Diel Vertical Migration

OCN 621
Outline

- Definition
- Who does it? How fast?
- Migration cues
- Why?
- Variations: seasonal, ontogenic, reverse
- Biogeochemical implications
Diel Vertical Migration: Definitions

- Usually involves migration into food-filled shallow water at night, and descent into relatively food-depleted depths during the day. Normal DVM is when migration occurs at dawn and dusk.

2 general patterns:

- Nocturnal migration (as above): most common
- Reverse migration: surface rise during the day, nighttime descent to a maximum depth.
How widespread?

- Freshwater and marine systems
- Occurs in all major groups of zooplankton
- Extent/occurrence varies with life stage and/or sex, season, geographic location, and general weather conditions
Examples of Diel Vertical Migrators

These phyla have representatives that DVM, but not all species within these phyla migrate:

- Crustacea: dominant group: copepods, especially the calanoids, and euphausiids (krill)
- Siphonophores
- Chaetognaths
- Squid
- Fish
- Protists: Reverse DVM (down at dusk, up at dawn)
  - Ciliates (e.g., autotrophic *Mesodinium rubrum*)
  - Dinoflagellates
Amplitude and extent of migration

- Amplitude (depth range): 10s of cm to 100s of meters, and at all depths down to the abyssopelagic zone, but down to 1700 m deepest that we have good evidence for.
- Occurs ocean-wide, but especially in highly productive tropical areas.
- Occurs over diel, seasonal and ontogenic time scales
How fast do they do it?

- Speeds ranging from 3.24 m/h (0.9 mm/s) in the small copepod *Paracalanus parvus* to 215 m/h (60.2 mm/s) in the krill *Meganyctiphanes norvegica* (i.e., slower in smaller swimmers than larger ones).

- Downward speeds are often faster than upward speeds, probably due to gravity.
Deep Scattering Layers

- Moving deep scattering layers are due to diel vertical migrators
- Look like false sea bottoms on echograms
- Formed by larger crustaceans, small fish with swim bladders, and occasionally copepods and heteropods

Day-time deep scattering layers in Saanich Inlet, BC, Canada

from Lalli & Parsons 1997
Example: ADCP, NE Atlantic

Main scattering layer: ascent at 3-4 cm/s, descent at 10 cm/s

Wade & Heywood 2001
Antarctica

VTS (db) 04/17/02 02:35:02-04/17/02 04:44:21 (Local)  MOC-1: 01

VTS (db) 04/17/02 07:09:21-04/17/02 09:30:18 (Local)  MOC-1: 02

Courtesy of M. Zhou

ADCP & MOCNESS
Euphausia superba
Vertical Migrators at BATS (Sargasso Sea, Atlantic Ocean)

Fig. 1. Proportion of total biomass contributed by common migrators. Time series of biomass of some of the important migrators at BATS. Data are averages of replicate night tows taken in the upper 200 m on all BATS cruises (202 μm mesh, 1 m² plankton net). Numbered months denote > 1 cruise in same month. The biomass of individual species was estimated by multiplying species counts in each tow by the mean dry weight determined for each species.

Steinberg et al. 2000
Proximate Cue

- Light the major cue: in particular the intensity of downwelling irradiance is linked to timing of migration and amplitude.
- Is the absolute magnitude of light or the rate of change of light that zooplankton use as cues? Rate of change hypothesis more widely supported by evidence and scientific community.
Total Solar Eclipse, 30 June 1973

- Solid Line: Vertical position of the 0.2 μW cm⁻² nm⁻¹ isolume
- DSL: Vertical position of the sonic scattering layer during the eclipse.
- The gap in the record was caused by ship repositioning for better observation.
Light cues: Longer residence time at the surface during winter months

North Atlantic copepods: size also impacted length of stay at the surface

Figure 1. The mean daily length of near-surface occupation by different populations of copepods in the North Atlantic, using samples from the Continuous Plankton Recorder survey. Filled circles = juvenile *Metridia*, open circles = adult *M. lucens*, filled squares = adult *M. longa*. For adult *Metridia longa*, adult *M. lucens* and juvenile *Metridia*, there were seasonal changes in the length of near-surface occupation in line with seasonal changes in the length of the night. For example, in winter, when nights are longer, populations spent longer at the surface each night compared to during the summer. In addition to this seasonal pattern, the length of near-surface occupation varied with body size, being shortest for the largest group, adult *M. longa*, and longest for the smallest group, juvenile *Metridia*. Adapted from Hays (1995).

Hays 2003
Why do it?

- Most favor the hypothesis that DVM allows zooplankton to avoid visual predation in the surface layers by taking temporary refuge in the darker depths during the day.

- Cost vs. Benefit: reduced feeding period vs. reducing probability of predation ("better hungry than dead").

- If this hypothesis true, then
  - expect ascent at dusk and descent at dawn, and
  - DVM will be more pronounced in more conspicuous individuals, and
  - the amplitude of migrations will vary with the abundance and activity of planktivorous fish.

- In fact, Reverse DVM also could be explained by this, as the predators of those doing the R-DVM are themselves doing DVM (invertebrate predators).
Visibility & Relative Predation Risk

Vulnerability to visual predation varies with light intensity & prey size

It should also depend upon optical transparency of the water (i.e., particle load).

DeRobertis 2002
**Calanus pacificus:** adult females

- Trawls for larval planktivorous fish
- Stomach contents of larval fish examined for presence/absence of *C. pacificus*
- Also looked at night/day distributions of *C. pacificus* (± 75 m)
- Found that when significant numbers of fish, DVM behavior strong and vice versa

\[ V = \text{index of vertical migration} \]
\[ F = \text{fish abundance} \]

Bollens & Frost 1989
Egg-bearing females more attractive to predators...

When presented with egg & non-egg bearing females, Pacific herring ingested 4.67 times as many ovigerous females.

Bollens & Frost 1991
Seasonal/Ontogenic Vertical Migration

Lalli & Parsons 1997

Figure 4.18  A schematic diagram of the life cycle of the copepod *Neocalanus plumchrus* in coastal waters off British Columbia, Canada. The depth distributions of the eggs, larvae (nauplii I–VI and copepodites I–V) and adults (copepodite VI) are shown over the course of one year. C, copepodite; N, nauplius.
Calanus pacificus

Figure 1. Life cycle of Calanus pacificus in the main basin of Puget Sound. Heavy lines indicate the daytime vertical distribution of developmental stages. Dots indicate the daily vertical migration performed by adult females.

lipid stores sufficient for winter
Acoustic observation of diel vertical migration and shoaling behaviour in Atlantic redfishes

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Acoustic methods were used to study Atlantic redfishes Sebastes spp. vertical migration and shoaling behaviour in Newfoundland waters. Redfishes exhibited consistent patterns of vertical migration in winter, spring and summer, but pelagic shoals were not observed in winter. Pelagic daytime aggregations were generally in close proximity to dense patches of redfishes along the sea floor. Pelagic shoals exhibited high degrees of variability in size, shape and density. Attempts to explain variations in shoal density and area with features of shoal position and structure were unsuccessful. Nearest neighbour distance between fish in shoals had a lower limit near one body length. During the night, fishes were dispersed in the water column and distributions were more homogenous. Diel vertical migration appeared to be a foraging strategy, in which redfishes followed the migration of their euphausioid prey.

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Persistence of Tidally-oriented Vertical Migration by Zooplankton in a Temperate Estuary

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ABSTRACT: Tidal vertical migration by zooplankton is a common phenomenon in estuaries, usually associated with landward movement of meroplankton or position maintenance of holoplankton. Little is known about the persistence of this behavior, its spatial variability, or its response to changing environmental conditions. We extended a previous study of tidal movements of zooplankton in the low-salinity zone (LSZ) of the San Francisco estuary in 1994 to include data from two additional years with very different hydrology. Freshwater flow during sampling in 1995 was about 7-fold greater than in 1994; the LSZ was about 28 km further seaward, and gravitational circulation in the LSZ was strong. In 1996 freshwater flow and LSZ position were intermediate but, because the LSZ was in shallower water in 1996 than in 1995, gravitational circulation was uncommon. Behavior of copepods in both years was similar to that reported in 1994 with some tidal migration observed during most cruises. An exception was the introduced carnivorous copepod 

Tortanus dextrolobatus, which did not migrate and maintained a position deep in the water column (1995 only). In 1996, mysids mainly stayed near the bottom with evidence for vertical migration from only 1 of 6 data sets, whereas amphipods migrated slightly on a diel schedule; these behaviors contrasted with the tidal migration observed in 1994. The bay shrimp 

Crangon franciscorum did not appear to migrate, but was more abundant in the water column during both ebb and flood, suggesting passive vertical dispersal. Zooplankton did not appear to maintain position by interactions with lateral circulation cells. The results for copepods suggest rigidity in behavior with little or no relaxation of the vertical movement in 1995 when strong gravitational circulation would have made upstream movement relatively easy. Mysids and amphipods altered their behavior depending on local conditions related to freshwater flow.
Reverse Diel Vertical Migration

- This is the opposite of DVM: organism come into surface waters during the day to feed, and sink to unlit depths at night.

Top: Vertical distribution of copepod during day (white) and night (black).

Bottom: Distributions of potential invertebrate predators of *Pseudocalanus*.

*Ohman et al. 1983*
Seasonal variation

*Pseudocalanus newmani*

- 2 stations (shallow & deep)
- displaying diel vertical migration, reverse DVM and no migration
- migration or absence thereof correlated with predator presence

![Graphs showing seasonal variation in P. newmani females](image)

**Fig. 9.** Seasonal change in day (○—○) and night (●—●) median depth of *Pseudocalanus newmani* females, at (A) Station D and (B) Station S. The distributions are from vertical series in 1979 excepting September (1978, both stations) and March (1980, Station S only). Vertical lines indicate the vertical distance between the 25th and 75th percentiles of the population distribution.

![Graph showing temporal variation in abundance](image)

**Fig. 1.** Temporal variation ($\bar{x} \pm sd$, when sd available) in abundance of the suspension-feeding copepod *Pseudocalanus newmani* and predators (the carnivorous copepod *Eucalanus elongata* and the chaetognath *Sagitta elegans*), at Station D in Dabob Bay.

Ohman 1990
Salp migrations in the Subarctic Pacific

Cyclosalpa bakeri

Top: Day and night distributions of *Cyclosalpa bakeri* at Stn. P in Aug. 1988

Bottom: Gut pigment contents as a function of time of day.

Purcell & Madin 1991
Figure 1.1 A simplified diagrammatic representation of the three main routes by which particulate and dissolved material may be exported from the surface layer of the ocean to depth (see text for details). DIC = dissolved inorganic carbon.
Contribution of Migrants to C & N flux

Table 8
Comparison of migrant flux estimates for carbon and nitrogen in tropical and subtropical open-ocean ecosystems. Flux estimates, mmol C or N m\(^{-2}\) d\(^{-1}\) and % trap particulate carbon (PC) or nitrogen (PN) at 150 m, are only for dissolved inorganic by-products of metabolism. All C flux estimates are computed assuming RQ = 0.8. Temp = mean temp at daytime depth of diel migrants.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Period</th>
<th>Migrant biomass (mg DW m(^{-2}) d(^{-1}))</th>
<th>Temp (°C)</th>
<th>Carbon Flux mmol C m(^{-2}) d(^{-1})</th>
<th>% PC</th>
<th>Nitrogen Flux mmol N m(^{-2}) d(^{-1})</th>
<th>% PC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Longhurst et al.</td>
<td>NFLUX 38°N, 65°W</td>
<td>Sept. 1988</td>
<td>72 (0.2–2 mm) 402 (2–20 mm)</td>
<td>18</td>
<td>0.186</td>
<td>3.1</td>
<td>0.051</td>
<td>7.6</td>
</tr>
<tr>
<td>Dam et al. (1995)</td>
<td>BATS 31°50’N, 64°10’W</td>
<td>Mar–Apr. 1990</td>
<td>479</td>
<td>18</td>
<td>0.967</td>
<td>29.7</td>
<td>0.136</td>
<td>37.3</td>
</tr>
<tr>
<td>Zhang and Dam (1997)</td>
<td>HNLC Equator 0°, 140°W</td>
<td>Mar–Apr. 1992</td>
<td>240</td>
<td>13</td>
<td>0.280</td>
<td>14.7</td>
<td>0.136</td>
<td>37.3</td>
</tr>
<tr>
<td></td>
<td>Oct. 1992</td>
<td></td>
<td>387</td>
<td>13</td>
<td>0.488</td>
<td>20.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Le Borgne and Rodier</td>
<td>HNLC Equator 0°, 150°W</td>
<td>Sept.–Oct. 1994</td>
<td>132 (0.2–2 mm)</td>
<td>14</td>
<td>0.529*</td>
<td>3.5</td>
<td>0.139*</td>
<td>4.9</td>
</tr>
<tr>
<td>(1997)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Steinberg et al. (2000)</td>
<td>Oligotrophic Equator</td>
<td>Sept.–Oct. 1994</td>
<td>118 (0.2–2 mm)</td>
<td>14</td>
<td>0.257*</td>
<td>5.5</td>
<td>0.106*</td>
<td>19.8</td>
</tr>
<tr>
<td>This study</td>
<td>BATS 31°50’N, 64°10’W</td>
<td>1994–97 37 cruises</td>
<td>123</td>
<td>18</td>
<td>0.100</td>
<td>4.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ALOHA 22°45’N, 158°W</td>
<td>1994–96 26 cruises</td>
<td>394</td>
<td>9</td>
<td>0.304</td>
<td>15.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Indicates flux estimates include authors’ correction for migrants > 2 mm.

note: these are minimum flux estimates, as they don’t include death of migrants at depth, under-sampled micro-nekton, dissolved organic excretion or inter-zonal fecal transport.
Table 2
Comparison of studies measuring the ratio of downward transport of carbon by migrating zooplankton to gravitational POC fluxes measured by sediment traps. Migratory and sediment trap fluxes are calculated across 150 m or the depth of the euphotic zone. Mean and range (given in parentheses). (Data not listed here were not provided in reference)

<table>
<thead>
<tr>
<th>Location of study and time of year</th>
<th>Migrating biomass (mg C m(^{-2}))</th>
<th>Migratory flux (mg C m(^{-2}) d(^{-1}))</th>
<th>% of mean POC flux</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>BATS (year-round)</td>
<td>50 (0–123)</td>
<td>2.0 (0–9.9)(^a)</td>
<td>8 (0–39)</td>
<td>(this study)</td>
</tr>
<tr>
<td>Subtropical and tropical Atlantic – several stations (September)</td>
<td>–</td>
<td>5.5 (2.8–8.8)(^b)</td>
<td>6 (4–14)</td>
<td>Longhurst et al. (1990)</td>
</tr>
<tr>
<td>BATS (March/April)</td>
<td>191 (82–536)</td>
<td>14.5 (6.2–40.6)</td>
<td>34 (18–70)</td>
<td>Dam et al. (1995)</td>
</tr>
<tr>
<td>Equatorial Pacific (March/April)</td>
<td>96</td>
<td>4.2(^c)</td>
<td>18</td>
<td>Zhang and Dam (1997)</td>
</tr>
<tr>
<td>(October)</td>
<td>155</td>
<td>7.3(^c)</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Equatorial Pacific Oligotrophic</td>
<td>47(^d)</td>
<td>3.8(^b,,e)</td>
<td>8(^e)</td>
<td>Le Borgne and Rodier (1997), and Rodier and Le Borgne (1997)</td>
</tr>
<tr>
<td>HNLC area (September/October)</td>
<td>53(^d)</td>
<td>7.9(^b,,e)</td>
<td>4(^e)</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Migratory flux includes DOC + CO\(_2\) (values in other studies are respiratory flux only).
\(^b\)Includes migrating micronekton or nekton in addition to zooplankton.
\(^c\)Does not include flux due to mortality.
\(^d\)Calculated from Table 10, Le Borgne and Rodier (1997), assuming C = 0.4 × dry weight.
\(^e\)Calculated from Table 8, Rodier and Le Borgne (1997).
Biogeochemical Implications

- Active transport of material from euphotic zone to deep (i.e. food in zp gut is metabolized at depth).
- Numerous studies to date have drawn five main conclusions
  1. inter-zonal migrants can significantly enhance oceanic export fluxes via their DVM behavior,
  2. the relative importance of the active flux is highly dependent on the biomass of the migrating community,
  3. the relative importance of the active versus the passive flux increases with increasing depth,
  4. inter-zonal migrants may provide a steady source of nutrients to deep-sea microbial communities, and
  5. we should be including the active flux caused by DVM when modeling the cycling of biogeochemically important elements.