

Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm

Craig E. Williamson,^{a,*} Janet M. Fischer,^b Stephen M. Bollens,^c Erin P. Overholt,^a and Joanne K. Breckenridge^c

^aDepartment of Zoology, Miami University, Oxford, Ohio

^bDepartment of Biology, Franklin & Marshall College, Lancaster, Pennsylvania

^cSchool of Earth and Environmental Sciences, Washington State University, Vancouver, Washington

Abstract

The current prevailing theory of diel vertical migration (DVM) of zooplankton is focused largely on two biotic drivers: food and predation. Yet recent evidence suggests that abiotic drivers such as damaging ultraviolet (UV) radiation and temperature are also important. Here we integrate current knowledge on the effects of abiotic factors on DVM with the current biologically based paradigm to develop a more comprehensive framework for understanding DVM in zooplankton. We focus on “normal” (down during the day, up at night) DVM of holoplanktonic, primarily herbivorous zooplankton. This new *transparency-regulator hypothesis* differentiates between *structural drivers*, such as temperature and food, that vary little over a 24-h period and *dynamic drivers*, such as damaging UV radiation and visual predation, that show strong variation over a 24-h period. This hypothesis emphasizes the central role of water transparency in regulating these major drivers of DVM. In less transparent systems, temperature and food are often optimal in the surface waters, visual predators are abundant, and UV radiation levels are low. In contrast, in more transparent systems, vertical thermal gradients tend to be more gradual, food quality and quantity are higher in deeper waters, and visual predator abundance is often lower and damaging UV radiation higher in the surface waters. This transparency-regulator hypothesis provides a more versatile theoretical framework to explain variation in DVM across waters of differing transparency. This hypothesis also enables clearer predictions of how the wide range of ongoing transparency-altering local, regional, and global environmental changes can be expected to influence DVM patterns in both inland and oceanic waters of the world.

Diel vertical migrations (DVM) of zooplankton in the world’s lakes and oceans comprise some of the most widespread and massive migrations of animals on Earth. These striking migrations across strong vertical habitat gradients have inspired numerous ecological and evolutionary studies addressing mechanisms of habitat selection and consequences for species interactions. These migrations also have important implications for water quality and fisheries production as well as biogeochemical cycling. Natural and anthropogenic environmental changes, such as shifting local land use patterns and regional to global climate change, are altering water transparency and have the potential to affect DVM in lakes and oceans worldwide. The purpose of this article is to provide a common theoretical framework for understanding variation in the drivers of DVM across transparency gradients with a particular emphasis on recent advances in our understanding of the role of ultraviolet radiation (UV).

Many environmental factors are recognized as providing both important proximate cues as well as ultimate consequences of adaptive significance for DVM, including light, temperature, food availability, and predation pressures (Table 1; Lampert 1989; Ringelberg 1993; Hays 2003). In spite of the widespread appreciation for the importance of multiple factors in regulating DVM, little consideration has been given to how the relative importance of these factors might vary more systematically across

transparency gradients in aquatic ecosystems. Very few papers to date have explicitly examined the relationship between DVM amplitude and water transparency. One freshwater study found a clear increase in the amplitude of DVM with increasing Secchi transparency, a pattern that was attributed to visual predation (Dodson 1990). Comparisons of zooplankton DVM at oligotrophic and mesotrophic stations in the North Pacific Ocean found the amplitude of DVM to be greater at the more transparent oligotrophic station (Steinberg et al. 2008). Similarly, DVM was more common in the oligotrophic Gulf of Mexico than in the more eutrophic Inland Sea of Japan (Checkley et al. 1992). However, other studies have found the strength of DVM in two species of marine copepods was related not to Secchi transparency but rather to the abundance of zooplanktivorous fishes (Bollens and Frost 1989a; Bollens et al. 1992).

Here we review some of the highlights of the historical development of ideas about DVM and propose a more comprehensive framework to explain the observed variation in DVM across lakes and oceans of differing transparency with an emphasis on recent advances in our understanding of the role of UV radiation. Our purpose is not to provide a comprehensive review of DVM theory, as numerous other reviews already exist, including two classical and comprehensive reviews (McLaren 1963; Hutchinson 1967) as well as more recent reviews (Hays 2003; Cohen and Forward 2009; Ringelberg 2010). Rather, we build on the “transparency-gradient” hypothesis

* Corresponding author: craig.williamson@muohio.edu

Table 1. Leading theories of “normal” (down by day, up at night) DVM, proximate cues, ultimate drivers, nature of the drivers (dynamic or structural), and generalized response of herbivorous zooplankton to each driver. Note that for each theory, there is both a proximate cue and an ultimate adaptive significance, while each driver can itself be considered either structural or dynamic. Although in some systems a given driver may be more dynamic than in others (e.g., diel temperature cycles), the temporal range of a structural driver is generally much less than its spatial range vertically within the water column.

Theory	Proximate drivers	Ultimate drivers	Nature of the drivers	Zooplankton response
UV avoidance	UV radiation	Photodamage, mortality	Dynamic	Down by day
Visual predation	Visible light, kairomones	Predation mortality	Dynamic	Down by day
Temperature	Temperature	Growth and reproduction	Structural	Up at any time
Food	Food	Survival, growth, and reproduction	Structural	Up or down at any time

(Kessler et al. 2008) and prior literature on DVM to develop a new hypothesis with a broader conceptual framework to evaluate how changes in water transparency and hence the threat of UV damage modify the relative importance of biotic (food and predation) vs. abiotic (temperature and UV radiation) factors that influence DVM in aquatic ecosystems of varying transparency. This *transparency-regulator hypothesis* includes a new approach for integrating both abiotic and biotic factors into a common framework that more explicitly distinguishes their functional role in DVM. In particular, we propose that drivers of DVM can be separated into structural drivers vs. dynamic drivers (Fig. 1). *Structural drivers* create a vertical habitat gradient that does not show any strong or consistent variation over a 24-h period but can change

markedly across seasons and locations. Thus, structural drivers vary too little on a diel basis to serve as proximate cues driving the observed changes in vertical distribution of zooplankton, yet they are important in determining the optimal depth that promotes maximum feeding, growth, survival, and reproduction (fitness correlates). Examples include nonmotile food and temperature for primarily herbivorous zooplankton. *Dynamic drivers*, on the other hand, include factors that show strong and systematic variation over a 24-h period and can thus drive diel changes in vertical distribution (i.e., DVM) of zooplankton. These variables are generally light dependent and include factors such as visual predation and damaging UV radiation. The dichotomy between structural and dynamic drivers is not meant to replace the classical and still useful distinction of

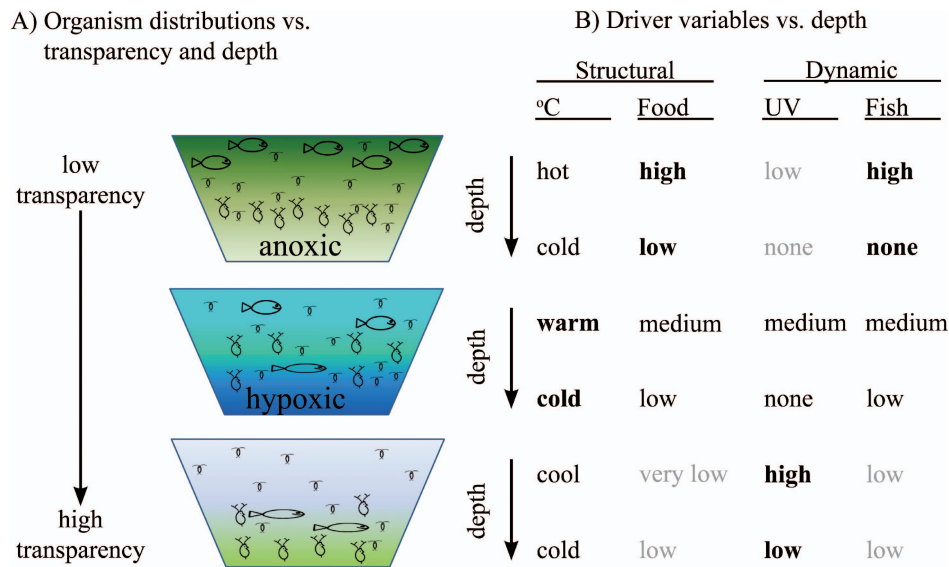


Fig. 1. (A) Conceptual diagram of the transparency-regulator hypothesis as it applies to *normal* DVM (migration up at night, down during the day) of primarily herbivorous zooplankton in lakes and some parts of the oceans. Shapes represent the daytime vertical distribution of the organisms, including warm-water (horizontal oval shape) and cold-water (more streamlined) fish, copepods (small, T-shape), and *Daphnia* (small, vertical oval with antennae). Green represents the general pattern of the vertical gradient in phytoplankton food concentration across lakes of differing transparency. Deep strata with low oxygen are also shown. (B) General patterns of the DVM drivers in shallow and deep waters of systems of differing transparency. Darker text indicates greater importance of a given variable in that type of system for *normal* DVM. In some parts of the oceans, more transparent waters are often warmer (e.g., the subtropical oligotrophic gyres), so the temperature profiles in this conceptual diagram would be reversed relative to the transparency gradient.

proximate cues vs. the ultimate adaptive significance of DVM. The two concepts are not mutually exclusive. The utility of the structural vs. dynamic approach is that it permits a clear separation of individual drivers into those that are relatively static over a 24-h period vs. those that show strong differences between day and night. In contrast, any single driver may involve both proximate cues and have ultimate adaptive significance (Table 1). For example, predation may involve important ultimate consequences for the prey in terms of increased mortality and involve proximate cues, such as kairomones, that induce behavioral responses, with no ultimate consequences of the kairomones themselves for the prey. Here we focus on “normal” downward migrations of primarily herbivorous holoplanktonic invertebrates (zooplankton) during the day in the open waters of the world’s lakes and oceans. Although not covered explicitly here, many of the basic concepts developed may be relevant to reverse migrations upward during the day; to migrations of phytoplankton, ichthyoplankton, and meroplanktonic invertebrates, and to more complex aspects of DVM, such as benthic-pelagic coupling and position maintenance in estuarine and coastal upwelling systems.

When the transparency-regulator hypothesis is applied to these more complex and diverse DVM systems, some variables may shift from being a structural driver for one organism or system to a dynamic driver for another organism or system. For example, food is most likely to be a structural driver for herbivorous zooplankton but a dynamic driver for ichthyoplankton or large invertebrates that feed on highly mobile zooplankton. Food may also be a dynamic driver for zooplankton feeding on food species that exhibit reverse, “cascading” DVM, such as dinoflagellates (Bollens et al. 2010). Similarly, while temperature is most frequently a structural driver, in intertidal estuaries temperature may switch to being a dynamic driver under some circumstances. The important point is to identify the functional role of each variable being considered in a given system to determine whether it is a structural driver that creates a vertical habitat gradient that influences vertical distribution or a more dynamic driver that varies over a 24-h period that can potentially drive vertical migrations. We conclude this synthesis by discussing how climate and other environmental changes are altering the transparency of natural waters and how the transparency-regulator hypothesis can be used to predict how DVM patterns will respond to these environmental changes.

A brief history of DVM theory

One of the earliest drivers proposed to explain DVM of both freshwater and marine zooplankton was the damaging effects of sunlight (Moore 1912; Huntsman 1924; Kikuchi 1930). Sunlight was proposed as both an important proximate cue that induced negative phototaxis and an ultimate factor for which DVM had a clear adaptive advantage because negative phototaxis led to downward migration of zooplankton during the day and hence reduction in exposure to potentially damaging short-wavelength solar radiation.

In subsequent years, strong evidence has accumulated for an important role of predation in driving zooplankton DVM. The first experimental evidence for the importance of predators came from studies of Gatun Lake in Panama and Fuller Pond in Connecticut (Zaret and Suffern 1976). Subsequent experiments that manipulated predators revealed that during the day, zooplankton migrate downward in the water column to avoid visual predators (Stich and Lampert 1981; Bollens and Frost 1991a; Neill 1992). Field data on zooplankton DVM in lakes in Vermont (Williamson and Magnien 1982) and in the Tatra Mountains of Poland (Gliwicz 1986) demonstrated that the presence of planktivorous fish increases the magnitude of DVM in the cyclopoid copepods *Mesocyclops edax* and *Cyclops abyssorum*, respectively. Similarly, the vertical distribution of the large calanoid copepod *Heterocope* during the day was found to be deeper in lakes and ponds with fish than those without fish (Luecke and O’Brien 1981). Field studies in coastal marine systems have found that DVM in a range of calanoid copepods is related to the abundance of zooplanktivorous fishes (Bollens and Frost 1989b; Bollens et al. 1992, 1993). Perhaps the most compelling evidence for the role of predators in DVM is the fact that zooplankton alter their vertical distribution in the water column in response to kairomones—chemicals released by both tactile and visually feeding predators (Dodson 1988; Neill 1990; Lass and Spaak 2003a). Predator-mediated mechanical or visual cues can also play a role in eliciting DVM in zooplankton (Bollens et al. 1994, 1995).

Food availability has also been found to be an important structural variable that influences the DVM response of zooplankton to visual predation. Experiments in a lake in Norway that added food to the surface waters of field mesocosms revealed that when food was scarce, *Daphnia* remained in the surface waters and did not migrate downward (Johnsen and Jakobsen 1987). This is consistent with prior studies that have shown that *Daphnia* are more positively phototactic when they are starved (Clarke 1932; Calaban and Makarewicz 1982).

Marine studies have similarly found that the amplitude of DVM is reduced when food densities are low (Huntley and Brooks 1982; Dagg 1985). Other experiments in both freshwater and marine systems have also demonstrated the important interaction between food as a structural variable and predators as a dynamic driver regulating zooplankton DVM (Leibold 1990; Bollens 1996). These and many other studies have led to the widespread belief that zooplankton DVM is controlled primarily by biotic factors such that zooplankton migrate down in the water column during the day to avoid visual predators and return to the food-rich surface waters at night to feed (Hays 2003; van Gool and Ringelberg 2003; Yoshida et al. 2004).

As evidence was growing for the importance of food limitation and predation in driving DVM, evidence was also increasing for the importance of damaging solar radiation in determining the daytime vertical distribution of zooplankton. Short wavelengths of UV in sunlight can damage DNA, membranes, and a variety of other biochemicals and can lead to high mortality rates of zooplankton that remain in the surface waters of high-

transparency systems for even a few days or less (Williamson et al. 1994a, 1999; Rautio and Tartarotti 2010). A central focus of many earlier studies was the relationship between pigmentation, photoprotection, and the vertical distribution of zooplankton. Although variations in carotenoid concentrations in zooplankton were found to be related to dietary availability (Ringelberg 1980, 1981; Moeller et al. 2005) and possibly temperature regulation (Byron 1981, 1982), extensive evidence accumulated on the important photoprotective function of carotenoids in copepods and melanin in cladocerans. In freshwater zooplankton, higher mortality of pale vs. pigmented individuals exposed to damaging wavelengths of light has been demonstrated for carotenoids in *Diatomus nevadensis* (Hairston 1976), *Heterocope septentrionalis* (Luecke and O'Brien 1981), *Acanthodiatomus denticornis* (Ringelberg et al. 1984), and *Leptodiatomus minutus* (Moeller et al. 2005) as well as for melanin in *Daphnia pulex obtusa* (Siebeck 1978), *Daphnia middendorffiana* (Luecke and O'Brien 1983), *Daphnia pulex* (Hessen 1996), and the *Daphnia pulex* group (Hebert and Emery 1990). In both copepods and cladocerans, pale individuals exhibit stronger avoidance of damaging sunlight and are usually distributed more deeply in the water column than pigmented individuals (Hairston 1979; Luecke and O'Brien 1981; Hebert and Emery 1990). The generally larger size and greater pigmentation of zooplankton in lakes without vs. with fish provides compelling evidence for the importance of visual predation yet simultaneously suggests that DVM alone is not adequate to reduce visual predation to unimportant levels. One of the more interesting aspects of these studies is the trade-off between high pigment concentrations that protect from photodamage and the tendency for these pigments to increase susceptibility of zooplankton to visual predators (Hairston 1979; Hansson 2000; Johnsen and Widder 2001). Zooplankton seem to be able to balance the conflicting selective pressures of visual predation and photodamage with a combination of photoprotection and DVM, though the extent to which these mechanisms are used may vary among zooplankton taxa (Hansson et al. 2007; Hylander et al. 2009). Some marine invertebrates are able to alter their color over even very short time intervals by modifying chromophore size or other mechanisms (Miner et al. 2000). The fact that some deep-dwelling marine copepods tend to be darker in color during the night than during the day suggests that avoidance of visual predation is a more likely explanation than photodamage (Vestheim and Kaartvedt 2006). Both the deep-dwelling nature of these copepods (mostly deeper than 100 m) and the darker color at night support this explanation. Yet there is also evidence that chromophore expansion does not necessarily enhance visual predation in other marine invertebrates (Morgan and Christy 1996), perhaps because chromophores also serve other functions, such as thermoregulation (Miner et al. 2000). In any case, such diel changes in pigmentation are an important consideration in examining trade-offs between visual predation and UV damage.

It was only after the discovery of the Antarctic ozone hole in the mid-1980s (Farman et al. 1985) that concerns about increasing levels of damaging UV shifted interest to

more extensive investigations of the role of UV in zooplankton DVM. The availability of new submersible UV radiometers was also critical to enabling these new studies. Although several lines of evidence have demonstrated that UV plays an important role in zooplankton DVM, these studies have yet to be fully integrated into DVM theory. In aquatic studies, UV is most commonly divided into the shortest, most damaging wavelength UV-B (280–320 nm) and the longer wavelength UV-A (320–400 nm; Williamson and Neale 2009). UV-A generally penetrates to about twice the depth of the more damaging UV-B wavelengths, though in the clearest of lakes, UV-A can penetrate as far as visible light (Rose et al. 2009b; Williamson and Neale 2009; Williamson and Rose 2010). Of key importance are the widespread observations that UV can penetrate to biologically significant depths in many marine waters (Tedetti and Sempéré 2006) as well as more transparent inland waters, including boreal lakes (Scully and Lean 1994), temperate glacial lakes in the northern and southern hemispheres (Morris et al. 1995), alpine lakes (Laurion et al. 1997; Rose et al. 2009a), Antarctic lakes (Vincent et al. 1998), and lakes in New Zealand (Rae et al. 2001) and Japan (Vincent et al. 2001).

Another key element has been the discovery of UV photoreceptors in the widespread freshwater cladoceran *Daphnia magna* with peak sensitivity in the UV-A at 348 nm (Smith and Macagno 1990). More recent laboratory studies with monochromatic light carefully adjusted for intensity among treatments revealed that *D. magna* was negatively phototactic to UV with the strongest response between 300 and 400 nm (340-nm peak) and positively phototactic to 420–600-nm visible light (Storz and Paul 1998). As discussed above, however, starvation can reverse phototactic responses in *Daphnia*. Earlier work had shown that early-instar larvae of the predatory freshwater midge *Chaoborus* were differentially phototactic to UV and visible light, but the patterns were opposite those of *Daphnia* with a positive phototaxis to UV (350–400 nm) and a negative phototaxis to visible light (440–690 nm; LaRow 1971). In this same study, late-instar *Chaoborus* larvae were observed to be negatively phototactic to all wavelengths tested (365–730 nm). More recent experiments have revealed a greater negative phototaxis of late-instar *Chaoborus punctipennis* to visible light than to UV-A (Persaud et al. 2003).

Laboratory behavioral experiments have also demonstrated pronounced differences in the behavioral responses of zooplankton to UV. For example, while the freshwater cladoceran *Daphnia* often exhibits a strong UV avoidance response, this is often not true for freshwater and some marine copepods that may even be attracted to UV. Experiments in 0.5–1-m-deep columns that manipulated UV under both artificial and natural solar light sources showed that UV stimulates a downward migration in several species of *Daphnia* (Hessen 1994; Rhode et al. 2001). On the other hand, the copepod *Cyclops serrulatus* shows only a slight (statistically untested) preference for visible light over UV-B (Barcelo and Calkins 1979). Similarly, only one of four coastal marine copepods tested showed any significant phototaxis: *Calanopia americana* exhibited a positive phototaxis to both visible and longer

wavelength UV-A, with a slightly stronger positive response to the visible wavelengths (Cohen and Forward 2002). Both nauplii and females of the marine copepod *Calanus finmarchicus* are negatively phototactic to UV, with nauplii responding more to UV-B and adults to UV-A (Wold and Norrbin 2004). Other marine copepod species showed variable responses to UV-B in vertical tank experiments—*Tortanus dextrilobatus* altered its vertical distribution in response to UV-B, whereas *Acartiura* spp. and *Acanthacartia* spp. showed no response (Speckmann et al. 2000). The intertidal copepod *Tigriopus californicus* is also able to detect UV-B radiation (Martin et al. 2000). Interestingly, the marine copepods *Acartia* spp. and *Pseudocalanus minutus* have been shown to exhibit positive phototaxis to short wavelengths of UV (280 nm) that are potentially very damaging (Martynova and Gordeeva 2010). The stronger UV avoidance of cladocerans vs. copepods may be related to the generally greater UV tolerance of copepods (Leech and Williamson 2000; Kessler et al. 2008).

A variety of other marine crustacean zooplankton have also been shown to respond to UV. Krill kept in 1.5-m vertical tanks responded to increased surface UV-A irradiance by increasing their depth but did not respond to UV-B (Newman et al. 2003). Even some mesopelagic zooplankton species have been reported to be responsive to UV despite their occupying daytime depths of several hundred meters or more (Frank and Case 1988; Frank and Widder 1994a,b). While caution must be observed in extrapolating laboratory phototaxis experiments to the field (Forward 1988; Ringelberg 1999), these observations indicate a clear behavioral response to UV and are not what one would expect if the visible light necessary for fish predation were the only driver of downward migrations of zooplankton during the day.

Field experiments in lakes generally support the laboratory experiments and the greater UV avoidance response in *Daphnia* than in copepods. For example, the first in situ DVM experiments manipulating solar UV were carried out with *Daphnia catawba* in 1.5-m-long vertical columns in a lake and showed that *D. catawba* migrated deeper in the presence of UV than in the absence of UV (Leech and Williamson 2001). In subsequent in situ experiments of a similar design in two lakes of differing transparency, UV stimulated a stronger downward migration in *D. catawba* than in diatomid copepods or the cyclopoid copepod *Cyclops scutifer* in the more transparent lake, while no response to UV was observed in any of the zooplankton in the less transparent lake (Leech et al. 2005a). In longer-term field experiments in 8-m-deep mesocosms that were either exposed to or shielded from UV, *D. catawba* showed a significant downward migration in response to UV, while the copepod *L. minutus* was more deeply distributed during day than at night but did not show a significant response to UV (Fischer et al. 2006). Similarly, manipulation of UV in 3-m-deep field enclosures revealed no significant change in the daytime vertical distribution of the marine copepod *Acartia hudsonica* (Bollens and Frost 1990).

Patterns of vertical distribution of zooplankton in field surveys also support the importance of UV in driving

zooplankton DVM, with again a stronger relationship for *Daphnia* than for copepods. An analysis of the depth distribution of zooplankton relative to seasonal and among-lake differences in UV levels in three lakes of differing transparency over 3 yr found stronger responses in *Daphnia* than in either cyclopoid or calanoid copepods (Leech et al. 2005b). This is the only study that we know of to date that also attempts to look at the relationship between (modeled) UV transparency and DVM by comparing the proportion of zooplankton that are present in the epilimnion during the day vs. during the night in three lakes of differing transparency at different times of the year. Species of zooplankton such as *Daphnia* that are less UV tolerant exhibited the strongest response to UV, and responses were much stronger in the lake with the highest UV transparency, consistent with UV driving DVM. A similar study that examined zooplankton vertical distribution in three Argentinean lakes of differing transparency revealed that the avoidance of the surface waters by zooplankton was also stronger in the more transparent lakes (Alonso et al. 2004). These patterns are difficult to explain using the visual predation hypothesis alone because in both studies planktivorous fish were less abundant in the more transparent lakes. Similarly, in two study lakes in the Tatra Mountains of Poland, both *Daphnia* and *C. abyssorum* exhibited significant downward migrations in a lake where salmonids had been stocked, while only *Daphnia* migrated down in a lake where there were no fish (Gliwicz 1986, 2003). A more recent survey of seven subalpine and alpine lakes in the Beartooth Mountains of Montana–Wyoming related the daytime peak distribution of several zooplankton species to UV and photosynthetically active radiation (PAR) transparency as well as the depth of the chlorophyll maximum (Kessler et al. 2008). The working hypothesis was that the relationships with PAR would be greater if visual predation by fish were the primary variable determining daytime vertical distribution, while the relationships with UV would be stronger if UV damage were the dominant variable. UV consistently explained a greater portion of the variance in the vertical distribution of *Daphnia* spp., *Holopedium gibberum*, and cyclopoid copepods than did either PAR or chlorophyll, while the more UV-tolerant calanoid copepods showed no relationship with UV, PAR, or chlorophyll. Other field studies have shown that nonmigrating *Daphnia* that remain in the surface waters exposed to UV may be more UV tolerant than those that migrate (Siebeck and Bohm 1994). Together, these field studies indicate that zooplankton in transparent waters employ a variety of strategies, including DVM, to reduce UV damage.

Temperature is also a critically important factor that can influence DVM. In contrast to UV, which is highly dynamic over a diel time scale, temperature is a structural driver that does not vary significantly between day and night. The demographic advantage for zooplankton that spend more time in the warmer surface waters of stratified systems has long been recognized: warmer temperatures in the surface waters induce higher growth and reproduction (Orcutt and Porter 1983; Stich and Lampert 1984; Leibold

1989). A combination of this demographic advantage and the fact that food quality is often suboptimal in the surface waters in fact makes temperature likely to be more important than food in creating a vertical habitat structure that leads zooplankton to migrate into the surface waters at night in some systems (Williamson et al. 1996a; Winder et al. 2003a; DeMott et al. 2004). The importance of temperature is apparent from experiments with experimental in situ columns incubated at three depths in a transparent lake. Both *D. catawba* and *L. minutus* showed a stronger avoidance of deeper depths at night when the columns were placed in cooler deeper waters than when the columns were placed in warmer metalimnetic or epilimnetic waters (Cooke et al. 2008). Laboratory experiments that carefully controlled for directional phototaxis and temperature-dependent changes in water density have shown that *D. magna* avoid migrating into colder-water strata (Calaban and Makarewicz 1982). Other laboratory experiments in a “plankton organ” (1-m-tall tubes) and larger-scale experiments in 11.5-m-tall plankton towers have demonstrated the importance of vertical temperature gradients; *Daphnia* were more likely to be distributed in the warmer surface waters rather than in food-rich deeper strata when there is a stronger vertical thermal gradient (Kessler 2004; Kessler and Lampert 2004b). In these experiments, the *Daphnia* showed strong differences in vertical distribution in response to the manipulation of the temperature gradients but had relatively similar vertical distributions during the day and night. This supports the strong role of temperature as a structural driver that influences vertical distribution rather than a dynamic driver that influences DVM.

The adaptive significance of zooplankton response to temperature is also apparent from several field studies. For example, experimental manipulation of both food and temperature combined with examination of field distributions of *Daphnia* in a suite of lakes demonstrated that temperature had more important life history consequences for zooplankton than food concentrations (Loose and Dawidowicz 1994). This study also estimated birth rate reduction due to differences in food to be always less than 10%, while that for temperature was generally 40–60% or more when comparing day vs. night depth distributions of *Daphnia* across six lakes. More recent studies have demonstrated that the demographic disadvantage to zooplankton that spend time at deeper depths with cooler waters may actually be similar to or greater than the lethal effects of predation (Pangle and Peacor 2006; Pangle et al. 2007). In oceanic surface waters, the relative importance of temperature on the one hand vs. food quantity and quality on the other hand in influencing zooplankton vertical distribution is less clear, although food quantity and quality can be more highly stratified (layered) than temperature in oceanic surface waters (Napp et al. 1988a,b).

Given this brief history of some of the DVM studies that are most relevant to the role of UV transparency in DVM, we next provide a critical examination of how the relative importance of two primary structural drivers (temperature and food) and two primary dynamic drivers (UV and visual

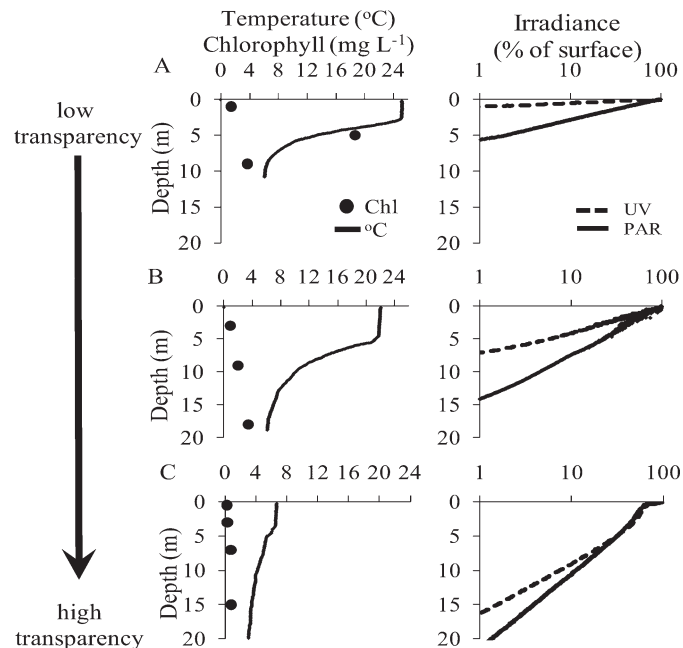


Fig. 2. Vertical profiles of temperature, food (chlorophyll), UV-A (380 nm), and PAR (400–700 nm) in three lakes of differing transparency. Note the steeper thermal gradients, higher concentration, and shallower distribution of food and more rapid attenuation of both UV-A and PAR with decreasing lake transparency. UV-A penetrates much deeper in both an absolute sense and relative to PAR with increasing lake transparency. In the low-transparency lake, the chlorophyll maximum is in the metalimnion rather than in the surface waters. In very low-transparency lakes where the 1% PAR depth does not reach below the epilimnion, chlorophyll would likely be maximal in the surface waters. Data are from two forested temperate lakes in northeastern Pennsylvania: (A) Lake Lacawac and (B) Lake Giles on 15 July 2010 and (C) alpine Lake Oesa in the Canadian Rocky Mountains, Alberta, Canada, on 28 July 2008. Chlorophyll data are from acetone-methanol extracts courtesy of Robert Moeller and Kevin Rose.

predation) are likely to vary in their influence on DVM across transparency gradients. We do this by posing four questions.

(1) *How do vertical temperature gradients vary across waters of differing transparency?*—Temperature is an important proximate and ultimate factor that structures the vertical habitat and can influence the amplitude of migrations, but it is not an actual dynamic driver of the diel migrations themselves. In most aquatic ecosystems, variation in temperature with depth is much stronger than variation over a diel cycle. Water transparency regulates the attenuation of sunlight in the water column and thus the nature of these vertical temperature gradients. This is particularly true in small lakes and ponds less than about 500 ha (Fee et al. 1996; Snucins and Gunn 2000). Increased water transparency tends to result in deeper surface mixed layers and more gradual changes in temperature with depth (Fig. 2). In larger lakes as well as in open oceans with greater fetch, however, wind plays a more important role in regulating thermal gradients, and surface mixed layers are

likely to be deeper. Because the incident sunlight has a greater volume of water to heat in systems with deeper mixing depths, larger water bodies are also likely to have cooler surface waters and more gradual thermal gradients that are similar to more transparent smaller lakes (Fig. 2). As discussed above, these more gradual thermal gradients are likely to decrease the importance of temperature as a structural variable in DVM because the difference in the demographic advantage of staying in warmer vs. cooler waters is lower when temperatures in the surface and deeper strata are more similar, and animals have to vertically migrate further to realize any given change in temperature. In estuarine and coastal waters, the situation is more complicated in that freshwater runoff can influence salinity stratification, which can have direct effects on zooplankton vertical distribution (Lougee et al. 2002) as well as indirect effects on mixed layer depths and thus vertical temperature gradients.

(2) *How do vertical gradients of food quantity and quality vary across waters of differing transparency?*—One of the central assumptions of the biotically based DVM theory is that food is best in the surface waters of lakes and oceans and that zooplankton migrate into the surface waters at night to feed on these high levels of food. There are several lines of evidence that indicate that in many systems—and particularly in more transparent water bodies—food is better in quality and quantity deeper in the water column. It has long been recognized that many lakes (Kiefer et al. 1972; Fee 1976) and oceans (Venrick et al. 1973; Cullen 1982; Estrada et al. 1993) are characterized by a deep-water chlorophyll maximum (DCM) wherein chlorophyll concentrations, a proxy for food availability for herbivores, are much higher in deeper waters than in surface waters. More recently a survey of 36 time points throughout the summer (June, July, and August) over a 5-yr period in three lakes that varied in their transparency revealed that the depth of the chlorophyll maximum was deeper in lakes with greater water transparency (Williamson et al. 1996a). The chlorophyll maximum was found in the epilimnion 23% of the time in the least transparent lake, 6% of the time in the lake with intermediate transparency, and never in the epilimnion of the most transparent lake. While a portion of the chlorophyll-depth patterns is due to physiological responses that lead to more chlorophyll per unit biomass at lower light levels, experimental evidence also supports the hypothesis that food quality is higher in the deeper strata (Williamson et al. 1996a; Winder et al. 2003a; but see Cole et al. 2002).

Water transparency affects the vertical distribution of algal food resources for zooplankton through effects on PAR and UV. In less transparent systems, phytoplankton productivity will be more constrained to the top few meters of the water column because of light limitation (PAR) and reduced UV photoinhibition (Vincent et al. 1984; Moeller 1994; Neale et al. 1998). In highly transparent waters, a combination of photoinhibition by UV in the top few meters and the deeper penetration of PAR will enable phytoplankton growth over a much broader and deeper depth range. Thus, vertical gradients in food are generally

weaker and peak food densities more deeply distributed in more transparent systems.

Stoichiometric arguments based on light and nutrient levels indicate that while increases in light at low irradiance levels may increase phytoplankton biomass and thus zooplankton growth, high light levels may reduce the nutritional quality of phytoplankton for higher trophic levels (Urabe and Sterner 1996; Dickman et al. 2008). Two important consequences of this are that more transparent lakes have lower food quality (higher carbon:phosphorus [C:P]) in the surface waters (Sterner et al. 1997) and that the food in the DCM is likely to be of higher nutritional quality than that in the surface waters (Rothhaupt 1991). A comparison of food quality across lakes of differing transparency showed that both oligotrophic and eutrophic lakes have lower seston C:P ratios (higher food quality) in deeper waters, and that the pattern is stronger in more oligotrophic lakes (DeMott et al. 2004). This same study also showed higher particulate carbon concentrations in the deeper waters of both types of lakes, higher edible chlorophyll in the deeper waters of the eutrophic lake, and similar edible chlorophyll across all depths in the oligotrophic lake. Heterotrophic microbial communities that often peak at deeper depths (Bennett et al. 1990) also have lower C:P and C:N ratios and thus higher stoichiometric food quality than phytoplankton (Hessen and Andersen 1990). Similarly, higher food quality was also found in deeper layers in the Southern California Bight (Napp et al. 1988b). In highly transparent lakes, lower food quality (higher C:P ratios) in surface waters may also reduce antioxidant enzyme activity critical for defending against damaging UV, potentially increasing susceptibility of *Daphnia* to UV damage and possibly even excluding them from more transparent high C:P lakes (Balseiro et al. 2008).

Studies that have fed zooplankton with seston collected from epilimnetic and deeper waters in controlled experiments frequently reveal equal or higher growth and reproductive rates on the food from deeper waters (Williamson et al. 1996a; Winder et al. 2003a; DeMott et al. 2004). In some cases, the depth of optimal food quality may vary seasonally (Hoenicke and Goldman 1987), and in others, food quality may actually be better in the surface waters (Cole et al. 2002). Experimental studies in plankton towers have also clearly demonstrated the ability of *Daphnia* to locate, remain in, and feed on DCM (Lampert and Grey 2003; Kessler and Lampert 2004a). Some species of marine zooplankton vertically collocate with maxima in their phytoplankton food, while others do not (Dagg et al. 1989; Pierson et al. 2005; Rollwagen-Bollens et al. 2006). So-called thin layers of phytoplankton in the ocean (Cowles et al. 1998; Boisdansky and Bollens 2009; Sullivan et al. 2010) are a type of DCM within which marine zooplankton have been shown to aggregate (Clay et al. 2004; Ignoffo et al. 2005) or visit for short-term feeding bouts (Boisdansky and Bollens 2004; Boisdansky et al. 2010).

In summary, the core assumption of the biotic theory of DVM that food is best in the surface waters is not likely to be valid in many lakes or in all parts of the ocean. This is particularly true in more oligotrophic transparent systems

where a DCM appears to be the norm (Kiefer et al. 1972; Sommaruga 2001; Saros et al. 2005). Furthermore, at least some species of zooplankton are able to detect these deeper food optima and spend more time at these depths.

(3) *Does UV penetrate deep enough to drive observed zooplankton DVM?*—The growing evidence that UV is important to the vertical distribution and migration of zooplankton combined with the well-established importance of food and predators argues for the need to combine these abiotic and biotic factors into a more comprehensive theory of zooplankton DVM. Before considering UV more thoroughly as a dynamic driver of zooplankton DVM, however, one important question that needs to be addressed is whether UV penetrates deep enough to account for observed zooplankton DVM patterns. There are three components to this question: (1) How deep do zooplankton migrate? (2) How deep does UV penetrate? (3) What levels of UV can zooplankton detect? Information exists on the first two of these components, but there is essentially no information on the third. While the ideal would be to have data on UV attenuation and migration amplitudes in the same systems, these data do not currently exist.

Zooplankton migrations are highly variable in their amplitude, ranging from less than a meter to several tens of meters in lakes and even hundreds of meters in some oceans. The most comprehensive assessment of the magnitude of zooplankton migrations in lakes is that of G. E. Hutchinson, who reviews the DVM patterns of numerous cladocerans and copepods from lakes around the world (Hutchinson 1967). Hutchinson's work showed that while the maximum daytime depth to which the majority of the species migrated is less than 10 m, there are several species, including *Daphnia*, that migrate to depths of 50 m or more and one species of copepod that was shown to migrate to depths of over 75 m in Lake Lucerne. A more recent study of the relationship between the amplitude of *Daphnia* DVM and Secchi transparency summarizes data from 25 DVM instances in 16 different lakes (Dodson 1990). This study found a strong relationship between the amplitude of migration and water transparency. In all cases, the migration amplitudes were less than 12 m, and in 19 of the 25 cases, the migration amplitudes were 6 m or less. In the coastal ocean, copepods often exhibit DVM with amplitudes ranging between 10 and 100 m (Bollens and Frost 1989b; Bollens et al. 1993; Frost 2005). In shallow marine lagoons, amplitude can be as small as only a few meters (Bollens and Frost 1989a; Bollens et al. 1992), whereas zooplankton in the open oligotrophic ocean can traverse distances of several hundred meters during their migrations (Sardou et al. 1996; Steinberg et al. 2008).

Data on the UV transparency of the world's lakes and oceans have increased in recent years. Estimates of UV transparency derived from dissolved organic carbon (DOC) data revealed that the depth (Z) to which 1% of 380-nm UV-A penetrates ($Z_{1\%380\text{nm}}$) is less than 2 m for at least 75% of lakes in 13 of 16 regions studied (Williamson et al. 1996b). However, the 75th percentile for $Z_{1\%380\text{nm}}$ depths exceeded 10 m in three regions (western United States, the

Cascades of the northwestern United States, and Newfoundland, Canada). Incident UV levels increase by as much as 10–20% per 1000-m elevation depending on the wavelength (Blumthaler et al. 1997). Corresponding reductions in DOC with increasing elevation make alpine lakes some of the highest UV exposure environments on Earth. For example, in a survey of 22 alpine lakes from different regions of the world, the $Z_{1\%380\text{nm}}$ averaged 15 m and ranged as deep as 78 m, while the $Z_{1\%380\text{nm}}$ values in nearby less transparent subalpine lakes averaged 4.3 m and ranged as deep as 11.8 m (Rose et al. 2009a). In some of the world's most transparent waters, studies based on the diffuse attenuation coefficients (K_d) in surface waters and the assumption that water transparency is constant across depths suggest that UV-A may penetrate to depths approaching 100 m or more. For example, these estimates suggest that $Z_{1\%380\text{nm}}$ may reach as deep as 98 m in Lake Tahoe, California and Nevada (Rose et al. 2009b); over 100 m in Crater Lake, Oregon (Hargreaves et al. 2007); and to 200 m in Lake Vanda, Antarctica (Vincent et al. 1998).

UV transparency also varies greatly in marine waters, especially in relation to colored dissolved organic matter concentration. Estimates of $Z_{1\%310\text{nm}}$ irradiance for coastal waters are most often less than 6 m but can exceed 10 m, whereas $Z_{1\%340\text{nm}}$ for the open ocean most often exceeds 20 m and has been recorded up to 90 m (Tedetti and Sempéré 2006). In North European coastal waters, UV penetration ($Z_{1\%380\text{nm}}$) ranged between 2.4 and 26 m (Aas and Højerslev 2001), whereas off the coast of Chile, $Z_{1\%380\text{nm}}$ penetrated 32–51 m during the austral winter (Montecino and Pizarro 1995). Deeper waters are often less transparent than shallow waters because of photobleaching in the surface waters, so these depths are upper limits in cases where diffuse attenuation coefficients were not estimated over the entire depth range. Biologically damaging UV-B has been detected at depths of 20–30 m in the oceans with DNA repair-deficient *Escherichia coli* or similar dosimeters (Karentz and Lutze 1990). The wavelengths of UV-A that zooplankton respond to with negative phototaxis may penetrate twice the distance of these DNA-damaging wavelengths (Storz and Paul 1998; Rose et al. 2009a,b).

Collectively, these data suggest that the UV transparency of many lakes and oceans is likely adequate to drive DVM to depths of only a few meters. This was clearly the thinking of many early prominent investigators who stated that “the lethal ultra-violet light is rapidly absorbed and would not affect the *Calanus* in deep water” (Marshall and Orr 1955), echoed by others as that “solar radiation has in the past been denied as an ultimate cause of vertical migration on the basis that ultraviolet light does not penetrate more than two meters into water” (Hairston 1976) and that “protection from UV-light damage would not require deep migrations, as UV is absorbed in the uppermost water column” (Lampert 1989). Yet in many of the clearer lakes and oceans of the world, the UV-A wavelengths to which zooplankton respond can penetrate to depths of tens to over 100 m and may thus be involved in driving DVM with much greater amplitudes than just a few meters.

One important consideration is that PAR is not likely to be an effective cue for UV across transparency gradients. Dissolved organic carbon, one of the major factors controlling variation in transparency in aquatic ecosystems, selectively absorbs shorter-wavelength UV. Thus, even the UV-A : UV-B ratio can vary by more than 1000 times over a change in DOC of just a few milligrams per liter (Williamson et al. 2001a). Given that the PAR : UV-B ratio is likely to vary even more than the UV-A : UV-B ratio over these transparency gradients, PAR would not be a good proxy to respond to in order to effectively avoid damaging UV.

(4) *How does predation risk from fish vary across waters of differing transparency?*—The second central assumption of the biotic theory of DVM is that zooplankton migrate down in the water column during the day to avoid visual predation. The potency of visual predators in altering zooplankton communities across a wide variety of lakes has been repeatedly demonstrated since the pioneering work published in the 1960s (Hrbáček 1962; Brooks and Dodson 1965). Evidence for the importance of visual predation in driving DVM also comes from the fact that visual predators are size selective and that smaller, less conspicuous zooplankton often migrate less than large zooplankton (Bollens and Frost 1991b; Gonzalez and Tessier 1997; Thys and Hoffmann 2005). Similarly, there is no question about the effectiveness of DVM in reducing predation risk in more productive, less transparent lakes where fish are abundant and a refuge from visual predators exists between an upper (shallow depth) boundary of low temperature or moderate hypoxia (3 mg L^{-1}) that excludes or at least minimizes the abundance of visual predators and a deep boundary of low oxygen (1 mg L^{-1}) that constrains zooplankton (Wright and Shapiro 1990; Tessier and Welser 1991; Klumb et al. 2004). Seasonally, as this refuge disappears, *Daphnia* populations decline even though food resources and reproductive rates are sustained. Perhaps even more important, except for a brief period in early spring, the depth at which visible light can serve as a potential refuge from visual predation may be so deep that oxygen levels are too low for *Daphnia* to survive (Wright and Shapiro 1990). While some predatory zooplankton such as *M. edax* and larval *Chaoborus* can migrate into anoxic strata (Williamson and Magnien 1982), this tolerance of anoxia has not been reported for *Daphnia* or other primarily herbivorous species. In highly transparent lakes and shallow coastal marine systems, the resident cold-water fish species are likely to be found deeper in the water column, and adequate light for visual predation may penetrate near or actually to the bottom such that a dark refuge from visual predation does not even exist for migrating zooplankton.

Here we discuss how the selective pressures associated with visual predation by planktivorous fish and the effectiveness of zooplankton DVM as a predator avoidance strategy change across aquatic ecosystems of differing transparency. We describe three main mechanisms through which changes in water transparency across lakes and oceans can alter the effects of planktivorous fish on

zooplankton DVM: changes in (1) fish density and kairomone concentration, (2) species composition and vertical distribution, and (3) reactive distance.

Fish density—Fish densities tend to be lower in more transparent waters. In both freshwater (Downing et al. 1990; Jeppesen et al. 1999; Karlsson et al. 2009) and marine (Ryther 1969; Iverson 1990) systems, transparent oligotrophic waters are known to have much lower abundances of fishes than less transparent, eutrophic waters. These lower densities of fish may also reduce the concentrations of kairomones, the infochemicals that often induce DVM (Dodson 1988; Tollrain and Harvell 1999; Lass and Spaak 2003a). The question that we ask here is whether results of studies in systems with higher productivity and lower transparency can be extended to more transparent oligotrophic lakes and oceans where fish production and species composition may be markedly different. To address this question, we conducted a literature survey in Web of Science focused on the effect of fish kairomones on DVM. We limited the review to studies where data on fish size and density were presented.

We found that the effectiveness of kairomones in stimulating DVM clearly depends on their concentration (Loose and Dawidowicz 1994; von Elert and Pohnert 2000; van Gool and Ringelberg 2002). The fish density needed to stimulate zooplankton DVM ranged from somewhat less than 1 fish m^{-3} up to 200 fish m^{-3} with a median of 16 fish m^{-3} (Table 2), and several authors raised concerns about the realism of kairomone concentrations in some of these studies (Dodson 1988; Leibold 1990; von Elert and Pohnert 2000). On the other hand, a few in situ studies have revealed that much lower fish densities were effective at inducing DVM (Bollens and Frost 1989b; Neill 1992), although the former authors acknowledged not sampling juvenile and deeper-dwelling fish. In addition, one elegant study conducted using water collected from a mesotrophic lake in the Netherlands demonstrated a strong correlation between the DVM response of *Daphnia* and natural seasonal changes in biomass of young-of-year (YOY) perch (van Gool and Ringelberg 2002). In this study, a standard clone of *Daphnia* exhibited a strong DVM response to lake water collected early in the summer when YOY perch biomass was high but was unresponsive to water collected later in the summer when YOY biomass had declined.

The high densities of fish needed to produce enough kairomones to induce DVM in most studies suggests that fish densities in more transparent oligotrophic or less productive dystrophic systems may not be adequate to induce DVM. While schooling fish may lead to much higher densities in local areas, the fact that kairomones last for only a few hours (Dodson 1988) makes it unlikely that adequate kairomone concentrations will accumulate to any great extent over time unless schools stay in the same location. In addition, the combination of cold temperatures and high UV in more transparent lakes may reduce kairomone concentration even further through temperature-dependent effects on kairomone production (Lass and Spaak 2003b) and UV-mediated kairomone degradation

Table 2. Minimum fish densities necessary to elicit DVM responses in zooplankton from the literature studies where adequate information was given to make this estimation.

Zooplankton type	Fish type (size)	Lab (L) or field (F)	Minimum fish density eliciting migration (fish m ⁻³)	Reference
Copepods	2 cyprinids (5 cm)	L	10–200	Loose and Dawidowicz (1994)
Daphnia	2 cyprinids	L	25	von Elert and Pohnert (2000)
Daphnia	Cyprinids (5 cm)	L	0.63	Loose (1993)
Daphnia, copepods	2 trout (6–7 cm)	F	0.2	Neill (1992)
Daphnia	Juvenile perch (5 cm) Perch larvae	F, L	1 (juvenile), 8000+ (larvae)	van Gool and Ringelberg (2002)
Daphnia	1 perch (4 cm)	L	200	van Gool and Ringelberg (1998)
Daphnia	1 bluegill (2.5 cm)	L	37	Dodson (1988)
Daphnia	1 bluegill (6–6.5 cm)	F	0.12	Leibold (1990)
Daphnia	2 cyprinids (5 cm)	L	25	Boersma et al. (1998)
Daphnia	1 bluegill (12 cm)	L	200	Brewer et al. (1999)
Daphnia	4 cyprinids	L	4	Pohnert and von Elert (2000)
Copepods	Natural assemblage	F	0.00186	Bollens and Frost (1989b)
Copepods	9 stickleback	L	3.5	Bollens and Frost (1989a)
Daphnia	2 cyprinids (8 cm)	L	10	De Meester (1996)
Daphnia	1 perch (4 cm)	L	70	van Gool and Ringelberg (1997)
Daphnia	1 perch (4 cm)	L	15	Ringelberg and van Gool (1998)

(Sterr and Sommaruga 2008). The effects of temperature on kairomone degradation, however, are not known.

The persistence of DVM in lakes without any fish predators also argues for the importance of factors other than visual predators in driving the downward migration of zooplankton. In recently deglaciated lakes in Glacier Bay, Alaska, both cladocerans and copepods exhibited DVM in several lakes without fish (Williamson et al. 2001b). In shallow, fishless subarctic ponds, *Daphnia longispina* shows stronger vertical migration downward during sunny days than on cloudy days (Rautio et al. 2003). In two lakes in the Tatra Mountains of Poland, one with and one without fish, *Daphnia* exhibited DVM in the lake without fish, albeit with a lower DVM amplitude than the lake with fish. At night, the peak *Daphnia* densities were in the top 10 m in both lakes. During the day, *Daphnia* population densities peaked at 10–20 m in the lake with no fish and at depths of 30–40 m in the lake that had been stocked with salmonids (Gliwicz 2003). In these same lakes, however, the cyclopoid copepod *C. abyssorum* showed DVM only in the lake that had fish (Gliwicz 1986). This is consistent with the generally greater DVM response to damaging UV of *Daphnia* compared to copepods as discussed above. In tropical high-elevation lakes in the Andes of Bolivia, *D. pulex* also showed DVM in lakes without fish (Aguilera et al. 2006). In a fishless high-elevation lake in the southern Andes in Argentina, the calanoid copepod *Boeckella gibossa* also exhibited deeper distributions during the day than at night (Marinone et al. 2006). Moreover, some species of marine zooplankton, such as the marine copepod *Metridia lucens*, always undertake DVM, even in the face of large seasonal and interannual variability in visual predators (Bollens et al. 1993).

The results of fish introductions to alpine lakes lend further support to the idea that DVM is unlikely to be an effective strategy to avoid fish predation in highly transparent lakes. For example, the introduction of

salmonids has been shown to lead to the disappearance of the larger zooplankton species in the Canadian Rockies (Parker et al. 1996, 2001; McNaught et al. 1999) and the Sierra Nevada of eastern California (Knapp et al. 2001; Sarnelle and Knapp 2004). In other transparent alpine lakes, the low densities and more benthic feeding habits of some salmonids may lead fish predation to be of little importance to *Daphnia* population dynamics or DVM (Winder et al. 2003b). In contrast, in a shallow (4-m maximum depth), eutrophic, highly turbid lake with anoxic deep waters, fish introduction led to the elimination of both *Daphnia* and a diaptomid copepod, while the cyclopoid *M. edax*, which can tolerate periods of anoxia and thus use an anoxic refuge from fish predation, showed no change in abundance but did start exhibiting a strong pattern of DVM (Williamson and Magnien 1982).

Fish species composition and vertical distribution—In addition to the generally lower planktivorous fish densities in more transparent systems, fish species composition and vertical distribution also change in ways that are likely to decrease the importance of visual predation in driving zooplankton DVM in these systems. In lakes, for example, as water transparency increases and lake productivity decreases across trophic gradients, increased light penetration leads to more well-oxygenated deep waters and a shift from warm-water fishes, such as bluegill and yellow perch, to cold-water fishes, such as salmonids (Helminen et al. 2000; Olin et al. 2002; Mehner et al. 2005). Many warm-water and cold-water fish are piscivorous but have planktivorous early life history stages that feed visually. Because cold-water species are not excluded from feeding in (or may even prefer to feed in) colder, deeper waters, predation pressure on zooplankton may actually increase with depth in more transparent lakes. One example of this comes from a yearlong study of zooplankton DVM in three cold-water Patagonian lakes in Argentina where the native

planktivorous galaxid fish larvae were generally most abundant in the deepest strata of the lakes (Alonso et al. 2004). In contrast, cold-water fish species are typically absent from more productive, less transparent lakes where hypolimnetic waters often lack oxygen. In these lakes, warm-water fish species dominate and are constrained to feeding in the surface waters. The hypoxic deeper waters may actually act as an important refuge for zooplankton from fish predation (Hanazato et al. 1989; Wright and Shapiro 1990; Tessier and Welser 1991) as well as visually feeding invertebrate predators, such as *Bythotrephes* (Manca et al. 2007; Manca and DeMott 2009).

In oceans, the more transparent systems are generally associated with warmer, open-ocean, low-latitude habitats, such as subtropical gyres, and therefore, in contrast to freshwater systems, are usually populated by warm-water fish species. These more transparent marine systems do have lower abundances of planktivorous fish that may reside deeper to avoid visual predation by larger piscivorous fish. Hypoxia may also play a role in affecting DVM in some shallow coastal areas, especially those suffering from eutrophication, such as the Gulf of Mexico and the Chesapeake Bay (Kimmel et al. 2009; Pierson et al. 2009). However, in deeper, offshore ocean waters where subsurface suboxic conditions occur (e.g., oxygen minimum or “dead zones”), a suppression in zooplankton DVM has more often been observed (Smith et al. 1998; Mincks et al. 2000; Liljebadh and Thomasson 2001). These hypoxic zones are also often areas of lower transparency caused by increased particle accumulation or reduced particle degradation.

Reactive distance—The reactive distance of visually feeding planktivorous fish can be defined as the maximum distance from which a predator can recognize a prey item (Confer and Blades 1975; Eggers 1977). The light dependence of reactive distance will cause reactive distance to generally increase with increasing water transparency (Utne-Palm 2002; Quesenberry et al. 2007; Chesney 2008), perhaps offsetting to some extent reduced predation rates due to the lower concentrations of fish. The mechanism is an increase in the potential encounter sphere of each individual fish. Planktivorous fish tend to maximize foraging by moving to areas that provide sufficient light for visual feeding (Masson et al. 2001; Gjelland et al. 2009). Fish can position themselves vertically in the water column based on light intensity and may remain at levels that exceed the 10^{-3} lux levels required for foraging (Bohl 1980). In eutrophic systems where light penetration is low, turbidity decreases the reactive distance of fish predators (Vinyard and O'Brien 1976; Sweka and Hartman 2003), potentially allowing zooplankton to reduce visual predation through migration to deeper waters. While the effectiveness of an optical refuge from visual predators has been hypothesized as discussed above, it has not been convincingly demonstrated. Nevertheless, the combination of higher fish densities and a more effective optical refuge in deeper waters may make DVM a more effective defense against visual predators in less transparent systems.

Some studies suggest that the effectiveness of this optical refuge in deeper waters may decrease with increasing water transparency. For instance, one model indicates that increasing water transparency by decreasing the diffuse attenuation coefficient from 0.11 to 0.07 m^{-1} could increase the feeding rate of visually feeding fish at a depth of 125 m by a factor of 150 (Aksnes and Giske 1993). Although these modeling efforts suggest that many transparent systems provide sufficient light for fish to forage at depths that exceed the migration depth of zooplankton, fish often do not exploit these environments. For example, in a deep, transparent lake in France, planktivorous YOY perch were concentrated in the epilimnion or nearshore regions, while the zooplankton (cladocerans and cyclopoids) were found at depths of 10–20 m or more during the day (Masson et al. 2001). Similarly, in Crater Lake, the light level required for kokanee foraging was adequate to a depth of 150 m. However, kokanee were concentrated at a mean daytime depth of 50–74 m, while cladocerans were most dense between 80 and 120 m (Buktenica et al. 2007). These relationships can be complicated by the fact that planktivorous fish can also migrate to avoid piscivorous predators (Scheuerell and Schindler 2003) and yet may themselves derive a demographic advantage by spending time in the warmer surface waters at certain times during the day (Wurtsbaugh and Neverman 1988). Overall, changes in fish density, species composition, and vertical distribution across transparency and productivity gradients suggest that avoidance of visually feeding predators in the surface waters is less likely to be an important dynamic driver of DVM in more transparent lakes and oceans. However, these effects could be somewhat offset by greater reactive distances of visual predators in more transparent systems.

Caveats and missing links

One of the important caveats for understanding DVM in freshwater systems is the overemphasis of past studies on *Daphnia*. This is warranted to some extent by the importance of *Daphnia* in pelagic ecosystems in inland waters (Pace 1984; Carpenter et al. 1998; Sarnelle 2005), yet other species are likely to be responsive to different selective pressures. For example, in a series of in situ experimental studies in a lake in Pennsylvania, *D. catawba* responded more strongly to UV than to fish kairomones, while the reverse was true for *L. minutus* (Leech et al. 2009). Smaller species, such as rotifers, will also tend to be less susceptible to visual predators because of their small size. Similarly, while we know that several species of *Daphnia* exhibit a negative phototaxis to UV and a positive phototaxis to visible light, very little is known about the spectral sensitivity of the many other species of zooplankton in freshwater and marine water. The attraction of some copepods and other zooplankton to damaging wavelengths remains unexplained. Even within a single species, clonal variation in phototactic responses is widely recognized (De Meester 1993, 1994).

While we focused here on spatial transparency gradients among different water bodies, in many if not most lakes

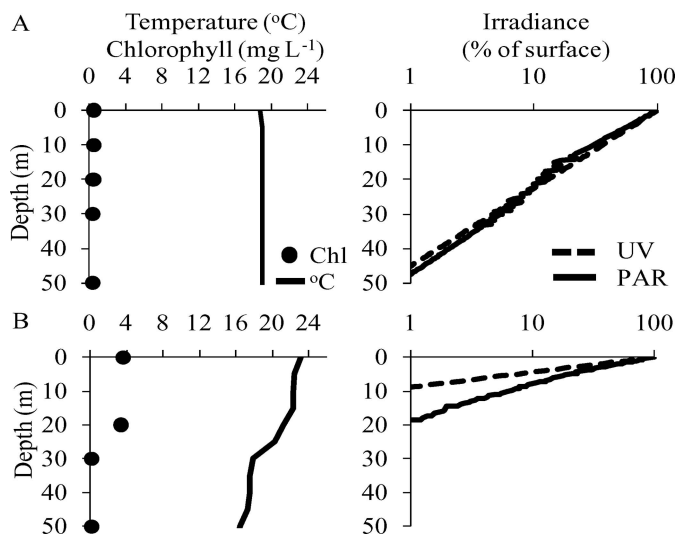


Fig. 3. In freshwater and marine systems, both structural and dynamic drivers that influence DVM of herbivorous zooplankton (and other organisms) are likely to show strong variations across seasons as illustrated by these data from the Pacific Ocean off the coast of Japan (35°10'N latitude). (A) Note the lack of any strong vertical gradients in temperature and food as well as high and similar water transparencies to UV-A and PAR in December and (B) the higher food concentrations and lower and more divergent water transparencies to UV-A vs. PAR in July. Modified from Kuwahara et al. (2000) with permission.

and oceans seasonal transparency gradients are also important (Fig. 3). Perhaps the best known and most widely studied phenological event in lakes is the clear-water phase, which can involve pronounced increases in both visible (Lampert et al. 1986; Sommer et al. 1986) and UV (Sommaruga and Augustin 2006; Williamson et al. 2007; Rose et al. 2009b) transparency during the spring to summer months. In freshwater lakes, the amplitude of DVM increases with increasing water transparency (Dodson 1990). While seasonal variation in zooplankton DVM has long been recognized (Hutchinson 1967), the relationship between transparency and DVM on a seasonal basis has not often been explored. In marine systems, the amplitude of zooplankton DVM has been shown to vary seasonally with illumination (Falkenhaug et al. 1997; Takahashi et al. 2009) but not necessarily with transparency per se (Bollens and Frost 1989b; Bollens et al. 1992). In addition, there can also be strong seasonal variation in visual predation pressures due to changes in temperature or production of YOY fish in both marine (Bollens and Frost 1989b; Bollens et al. 1992) and freshwater (van Gool and Ringelberg 2002) systems. This is particularly important given that UV may enhance the feeding ability of YOY fish (Leech et al. 2009). These seasonal shifts in predation pressure across seasonal transparency gradients may or may not parallel those observed across water bodies of differing transparency.

There are still some fundamental missing links in understanding the role of UV in driving DVM. One is that although there is evidence that daytime vertical distributions of zooplankton are related to UV transparency across

a range of lakes of differing transparency (Alonso et al. 2004; Leech et al. 2005b; Kessler et al. 2008), there are no studies to date that have examined the relationship between UV transparency and amplitude of DVM. The other is the lack of knowledge on what levels of UV zooplankton can detect. For example, if zooplankton are able to detect and respond to UV levels that are 0.1% of incident solar radiation, these depths are about twice as deep as the 1% attenuation depths (1% of surface irradiance) discussed above because light attenuates exponentially with depth. The inability of zooplankton to detect and avoid damaging levels of UV in surface waters on the other hand may lead to “solar ambush” (Williamson 1995), which may result in the elimination of UV sensitive species that do not have either high levels of photoprotection or photorepair. UV transparency and UV tolerance data for *Boeckella gracilipes* have been used to estimate that this copepod must migrate to a depth of at least 12 m to avoid damaging UV in an Argentine lake, Lago Moreno, East (Ringelberg 2010). For reference, previously published UV data from this same lake (Morris et al. 1995) give 1% attenuation depths of 8.8, 11.8, and 20.0 m for 320, 340, and 380 nm UV, respectively. As Ringelberg (2010) indicates, 50% mortality rates are not likely sustainable, and the LD₅₀ values do not consider sublethal effects of UV, so the 12-m UV depth refuge is likely an underestimate of how deep these copepods must migrate to avoid UV damage.

One of the more interesting yet almost totally unexplored aspects of light and DVM is the potential ability for habitat partitioning or predator avoidance based on differential responses of competitors or predators and their prey to different wavelengths of sunlight. For example, two of the major freshwater crustacean groups of plankton, Daphniids and Diaptomid copepods, exhibit different responses to UV radiation. Daphniids exhibit a negative phototaxis to UV and a positive phototaxis to visible light (Storz and Paul 1998) that leads them to occur deeper in the water column during the day than Diaptomid copepods, which often exhibit little or no avoidance of UV radiation (Leech et al. 2005a). DOC strongly alters the UV:visible light ratio (Williamson et al. 2001a) such that the extent of this habitat partitioning may vary greatly across lakes or over time. This may in part explain the patterns of variation in the relative abundance of copepods and cladocerans that have classically been observed among lakes of differing productivity (McNaught 1975). In terms of predator avoidance, *Daphnia* is prey to the larvae of the phantom midge *Chaoborus*, and predator avoidance may at least in part explain the positive phototaxis of *Daphnia* to visible light, while *Chaoborus* has a generally negative phototaxis to all wavelengths.

Clearly, there are often important trade-offs among dynamic drivers of DVM across transparency gradients. For example, photoprotective compounds such as carotenoids and melanin are highly effective defenses against damaging sunlight, but they also increase susceptibility to visual predation (Johnsen and Widder 2001; Hansson et al. 2007; Hylander et al. 2009). Zooplankton are not limited to just a single type of response to these threats but rather respond with more than one defense at the same time,

balancing these selective pressures between predation and UV damage (Hansson et al. 2007; Hansson and Hylander 2009). In marine systems, the effect of climate change drivers on zooplankton dynamics may be stronger when fish predation is low (Stige et al. 2009), again suggesting the importance of interactive effects.

Another example of important interactive effects of predation and UV is reverse migrations by smaller zooplankton into the surface waters during the day to avoid tactile predators (Neill 1990; Frost and Bollens 1992; Lagergren et al. 2008). These migrations would tend to expose smaller zooplankton to higher levels of damaging UV in more transparent lakes. The evidence to date suggests that at least some smaller species that are found in surface waters tend to be more UV tolerant (Williamson et al. 1994b; Leech and Williamson 2000; Leech et al. 2005b). In addition, the concentration of photoprotective compounds is often higher in more UV-transparent lakes (Tartarotti et al. 2004) and in smaller, juvenile zooplankton than in adults (Tartarotti and Sommaruga 2006). Experimental *in situ* tests that manipulated tactile predators and UV demonstrated the importance of these conflicting selective pressures: in the presence of both predators and UV zooplankton adopted an intermediate depth distribution (Boeing et al. 2004). In shallow Arctic ponds with no visual predators, *Daphnia* were found to migrate down on sunny days in apparent response to high light but upward during cloudy days in response to the predator *Chaoborus* (Rautio et al. 2003).

Interactive effects of predation and UV are likely to be different for zooplankton of different trophic levels. While our review is focused on herbivorous zooplankton, it is worth noting that migrations that occur at one trophic level can affect the opposite (or out-of-phase) vertical migration of the next lower trophic level and so on throughout the food web (i.e., “cascading migrations,” *sensu* Bollens et al. 2010). Such out-of-phase migrations would allow a normally migrating zooplankton (residing at depth during the day) to avoid both predation and UV, while its reverse migrating prey (residing at the surface during the day) may face severe trade-offs between avoiding predation and experiencing increased exposure to UV.

Implications

The transparency-regulator hypothesis provides a broad conceptual framework for zooplankton DVM that enables us to more clearly distinguish the functional importance of structural vs. dynamic drivers across transparency gradients (Fig. 1). In both marine and freshwater systems, variations in water transparency create fundamental differences in both the structural (vertical habitat gradient) and the dynamic drivers of DVM. More transparent systems often have greater food availability in deeper waters because of a deeper compensation depth and lower food quality in surface waters because of higher light:nutrient ratios in comparison to deeper waters. This suggests that food is not a likely reason for zooplankton to migrate into the surface waters at night in clear-water lakes and oligotrophic oceans, as is suggested by the

currently prevalent biotic DVM paradigm. The absorption of sunlight over a broader range of depths in more transparent systems will also alter the structure of the vertical habitat gradient by creating more gradual thermal gradients that reduce the demographic costs of spending time in the deeper, cooler strata vs. in the surface waters. The dynamic drivers of DVM in more transparent systems are likely to include higher levels of potentially damaging UV in the surface waters, a reduction in the abundance of visually feeding planktivores in the surface waters, and increases in the depth to which visible light penetrates. Collectively, these patterns lead to a greater importance of UV relative to visual predation as a dynamic driver of DVM in more transparent systems.

In order for DVM to be induced and have some adaptive significance, dynamic drivers must create selective pressures at different depths in the water column that oppose selective pressures of structural or other dynamic drivers. However, structural drivers alone that create opposing selective pressures in the water column are not adequate to induce DVM. For example, in highly transparent systems that are largely fishless and relatively isothermal with a DCM (common in many subalpine, alpine, and polar lakes), there may be no selective advantage to migrating into the surface waters. Instead, zooplankton may seek a single optimum depth that balances structural drivers such as temperature and food. Similarly, if food concentrations are relatively uniform in the water column and temperature is optimal in the surface waters of a transparent system with few or no visual predators, the magnitude of DVM in response to UV is likely to be less than that in response to visual predation both because of the ability of zooplankton to develop photoprotective pigments and because UV generally does not penetrate as far as visible light. In his original 1990 paper, Dodson recognized that *Daphnia* exhibited a reduced DVM amplitude in transparent lakes when they had few fish (Dodson 1990). In less transparent lakes, oxygen depletion may also block migrations of many species to deeper depths, also reducing the amplitude of DVM.

Longer-term trends of change in transparency related to climate change or other natural or human disturbances may lead to pronounced changes in DVM. In fact, DVM may be one of the best biotic sentinels of the effects of climate change on aquatic ecosystem structure and function (Williamson et al. 2009). Climate warming is increasing the strength and duration of thermal stratification in lakes (Jankowski et al. 2006) and oceans (Palacios et al. 2004; Boyce et al. 2010), leading to shallower mixing depths, reductions in oceanic primary productivity, and greater oxygen depletion in deeper waters that may in turn alter food web dynamics and lead to major regime shifts (Beaugrand et al. 2008). DVM can be highly responsive to climate-driven changes in aquatic ecosystems (De Stasio et al. 1993; Kimmel et al. 2009; Pierson et al. 2009). Other consequences of these changes in vertical habitat gradients and their subsequent effects on DVM include alteration of the overlap between predators and their prey (Williamson and Stoeckel 1990), parasite–host dynamics and rates of parasitism (Caceres et

al. 2009), and DVM-mediated vertical biogeochemical fluxes (Bollens et al. 2010).

Many lakes and rivers in the northeastern United States and parts of Europe have also shown strong changes in dissolved organic carbon (DOC) concentrations over the past 15–20 yr (Findlay 2005; Evans et al. 2006; Monteith et al. 2007). In some systems, DOC concentrations have as much as doubled over this time period, while in other systems they have decreased. Since UV transparency is much more heavily influenced by changes in DOC than is visible light transparency (Morris et al. 1995; Laurion et al. 1997; Rose et al. 2009a), increases in DOC will selectively decrease the importance of UV relative to visual predation as a regulator of DVM in UV-transparent lakes. In regions where DOC concentrations are decreasing, UV may become a relatively more important driver. Changes in DOC may also alter the structural drivers of DVM because DOC concentration influences thermal gradients in lakes (Fee et al. 1996; Gunn et al. 2001) as well as the compensation depth and thus the vertical distribution of food resources.

Many inland and coastal systems are also experiencing eutrophication, which may alter both structural drivers of DVM such as oxygen refugia and dynamic drivers, including both UV and visual predator abundance and depth distribution. Increases in harmful algal blooms (HAB) in inland and coastal waters, due largely to enhanced nutrient inputs (Rabalais et al. 2007; Heisler et al. 2008; Lopez et al. 2008), will also alter the quality, quantity, and vertical distribution of zooplankton food resources and hence the structure of vertical habitat gradients for DVM. In contrast to the increased incidence of HAB in coastal and inland waters, in 8 out of 10 regions of the world's open oceans, climate-driven changes in vertical stratification appear to have led to reductions in chlorophyll concentrations and increases in water transparency (Boyce et al. 2010). The transparency-regulator hypothesis provides a potentially valuable framework to interpret how these important changes in transparency influence the structural and dynamic drivers of zooplankton DVM. Further studies of zooplankton DVM conducted across transparency gradients in lakes and oceans will advance our understanding of overlap between consumers and their resources, predators, and parasites as well as the subsequent consequences for food web dynamics and vertical biogeochemical fluxes.

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