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Temporal resolution in mesopelagic crustaceans

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Mesopelagic crustaceans occupy a dim-light environment that is similar to that of nocturnal insects. In a light-limited environment, the requirement for greater sensitivity may result in slower photoreceptor transduction and increased summation time. This should be reflected by a lower temporal resolution, as indicated by a lower critical flicker fusion frequency (CFF). Therefore, one would predict that the CFFs of mesopelagic organisms would be relatively low compared with those of their shallow-water relatives, just as nocturnal insects tend to have lower CFFs than diurnal insects. Using an electrophysiological apparatus that was adapted for shipboard use, the dark-adapted CFFs of a variety of species of mesopelagic crustaceans were determined using the electroretinogram. The parameter examined was the maximum CFF—the point at which further increases in irradiance no longer result in a faster flicker fusion frequency. The results summarized here indicate that there is a trend towards lower CFFs with increasing habitat depth, with some interesting exceptions.

Keywords: temporal resolution; vision; crustaceans; deep sea; flicker fusion

1. INTRODUCTION

Most studies on the visual acuity of mesopelagic species have been restricted to studies of spatial resolution (for a review, see Land 1990), which is a function of the structure of the eye. However, for species living in an environment such as the water column where their visual targets are never stationary, as would be the case in the mesopelagic zone, visual acuity depends on both spatial resolution and temporal resolution (Srinivasan & Bernard 1975). Temporal resolution is a function of the membrane properties of the receptor cells and must be measured in a living eye. For this reason, studies of mesopelagic species, which are difficult to collect and maintain alive, are quite rare.

2. METHODS AND RESULTS

The work reported here was conducted using an electrophysiological apparatus adapted for use at sea. Temporal resolution was studied by recording an extracellular signal called the electroretinogram, which is the summed response of a large number of receptor cells. This signal remains in synchrony with a flashing light stimulus until critical flicker fusion is achieved, which is defined as the stimulus rate at which the eye can no longer produce an individual response to each light flash. Because flicker fusion frequency depends on the stimulus intensity (Bröcker 1935; Crozier & Wolf 1939; Crozier *et al.* 1939), the characteristic used to compare temporal resolution between the various species in this study was the maximum critical flicker fusion frequency (maximum CFF), which is the highest flicker rate that the eye is capable of following at any intensity.

Organisms used in this study were collected with a trawl net with a light-tight, thermally insulated cod-end, which could be closed at depth. Animals were sorted under dim red light, and maintained in chilled, aerated seawater in the dark. Electrophysiological recordings were carried out as described in Frank (1999). Test flashes of 490 nm light were delivered to the dark-adapted eye via a fused silica light guide. The flicker rate and/or irradiance was increased until the maximum CFF was reached. Sufficient time was allowed between each stimulus to ensure that the eye remained fully dark adapted. Temperature was maintained at 7 °C for all experiments.

The results from the current study and a previous study (Frank 1999), are summarized in table 1. Four new species in two new families were examined: *Phronima sedenteria*, a hyperiid amphipod, and the only species with an apposition eye; *Pasiphaea multidentata*, a pasaphaeid shrimp; and the sergestids *Sergestes arcticus* and *Sergia grandis*. In addition, more data were obtained on several species used in the previous study (*Stylocheiron maximum*, *Funchalia villosa* and *Sergia filictum*). In total, there are data from 12 species of mesopelagic crustaceans from a variety of depths. With the addition of these new species, a trend is now apparent. In general, maximum CFF is higher in those species whose daytime depth is shallower than 600 m, compared with those species whose daytime depth range is deeper than 600 m (figure 1). As there is an inverse correlation between maximum CFF and sensitivity of the eye (Frank 1999), one might have predicted this trend, i.e. that maximum CFF would decrease with increasing habitat depth, much as the flicker fusion frequency of nocturnally active insects is lower than that of day-active insects (Autrum 1958). However, there are

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Table 1. *Approximate daytime depth ranges and maximum CFF of dark-adapted adult mesopelagic crustaceans*

(Equivalent optical depths in type 1A water were calculated for those species where the only available data were for type 1B water.)

family, genus and species	daytime depth (m)	water type[h]	maximum CFF ± s.e. (Hz)
Euphausiacidae			
Stylocheiron maximum	250–500[a]	1, 1A, 1B	40 ± 1.6 ($n = 7$)
Nematobrachion sexspinosus	400–600[a]	1, 1A, 1B	56 ± 2.0 ($n = 4$)[i]
Nematobrachion flexipes	450–600[a]	1, 1A, 1B	44 ± 1.0 ($n = 2$)[i]
Hyperiidae			
Phronima sedenteria	100–500[b]	1B	27 ± 1.0 ($n = 2$)
equivalent 1A depth	120–600		
Oplophoridae			
Janicella spinacauda	500–600[c]	1, 1A	31 ± 0.3 ($n = 3$)[i]
Oplophorus gracilirostris	500–650[c]	1, 1A	32 ± 0.5 ($n = 2$)[i]
Systellaspis debilis	600–900[c]	1, 1A	21 ± 0.6 ($n = 4$)[i]
Pasiphaeidae			
Pasiphaea multidentata	500–800[d]	1B	17 ± 1.0 ($n = 3$)
equivalent 1A depth	600–960		
Penaeidae			
Funchalia villosa	300–550[e]	1A	21 ± 0.9 ($n = 8$)
Sergestidae			
Sergestes arcticus	500–800[b]	1B	17 ± 1.3 ($n = 3$)
equivalent 1A depth	600–960		
Sergia filictum	600–900[e]	1, 1A, 1B	24 ± 1.0 ($n = 2$)
Sergia grandis	600–900[f,g]	1, 1A, 1B	22 ($n = 1$)

[a] Roger 1978; [b] T. M. Frank and E. A. Widder, unpublished data; [c] Hopkins *et al.* 1989; [d] Sardou *et al.* 1996; [e] Hopkins *et al.* 1994; [f] Donaldson 1975; [g] Flock & Hopkins 1992; [h] Jerlov 1976; [i] Frank 1999.

several exceptions to this trend, possibly explained by factors other than the downwelling light intensity.

As previously reported, the three krill species, all of which possess bilobed eyes, have the highest flicker fusion frequencies of any mesopelagic species studied to date, in spite of the fact that their depth distribution falls in the middle of the shallower (< 600 m) depth division (Frank 1999). All the krill species with bilobed eyes possess an elongated second and third thoracic appendage, which has been hypothesized to be an adaptation for active carnivorous feeding (Mauchline & Fisher 1969), and higher temporal resolution would enhance their tracking ability. However, the two euphausiid species with the deeper depth distributions (*Nematobrachion sexspinosus* and *Nematobrachion flexipes*) have higher maximum CFFs (and hence lower sensitivity) than the shallower-living species (*S. maximum*), which is contrary to what one would expect when considering only the downwelling light environment. In the mesopelagic realm, however, bioluminescence is an extremely common phenomenon, and it would not be surprising if bioluminescence had as strong an effect on the evolution of visual systems as downwelling light. Both *Nematobrachion* species specialize on bioluminescent prey, while the primary prey of *Stylocheiron* is not luminescent. The greater contrast provided by a bioluminescent organism against a dim background versus that provided by a dark organism implies that the *Nematobrachion* species might be able to sacrifice sensitivity (contrast detection) in return for greater temporal resolution (for a complete discussion, see Frank 1999).

The other exception to the general trend of higher temporal resolution in the shallower mesopelagic organisms is *F. villosa*. *F. villosa* has one of the shallowest depth distributions in the study (figure 1), and lives in fairly clear water, yet its dark-adapted maximum CFF (21 Hz) was one of the lowest in the study. However, *F. villosa* possesses screening pigments which change its eye optically from a spatially acute, apposition-like eye during the day to a less spatially acute superposition-like eye at night (Herring & Roe 1988). If screening pigment migration in *F. villosa* is accompanied by changes in the photoreceptor frequency response, then the temporal resolution of the eye would be higher in the light-adapted eye, as is the case for shallow-water crustacean species with mobile screening pigments (Crozier & Wolf 1939; Crozier *et al.* 1939; Bröcker 1935), as well as insects (for a review, see Laughlin 1990). This was the hypothesis originally put forth by Frank (1999) to explain the anomaly of such low temporal resolution in one of the shallower-living mesopelagic species. However, new data presented here indicate that this is not the case.

Five out of the eight dark-adapted experiments on *F. villosa* were conducted during the day, while three of them were conducted during the night. There was no difference between data collected during the day (maximum CFF = 20.6 ± 1.5 Hz (s.e.)) and those collected at night (maximum CFF = 20.7 ± 1.5 Hz), so in this species, daytime 'dark adaptation' appears to be as effective as night-time dark adaptation, at least with respect to flicker fusion frequency. Three light-adaptation experiments were also carried out with *F. villosa*. Maximum

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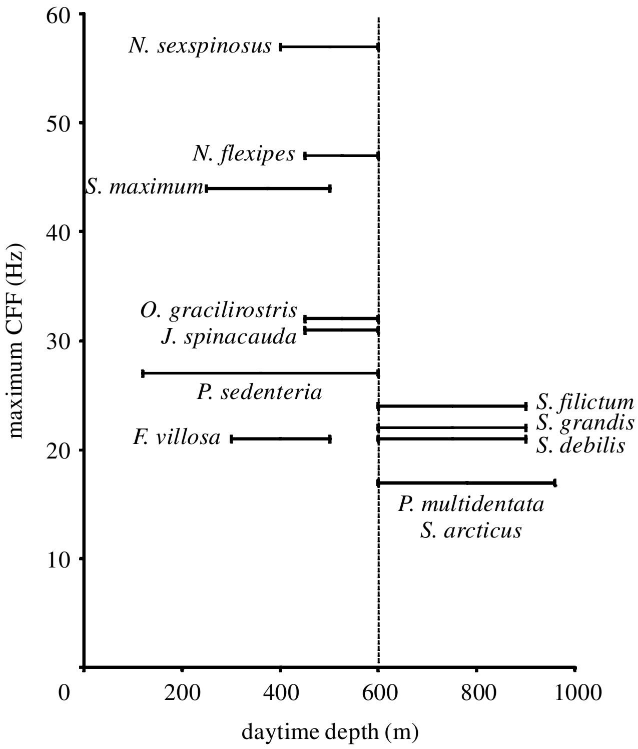
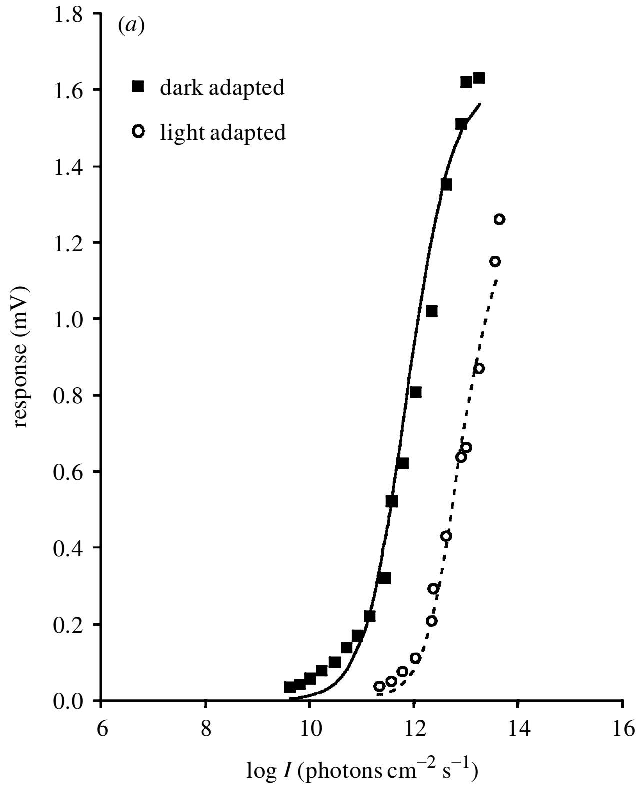


Figure 1. Maximum CFF as a function of daytime depth distribution in type 1 and 1A water. (For full genera names see table 1.)



(*b*)

	max CFF (Hz) (n = 3)
dark adapted	light adapted
20.3 (+/− 1.7)	21.3 (+/− 1.2)

Figure 2. Data from *F. villosa*. (*a*) Irradiance–response function from one individual under conditions of dark and light adaptation. Curves were calculated according to the well-known expression derived by Naka & Rushton (1966): $V/V_{\max} = I^n/(I^n + K^n)$ where here n is the slope of the near linear part of the $V/\log I$ function, I is the stimulus irradiance, K is the irradiance needed to produce a half-maximal response, V is the response amplitude and $V_{\max}$ is the maximum response amplitude. (*b*) Mean maximum CFFs for dark- and light-adapted eyes.

CFF was first determined in the dark-adapted eye using the methods described above, with light stimuli presented to the eye through one branch of a bifurcated light pipe. Subsequent to this, an adapting light illuminated the eye via the other branch of the bifurcated light pipe. Once the response of the eye had stabilized (between 1 and 2 h after onset of the adapting light), maximum CFF was again determined with light stimuli superimposed on the adapting light via the bifurcated light pipe. As shown by the representative example in figure 2*a*, the light adaptation reduced the sensitivity of the eye by 1.5–2 log units. However, this degree of light adaptation had no significant effect on the maximum CFF, which was 20.3 ± 1.7 Hz in dark-adapted eyes versus 21.3 ± 1.2 Hz ($n = 3$) in light-adapted eyes (figure 2*b*). Two of these light-adaptation experiments were conducted at night (maximum CFF = 21 ± 2.8) and one was conducted during the day (maximum CFF = 22), and again, time of day did not appear to affect the experimental results.

There are several possible explanations for the lack of an effect of light adaptation on the CFF of *F. villosa*. One is that this degree of light adaptation might have been insufficient, or of too short a duration, to induce significant changes in the photoreceptor frequency response. It may also be that this species does in fact have a very low temporal resolution, and factors other than the downwelling light intensity, such as the mode of bioluminescence of its prey or primary predator, may have been the driving force.

3. DISCUSSION

The available evidence indicates that mesopelagic crustaceans, in general, have photoreceptors with fairly low temporal resolution, as would be expected from organisms living in a light-limited environment, and comparable with those found in nocturnal insects (for references see Frank 1999). And, within the mesopelagic zone, the species whose daytime depth ranges are shallower than 600 m have better temporal resolution than those species whose depth ranges are deeper than 600 m. The exceptions to these trends are the bilobed krill species, whose unexpectedly high maximum CFFs may be correlated with their method of prey capture and the bioluminescence of their prey, and *F. villosa*, whose very low maximum CFF, for now, defies explanation.

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