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Abstract

We adopt a trait-based approach to explain Diel Vertical Migration (DVM) across a diverse assemblage of planktonic copepods, utilizing body size as a master trait. We find a reproducible pattern of body size-dependence of day and night depths occupied, and of DVM. Both the smallest surface-dwelling and the largest deeper-dwelling copepods refrain from migrations, while intermediate-sized individuals show pronounced DVM. This pattern apparently arises as a consequence of size-dependent predation risk. In the size classes of migratory copepods the amplitude of DVM is further modulated by optical attenuation in the ocean water column because increased turbidity decreases encounter rates with visually hunting predators. Long-term changes in the ocean optical environment are expected to alter the vertical distributions of many copepods and thus to affect predator-prey encounters as well as oceanic carbon export.

Copepods are ubiquitous aquatic crustaceans that play a key role in food webs and biogeochemical cycles. Copepods are known from all bathymetric provinces extending from hadal depths in the deep sea (Beliaev 1989) to transient melt ponds high in the Himalaya mountains (Kikuchi 1994). Many copepods and other zooplankton in the ocean and lakes undergo Diel Vertical Migration (DVM), purportedly the largest biomass of animal migration on earth. Zooplankton utilize different sectors of the water column at different times of day as refuges from predators (Ohman 1990; DeRobertis et al. 2000), to maximize or minimize dispersal (Batchelder et al. 2002), to encounter mates (Madin and Purcell 1992), or, in shallow waters, to avoid ultraviolet light (Williamson et al. 2011). However, copepods are highly diversified, encompassing >14,500 described species from 10 taxonomic orders (Walter and Boxshall 2015). They exhibit disparate life histories, morphologies, trophic niches, metabolic potential, and vertical and geographic distributions, and their DVM behaviors vary widely among species and across life history stages in a complex manner (Frost 1988; Mauchline 1998; Ringelberg 2010).

Here, we adopt a trait-based approach (Litchman et al. 2013) as an alternative to interspecific analyses to explain variations in DVM in the southern sector of the California Current System, a major coastal upwelling biome. Among traits considered for the zooplankton, body size has been considered a master trait because so many aspects of metabolism, predation risk, and other characteristics covary with size (Litchman et al. 2013). Variations in body size are also well suited to applications of digital image analysis and associated machine learning methods, which currently show higher fidelity for morphometric measurements than for taxonomic identifications. Because free-living planktonic copepods span at least five orders of magnitude variation in body mass, there are substantial variations in predation risk across this range (cf. Aksnes and Giske 1993). Here, we find body size (as feret diameter, the longest dimension of an imaged object) to be a good predictor of both day and night vertical distributions of planktonic copepods, and that copepod vertical distributions are further modulated by variations in the optical properties of the ocean water column.

Materials and methods

Zooplankton sampling and digital analysis

Sampling was conducted on two springtime cruises of the California Current Ecosystem Long-Term Ecological Research program (P0605: 8 May–7 June 2006; 5 experimental "cycles"; P0704: 2-21 April 2007; 4 experimental "cycles"). Discrete water parcels of different hydrographic characteristics were selected using satellite remote sensing imagery and Moving Vessel Profiler (Ohman et al. 2012) site surveys. Zooplankton were sampled in a quasi-Lagrangian manner while following a
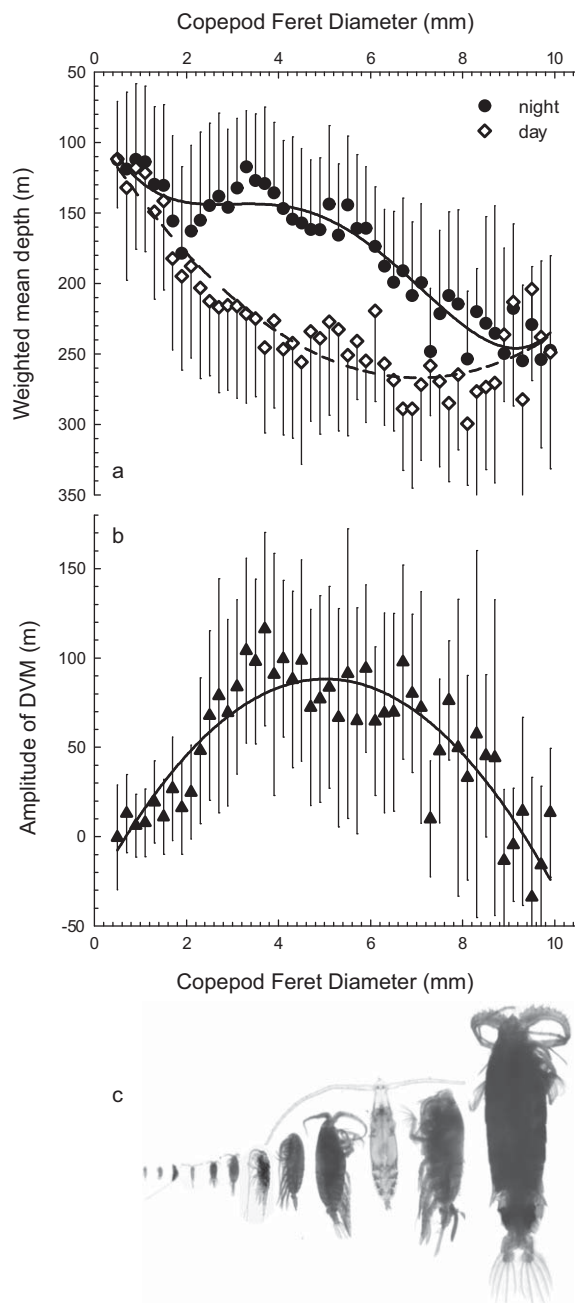
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Copepod Feret Diameter (mm)

a

b

c

Fig. 1. Body size-dependence of copepod Diel Vertical Migration (DVM) in the California Current Ecosystem in spring. (a) Weighted mean depth by day (◇) and night (●) of the copepod assemblage. Means + or − 95% C.I. averaged over 9 different locations in the study region over two years, together with polynomial fits. (b) Body size-dependence of the amplitude of DVM, as the difference between day and night values in panel (a) (mean ± 95% together with polynomial fit. (c) Body size variation of adult copepods across four different orders (Calanoida, Cyclopoida, Poecilostomatoida, Harpacticoida) from the study site. Equations are reported in Table 1.

modified holey sock drifter drogued at 15 m depth (Niiler et al. 1995; Landry et al. 2009) using Globalstar satellite telemetry. Vertically stratified sampling was done with a 1 m², 202-μm

mesh MOCNESS (Wiebe et al. 1985), towed between 450 m and 0 m, typically with 2 d and two night MOCNESS vertical series at each of the nine repeated Lagrangian cycles of activity. Strata were sampled at 50 m intervals, except on the shallow continental shelf (Cycle 3) on P0605, where 10–15 m strata were sampled from 120 m to 0 m. Samples were fixed at sea in 1.8% formaldehyde buffered with sodium tetraborate, then images of individual copepods digitized ashore using a ZooScan (Gorsky et al. 2010). To ensure adequate representation of all size classes, each plankton sample was passed sequentially through 1 mm and 0.2 mm meshes, then aliquoted to scan, on average, 1500–2000 animals from the 0.2–1 mm fraction and 400–700 animals from the >1.0 mm fraction. Organisms were carefully distributed manually on the scanning glass so as to avoid overlap of adjacent specimens. Images were digitally segmented into regions of interest (ROI) and morphometric measurements made using ImageJ routines (Gorsky et al. 2010). ROI's were classified initially with a Random Forest algorithm (Gorsky et al. 2010), then 100% of the ROI's were examined and classification errors corrected manually. The body size of copepods was measured as maximum feret diameter, an image analysis metric defined as the longest distance between any two points along the object boundary. For copepods, feret diameter is typically 5–17% greater than copepod total length, but the two are highly correlated ($r^2 = 0.954$ [Gorsky et al. 2010]). Sampling depth, volumes of water filtered by each net in situ, and aliquot ratio of samples scanned were used to calculate numbers of copepods per cubic meter. The weighted mean depth of each size category was calculated for each vertical MOCNESS series, weighting the mean depth of occurrence by the number of individuals in each stratum, after assigning all organisms sampled in a stratum to its mid-point depth (Ohman et al. 2002).

Optical attenuation coefficient

The diffuse attenuation coefficient for downwelling irradiance at 490 nm (k_{490}) was calculated from empirical polynomial fits to in situ satellite data, using standard NASA algorithms (NASA Ocean Biology 2015). Results from SeaWifs and MODIS-Aqua sensors were averaged. k_{490} was averaged along the in situ drifter tracks corresponding to the time periods for each of the experimental cycles where MOCNESS tows were carried out.

Results and discussion

Both day and night vertical distributions deepen progressively with increasing copepod body size (Fig. 1a; equations reported in Table 1).This descent likely occurs because of the body size-dependent risk of detection and capture by visually hunting predators like planktivorous fishes, which detect prey at greater distances in better illuminated surface waters (Aksnes and Utne 1997). Some fishes can detect prey even in dim nocturnal illumination (Macy et al. 1998), hence larger animals have deeper depth distributions even at night. However, the nonlinear relationship between body size, vertical

Table 1. Polynomial equations fitted to the relationships in Fig. 1. Equations are of the form: $Y = Y_0 + a \times X + b \times X^2 + c \times X^3 + d \times X^4$, where Y = Nighttime weighted mean depth (m), Daytime weighted mean depth, or Amplitude of diel vertical migration. X is copepod body size (feret diameter, μm). R^2 indicates the proportion of variance explained; p is the probability associated with the equation fit.

Variable	Y_0	a	b	c	d	R^2	p
Nighttime depth (m)	80.559	0.071	-2.780 E -05	4.408 E -09	-2.184 E -13	0.90	<0.0001
Daytime depth (m)	93.784	0.049	-3.511 E -06			0.85	<0.0001
Amplitude (m)	-29.988	0.047	-4.703 E -06			0.76	<0.0001

distribution (Fig. 1a), and amplitude of DVM (Fig. 1b) was unexpected. The smallest-bodied copepods are non-migratory, remaining in shallower waters day and night (Fig. 1a). The largest-bodied animals are also nonmigratory, but remain continuously in deeper, subsurface waters (Fig. 1a). In contrast, intermediate-sized animals, between approximately 2.5–7 mm feret diameter, reside in deeper subsurface waters by day, but show nightly excursions into shallower waters (Fig. 1b), where concentrations of their prey are higher (http://oceaninformatics.ucsd.edu/datazoo/data/ccelter/datasets). We detected this nonlinear size-dependent migration consistently across nine different sampling locations in two different study years.

Figure 1b also reveals that within the migratory size classes of copepods, there is considerable unexplained variability in the amplitude of DVM. While this variance is expected because of behavioral differences among different species and life history stages present within each of our size categories, we found that most (70.5%) of the variation in DVM amplitude is explained by spatial variations in transparency of the ocean water column. Fig. 2a illustrates spatial variations in the optical attenuation coefficient (k_{490}) in the upper water column as measured by SeaWifs and MODIS-Aqua satellites, together with our zooplankton sampling locations at a series of sites across the southern California Current Ecosystem. k_{490} varies from 0.03 m^{-1} to 0.6 m^{-1} in the upper ocean across our zooplankton sampling locations (Fig. 2a), reflecting much of the variability of optical attenuation found across the world ocean, outside estuarine and nearshore coastal habitats. Within the migratory size classes of copepods (shaded region in Fig. 2b), there is an onshore-to-offshore progression in daytime depths and the amplitude of DVM, both of which increase in optically clearer waters. The amplitude of DVM is directly proportional to the reciprocal of the light extinction coefficient (Fig. 3, $p < 0.01$, across two different sampling years in this study site). Residuals from the regression in Fig. 3 were uncorrelated with lunar phase ($p > 0.10$, Spearman's rank). In optically clearer waters, copepods consistently descend deeper and migrate farther than in turbid waters. Such a response has also been found for freshwater *Daphnia* (Dodson 1990), oceanic copepods in the Sargasso Sea (Buskey et al. 1989), and zooplankton elsewhere (Ringelberg 2010). The vertical extent of

descent is related to water transparency and in turn is likely caused by risk of visual predation.

The smallest-bodied copepods remain continuously in near-surface waters both day and night because of their very small body size and reduced risk of encounter with visually hunting predators. The largest-bodied copepods remain continuously in deep strata because of the steep body-size dependence of encounter rate with visual predators (Aksnes and Giske 1993), hence elevated predation risk in shallower waters even at night. There appears to be no time of day or night when the largest bodied forms can safely enter surface waters. Intermediate-sized copepods, however, utilize deeper waters as a refuge by day, but forage in shallow strata by night where the net energy gain in regions of elevated food concentration compensates for the somewhat elevated predation risk, thereby achieving a fitness advantage (Aksnes and Giske 1990).

Copepod body size is an imperfect trait that ignores many important sources of biological variability. Using body size alone as an independent variable does not permit us to evaluate whether optically related changes in habitat depths are caused by changes in behavior of individual species (Buskey et al. 1989; Frank and Widder 2002) or by spatial differences in the species composition of the zooplankton (e.g., assemblage changes across ocean fronts [Powell and Ohman 2015]). Also, it is well known that deeper-dwelling zooplankton may show DVM extending to deeper depths than the upper 450 m strata sampled here, and that smaller shallow-dwelling zooplankton may show DVM of only a few meters amplitude (Bollens and Frost 1991), much less than our sampling resolution. In addition, other, nonvisually hunting predators can be more important and induce reverse vertical migrations of small-bodied copepods in some ocean environments (Ohman 1990). Nevertheless, considered across the high diversity of copepods occupying the marine environment, body size, mediated by optical characteristics of the ocean water column, is a key determinant of habitat occupied and migration behaviors in the contemporary ocean, most likely because of the importance of size-dependent predation due to visually hunting predators (DeRobertis et al. 2000; Ringelberg 2010).

The optical environment of the ocean is changing and our results suggest that such changes may have consequences for
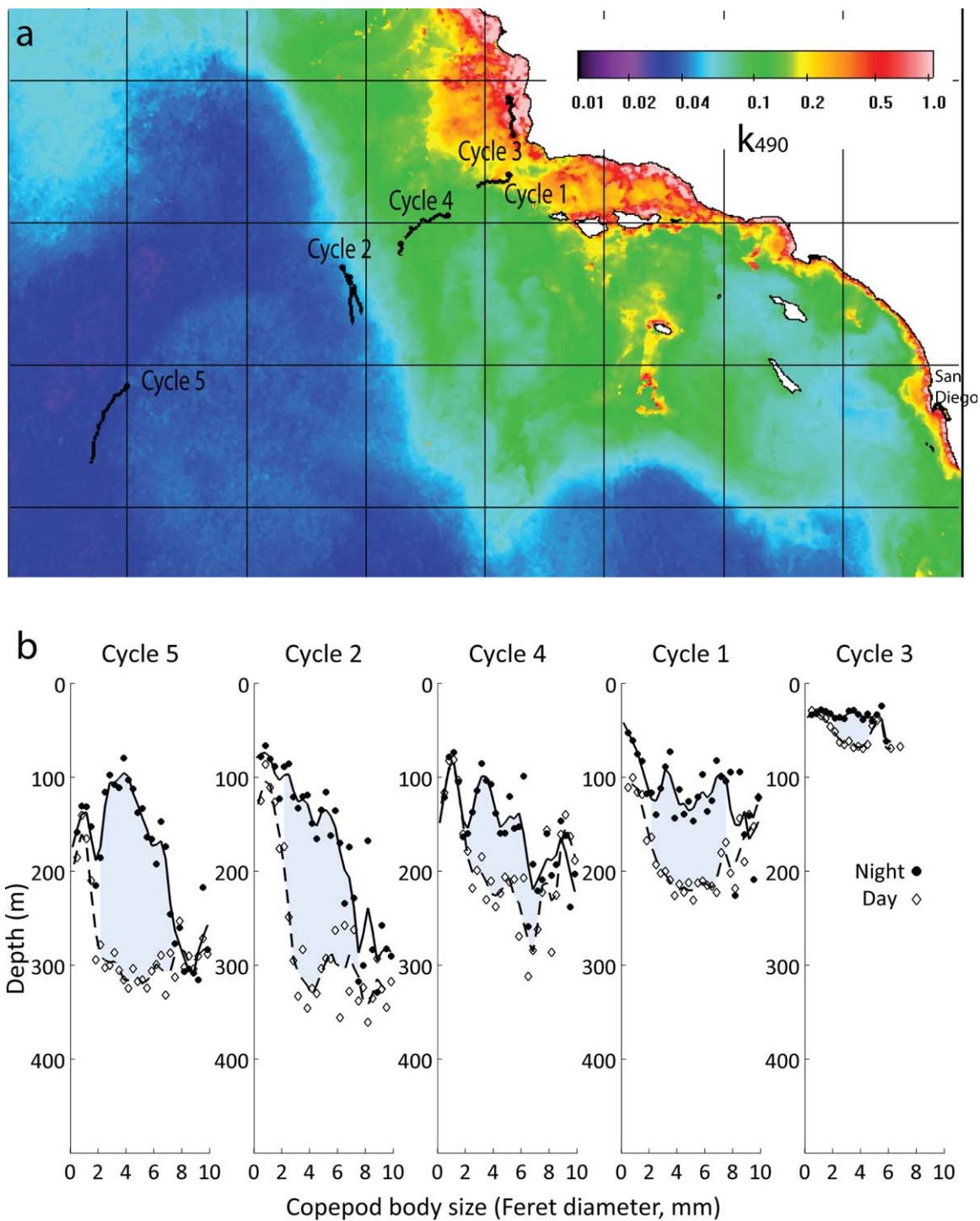
Fig. 2. (a) Variations in diffuse attenuation coefficient (k_{490}) across the California Current Ecosystem, with Lagrangian drifter tracks (black lines) for five experimental cycles on cruise P0605. Drifters were followed while sampling planktonic copepods. (b) Weighted mean depth as a function of copepod body size (as feret diameter) by day (open symbols, dashed lines) and night (solid symbols and lines), across the five experimental cycles in (a). Plots arranged from offshore, clearer waters (left) to onshore more turbid waters (right). Points indicate means of duplicate profiles and lines illustrate loess fits. Shaded region indicates size classes of copepods that show Diel Vertical Migration.

zooplankton distributions, predator–prey interactions, and ocean biogeochemistry. In coastal upwelling ecosystems such as the California Current Ecosystem, both empirical (Sydeman et al. 2014) and modeling (Wang et al. 2015) studies indicate that coastal upwelling is intensifying, primarily due to a greater sea-land temperature differential as the continental
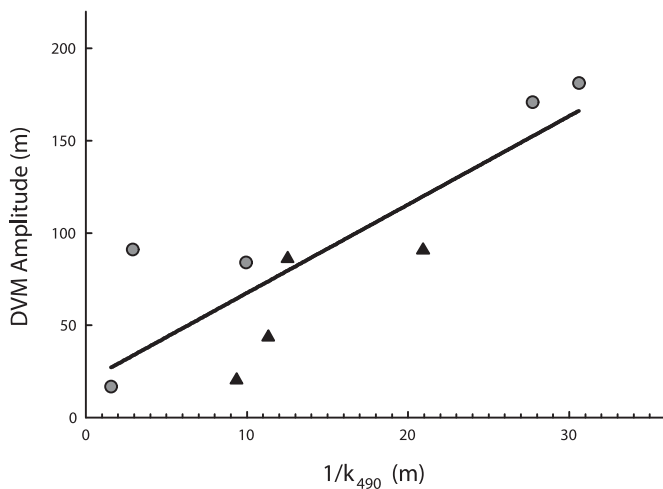
Fig. 3. Dependence of the amplitude of copepod Diel Vertical Migration on the diffuse attenuation coefficient ($1/k_{490}$) in the upper ocean. Amplitude is for intermediate sized (3–6 mm feret diameter) migratory copepods, at nine different water parcels sampled over two years (gray circles = P0605, black triangles = P0704). $Y = 4.79X+19.61$, $r^2 = 0.705$, $p < 0.01$.

land masses warm faster than the coastal ocean (Wang et al. 2015). Enhanced primary production is expected to result from increased wind stress and elevated vertical fluxes of nutrients. Elevated concentrations of phytoplankton have indeed been detected in recent years, together with an increase in the optical attenuation coefficient in the California Current Ecosystem (CCE) since the advent of CalCOFI in 1949 (Aksnes and Ohman 2009). Our results suggest that this increased turbidity leads copepod distributions to shoal with time, with a corresponding decrease in amplitude of DVM. Based on the documented rate of change in the diffuse plus beam attenuation coefficient in the CCE (Aksnes and Ohman 2009), and assuming that this rate of change is applicable to the diffuse attenuation coefficient k_{490}, the relationship in Fig. 3 suggests that the amplitude of copepod DVM has already declined by approximately 20 m since the beginning of the CalCOFI sampling record and will continue to decline at the rate of $\sim$30 m century^{-1}. Such changes in vertical distributions of the dominant mesozooplankton grazers in ocean food webs are expected to alter vertical carbon export and carbon sequestration potential. Shallower copepod distributions in the water column will lead to longer residence times and greater microbial degradation of zooplankton fecal pellets in the upper ocean. Lower amplitude DVM will lead to less translocation and vertical export of respired carbon into deeper waters (known as "active transport"). In contrast, in regions such as open ocean oligotrophic gyres, which are enlarging (Polovina et al. 2008) as phytoplankton concentrations and optical attenuation decrease, we expect copepods will occupy progressively deeper strata, with enhanced C export as a proportion of surface production.

In summary, a trait-based approach has revealed the importance of body size and optical environment in regulating cope-pod vertical distributions and Diel Vertical Migration behavior. Such relationships can now be predicted from remotely sensed optical measurements and readily incorporated into prognostic models of future states of ocean food webs and the ocean carbon cycle.

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Acknowledgements