Effects of bottom-layer hypoxia on spatial distributions and community structure of mesozooplankton in a sub-estuary of Puget Sound, Washington, U.S.A.

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Abstract

We investigated the response of mesozooplankton to low dissolved oxygen (DO) concentrations in Hood Canal, Washington, a seasonally hypoxic sub-estuary of Puget Sound. Depth-stratified zooplankton net tows were conducted above and below the oxycline during day and night in midsummer (July), late summer (September), and early winter (December) 2008 using closing nets. Bottom DO concentrations declined slowly through summer. In July, DO at most stations was low but not hypoxic. By late summer, bottom waters throughout the study area were hypoxic (≤ 2 mg L^{-1}) and were severely hypoxic (< 1 mg L^{-1}) at some stations. In winter, water-column mixing and lower surface primary production resulted in higher DO, although sub-pycnocline hypoxia persisted through December at some locations. Zooplankton abundance decreased from midsummer to winter. The community was dominated by gelatinous zooplankton and copepods. A shift in community structure towards a higher dominance of polychaetes and the cyclopoid copepod *Oithona similis* occurred over the season. Temporal and spatial patterns in zooplankton communities were primarily structured by month and bottom depth. DO played a lesser role in structuring the species composition, but vertical distributions of several taxa changed in response to hypoxia, with a greater proportion of their populations found above the oxycline during both day and night where bottom oxygen was low. However, some taxa were abundant below the oxycline, even at oxygen levels < 0.5 mg L^{-1}; these taxa may have a high tolerance to hypoxia, use low-oxygen regions as a predation refuge, and be useful indicators of poor water-quality conditions.

Hypoxia can dramatically affect aquatic communities through its effects on mortality, physiology, and behavior of organisms, which can indirectly lead to changes in distributions, predation, and food webs (Pihl et al. 1992; Breitburg et al. 1997). Together, these effects may be increasingly altering ecosystems as anthropogenic eutrophication and climate change increase the occurrence and spatial extent of hypoxia in many estuarine and coastal aquatic systems (Keeling et al. 2010).

A sizable body of literature exists on the effects of hypoxia on fished species, but relatively little is known about the responses of zooplankton, despite their importance to fisheries, ecosystems, and carbon cycling. Studies indicate that zooplankton response is mixed and likely varies by species, region, and conditions. Studies of the direct effects of hypoxia on zooplankton have mainly focused on survival and reproduction of copepods, which have been reported to decrease with declining oxygen concentrations (Roman et al. 1993; Invidia et al. 2004; Marcus et al. 2004). In contrast, several studies on ctenophores and scyphozoan jellyfish indicate that they may be more tolerant of hypoxia; many of those species are capable of tolerating very low oxygen levels and can be voracious predators under hypoxic conditions (Purcell and Decker 2005). In Chesapeake Bay, copepods are rare in bottom layers where oxygen concentrations are < 1–3 mg L^{-1} (Roman et al. 1993; Keister et al. 2000). In other systems, abundant copepods have been found in hypoxic bottom water under some conditions (Taylor and Rand 2003; Kimmel et al. 2010). Overall, more research is needed to understand the complexities of the effects of hypoxia on zooplankton and the resultant trophic effects.

Puget Sound, Washington, is a glacially carved fjord and is the second largest estuary in the U.S. As in many estuaries and coastal seas, the combination of high primary production, stratification, sluggish deep circulation, and long residence times leads to strong seasonal drawdown of dissolved oxygen (DO) below the pycnocline. Hood Canal (HC), a subbasin of Puget Sound, experiences the most severe hypoxia in the sound. Hypoxic conditions first develop near bottom in summer, moving increasingly toward the surface below the pycnocline as the season progresses and near-bottom oxygen declines. Although DO conditions vary interannually, hypoxia typically persists in HC for several months from midsummer to fall (Newton et al. 2002).

This study was conducted as part of a larger collaboration among the University of Washington, the Washington Department of Fish and Wildlife, and the Hood Canal Salmon Enhancement Group to evaluate the effects of seasonal hypoxia in lower HC (LHC; Puget Sound, Washington) on species composition, abundance, distribution, and habitat utilization of pelagic fish and zooplankton. Sampling was conducted from midsummer to early winter, encompassing pre-hypoxic, hypoxic, and post-hypoxic conditions. In this paper, we focus on patterns in mesozooplankton abundance and distribution over time and in response to oxygen concentrations.

Methods

Study location—Our study site was the lower portion of HC (Fig. 1). HC is separated from the Main Basin by a

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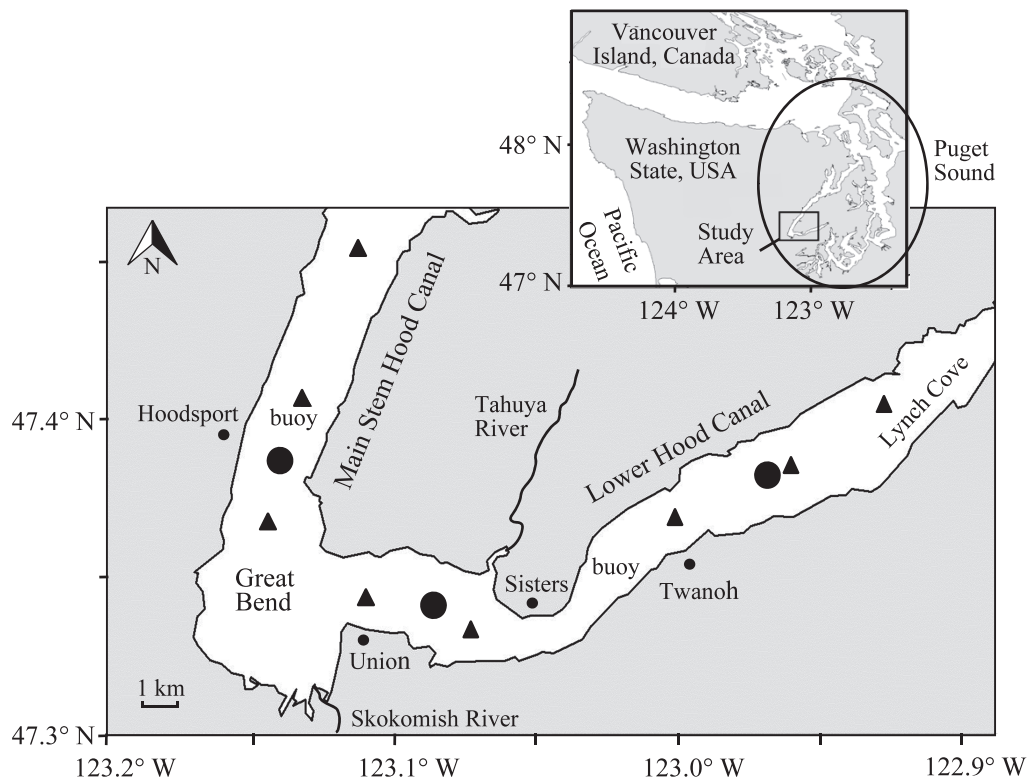* Corresponding author: jkeister@u.washington.edu

Fig. 1.   Map of the HC study area showing the location of landmarks and buoys mentioned in the text. Triangles show locations of all net tows and CTD casts made during the study; large filled circles show locations of the CTD profiles shown in Fig. 2.

shallow (55 m) sill that restricts tidal mixing and the exchange of deep waters. The Main Stem of HC (regions north of the Great Bend) is deep (> 200 m) and narrow (< 5 km). LHC, defined here as the portion of HC to the east and south of the Great Bend, is relatively shallow (< 50 m in most places). Water exchange with the Main Stem is weak, especially in summer when the water column is strongly stratified. LHC experiences the most severe and persistent hypoxia in Puget Sound.

The deep basins and low river inputs in Puget Sound create hydrographic conditions that support zooplankton assemblages that are more similar to coastal oceans than to most estuaries. The mesozooplankton community of Puget Sound is diverse and consists of predominantly oceanic species similar to the communities found in offshore areas of the California Current and the southeast Alaska Gyre. Copepods typically dominate the zooplankton biomass, but, as in many estuaries, gelatinous zooplankton can dominate in retentive areas. Euphausiids, shrimp, and amphipods are abundant where bottom depths are > 50 m.

Sampling methods—We used vertically and obliquely towed zooplankton nets and a SeaBird Seacat 19 conductivity, temperature, and depth (CTD) sensor fitted with an annually calibrated SBE43 DO sensor to characterize the biological and physical patterns in LHC during July, September, and December 2008. Sampling was conducted aboard the fishing vessel *Memories*. Two types of nets were used to sample the zooplankton: a 60 cm diameter, 200 μm mesh Puget Sound–style closing net was lifted vertically

through the water column to sample small, weakly motile zooplankton, and a 1 m diameter, 335 μm mesh ring net was towed obliquely through the water column at 0.5– 1.0 m s^{-1} (1–2 knots) to sample larger, more strongly swimming species. A Tsurumi–Seiki Company flow meter and a combination temperature and depth sensor were attached to the nets to accurately measure the volume filtered and the depth ranges sampled.

Discrete layers above and below the oxycline were targeted with net tows at each station as time allowed, using CTD profiles to determine target depths. When ship time was limited, full water column tows replaced depth-stratified tows. In September and December, some stations were sampled in both day and night to assess changes in distributions due to diel vertical migration (DVM).

Samples were preserved in 5% buffered formalin in seawater and returned to the laboratory for analysis, where they were diluted to 5–10 times the settled volume and subsampled with a 1 mL Stempel pipette; two to four subsamples were counted, for a total of 500–700 individuals per sample and 125–250 individuals of the dominant taxa. Zooplankton were counted and identified to the lowest possible taxonomic level: calanoid copepods, euphausiids, shrimp, and amphipods were identified to species and life history stage. Eggs and nauplii of those organisms were excluded from analyses; for copepods, all copepodite stages were combined for statistical analyses. All other taxa were identified to larger groups (e.g., chaetognaths, medusae, siphonophores, barnacles) and not separated by life stage.

Statistical analyses—To examine vertical distributions in relation to below-oxycline DO concentrations, the proportional abundance of each taxon in each layer was calculated. The proportional abundance was calculated as the proportion of the whole water column abundance of organisms that was above (or below) the oxycline at any station during a day or night occupation. For example, the proportional abundance above the oxycline = P_a = $No._a$/($No._a$ + $No._b$) where $No._a$ is the number of organisms m^{-3} or m^{-2} above the oxycline and $No._b$ is the number of organisms m^{-3} or m^{-2} below the oxycline at a particular station. A total of seven day and seven night samplings were included in the analysis: five stations were fully sampled above and below the oxycline during both day and night, including two stations that were hypoxic in both September and December and one normoxic station in December; an additional two normoxic stations were sampled both above and below the oxycline during either day or night. Proportional abundances of taxa were averaged over hypoxic vs. normoxic and day vs. night sampling for comparisons.

We used nonparametric multivariate analyses to examine spatial and temporal patterns in zooplankton community structure using PC-ORD 5.05 for Windows (McCune and Grace 2002; McCune and Mefford 2005). A species density by sample matrix was constructed using data collected from vertical net tows. Values in the matrix were equal to the density (No. m^{-3}) of each species separated by life stage for organisms that undergo large ontogenetic changes in swimming ability (i.e., euphausiids). Rare species, defined as those occurring in < 5% of samples, were discarded and data were $Log_{10}(Y + 0.01) + 2$ transformed to normalize variances prior to analysis (McCune and Mefford 2005); the use of (Y + 0.01) + 2 rather than (Y + 1) helps prevent distorting the relationship between zeros and small values in the dataset (McCune and Grace 2002). Finally, the species' densities were relativized by total sample density (i.e., each density estimate was expressed as the proportion of the total density in the sample). The final matrix consisted of 46 samples × 47 taxa.

We sought groupings based on zooplankton community structure in the species by sample matrix using agglomerative hierarchical cluster analysis with a Euclidean distance measure and Ward's linkage method (McCune and Grace 2002). For presentation, the cluster dendrogram is scaled both by Wishart's (1969) objective function and by percentage of information remaining. Wishart's objective function is a measure of information loss as clustering proceeds, and is calculated as the sum of the error sum of squares from the centroid of each group to the items in that group.

We used nonmetric multidimensional scaling (NMDS) ordination to explore patterns among samples. NMDS is considered one of the most robust ordination methods when dealing with community data because it deals well with nonlinear relationships that are common in ecological data, and any distance measure can be used, allowing incorporation of ones that are robust with respect to zero–zero species density pairs (Field et al. 1982). We used the Sørensen distance measure, calculated as

$$D_{ik} = \frac{\sum_{j=1}^{p} |a_{ij} - a_{kj}|}{(\sum_{j=1}^{p} a_{ij}) + (\sum_{j=1}^{p} a_{kj})}$$

where p is the total number of species (here = 47), a_{ij} represents the abundance of species j on the ith sample date, and a_{kj} represents its abundance on the kth sample date. The final "stress" (a measure of the goodness of fit between the data and the final ordination) was examined in relation to the ordination dimensionality to help choose the fewest dimensions necessary to adequately describe the data. Dimensionality was increased if the addition of an axis reduced the stress by > 5, to a maximum of three dimensions, above which interpretation is prohibitively difficult. Stress values approaching or exceeding 20 are considered high; a value of zero indicates perfect monotonicity (McCune and Grace 2002). Following ordination of the matrix, we rigidly rotated the resultant ordination such that the maximum possible correlation between DO and the community structure as expressed along the first axis was obtained. This rigid rotation did not affect the geometry of points in the ordination space or the total variance explained by the ordination, but simply realigned the ordination points such that the greatest dissimilarity in community structure among samples as related to DO was expressed along the first axis (McCune and Grace 2002).

We correlated environmental variables with axes in the final, rotated NMDS ordination to examine which of the measured variables may be important in the relationships among zooplankton communities. The coefficient of determination (r^2) of each axis determines the proportion of the variation in the original distances that is represented by the axis. The Pearson correlation between each ordination axis and individual species and environmental parameters was used to measure the strength and direction (in relation to the axes) of relationships. Environmental variables examined were minimum sub-oxycline DO concentration, station depth, and month (i.e., season). We used indicator species analysis (ISA) and correlations between relative species abundances and the NMDS axes to determine taxa that were important in defining clusters and in ordination of the communities. In ISA, the indicator value (IV) for a species in a group is calculated as the product of the relative abundance of the species in the group (the mean abundance in the group divided by the sum of the mean abundances in all groups) and the frequency of occurrence of the species in samples in the group. The statistical significance of each species IV was determined by a Monte Carlo method, in which sample units were randomly reassigned 1000 times to test if the IV was higher than expected by chance (Dufrêne and Legendre 1997).

Results

Physical conditions—CTD profiles of DO, temperature, and salinity show the spatial and temporal development of stratification and hypoxia in our study area over the year (Fig. 2). The water column was strongly stratified at all locations in July, with slightly shallower thermoclines
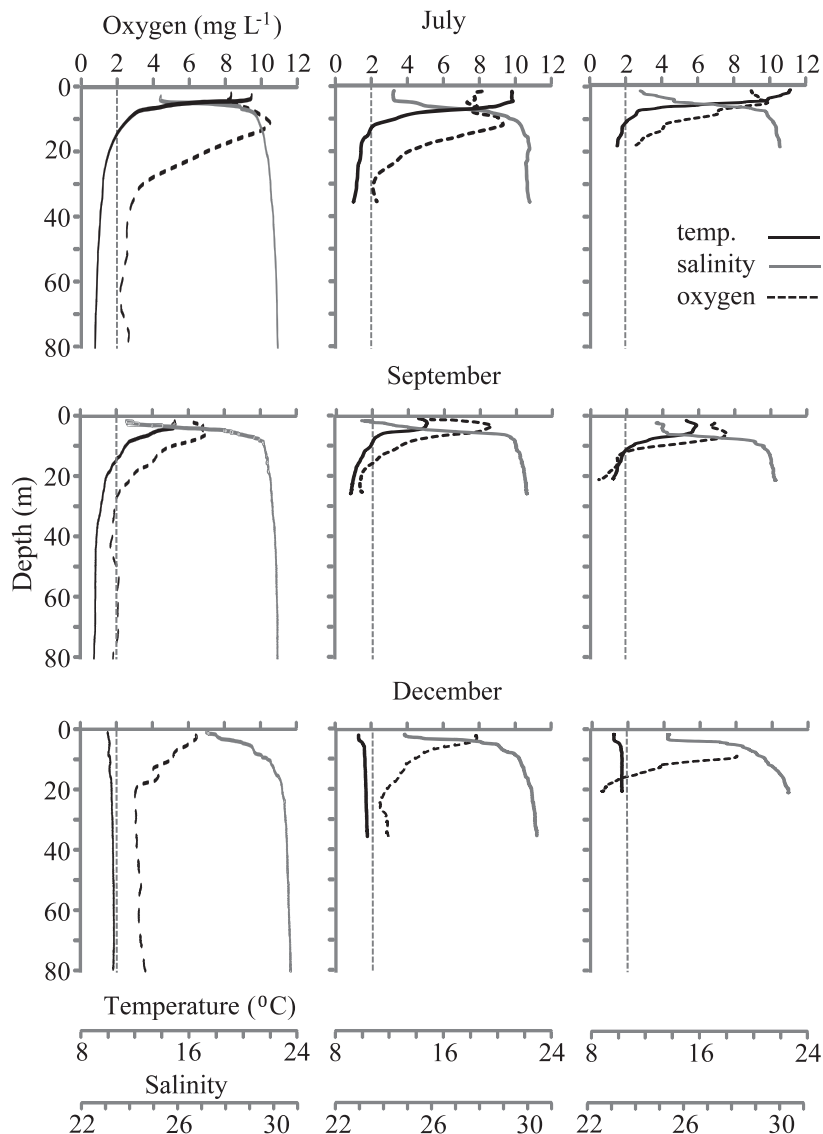
Fig. 2. Temperature (temp., solid black), salinity (solid gray), and DO (dashed black) profiles at three stations along the canal in July, September, and December 2008. Three stations are shown, ordered from Main Stem (left) to western (middle) and eastern (right) LHC as shown in Fig. 1. Vertical dashed line is at 2 mg DO L^{-1} in all panels.

occurring at shallower stations. Bottom DO, although low, had not declined to hypoxic levels. Surface temperatures were between 20°C and 25°C; bottom temperatures were ~ 9–10°C. DO showed supersaturated subsurface maxima at approximately the base (or occasionally top) of the pycnocline, then dropped sharply to 2–3 mg L^{-1} near bottom at all stations. DO did not closely track salinity, but instead continued to decline below the halocline to a minimum, usually near bottom. The lowest DO recorded in July was 2.1 mg L^{-1}.

In September, the surface layer was cooler (14–16°C) whereas bottom temperatures were similar to July. A strong thermocline was present in the upper 5–10 m throughout the study area. DO more closely tracked temperature and salinity, exhibiting sharper oxyclines and a larger depth range of low DO, reaching hypoxic levels

below 30 m depth at most stations. Near-bottom DO reached 0.4 mg L^{-1} near the terminus of the canal. At the deepest stations seaward of the Great Bend, a weak hypoxic mid-water oxygen minimum occurred between 25 and 45 m depth; this mid-water minimum is known to occur when the bottom layer is displaced upward by saline deep-water intrusions that enter the canal over the northern sill (Parker-Stetter and Horne 2009). Below the mid-water minimum, DO concentrations increased to slightly above 2 mg L^{-1} and dropped again very near bottom.

In December, the water column was weakly stratified by a thin (5–10 m), relatively low salinity lens (Fig. 2, lower panels). Temperatures were nearly uniform with depth and DO concentrations were > 2 mg L^{-1} everywhere except near Twanoh in LHC, where near-bottom DO was < 0.7 mg L^{-1}.

Table 1. Seasonal abundances (No. m^{-3}) of numerically dominant taxa averaged over stations in UHC and LHC. The 10 most abundant taxa in summer and winter (if different) are shown for each region. Standard error is given in parentheses. *See* Web Appendix, Table A1 (www.aslo.org/lo/toc/vol_58/issue_2/0667a.html) for additional taxa.

	Summer (Jul)	Fall (Sep)	Winter (Dec)
Upper HC	*n*=1	*n*=4	*n*=1
Paracalanus parvus	11613	2770 (820.0)	562
Pseudocalanus spp.*	9718	54 (18.8)	2
Oithona similis	1916	1680 (140.7)	761
*Calanus pacificus**	1223	203 (20.2)	16
Gastropods	414	170 (19.5)	76
Corycaeus spp.	412	261 (86.1)	93
Bivalves	262	91 (14.6)	29
Barnacles	157	464 (406.0)	36
Pteropods	125	3 (17.0)	75
Crabs	49	0 (1.6)	0
Siphonophores	0	48 (89.3)	86
Bryozoans	37	71 (21.5)	58
*Metridia pacifica**	42	183 (4.8)	33
Lower HC	*n*=4	*n*=7	*n*=4
Evadne sp.	8031 (4234.4)	1220 (26.7)	8 (3.6)
Paracalanus parvus	7661 (2331.0)	2983 (1124.3)	1178 (240.5)
Oithona similis	523 (180.1)	885 (628.2)	997 (338.0)
Polychaetes	374 (140.9)	386 (16.3)	575 (228.8)
Barnacles	348 (222.7)	1561 (276.8)	183 (79.2)
Acartia clausi	333 (214.1)	0 (0.4)	22 (18.2)
Bivalves	285 (145.3)	58 (45.4)	31 (12.6)
*Calanus pacificus**	261 (99.6)	61 (90.8)	2 (0.8)
Corycaeus	214 (118.2)	252 (90.4)	79 (18.2)
Gastropods	193 (71.3)	93 (71.6)	112 (18.7)
Siphonophores	28 (15.7)	297 (32.7)	429 (82.1)
Larvaceans	192 (77.5)	607 (191.9)	186 (36.5)
Bryozoans	14 (11.4)	52 (23.6)	54 (26.2)

* Diapause late summer through winter in Puget Sound.

Zooplankton—Abundance and taxonomic composition: Gelatinous taxa dominated the zooplankton biovolume, particularly in late summer when individual *Cyanea capillata*, the lion's mane medusa, were up to 0.5 m in diameter and visibly abundant. The largest taxa were not quantitatively sampled, so data are not shown here. Other common gelatinous zooplankton included the medusae *Aequorea victoria* (water jelly) and *Aurelia labiata* (moon jelly), and larvaceans. Zooplankton abundance was highest in July and lowest in December. Copepods numerically dominated the zooplankton; diversity was high, with *Paracalanus parvus, Oithona similis*, *Pseudocalanus* spp. (mostly *newmani*), *Calanus pacificus*, *Acartia clausi*, and *Acartia longiremis* being most abundant. *Metridia pacifica*, *Mi. pusillus*, *Corycaeus anglicus*, and *Oncaea subtilis* were also important. Euphausiids (primarily *Euphausia pacifica*), shrimp, and hyperiid amphipods were common in the deepest areas north of the Great Bend. Cladocerans, meroplankton (especially barnacles and bivalves), and polychaetes were also abundant.

Abundances of most zooplankton decreased from summer through early winter in both upper HC (UHC) and LHC (Table 1), but a few taxa (the calanoid copepod *Aetidius divergens*, bryozoan cyphonautes larvae, echinoderm plutei, and siphonophores) increased abundance over the sampling period. Larvaceans, barnacle nauplii, medusae, and the calanoid copepod *M. pacifica* peaked in midsummer

(September). Two dominant taxa, polychaete larvae and the cyclopoid copepod *O. similis*, increased in abundance in LHC over the season but decreased in UHC (Table 1).

Relative changes in species abundances resulted in shifts in community composition and species dominance. The largest temporal changes were the large jellyfish "blooms" that developed in LHC by September and an increasing dominance from July to December of the cyclopoid copepod *O. similis*, siphonophores, and polychaetes in LHC concurrent with decreased dominance of all calanoid copepods, particularly *P. parvus*, *Ca. pacificus,* and *Pseudocalanus* spp., as well as cladocerans. The latter three taxa all undergo diapause in winter (Ohman 1985; Osgood and Frost 1994; Egloff et al. 1997); their water-column abundances had dropped sharply by December.

Vertical distributions in relation to DO: We examined the influence of bottom DO on vertical habitat of the most abundant taxa by plotting the proportions that occurred in the surface vs. below-oxycline layer of the water column (Fig. 3). A variety of patterns in vertical distribution were exhibited. Several taxa were almost exclusively found in the surface layer above the oxycline: these taxa included most meroplankton, larvaceans (Fig. 3A), jellyfish medusae, the copepod *P. parvus* (Fig. 3B), crab larvae (Fig. 3C), and siphonophores (Fig. 3D). *Corycaeus* spp. (Fig. 3D) showed a hint of increasing abundances below the oxycline as bottom DO increased. A few taxa, including the copepods
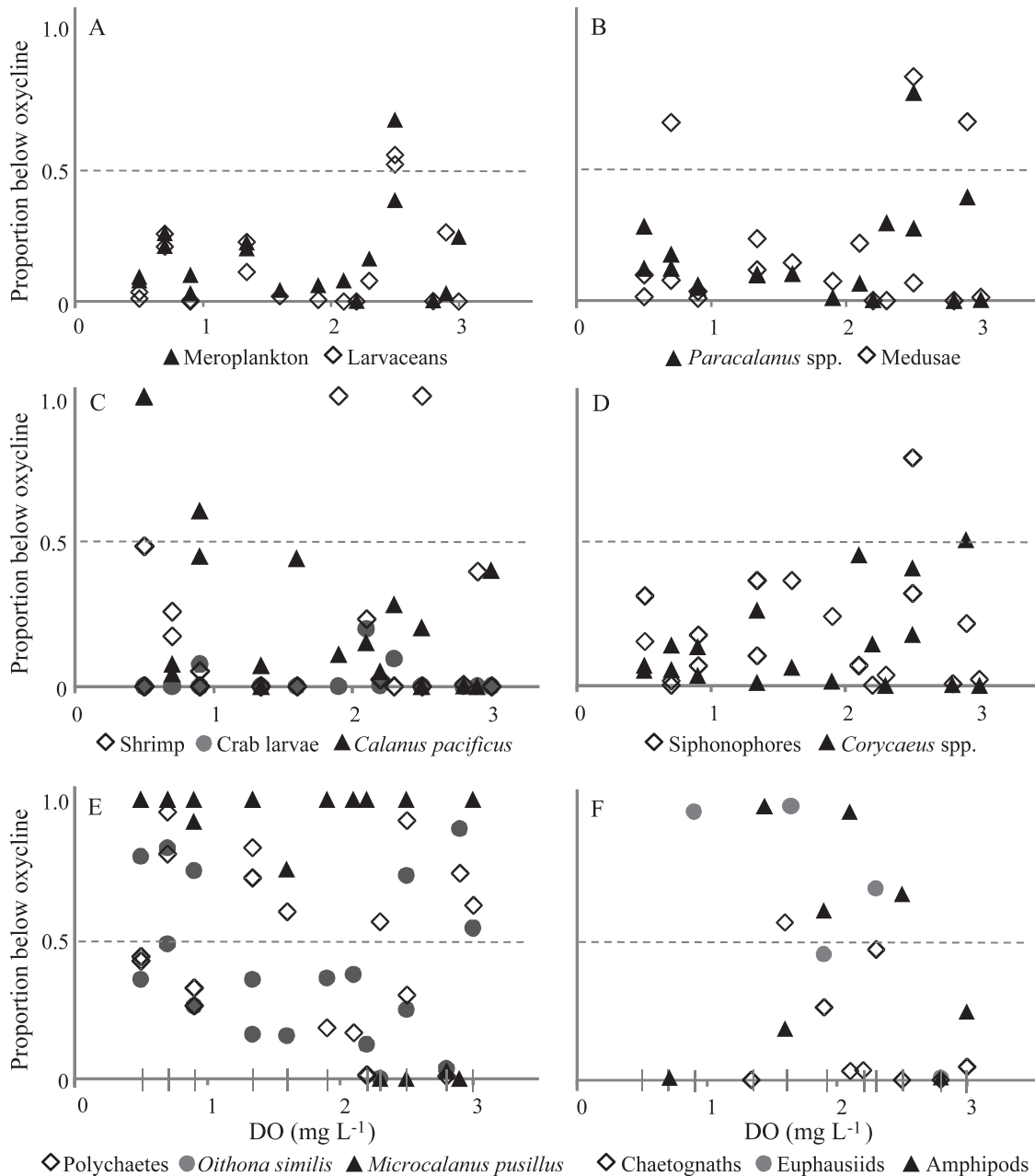
Fig. 3. Relationship between minimum water column DO concentration and proportion of zooplankton populations found below the oxycline from stations where paired above- and below-oxycline vertical net tows were conducted (day and night). (A) Meroplankton and larvaceans, (B) *Paracalanus* spp. and medusae, (C) shrimp, crab larvae, and *Calanus pacificus*, (D) siphonophores and *Coryceaus* spp., (E) polychaetes, *Oithona similis*, and *Microcalanus pusillus*, (F) chaetognaths, euphausiids, and amphipods. (E, F) Long tick marks indicate where samples were taken; lack of a symbol at those values indicates the taxon was too rare in those paired samples to include in analysis.

Mi. pusillus and polychaetes, were most often below the oxycline, even at DO levels < 0.5 mg L^1. *O. similis* showed no pattern in relation to DO (Fig. 3E). Chaetognaths, euphausiids, and amphipods were rarely found at stations where bottom oxygen was < 1 mg L^{-1} (Fig. 3F); these stations were also in shallow areas where those taxa may not have been able to escape visual predators during the day.

DVM in relation to DO: Most zooplankton did not exhibit strong changes in DVM behavior when bottom DO was < 2 mg L^{-1} (Fig. 4, top panels). Abundances above vs.

below the oxycline were highly variable, particularly when bottom oxygen was normoxic. Some taxa were consistently more abundant above; others were consistently more abundant below. Distributions of several taxa, including bryozoan cyphonautes larvae, *Aet. divergens*, *M. pacifica*, and *Mi. pusillus*, suggested a downward movement at night (i.e., reverse DVM).

Taxa that showed stronger evidence of altered migrations during hypoxia (Fig. 4, lower panels) included several copepods (*Coryceaus* spp., *P. parvus*, *Acartia* spp., and
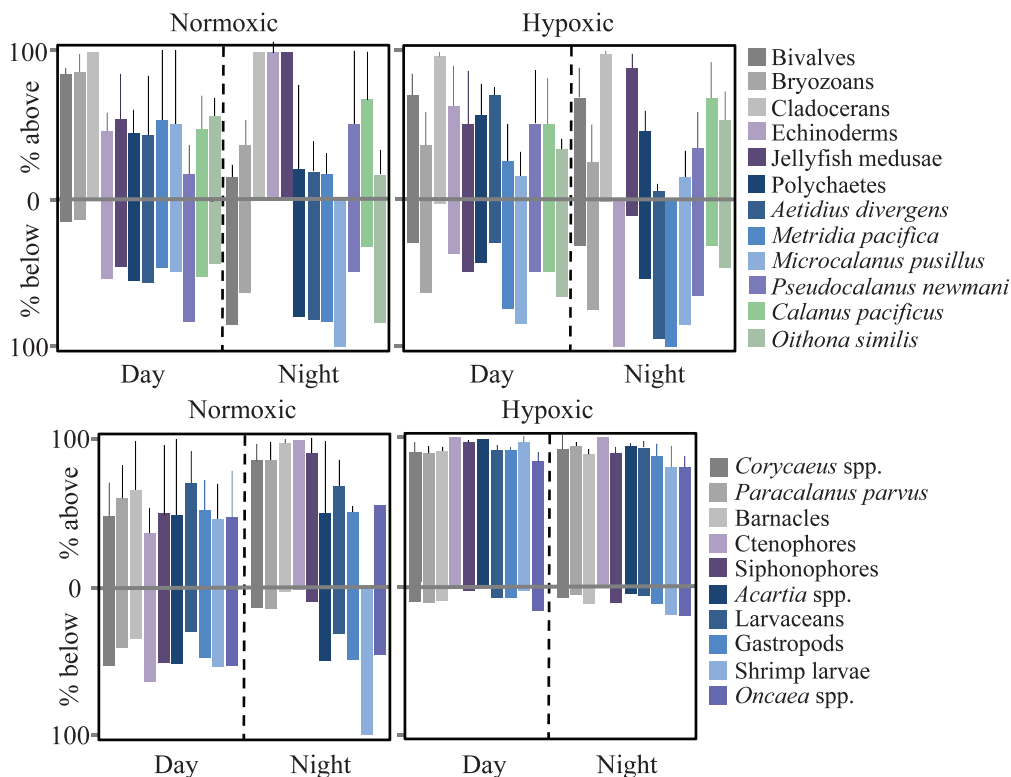
Fig. 4. Percentage of zooplankton sampled above vs. below oxycline during day and night at stations where bottom DO was hypoxic (≤ 2 mg L^{-1}) or normoxic (> 2 mg L^{-1}). Top panels show taxa that did not show an apparent response to hypoxia. Bottom panels show taxa that exhibited altered distributions at stations where bottom water was hypoxic compared to where bottom-layer DO was > 2 mg L^{-1}. Error bars are 1 SE of the proportions.

Oncaea spp.), barnacle larvae, ctenophores, siphonophores, gastropods, and shrimp larvae. Those taxa either moved into deep layers during the day or were more abundant below the oxycline both day and night where bottom oxygen was > 2 mg L^{-1}, but remained above the oxycline at hypoxic stations. Notably, the variance in the distribution of individual taxa was high when DO was high, but very low during hypoxia.

Community analysis: Cluster analysis on vertical net samples identified five zooplankton community groupings that separated seasonally and spatially (Fig. 5). Most samples taken from the deep Main Stem clustered differently than those in LHC and were represented by Cluster 2a (black triangle); amphipods, chaetognaths, and the relatively large-bodied copepods *Calanus* and *Metridia* as well as smaller copepods of the genera *Oithona*, *Oncaea*, and *Pseudocalanus* were good indicators of that cluster, meaning that those taxa were found relatively consistently and in highest abundances at those locations (Table 2). Communities in the Main Stem also differed from those of LHC in that they showed relatively little seasonal change in composition compared to LHC.

In July, Clusters 1a (black inverted triangle), 2a (black triangle), and 2c (black star) dominated in LHC; too few samples were taken to draw conclusions from their spatial distributions. In September, Cluster 2c occurred exclusively below the oxycline at hypoxic stations whereas Cluster 1a was primarily found in the upper portion of the water

column. Indicator species for Cluster 1a were barnacle cyprids, cladocerans, crab larvae, and *Ca. pacificus*; indicators for 2c were chaetognaths, cladocerans, and the copepods *Ca. pacificus*, *M. pacifica*, and *Pseudocalanus* spp. (Table 2).

In December, LHC communities clustered separately from those found earlier in the season (Fig. 5). Two communities were present: at the normoxic station at ~ 123.1°W, a community represented by Cluster 1b (black circle) showed a diel shift from below oxycline during the day to above oxycline at night; that community was found exclusively above the oxycline at hypoxic stations and throughout the water column at the shallowest station.

A three-dimensional NMDS ordination with a final stress of 10.3 was cumulatively able to express 91.4% of the variance in the total zooplankton community structure (Axes 1, 2, 3 = 13.0%, 46.1%, and 32.3%, respectively) (Fig. 6). Of the station characteristics measured, station depth and minimum sub-oxycline DO were cross-correlated during September with $R^2 = 0.70$; both correlated with Axis 1 of the ordination, although DO explained slightly more of the variance in community structure along that axis ($r = 0.51$ and 0.63, for depth and DO respectively). Station depth was the only variable that strongly correlated with Axis 2 ($r = -0.66$). Month was a strong correlate with Axis 3 ($r = 0.84$).

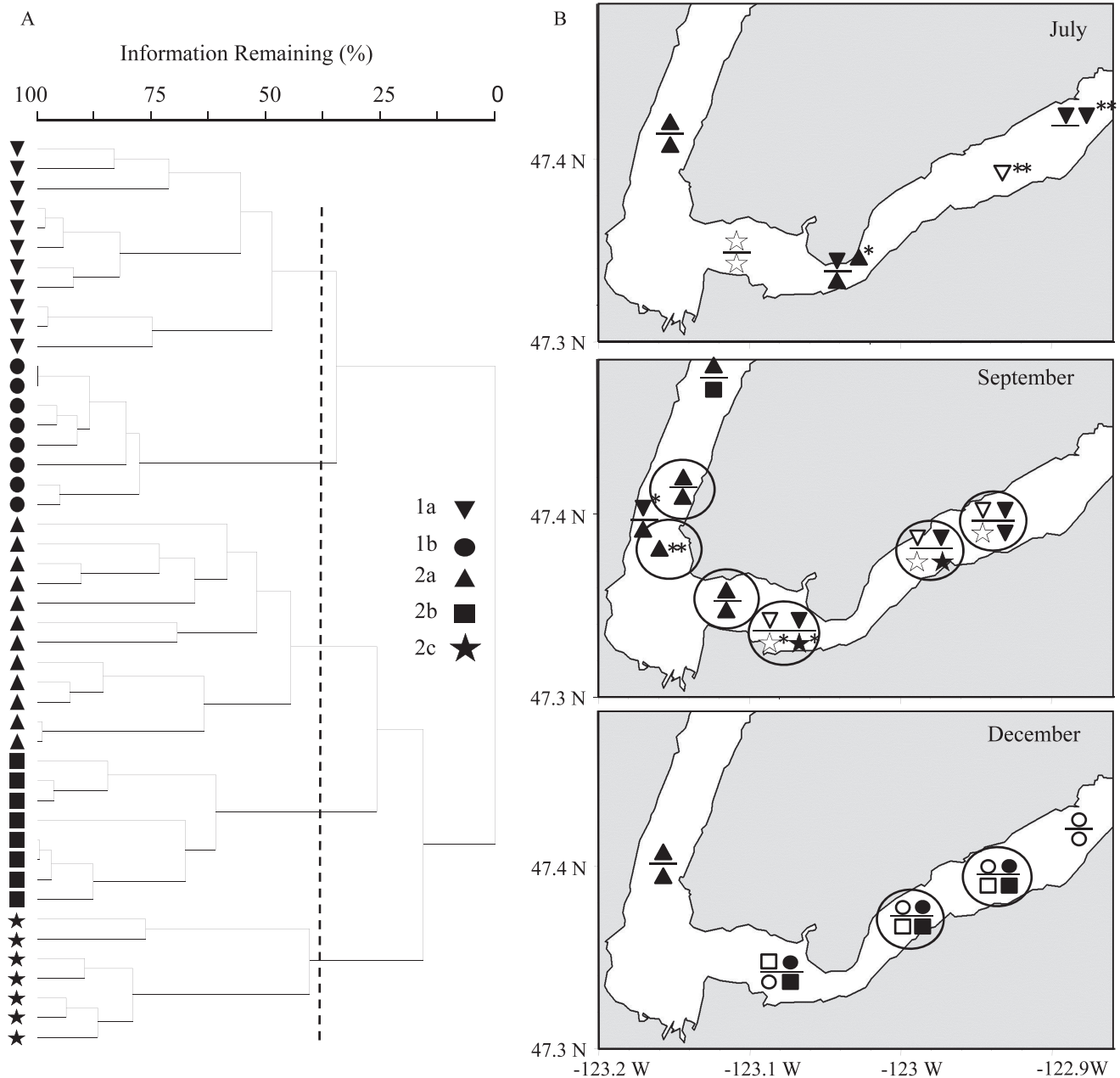The percentage variance in communities explained by each of Axes 1, 2, and 3, combined with the correlation of

Fig. 5.   (A) Dendogram from cluster analysis showing stations clustered in species space. (B) Stations sampled during the 3 months of the study coded by zooplankton community cluster group from cluster analysis. Black-filled shapes = night samples, white-filled shapes = daytime. Stations at which minimum DO was ≤ 2 mg L^{-1} are circled. Vertically stratified samples collected above and below the oxycline are separated by horizontal lines.

variables with each axis, suggests that the largest separation in community structure in our study was related to spatial and depth differences between deep (UHC) and shallower (LHC) locations, a depth gradient that was also confounded with the pattern of weaker to stronger bottom hypoxia. Secondarily, temporal shifts from summer to early winter were important. Clear separation of the cluster groups along Axes 2 and 3 (Fig. 6) reinforced our inference that separation along those axes captured the dominant differences among communities. Bottom oxygen concentration played a lesser role in structuring community

differences, but was more important in structuring separation along Axis 1 than the other variables measured.

Several taxa strongly correlated ($p < 0.001$) with one or more ordination axes (Table 2). Examples of the correlations are shown in Fig. 7. Most that correlated with an axis had also been identified by ISA as good indicators of one or more clusters. Most showed patterns of increased relative abundance along depth gradients (i.e., negative correlation with Axis 2, positive with Axis 1), but barnacle cyprids, cladocerans, and ctenophores were more important at shallower locations than at deeper ones. Several

Table 2. Correlations between NMDS ordination axes and taxa or variables given as the linear (Pearson's r, R^2) correlation coefficient. Only taxa and variables that correlated $R^2 \geq 0.3$ with at least one axis are shown; those correlations are in bold. Cluster groups that the taxon was a strong indicator of ($p < 0.001$) are shown in parentheses.

	Axis 1		Axis 2		Axis 3	
	r	R^2	r	R^2	r	R^2
Amphipods (2a)	0.37	0.13	−0.67	**0.44**	−0.23	0.05
Barnacle cyprids (1a)	0.08	0.01	0.59	**0.34**	−0.33	0.11
Chaetognaths (2a, 2c)	0.11	0.01	−0.57	**0.33**	−0.50	0.25
Cladocerans (1a, 2c)	−0.14	0.02	0.70	**0.49**	−0.56	**0.31**
Crab larvae (1a)	0.21	0.04	0.33	0.11	−0.72	**0.52**
Ctenophores (1b)	0.04	0	0.59	**0.35**	0.21	0.04
Euphausiid calyptopes	0.35	0.12	0	0	−0.70	**0.49**
Ostracods	−0.02	0	−0.64	**0.41**	−0.31	0.10
Polychaetes	−0.68	**0.47**	0.44	0.19	0.17	0.03
Copepods						
Aetidius divergens	0.18	0.03	−0.58	**0.33**	0.56	**0.32**
Calanus pacificus (1a, 2a, 2c)	0.23	0.05	−0.34	0.11	−0.63	**0.40**
Metridia pacifica (2a,b,c)	−0.15	0.02	−0.81	**0.66**	−0.15	0.02
Microcalanus pusillus	−0.62	**0.38**	−0.55	**0.30**	−0.01	0
Oithona similis	−0.26	0.07	−0.72	**0.52**	0.31	0.10
Oithona spinirostris (2a)	0.21	0.04	−0.71	**0.50**	0.12	0.02
Oncaea borealis (2a)	0.01	0	−0.70	**0.48**	0.08	0.01
Paracalanus parvus	−0.03	0	0.57	**0.32**	−0.41	0.17
Pseudocalanus spp. (2a, 2c)	0.08	0.01	−0.36	0.13	−0.77	**0.59**
Month	−0.17	0.03	−0.02	0	0.84	**0.70**
Station depth	0.51	0.26	−0.66	**0.44**	−0.11	0.01
Minimum DO	0.63	**0.40**	−0.09	0.01	−0.03	0

taxa showed strong seasonal patterns, as indicated by positive (increasing from July to December) or negative (decreasing July to December) correlations with Axis 3. Not surprisingly, crab larvae and euphausiid calyptopes, which progress to later life stages over the season, and the diapausing copepods *Ca. pacificus* and *Pseudocalanus* spp. were increasingly less important in the community throughout the year. Only two taxa—*Mi. pusillus* and polychaetes—correlated with Axis 1, the axis that was most strongly associated with bottom DO.

Discussion

Hypoxia can have strong effects on pelagic populations through direct mortality, but some of the largest effects are likely to act indirectly through changes in distribution and behavior that alter susceptibility to predation and predator–prey encounter rates. These indirect effects can result in shifts in community structure, favoring taxa with greater physiological tolerance of hypoxic conditions or that have life history strategies to avoid them. Furthermore, changed distributions will alter advection and retention of populations, particularly in highly advective coastal systems where many taxa use vertical migrations to maintain retention in estuaries or on the continental shelf.

Altered distributions—DVM is a behaviorally plastic predator avoidance mechanism undertaken by a majority of mesozooplankton and many ichthyoplankton (Irigoien et al. 2004). The extent to which individuals migrate is variable on daily and seasonal time scales and can be affected by predator abundance and distribution (Bollens

and Frost 1989), life stage and reproductive status (Haney 1988; Osgood and Frost 1994), seasonality (Bollens et al. 1993), and food distribution (Dagg et al. 1998). This variability was reflected in the within-species variance in day vs. night vertical distributions we observed when bottom oxygen was > 2 mg L^{-1} (Fig. 4).

In contrast, the low variance and higher proportions of several species found near surface at hypoxic stations (Fig. 4) strongly suggests consistent avoidance of sub-oxycline hypoxia by those taxa. Several copepods (*Corycaeus* spp., *Acartia* spp., *Oncaea* spp., and *P. parvus*) are among those that exhibited avoidance, as were several broader groups (barnacles, ctenophores, siphonophores, gastropods, larvaceans, and shrimp larvae). If finer taxonomic resolution had been available for all taxa, more might have revealed responses that, when aggregated, were obscured by species-specific differences. Similarly, if we had chosen an oxygen threshold other than 2 mg L^{-1} across which to look for response, we might have drawn different conclusions.

Vertical avoidance of hypoxia by nonmigrating taxa may be characterized by decreasing bottom-layer abundances as DO decreases or as a threshold response in which organisms are rare below a certain DO concentration, but not correlated to DO above the threshold. If variability in zooplankton behavior is similar to that observed for some fish and benthic invertebrates, their response to threshold conditions may vary depending on factors such as nutritional state (Bernatis et al. 2007) and predation risk (Robb and Abrahams 2002). We found a mix of responses to hypoxic bottom water, ranging from no apparent response in most taxa to decreased proportions below the oxycline as oxygen decreased (e.g., siphonophores, *Corycaeus*).
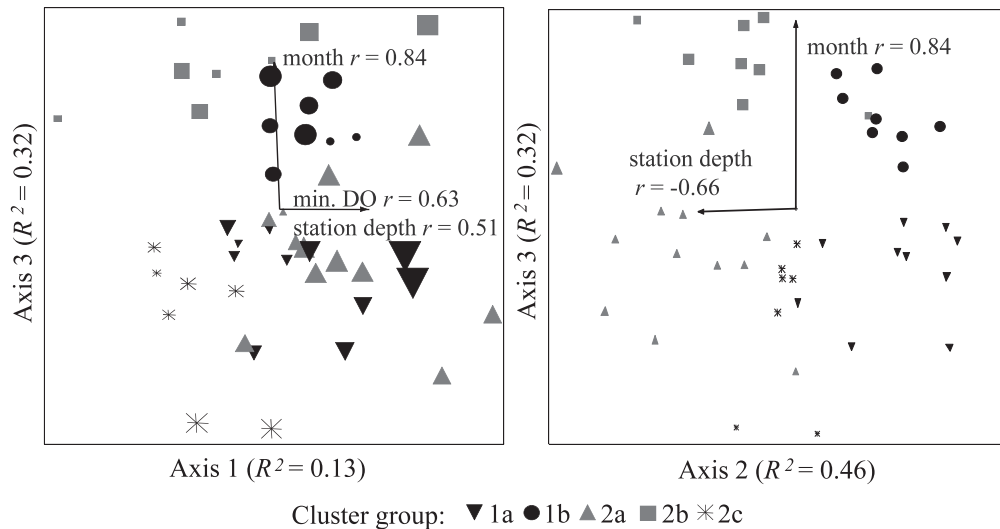
Fig. 6.   NMDS ordination of samples based on species composition. Correlations of each axis with original (preordination) distances among samples are given as R^2 values; correlations between variables and axes are shown with arrows depicting the direction of positive correlation. Samples are symbol coded by their cluster grouping from the cluster analysis shown in Fig. 5. (A) Symbols are scaled to minimum (min.) water column DO with larger symbols indicating higher DO; (B) Symbols are scaled to month with December shown as largest symbols.

The apparent avoidance of hypoxic bottom water we observed could alternatively have been caused by high mortality. Experiments show that lethal limits for zooplankton vary greatly among species; for example, < 2 mg DO L^{-1} is potentially lethal for some decapod larvae (Miller et al. 2002), < 0.9–1.4 mg L^{-1} is for *Acartia tonsa* (Roman et al. 1993; Stalder and Marcus 1997), and < 0.5 mg L^{-1} is for the Chesapeake Bay ctenophore *Mnemiopsis leidyi* (Breitburg et al. 2003). The minimum DO measured at our hypoxic stations was 0.4 mg L^{-1}, a value low enough to cause mortality in many species. However, oxygen concentrations were generally > 1 mg L^{-1} across most of the depth range that the net sampled in lower layers, which is above the critical threshold for many planktonic species (Breitburg 1994; Breitburg et al. 1994; Stalder and Marcus 1997).

Even where sub-oxycline waters were severely hypoxic, direct mortality would be indicated only if organisms cannot sense and move to avoid stressful conditions. Laboratory experiments have demonstrated that some ichthyoplankton move vertically when exposed to bottom hypoxia (Breitburg 1994), but the experimental evidence on zooplankton is mixed. Clear behavioral avoidance of hypoxia by Chesapeake Bay populations of the copepod *Ac. tonsa* has been shown in the laboratory, but Gulf of Mexico populations of the same species did not avoid hypoxia, even when exposed to quickly lethal levels of < 0.1 mg DO L^{-1} (Stalder and Marcus 1997; Decker et al. 2003). Decker et al. (2003) hypothesized that the behavioral differences reflected different evolutionary pressures on populations that inhabit regions of predictable vs. episodic hypoxia. Reports of HC fish kills dating back to the 1920s indicate that, as in Chesapeake Bay (Hagy et al. 2004), hypoxia is a natural condition that has occurred in HC seasonally since before oxygen records began in 1950. Together, the laboratory evidence of active avoidance, the generally > 1 mg L^{-1} bottom DO concentrations we

measured during our study, and the time scales over which local zooplankton populations have had to evolve a response to hypoxia suggest that avoidance of bottom-layer hypoxia likely influenced the zooplankton distributions we observed.

Although individual species of zooplankton have been shown to be distributed differently during hypoxia, multispecies assemblages of zooplankton have generally not, in aggregate, shown clear patterns of avoidance, perhaps because of species-specific differences in their oxygen response. In the Gulf of Mexico, several studies have indicated a general increase in zooplankton abundance toward surface when bottom oxygen is depleted, but high abundances have also been found in hypoxic bottom water (Zhang et al. 2009; Kimmel et al. 2010). In contrast, in upper Chesapeake Bay, where communities are less diverse and populations are more isolated so potentially more adapted to local conditions, several studies have found that fish larvae, scyphomedusae, ctenophores, and copepods are less abundant below the oxycline when bottom-layer DO is < 2 mg L^{-1} (Roman et al. 1993; Keister et al. 2000; Kolesar et al. 2010). The estuarine residence time of southern HC is similar to those of Chesapeake Bay and its sub-estuaries (Hagy et al. 2000; Babson et al. 2006), so populations may be similarly isolated and adapted to seasonal hypoxia; but, like the Gulf of Mexico, HC supports a diverse zooplankton community, with presumably equally diverse responses to hypoxia.

Predator–prey interactions—Differential physiological responses to oxygen depletion can lead to changes in predation through impaired capture ability, swimming speeds, predator avoidance, and escape responses (Breitburg et al. 1994; Shoji et al. 2005). The net effect of hypoxia on predator–prey interactions and thus food chains and trophic energy transfer will depend on individual responses of the interacting species and is likely to results in winners and
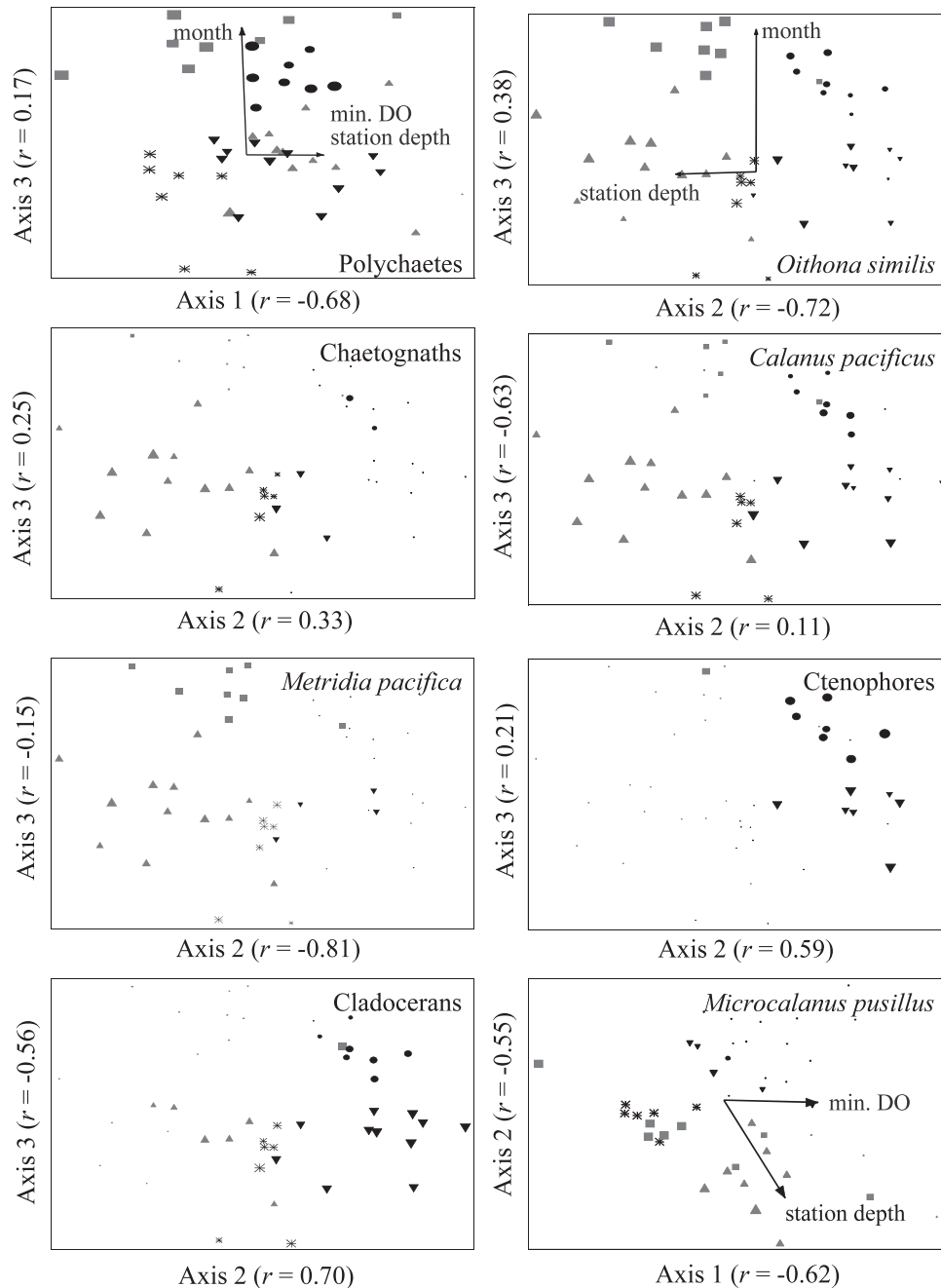
Fig. 7.   Alignment of individual taxa in NMDS ordination of samples; correlation between the species and each axis is shown as Pearson's *r* following the axis labels. Symbol codes are from cluster groupings shown in Fig. 5. Size of symbol is related to the relative proportion of the taxa within each sample. Note that the two dominant axes for each taxon are shown so axes differ among panels.

losers in the community. Tolerance of low DO generally increases from vertebrates to crustaceans to gelatinous zooplankton (Ekau et al. 2010), many of which are tolerant of < 1 mg DO L^{-1} (Purcell et al. 2001; Rutherford and Thuesen 2005; Thuesen et al. 2005). Some medusae have been shown to maintain or increase predation rates under hypoxic conditions (Breitburg et al. 1997; Shoji et al. 2005), whereas vertebrate predators decrease predation under the same conditions (Breitburg et al. 1997). These differences

could lead to increased dominance of gelatinous predators as oxygen declines, particularly in estuaries where jellyfish abundances are already high (Shoji et al. 2005).

However, because many pelagic organisms can move vertically to avoid physiological stress, predator–prey interactions may be more affected by altered habitat use and encounter rates than by changes in physiology per se (Kolesar et al. 2010). Prey that move up in the water column to avoid hypoxia may increase their overlap with,

and susceptibility to, visual predators (Keister et al. 2000; J. E. Keister unpubl). Some field studies have reported that organisms aggregate at short distances from the edge of hypoxic zones, potentially in dense aggregations that can be targeted by predators (Zhang et al. 2009; Craig 2012). On the other hand, if predators' avoidance of hypoxia is stronger than their prey's, hypoxic layers may act as a predation refuge (Parker-Stetter and Horne 2009; Vanderploeg et al. 2009).

As in previous studies, we found that changes in vertical distribution varied with DO concentration in complex and species-specific ways. Behavioral experiments and field observations show that some organisms demonstrate threshold-like behavior changes to DO whereas others show a more linear response (Breitburg 1994; Keister et al. 2000). Such differences make it difficult to assess how energy flow through food webs may be affected by hypoxia in ecosystems with diverse species assemblages.

Community changes—Hypoxia has been shown to alter community structure and decrease species diversity in fish and benthic communities (Diaz and Rosenberg 1995). In our study, we observed spatial and temporal patterns in species composition that may have been influenced by hypoxia, but the relationship between bottom DO and community assemblages was confounded with both station depth and seasonal changes so cannot be conclusively separated. NMDS ordination revealed that spatial patterns in communities were strongly structured along depth gradients, particularly for large, motile taxa such as euphausiids, chaetognaths, and amphipods, which are heavily preyed on by visual predators. Those taxa were always uncommon in shallow regions, were never found below the oxycline when lower-layer DO was < 1.5 mg L^{-1}, and were absent throughout the water column where bottom DO was < 1 mg L^{-1}. Those zooplankton perform DVM to depths of > 100 m of necessity to avoid visual predators; their absence from shallower, hypoxic regions may indicate their inability to escape visual predators in those areas regardless of oxygen conditions. Avoidance of bottom waters would likely increase their susceptibility to predators and reinforce the observed patterns.

The temporal changes in community structure we observed are also difficult to interpret given the tight coupling between the seasonal development of hypoxia and other environmental changes (e.g., temperature and production cycles). Seasonal changes in most taxa probably reflect their typical production cycles, but the relative abundances of medusae, cyclopoid copepods, and polychaetes all increased through the year in LHC and may indicate a hypoxia-driven shift in species composition. Members of all of those taxa are known to be hypoxia tolerant and have indicated degraded habitat conditions in previous studies (Purcell et al. 2001; Baustian and Rabalais 2009).

Among the copepods, the increased dominance of the small cyclopoid copepod *Oithona* over the season is notable. Previous studies have suggested that *Oithona* can be a useful indicator of eutrophication and low oxygen concentrations (Richard and Jamet 2001). Its relatively low metabolism and high tolerance for hypoxia compared to

many calanoid copepods (Paffenhofer 1993; Roman et al. 1993) and a dietary preference for flagellates, which can dominate over diatoms in eutrophied areas (Uye 1994), may allow it to proliferate under degraded conditions. In addition, because *Oithona* carries its egg sacs, its entire life cycle can be dissociated from hypoxic bottom waters, whereas the eggs of broadcast spawners would likely sink into hypoxic bottom waters during their development. All of these factors could result in an increasing dominance of *Oithona* under degraded environmental conditions.

On the other hand, the observed proliferation of *Oithona* in late summer and winter could be related to the balance between its fecundity and predation mortality. *Oithona* maintains almost constant weight-specific egg production year round (Sabatini and Kiørboe 1994) and maintains relatively high abundances in winter when other copepods decline (Nielsen and Sabatini 1996). Because of its small size, larval but not juvenile fish prey upon it, so *Oithona* is also likely to experience relief from its vertebrate predators as the season progresses. These different mechanisms for *Oithona*'s seasonally increased dominance cannot be separated in this study so remain to be explored.

The large medusae that were abundant in LHC during our study—*C. capillata*, *A. victoria*, and *Aur. labiata*—oxyregulate using intragel oxygen storage to sustain their metabolism, so can inhabit very low oxygen waters for extended periods (Purcell et al. 2001; Rutherford and Thuesen 2005). Scyphomedusae can be voracious predators on copepods and ichthyoplankton (Purcell et al. 2001). Their high predation rates may feed back to increase eutrophication if their consumption of zooplankton releases phytoplankton and as they themselves senesce and are decomposed on the benthos (West et al. 2009). Jellyfish biomass is higher in regions of HC that are subject to hypoxia than in northern HC or elsewhere in northern Puget Sound (Reum et al. 2010), possibly indicating their competitive advantage in degraded areas as has been noted in other parts of the world (Purcell et al. 2001; Riisgard et al. 2012). Furthermore, because the nonvisual medusae do not strongly discriminate among copepod prey, Uye (1994) suggested that a shift in copepod communities from larger calanoids to smaller cyclopoids may be a reason for the relative success of medusae over fish in eutrophied areas.

Management implications—There is good reason to believe that hypoxia in many aquatic systems will increase over the coming years as a result of climate change and human population growth. Global warming is increasing ocean temperatures and stratification, leading to increased isolation of deep layers from oxygenated surface water while anthropogenic eutrophication of watersheds and enclosed seas is intensifying. Indicators of ecosystem stress are being seen in Puget Sound as in many other estuaries around the world; without restoration efforts, ecosystem health is likely to continue to decline (Mumford 2002). Seasonal hypoxia naturally occurs in HC, but managers are increasingly concerned that additional declines in water quality may increase the frequency of fish kills, alter community structure, and ultimately decrease the capacity of the region to support fisheries. An increased understanding of how the

base of the food chain responds to oxygen depletion will improve our understanding of ecosystems and help predict their response to future changes.

Hypoxia has the potential to substantially alter trophic pathways and ultimately the transfer of energy up the food chain to fish. We found evidence of shifts in distributions and altered community structure of mesozooplankton as a consequence of hypoxia in HC, changes that are likely to affect the ecosystem and trophic transfer of energy through food webs. Vertical distributions indicated that not all taxa were similarly affected—several taxa showed apparent tolerance of the conditions present during our sampling, indicating the potential for ecosystem function to be maintained even as changes occur if those taxa fill ecological roles vacated by less tolerant organisms. Small sample sizes and our inability to distinguish live from recently dead or dying organisms caution against drawing strong conclusions from the details of our results, but the patterns observed are suggestive of fundamental changes that warrant further investigation.

References

BABSON, A. L., A. KAWASE, AND P. MACCREADY. 2006. Seasonal and interannual variability in the circulation of Puget Sound, Washington: A box model study. Atmos. Ocean **44:** 29–45, doi:10.3137/ao.440103

BAUSTIAN, M. M., AND N. N. RABALAIS. 2009. Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. Estuaries Coasts **32:** 975–983, doi:10.1007/s12237-009-9187-3

BERNATIS, J. L., S. L. GERSTENBERGER, AND I. J. MCGAW. 2007. Behavioural responses of the Dungeness crab, *Cancer magister*, during feeding and digestion in hypoxic conditions. Mar. Biol. **150:** 941–951, doi:10.1007/s00227-006-0392-3

BOLLENS, S. M., AND B. W. FROST. 1989. Predator-induced diel vertical migration in a planktonic copepod. J. Plankton Res. **11:** 1047–1065, doi:10.1093/plankt/11.5.1047

———, K. OSGOOD, B. W. FROST, AND S. D. WATTS. 1993. Vertical distributions and susceptibilities to vertebrate predation of the marine copepods *Metridia lucens* and *Calanus pacificus*. Limnol. Oceanogr. **38:** 1827–1837, doi:10.4319/lo.1993.38.8.1827

BREITBURG, D. L. 1994. Behavioral-response of fish larvae to low dissolved-oxygen concentrations in a stratified water column. Mar. Biol. **120:** 615–625, doi:10.1007/BF00350083

———, T. LOHER, C. A. PACEY, AND A. GERSTEIN. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecol. Monogr. **67:** 489–507, doi:10.1890/0012-9615(1997)067[0489:VEOLDO]2.0.CO;2

———, N. STEINBERG, S. DUBEAU, C. COOKSEY, AND E. D. HOUDE. 1994. Effects of low dissolved-oxygen on predation on estuarine fish larvae. Mar. Ecol. Prog. Ser. **104:** 235–246, doi:10.3354/meps104235

———, AND OTHERS. 2003. The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. Estuaries **26:** 280–297, doi:10.1007/BF02695967

CRAIG, J. K. 2012. Aggregation on the edge: Effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar. Ecol. Prog. Ser. **445:** 75–95, doi:10.3354/meps09437

DAGG, M. J., B. W. FROST, AND J. NEWTON. 1998. Diel vertical migration and feeding in adult female *Calanus pacificus*, *Metridia lucens* and *Pseudocalanus newmani* during a spring bloom in Dabob Bay, a fjord in Washington USA. J. Mar. Syst. **15:** 503–509, doi:10.1016/S0924-7963(97)00093-6

DECKER, M. B., D. L. BREITBURG, AND N. H. MARCUS. 2003. Geographical differences in behavioral responses to hypoxia: Local adaptation to an anthropogenic stressor? Ecol. Appl. **13:** 1104–1109, doi:10.1890/1051-0761(2003)13[1104:GDIBRT]2.0.CO;2

DIAZ, R. J., AND R. ROSENBERG. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna, p. 245–303. *In* A. D. Ansell, R. N. Gibson and M. Barnes [eds.], Oceanography and marine biology—an annual review. V. 33. UCL Press.

DUFRÊNE, M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. **67:** 345–366.

EGLOFF, D. A., P. W. FOFONOFF, AND T. ONBE. 1997. Reproductive biology of marine cladocerans. Adv. Mar. Biol. **31:** 79–167, doi:10.1016/S0065-2881(08)60222-9

EKAU, W., H. AUEL, H. O. PORTNER, AND D. GILBERT. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences **7:** 1669–1699, doi:10.5194/bg-7-1669-2010

FIELD, J. G., K. R. CLARKE, AND R. M. WARWICK. 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. **8:** 37–52, doi:10.3354/meps008037

HAGY, J. D., W. R. BOYNTON, C. W. KEEFE, AND K. V. WOOD. 2004. Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. Estuaries **27:** 634–658, doi:10.1007/BF02907650

———, L. P. SANFORD, AND W. R. BOYNTON. 2000. Estimation of net physical transport and hydraulic residence times for a coastal plain estuary using box models. Estuaries **23:** 328–340, doi:10.2307/1353325

HANEY, J. F. 1988. Diel patterns of zooplankton behavior. Bull. Mar. Sci. **43:** 583–603.

INVIDIA, M., S. SEI, AND G. GORBI. 2004. Survival of the copepod *Acartia tonsa* following egg exposure to near anoxia and to sulfide at different pH values. Mar. Ecol. Prog. Ser. **276:** 187–196, doi:10.3354/meps276187

IRIGOIEN, X., D. V. P. CONWAY, AND R. P. HARRIS. 2004. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. Mar. Ecol. Prog. Ser. **267:** 85–97, doi:10.3354/meps267085

KEELING, R. F., A. KORTZINGER, AND N. GRUBER. 2010. Ocean deoxygenation in a warming world. Annu. Rev. Mar. Sci. **2:** 199–229, doi:10.1146/annurev.marine.010908.163855

KEISTER, J. E., E. D. HOUDE, AND D. L. BREITBURG. 2000. Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. Mar. Ecol. Prog. Ser. **205:** 43–59, doi:10.3354/meps205043

KIMMEL, D. G., W. C. BOICOURT, J. J. PIERSON, M. R. ROMAN, AND X. S. ZHANG. 2010. The vertical distribution and diel variability of mesozooplankton biomass, abundance and size in response to hypoxia in the northern Gulf of Mexico USA. J. Plankton Res. **32:** 1185–1202, doi:10.1093/plankt/fbp136

KOLESAR, S. E., D. L. BREITBURG, J. E. PURCELL, AND M. B. DECKER. 2010. Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: Clearance rates and vertical habitat overlap. Mar. Ecol. Prog. Ser. **411:** 173–188, doi:10.3354/meps08656

MARCUS, N. H., C. RICHMOND, C. SEDLACEK, G. A. MILLER, AND C. OPPERT. 2004. Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana. J. Exp. Mar. Biol. Ecol. **301:** 111–128, doi:10.1016/j.jembe.2003.09.016

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities [Internet]. MjM Software Design [accessed 2012 December 11]. Available from http://home.centurytel.net/~mjm/

———, AND M. J. MEFFORD. 2005. PC-ORD, 5.0 [Internet]. MjM software design [accessed 2012 December 11]. Available from http://home.centurytel.net/~mjm/

MILLER, D. C., S. L. POUCHER, AND L. COIRO. 2002. Determination of lethal dissolved oxygen levels for selected marine and estuarine fishes, crustaceans, and a bivalve. Mar. Biol. **140:** 287–296, doi:10.1007/s002270100702

MUMFORD, T. F. J. 2002. Emerging issues: Changing paradigms, unseen signs and neglected science, p. 1–14. *In* T. Droscher [ed.], Proceedings of the 2001 Puget Sound research conference. Puget Sound Action Team.

NEWTON, J. A., S. L. ALBERTSON, K. V. VOORHIS, C. MALOY, AND E. SIEGEL. 2002. Washington State marine water quality in 1998 through 2000 [Internet]. Washington State Department of Ecology, Pub. No. 02-03-056 [accessed 2012 December 11]. Available from http://www.ecy.wa.gov/biblio/0203056.html

NIELSEN, T. G., AND M. SABATINI. 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. Mar. Ecol. Prog. Ser. **139:** 79–93, doi:10.3354/meps139079

OHMAN, M. D. 1985. Resource-satiated population growth of the copepod *Pseudocalanus* sp. Ergeb. Limnol. **21:** 15–32.

OSGOOD, K. E., AND B. W. FROST. 1994. Ontogenic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. Mar. Ecol. Prog. Ser. **104:** 13–25, doi:10.3354/meps104013

PAFFENHOFER, G. A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). J. Plankton Res. **15:** 37–55, doi:10.1093/plankt/15.1.37

PARKER-STETTER, S. L., AND J. K. HORNE. 2009. Nekton distribution and midwater hypoxia: A seasonal, diel prey refuge? Estuar. Coast. Shelf Sci. **81:** 13–18, doi:10.1016/j.ecss.2008.09.021

PIHL, L., S. P. BADEN, R. J. DIAZ, AND L. C. SCHAFFNER. 1992. Hypoxia-induced structural-changes in the diet of bottom-feeding fish and crustacea. Mar. Biol. **112:** 349–361, doi:10.1007/BF00356279

PURCELL, J. E., D. L. BREITBURG, M. B. DECKER, W. M. GRAHAM, M. J. YOUNGBLUTH, AND K. A. RASKOFF. 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review, p. 77–100. *In* N. N. Rabalais and R. E. Turner [eds.], Coastal hypoxia: Consequences for living resources and ecosystems. American Geophysical Union, Coastal and Estuarine Studies.

———, AND M. B. DECKER. 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnol. Oceanogr. **50:** 376–387, doi:10.4319/lo.2005.50.1.0376

REUM, J. C. P., M. E. HUNSICKER, AND C. E. PAULSEN. 2010. Species composition and relative abundance of large medusae in Puget Sound, Washington. Northwest. Sci. **84:** 131–140, doi:10.4319/lo.2005.50.1.0376

RICHARD, S., AND J. L. JAMET. 2001. An unusual distribution of *Oithona nana* Giesbrecht (1892) (Crustacea: Cyclopoida) in a bay: The case of Toulon Bay (France, Mediterranean Sea). J. Coast. Res. **17:** 957–963.

RIISGARD, H. U., P. ANDERSEN, AND E. HOFFMANN. 2012. From fish to jellyfish in the eutrophicated Limfjorden (Denmark). Estuaries Coasts **35:** 701–713, doi:10.1007/s12237-012-9480-4

ROBB, T., AND M. V. ABRAHAMS. 2002. The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. Behav. Ecol. Sociobiol. **52:** 25–30, doi:10.1007/s00265-002-0474-2

ROMAN, M. R., A. L. GAUZENS, W. K. RHINEHART, AND J. R. WHITE. 1993. Effects of low-oxygen waters on Chesapeake Bay zooplankton. Limnol. Oceanogr. **38:** 1603–1614, doi:10.4319/lo.1993.38.8.1603

RUTHERFORD, L. D., AND E. V. THUESEN. 2005. Metabolic performance and survival of medusae in estuarine hypoxia. Mar. Ecol. Prog. Ser. **294:** 189–200, doi:10.3354/meps294189

SABATINI, M., AND T. KIØRBOE. 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis*. J. Plankton Res. **16:** 1329–1351, doi:10.1093/plankt/16.10.1329

SHOJI, J., R. MASUDA, Y. YAMASHITA, AND M. TANAKA. 2005. Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. Fish. Sci. **71:** 748–753, doi:10.1111/j.1444-2906.2005.01024.x

STALDER, L. C., AND N. H. MARCUS. 1997. Zooplankton responses to hypoxia: Behavioral patterns and survival of three species of calanoid copepods. Mar. Biol. **127:** 599–607, doi:10.1007/s002270050050

TAYLOR, J. C., AND P. S. RAND. 2003. Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. Aquat. Living Resour. **16:** 191–196, doi:10.1016/S0990-7440(03)00012-3

THUESEN, E. V., L. D. RUTHERFORD, AND P. L. BROMMER. 2005. The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. J. Mar. Biol. Assoc. U. K. **85:** 627–633, doi:10.1017/S0025315405011550

UYE, S. 1994. Replacement of large copepods by small ones with eutrophication of embayments—cause and consequence. Hydrobiologia **293:** 513–519, doi:10.1007/BF00229979

VANDERPLOEG, H. A., AND OTHERS. 2009. Hypoxic zones as habitat for zooplankton in Lake Erie: Refuges from predation or exclusion zones? J. Exp. Mar. Biol. Ecol. **381:** S108–S120, doi:10.1016/j.jembe.2009.07.015

WEST, E. J., D. T. WELSH, AND K. A. PITT. 2009. Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. Hydrobiologia **616:** 151–160, doi:10.1007/s10750-008-9586-7

WISHART, D. 1969. An algorithm for hierarchical classifications. Biometrics **25:** 165–170, doi:10.2307/2528688

ZHANG, H. Y., AND OTHERS. 2009. Hypoxia-driven changes in the behavior and spatial distribution of pelagic fish and mesozooplankton in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. **381:** S80–S91, doi:10.1016/j.jembe.2009.07.014