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# Ultraviolet-absorbing compounds in the mucus of temperate Pacific tidepool sculpins: variation over local and geographic scales

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ABSTRACT: Temperate tidepool fishes of the family Cottidae (Teleostei) display biogeographic distribution patterns that vary with latitude and elevation within the intertidal zone. Middle and high intertidal pool species show a pattern of 'species replacement', with southern species being replaced by northern species at discrete locations along the coast. Lower intertidal pools, on the other hand, are dominated by a single species, *Oligocottus snyderi*, that occurs over an extremely wide latitudinal range. As a consequence of both latitudinal and elevational patterns, these fish experience variable amounts of ultraviolet (UV, 280 to 400 nm) irradiation both between and within species. The mucus of tidepool sculpins was analyzed by absorbance spectrophotometry to compare concentrations of UV-absorbing compounds in the mucus of fish, with regard to geographic location or intertidal microhabitat. Mucus from northerly fishes absorbed significantly less UV than the mucus of southerly fishes. Overall, mucus from high intertidal pool fishes absorbed significantly more UV than mucus from middle or lower intertidal pool fishes, but differences were not detectable within a site. The mucus spectra of all fish surveyed contained a single UV absorption peak with maximum absorbance ($\lambda_{max}$) in the short-wavelength UVA (UVA = 320 to 400 nm, $\lambda_{max}$ range = 323 to 331 nm). Compounds with $\lambda_{max}$ in the UVB (280 to 320 nm) or longer-wavelength UVA (ca. 360 nm) were not found, although these compounds were present in 38 (UVB) and 59% (longer UVA) of tropical species' mucus (138 species surveyed).

KEY WORDS: UV · Mycosporine-like amino acid · MAA · Mucus · *Oligocottus* · *Clinocottus*



## INTRODUCTION

Sculpins (Cottidae: Teleostei) are an abundant and well-studied component of temperate Pacific tidepool communities (Morris 1962, Yoshiyama 1981, Yoshiyama et al. 1986, 1992). These fishes show species-specific distribution patterns, both vertically, within the intertidal zone, and along a latitudinal gradient. Within the intertidal zone, different species dominate high, mid-level, and low intertidal pools (Yoshiyama et al. 1986). The predominant fishes in high- and mid-intertidal pools show a latitudinal pattern of 'geographical replacement' by closely related and ecologically similar species (Morris 1962, Yoshiyama et al. 1986). South of San Francisco Bay, *Clinocottus analis* is the most common fish in high intertidal pools, whereas to the north, *Oligocottus maculosus* occupies this niche. Similarly, in mid-intertidal pools, the southerly *C. recalvus* is replaced by the northerly (and morphologically nearly identical) *C. globiceps* between San Francisco Bay and Monterey Bay. However, *O. snyderi* is the predominant low-intertidal species over a wide latitudinal range, from Alaska to Baja California (Eschmeyer et al. 1983).

Because of these variable distribution patterns, tidepool sculpins experience a wide range of incident ultraviolet radiation (UV, 280 to 400 nm), both between and within species. By virtue of their shallow water environment, these fish experience potentially maximal incident UV (barring behavioral avoidance). The

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damaging effects of UV radiation, particularly shorter UVB (280 to 320 nm) wavelengths, on fishes include cataracts, corneal damage, and epithelial 'sunburn' damage (Bullock 1982, Ahmed & Setlow 1993, Cullen & Monteith-McMaster 1993, Cullen et al. 1994). For fishes, sunburn can be fatal, but different fish species (and even strains within a species) are differentially tolerant of UV exposure (Blazer et al. 1997, Armstrong et al. 2002). The epithelial mucus of coral reef fishes (n = 138 species) contains varying amounts of several 'sunscreen' compounds that absorb both UVB and UVA (320 to 400 nm) radiation (Zamzow & Losey 2002, J. P. Zamzow unpubl.). The UV-absorbing compounds of one species, *Thalassoma duperrey*, have been identified by high-performance liquid chromatography as the mycosporine-like amino acids (MAAs) palythine ($\lambda_{max}$ [maxiumum absorbance] = 320 nm), palythinol ($\lambda_{max}$ = 332 nm), and asterina-330 ($\lambda_{max}$ = 330 nm, J. P. Zamzow unpubl.). These compounds, along with palythene at $\lambda_{max}$ = 360 nm, occur in the ocular tissues of coral reef fishes (Dunlap et al. 1989). The UVB-absorbing peak in coral reef fish mucus is presumed to arise from gadusol or deoxygadusol ($\lambda_{max}$ = 294 to 296 nm at pH > 7), compounds which occur in fish roe (Plack et al. 1981, Shick & Dunlap 2002). The concentration of these sunscreens in the mucus changes according to the UV exposure of the fish (Zamzow & Losey 2002), and they are sequestered from the diet (Mason et al. 1998, Zamzow in press).

The diets of Pacific tidepool fishes are well documented. *Oligocottus snyderi* feeds primarily on gammarid amphipods, as does *O. maculosus* (Grossman 1986). *Clinocottus globiceps* eats anemones and algae, whereas *C. analis* feeds on polychaetes and shrimp (Grossman 1986, Yoshiyama et al. 1996). Gammarid amphipods (Helbling et al. 2002), anemones (Banaszak & Trench 1995), algae (Karsten et al. 1998), and shrimp (Grant et al. 1985) are known to possess MAAs, and these compounds are nearly ubiquitous in marine taxa (Shick & Dunlap 2002).

Incident UV radiation varies widely with both latitude (Gleason et al. 1993, Madronich et al. 1998) and depth in the water column (Jerlov 1976). Additionally, due to the nature of the tidal cycle, fishes in high intertidal pools spend more time exposed to high UV levels than fishes in low intertidal pools (Ricketts et al. 1992). This study investigated whether the UV absorbance of the epithelial mucus of tidepool sculpins varied with latitude, vertical location within the intertidal zone, or both. I hypothesized that fishes from higher latitudes would possess less sunscreen in the mucus than fishes from lower latitudes, and that fish from higher tidepools would possess more sunscreen than those from lower tidepools.

## MATERIALS AND METHODS

Fishes were collected with dip nets at low tide from 3 sites along the Pacific Coast of North America (Table 1). The sites were Soberanes Point, California (36° 27′ N, 121° 56′ W; July 10 to 12, 2002); Arena Cove, California (38° 55′ N, 123° 43′ W; July 23 to 25, 2002); and Sitka, Alaska (57° 02′ N, 135° 21′ W; August 7 to 11, 2002). The first 2 sites were chosen from Yoshiyama (1986), and were expected to represent the southern species complex, and an overlap zone between southern and northern species, respectively. The third site was chosen from Eschmeyer (1983) as the extreme northern range of *Oligocottus snyderi*, and was expected to elucidate any subtle changes that might occur with latitude, as well as representing the northern species complex. Sites were sampled beginning in the south, in order to bias the results against any possible cumulative effect of summertime UV exposure. The Arena Cove site was expected to be a zone of overlap for direct comparison of the mucus of *Clinocottus analis* and *O. maculosus* (Yoshiyama et al. 1986); however, no *C. analis* were present at the time of sampling (approximately 25 work-hours of search time).

The relative height of tidepools within the intertidal zone was characterized as low, mid, or high, modified from Yoshiyama (1981). For this study, mid-intertidal pools were defined as Yoshiyama's 'high-offshore' and 'high-intermediate' pool categories, whereas high intertidal pools were his 'high-nearshore' pool category (Yoshiyama 1981). All 3 sites consisted of wave-exposed rocky benches, and the types of tidepools present were quite similar. Low-intertidal pools were of

Table 1. Cottid species used in general linear model of integrated UV absorbance (see also Fig. 2)

| Site (Latitude) | Date (2002) | Zone | Species | n |
|---|---|---|---|---|
| Soberanes Point (36° 27′ N, 121° 56′ W) | Jul 10–12 | High | *Clinocottus analis* | 8 |
| | | Mid | *Clinocottus recalvus* | 10 |
| | | Low | *Oligocottus snyderi* | 9 |
| Arena Cove (38° 55′ N, 123° 43′ W) | Jul 23–25 | High | *Oligocottus maculosus* | 10 |
| | | Mid | *Clinocottus globiceps* | 10 |
| | | Low | *Oligocottus snyderi* | 11 |
| Sitka (57° 02′ N, 135° 21′ W) | Aug 7–11 | High | *Oligocottus maculosus* | 10 |
| | | Mid | *Clinocottus globiceps* | 2 |
| | | | *Clinocottus embryum* | 5 |
| | | Low | *Oligocottus snyderi* | 8 |

moderate depths (~0.25 to 1.5 m) and contained the most macroalgal cover, mid tidepools were generally deep (~0.75 to 1.5 m) potholes or gorges with less macroalgal cover than low pools, and high tidepools had large surface-area-to-volume ratios (<1 m depths and 1 to 3 m across) and the least amount of macroalgal cover.

Fishes were held in buckets of aerated seawater prior to sampling for no more than 3 h post-capture. One fish of each species was euthanized, and transmission of the ocular media was determined following Losey et al. (2000). After sampling, fishes were returned to their home tidepools, and any subsequent collections took place at least 100 m distant.

Spectrophotometric methods followed Zamzow & Losey (2002). Briefly, a mucus sample was taken from the dorsal flank of each fish and 'squashed' to a standard depth of 0.25 mm between 2 UV-transparent microscope slides, with coverslips at either end to act as spacers (Zamzow & Losey 2002). While mucus of the fishes in this study was not examined, microscopic examination of mucus samples from Hawaiian fishes did not indicate the presence of epithelial cells (J. P. Zamzow unpubl.). Absorbance of each sample was measured from 280 to 400 nm with a fiber-optic spectrophotometer (Fig. 1). For the purposes of data analysis, the variable 'integrated absorbance' was used. Integrated absorbance consists of the sum of the absorbance values (units = optical density [OD]) at each wavelength integer from 280 to 400 nm.

General linear model (GLM) analysis was performed with SAS systems, Release 8.02. The initial GLM tested the effects of geographic site, relative intertidal elevation, standard length, species of fish, and interaction terms, on integrated absorbance. Non-significant independent variables (p > 0.5) were sequentially excluded, and the explanatory variables in the final model were geographic site, intertidal elevation, and their interaction. A second GLM tested for effects of site and location (and their interaction) on the $\lambda_{max}$ of the fishes' mucus.

## RESULTS

The mucus of both *Oligocottus* spp. and *Clinocottus* spp. absorbed UV, with the main absorbance peak located at ca. 330 nm. This is unlike the mucus of tropical fishes that often contains either a UVB-absorbing peak at ca. 294 nm (38% of 138 species from 25 families, J. P. Zamzow unpubl.), or evidence of longer-wavelength ($\lambda_{max}$ ≈360 nm) absorbing compounds (59% of 138 species). The mucus absorbance spectrum of a phylogenetically unrelated, but ecologically similar, high intertidal-zone fish, *Istiblennius lineatus* (family Bleniidae), from Majuro Atoll (7° 09' N, 171° 12' E, June 13, 2001), is shown for purposes of comparison (Fig. 1a).

Integrated absorbance showed significant effects of both site and relative height within the intertidal zone (Table 2, Fig. 2, ANOVA: Site $F_{2,70}$ = 46.44, p < 0.0001; Height $F_{2,70}$ = 9.41, p < 0.001). Fishes from high intertidal pools had significantly greater UV absorbance than those from low- or mid-intertidal pools (least square means [LSM] comparison, Tukey post-hoc adjustment, Mid: p < 0.001, Low: p < 0.01), but the mucus of low- and mid-intertidal pool fish could not be distinguished from one another (LSM, Tukey, p = 0.94). Overall, fish from Soberanes Point had significantly higher mucus absorbance than fish from Arena Cove (LSM, Tukey, p = 0.02) or Sitka (LSM, Tukey, p < 0.0001), and fish from Arena Cove had significantly higher integrated UV absorbance than fish from Sitka (LSM, Tukey, p < 0.0001). There was no interaction between relative height and geographic location.

The $\lambda_{max}$ of fishes' mucus varied significantly by intertidal height but not by location (ANOVA: Height

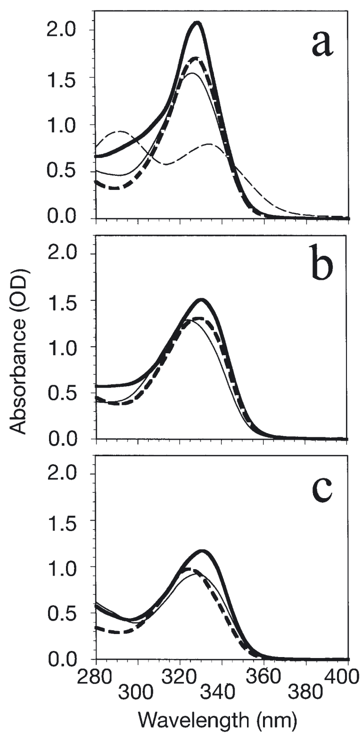


Fig. 1. Representative absorbance spectra of temperate Pacific cottid mucus. Heavy solid lines: high-tidepool species; heavy dashed lines: mid-tidepool species; thin lines: low-tidepool species (*Oligocottus snyderi* in all panels). (a) Soberanes Point. High species: *Clinocottus analis*; mid species: *C. recalvus*. *Istiblennius lineatus*, a tropical blenniid high tidepool species from Majuro Atoll, is shown for comparison (thin dashed line). (b) Arena Cove. High species: *O. maculosus*; mid species: *C. globiceps*. (c) Sitka. Species sampled as in (b)

Table 2. Post-hoc comparison p-values, Tukey corrected, for the 2-way ANOVA of integrated absorbance by site and intertidal height. Sites: SP = Soberanes Point, AC = Arena Cove, S = Sitka; HI = high-, MID = mid-, and LO = low-intertidal pools (see 'Materials and methods' for details)

| Site | S HI | S MID | S LO | AC HI | AC MID | AC LO | SP HI | SP MID |
|---|---|---|---|---|---|---|---|---|
| SP LOW | 0.002 | 0.002 | 0.0002 | 0.992 | 0.707 | 0.852 | 0.212 | 1.00 |
| SP MID | 0.014 | 0.014 | 0.001 | 0.836 | 0.935 | 0.993 | 0.021 | |
| SP HI | <0.0001 | <0.0001 | <0.0001 | 0.637 | 0.0004 | 0.003 | | |
| AC LOW | 0.093 | 0.061 | 0.012 | 0.227 | 1.00 | | | |
| AC MID | 0.244 | 0.173 | 0.039 | 0.138 | | | | |
| AC HI | <0.0001 | 0.0001 | <0.0001 | | | | | |
| S LOW | 0.99 | 1.00 | | | | | | |
| S MID | 0.99 | | | | | | | |

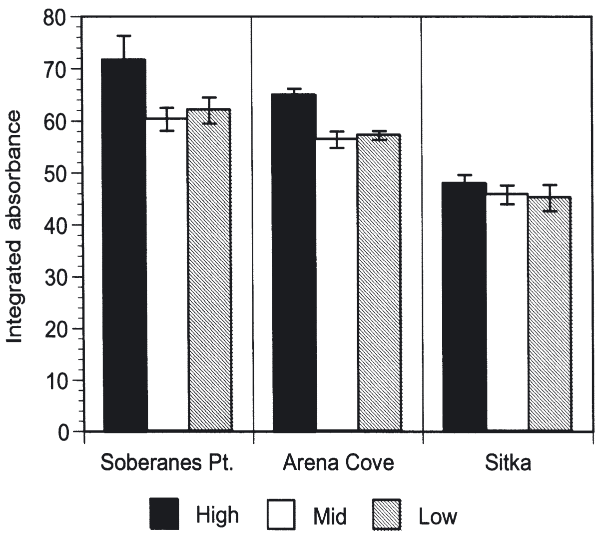


Fig. 2. Integrated absorbance for *Clinocottus* and *Oligocottus* species from high-, mid-, and low-intertidal pools at each site (mean ± SE). Low-tidepool data for all 3 sites are from *O. snyderi* mucus. Species sampled: Soberanes Point, *C. analis* (high tidepools) and *C. recalvus* (mid tidepools); Arena Cove, *O. maculosus* (high tidepools) and *C. globiceps* (mid tidepools); Sitka, *O. maculosus* (high tidepools) and *C. globiceps* and *C. embryum* (mid tidepools). See Table 2 for post-hoc pair-wise comparisons

$F_{2,70}$ = 35.44, p < 0.0001; Site $F_{2,70}$ = 0.2, p = 0.8). However, a significant interaction between height and location (ANOVA: Height × Site $F_{4,70}$ = 12.96, p < 0.001) reflects the fact that the height effect varied depending on the site, and therefore no clear trend was evident in terms of either height or location.

Additional intertidal species were opportunistically surveyed for mucus transmission, and the non-cottids had very low integrated absorbance values (Table 3). Among the cottids, *Artedius* spp. mucus had integrated absorbance values similar to those found for *Oligocottus* and *Clinocottus* species, whereas the mucus of *Enophrys bison* demonstrated little UV absorbance.

The ocular media of all species surveyed blocked UV radiation from reaching the retina; the wavelength of 50% transmission ($T_{50}$) of the lens for each species was 399 nm or higher (Table 4). For *Artedius lateralis*, *Clinocottus globiceps* and *Oligocottus snyderi*, corneal absorbance resulted in higher $T_{50}$ values for whole-eye transmission.

## DISCUSSION

The UV absorbance of *Oligocottus* and *Clinocottus* species mucus was clearly reflective of their habitat, both along a latitudinal gradient and within the intertidal zone. Overall, fishes from high-intertidal pools had more sunscreen in the mucus than those from mid- or low-intertidal pools, though differences were not detectable within a site (Table 2). Fish in high-intertidal pools experienced more potentially damaging UV radiation than those in low-intertidal pools,

Table 3. Additional temperate tidepool species sampled for mucus and ocular media

| Site | Species (family) | Integrated absorbance (mean ± SE) | n |
|---|---|---|---|
| Soberanes Point | *Cebidichthys violaceus* (Stichaeidae) | 11.1 | 1 |
| | *Gobiesox maeandricus* (Gobiesocidae) | 25.5 | 1 |
| | *Xererpes fucorum* (Pholidae) | 10.9 | 1 |
| Arena Cove | *Artedius lateralis* (Cottidae) | 51.1 ± 0.9 | 2 |
| Sitka | *Artedius harringtoni* (Cottidae) | 35.5 | 1 |
| | *Artedius lateralis* (Cottidae) | 40.7 ± 1.8 | 8 |
| | *Enophrys bison* (Cottidae) | 15.4 ± 1.2 | 3 |

Table 4. Cottid species sampled for ocular media transmission. $T_{50}$: wavelength of 50% transmission. For *Artedius lateralis*, *Clinocottus globiceps* and *Oligocottus snyderi*, corneal absorbance resulted in higher $T_{50}$ values for whole eye transmission

| Species | Site | Lens $T_{50}$ (nm) |
|---|---|---|
| *Artedius lateralis* | Sitka | 410 |
| *Clinocottus analis* | Soberanes Point | 409 |
| *C. globiceps* | Arena Cove | 412 |
| *C. recalvus* | Soberanes Point | 412 |
| *Cebidichthys violaceus* | Soberanes Point | 407 |
| *Enophrys bison* | Sitka | 402 |
| *Oligocottus maculosus* | Arena Cove | 408 |
| *O. snyderi* | Soberanes Point | 399 |

both due to increased tidal exposure and because high pools were shallow with sparse macroalgal cover. High-tidepool fish may mitigate their exposure to this radiation through increased mucus absorbance. Both *O. maculosus* and *C. analis* commonly occur in open sandy areas of large high tidepools, whereas *O. snyderi* shows a preference for plant cover in low tidepools (Nakamura 1976, pers. obs.). These behavioral differences may contribute to the differences found in mucus absorbance between the species.

Fishes from lower latitudes experience higher levels of UV radiation than species from higher latitudes (Gleason et al. 1993, Madronich et al. 1998). In the 2 wk prior to sampling, the average integrated UV irradiance (erythmally weighted) at each site was as follows (mean ± SE): Soberanes Point, 5571 ± 193 J $m^{-2}$; Arena Cove, 4936 ± 237 J $m^{-2}$; Sitka, 2264 ± 120 J $m^{-2}$ (total ozone mapping spectrometer [TOMS] UV data, available at http://toms.gsfc.nasa.gov/ery_uv/euv.html). The irradiance at each site was significantly different from the next (1-way ANOVA, $F_{2,41} = 95.9$, $p < 0.0001$; Tukey post-hoc, Soberanes vs Arena Cove $p = 0.04$, Arena Cove vs Sitka $p < 0.0001$). Similarly, the overall integrated UV absorbance of tidepool fish mucus increased significantly from one site to the next. Soberanes Point tidepool fishes, exposed to 2.5 times the weighted irradiance of Sitka tidepool fishes, had approximately 1.5 times higher integrated mucus absorbance, which may protect them from increased UV levels.

Another possible factor influencing the UV absorbance of fish mucus is temperature. Both seawater temperature and UV radiation fluctuations significantly affect MAA tissue concentrations in soft coral colonies (Michalek-Wagner 2001). Temperature, which varies in the same manner as UV irradiance over latitude and intertidal height, may also play a role in the UV absorbance patterns found in this study. However, as temperature is generally tightly correlated with UV irradiance, experimental manipulations would be necessary to determine the role of each environmental factor.

UV-absorbing compounds in the mucus and ocular media of fishes are derived from the diet (Mason et al. 1998, Zamzow in press). Judging from the ocular media transmission values (Table 4), as well as the mucus absorbance spectra (Fig. 1), all of the *Clinocottus* and *Oligocottus* species surveyed were capable of sequestering UV-absorbing compounds from their diet. However, the compounds sequestered in the ocular tissues clearly differ from those found in the mucus. The fact that these UV-absorbing compounds are accumulated up the food web suggests that they are ecologically important in terms of sunscreen protection.

Intertidal fishes do not seem to be simply passively excreting all available dietary compounds in their mucus. *Oligocottus maculosus*, *O. snyderi*, and *Xererpes fucorum* consume primarily gammarid amphipods (Grossman 1986). However, in contrast to the 2 *Oligocottus* species, *X. fucorum* showed almost no sunscreen in the mucus. This may be due to phylogenetic differences in the ability to sequester UV-absorbing compounds in the mucus, but high mucus absorbance did not occur in all cottids (see *Enophrys bison*, Table 3). *X. fucorum* is generally found under rocks or in crevices (Eschmeyer et al. 1983), and thus may behaviorally regulate its UV exposure, precluding the need for high mucus absorbance. *Cebidicthys violaceus* (a herbivore) and *Gobiesox maeandricus* (an invertebrate predator) often shelter under rocks and algae (Yoshiyama 1981, Martin & Bridges 1999), and these species also had low levels of sunscreen in the mucus (Table 3). The dietary source of MAAs for these species may vary due to bathymetric or latitudinal patterns in MAA concentrations in prey items (Karsten et al. 1998, Hoyer et al. 2001), and this may also contribute to the observed patterns of absorbance.

UV absorbance of the mucus varies not only between species, but also within species as a function of latitude, where individuals from higher latitude sites have significantly less sunscreen in the mucus than those from lower latitudes. It is likely that the dietary availability of MAAs varies over a latitudinal gradient (Karsten et al. 1998). However, the aforementioned differences in mucus absorbance between tidepool species with similar diets (and particularly the lack of compounds in *Xererpes fucorum* mucus) suggest that differential sequestration or secretion of MAAs, as well as differential dietary availability, may result in the latitudinal patterns found in this study. Experiments with coral reef fish have shown that fish fed an identical diet rich in MAAs sequester compounds in the mucus only in response to UV exposure (Zamzow in press). A study on the ovaries of sea urchins, however, found no UV exposure effect on MAA sequestration (Adams et al. 2001), so this ability to acclimate is clearly not universal across taxa.

The lack of UVB- and longer-wavelength UVA-absorbing compounds in the mucus of temperate tidepool fishes is noteworthy. Thirty-eight percent of tropical fishes (138 species surveyed from 25 families) have compounds in their mucus with $\lambda_{max}$ in the UVB range (J. P. Zamzow unpubl.). Whether the absence of these compounds in the mucus of temperate fishes is due to dietary limitations, or phylogenetic differences in sequestration ability, is unknown. Furthermore, there is no evidence for the secretion of longer-wavelength UVA compounds, such as palythene ($\lambda_{max}$ = 360 nm), into the mucus of temperate tidepool fishes, as has been found in many tropical species (59% of 138 species showed evidence of a compound with $\lambda_{max}$ = 360 nm, J. P. Zamzow unpubl.). The ocular media data (Table 4) demonstrate that temperate tidepool fishes are able to sequester longer wavelength UVA-absorbing compounds, and therefore these compounds must be available in the diet.

It is impossible to say with the data presented here whether the observed patterns of variability in mucus absorbance of different species is simply acclimatization to their habitat, or whether the ability to sequester large amounts of sunscreen may be a limiting factor determining the geographic distribution of sister species. Experimental manipulations might help to elucidate this question. Nonetheless, it does seem that tidepool sculpins are able to acclimatize to their UV environment, on both local and geographic scales.

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