Visual Predation during Springtime Foraging of the North Atlantic Right Whale (*Eubalaena glacialis*)

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ABSTRACT

To assess the role that vision plays in the ability of the North Atlantic right whale (*Eubalaena glacialis*) to detect its primary prey species, the calanoid copepod *Calanus finmarchicus*, we have compared the absorbance spectrum of the *E. glacialis* rod visual pigment, the transmittance spectra of *C. finmarchicus* carotenoid pigments, as well as the downwelling irradiance and horizontal radiance spectra collected during springtime at three locations in the western Gulf of Maine. The *E. glacialis* rod visual pigment absorbs light maximally at 493 nm, while microspectrophotometric measurements of the *C. finmarchicus* carotenoid pigments reveal transmission spectra with minima matching very well with the *E. glacialis* rod visual pigment absorbance spectra maximum. Springtime spectral downwelling irradiance and horizontal radiance values from the surface waters of Cape Cod Bay and at all depths in Great South Channel overlap the *E. glacialis* rod absorbance spectrum, allowing *C. finmarchicus* to appear as a high-contrast dark silhouette against a bright background space-light, thus facilitating visually-guided contrast foraging. In contrast, spectral downwelling irradiance and horizontal radiance at depth in Cape Cod Bay, and all depths in Wilkinson Basin, do not overlap the *E. glacialis* rod absorbance spectrum, providing little if any useful light for contrast vision.

Key Words: *Eubalaena glacialis*, Vision, Foraging Ecology, *Calinus finmarchicus*, downwelling irradiance spectrum, horizontal radiance spectrum

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is a critically endangered species with an estimated population size of 524 individuals (Pettis and Hamilton 2016). In order to provide strong conservation efforts for this species and reduce by-catch events, it is important to understand the sensory systems by which these animals perceive and interact with their environment. The purpose of the current project was to describe the visual foraging ecology of the right whale. The study required knowledge of three key components that underlie visual foraging: 1) the spectral sensitivity of the right whale retina, 2) the spectral transmission of prey items, and 3) the background spacelight against which the detection of this prey occurs.

In general, the underwater photic environment strongly influences the evolution of spectral sensitivity of the photoreceptors in aquatic animals: the wavelength of maximum absorbance (λ_{max}) of the rod photoreceptor lies near the peak radiance of the ambient light (Lythgoe and Dartnall 1970, McFarland 1971, Lythgoe and Partridge 1989). Previous studies have shown that the rod visual pigments of cetaceans and pinnipeds have a much wider range in the λ_{max} values of their rod visual pigments than those of terrestrial mammals (Lythgoe and Dartnall 1970, McFarland 1971, Fasick *et al*. 1998, Fasick and Robinson 2000, Bischoff *et al*. 2012). Unlike terrestrial mammals, whose rod visual pigments generally absorb maximally around 500 nm, marine mammals have rod pigments with absorption maxima that range from 479 to 505 nm (Lythgoe and Dartnall 1970, McFarland 1971, Lavigne and Ronald 1975, Piggens *et al*. 1983) with decreasing λ_{max} values being associated with increasing depths of foraging. Recently, the rod visual pigment from the North Atlantic right whale has been cloned, sequenced, and expressed *in vitro*, allowing its absorption spectrum to be measured. Bischoff *et al*. (2012) found that the right whale rod visual pigment possesses a λ_{max} of 493 nm, thus lying between the marine odontocete rod pigments, which have absorbance maxima between 478-486 nm and terrestrial vertebrate rod pigments, most of which absorb maximally near 500 nm. The right whale's rod visual pigment is similar to that of other coastal mysticete whales, such as the grey whale (*Eschrichtius robustus*; λ_{max}=496.6 nm, McFarland 1971) and the humpback whale (*Megaptera novaeangliae*; λ_{max}=492 nm (Dartnall 1962). Because the Balaenidae whales are rod monochromats (Meredith *et al*. 2013, Schweikert *et al*. 2016), the spectral sensitivity of the rod visual pigment also describes the spectral sensitivity of the retina as a whole.

The life history of *C. finmarchicus*, the primary prey species of the North Atlantic right whale, has been thoroughly reviewed (Baumgartner *et al*. 2007). Like many zooplankton, *C. finmarchicus* exhibits diel vertical migration, or the tendency to migrate into surface waters at dusk and below the euphotic zone at dawn, although notable exceptions to this basic behavior have been observed (Baumgartner *et al*. 2011). *C. finmarchicus* possesses regions of red carotenoid pigments (Fig. 1) whose functions are unknown. While they may confer photoprotection in shallow marine waters (Hairston 1976), they greatly increase visibility of the animals to predators with blue-sensitive visual receptors. The prevalence of surface aggregations of late-stage C5 copepods during spring often coincide with high abundances of phytoplankton which are restricted to well-lit, near surface waters. After spring, most *C. finmarchicus* enter a hibernation state called diapause and are typically found at depth, although some remain in surface waters where they molt into adults and reproduce.

During winter, right whales occur in calving grounds off the coastal southeastern United States, in a migratory corridor throughout the mid-Atlantic, and in the Gulf of Maine. Right whales visit Cape Cod Bay in the Gulf of Maine during winter to feed primarily on *Pseudocalanus* species and other small copepods both at the surface and at depth; during early spring, they transition to feeding on late-stage *C. finmarchicus* in the near surface waters of Cape Cod Bay. From mid-spring to early summer, right whales can be found in the Great South Channel just east of Cape Cod and Nantucket, Massachusetts. Right whales transition to eastern habitats in the summer, including the northern edge of Georges Bank, the Bay of Fundy, the Scotian Shelf, and even the Gulf of St. Lawrence (Winn *et al*. 1986, Kenney *et al*. 1995, Kenney *et al*. 2001). Foraging depths vary widely depending on location; for example, foraging dives in the Bay of Fundy during summer span 80-175 m (Baumgartner and Mate 2003) while surface feeding is most often observed in Cape Cod Bay and the Great South Channel in late winter and spring (Watkins and Schevill 1979, Wishner *et al*. 1988, Mayo and Marx 1990, Kenney *et al*. 1995).

To maximize prey detection, marine predators have adopted a variety of sensory strategies including increasing photoreceptor density, enhancing photon capture with a tapetum, as well as overlapping the visual pigment spectral sensitivity to that of the radiance spectrum at foraging depths (Wartzok and Ketten 1999). Cetaceans typically have photoreceptors that have their greatest sensitivity near the wavelength of light that is best transmitted through the type of ocean water in which they forage (Munz 1965) which would be perceived by the animal as a bright background spacelight. Prey items whose spectral transmittance falls outside of the spectral sensitivity of the predator's photoreceptors would be silhouetted against this bright background. As seen in Figure 2 (top panel), a predator whose photoreceptor sensitivity (black trace) overlaps well with the transmission spectrum of the underwater light (blue trace) would easily be able to visually detect prey items whose transmission spectrum (red trace) was located outside of the sensitivity spectrum of the predator's photoreceptor by luminance contrast, in this case the perception of a dark object against a bright background in silhouette (Fig. 2; right whale perception). As the transmission spectrum of the underwater spacelight shifts away from the sensitivity spectrum of the predator's photoreceptors and nearer to the transmission spectrum of the prey, the ability to visually detect the prey item by silhouette diminishes as shown in the middle and bottom panels of Figure 2.

The current study attempts to describe the role that vision may play in utilizing the underwater photic environment for the detection of the whale's principal prey, *C. finmarchicus*. To accomplish this, we obtained the rod visual pigment absorbance spectrum of the right whale, the percent transmission spectrum of the North Atlantic right whale's primary prey species, *Calanus finmarchicus*, and finally the downwelling irradiance and horizontal radiance spectra at a range of depths at several locations in the western Gulf of Maine, an area in which right whales feed during the spring.

MATERIALS AND METHODS

Expression and Spectral Absorbance of the Eubalaena glacialis rod visual pigment. The right whale (*Eubalaena glacialis*) rod visual pigment was expressed as in Bischoff *et al* (2012). The *E. glacialis* rod opsin coding region was cloned into the pMT3 expression vector (Franke *et al*. 1988) and transiently transfected into COS-1 cells (Nickle *et al*. 2006). COS-1 cells expressing opsin were resuspended in phosphate buffered saline (PBS) and incubated with 40 μM 11-*cis* retinal. Cells were solubilized in 1% (w/v) n-Dodecyl-β-D-maltoside (DDM, Calbiochem, San Diego, CA) PBS, samples were centrifuged at 4000 x g for 10 minutes, and supernatant was added to 1D4-antibody bound Sepharose beads. Pigment was eluted using 50 μM of a peptide corresponding to the last 9 amino acids of bovine rod opsin's C-terminal tail (sequence: TETSQVAPA) in 0.02% DDM PBS. Spectral analysis was performed using a

Hitachi U-3210 dual-beam spectrophotometer that was modified by the manufacturer for use in a darkroom. Templates designed for visual pigments with a retinal chromophore were used to determine λ_{max} values (Govardovskii *et al*. 2000).

In order to confirm the expressed pigment as a rod opsin, samples were incubated for 6 hrs in the presence of 50 mM hydroxylamine (pH 7.0) in the dark with absorbance spectra being recorded every 2 hrs after which the samples were photobleached with light.

Copepod Collection and Microspectrophotometry. Thirty to 50 late-stage *Calanus finmarchicus* were collected on May 18, 2010 in the Great South Channel (southwestern Gulf of Maine) at 69.64 W, 41.75 N in 148 m depth using a 70-cm diameter ring net equipped with a 150-µm mesh conical net hauled slowly from 20 m to the surface. Copepods were held overnight in an ice-chilled container and then transported overnight from Provincetown, Massachusetts to Baltimore, Maryland. Spectral analysis of the copepods was conducted within 48 hours of collection.

For spectral measurements, copepods were placed on a coverslip in a drop of seawater or mineral oil, compressed between coverslips and placed in the microspectrophotometer. Microspectrophotometry was performed using a single-beam instrument that obtains spectral data at 1-nm intervals from 400-700 nm (Cronin *et al*. 1994). Absorbance values were computed by comparing the amount of light passing through the red pigments in the copepods at each wavelength with the amount of light measured when the beam was placed in a clear area of the preparation devoid of copepods. Percent transmittance (T) values were generated from these absorbance values using the equation: $T = (10^{-Abs})*100\%$.

Radiance and irradiance measurements from Wilkinson Basin, Cape Cod Bay and the Great South Channel. Two deployments were conducted on April 4, 2012 from the R/V *Tioga*:

the first at a station in Wilkinson Basin 36 km northeast of Race Point (Provincetown), Massachusetts, and the second at a station 2 km northwest of Race Point at the entrance to Cape Cod Bay (Table 1). A third deployment was conducted the following year in the Great South Channel on May 9, 2013 from the NOAA Ship *Gordon Gunter* (Table 1). Cape Cod Bay and the Great South Channel are documented springtime feeding grounds for right whales (Mayo and Marx 1990, Kenney *et al*, 1995). Although right whales visit Wilkinson Basin (Baumgartner and Mate 2005), it is not thought to be a major feeding ground; we chose to study the underwater light field in Wilkinson Basin as a contrast to areas where right whales are known to feed. Conditions at all three stations were characterized by clear skies with no or thin cloud cover and calm seas. At each station, three replicate casts were conducted with a free-falling Profiler II instrument (Satlantic, Halifax, Nova Scotia) equipped with radiometers to measure spectral profiles of downwelling irradiance ($\mu W/cm^2/nm$, model HYPEROCR ICSW, Satlantic) and horizontal radiance ($\mu W/cm^2/nm/sr$, model HYPEROCR R08W, Satlantic). Horizontal radiance was collected to estimate the light field viewed in the forward direction by a right whale moving horizontally through the water, whereas the downwelling irradiance measures the amount of light reaching a particular depth integrated over the entire hemisphere above (note that the mammalian eye perceives radiance, *i.e.*, light from a particular direction, not irradiance). We use downwelling irradiance here as a proxy for the average of downward radiance as the shape of the downwelling irradiance spectrum will approximate the shape of the vertical radiance spectrum. During the casts, spectral profiles of skyward irradiance ($\mu W/cm^2/nm$) were simultaneously collected with a radiometer mounted on the ship's mast (model HYPEROCR ICSA, Satlantic). All of the radiometers periodically closed a shutter over the sensor, allowing the recording of a dark spectrum to provide a baseline. Underwater spectral data consisted of averaged spectra for

4-m depth bins from the surface to either the sea floor or to the maximum depth allowed by the profiler's tether (120 m). Both light and dark spectra were averaged over the indicated depth intervals as well as over the 3 replicate casts. Skyward irradiance spectra (light and dark) were averaged over time in 10-second intervals spanning the exact time that the Profiler II was in the water collecting both horizontal radiance and downwelling irradiance spectra.

At each depth, light and dark spectra were measured from 349-803 nm at ~3 nm resolution. To generate Figures 4-7, dark values at each wavelength were first subtracted from the corresponding light values and the resulting spectra were converted to photon units; *e.g.* for irradiance in photons/s/cm^2/nm and for radiance, photons/s/cm^2/nm/sr. Although it would seem that frequency, rather than wavelength, of light would be more fundamental to this study as the frequency of light does not depend on the medium the light is going through, *e.g*. the frequency of light does not change from air to water (Johnsen 2012). However, wavelength, rather than frequency, of light as measured in air is typically used in studies of visual ecology (Cronin *et al*. 2014) and we use wavelengths throughout this study.

RESULTS

Analyses of Visual and Carotenoid Pigments

The expression of the North Atlantic right whale (*Eubalaena glacialis*) rod visual pigment has been previously described (Bischoff *et al*. 2012). In our study, after opsin expression, reconstitution with 11-*cis* retinal and purification, the right whale rod visual pigment was found to have an absorbance maximum (λ_{max})= 493 nm (Fig. 3A), identical to the value reported by Bischoff *et al*. (2012). Hydroxylamine assays were performed to distinguish rod and cone opsins. The protein conformation of cone opsins, unlike rod opsins, allows the Schiff base to be easily accessible to hydroxylamine, resulting in rapid bleaching of dark adapted pigments (Wald *et al*. 1955, Fager and Fager 1981, Okano *et al*. 1989). Characteristic of rod opsins, the right whale rod pigment showed little susceptibility to bleaching in the presence of 50 mM hydroxylamine over a six hour time course (Fig. 3A insert). The λ_{max} of the right whale rod visual pigment was slightly blue-shifted (3 nm) from that of the more commonly studied bovine rhodopsin (λ_{max} = 496 nm, data not shown).

Microspectrophotometric measurements of freshly mounted individuals of *Calanus finmarchicus*, as shown in Figure 3B, produced generally similar results depending on the individual and region measured, possibly because of the mixture of carotenoid pigments in these animals, as has been found in *Calanus pacificus* (Juhl *et al*. 1996). The decreases in the transmittance minima shown in Figure 3B are associated with increases in carotenoid pigment density. The normalized average from the three calanoid carotenoid pigment transmittance spectra in Figure 3B is plotted in Figure 3C (red trace) revealing high transmittance at wavelengths greater than ~625 nm and very little transmittance between 450 and 475 nm. Plotted with the right whale rod visual pigment absorbance spectrum (Fig. 3C, black trace), it is evident that the calanoid carotenoid pigments transmit light in a region of the spectrum where the right whale rod visual pigment absorbs relatively little light. As described in Figure 2, light transmitted outside of the spectral range that the right whale is capable of detecting would appear dark against the background spacelight.

Subsurface Irradiance and Radiance Spectra at Wilkinson Basin, Cape Cod Bay and the Great South Channel

In order to define the backlight illumination that right whales could utilize to visualize prey during foraging, we examined both the downwelling spectral irradiance and the horizontal spectral radiance with depth in Wilkinson Basin and Cape Cod Bay in early spring, and the Great South Channel in mid-spring. The spectrum of irradiance and radiance present at any given subsurface depth is influenced by the angular position of the sun during daylight hours. Because the underwater light profile casts were made at different times of the day, we measured skyward spectral downwelling irradiance above the surface of the water during each cast to determine if changes in irradiance values based on time of day would impact the underwater light profiles. Figure 4A shows skyward irradiance spectra from Wilkinson Basin (blue trace), Cape Cod Bay (red trace) and the Great South Channel (green trace). The skyward spectral irradiance at Wilkinson Basin shows a value at 575 nm (the midpoint value of the scanned spectra) that is ~1.5x to 2x those of the equivalent irradiance values at the Great South Channel and Cape Cod Bay, respectively, due to the higher solar elevation at the former location (47° compared to 30.5° and 23°, respectively). When skyward irradiance was normalized by the solar elevation at each location (Fig. 4B), the three spectra agree well with each other, with slightly elevated values at Wilkinson Basin across most of the irradiance spectrum possibly due to less cloud cover at that location.

To understand the underwater photic environment utilized by right whales for visually guided foraging, we examined the downwelling irradiance and horizontal radiance at three different locations in the western Gulf of Maine in early and mid-spring. Data from Wilkinson Basin are shown in Figure 5. The depth at the Wilkinson Basin station was 209 m, however the length of the cable suspending the radiometer limited light profiling measurements to a maximum depth of 120 m. Both the downwelling irradiance (Fig. 5A) and horizontal radiance (Fig. 5B) at Wilkinson Basin were maximal near 569 nm where the instrument could detect enough light to record a signal: 0-44 m for downwelling irradiance measurements (Fig. 5A) and

0-40 m for horizontal radiance measurements (Fig. 5B). Downwelling irradiance ranged from 1.18 x 10^14 photons/s/cm^2/nm at 0-4 m to 7.18 x 10^9 photons/s/cm^2/nm at 40-44 m, a decrease of nearly five log units between these two depths when measured at 569 nm. Horizontal radiance ranged from 9.31x 10^11 photons/s/cm^2/nm/sr at 0-4 m to 6.09 x 10^8 photons/s/cm^2/nm/sr at 36-40 m, decreasing nearly 3 log units between these two depths when measured at 569 nm. The radiometer was insensitive to downwelling irradiance below 44 m and horizontal radiance below 40 m.

Data from Cape Cod Bay are shown in Figure 6. The depth at this station was 58 m, allowing measurements to be taken throughout the entire water column. Spectra from Cape Cod Bay were broader and more variable with increasing depth than at the other locations: downwelling irradiance maxima moved to longer wavelengths with depth (Fig. 6A); 0-24 m (549 nm), 24-44 m (563 nm) and 48-56 m (569 nm); and horizontal radiance followed a similar trend (Fig. 6B); 0-12 m (549 nm), 12-24 m (556 nm), 24-48 m (563 nm) and 48-52 m (569 nm). The radiometer was insensitive to downwelling irradiance below 48 m and horizontal radiance below 52 m. Compared to Wilkinson Basin (Fig. 5), the downwelling irradiance and horizontal radiance spectra from Cape Cod Bay were blue-shifted by ~20 nm near the surface (0-12 m) and gradually red-shift to maxima near 569 nm at 48 m. Downwelling irradiance at Cape Cod Bay ranged from 6.89 x 10^13 photons/s/cm^2/nm at 0-4 m (measured at 549 nm) to 3.96 x 10^9 photons/s/cm^2/nm at 44-48 m (measured at 563 nm), decreasing by a factor of 2.93 x 10^4 between these two depth bins, slightly less than that observed at Wilkinson Basin (4.62 x 10 ^4, 0-44 m) despite the greater range of depth measurements made at Cape Cod Bay. Horizontal radiance ranged from 4.43x 10^12 photons/s/cm^2/nm/sr at 0-4 m (measured at 549 nm) to 2.69x

10^8 photons/s/cm^2/nm/sr at 48-52 m (measured at 569 nm), decreasing by a factor of 1.74 x 10^4 between these two depth bins.

Light profiles from the Great South Channel are shown in Figure 7. The depth at this station was 84 m, allowing measurements to be taken throughout the entire water column. Unlike Wilkinson Basin and Cape Cod Bay, spectral maxima from the Great South Channel decreased in wavelength with depth and revealed two well defined peaks below 32 m: downwelling irradiance maxima (Fig. 7A); 0-24 m (556 nm), 24-40 m (546 nm) 40-52 (502, 539 nm), and 52-84 m (500, 533 nm); horizontal radiance maxima (Fig. 7B); 0-20 m (556 nm), 20-28 m (543 nm), 28-38 m (502, 539 nm) and 38-80 m (499,536 nm). When compared to the spectra from Wilkinson Basin (Fig. 5) and Cape Cod Bay (Fig. 6), the spectra from the Great South Channel were broader near the surface, with maxima near 555 nm, and gradually shifted to shorter wavelengths with depth. Interestingly, the spectra from the Great South Channel possessed unusual twin peaks below 32 m with the shorter wavelength peaks near 500 nm and the longer wavelength peaks near 535 nm. Downwelling irradiance at the Great South Channel ranged from 1.07 x 10^14 photons/s/cm^2/nm at 0-4 m (measured at 556 nm) to 2.94 x 10^10 photons/s/cm^2/nm at 80-84 m (measured 500 nm), decreasing by a factor of 7.76 x 10^3. This decrease is somewhat less than that observed over the measurable range at both Wilkinson Basin (4.62 x 10^4, 0-44 m) and Cape Cod Bay (2.93 x 10^4, 0-48 m), even though the measurement range at the Great Sound channel extended 40 m deeper (0-88m) than those made at either Cape Cod Bay or Wilkinson Basin. Horizontal radiance at the Great South Channel ranged from 4.43 x 10^12 photons/s/cm^2/nm/sr at 0-4 m (measured at 556 nm) to 6.34 x 10^8 photons/s/cm^2/nm/sr at 76-80 m (measured 499), decreasing by a factor of 3.8 x 10^4. Although this total decrease is greater than those reported at either Wilkinson Basin (3.22 x 10^3, 0-40 m) and Cape Cod Bay

(1.74 x 10^4, 0-52 m), the depth range covered at the Great South Channel was also much greater (0-80m) than measurements made at either Cape Cod Bay or Wilkinson Basin. Being both clearer and bluer, the waters of the Great South Channel (during the spring, at least) attenuated light less and most likely contained fewer particulates (particularly phytoplankton) and dissolved organic material ~~that~~ those of Wilkinson Basin and Cape Cod Bay.

Spectral comparisons of predator and prey pigments, and environmental light.

The right whale rod visual pigment is rather insensitive to the wavelengths transmitted by its primary prey, the calanoid copepod *C. finmarchicus*, as shown in Figure 3. To determine if the right whale visual pigment is spectrally positioned to adequately absorb the available subsurface light for contrast-based vision at foraging locations and depths during early and mid-spring, we compared normalized values of the pigment's absorbance spectrum to normalized prey percent transmittance, and plotted both with normalized horizontal radiance and downwelling irradiance spectra taken at the surface and the greatest recorded depth from the three sampling stations.

At the surface of Wilkinson Basin in early spring (0-4 m, Fig. 8A), the downwelling irradiance (blue trace) and horizontal radiance (yellow trace) spectra had similar maxima near 569 nm. However, the downwelling irradiance spectrum at the surface was somewhat broader than the corresponding horizontal radiance spectrum, so that the former overlapped the visual pigment absorbance spectrum over a greater spectral range presumably providing the whale with more light to visually contrast prey. In contrast, at depth both downwelling irradiance and horizontal radiance had similar spectral shapes and had little or no overlap with the visual pigment's absorbance spectrum (Fig. 8B) thus providing the whale little light to visually contrast prey.

In early spring, at the surface of Cape Cod Bay (0-4 m, Fig. 8C) both the downwelling irradiance and horizontal radiance spectra resemble the absorbance spectrum of the visual pigment. While these spectra were blue-shifted by a few nm from the corresponding spectra seen in Wilkinson Basin, both spectra at Cape Cod Bay were much broader than those from Wilkinson Basin, and overlapped very well with the right whale rod visual pigment absorbance spectrum. At depth, as was the case at Wilkinson Basin, both spectra at Cape Cod Bay were relatively narrow compared to the surface spectra, and maintained similar peak spectral values which were distinctly blue-shifted compared to those of Wilkinson Basin (Fig. 8D). Although these deeper spectra still overlap with the visual pigment absorbance spectrum, they do so to a lesser degree than at the surface.

In mid-spring, the downwelling irradiance at the surface of the Great South Channel (0-4 m, Fig. 8E) resembled that of Cape Cod Bay in early spring, and both had broad overlap with the visual pigment absorbance spectrum. The horizontal irradiance spectrum at the surface of the Great South Channel appeared to be intermediate between the corresponding surface values from Wilkinson Basin and Cape Cod Bay. An interesting spectral change in both downwelling irradiance and horizontal radiance was observed at depth (64-68m, Fig. 8F) in the Great South Channel with the appearance of two peaks around 500 nm and 530 nm. While the downwelling and horizontal light at this depth were much dimmer than at the surface, the shorter-wavelength peak was spectrally quite similar to the absorbance spectrum of the visual pigment when plotted in wavelength units.

DISCUSSION

We present here a study of the visual foraging ecology of the North Atlantic right whale (*Eubalaena glacialis*) by comparing the spectral placement of the right whale rod visual pigment absorbance spectrum with the spectra from subsurface light in three areas visited by right whales in the spring: Wilkinson Basin, Cape Cod Bay and the Great South Channel. Transmission spectra from the primary prey species of the North Atlantic right whale, *Calanus finmarchicus*, were also examined to assess the visibility of prey in the springtime waters of the western Gulf of Maine.

A recent study has determined that the right whale, as well as most other mysticete whales, is a rod monochromat, lacking cone photoreceptors altogether (Meredith *et al*. 2013). Because mammalian photoreceptors generally lack strong spectral filters, unlike some other vertebrates, we can estimate the spectral sensitivity of the right whale retina from the spectrum of the rod photoreceptor visual pigment. We confirmed the absorbance maximum (λ_{max}) of the right whale rod pigment to be 493 nm from an *in vitro* expressed, reconstituted and purified pigment. The spectrum of the right whale rod pigment is red-shifted compared to pelagic cetacean species' rod pigments (Ziphiidae: ~480 nm; Delphinidae & Balaenopteridae: λ_{max} ~484 nm; (Fasick and Robinson 2000, Bischoff *et al*. 2012), and is blue-shifted relative to typical terrestrial mammalian rod pigments (λ_{max} ~500 nm).

Absorbance spectra from the carotenoid pigments of *C. finmarchicus* were converted into percent transmission spectra to examine the spectrum of light transmitted by the primary prey species of the North Atlantic right whale. The carotenoid pigment spectra varied somewhat between individuals. There is evidence that some copepod species reduce their pigment concentrations when living in shallow water (Vestheim and Kaartvedt 2006), and in fact, many of the copepods collected for this study had relatively little pigmentation. Nevertheless, *C. finmarchicus* carotenoid pigments show absorbance profiles (not shown) that overlap very well with the absorbance spectrum of the right whale rod visual pigment.

Because the right whale probably does not focus on individual copepods while foraging, but rather on the densest prey patches available, the variable nature of carotenoid concentration between individuals is not very significant. Instead, the averaged transmittance or scattering of light from an entire patch is likely to be much more important for a visual predator. Because copepod patches are likely to be quite large, the individual variation in either carotenoid concentration or location within the patch would be irrelevant. Here, we observe that the averaged spectral transmittance of *C. finmarchicus* increases significantly at wavelengths >575 nm, placing this spectrum for all practical purposes outside of the spectral sensitivity range of the right whale retina. This spectral "mismatch" between predator spectral sensitivity and prey transmittance provides an opportunity for visualizing prey by its contrast with the background light. On this basis, then, it is to the advantage of the predator if its retina is spectrally tuned, or matched, to the spectrum of the background spacelight against which prey could be seen in contrast.

To learn more about the spectrum of light available to foraging right whales at various depths, we measured the downwelling irradiance and horizontal radiance values at three locations in the Gulf of Maine in early and mid-spring: Wilkinson Basin and Cape Cod Bay on ~~April 4, 2012~~ and the Great South Channel on ~~May 9, 2013~~. The observed spectral changes in subsurface light occurring during either early or mid-spring are undoubtedly related to phytoplankton abundance. The presence of phytoplankton moves the peak of transmitted light to longer wavelengths, near 550-650 nm (Lutz et al. 1996). This leads to relatively red-shifted spectra, peaking near 570 nm, in Wilkinson Basin at both the surface as well as at depth. In early spring at Wilkinson Basin, it appears that the light spectrum at the surface may be useful for visually contrasting prey against both the surface and against the horizontal background spacelight. However, at depth, the light becomes red-shifted beyond the absorption range of the right whale's rod pigment, thereby providing little if any useful light for vision. In comparison, the light spectrum at the surface of Cape Cod Bay (on the same day) is well suited for visual processes in right whales, as it is within the absorption range of the visual pigment. At depth in Cape Cod Bay, as was the case in Wilkinson Basin, spectra are red-shifted relative to surface spectra, making the light less suitable for visual processes. In mid-spring, the spectral quality of the subsurface light changes again, at least in the Great South Channel, most likely due to the reduction of phytoplankton abundance. Although the spectra in the Great South Channel resemble the surface spectra at Cape Cod Bay, at depth they are substantially blue-shifted relative to the spectra at depth at either Cape Cod Bay or Wilkinson Basin. Thus, despite the relatively low levels of light (2.94^10 photons/s/cm^2/nm at 80-84 m), it seems likely that there is light available to support visually guided predation by whales. The data portrayed in Figure 8 provide evidence that the surface light at all three locations during the spring could support contrast based visual predation by foraging right whales. Interestingly, it appears that both the spectral horizontal radiance and downwelling irradiance at depth in mid-spring at the Great South Channel provide the most useful light for contrast vision as shown with the close overlap of these subsurface light spectra with that of the right whale rod absorbance spectrum. Although it is not clear if right whales foraging in these locations take advantage of downwelling or horizontal light, the former provides greater illumination at all depths for vision during the day.

Right whale foraging strategies in Cape Cod Bay and the Great South Channel have been well documented, with dive patterns of the whales being closely correlated with the horizontal and vertical distributions and movements of dense patches of zooplankton prey (Mayo and Marx 1990, Mayo and Goldman 1992, Winn *et al*. 1995, Kenney *et al*. 2001). Right whales feed on *Pseudocalanus* species in Cape Cod Bay during the early winter, but transition to the much more lipid rich *C. finmarchicus* in early spring (Mayo and Marx 1990, Parks *et al*. 2012). The depth of foraging in Cape Cod Bay in early spring is frequently in the upper 5 m of the water column (Parks *et al*. 2012). Based on our observations, we hypothesize that right whales use vision to facilitate foraging at the surface during the day in Cape Cod Bay, taking advantage of the relatively bright background light to silhouette dense patches of red-pigmented prey. Although Cape Cod Bay is relatively shallow, with an average depth of 25 m, it appears to provide relatively poor light for vision at depth in early spring if copepods were to migrate to near the sea floor during the day.

Although the onset and termination of spring algal blooms vary from year to year, they typically are completed in the Great South Channel by mid- to late spring when right whales visit this area. Dive patterns of right whales in the Great South Channel appear to vary with the movements of their copepod prey. Winn *et al*. (1995) reported right whales diving to a mean depth of 7.3 m with only a few dives greater than 30 m depth during late May and early June, 1989 in the Great South Channel. During that year, copepods exhibited no diel migration behavior, remaining at or near the surface throughout the day and night. However, right whales were rarely seen foraging at the surface in the same location and at the same time of year during 1981 and 1988; instead, they were thought to be foraging at or near the sea floor where the main prey concentration was found during the day (Winn *et al*. 1995). Baumgartner *et al*. (2011)

observed intra-annual variability in diel vertical migration of *C. finmarchicus* in the presence of right whales, suggesting that right whales feed both at the surface and at depth in the Great South Channel. Like Cape Cod Bay, the surface light profiles from the Great South Channel provide suitable light for contrast-based vision during the day. When *C. finmarchicus* are at depth during the day (during periods of diel vertical migration), there is still sufficient spectral overlap between the background light and the right whale rod pigment to facilitate contrast-based vision of *C. finmarchicus* aggregations (Fig. 8F).

We show that the spectral placement of the North Atlantic right whale rod visual pigment is offset from the spectral transmission of its primary prey species *C. finmarchicus*, but is spectrally tuned fairly well to absorb the downwelling irradiance and horizontal radiance spectra at foraging locations in early and mid-spring in the western Gulf of Maine. It remains to be determined if right whales rely, to a greater or lesser degree, on vertical radiance, whereby prey patches would be contrasted against light transmitted from the surface, or by horizontal radiance where prey patches would be contrasted against scattered light. Here we used downwelling irradiance to estimate the potential range of vertical radiance. This distinction is important as irradiance provides overall illumination rather than the typical properties of light at a particular location in the visual field. Although downwelling irradiance and horizontal radiance have similar spectral shapes at depth, this is not the case at the surface, and in any case it is not possible to predict surface horizontal radiance from downwelling irradiance spectra (Johnsen 2012). This discrepancy in light viewed in different directions at different depths (*e.g.* surface vs. horizontal radiance) may provide some insights as to how right whales take advantage of available light to contrast prey.

While this study focuses on the spectral placement of available light relative to the absorption spectrum of the right whale rod visual pigment, we do not address here the spectral sensitivity of the right whale eye. Can the right whale eye detect and use the limited number of photons in the Great South Channel at 120 m? Our current understanding of right whale retinal sensitivity suggests that this is the case. A recent study by Cronin *et al* (in press) examines the right whale's visual spectral sensitivity based on Land's (Land 1981, Land and Nilsson 2012) equation for sensitivity which is calculated using the retinal absorbance spectrum reported by Bischoff *et al* (2012) as well morphological measurements of the eye including pupil diameter, lens focal length and the rod photoreceptor outer segment diameter and length (Zhu *et al*. 2001, Buono *et al*. 2012, Schweikert *et al*. 2016). Using spectral attenuation measurements of live copepods and a subset of the field radiometric measurements reported here (0-22 m at Wilkinson Basin and the Great South Channel as well as the spectral attenuation at the surface and depth at the Great South Channel), it was proposed that the right whale retinal sensitivity would allow the whales to visually locate *C. finmarchicus* during the day at depths throughout their springtime foraging range. Depending on the number of rod photoreceptors that summate on each retinal ganglion cell, it was calculated that contrast based vision is perceptible down to 160 m with the summation of 8,000 rod photoreceptors, a reasonable summation value for an animal adapted for dim light vision (Cronin *et al*. in press). The available light at this depth will be visible to the right whale retina only if it is sufficiently bright for rod summation to occur. Given that foraging at depth most likely does not demand high-quality spatial vision as it is assumed that the whale focuses on dense patches of prey rather than individual prey items, evolution no doubt favors high contrast sensitivity. Furthermore, in very dim light (at depths >160 m or at night), right whales certainly must rely on other sensory systems to detect dense patches of prey. It has been proposed that they may use touch utilizing sensory hairs on the snout to sense prey patches when light suitable for vision is absent[1]. Finally, it is our hope that the study presented here will lend favorably to conservation efforts of the right whale and assist fisheries in by-catch reduction. Applications of this work may include improving the design of new fishing gear, or amending current gear, in such a fashion that it could be visually detected by the animal at some distance and possibly avoided.

[1]Murphy C, *et al*. Naval Undersea Warfare Center, Division Newport, Newport, RI. The vibrissal vystem of the North Atlantic right whale: Insight into sensory ecology and inspiration for biomimetic technology. Presented at the North Atlantic Right Whale Consortium Annual Meeting. The New England Aquarium, New Bedford, MA, November, 2015.

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Table I. Deployment information for free-falling Profiler II instrument.

Location	**Date**	**Time (GMT)**	**Location**	**Solar elevation (º)**	**Conditions**	**Water depth (m)**
Wilkinson Basin	4/4/12	14:52-15:07	42.23 N, 69.86 W	47	Clear sky	209
Cape Cod Bay	4/4/12	20:56-21:11	42.07 N, 70.27 W	23	Clear sky	58
Great South Channel	5/9/13	20:55-21:09	41.32 N, 69.32 W	30.5	Clear sky	83

FIGURE LEGENDS

Figure 1. The C5 copepodite stage of the calanoid copepod *Calanus finmarchicus*. Carotenoid pigments are associated with the posterior tip of the oil sac (OS), antennae (A), urosome (U), mouth (M), and insertion points of the legs (IP). Note that there is considerable variability in pigmentation among individuals.

Figure 2. Luminance contrast visual detection of prey by a monochromatic predator. Three underwater scenes are diagrammed showing varying degrees of overlap between the underwater spacelight spectrum, the predator's spectral sensitivity, and the resulting visual perception of a red prey item to the predator. Top-right: Complete overlap of the underwater light spectrum with the predator's spectral sensitivity results in the perception of a highly contrasted red prey item. Middle-right: Partial overlap of the underwater light spectrum with the predator's spectral sensitivity results in the perception of a lower contrasted red prey item. Bottom-right: No overlap of the underwater light spectrum with the predator's spectral sensitivity results in little or no perception of a red prey item. Human trichromatic color vision (left panels) extends visual perception of the copepod to a wider spectrum of underwater light by color contrast. Note that *Calanus finmarchicus* copepods are largely transparent with localized regions of red pigment (Fig. 1); the copepods depicted here are opaque and a single color to better illustrate silhouette detection by luminance contrast.

Figure 3. Absorbance and percent transmittance spectra of the North Atlantic right whale (*Eubalaena glacialis*) rod visual pigment and the carotenoid pigments from the calanoid copepod

Calanus finmarchicus. A. Absorbance spectrum of the right whale rod visual pigment (absorbance maximum = 493 nm) in the presence of hydroxylamine over 6 ~~hrs~~ (solid lines) and the formation of all-trans retinal after photobleaching (dashed line). Inset: Time course dark-adapted bleaching assay plotting the percentage of 493 nm pigment against time in the presence of hydroxylamine. B. Normalized transmission spectra of carotenoid pigments from *C. finmarchicus*. C. Normalized spectrum of the right whale rod visual pigment (black trace) and the average of the three transmittance spectra (red trace) shown in B. The absorbance maximum for the *E. glacialis* rod visual pigment falls within the range of minimum light transmittance from the *C. finmarchicus* carotenoid pigments.

Figure 4. Comparison of skyward solar irradiance spectra taken during collection periods at Wilkinson Basin, Cape Cod Bay and the Great South Channel. A. Skyward irradiance spectra were measured at Wilkinson Basin [spectrum taken on ~~April 4, 2012~~ at T_0 (14:52 GMT, solar elevation ≈47°), blue trace], at Cape Cod Bay [spectrum taken on April 4, 2012 at T_0 (20:56 GMT, solar elevation ≈23°), red trace] and at the Great South Channel on ~~May 9, 2013~~ at T_0 (20:09 GMT, solar elevation ≈30.5°, green trace). B. Normalized solar irradiance spectra from Figure 2A. Spectra were normalized by dividing each spectrum by the sin of the solar elevation.

Figure 5. Spectral light profiles from Wilkinson Basin, April 4, 2012. Downwelling irradiance spectra (A) or horizontal radiance spectra (B) averaged over 4-meter intervals from 0-52 m. Top left spectral profiles in both A and B, as examples, include the intervals 0-4 m (greatest irradiance and radiance) followed by 4-8 m, 8-12 m and 12-16 m (least irradiance and radiance) with averaged 4 m intervals being reiterated in subsequent spectral profiles. All spectra with a

clearly defined maximum have a peak irradiance or radiance at 569 nm. Spectra recorded below 44 m (A) and 40 m (B) do not possess defined maxima due to the sensitivity limitations of the radiometer.

Figure 6. Spectral light profiles from Cape Cod Bay, April 4, 2012. A. Downwelling irradiance spectra averaged over 4 meter intervals from 0-52 m (spectra are organized as in Fig. 4). Spectra from 0-20 m have peak irradiance at 549 nm, while spectra from 20-48 m have peak irradiance at 563 nm, after which the light meter was insensitive. B. Horizontal radiance spectra averaged over 4 meter intervals from 0-52 m. Spectra are organized as described in A. Spectra from 0-12 m have peak irradiance at 549 nm, while spectra from 12-48 m have peak irradiance at 563 nm, after which the light meter was insensitive.

Figure 7. Spectral light profiles from the Great South Channel, May 9, 2013. A. Downwelling irradiance spectra averaged over 4-meter intervals from 0-88 m (spectra are organized as in Fig. 4). Spectra from 0-32 m have broad peak irradiance values ranging from 555-562 nm, while spectra from 32-84 m have two clearly defined peak irradiances with a long wavelength peak at 542 nm and a short wavelength peak at 502 nm. B. Horizontal radiance spectra averaged over 4-meter intervals from 0-84 m. Spectra are organized as described in A. Spectra from 0-32 m have a peak radiance values around 550 nm, while spectra from 32-80 m have two clearly defined peak radiances with a long-wavelength peak at 532 nm and a short-wavelength peak at 498 nm.

Figure 8. Normalized right whale rod pigment absorbance (black trace) and copepod percent transmittance (red trace) plotted with normalized downwelling irradiance (blue trace) and horizontal radiance (yellow trace). Irradiance and radiance values are shown for surface light (A, C & E) and at the greatest depth resulting in peak maxima (B, D & F) at Wilkinson Basin (A & B), Cape Cod Bay (C & D) and the Great South Channel (E & F). Right whale rod visual pigment and copepod percent transmittance spectra are normalized to their respective maximum absorbance. Downwelling irradiance and horizontal radiance spectra are normalized to their respective peak maxima.

Figure 1

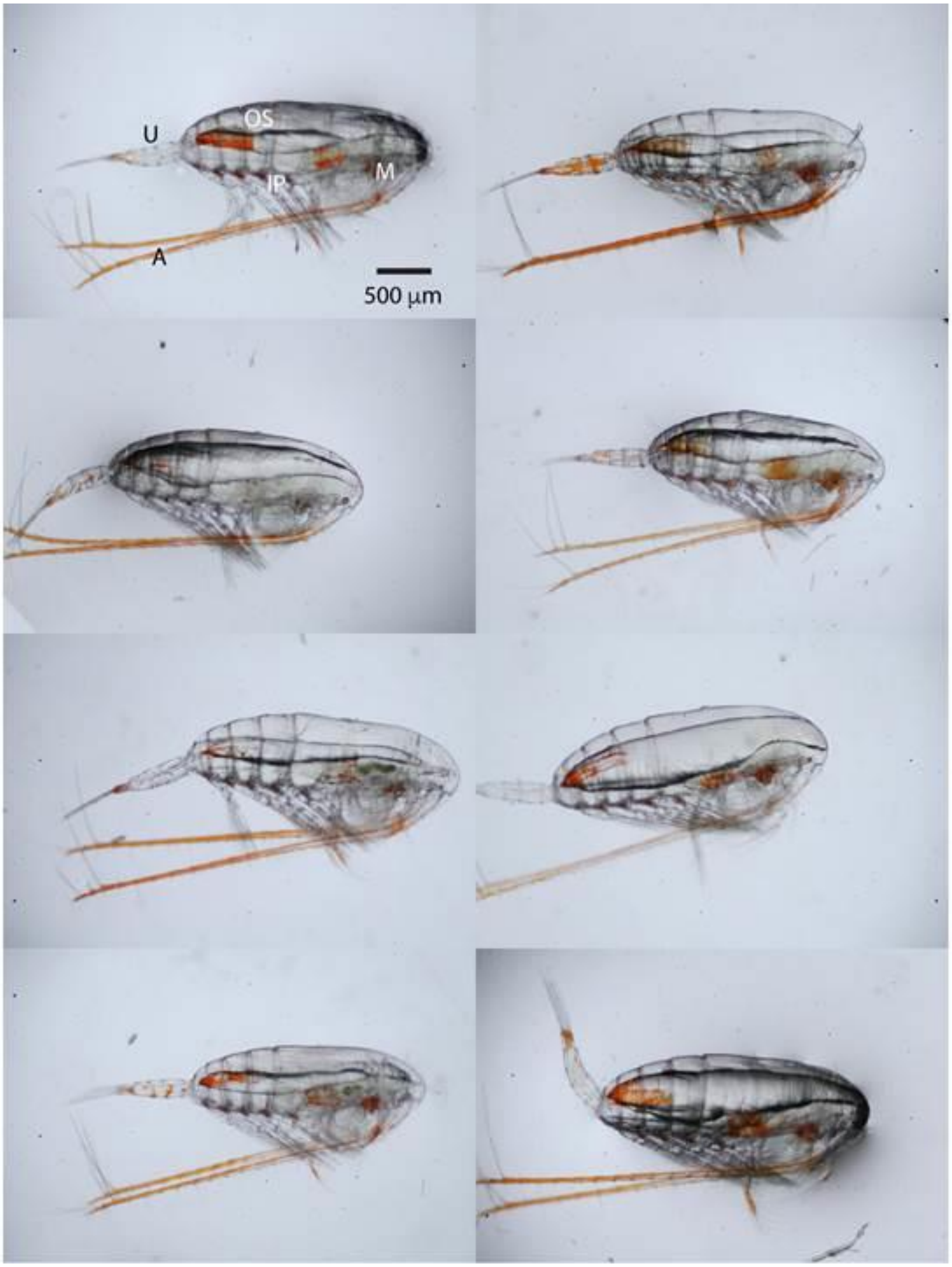


Figure 2

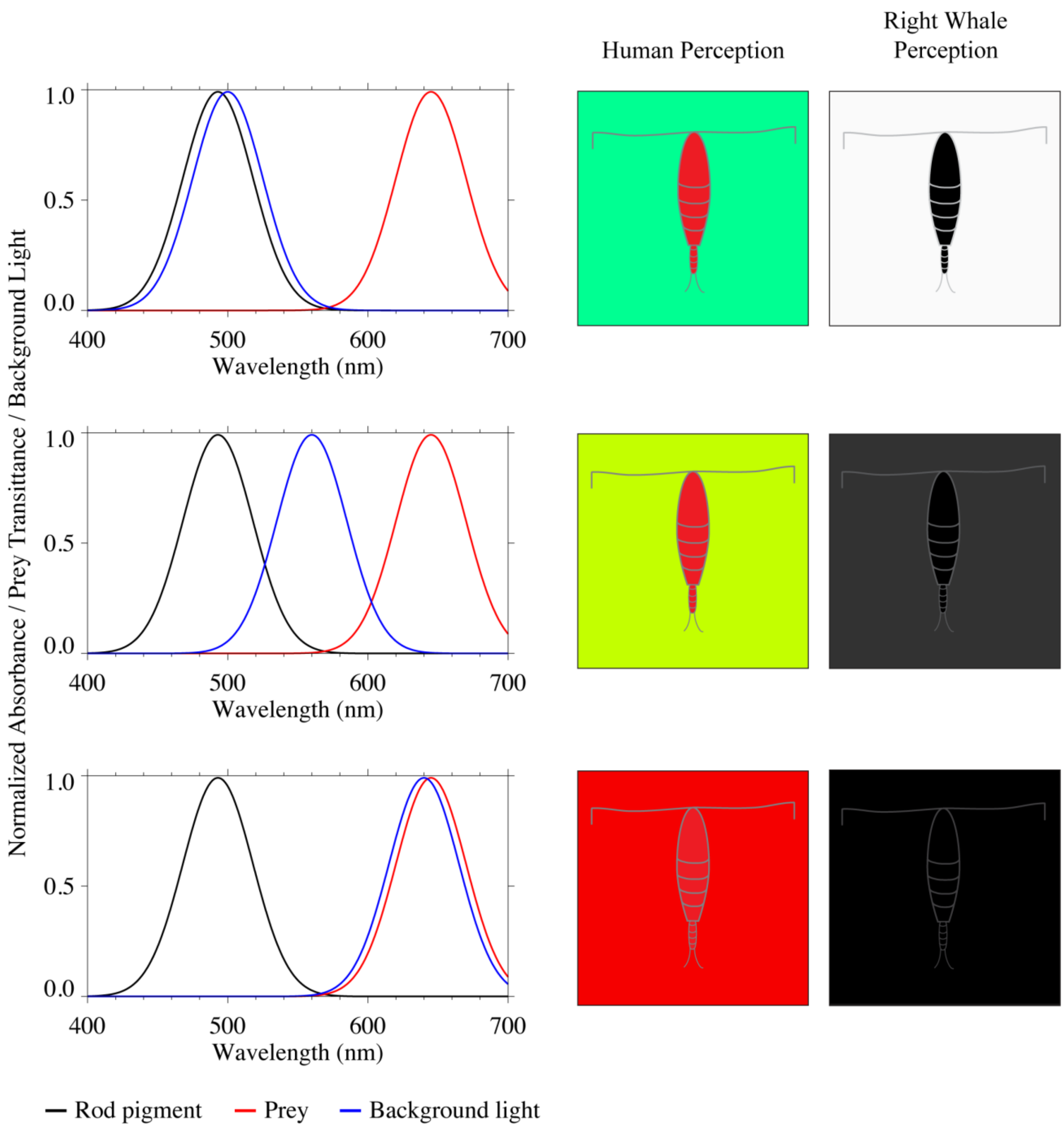
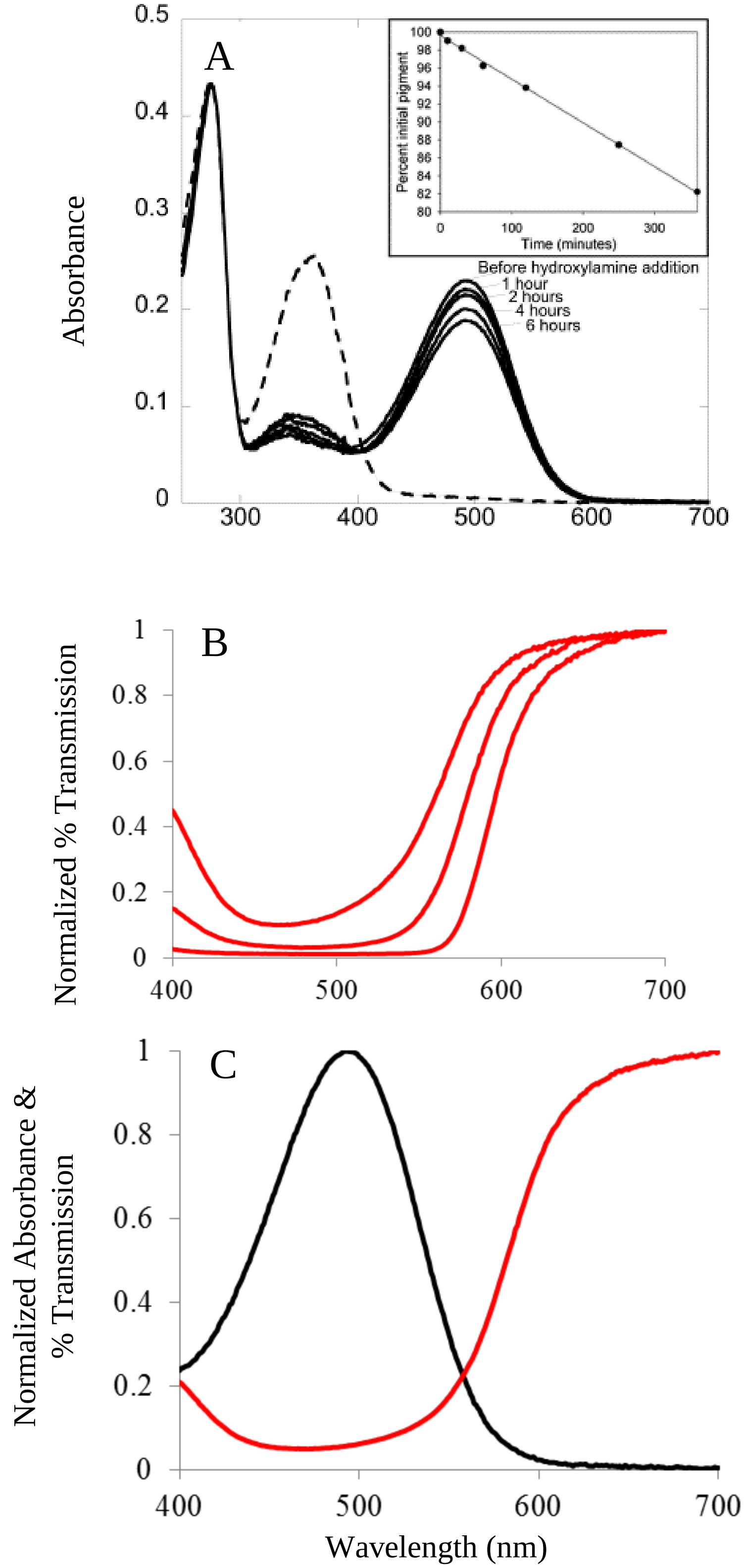

Human Perception
Right Whale Perception
Normalized Absorbance / Prey Transittance / Background Light
1.0
0.5
0.0
400
500
600
700
Wavelength (nm)
Rod pigment
Prey
Background light

Figure 3



A
B
C
Absorbance
Percent initial pigment
Time (minutes)
Before hydroxylamine addition
1 hour
2 hours
4 hours
6 hours
Normalized % Transmission
Normalized Absorbance &
% Transmission
Wavelength (nm)

Figure 4

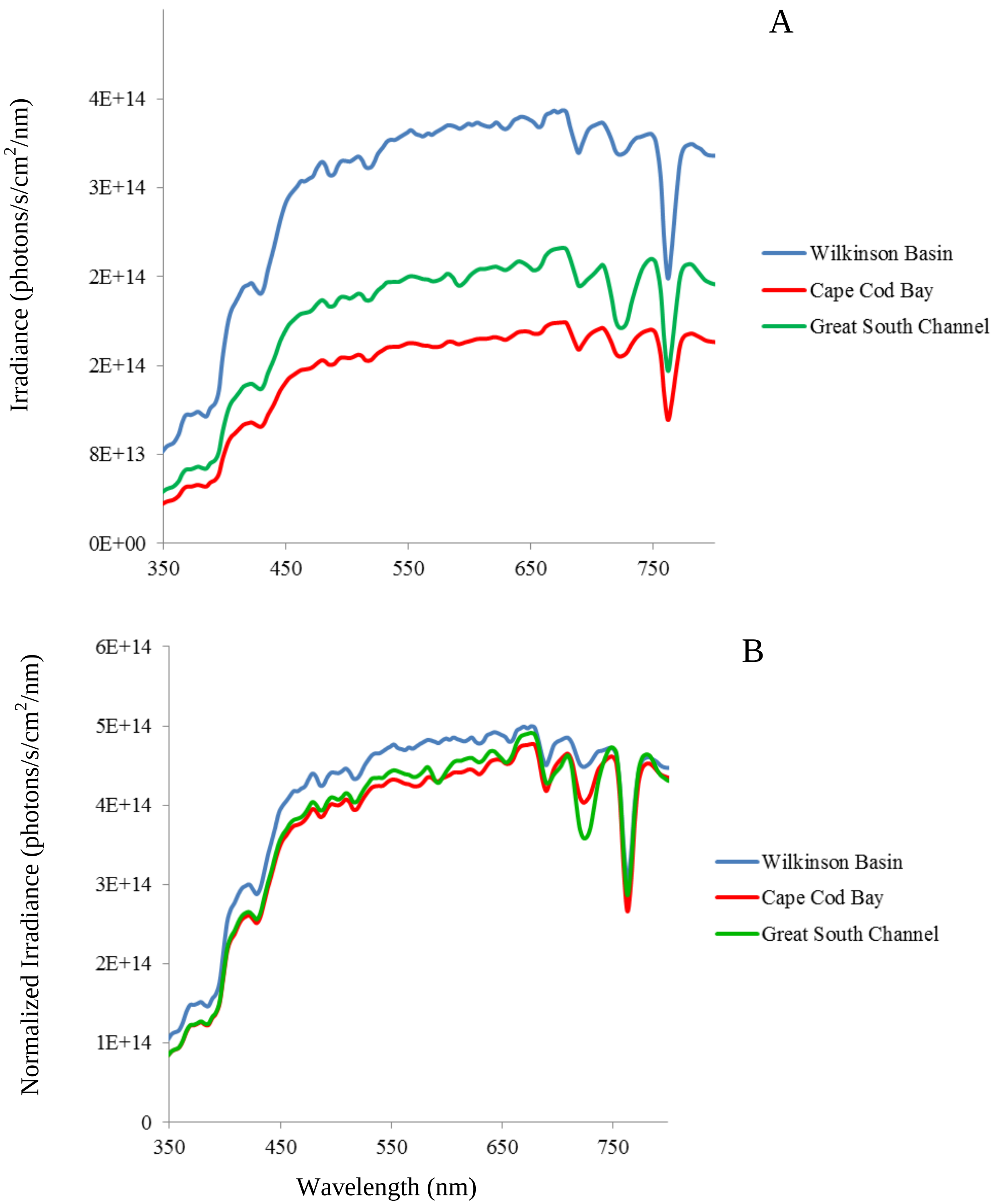
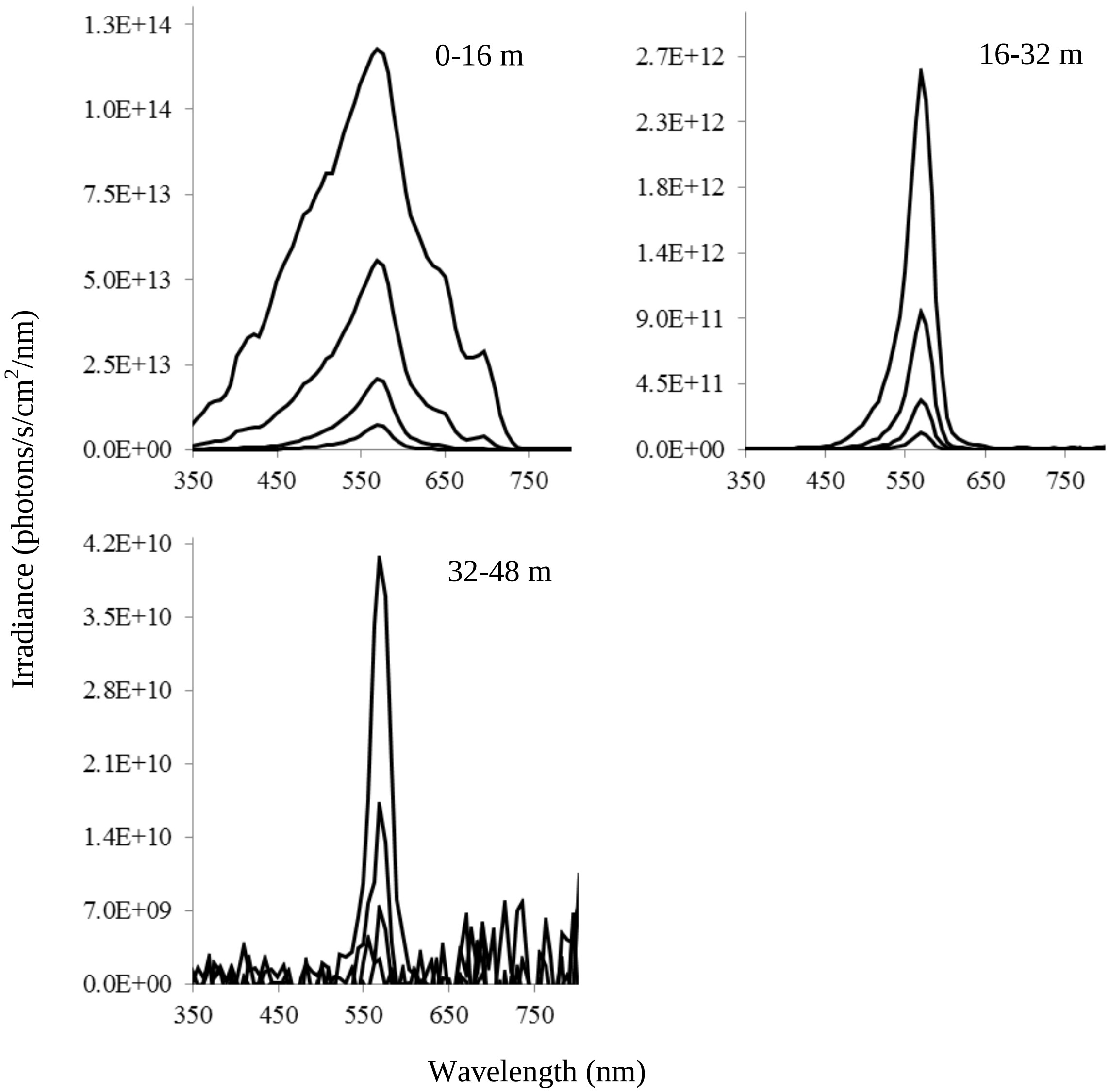

A
Irradiance (photons/s/cm2/nm)
4E+14
3E+14
2E+14
2E+14
8E+13
0E+00
350
450
550
650
750
Wilkinson Basin
Cape Cod Bay
Great South Channel
B
Normalized Irradiance (photons/s/cm2/nm)
6E+14
5E+14
4E+14
3E+14
2E+14
1E+14
0
350
450
550
650
750
Wavelength (nm)
Wilkinson Basin
Cape Cod Bay
Great South Channel

Figure 5

A. Wilkinson Basin



B. Wilkinson Basin

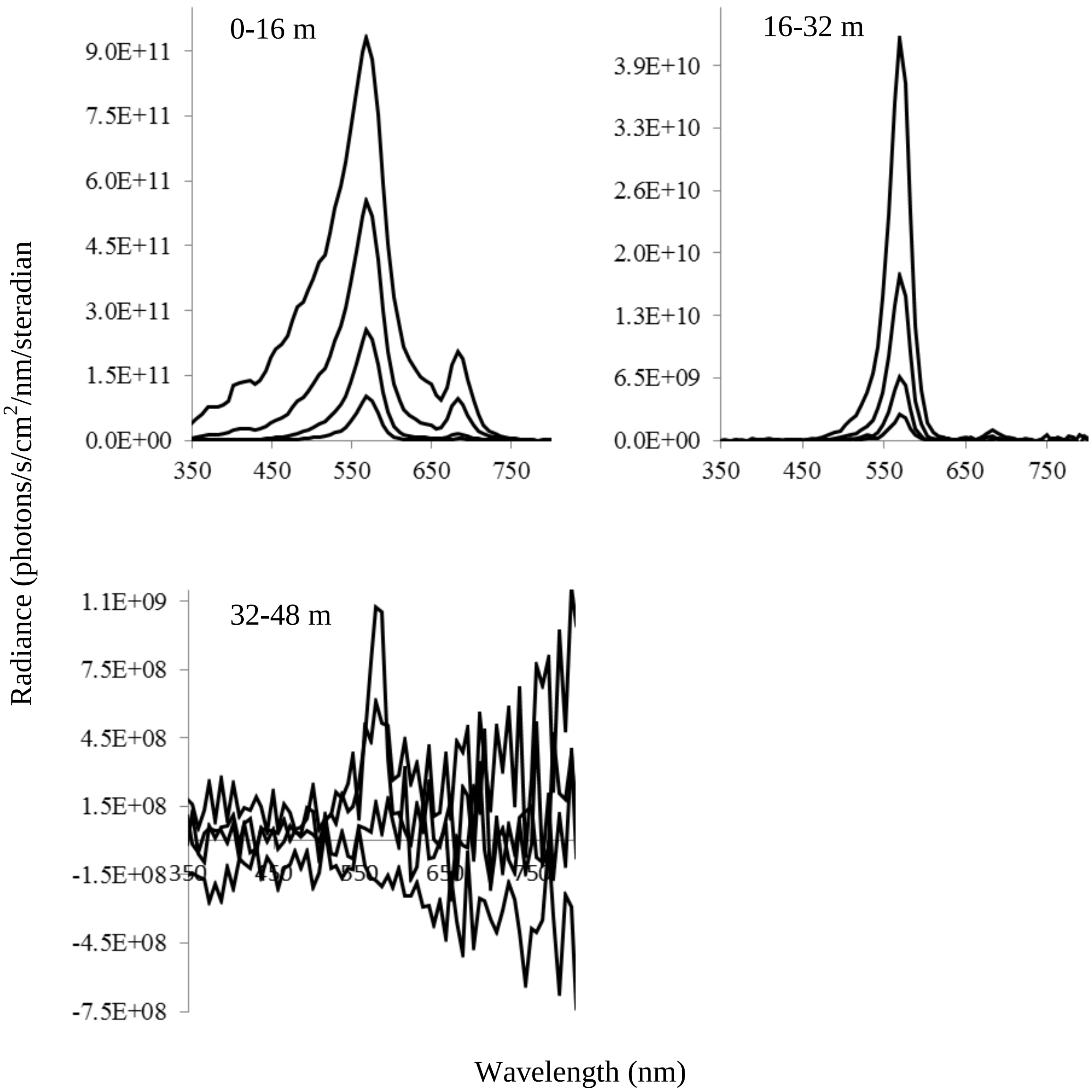
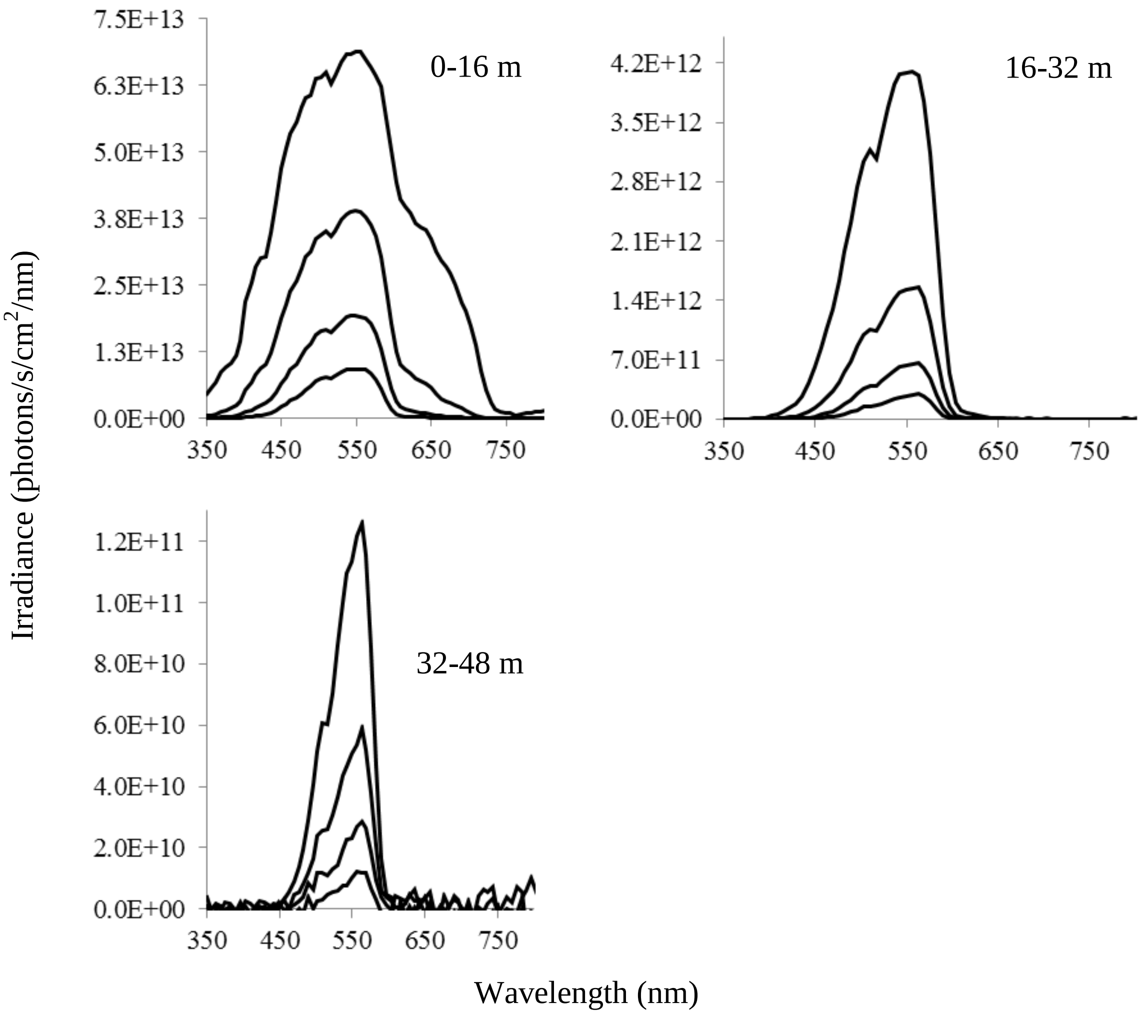


Figure 6

A. Cape Cod Bay



B. Cape Cod Bay

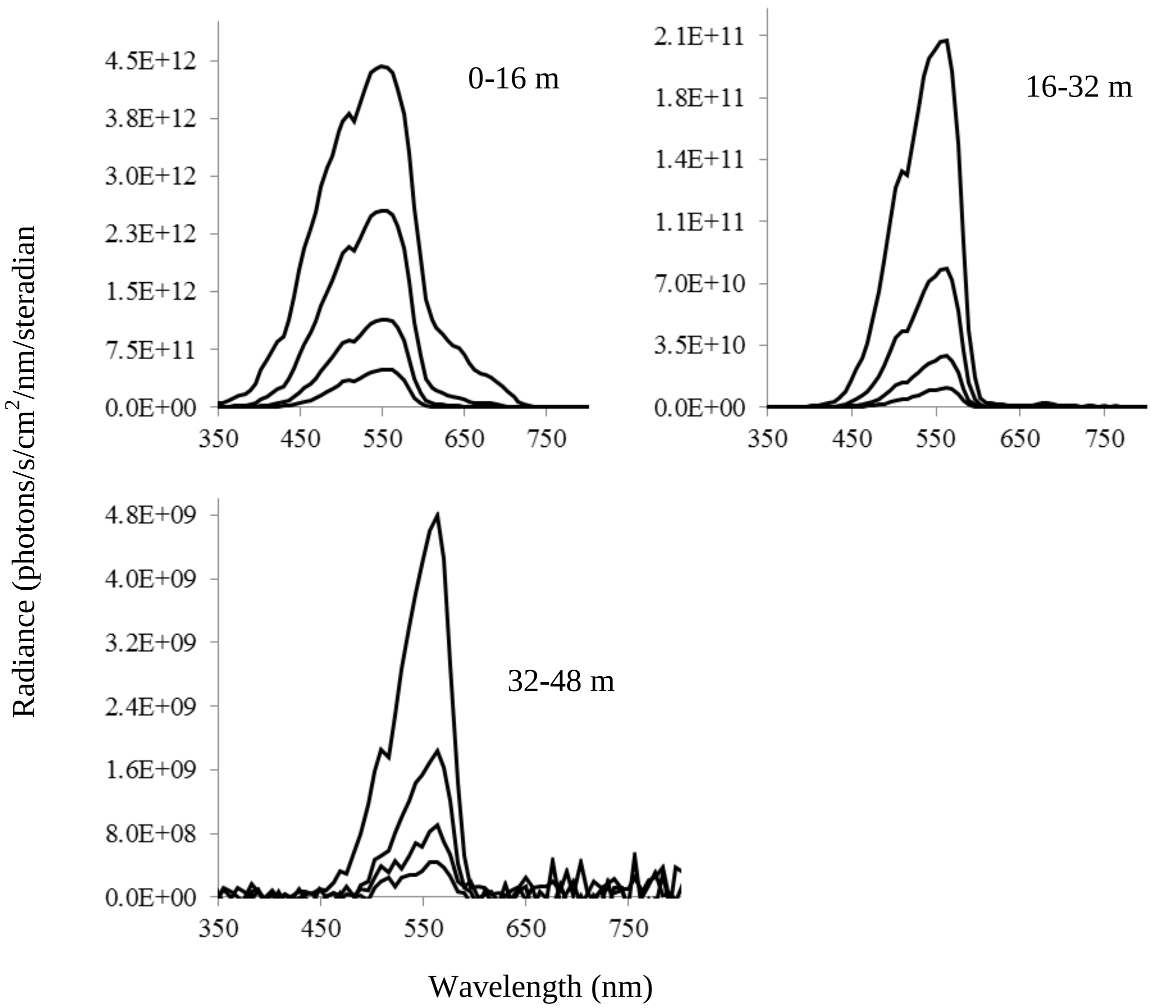
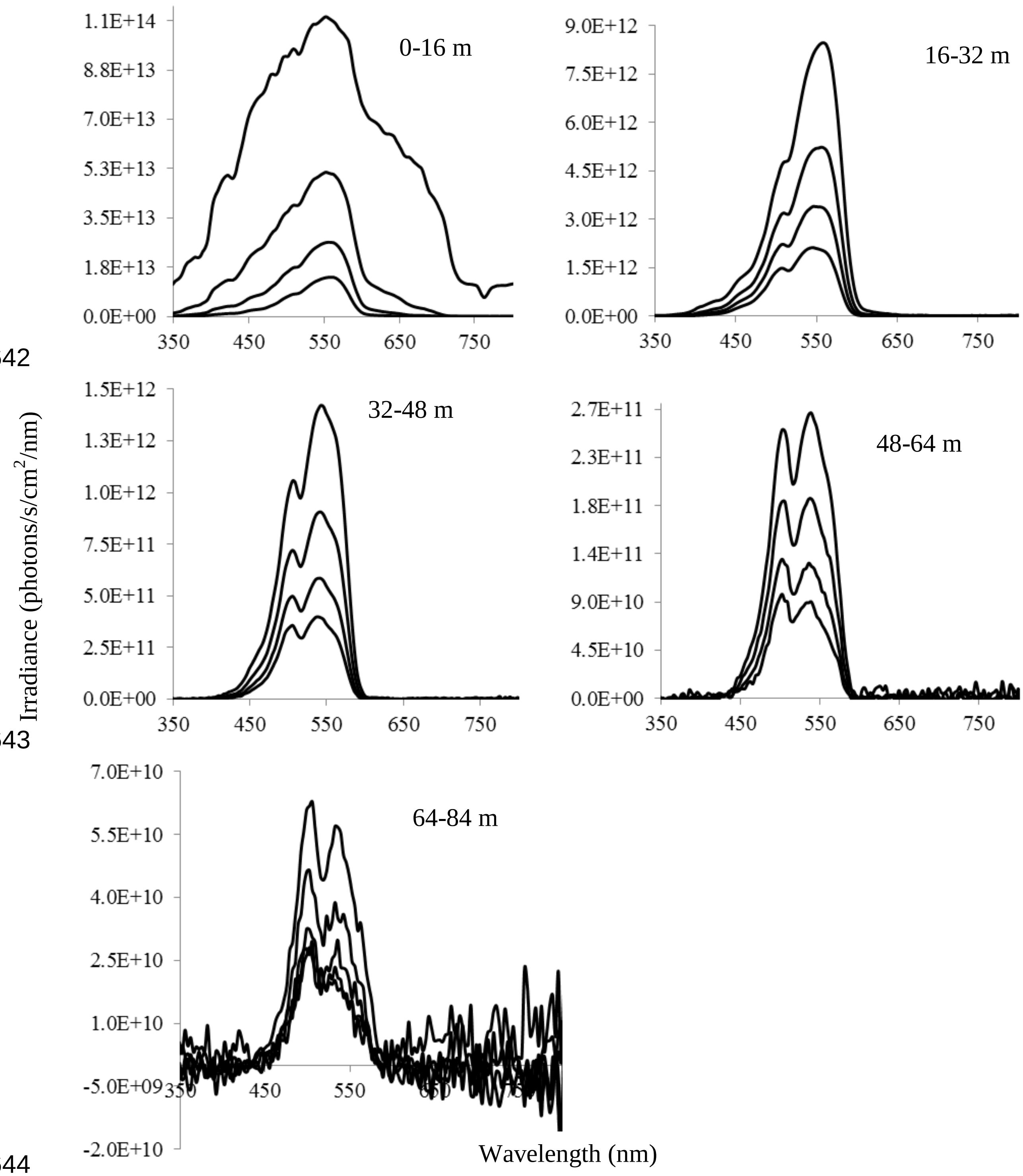


Figure 7

A. Great South Channel



B. Great South Channel

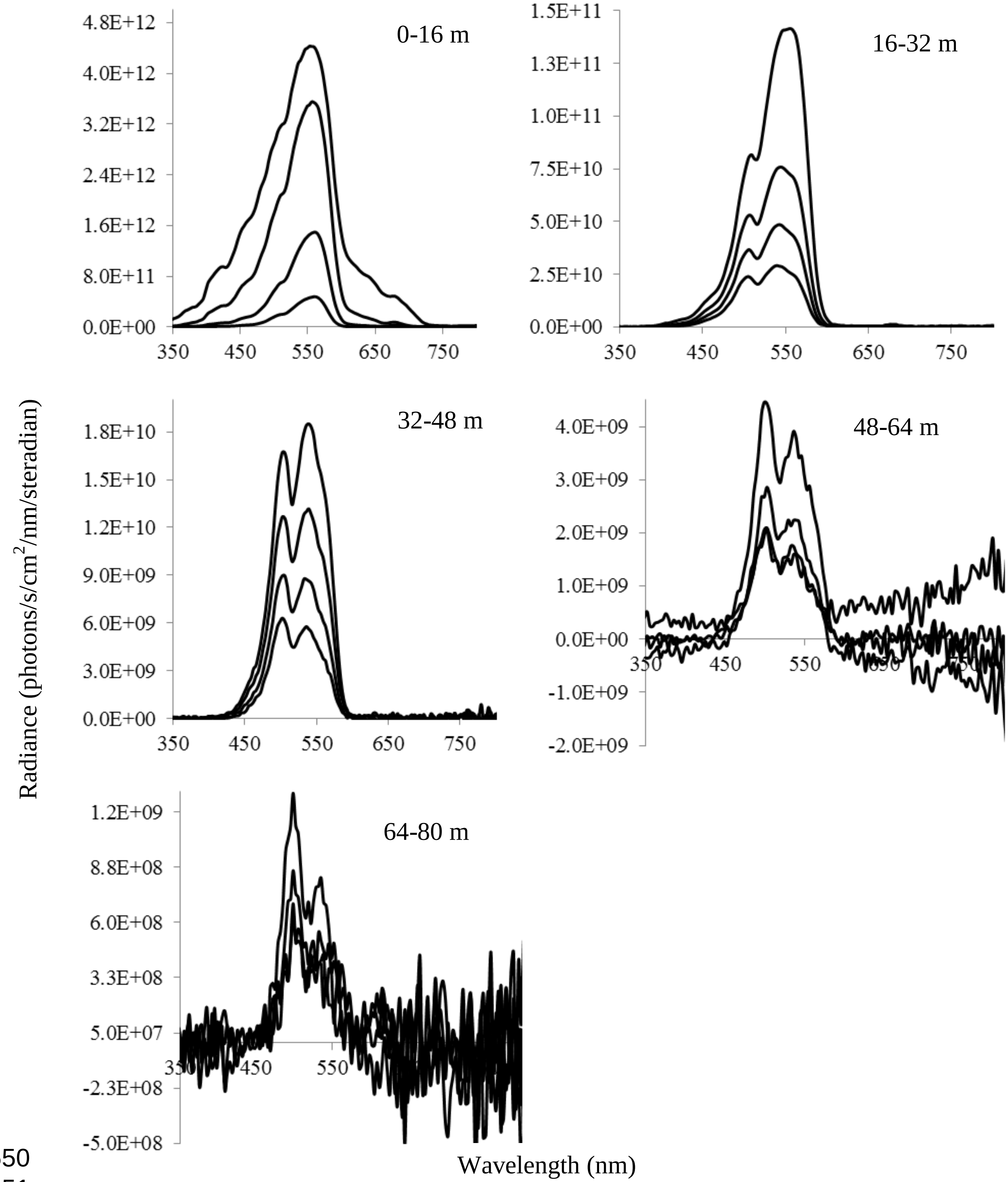
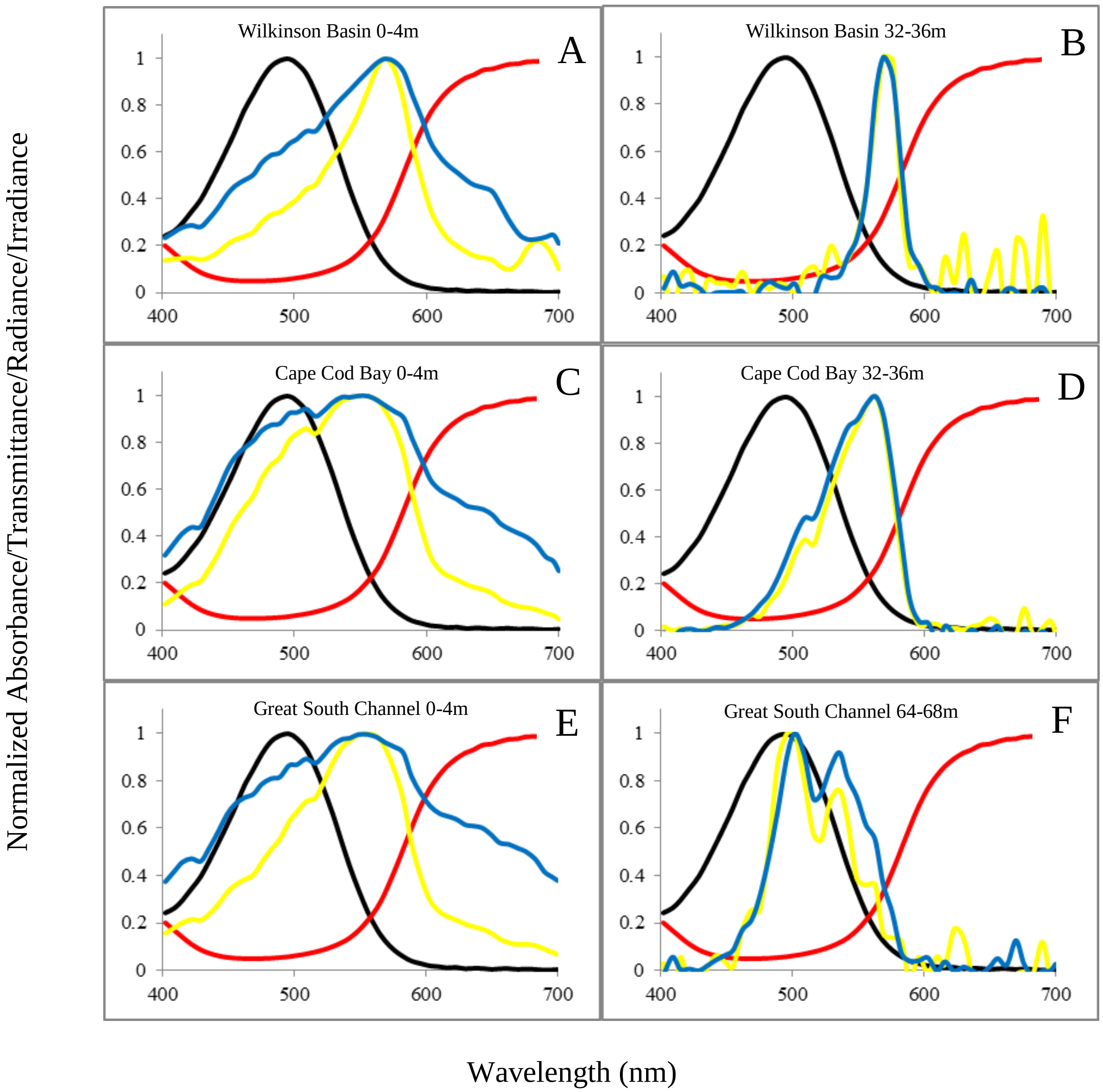


Figure 8


Normalized Absorbance/Transmittance/Radiance/Irradiance
Wilkinson Basin 0-4m
A
Wilkinson Basin 32-36m
B
Cape Cod Bay 0-4m
C
Cape Cod Bay 32-36m
D
Great South Channel 0-4m
E
Great South Channel 64-68m
F
0
0.2
0.4
0.6
0.8
1
400
500
600
700
Wavelength (nm)

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