

Temporal resolution in mesopelagic crustaceans

Tamara M. Frank

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 Temporal resolution in mesopelagic crustaceans

Tamara M. Frank

Division of Marine Science, Harbor Branch Oceanographic Institution, 5600 US 1 N, Fort Pierce, FL 34946, USA (*frank@hboi.edu*)

on of Marine Science, Harbor Branch Oceanographic Institution, 5600 US 1 N, Fort Pierce, FL 34946, USA (frank@hboi.ea
Mesopelagic crustaceans occupy a dim-light environment that is similar to that of nocturnal insects. In 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 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 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 lo 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 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 noctur 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 wa 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 meso-
pelagic crustaceans apparatus that was adapted for shipboard use, the dark-adapted CFFs of a variety of species of meso-
pelagic crustaceans were determined using the electroretinogram. The parameter examined was the
maximum CFF—the point at pelagic 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 resu 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 de

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

1. INTRODUCTION

1. INTRODUCTION
Most studies on the visual acuity of mesopelagic species
have been restricted to studies of spatial resolution (for a **HAVELOUS HOW**
Most studies on the visual acuity of mesopelagic species
have been restricted to studies of spatial resolution (for a
review see I and 1990), which is a function of the 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 eve However for species living in an have been restricted to studies of spatial resolution (for a under dim red light, and maintained in chilled, aerated
review, see Land 1990), which is a function of the seawater in the dark. Electrophysiological recordings
 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 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 mesonelagic zone, visual acuity depends on both spat 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 & targets are never stationary, as would be the case in the
mesopelagic zone, visual acuity depends on both spatial
resolution and temporal resolution (Srinivasan & re
Bernard 1975) Temporal resolution is a function of 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 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 mesomembrane properties of the receptor cells and must be
measured in a living eye. For this reason, studies of meso-
pelagic species, which are difficult to collect and maintain
alive are quite rare measured in a living e
pelagic species, which
alive, are quite rare. **2. METHODS AND RESULTS**

ELECTRODS AND RESOLTS
The work reported here was conducted using an electrophysiological apparatus adapted for use at sea.
Temporal resolution was studied by recording an extra-The work reported here was conducted using an
electrophysiological apparatus adapted for use at sea.
Temporal resolution was studied by recording an extra-
cellular signal called the electroretinogram which is the electrophysiological apparatus adapted for use at sea.
Temporal resolution was studied by recording an extra-
cellular signal called the electroretinogram, which is the
summed response of a large number of receptor cells. Temporal resolution was studied by recording an extra-
cellular 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 cellular 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, whi 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 eve can no 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. 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 i 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. 193 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 resolut 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 (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 the characteristic used to compare temporal resolution
between the various species in this study was the the
maximum critical flicker fusion frequency (maximum in
CEE) which is the bighest flicker rate that the eye is 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 canable of following at any intensity maximum critical flicker fusion free
CFF), which is the highest flicker r.
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, 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 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 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 under dim red light, and maintained in chilled, aerated of 490 nm light were delivered to the dark-adapted eye 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 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 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 eve remained fully dark 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 $7\degree C$ for all 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 experiments. 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

2. WETHODS AND RESOLTS
The work reported here was conducted using an shrimp; and the sergestids *Sergestes arcticus* and *Sergia*
ectrophysiological apparatus adapted for use at sea. *grandis*. In addition, more data were 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* 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 amphinod and the only species with an (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
annosition ever *Pasiphaea multidentata* a pasaphaeid 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* 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 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 (Stylocheiro 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*) 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 denths With the addition of these new 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 CEE 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 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 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 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 CEF and sensi-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 sensi-
tivity of the eye (Frank 1999) one might have predicted 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 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 tivity 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 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 dav-active insects (Autrum 1958) However, there are 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

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

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

^a Roger 1978; ^bT. M. Frank and E. A. Widder, unpublished data; "Hopkins *et al.* 1989; ^d Sardou *et al.* 1996; "Hopkins *et al.* 1994; ^fDonaldson 1975; ^gFlock & Hopkins 1992; ^hJerlov 1976; ⁱ Frank 1999.

several exceptions to this trend, possibly explained by
factors other than the downwelling light intensity several exceptions to this trend, possibly explair
factors other than the downwelling light intensity.
As previously reported, the three krill species As previous to this trend, possibly explained by
As previously reported, the three krill species, all of
As previously reported, the three krill species, all of
bich possess bilobed eves, have the highest flicker fusion

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 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 (ϵ 600 m) depth frequencies of any mesopelagic species studied to date, in spite of the fact that their depth distribution falls in the middle of the shallower $(<600 \text{ m})$ depth division (Frank 1999) All the krill species with bilobed ev spite of the fact that their depth distribution falls in the was one of the lowest in the study. However, F villosa
middle of the shallower $(< 600 \text{ m})$ depth division (Frank possesses screening pigments which change it elongated second and third thoracic appendage, which 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 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 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 cuphausiid species with the 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 sershinosus* and higher temporal resolution would enhance their tracking
ability. However, the two euphausiid species with the
deeper depth distributions (*Nematobrachion sexspinosus* and
Nematobrachion flexibes) have bigher maximum CEEs *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-livi 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 *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 env hence lower sensitivity) than the shallower-living species (*S. maximum*), which is contrary to what one would expect when considering only the downwelling light environ-
ment. In the mesonelagic realm, however, hiolumines when considering only the downwelling light environment. In the mesopelagic realm, however, biolumineswhen considering only the downwelling light environ-
ment. In the mesopelagic realm, however, biolumines-
cence is an extremely common phenomenon, and it
would not be surprising if bioluminescence had as strong ment. In the mesopelagic realm, however, biolumines-
cence 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 downcence 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 down-
welling light. Both *Nematohrachion* species specialize on would not be surprising if bioluminescence had as strong presented here indicate that this is not the case.

an effect on the evolution of visual systems as down-

Welling light. Both *Nematobrachion* species specialize on an effect on the evolution of visual systems as down-
welling light. Both *Nematobrachion* species specialize on
bioluminescent prey, while the primary prey of
Stylocheiron is not luminescent. The greater contrast welling 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 bioluminescent prey, while the primary prey of the *Stylocheiron* is not luminescent. The greater contrast diprovided by a bioluminescent organism against a dim (m *Stylocheiron* is not luminescent. The greater contrast diprovided by a bioluminescent organism against a dim (n
background versus that provided by a dark organism at
implies that the *Nematobrachion* species might be able 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 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 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). greater temporal resolution (for a complete discussion,

factors other than the downwelling light intensity.
As previously reported, the three krill species, all of isms is *F. villosa. F. villosa* has one of the shallowest depth
which possess bilobed eyes, have the highest flic The other exception to the general trend of higher
moral resolution in the shallower mesonelagic organ-The other exception to the general trend of higher
temporal resolution in the shallower mesopelagic organ-
isms is F villegg F villegg has one of the shallowest denth The other exception to the general trend of higher
temporal resolution in the shallower mesopelagic organ-
isms is *F. villosa*. *F. villosa* has one of the shallowest depth
distributions in the study (figure 1) and lives isms is F *villosa*. *F villosa* has one of the shallowest depthisms 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 (21Hz)
was one of the lowest in the study However 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 eve 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 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 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 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 $F \frac{vil\log s}{s}$ is accompanied by chang 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 temp eye at night (Herring & Roe 1988). If screening pigment migration in $F.\,vildes a$ 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 speci 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 1939resolution 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 insect 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 I aughlin 1990). This was the hypothe 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 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 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 anomaly of such low temporal resolution in or
shallower-living mesopelagic species. However, a
presented here indicate that this is not the case.
Five out of the eight dark-adanted experiments allower-living mesopelagic species. However, new data
esented here indicate that this is not the case.
Five out of the eight dark-adapted experiments on
willow were conducted during the day while three of

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 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 *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 CEF – 20.6 + 1.5 Hz $(s e)$) and those collected 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 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 effec-(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 effec-
tive as night-time dark adaptation at least with r 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 e 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. Ma to flicker fusion frequency. Three light-adaptation experi-

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

see table 1.)
CFF was first determined in the dark-adapted eye using the methods described above, with light stimuli presented 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 th 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 pip 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 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 CEE was 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 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 b 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 $2a$, the light again determined with light stimuli superimposed on the adapting light via the bifurcated light pipe. As shown by
the representative example in figure $2a$, the light
adaptation reduced the sensitivity of the eye by 1.5–2 log
units. However, this degree of light adaptation had the representative example in figure $2a$, 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 CEE which was 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
 $20.3+1.7 \text{ Hz}$ in dark-adapted eyes versus $21.3+1.2 \text{ Hz}$ 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 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 $(n=3)$ in light-adapted eyes (figure 2b). Two of these ($n = 3$) 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 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 (maximum $CFF = 21 \pm 2.8$) and one was conduc
during the day (maximum $CFF = 22$), and again, time
day did not appear to affect the experimental results.
There are several possible explanations for the lack 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 hav 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 i 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 photorecentor frequency resp 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 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 resolu-
tion and factors other than the downwelling the photoreceptor frequency response. It may also be that
this species does in fact have a very low temporal resolu-
tion, and factors other than the downwelling light intensity,
such as the mode of biolyninescence of its 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 tion, 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

3. DISCUSSION
The available evidence indicates that mesopelagic crus-S. DISCUSSION
The available evidence indicates that mesopelagic crus-
taceans, in general, have photoreceptors with fairly low taceans, in general, have photoreceptors with fairly low
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Figure 2. Data from *F. villosa.*(*^a*) Irradiance^response 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 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 & Rusht 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*/*I*_{*O*}*n*</sub> *L*^{*n*}(*I*^{*n*} + *K*^{*n*}) where here *n* is the slope of the near linear part of the *V*/*I*_{*O}* well-known expression derived by Naka & Rushton (1966):
 $V/V_{\text{max}} = I^n/(I^n + K^n)$ 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 prod $V/V_{\text{max}} = I^n/(I^n + K^n)$ where here *n* is the slope of the near part of the $V/\log I$ function, *I* is the stimulus irrad K is the irradiance needed to produce a half-maximal response *V* is the response amplitude and *V* is linear part of the $V/\log I$ function, *I* is the stimulus irrad 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 maxim *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-adanted eves response, *V* is the response amp
maximum response amplitude.
dark- and light-adapted eyes.

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
 $\frac{600 \text{ m}}{2}$ have better temporal resolution than dark- and light-adapted eyes.

temporal resolution, as would be expected from organ-

isms living in a light-limited environment, and compartemporal resolution, as would be expected from organisms living in a light-limited environment, and compar-
able with those found in nocturnal insects (for references 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 mesonelagic zone the isms 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 denth ranges are shallower than able 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 speci 600 m have better temporal resolution than those species 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 excep-
tions to these trends are the bilobed krill species whose 600 m have better temporal resolution than those species
whose depth ranges are deeper than 600 m . The excep-
tions to these trends are the bilobed krill species, whose
unexpectedly high maximum CFEs may be corr 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 prev capture and the bioluminestions to these trends are the bilobed krill species, whose
unexpectedly high maximum CFFs may be correlated
with their method of prey capture and the bioluminesunexpectedly high maximum CFFs may be correlated
with their method of prey capture and the biolumines-
cence of their prey, and *F. villosa*, whose very low
maximum CEF for now defies explanation with their method of prey capture and the cence of their prey, and *F. villosa*, whose maximum CFF, for now, defies explanation.

maximum CFF, for now, defies explanation.
I thank the captains and crews of the research vessels *Edwin Link* I thank the captains and crews of the research vessels *Edwin Link*
and *Suncoaster* for their help with animal collections, and Tracey
Sutton and Jose Torres for allowing me to participate on their I thank the captains and crews of the research vessels *Edwin Link*
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cruises This work was f and *Suncoaster* for their help with animal collections, and Tracey
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