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Effect of net avoidance on estimates of diel vertical migration

Abstract—Diel vertical migration (DVM) has been hypothesized to actively transport organic material out of the euphotic layer, thus forming a novel part of the ''biological pump.'' However, quantifying DVM is made difficult by observational limitations. Conventionally, the difference between night and day biomass from net trawls in the surface has been assumed to be a consequence of species that have migrated up from their deep daytime depths. However, some of this difference might be an artifact of visual net avoidance. Here, we present a method that facilitates quantification of zooplankton that are migrating, those that are not migrating, and those able to avoid net capture. The algorithm is applied to an extensive data set gathered in the Azores Front region. Results indicate that DVM, and thus active carbon transport, calculated in the traditional manner would overestimate the true value by ~50%.

Diel vertical migration (DVM) by zooplankton and micronekton is a ubiquitous occurrence in the ocean (e.g., Banse 1964). It is assumed that organisms rise up into the surface layer at night and descend below during the day to optimize feeding potential and minimize the probability of visual predation. (Note that specific variations and deviations in this behavior occur, e.g., Ohman 1990; Tarling et al. 2002.) Depending on the animal, ranges of diel migration vary tremendously, both in overall distance of ascent and in upper limit of ascent.

DVM is important to many areas of oceanography, including the study of carbon dynamics. Diel vertically migrating organisms move carbon out of the surface layer to the lower depths of their migratory range, thus forming an active part of the ''biological pump'' (sensu Volk and Hoffert 1985). These organisms feed (taking up carbon) in the surface layer but metabolize (releasing carbon) throughout the water column. The form of carbon released can be particulate organic carbon (POC), dissolved organic carbon (DOC), or dissolved inorganic carbon (DIC). POC export can take the form of fecal pellets, if organisms have sufficiently long gut clearance rates, or the organisms themselves if they are preyed on in the mesopelagic layer (e.g., Angel and Pugh 2000; Schnetzer and Steinberg 2002). DOC is excreted as a byproduct of metabolism at depth (Longhurst and Harrison 1988; Steinberg et al. 2000), and DIC is produced by respiration at depth (Longhurst et al. 1990). This active vetical transport has been estimated to be a significant fraction—as much as 50%—of the total export flux below the euphotic zone (e.g., Longhurst and Harrison 1988; Longhurst et al. 1990; Steinberg et al. 2000).

Zooplankton also alter particulate flux by eating particles and each other (Jackson and Burd 2002) and thus play an important role in determining remineralization depth scales, a crucial parameter in the carbon system (e.g., Najjar 1992). Their migrant behavior might cause coherent fluctuations in particulate flux (Lampitt et al. 1993; Stemmann et al. 2000).

Traditionally, zooplankton distributions have been measured with the use of net trawls of varying diameter and mesh size. The main difficulty with interpreting trawl data is the uncertain efficiency by which the different plankton components are fished. Creatures that are close in size or smaller than the nominal mesh size can pass through and are caught with poor efficiency (e.g., Gallienne and Robins 2001); creatures that are large relative to the mesh size are more likely to avoid actively being caught by the nets (Clutter and Anraku 1968). In addition, larger animals are more rare and likely to be under- (or over)-sampled (Colinvaux 1978). Organisms might avoid capture by visual or mechanical cues. Visual cues can come from natural light and, potentially, from bioluminescence caused by a net's passage, whereas mechanical cues result from the pressure wave associated with the net (Fleminger and Clutter 1965; Clutter and Anraku 1968). Bioluminescence might also attract zooplankton or cause them not to avoid capture. For example, euphausiid catches were significantly enhanced by a factor of 10–20 during the day when artificial lights were attached to nets (Sameoto et al. 1993). The main advantage of net trawls is that organisms collected can be identified and analyzed, yielding full taxonomic information, as well as data on biomass and chemical composition.

Acoustics can also be used to measure zooplankton distributions. Although they do not suffer the disadvantage of net avoidance, shipboard and towed sounders do not necessarily yield consistent results. Where salinity gradients are present, it is difficult to distinguish turbulence from zooplankton backscatter (Ross and Lueck 2003). In addition, backscatter is highly dependent on species and therefore does not provide viable data on biomass or abundance. Results depend heavily on the particular backscatter–biomass model used (Cochrane and Sameoto 1991). Models continue to improve (e.g., Wiebe et al. 1997; McGehee et al. 1998), but acoustic results still require ground truthing (e.g., net trawls) to verify taxonomic composition and determine total biomass (Benfield et al. 1998; Kringel et al. 2003; M. Stutor pers. comm.). Acoustics do, however, demonstrate conclusively that DVM occurs.

Much of the previous work on DVM assumes that differences between day and night net collections in the euphotic zone are a result of DVM only (Longhurst et al. [1990] is an exception). Total DVM biomass is estimated from this difference accordingly. We call this the surface-only method (SOM). It implicitly assumes that capture efficiency is independent of light level. This assumption is inconsistent with our observations in which integrated biomass over the entire habitat depth range (e.g., 800 m) is almost always greater during the night than day. Furthermore, there is good anecdotal evidence of visual net avoidance (VNA) by zooplankton (e.g., euphausiids, Mackintosh 1934).

Here, we present an objective method to determine the DVM component in zooplankton net trawl data and correct for visual net avoidance. The method requires vertically re-

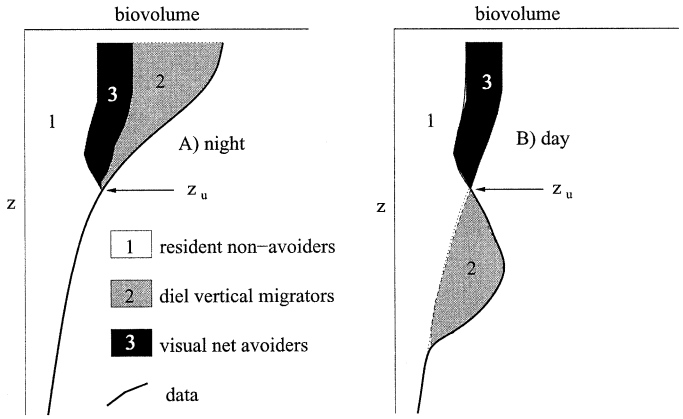

Fig. 1. (A) Night and (B) day biovolume illustrating the three populations of zooplankton that our algorithm isolates from the trawl data. The bold line in each plot represents the net catch. z_u is the upper depth limit for DVM organisms during the day.

solved samples collected during the day and night and extending over the entire DVM range (>800 m) at a given location. We compare results from our algorithm with those calculated by SOM with data gathered in the Azores Front region (Angel 1989).

Methods—The ecology and behavior of the zooplankton community is diverse. This diversity must be represented as reasonably as possible by rigid categories in order for our algorithm to work. In addition, organisms are not likely to be caught in their natural proportions by nets. For example, some animals can avoid capture at all depths. We assume that there are three distinct populations of plankton captured in nets that we can identify (Fig. 1): (1) the resident population—animals living throughout the water column who do not migrate or avoid nets, (2) the DVM portion—animals who migrate below the euphotic zone during the day and into it at night; these animals do not avoid net capture, and (3) the VNA portion—animals resident in the euphotic zone who avoid net capture during the day but not at night.

Data requirements and assumptions: Vertically resolved day and night profiles of horizontal (oblique) net trawls from the same location, collected with the same net system and mesh diameter to avoid dealing with biases associated with different net sampling gear, are required. Our algorithm applies only to the portion of the community caught by nets. We do not account for species or specimens that are either extruded through meshes or rendered unquantifiable (i.e., those that are too small or fragile). Likewise, we do not consider organisms that avoid capture by mechanical cues, bioluminescence associated with the net's passage, or low light, such as moonlight at night. In addition, we assume that none of these potential cues vary with depth. Therefore, in our algorithm, the night data require no correction and are considered representative of the population of interest at all depths sampled. Similarly, we assume VNA occurs only during the day within the euphotic zone. We further assume that the day and night vertical zones of a vertically migrating population do not overlap. In other words, all migrants go below their maximum night depth during the day. Finally, we assume that all migrators rise up at night and descend during the day, even though nature provides exceptions (e.g., Ohman 1990).

Data processing: Raw displacement volume of animals is normalized by the total water volume passing through the net to yield biovolume, a volumetric concentration, expressed here as (volume of animals)/(volume of water). We do not convert to biomass to avoid an additional error. Day and night bioviolume must be interpolated (gridded) to common depths. First cumulative sums from the bottom are calculated. Gaps and overlaps with respect to depth in net trawl data are accounted for by linear interpolation within this numerical integration routine. The data are then gridded to a standard set of depth intervals chosen to match the collection depths as closely as possible. The intervals do not need to be uniform. Finally, the data are differentiated back to biovolume.

Algorithm—On the basis of these assumptions, we isolate three distinct populations: resident, DVM, and VNA (Fig. 1). Discrete depths (z_i) correspond to the midpoint of the gridded interval (Δz_i). Both depth (z) and index i are defined as increasingly positive with depth. Symbols are summarized in Table 1. The algorithm for the gridded data is as follows.

Table 1. Definitions of symbols and acronyms used in the text, with units shown as dimension.

	Definition	Unit (L = length)
A_T	Total VNA biovolume	L^3(animal) L^{-2}
D_T	Total DVM biovolume	L^3(animal) L^{-2}
N_T	Total DVM biovolume predicted by SOM	L^3(animal) L^{-2}
$D(z_i)$	Vertical distribution of DVM during day	L^3(animal) L^{-3}
$N(z_i)$	Vertical distribution of DVM at night	L^3(animal) L^{-3}
Δz_i	ith grid interval	L
z	Depth	L
z_i	ith gridded depth (midpoint of Δz_i)	L
z_u	Upper gridded depth limit of day migration	L
DVM	Diel vertical migration	
SOM	Surface-only method	
VNA	Visual net avoidance	

1. Determine the upper depth of the daytime migrating profile, z_u (Fig. 1): Find the shallowest gridded depth below 100 m (nominal depth of euphotic zone) at which day biovolume exceeds night for at least two consecutive depths. By requiring two values here rather than one, we hope to avoid being misled by statistical fluctuations.

2. Determine the vertical distribution of vertical migrators during the day, $D(z_i)$ (shaded area 2, Fig. 1B): For $z_i < z_u$, $D = 0$, and for $z_i \geq z_u$, $D =$ [day biovolume(z_i) − night biovolume(z_i)]. Note that negative values in $D(z_i)$ are retained to avoid biasing the results.

3. Calculate the total migrating biovolume (D_T): Integrate $D(z_i)$ with respect to z_i. D_T is preserved as the total (maximum) biovolume of vertical migrators in the surface at night. D_T is negative or zero, there are no vertical migrators.

4. Determine the VNA fraction (shaded area 3, Fig. 1): (a) Predict the total biovolume of vertical migrators at night (N_T) in the absence of net avoidance. Calculate [night biovolume(z_i) − day biovolume(z_i)] for $z_i < z_u$ and integrate with respect to z_i. (b) Is there net avoidance? If $N_T > D_T$ (as anticipated), the difference $N_T - D_T$ is the net-avoiding portion, A_T (corresponding to shaded section 3, Fig. 1). Continue with the next step; otherwise $N_T \leq D_T$ and there is no net avoidance. Skip steps 5 and 6 (no correction necessary) and proceed to step 7b.

5. Determine the VNA profile: Choose how the avoiders were distributed within the euphotic zone during the day. We suggest two vertical profile shapes (rectangular or triangular, each with area A_T) of net avoiders. The rectangle represents a vertically uniform concentration of VNA, the simplest assumption in the absence of knowledge. The triangle assumes that avoidance decreases linearly with depth, mimicking exponential light decrease. The lower limit of net avoiders (i.e., location of the bottom of the rectangle or triangle) could be the upper limit of the day migrators (z_u, Fig. 1)—specifically, one interval above the upper limit of $D(z_i)$, z_{u-1} or the nominal euphotic zone depth. Acoustic scattering data will aid in making these decisions if it is available. These choices do not affect quantitative results of the algorithm, only profiles shapes (*see Discussion*).

6. Correct (total) day vertical profiles: Add the net-avoiding profile (estimated in step 5) to the gridded day profile.

7. Determine the night profile of vertical migrators, $N(z)$ (shaded section 2, Fig. 1A): (a) If $N_T > D_T$, $N(z_i) =$ [corrected day biovolume(z_i) − night biovolume(z_i)] for $z_i < z_u$ and $N(z_i) = 0$ for $z_i \geq z_u$. (b) In the rare case that $N_T < D_T$ (implying negative net avoidance), we do not account for the discrepancy between N_T and D_T. There is no correction to the day profile; thus, $N(z_i) =$ [night biovolume(z_i) − day biovolume(z_i)] for $z_i < z_u$ and $N(z) = 0$ for $z_i \geq z_u$. Sampling difficulties that can lead to this case are mentioned in the Discussion.

We are left with vertical profiles of biovolume for total night (uncorrected), visual net avoiders, corrected total day, day DVM, and night DVM. The author (D. Ianson) will supply a MATLAB computer program that implements this algorithm on request.

Results—To test the algorithm, we used an extensive data set that was collected in the Azores Front region (~33°N, 33°W) as part of a series of general surveys. The Azores current is an eastward continuation of the Gulf Stream. The front associated with it is weak, forming a meandering boundary between the more productive eastern Atlantic water that lies to the north of the front and the western Atlantic water that lies to the south (Angel 1989 and references therein). Eight stations were sampled (including stations north and south of the front) during both day and night with multiple opening/closing rectangular midwater trawl (RMT) nets. Specifically, RMT1 (macroplankton, 0.32-mm mesh size, 1-m^2 opening) and RMT8 (micronekton, 4.5-mm mesh size, 8-m^2 opening) from depths >1,000 m to the surface with ~100 m resolution. Tow speeds were ~1 m s^{-1}, and roughly 3,000 m^3 and 30,000 m^3 of water were filtered for each sample by RMT1 and RMT8 nets, respectively. (For a full description of collection methods, location, and timing, *see* Angel 1989.) Total displacement volume has been analyzed and normalized to biovolume (*see Methods: Data Processing*) for both net sizes. The RMT8 samples also were sorted into taxonomic displacement volumes then normalized to taxonomic biovolume. Note that biovolumes can be converted to biomass (or carbon) with the use of a taxonomic conversion factor. Gelatinous organisms have approximately one-third the carbon per biovolume relative to nongelatinous organisms (Wiebe 1988; Pugh et al. 1997). We present profiles assuming a rectangular distribution of net avoiders with a lower depth limit of z_{u-1} (algorithm step 5).

The algorithm yields scenarios in which the day–night disparity is due almost entirely to DVM (Fig. 2A) and, alternatively, in which the disparity results mainly from net avoidance (Fig. 2B). In the first example from north of the Azores Front, there is an obvious deep bulge (500–700 m) in total biovolume during the day relative to the night (Fig. 2A). This bulge is equal to the excess biovolume found in the surface at night, suggesting that migration is responsible for both the surface and lower layer day–night differences (equivalent to the result obtained by SOM). The migrating population makes up 30% of the total biovolume (area 2, day and night; Fig. 2A, right panel). On the other hand, at Sta. 78 just south of the front, the algorithm predicts that the difference between the day and night surface data (as with SOM) is mostly due to net avoidance (Fig. 2B). In the lower layer, biovolume increases little during the day. Thus, the algorithm suggests that 40% of the total biovolume avoids capture via visual cues, with only 15% of the population migrating (profiles of the migrating portion, Fig. 2B, right panel).

The RMT8 data show that the algorithm describes net avoidance (and lack of avoidance) by distinct taxonomic groups, as expected. The taxa Mysidacea and Chaetognatha have low metabolic rates, lack escape responses, and are considered to be nonavoiders (Childress and Thuesen 1992; Thuesen and Childress 1993; Angel and Pugh 2000). The

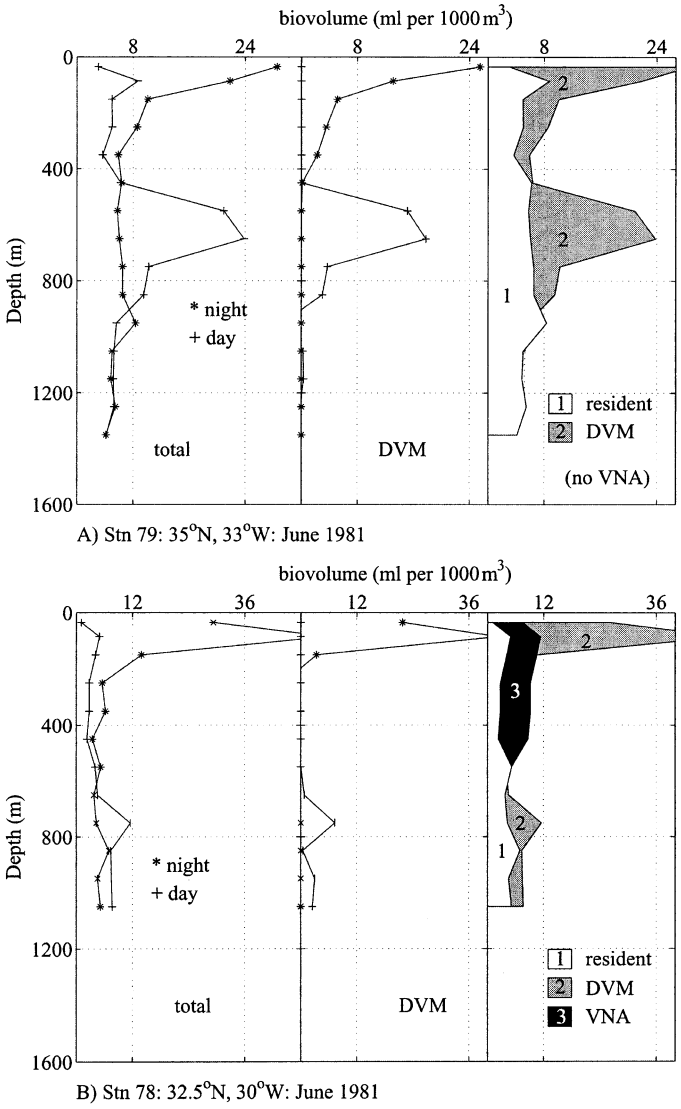

Fig. 2. RMT8 vertical profiles of day and night total biovolume (bv, left panel) at (A) Sta. 79 (well outside of the front, northward) and (B) Sta. 78 (just south of the front and likely influenced by it). The diel migrating fraction (DVM, day and night) and the three populations (1, resident; 2, DVM [both day and night shown]; 3, visual net-avoiding fraction (VNA) predicted by the algorithm are also shown for each station in the middle and right panels, respectively.

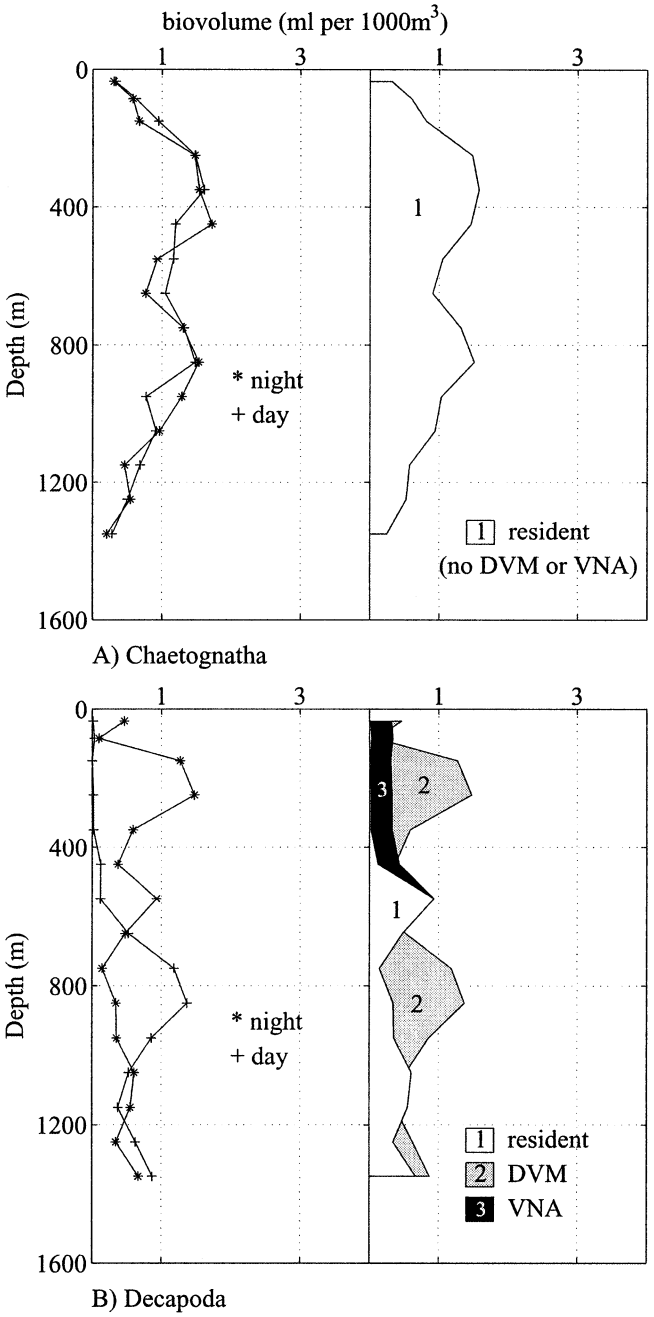

Fig. 3. Vertical profiles of day and night taxonomic biovolume (bv, left panel) with the three populations isolated by the algorithm (1, resident; 2, DVM [both day and night shown]; 3, VNA) (right panel) for (A) Chaetognatha (no avoidance or migration) and (B) Decapoda (33% DVM and 22% VNA) from Sta. 79: 35°N, 33°W, June 1981.

algorithm yields no net avoidance for mysids at all eight stations, and for chaetognaths (Fig. 3A) at seven of eight stations. At the only station where chaetognaths appear to avoid (<20%), they are more numerous in the lower portion of the water column at night, whereas the upper portion shows little difference between day and night biovolume. This station is within the frontal region where advection between sampling times could easily influence catches. Decapoda and Euphausiacea are capable net avoiders, particularly the latter (Marschoff et al. 1998; Angel and Pugh 2000). The data show that, on average, 20–30% of the total population for each taxon avoids, which is as anticipated for decapods (Fig. 3B) but lower than anticipated for euphausiids. However, there is considerable variation within the euphausiid data, and total biovolume of this taxon was lower than expected (Angel 1989). In addition, euphausiids are likely to use nonvisual as well as visual cues to avoid nets.

The algorithm was applied to all of the Azores Front data (16 sets; RMT1 and RMT8 samples from eight stations). Uncertainties as a result of sampling variability (*see Discussion*) are expected to be high in each individual sample. This

Table 2. RMT1 and RMT8 mean values reported with standard errors ($n = 8$) for diel vertical migrators (DVM) and visual net avoiders (VNA), expressed as fractions of the total biovolume in the sample. Weighted fractions are normalized by the size of the sample, that is, (total biovolume)/(mean biovolume for the given net size from all eight samples). VNA/SOM migrators is the fraction of the vertical migrators predicted by SOM that are net avoiders in our scheme.

	RMT1	RMT8
DVM	11±3%	16%±5%
Weighted DVM	8%±2%	15%±5%
VNA	17%±4%	13%±6%
Weighted VNA	20%±4%	15%±8%
VNA/SOM migrators	60%±10%	40±10%

variability is reflected in the standard errors of the means that summarize our results (Table 2).

We estimate that the fraction of the total biovolume avoiding nets visually is around 15–20%, whether the samples are weighted by total biovolume or not (Table 2). Meanwhile, the DVM fraction is ~10–15% (again, whether weighted or not). If we apply SOM, we find that ~40–60% of the vertical migrators predicted by SOM are avoiding nets according to our scheme. In other words, SOM overpredicts the amount of diel migration by roughly 50% in these data.

Discussion—Conceptually, our method is rational and straightforward. In practice, it is limited by the intrinsic difficulties associated with the data.

Collecting zooplankton samples is time consuming and challenging. Our data have no repeat tows. However, data from another study show repeatability for the same location and depth range within a factor of 2 over a 48-h period (Roe et al. 1984). This variability results in part because profiles are often compiled from trawls collected over periods of days (e.g., each profile used here was collected over ~3 d). Spatial and temporal variation is often high within zooplankton populations and is likely to influence zooplankton profiles such as these, especially in the upper layer of the ocean where horizontal advection is generally greatest. In addition, many organisms cue to preferred light depths, which will change depending on cloud cover and time of day.

Our method is sensitive to such variability because we calculate the difference between two measurements, each with its uncertainty. For example, one exceptionally large surface datum at night could alter the results of our algorithm significantly (e.g., from 0% to 30% avoiding). Large swarms of gelatinous creatures (such as *Pyrosoma*) tend to be patchy and occur in the surface at night; when they occurred in this study, they were handpicked from the samples in an attempt to avoid misleading results (*see* Angel 1989).

This sensitivity could also cause negative biovolume estimates. Roe et al. (1984) were concerned with DVM in their repeat survey and found that day and night samples were significantly different to a minimum of the 95% confidence level at all depths despite the high sampling uncertainty. Their results suggest that day–night differencing, as in our algorithm, is feasible. Similarly, sampling variability in our data does not appear to limit the algorithm. Negative biovolume estimates do not occur in any of the 16 total biovolume results. Two rare cases in which negative estimates result for separate taxonomic biovolumes are discussed (chaetognaths, discussed earlier, and salps).

Meaningful surface data are particularly difficult to obtain because the upper 5 m of the water column is disrupted by the passage of the ship. One might expect avoidance by micronekton (RMT8) to be greater on average than that of macroplankton (RMT1), simply because the nekton are larger and potentially more mobile and more capable of avoiding. The Azores Front data suggest that the avoiding fraction is roughly the same in each size fraction (Table 2). However, it is likely that we underestimated avoidance in some of the RMT8 data because of the surface sampling problem. Salps were often abundant and found at the surface at night during collection of these data. As such, salps within the RMT8 samples are the only taxon that often have higher biovolume (integrated) during the day relative to night (i.e., apparent negative avoidance). This oddity influences the total biovolume samples by lowering the avoiding fraction (and is likely the reason that no avoidance is seen at Sta. 79; Fig. 2A). Given this challenge with the salp data, our method should be more powerful if used on each taxon separately. Taxon results can then be combined to yield total biovolume. In addition, the gelatinous organisms are generally more difficult to sample. Thus, we expect the algorithm to be most successful when used with crustaceans or nongelatinous organisms alone or when they dominate the total biovolume.

Our data indicate that daylight visual avoidance is important. However, the algorithm is unable to account for other potential avoidance cues, which are listed with the assumptions in Methods (e.g., mechanical, bioluminescence, and low light). We have stressed that this method applies to the population caught by nets. One must be aware, however, that unaccounted for cues might have some depth dependence. With depth variation, each potential cue is most likely to increase in the upper layer. Wire angle increases as nets approach the surface and is expected to alter flow properties, increasing the level of disturbance that organisms perceive. Similarly, bioluminescence can be greatest in the surface and most important at night. The resident population predicted by our algorithm would be unaffected by these variations. However, if a significant fraction of DVM are able to avoid in the surface at night, our algorithm would underestimate the VNA portion because the surface day–night disparity, were we able to catch these organisms, would increase.

The method will fail if vertical migrators travel beneath the deepest net trawl. (This situation is assumed to account for higher integrated biovolume during night relative to day when using SOM (e.g., Angel and Pugh 2000). Certainly, the macroplankton are not expected to migrate to <1,000 m on a diel basis (Angel et al. 1982). Some of the micronekton, such as Decapoda, do migrate to surprising depths (e.g., 1,200 m; Domanski 1986). However, DVM organisms do not appear to be travelling outside of the sampling range in the Azores Front data. Biovolume is relatively constant below ~800 m and varies little between day and night.

Although we can estimate the fraction of net avoiders from the data, we cannot use the net data to constrain their vertical distribution. In many cases, the biovolume caught

by day is near zero throughout the upper layer. Avoiding organisms might be evenly distributed in the euphotic zone, or they might be concentrated at particular depths. We present choices of VNA profile shapes on the basis of simplicity and light levels (algorithm step 5).

Despite variability in the data, our method provides a useful means of determining the vertical migrating fraction—both biovolume and day–night vertical profiles—from net trawl data. It illustrates the utility of midwater sampling and provides substantial improvement over the conventional method of simply subtracting day from night biomass in the upper layer (SOM). When used with appropriate caution, our algorithm allows as much information as possible to be gained from day and night trawl data.

We present a method for determining the biovolume (or biomass) of diel vertical migrators and of visual net avoiders. The method requires zooplankton net trawls during day and night at the same location. Trawls must extend from the surface to depths well below the euphotic zone, where migrators go during the day, to a minimum depth of ~800 m. Our method predicts the level of net avoidance, and results suggest that the conventional method of estimating the biomass of diel migrators (SOM) overestimates DVM, and thus active vertical export of carbon, by about 50%.

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Taxonomic variability of phosphorus stress in Sargasso Sea phytoplankton

Abstract—Low inorganic phosphorus (SRP) concentrations and high inorganic nitrogen to phosphorus ratios suggest that phytoplankton production in the northwestern Sargasso Sea may be controlled to some extent by the availability of phosphorus. Phosphorus stress in marine phytoplankton was qualitatively assessed by using a single-cell enzyme-linked fluorescent (ELF) assay for the enzyme alkaline phosphatase, which is induced at low SRP concentrations. During the highly stratified summer period, ~30% of the observed autotrophic eukaryotes in the surface waters were ELF-labeled, whereas in the well-mixed fall period, nearly 70% of the observed autotrophic eukaryotes in the surface waters were ELF-labeled. During the summer, autotrophic flagellates displayed significantly higher ELF-labeling than did both diatoms and dinoflagellates, and this labeling did not vary with depth, whereas in the fall, autotrophic flagellates and diatoms displayed statistically similar and decreasing percentages of ELF-labeled cells as a function of depth. This assay allowed for rapid assessment of the in situ physiological condition of individual autotrophic phytoplankton in the Sargasso Sea. By using this assay, we were able to identify taxonomic and potential seasonal variability of phosphorus stress within the autotrophic phytoplankton community.

For decades, biologists and geochemists have debated which nutrient, nitrogen or phosphorus, limits marine primary production (e.g., Codispoti 1989). In the 1960s and 1970s, the open-ocean new production (Dugdale and Goering 1967) and export production (Eppley and Peterson 1979) paradigms were developed based upon a nitrogen-limited ocean, a view that found support in prominent publications (e.g., Hecky and Kilham 1988). In the past two decades this view has changed and it is now widely accepted that marine primary production can be limited by inorganic phosphorus (SRP), iron, and silica, as well as nitrogen (e.g., Martin and Fitzwater 1988; Boyd et al. 1999). Part of this change in thought is due to a greater appreciation of nitrogen-fixing organisms that by definition cannot be nitrogen-limited.

A number of studies in the Sargasso Sea have presented evidence supporting the hypothesis that this region may currently be SRP-limited. Early geochemical studies (Fanning 1992; Michaels et al. 1996) noted dissolved inorganic N : P ratios that were substantially greater than the canonical Redfield (1958) ratio, and that have recently been confirmed by high-sensitivity nutrient analytical methods (Wu et al. 2000; Cavender-Bares et al. 2001). The biological interpretation of nutrient limitation associated with these high N : P ratios is not straightforward, because there is little physiological information on the N : P ratio at which phytoplankton transition from nitrogen to phosphorus limitation. Examination of available data suggests that this ratio may range from ~20 to 50 (reviewed by Geider and LaRoche 2002).

The enzyme alkaline phosphatase (AP), which is induced by SRP limitation in many phytoplankton species (Cembella