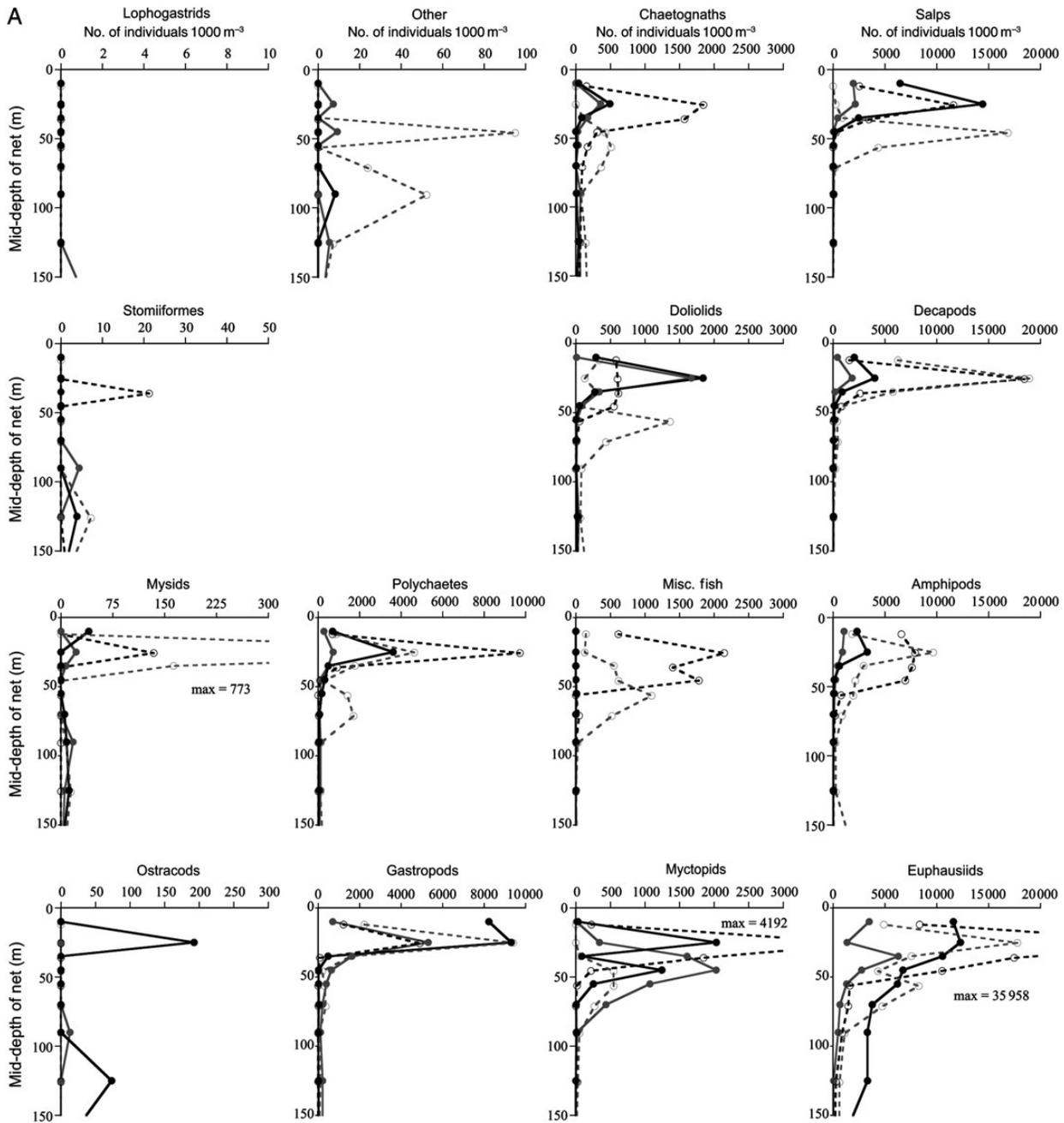


Fig. 3. Day (grey) and night (black) distributions of various taxa during 2007 (solid) and 2008 (dashed) in the standard depth categories of upper (A: 0–150 m) middle (B: 150–550 m) and lower water column (C: 550–1000 m). Note the different abundance (no. of individuals 1000 m^{-3}) scales within and between figures.

(>22 mm), were completely absent from the surface waters during the day, and found predominantly in the surface during the night during both years.

The oxygen minimum zone core

The OM, defined as the region where oxygen levels were $\leq 1.8\ \mu\text{M O}_2$, was found from 350 to 550 m during 2007

and 300 to 500 m in 2008. In this zone, there were daytime layers of euphausiids and myctophids in both years (Fig. 3B). Occasionally, there were also high densities of other groups, such as a daytime peak in salps between 300 and 400 m and in mysids and polychaetes between 400 and 450 m in 2007 and a nighttime salp layer between 400 and 450 m in 2008.

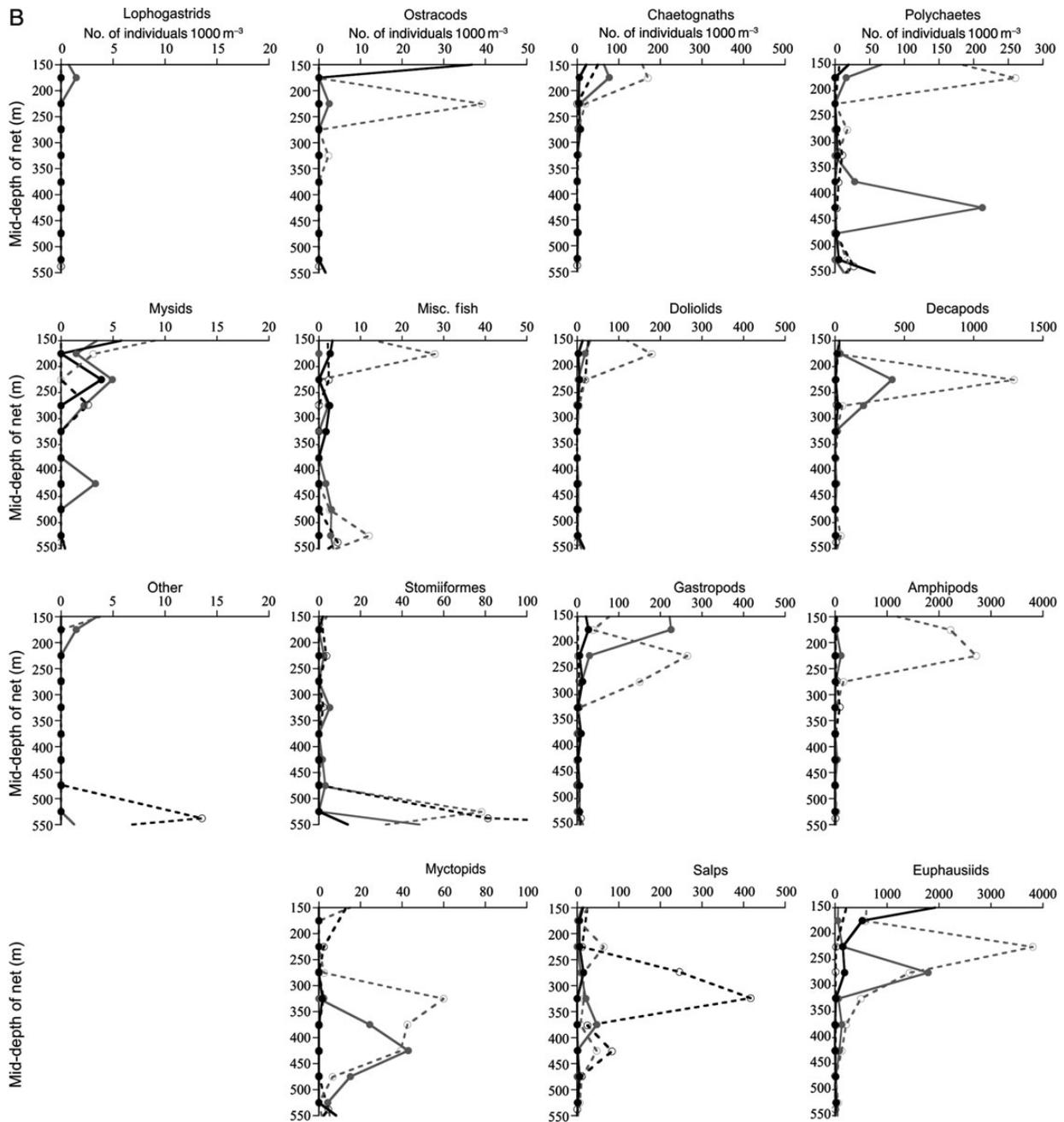


Fig. 3. Continued

The lower oxycline

There was a unique community (termed the “lower oxycline community” Wishner *et al.*, 2013) in and below the OMZ that consisted of, in decreasing abundance, Stomiiformes fish (almost exclusively made up of *Cyclothone* spp.), polychaetes, decapods, ostracods, doliolids, myctophids, salps and amphipods (Fig. 3C). In 2007, there were less strongly defined peaks of these taxa below the OM, with the LO community being somewhat more

spread out through the lower water column during both the day and night. In contrast, the LO community was much more localized in 2008, with ~60% of the lower water column depth integrated abundances (550–1000 m, no. of individuals per square meter) being found between 575 and 600 m during the day. This pronounced peak consisted of decapods, amphipods, Stomiiformes and myctophid fish, salps, polychaetes and ostracods. During the night in 2008, only the

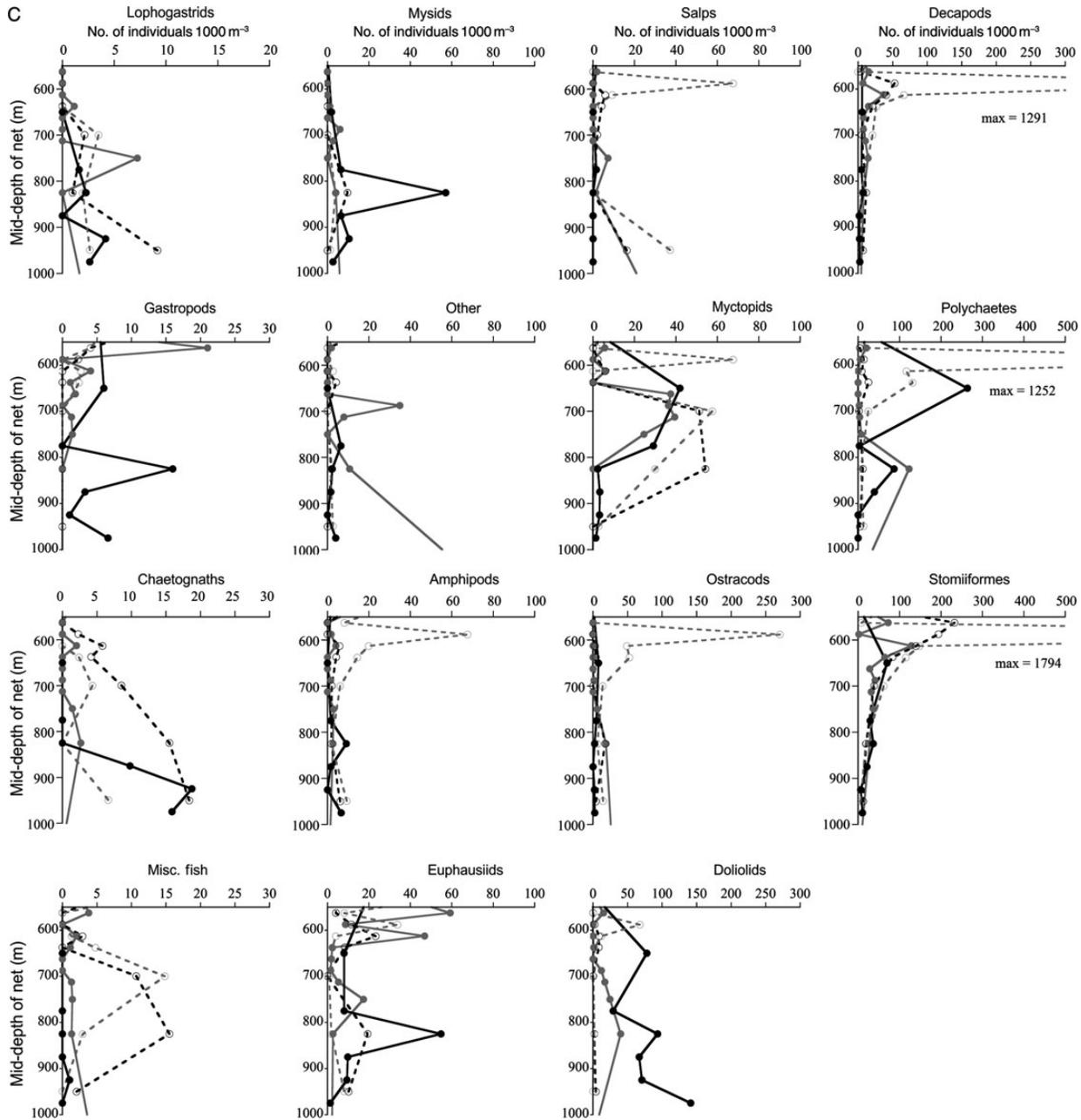


Fig. 3. Continued

decapods and Stomiiformes fish remained concentrated in this layer.

The suboxycline

The SO region (below 750 m) had a distinct taxonomic profile, made up of persistent populations of chaetognaths, euphausiids (*B. amblyops*), decapods (predominantly *Gennadas* spp. and Caridean shrimp), Stomiiformes (hatchetfish and *Cyclothone* spp.), lophogastrids, salps, doliolids and

mysids (Fig. 3C). At this depth, where oxygen levels began to increase, there was an influx of new taxa and a greater taxonomic evenness as indicated by the proportionate composition of taxa (Supplementary data, Fig. S1).

Analysis

Clusters from Bray–Curtis analyses using taxa abundances from each net were arbitrarily defined to produce

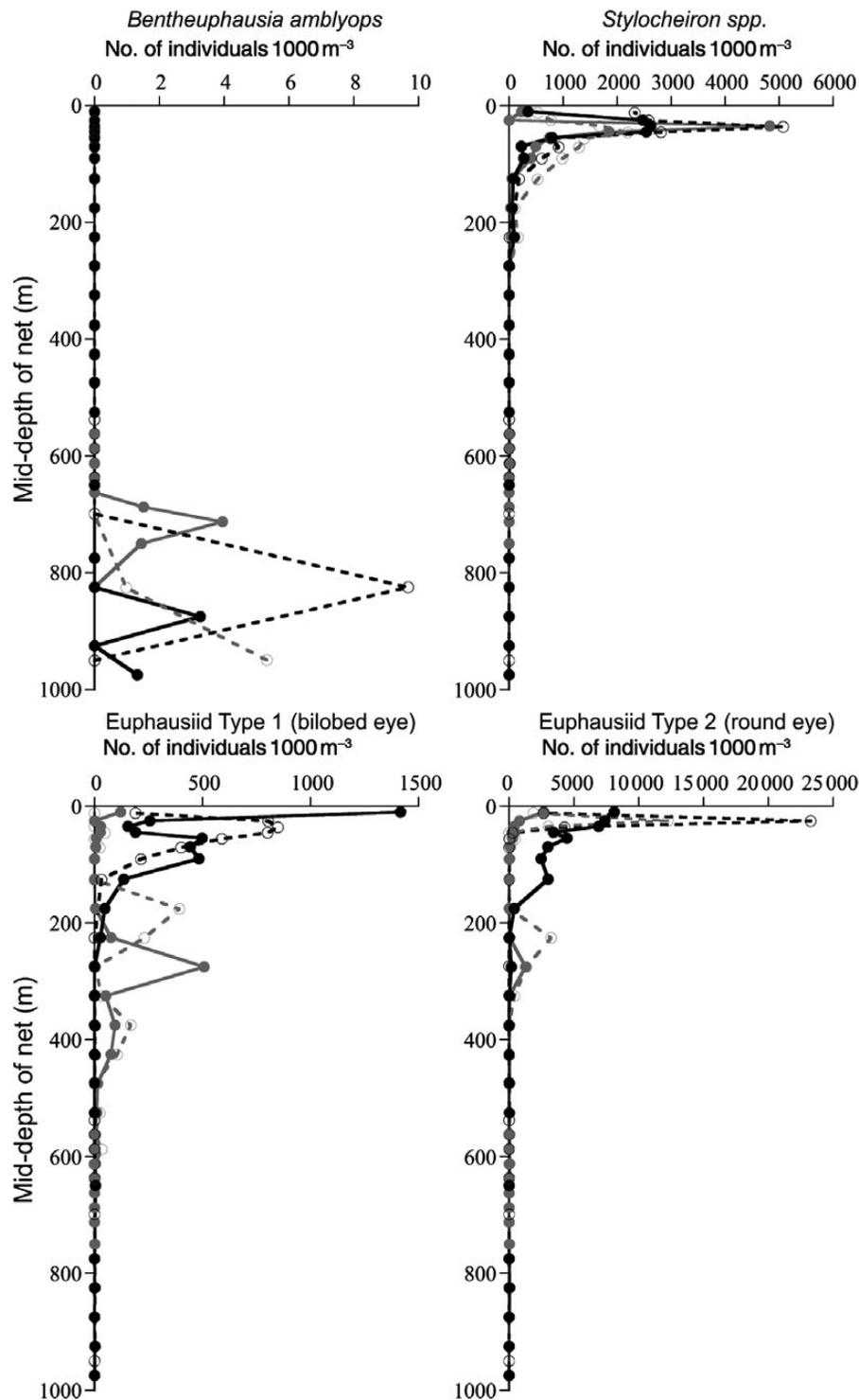


Fig. 4. Day (grey) and night (black) distributions of euphausiids during 2007 (solid) and 2008 (dashed). Note the different abundance (no. of individuals 1000 m⁻³) scales and the difference in vertical habitat use among and within the groups.

11 meaningful groups at 40% similarity and above. MDS plots captured these patterns of compositional similarity, and supported the *a priori* grouping of taxa by depth and

ecological zone, placing the lower water column nets in a separate group from the upper and midwater nets during both years (Fig. 6). A Pearson correlation further

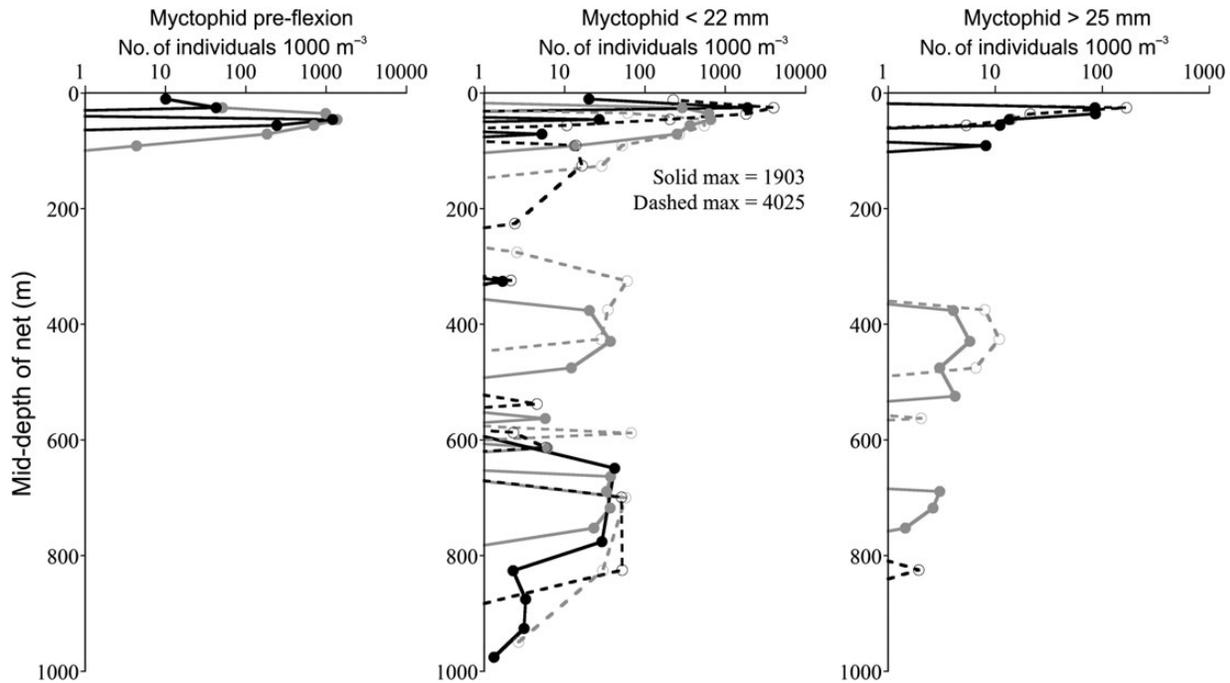


Fig. 5. Day (grey) and night (black) distributions of pre- and post-flexion myctophid fish during 2007 (solid) and 2008 (dashed). Abundance scales are logarithmic and differ between years (no. of individuals 1000 m^{-3}). Note the ontogenetic differences in vertical habitat use and the high proportion of individuals in the upper water column.

suggested that the divisions among groups were strongly correlated ($-0.6 < R < 0.6$) with the *a priori* physical factors used to define the ecological zones (depth, temperature and oxygen; statistics in Supplementary data, Table SII). SIMPER analyses of similarity within ecological zone groups suggested that the ML and SO were more homogeneous environments, with $\sim 60\%$ similarity in the patterns of abundance, while the OM was a more heterogeneous environment with $> 33\%$ similarity in patterns of abundance (Table V). Further SIMPER and ANOSIM analyses showed that there was 90–60% dissimilarity among the ecological zones and highlighted their unique communities and abundances (see Supplementary data, Table SIII for taxon contributions to similarity and dissimilarity). Using only the depth factor, similar patterns emerged, but there was less similarity within depths.

Unlike ecological zone and depth factors, analysis of abundance patterns based on year and day/night factors showed no significant differences (Table V). The lack of significant differences between the day and night nets may be attributable to the broad taxonomic groups and the zonal patterns of DVM. When a two-way SIMPER analysis of day/night and ecological zone was applied, the similarities and differences doubled in percentage, but remained insignificant.

No single variable was strongly predictive of community composition (BEST-ENV analysis). The vertical profiles were relatively consistent between the 2 years, with the thermocline, OMZ and LO at similar depths. Depth correlated strongly with temperature and oxygen across the dataset and was the best predictor of community makeup when considering the 0–1000-m water column ($R = 0.503$). An analysis of the combined upper and middle water column (0–550; the range inclusive of much of the DVM) revealed that depth remained the best predictor of abundances ($R = 0.632$). When analyzed separately by time of day, depth remained the best factor to predict net composition similarity for both the day ($R = 0.704$) and night ($R = 0.679$) in the upper water column (0–550 m). The lower water column samples (550–1000 m) were best correlated with temperature ($R = 0.372$).

DISCUSSION

General population structure

Macroplankton and micronekton abundance data contribute to a descriptive understanding of the community structure of OMZ regions, and these results provide greater vertical resolution for evaluating the pronounced

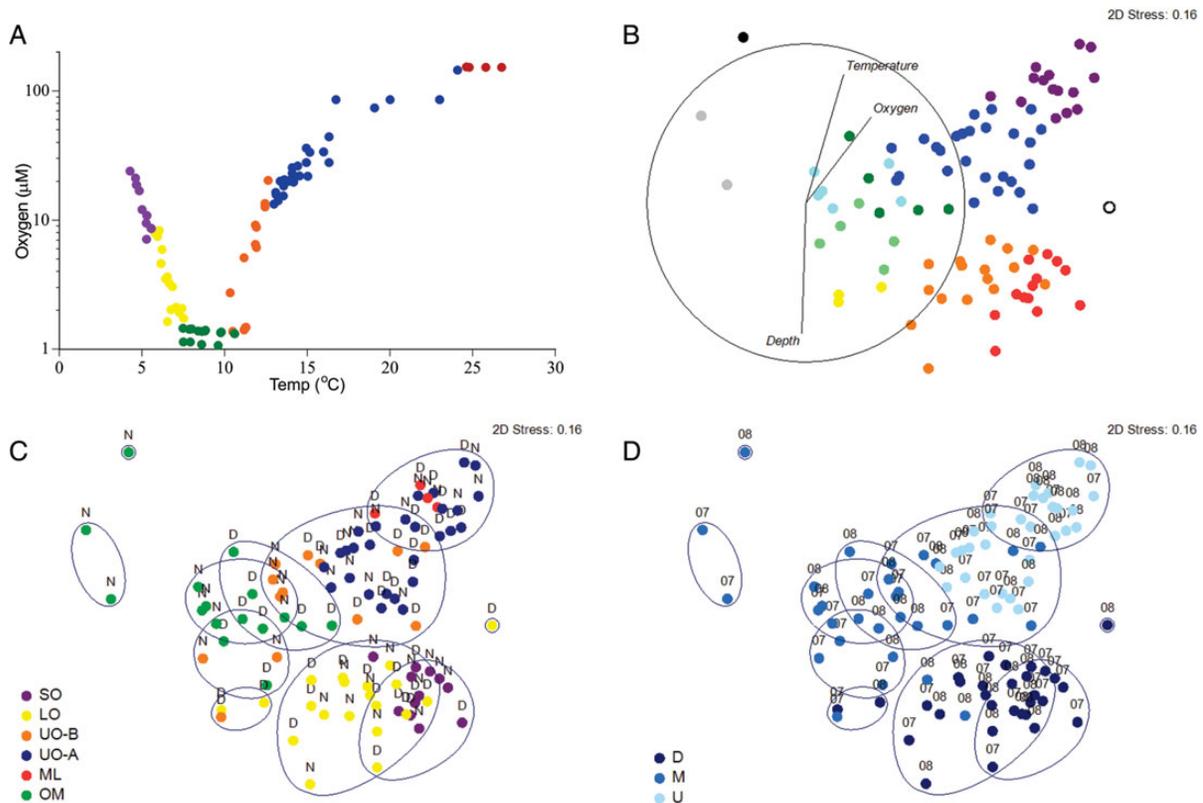


Fig. 6. (A) A temperature (°C) and oxygen (µM) plot showing the hydrographic parameters that define the ecological zones (abbreviations in Fig. 1) of nets from both years during the day and night. Values are averages of MOCNESS sensor data across the net interval. These factors and the taxon abundances (no. of individuals 1000 m⁻³) in each net were applied to form MDS plots from cluster analyses. Each point represents a net sample, the axes are nondimensional and the distance between points indicates their compositional similarity. (B) Clusters of >40% similarity (colors and shapes) are from Bray–Curtis analysis and are plotted with Pearson correlated normalized environmental vectors. This original 40% similarity plot (expressed with ovals) is re-plotted with both the (C) ecological zones pictured in panel A with the day/night factor and the (D) depth zone (Deep, Mid and Upper water column) with the year factor.

Table V: Analyses of environmental factors measuring the similarity within (grey boxes) and dissimilarities between (unboxed) groups were performed using ANOSIM and SIMPER tests.

Paired comparison of average similarity and dissimilarity by factor													
Total <i>R</i> 0.647	Ecological zones						Total <i>R</i> 0.613	Depth zones			Total <i>R</i> 0.02	Day/night	
	ML	UO-A	UO-B	OM	LO	SO		U	M	D		D	N
ML	61.69	54.64	76.94	89.21	88.08	87.36	U	44.26	79.41	81.71	D	27.46	74.41
UO-A		43.66	72.0	84.04	82.13	78.56	M		29.74	79.81	N		24.64
UO-B			34.85	72.62	78.60	77.63	D			41.88	Total <i>R</i> :	Years	
OM				33.36	81.21	86.84					0.022	2007	2008
LO					43.35	64.16					2007	26.90	74.64
SO						59.82					2008		25.89

Total *R* values for ANOSIM analyses are shown and significance is reported when $P < 0.01$ (italics) and $P < 0.001$ (bold italics) for differences between groups.

impact of OMZs on the distribution of pelagic animals (Saltzman and Wishner, 1997a; Rapien, 2004; Ekau and Verheye, 2005; Criales-Hernández *et al.*, 2008; Escribano *et al.*, 2009). As expected, we saw a marked decrease in abundances with decreasing oxygen concentration,

with the lowest densities found in the OM core. There were, however, significant numbers of migrators above and within this region during the daytime, primarily euphausiids and myctophid fish. Finally, below the LO, where oxygen levels rose above 9 µM, the taxa

changed to a richer community of typical bathypelagic animals.

DVM (upper and middle water column, 0–550 m)

Portions of the abundant surface community made DVMs into the hypoxic waters of the UO during the daytime, as evidenced by secondary peaks in abundance and an increased proportion of total abundance found below the ML during the day. OMZ waters are, however, known to reduce the depth to which many species migrate (Wishner *et al.*, 1998; Fernández-Álamo and Färber-Lorda, 2006). Compared with regions without OMZs, there was a drop in the proportion of migrating biomass, with a ratio of mean night:day biomass in the upper 150 m of 1.1 for the ETNP (Wishner *et al.*, 2013) in contrast to 2.5 at K2 off of Japan and 1.7 at ALOHA near Hawaii (Steinberg *et al.*, 2008a). This indicated that DVM for at least some macroplankton and micronekton may be compressed, presumably to avoid hypoxic waters, as has been shown for some higher trophic levels (Prince and Goodyear, 2006; Prince *et al.*, 2010; Koslow *et al.*, 2011) and in a meta-analysis of DVM acoustic backscatter (Bianchi *et al.*, 2013). Organisms which did migrate, however, were found at similar depths regardless of the oxygen concentration at depth (this analysis and Wishner *et al.*, 2013). It may be that the ecological pressures instigating DVM, particularly seeking out low-light environments to achieve visual predator avoidance, have a certain minimum depth to be worth the energetic expenditure. Thus, in our study region, the proportion of organisms physiologically capable of performing the DVM may be smaller in comparison with other regions in the Pacific, but those species which are adapted to low oxygen consistently seek a similar depth of migration.

The taxa that performed DVM from epipelagic waters into the UO consisted of euphausiids, amphipods, decapods, ostracods, myctophid fish, chaetognaths and polychaetes. This taxonomic resolution was useful to differentiate patterns of vertical distribution and behavior. In Wishner *et al.* (Wishner *et al.*, 2013), the 2007 DVM daytime depth extended from 150 to 350 m based on biomass samples. With taxonomic abundance data, it is seen that there are subpeaks, comprised of discrete overlapping taxa contributing to this feature.

The ability to explore these finer scale differences in DVM peaks may help us understand broader scale patterns in vertical distribution and hypoxia tolerance. For example, there were consistent patterns in the peaks of the crustacean vertical distribution, and as a result, the hypoxia exposure of certain groups. Amphipod daytime abundance was at a shallower, more oxygenated depth

than decapods. The euphausiids had a broad daytime distributional peak, but type-2 (round-eyed) euphausiids had a single shallower, more oxygenated peak in distribution than type 1 (bilobed; Fig. 4). This is similar to the results of Sameoto *et al.* (Sameoto *et al.*, 1987) who reported high concentrations of adult euphausiids near 300–350 m during the day in the ETNP. Brinton (Brinton, 1979) also found a secondary peak of daytime migrating euphausiids between 200 and 400 m, while *Stylocheiron* species and juveniles remained in surface waters throughout the diel cycle, as in our study. In the eastern tropical South Pacific, the site of another OMZ with profound severity and extent, Escribano *et al.* (Escribano *et al.*, 2009) found higher euphausiid abundance, by about an order of magnitude, than in this study. At their site, however, *Euphausia* spp. and *Nematoscelis megalops* euphausiid populations migrated from the surface to 200–400 m during the day, while *Stylocheiron affinis* remained between 60 and 80 m, similar to our observed distributional patterns.

In the OM core, we also observed diel vertical migratory patterns for a few groups. The type-1 euphausiids had a small DVM peak in abundance in the OM core during both years, co-habiting this region with salps and myctophid fish during the day. The presence of myctophids at midwater depths was expected, but only a small proportion of the population occurred in the lower and midwater column at low oxygen (<2% of the abundance), an unusually small amount for this mesopelagic migratory group. Much of the myctophid population was in the upper water column and consisted of a large cohort of pre-flexion juveniles in 2007 and a portion of the smaller-size class of post-flexion individuals during both years. A similar absence of a resident myctophid (*Benthoosema pterotum*) at midwater depths in low oxygen was observed by Dypvik and Kaartvedt (Dypvik and Kaartvedt, 2013) in the Red Sea; this was attributed to the combined physiological stresses of high temperature, low oxygen and low food availability. Instead, individuals in that study migrated very deep and were found below the oxycline at 600–750 m. In the ETNP, a deeper peak may occur below our sampling depth. Alternately, myctophid fish are good at avoiding nets (Kaartvedt *et al.*, 2012). Our daytime abundances of large post-flexion myctophids were 50 and 56% lower than at night in 2007 and 2008, respectively, while small post-flexion individuals were similar in abundance in 2007 but 48% lower during the day versus the night in 2008. This suggests that capture avoidance contributed to apparent patterns of nonmigration in myctophids. Regardless, the persistent peak (>20 individuals m⁻²) of the small-size class of post-flexion individuals in the upper water column (0–150), suggested that the oxygen and resource

limited habitat associated with the OMZ in the ETNP influenced the DVM of smaller younger individuals of this generally mesopelagic group.

LO and deep communities (550–1000 m)

Below the OM, where oxygen concentration began to increase, we characterized a distinct LO community with a peak in abundance. This persistent peak was observed in earlier studies (Vinogradov and Voronina, 1961; Sameoto, 1986; Wishner *et al.*, 1995), but the narrower depth ranges of our sampling regime revealed that some of the macroplankton and micronekton associated with this phenomenon were aggregated quite densely, within a 25 m depth interval at an oxygen concentration of 2 μM (Wishner *et al.*, 2013). This assemblage, which during the daytime in 2008 was $\sim 60\%$ of the lower water column abundance, was comprised of myctophids, amphipods, salps, ostracods, and most abundantly polychaetes, decapods and *Cyclothone* spp. fish, in addition to the unique copepod assemblage previously described at the LO (Wishner *et al.*, 2013). The layer was less distinct during 2007 and during the night in 2008, although smaller abundance peaks of similar taxonomic composition were spread out across a larger depth range within the LO (75–100 m in vertical extent). The LO peak was of a similar taxonomic composition to that found in the Arabian Sea in earlier work. In that region, there was a strong consistent peak of *Cyclothone* spp. and the decapod *Gennadas* sp. in association with the oxygen threshold below the OM (Rapien, 2004). Below the LO layer in the ETNP study, the community became more taxonomically rich and varied, including salps, myctophids, Stomiiformes fish, the specialized euphausiid *B. amblyops*, *Gennadas* spp. and Caridean shrimp, chaetognaths, lophogastrids, doliolids and mysids.

Comparisons with other Pacific regions

Overall abundances (0–1000 m, no. of individuals per square meter) and organism concentration at any particular depth (no. of individuals per cubic meter) are difficult to compare with previous studies because of differences in sample sorting methodology. In our study, smaller size classes of some taxa were counted separately along with copepods; those data are still being analyzed (Table II). In macroplankton groups for which it was possible to make direct comparisons, there were higher abundances of euphausiids and salps compared with other Pacific regions without OMZs such as time-series stations K2 off Japan and ALOHA off Hawaii (Steinberg *et al.*, 2008a). There were similar abundances of decapods, polychaetes, mysids and doliolids in comparison with ALOHA and K2 in 2007, although a much higher

abundance of decapods and polychaetes in 2008. As described above, there was an impact of the pronounced OMZ on the proportion and behavior of diel migratory species in comparison with other Pacific regions.

Hydrographic parameters

One of the goals of this study was to disentangle the environmental parameters influencing the abundance and community composition of the OMZ. However, since temperature and oxygen concentration were both strongly correlated with depth as a consequence of similar hydrographic profiles during both years, it was not possible to isolate these effects. The *a priori* ecological zones, however, were effective in predicting community composition, with ecological groups clustered together statistically. Each ecological region, excluding the ML and UO-A, was statistically distinct from all other regions of the water column.

Sampling limitations

Historical sampling of midwater depths typically averaged distributions over large vertical strata probably because of lower biomass and an expectation of little differentiation in midwater ecosystem niches. However, the fine-scale layering and patchiness of mesopelagic distributions, revealed by recent acoustic and vehicle observations and supported by our analysis, re-emphasizes the need to carefully consider the dynamics of midwater distributions (Robison, 2004; Cheriton *et al.*, 2007; Opdal *et al.*, 2008). Acoustic and optical analysis of near-surface thin layers suggested that the thickness of these features in the upper water column was ~ 1 m for zooplankton, and that the shape of the gradient is potentially strongly mediated by predator–prey interactions (Benoit-Bird *et al.*, 2009). In our study, much care was taken to correlate discrete net sampling strata with hydrographic parameters using adaptive targeted sampling. Our results suggest that a macroplankton and micronekton thin layer exists at very low oxygen within the oxygen gradient of the LO. Even this fine-scale sampling, however, covered a vertical range of 25 m. Whether these deeper oxycline layers have a similar vertical extent and physical/biological origin as surface thin layers can be tested in the future by pairing net tows with an optical or acoustic investigation, particularly as variations in the vertical displacement caused by internal waves make pinpointed localized net capture on a scale of <10 m difficult.

Distribution patterns in our dataset were complicated by the unique species-specific and ontogenetic patterns embedded in the broad taxonomic groups of the study.

In particular, differential patterns of migration were exemplified by the distribution of euphausiid subgroups and by myctophid fish. Other work performed on the same set of cruises further described ontogenetic and species-specific patterns of DVM for copepods and thecosomatous pteropods (Maas *et al.*, 2012b; Wishner *et al.*, 2013). Specific life history events such as molting, egg laying or diapause can also modify diel migratory behavior (e.g. Endo and Yamano, 2006) and can be associated with bimodal vertical distributions within species. As a consequence, populations within a species may have differences in both exposure and sensitivity to low oxygen. As the oceans warm and regions of hypoxia expand, it is important to understand environmental constraints on these processes and implications for biotic transfer of nutrients, such as nitrogenous waste or respiratory and waste carbon (Burd *et al.*, 2010; Robinson *et al.*, 2010). Higher resolution species and stage-specific sampling of populations, incorporating physiological and biogeochemical studies, are needed to quantify changes in the carbon and nitrogen cycles. The patterns in distribution and associated hydrography from this study are important basic characterizations of OMZ communities.

CONCLUSION

The fine-scale detail provided by our sampling strategy, which focused on relatively narrow depth intervals near changes in oxygen concentration, allowed us to describe distinct communities associated with specific regions of the water column of an OMZ in the ETNP. Community composition was strongly correlated with depth, temperature and oxygen concentration, supporting our classification of the water into ecological zones that were comprised of distinct macrozooplankton and micronekton communities.

The upper water column DVM community, which was dominated by fish, amphipods, gastropods, euphausiids, decapods, chaetognaths and polychaetes, migrated from the ML down into the UO and OMZ core during the day. Peak daytime abundances showed vertical segregation in the water column. Although the migratory macroplankton and micronekton in this region were less abundant than in other Pacific open ocean sites, they persisted at a similar daytime depth despite the severely oxygen limited habitat (oxygen $< 10 \mu\text{M}$). Euphausiids and myctophids in particular were found in very low oxygen environments during the day, and there was evidence that their distributions were shaped by oxygen limitation. Of particular interest, we characterized the macrozooplankton and micronekton community

associated with the secondary biomass peak (Wishner *et al.*, 2013) found at the LO ($\sim 600 \text{ m}$, $\sim 2 \mu\text{M}$ oxygen). This community consisted of a distinct group of taxa including abundant cyclothone fish, *Gennadas* spp. and other decapods, myctophids, polychaetes and amphipods.

If OMZs expand, these unique populations of migrators and OMZ residents that are highly adapted to extremely low oxygen concentrations, may expand their ranges horizontally if they out-compete organisms that have not undergone selection for such hypoxia tolerance. The global diel vertical distribution of midwater animals may, however, be limited by hypoxia (Bianchi *et al.*, 2013). As OMZs become shallower, midwater animals may be forced into more illuminated regions of the water column where they may be more easily preyed on by visual predators (Koslow *et al.*, 2011; Stewart *et al.*, 2013). Repercussions for the re-distribution of biomass in the water column and the effects of habitat compression on fisheries and biogeochemical cycling are already being explored (Prince *et al.*, 2010; Bertrand *et al.*, 2011; Seibel, 2011, Wishner *et al.*, 2013). Characterizing the animals that will encounter this expanding low oxygen ecosystem, and understanding the limits of their physiology and distribution will provide insight into the ecosystems that will evolve as climate change causes warming waters, ocean acidification and expanding regions of hypoxia in the open oceans. These changes, which are clearly of both scientific and economic interest, require zooplankton distribution studies spanning more geographic and seasonal variations, along with greater species-specific data and environmental resolution.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

ACKNOWLEDGEMENTS

We would like to acknowledge the hard work and expertise of the captains, crews and marine technicians of the *R/V Seward Johnson* and *R/V Knorr* as well as the organization and leadership of K. Daly who served as chief scientist on both cruises. We are thankful for the assistance of N. Charriere, A. Cleary, L. Elder, J. Graff, M. McNamara, M. O'Brien, J. Pelsler, B. Phillips, J. Schneider, K. Vogel and R. Williams for help at sea and in the laboratory collecting, sorting and identifying zooplankton. R. Williams processed the MOCNESS hydrographic measurements.

FUNDING

The work was supported by the National Science Foundation (OCE-0526545 to K.D., OCE-0526502 to K.W. and B.S. and OCE-0851043 to B.S.). Student and faculty funding was provided by the University of Rhode Island, the Rhode Island Experimental Program to Stimulate Competitive Research Fellowship program (to A.E.M.) and the Graduate School of Oceanography's summer REU program, SURFO (S.E. NSF grant OCE-0851794 to R. Pockalny).

REFERENCES

- Antezana, T. (2009) Species-specific patterns of diel migration into the oxygen minimum zone by euphausiids in the Humboldt current ecosystem. *Prog. Oceanogr.*, **83**, 228–236.
- Benoit-Bird, K. J., Cowles, T. J. and Wingard, C. E. (2009) Edge gradients provide evidence of ecological interactions in planktonic thin layers. *Limnol. Oceanogr.*, **54**, 1382–1392.
- Bertrand, A., Chaigneau, A., Peraltila, S. *et al.* (2011) Oxygen: a fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical pacific. *PLoS ONE*, **6**, e29558.
- Bianchi, D., Galbraith, E. D., Carozza, D. A. *et al.* (2013) Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat. Geosci.*, **6**, 545–548.
- Brinton, E. (1979) Parameters relating to the distributions of planktonic organisms, especially euphausiids in the eastern tropical pacific. *Prog. Oceanogr.*, **8**, 125–189.
- Burd, A. B., Hansell, D. A., Steinberg, D. K. *et al.* (2010) Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the @ \$! Is wrong with present calculations of carbon budgets? *Deep Sea Res. II*, **57**, 1557–1571.
- Cheriton, O. M., Mcmanus, M. A., Holliday, D. *et al.* (2007) Effects of mesoscale physical processes on thin zooplankton layers at four sites along the west coast of the us. *Estuaries Coast.*, **30**, 575–590.
- Cheung, W. W. L., Dunne, J., Sarmiento, J. L. *et al.* (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the northeast Atlantic. *ICES J. Mar. Sci. J. Conseil*, **68**, 1008–1018.
- Childress, J. J. and Seibel, B. A. (1998) Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J. Exp. Biol.*, **201**, 1223–1232.
- Clarke, K. R. and Gorley, R. N. (2006) *Primer v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Clarke, K. R. and Warwick, R. M. (2001) *Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E, Plymouth.
- Criales-Hernández, M., Schwamborn, R., Graco, M. *et al.* (2008) Zooplankton vertical distribution and migration off central Peru in relation to the oxygen minimum layer. *Helgoland Mar. Res.*, **62**, 85–100.
- Dam, H. G., Roman, M. R. and Youngbluth, M. J. (1995) Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time-series station. *Deep Sea Res. I*, **42**, 1187–1197.
- Dypvik, E. and Kaartvedt, S. (2013) Vertical migration and diel feeding periodicity of the skinnycheek lanternfish (*Benthoosema pterotum*) in the red sea. *Deep Sea Res. I*, **72**, 9–16.
- Ekau, W. and Verheye, H. (2005) Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. *Afr. J. Mar. Sci.*, **27**, 629–639.
- Endo, Y. and Yamano, F. (2006) Diel vertical migration of *Euphausia pacifica* (Crustacea, Euphausiacea) in relation to molt and reproductive processes, and feeding activity. *J. Oceanogr.*, **62**, 693–703.
- Escribano, R., Hidalgo, P. and Krautz, C. (2009) Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. *Deep Sea Res. II*, **56**, 1083–1094.
- Fernández-Álamo, M. A. and Färber-Lorda, J. (2006) Zooplankton and the oceanography of the eastern tropical pacific: a review. *Prog. Oceanogr.*, **69**, 318–359.
- Fiedler, P. C. and Talley, L. D. (2006) Hydrography of the eastern tropical pacific: a review. *Prog. Oceanogr.*, **69**, 143–180.
- Gowing, M. M. and Wishner, K. F. (1998) Feeding ecology of the copepod *Lucicutia aff. L. Grandis* near the lower interface of the Arabian Sea oxygen minimum zone. *Deep Sea Res. II*, **45**, 2433–2459.
- Hays, G. C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.
- Hays, G. C., Harris, R. P. and Head, R. N. (1997) The vertical nitrogen flux caused by zooplankton diel vertical migration. *Mar. Ecol. Prog. Ser.*, **160**, 57–62.
- Honjo, S., Manganini, S. J., Krishfield, R. A. *et al.* (2008) Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: a synthesis of global sediment trap programs since 1983. *Prog. Oceanogr.*, **76**, 217–285.
- Kaartvedt, S., Staby, A. and Aksnes, D. L. (2012) Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar. Ecol. Prog. Ser.*, **456**, 1–6.
- Kamykowski, D. and Zentara, S. J. (1990) Hypoxia in the world ocean as recorded in the historical data set. *Deep Sea Res. A*, **37**, 1861–1874.
- Karstensen, J., Stramma, L. and Visbeck, M. (2008) Oxygen minimum zones in the eastern tropical Atlantic and pacific oceans. *Prog. Oceanogr.*, **77**, 331–350.
- Keeling, R. F., Körtzinger, A. and Gruber, N. (2010) Ocean deoxygenation in a warming world. *Ann. Rev. Mar. Sci.*, **2**, 199–229.
- Koslow, J. A., Goericke, R., Lara-Lopez, A. *et al.* (2011) Impact of declining intermediate-water oxygen on deepwater fishes in the California current. *Mar. Ecol. Prog. Ser.*, **436**, 207–218.
- Longhurst, A. R. (1967) Vertical distribution of zooplankton in relation to the eastern pacific oxygen minimum. *Deep Sea Res.*, **14**, 51–63.
- Longhurst, A. R. and Harrison, W. G. (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Prog. Oceanogr.*, **22**, 47–123.
- Maas, A. E., Wishner, K. F. and Seibel, B. A. (2012a) The metabolic response of pteropods to acidification reflects natural CO₂-exposure in oxygen minimum zones. *Biogeosciences*, **9**, 747–757.
- Maas, A. E., Wishner, K. F. and Seibel, B. A. (2012b) Metabolic suppression in thecosomatous pteropods as an effect of low temperature and hypoxia in the eastern tropical north. *Mar. Biol.*, **159**, 1955–1967.
- Morrison, J. M., Codispoti, L. A., Smith, S. L. *et al.* (1999) The oxygen minimum zone in the Arabian sea during 1995. *Deep Sea Res. II*, **46**, 1903–1931.

- Motoda, S. (1959) Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.*, **7**, 73–94.
- Opdal, A., Godøy, O., Bergstad, O. *et al.* (2008) Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the northern mid-Atlantic ridge. *Deep Sea Res. II*, **55**, 45–58.
- Oschlies, A., Schulz, K. G., Riebesell, U. *et al.* (2008) Simulated 21st century's increase in oceanic suboxia by CO₂-enhanced biotic carbon export. *Glob. Biogeochem. Cycles*, **22**, GB4008.
- Paulmier, A. and Ruiz-Pino, D. (2009) Oxygen minimum zones (omzs) in the modern ocean. *Prog. Oceanogr.*, **80**, 113–128.
- Podlaska, A., Wakeham, S. G., Fanning, K. A. *et al.* (2012) Microbial community structure and productivity in the oxygen minimum zone of the eastern tropical north Pacific. *Deep Sea Res. I*, **66**, 77–89.
- Prince, E. D. and Goodyear, C. P. (2006) Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.*, **15**, 451–464.
- Prince, E. D., Luo, J., Phillip Goodyear, C. *et al.* (2010) Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fisheries Oceanogr.*, **19**, 448–462.
- Rapien, M. (2004) *Macrozooplankton and Micronekton in the Arabian sea Oxygen Minimum Zone*. University of Rhode Island: Kingston, Rhode Island.
- Robinson, C., Steinberg, D. K., Anderson, T. R. *et al.* (2010) Mesopelagic zone ecology and biogeochemistry—a synthesis. *Deep Sea Res. II*, **57**, 1504–1518.
- Robison, B. H. (2004) Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.*, **300**, 253–272.
- Rosa, R. and Seibel, B. A. (2008) Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci.*, **105**, 20776–20780.
- Rosa, R. and Seibel, B. A. (2010) Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Prog. Oceanogr.*, **86**, 72–80.
- Saltzman, J. and Wishner, K. F. (1997a) Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 1. General trends. *Deep Sea Res. I*, **44**, 907–930.
- Saltzman, J. and Wishner, K. F. (1997b) Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. Vertical distribution of copepods. *Deep Sea Res. I*, **44**, 931–954.
- Sameoto, D. (1986) Influence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in the eastern tropical Pacific. *Mar. Biol.*, **93**, 263–279.
- Sameoto, D., Guglielmo, L. and Lewis, M. (1987) Day/night vertical distribution of euphausiids in the eastern tropical Pacific. *Mar. Biol.*, **96**, 235–245.
- Seibel, B. A. (2011) Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.*, **214**, 326–336.
- Smith, S. L. and Madhupratap, M. (2005) Mesozooplankton of the Arabian sea: patterns influenced by seasons, upwelling, and oxygen concentrations. *Prog. Oceanogr.*, **65**, 214–239.
- Steinberg, D. K., Carlson, C. A., Bates, N. R. *et al.* (2000) Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso sea. *Deep Sea Res. I*, **47**, 137–158.
- Steinberg, D. K., Cope, J. S., Wilson, S. E. *et al.* (2008a) A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic north Pacific ocean. *Deep Sea Res. II*, **55**, 1615–1635.
- Steinberg, D. K., Van Mooy, B. A. S., Buesseler, K. O. *et al.* (2008b) Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnol. Oceanogr.*, **53**, 1327–1338.
- Stewart, J. S., Field, J. C., Markaida, U. *et al.* (2013) Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones. *Deep Sea Res. II*, **95**, 197–208.
- Stramma, L., Johnson, G. C., Sprintall, J. *et al.* (2008) Expanding oxygen-minimum zones in the tropical oceans. *Science*, **320**, 655–658.
- Stramma, L., Schmidt, S., Levin, L. A. *et al.* (2010) Ocean oxygen minima expansions and their biological impacts. *Deep Sea Res. I*, **57**, 587–595.
- Vinogradov, M. E. and Voronina, N. M. (1961) Influence of the oxygen deficit on the distribution of plankton in the Arabian sea. *Deep Sea Res.*, **9**, 523–530.
- Wiebe, P., Morton, A., Bradley, A. *et al.* (1985) New development in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar. Biol.*, **87**, 313–323.
- Wiebe, P. H., Ashjian, C. J., Lawson, G. L. *et al.* (2011) Horizontal and vertical distribution of euphausiid species on the western Antarctic Peninsula U.S. GLOBEC Southern Ocean Study Site. *Deep Sea Res. II*, **58**, 1630–1651.
- Wiebe, P. H., Burt, K. H., Boyd, S. H. *et al.* (1976) A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J. Mar. Res.*, **34**, 313–326.
- Wishner, K. F., Ashjian, C. J., Gelfman, C. *et al.* (1995) Pelagic and benthic ecology of the lower interface of the eastern tropical Pacific oxygen minimum zone. *Deep Sea Res. I*, **42**, 93–115.
- Wishner, K. F., Gelfman, C., Gowing, M. M. *et al.* (2008) Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian sea oxygen minimum zone. *Prog. Oceanogr.*, **78**, 163–191.
- Wishner, K. F. and Gowing, M. M. (1992) The role of deep-sea zooplankton in carbon cycles. *Deep Sea Food Chains Glob. Carbon Cycle*, **360**, 29–43.
- Wishner, K. F., Gowing, M. M. and Gelfman, C. (1998) Mesozooplankton biomass in the upper 1000 m in the Arabian sea: overall seasonal and geographic patterns, and relationship to oxygen gradients. *Deep Sea Res. II*, **45**, 2405–2432.
- Wishner, K. F., Gowing, M. M. and Gelfman, C. (2000) Living in suboxia: ecology of an Arabian sea oxygen minimum zone copepod. *Limnol. Oceanogr.*, **45**, 1576–1593.
- Wishner, K. F., Outram, D. M., Seibel, B. A. *et al.* (2013) Zooplankton in the eastern tropical north Pacific: boundary effects of oxygen minimum zone expansion. *Deep Sea Res. I*, **79**, 122–140.
- Wyrki, K. (1962) The oxygen minima in relation to ocean circulation. *Deep Sea Res. Oceanogr. Abs.*, **9**, 11–23.