

Zooplanktivory by a nocturnal coral-reef fish: Effects of light, flow, and prey density

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Abstract

Visual predation by nocturnal zooplanktivorous fish is assumed to be sufficiently limited to allow the evolution of vertical migration as means for predation avoidance by zooplankton. However, in situ measurements of predation rates by nocturnal fish are lacking. Most of our knowledge of this predation is based on stomach contents and laboratory experiments. Our objectives were to measure the in situ rate of zooplanktivory by a common, nocturnal coral-reef fish, *Apogon annularis*, and to assess, through laboratory and field experiments, the effects of light, prey density, and flow on the fish's predation. In situ, the fish selectively fed on large zooplankton (>1 mm) at a rate of 0.12 prey min⁻¹, or 52% efficiency. Predation rates increased linearly with prey density, with no apparent effects of current speed and light intensity. Flume experiments indicated that feeding rates were saturating at a level corresponding to that found at 3 m depth on a moonless night and were negligible at >18 m. Predation rates by *A. annularis* were two orders of magnitude lower than those of diurnal fishes; however, the difference in carbon gain was largely offset by the greater size of nocturnal prey. Nocturnal vision in *A. annularis* is sufficiently sensitive to allow a remarkable detectability of large prey in its natural habitat. If this fish is representative of other nocturnal fishes, reconciliation between the potential for substantial nocturnal predation, as is demonstrated in the present study, and the evolution of vertical migration in large zooplankton could be related to the total abundance of those fishes and their depth distribution. Both parameters are as yet poorly known.

Predation on zooplankton by fish is a major trophic pathway in aquatic communities. In lakes, this predation, or its absence, can determine the overall trophic state of the ecosystem (Kerfoot and Sih 1987). In marine benthic communities, it can affect larval recruitment (Roughgarden et al. 1988) and the import of allochthonous carbon (Hamner et al. 1988) and nutrients (Bray et al. 1981).

It is widely accepted that zooplankton detection by visual predators is much reduced at night (O'Brien 1987; Giske et al. 1994) and that this reduction is the main reason for the evolution of zooplankton diel vertical migration in lakes (e.g., Gliwicz 1986), oceans (e.g., Bollens and Frost 1989), and coastal waters (Alldredge and King 1985). De Robertis et al. (2000) showed that large zooplankton ascend to the

upper water column later at night than small individuals, apparently because of their higher detectability under twilight conditions. Similarly, Onsrud and Kaartvedt (1998) suggested that the reason krill retain low-intensity isolum at night is an adaptation to avoid visual predation.

Although the above behaviors indirectly indicate that visual predation during the night is important, no direct, in situ measurements of predation rates are available. Most of our knowledge of in situ zooplanktivory by nocturnal fishes is based on stomach contents (Hobson and Chess 1976; Gladfelter 1979; Marnane and Bellwood 2002), and the effects of environmental factors on this predation are, by and large, based on laboratory experiments (Bergman 1988; Macy et al. 1998; Ryer and Olla 1999).

Although both diurnal and nocturnal fish are selective for large planktonic prey (O'Brien 1987), nocturnal fish feed primarily on zooplankton longer than ~2 mm, with a modal prey size >5 mm (Hobson and Chess 1978; Gladfelter 1979; Sudo and Azeta 1992). Mostly because of their characteristic large size, demersal zooplankton usually make up a major part of the diet of nocturnal fish (Hobson and Chess 1976, 1978; Marnane and Bellwood 2002).

The effect of light on nocturnal predation by juvenile walleye pollock and sablefish was studied in the laboratory by Ryer and Olla (1999). Predation rates by these fish increased with increasing light intensity, exhibiting a threshold

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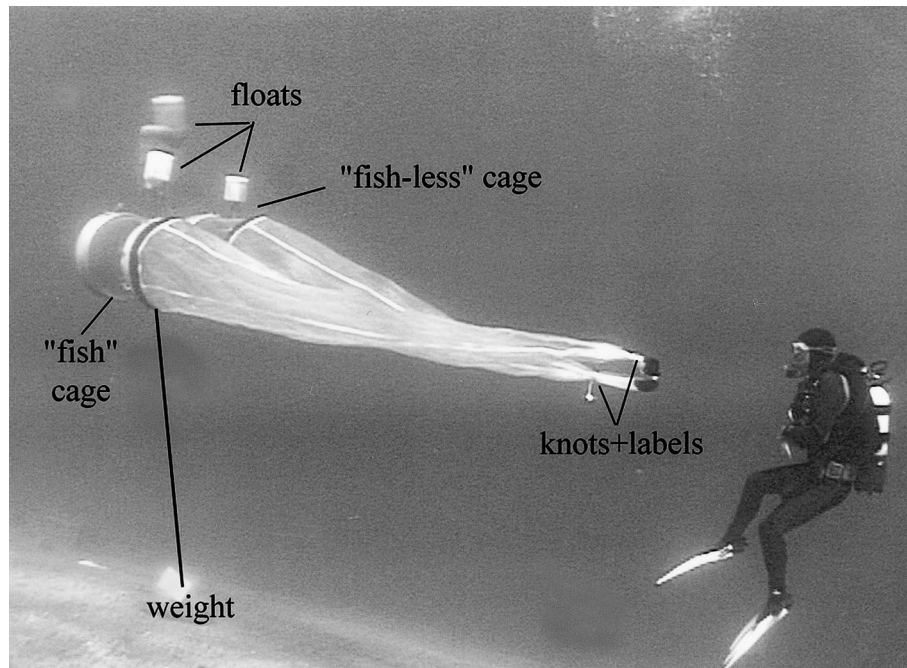


Fig. 1. The Bongo experimental setup located at 3 m above bottom and 3 m beneath the sea surface (picture taken during daytime). Heavy ballast and a set of floats were used to keep the setup tight at a constant depth and to keep the cages horizontal. A cod end was too heavy to use, so a string was used to tie chalk the net ends and to label the fish and fishless nets. Note the current direction (current speed, $\sim 6 \text{ cm s}^{-1}$).

below which no visual predation occurred. The threshold was species specific, ranging from light levels on a moonless night at 20 m depth to that of a full moon at the surface, whereas the relationships between light and predation rates reflected the light dependency of the fish's reactive distance (O'Brien 1987 and references therein). Nocturnal fishes can use senses other than vision to detect prey, including mechanoreceptors (Montgomery and Macdonald 1987; Janssen 1997), electroreceptors (Wilkens et al. 2001), and, possibly, chemical cues (Von Der Emde and Bleckmann 1998; Wilkens et al. 2001). However, nonvisual senses require a close proximity to the prey, typically below a few centimeters (Janssen 1997; Ryer and Olla 1999), compared with $>10 \text{ cm}$ in visual nocturnal predation (O'Brien 1987). Therefore, in situations where prey density is below saturation and light is sufficient, visual predation is expected to be more effective.

Given the high abundance of large zooplankton in the upper water column at night, one would expect a utilization of this vast resource to evolve. Fish capable of foraging effectively under low light conditions would gain enormously. Herein we report on the rates of in situ zooplanktivory by a common, nocturnal coral-reef fish, *Apogon annularis* (Rüppell 1829) and assess, through laboratory and field experiments, the effects of light, prey density, and flow on its predation.

Methods

A. annularis—Apogonid fishes dominate the guild of nocturnal planktivores in Indo-Pacific coral reefs, where they

are most abundant in lagoons and the leeward sections of the reef (Hobson and Chess 1978; Marnane and Bellwood 2002). *A. annularis* is a small (7–10 cm) planktivore reef fish, with large eyes ($\sim 5 \text{ mm}$ diameter, or 47% of head length) and a moderately large mouth ($\sim 8 \text{ mm}$). During the night, the fish forages either individually or in small groups in the shallow waters above the coral reef, exhibiting intermittent bursts and drift intervals, with a general retention of their position relative to the reef for at least a few minutes (R. Holzman unpubl. observations). During the day, the fish hide in deep crevices and caves.

Study site—The field study was carried out at the coral reef in front of the Steinitz Marine Biology Laboratory ($29^{\circ}30' \text{N}$, $34^{\circ}56' \text{E}$), Eilat, Red Sea. The local coral reef community has been described by Fishelson (1971), Benayahu and Loya (1977), and Rilov and Benayahu (2000). In brief, it is a flourishing reef dominated by stony corals extends on a steep ($10\text{--}30^{\circ}$) slope from the subtidal zone to $>50 \text{ m}$. Zooplankton abundance approximately doubles during the night. Larger individuals (trapped on a $200\text{-}\mu\text{m}$ mesh) consisted most of the nocturnal increase, with the fraction trapped on a $500\text{-}\mu\text{m}$ mesh appearing almost exclusively at night (Yahel et al. 2002).

Stomach contents—Nineteen *A. annularis* were collected $\sim 2 \text{ h}$ after sunset, on three full-moon and four moonless nights (9 and 10 fish, respectively), at 2–3 m depth, using a hand net. Within 1 h, the fish were brought to the laboratory, measured (standard and total length), weighed, and dissected to remove the stomach contents, which were immediately

preserved in 4% buffered formaldehyde in seawater. Later, the preserved contents were recorded using a video camera (Watec 902H CCD) mounted on a dissecting microscope (Wild). The recorded prey were sorted and their body size measured using the video analysis software ImagePro (version 4; Media Cybernetics). The prey were sorted into eight taxonomic groups: decapods, mysids, copepods, zoea larvae, tanaids, brachyuran megalopa, polychaetes, and a pooled group of all other prey (<11% of the sample).

In situ experiment—A Bongo net, 70 cm in diameter (General Oceanic) was used as a frame for a pair of underwater cages in which the fish were kept during the experiment (Fig. 1). The cylindrical cages (120 cm long and 69.8 cm diameter) were made of hard-wire net (1.2 cm mesh size). Each cage was attached and slightly inserted into the downstream side of one of the paired Bongo rings. The original zooplankton net (335 μm mesh size) was attached behind (downstream of) each cage. One cage was inhabited by three *A. annularis*, whereas the other contained no fish. Each cage contained a small plastic box (20 \times 10 \times 10 cm) that was open on both sides, in which the fish hid during the day. Using a heavy ballast weight and a large subsurface float, the Bongo frame was moored suspended 3 m above the bottom (total water depth, 6 m). The swivels of the original Bongo net ensured that the net was constantly facing into the current as long as the speed was $>4 \text{ cm s}^{-1}$. In this position, the two nets trapped zooplankton after they had passed through the cages. Thus, the net downstream of the empty cage (the fishless net) sampled the ambient zooplankton density, whereas the fish net sampled the zooplankton surviving the predation by the caged fish. The difference between the two samples was considered to be an estimate of the prey the fish consumed during the duration of the run (85–100 min; mean \pm standard deviation, 91 ± 7 min). The quality of this estimate was evaluated in a series of control experiment during which both cages were kept fishless. A total of 20 runs with fish and 9 without were carried during June 2000–July 2001. For logistical reasons, we could use only nine different triplicates of *A. annularis*, so that each triplicate was used in 1–4 consecutive runs.

The fish were caught and transferred to the cages, to acclimatize in the Bongo cage for at least 24 h. The selection of the fish and fishless cages alternated between different groups. The experiments started at least 1 h after sunset. A pair of SCUBA divers simultaneously attached a plankton net to the downstream end of each cage and immediately retreated to the shore for the duration of the run. At the end of the run, the two divers returned to the site, simultaneously choked closed the two nets, removed them from the frame, and retrieved them to shore. On shore, the zooplankton were transferred to glass jars and preserved in buffered 4% formaldehyde solution with seawater (Omori and Ikeda 1984). To minimize disturbance to the fish, no artificial light was used throughout the underwater operation.

Analysis of the stomach contents indicated that large zooplankton retained on a 1-mm mesh made up, on average, $85.3\% \pm 8.6\%$ of the fish diet (see “Results” section). Therefore, prior to the microscopic sorting, the preserved Bongo net samples were separated, using a 1-mm sieve, into

two fractions of large and small zooplankton. The latter fraction, from which the fish were expected to eat very little, was used as an internal control to examine for inherent differences between the Bongo’s right and left nets. Although the fraction of large zooplankton was always fully counted, the fraction of the smaller animals, which typically consisted of thousands of specimens, was subsampled using a Stempel Pipette (Omori and Ikeda 1984) prior to counting. Each subsample consisted of >250 animals. Replicated counts of different aliquots from the same sample differed by $<10\%$. The animals were sorted to the same taxonomic groups as the stomach contents (see above).

Light was measured in situ, using a sensitive photo sensor (Hamamatsu H6780; Hamamatsu Photonics) for which we built an underwater housing with a bore-silica glass window. Measurements were made by the divers immediately before and after each run. Each measurement consisted two readings: one of the downwelling light, for which the sensor was oriented upward, and the other of the horizontal-forward light, for which the sensor was oriented directly upstream. Because these two measurements were highly correlated (Pearson’s $r = 0.98$, $df = 14$, $P < 0.001$), only the downwelling value is reported herein.

An acoustic Doppler current profiler (600 KHz ADCP; RD Instruments) or an electromagnetic current meter (model S4; InterOcean) were deployed ~ 15 m away from the Bongo nets, to measure the current velocity during each run at the same depth. The samples were discarded if the currents became weaker than 4 cm s^{-1} .

Because traditional flow meters used in zooplankton nets do not function reliably at weak flow levels, the volume of water filtered by the Bongo nets was calculated on the basis of the measured currents during the run and the knowledge of the net’s filtration efficiency at different flow speeds. The net’s efficiency was measured in a separate set of runs (without fish) for which the flow through the Bongo net was compared with the ambient current speed. The former was measured using a MicroADV (Acoustic Doppler Velocimeter; Sontek) attached on the outer side of the Bongo net frame and oriented to measure the flow at the center of Bongo net’s mouth. In the range of ambient currents of $4\text{--}20 \text{ cm s}^{-1}$, the two parameters were highly correlated (linear regression, $F_{1,67} = 1,514$, $P < 0.001$, $r^2 = 0.96$), following the regression curve

$$V_{\text{net}} = 0.81 \times V_{\text{ambient}} + 0.16$$

Flume experiments—The feeding rate of *A. annularis* was measured under controlled flow and light conditions in a laboratory flume. We used the flume described by Kiflawi and Genin (1997). In brief, this recirculating flume was 320 liters in volume, 2 m long, 30 cm wide, and 30 cm deep. The sides of the working section were made of transparent glass. The flow was generated with a propeller with an electric frequency controller. Two plastic-coated fencing screens (1 \times 1 cm mesh size) were placed in the downstream end of the working section, delimiting a 30-cm experimental arena through which the fish could move. Runs were made with a single fish in the flume. The fish motions were recorded using an infrared (IR)–sensitive video camera (Watec 902H

with a Tamron zoom lens 8–80 mm f/1.8). A mirror attached above the working section inclined 45° allowed us to track the fish movements in three dimensions (Kiflawi and Genin 1997). Three molded packages, each of which contained 30 light-emitting diodes, were used as a submersible source for IR illumination (880 nm). An external 25-W halogen lamp, controlled by a potentiometer, was used as a source of ambient visible light. The light in the flume was characterized using a fiber optic spectrometer (USB2000; Ocean Optics), indicating a similarity in the spectral properties of the different light levels (except the lowest intensity, which was undetectable with that instrument). Especially important was the similarity in the range of rod visual pigments of nocturnal reef fish (480–500 nm; McFarland 1991). The IR illumination had no apparent effect of the fish's feeding rates (Ryer and Olla 1999; see "Results" section), and its intensity was not recorded.

All experiments were run at a single flow speed (4 cm s⁻¹) and six light levels: 1×10^{-6} , 1.5×10^{-5} , 4.6×10^{-5} , 8.9×10^{-5} , 1.8×10^{-4} , and 4.4×10^{-4} $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. These levels ranged from the level of light at 20 m in a clear moonless night through the level on a full-moon night near the surface (Macy et al. 1998; R. Holzman unpubl. data). Light was measured outside the flume with the aforementioned light meter.

The fish were acclimatized in the flume for >24 h before the experiment started. During acclimatization, the natural day-night cycle was retained by illuminating the flume with dim light (4.6×10^{-5} $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) for 14 h, overlapping the night hours outside, followed with 10 h of full light, generated by four neon lamps. A small (10 × 5 × 5 cm) plastic cube provided a dark shelter in which the fish could hide during the 10 "day" h. During the dark hours, the flow speed was occasionally raised to 8–12 cm s⁻¹ for 15–20 min, to acclimatize the fish to variations in the flow. A total of 12 fish were used. For each fish, the feeding rate was measured once under each of six light levels (listed above). It took about ~3 d to complete the runs for a single fish.

Prey used in the experiment were live, adult, nonbreeding brine shrimp (*Artemia salina*), ~1 cm in length. Each fish was fed with 15 *Artemia* immediately after its transfer to the flume and maintained unfed for 24 h prior to the run. At the start of a run, 15 *Artemia* were put in the flume by gradually releasing them above the flume's propeller while the flume was running at 4 cm s⁻¹. The fish were allowed to feed for precisely 80 s from the time the first prey entered the working section. During that period, all 15 *Artemia* passed the fish once (it took 90 s for the water to make a complete turn of the flume). Considering that 288 liters of water passed by the fish during those 80 s, the fish was exposed to an "apparent" prey density of 52 m⁻³, more than an order of magnitude higher than that in nature (see below).

The run was terminated by inserting a plankton net (100 μm) into the flume, upstream of the fish, on which the fish immediately escaped to its shelter. The net, mounted on a square aluminum frame to tightly fit the flume's inner cross-section, was used to collect the *Artemia* that survived predation by filtering the flume water for 5 min after enhancing the flow speed to 8 cm s⁻¹. The retrieval efficiency in control

runs, without fish in the flume, was $99\% \pm 2\%$ ($n = 27$; 12 in the lowest light level and 2–3 in each of the other levels). The number of prey lost in a control run never exceeded one *Artemia*.

The video records were processed using a personal computer equipped with a frame grabber (Mvc Ic-Pci; Imaging Technologies) and image analysis software (Imagepro for windows version 4.0; Media cybernetics). Because both the fish and the prey were seen in the video, we could measure the strike distance, defined as the distance between the fish and the *Artemia* when the attack started, and the strike angles, both in three dimensions (Kiflawi and Genin 1997). The handling time, defined as the time it took the fish to strike and consume a single prey, was measured as well.

Because *Artemia* are different from natural prey, specifically in their lack of escape response, no inference on the fish's absolute rates of predation at sea should be made. On the other hand, the use of an identical prey under different illumination levels was appropriate to elucidate the mechanistic effect of light intensity, and the lack of escape response in *Artemia* allowed accurate measurements of strike distances.

To study the fish swimming behavior when prey were not present, their motions were recorded with the aforementioned IR video for several minutes prior to each run. A subsample of six randomly selected fish was analyzed in these records. The parameter measured for each fish was the proportion of time of active fin movement during five intervals, each 10 s long, at each of the six light levels (a total of 30 measurements per fish).

Statistical analysis—Because each fish was tested for feeding rates at all six levels of light intensities, a repeated-measures analysis of variance (ANOVA) was used to test for the effect of light on the feeding rate and strike distance. The effect of light intensity on the proportion of time of active fin motions was also tested using repeated-measures ANOVA, with light intensity (six levels) and the replicate (each of the five 10-s intervals) as repeated measured factors. The compliance with the sphericity assumption (Rao 1998) was verified in both analyses.

The total number of strikes executed by a fish was different at different light levels. Hence, data on the effect of light on strike's distance and speed were not balanced. To make the statistical design balanced, a single strike was used for each fish for each light level, arbitrarily selected as the most horizontal strike in the run (the one with minimal vertical displacement).

For all other analysis, ANOVA and Student's *t*-test were used after testing for homogeneity of variance using the Cochran statistics. Because of nonhomogeneity of variance, the Wilcoxon matched-pairs test was used to test the difference in the number of zooplankton between the two Bongo nets in the control runs and to test the effect of IR illumination on the fish's feeding rate in the flume. Similarly, the Mann-Whitney *U*-test was used to test the effect of moonlight on stomach contents of the fish.

A χ^2 test was used to compare the distribution of the strike angles in the flume to a homogenous distribution. Observed strike angles in each of the plains (*XY*, *YZ*) were grouped in

18 bins of 10° each. The expected number of strike angles in each bin was calculated by dividing the total number of strikes by the number of bins. Strike angles in the XY plane were plotted against those in the YZ plane, to test for an interaction between the two (e.g., such that a narrow angle in one plane is associated with a narrow angle on the other). All the statistical analyses were done using Statistica software (version 6.0 for Windows; StatSoft).

Results

Stomach contents—The number of prey in the fish stomach did not differ (Mann-Whitney U -test, $P > 0.18$, $n = 19$) between moonless nights (average, 42.8 ± 34.1 stomach $^{-1}$, $n = 10$) and full-moon nights (25.1 ± 17.7 stomach $^{-1}$, $n = 9$). Similarly, the prey eaten on dark nights were not significantly larger (Mann-Whitney U -test, $P > 0.16$, $n = 19$) than those eaten on full-moon nights (average median lengths, 3.29 ± 0.41 and 2.76 ± 0.80 mm, respectively). Overall, the median length of the prey in the fish stomachs was 3.01 mm ($n = 655$, average 3.49 ± 1.98 mm). More than 90% of the prey were longer than 1.6 mm.

Three groups—Polychaeta, Decapoda, and Amphipoda—made up $\sim 60\%$ of the fish diet (392 of 656 prey). Altogether, taxa that included many demersal species (Polychaeta, Stomatopoda, Amphipoda, Cumacea, Molluska, Megalopa, Tanaidacea, and Isopoda but not Decapoda) made up 66% of the prey. Neither eggs nor appendicularia were found in the stomachs we analyzed, although both taxa were abundant in the ambient waters (forming $21.3\% \pm 14.9\%$ and $4.7\% \pm 3.9\%$, respectively, of the fraction of “big” zooplankton sampled with our fishless Bongo net).

In situ experiment—The number of large zooplankton (retained on 1-mm mesh) was significantly lower in the net with fish than in the fishless net (one-tailed paired t -test, $P < 0.005$, $df = 19$). The mean difference between the two nets was 28.3 ± 38.7 prey ($n = 20$), equivalent to $25.6\% \pm 36.1\%$ of the catch in the fishless net.

The “internal control,” based on the counts of small zooplankton (passing through 1 mm mesh), indicated no significant difference (t -test, $P > 0.8$, $df = 14$) in zooplankton abundance between the fish and fishless nets (mean difference, $2.3\% \pm 8.0\%$). Similarly, no significant (Wilcoxon matched-pairs test, $P > 0.9$, $n = 9$) internet difference was found in the control runs without fish (mean difference, $1.5\% \pm 6.5\%$). Two of the 20 runs with fish yielded substantially more prey in the fish net, by far (2 and 8 times) exceeding the internal and fishless controls, indicating “negative” feeding. These two obvious outliers were excluded from the calculations of the fish’s feeding rates described below. This exclusion hardly affected ($<10\%$) the resulting values.

The fish’s feeding rate (0.12 ± 0.11 prey min^{-1} fish $^{-1}$, $n = 18$) was significantly correlated ($F_{1,16} = 45.7$, $P < 0.001$, $r^2 = 0.72$) with ambient prey density, following the regression equation

$$FR = 0.206D \quad (1)$$

where FR is feeding rate (in prey min^{-1}) and D is the prey density (in prey m^{-3}) (Fig. 2A). No correspondence between

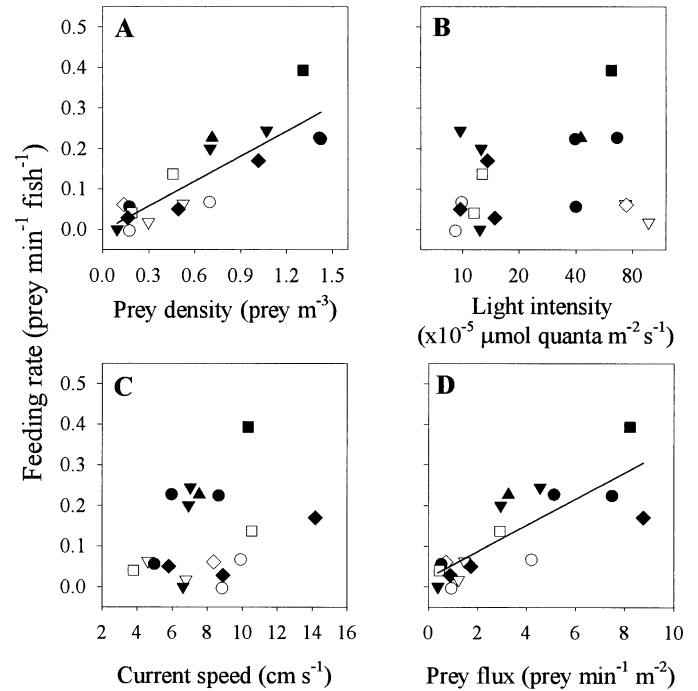


Fig. 2. In situ feeding rates as a function of (A) ambient prey density (zooplankton >1 mm), (B) light intensity, (C) current speed, and (D) prey flux. Each symbol indicates a different group of fish. Feeding rates correlated best with prey density ($F_{1,16} = 45.7$, $P < 0.001$, $r^2 = 0.72$), and the correlation can be described by the empirical equation $FR(\text{prey min}^{-1} \text{ fish}^{-1}) = 0.206 \times (\text{prey m}^{-3})$.

feeding rate and either light intensity or flow speed was apparent (Spearman $r = 0.19$ and 0.27 , respectively, $n = 18$; Fig. 2B,C). When current speed was multiplied by prey density, resulting in prey flux (Fig. 2D), the r^2 value decreased from 0.72 (for density alone) to 0.65. This could have resulted from a compounding effect of noise or a nonlinear effect of current (Hill and Grossman 1993; Kiflawi and Genin 1997), as is discussed in the “Discussion” section.

No taxonomic selectivity was apparent within the fraction of large zooplankton, with the proportions of the preyed taxa similar to those in the ambient water. Therefore, the values of the Chesson index for selectivity were not significantly different from the expected under random selectivity for each of the preyed taxa (t -test, $P > 0.1$, $df = 19$). The most abundant taxa in the fraction removed by the fish included decapods, zoea, fish larva, amphipods, and megalopa larva, which accounted for 85% of the removed individuals. The density of fish eggs and appendicularia, both of which were absent from the fish stomachs, did not differ between the fish and fishless samples (t -test, $P > 0.5$, $df = 19$ for eggs and $P > 0.16$, $df = 8$ for appendicularia). No correlation was found between light level and the ambient abundance of zooplankton sampled with the fishless net (Spearman $r = 0.05$, $P > 0.8$, $df = 28$).

Flume experiments—An increase in light intensity significantly affected both the feeding rate (ANOVA, $F_{5,55} = 28.28$, $P < 0.001$) and strike distance (ANOVA, $F_{5,10} = 5.61$, $P < 0.01$) (Fig. 3). The best fit of both parameters with light

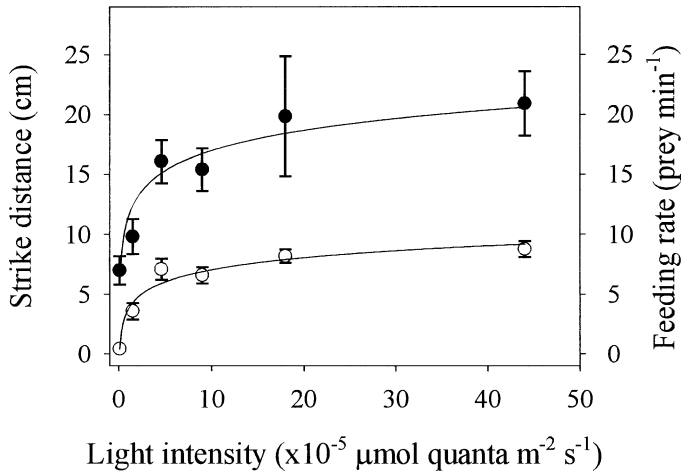


Fig. 3. The effect of light intensity on *A. annularis* strike distance (left axis; filled circles) and feeding rate (right axis; open circles) in a recirculating flume. A log-linear regression line was fitted to the means of all fish. Strike distance can be described as, strike distance (in cm) = $2.43 \times \ln[\text{light intensity } (\mu\text{mol quanta m}^{-2} \text{s}^{-1})] + 39.37$ (log-linear regression, $F_{1,4} = 42.5$, $P < 0.005$, $r^2 = 0.914$). Feeding rate can be described as, $FR(\text{prey min}^{-1}) = 1.44 \times \ln[\text{light intensity } (\mu\text{mol quanta m}^{-2} \text{s}^{-1})] + 20.3$ (log-linear regression, $F_{1,18} = 86.7$, $P < 0.001$, $r^2 = 0.955$). Error bars represent standard errors.

intensity was logarithmic, with the steepest response in the range of $0.1\text{--}4.6 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and an apparent saturation at higher levels (Fig. 3). The strike distance was best described by

$$L_r = 2.4 \times \ln(E) + 39.3 \quad (2)$$

where L_r is the strike distance (in cm) and E is the light intensity (in $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) (log-linear regression, $F_{1,4} = 42.5$, $P < 0.005$, $r^2 = 0.91$). The feeding efficiency, calculated as the proportion of the prey captured from the 15 *Artemia* introduced, increased from a negligible level ($<2\%$) at $10^{-6} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, to 45% at $4.6 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, to 57% at maximal light intensity. Because the strike speed ($12.8 \pm 3.6 \text{ cm s}^{-1}$) was not affected by changes in light intensity (ANOVA, $F_{5,10} = 0.81$, $P > 0.56$), the time it took the fish to strike and consume a prey (hereafter “handling time,” 0.6–2.3 s) was affected only by strike distance.

Strike angles were almost uniformly distributed across the horizontal and vertical planes (χ^2 , $P > 0.11$ and 0.4, respectively, $n = 18$), with no apparent correlation between vertical and horizontal strike angles (linear regression, $F_{1,186} = 0.96$, $P > 0.32$, $r^2 = 0.005$).

The effect of IR illumination, examined under the darkest illumination ($10^{-6} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), indicated no significant difference (Wilcoxon matched-pairs test, $P > 0.9$, $n = 8$ fish) in the fish’s feeding rates with and without IR illumination ($FR = 0.21 \pm 0.43$ and $0.25 \pm 0.53 \text{ prey min}^{-1}$, respectively).

The fish were more active, spending higher proportion of their time moving their fins as light intensity increased (ANOVA, $F_{5,15} = 4.57$, $P < 0.01$). The most striking difference was between the fish’s infrequent activity ($31.8\% \pm 8.9\%$

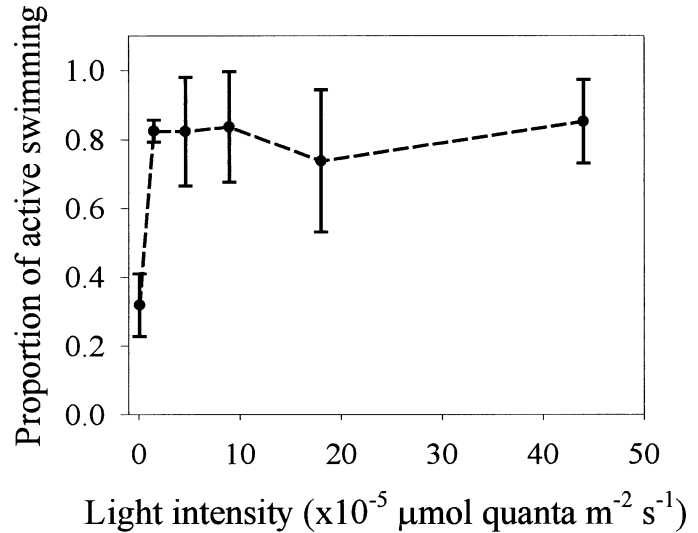


Fig. 4. The effect of light intensity on *A. annularis* swimming mode in a recirculating flume, prior to prey introduction. Data are the mean proportion of active swimming periods in six fish (five replicates per fish per light intensity). Error bars represent standard errors.

of the time) at the lowest light level to sharp increase to $82.5\% \pm 3.2\%$ of the time at the next light level (Fig. 4). Under the lowest light intensity, fish tended to swim intermittently, with infrequent thrusts followed by a long motionless drift. As the light level increased, the periods of passive drift were shorter and less frequent. No significant changes were observed in the proportion of fin movements within a light level (ANOVA, $F_{4,12} = 1.05$, $P > 0.4$), indicating no habituation during the course of the “within-fish” repeated observations.

Discussion

A. annularis consumes large zooplankton that are rare during the day but becomes abundant at night (Yahel et al. 2002), thereby taking advantage of the prey’s diel migration. The combination of the flume and in situ experiments demonstrated how well the fish is adapted for this mode of visual predation, where light saturation is reached at levels that correspond to light intensity during a moonless night at 3 m depth. Small zooplankton ($<1 \text{ mm}$), which are readily consumed by diurnal fish (e.g., Hobson and Chess 1978), are apparently not detectable by *A. annularis*.

More than 90% of the prey found in the fish stomachs was $>1.6 \text{ mm}$ in length. A similar selectivity was reported by Hobson and Chess (1978) and Gladfelter (1979) for other nocturnal coral-reef fishes. The selectivity for large prey by *A. annularis* was apparently related to a fish’s inability to detect small prey rather than to active preference of one prey over the other. Such a preference would require that at least two prey would be found together within the fish’s reactive volume ($\leq 0.015 \text{ m}^3$), an unlikely situation where the density of large ($>0.9 \text{ mm}$) zooplankton is $\sim 7 \text{ m}^{-3}$ (based on the fishless Bongo net). Moreover, our observations in the flume showed that *A. annularis* never struck or captured *Artemia*

Table 1. The abundance of diurnal and nocturnal zooplankton in different locations and size ranges. Diurnal values are from Hamner et al. (1988), referring to salps, larvaceans, and copepods at 5 m depth in the Great Barrier Reef, Australia, and from Genin (unpubl. data), referring to all species at 12 m depth in our study site. Nocturnal values are from the present study (in situ experiment) and from Yahel et al. (2002).

	Diurnal zooplankton		Nocturnal zooplankton	
	Hamner et al. (1988) (250 μm)	Genin unpubl. data (200 μm)	Present study (1,000 μm)	Yahel et al. (2002) (100 μm)
Density (no. m^{-3})	76	687	0.63	1,651
CV of density	1.0	1.25	0.68	1.23
n	6	17	28	9

nauplii (0.6 mm in length). Small size seems to provide an effective refuge from predation by this nocturnal fish.

The prey captured by *A. annularis* (mean length, 3.5 mm) was much larger than that captured by the diurnal Reef Anthias, *Pseudanthias squamipinnis*, at our study site (mean, 0.75 mm; A. Genin unpubl. data). Thus, when the realized prey is considered, the prey density for nocturnal fish such as *A. annularis* is 2–3 orders of magnitude lower than that of diurnal fishes (Table 1). Correspondingly, in situ feeding rates of diurnal fishes (mean, 27 prey min^{-1} for *P. squamipinnis* [A. Genin unpubl. data] and 34 prey min^{-1} for *Chromis dispilus* [Kingsford and MacDiarmid 1988]) are >2 orders of magnitude higher than those of *A. annularis*. However, in terms of energetic yield, the low predation rates by the nocturnal fish are partly offset by the larger size of their prey. Calculations based on body length-carbon relationships in zooplankton (Rodríguez and Mullin 1986) have indicated that the consumption rate of *A. annularis* is only about six times lower than that of the reef Anthias (25 and 138 $\mu\text{g C fish}^{-1} \text{min}^{-1}$, respectively).

A possible adaptation to a reduced prey density is a greater reactive distance. Under light levels equal to those near the surface on a moonless night ($4.6 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), the reactive distance of *A. annularis* (Fig. 3) was twice that measured by Kiflawi and Genin (1997) for two diurnal damselfishes from our study site under daylight conditions. Only at the two lowest light intensities used in the flume did the reactive distance become similar to that of the diurnal fish. The larger size of prey undoubtedly contributed to the occurrence of long reactive distance for *A. annularis* (e.g., O'Brien 1987; Giske et al. 1994). Yet our findings indicate that this nocturnal fish is well adapted for detecting large prey at a relatively long distance, but, unlike diurnal fishes, it seems to be unable to detect (or strike) small prey at short range. This inability is surprising, given that it renders inaccessible a major pool of potential prey.

The flume experiment showed that the fish's functional response (Fig. 3) nearly saturated at light intensity that corresponds to the level of a dark, moonless night in the upper 3 m of the water column ($4.6 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$). A similar absence of light effect in the reef was suggested by Acosta and Butler (1999) on the basis of their observation that predation on tethered lobster larvae was similar during new- and full-moon nights. Visual feeding by *A. annularis* in the flume became significant at light levels $>1.5 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, a level 2 orders of magnitude weaker

than that found for apogoniid larvae in the Great Barrier Reef, Australia (Job and Bellwood 2000). At the other extreme are Atlantic mackerel and juvenile walleye pollock, which have feeding thresholds at 10^{-7} and $5 \times 10^{-7} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, respectively (Macy et al. 1998; Ryer and Olla 1999).

Our Bongo net experiment corroborates the conclusion that, at 3 m depth, light was almost always saturating (Fig. 2B), regardless of the lunar phase. Subsaturating levels are expected, even under full moon, at greater depths or under heavy overcast. Considering a local light attenuation coefficient of 0.12 m^{-1} (Rickett 2000), the depth at which visual feeding by *A. annularis* becomes significant under clear skies would be 18 m on moonless nights and 47 m at the full moon. Marnane and Bellwood (2002) reported that *Apogon* spp. were foraging at 3–5 m depth in the shallow lagoon of One Tree Reef, Australia. However, no information was provided on the fish distribution at the deeper waters outside the lagoon. Similarly, Gladfelter (1979) and Golani and Diamant (1991) reported that the nocturnal sweepers (*Pempheris* spp.) foraged in the shallow subtidal zone, perhaps because of their inability to detect prey at greater depths. The vertical distribution of *A. annularis* in Eilat is yet unknown.

The fish's success to capture prey in the flume under the lowest light level suggests that senses other than vision are utilized. Possible senses include the lateral line and olfactory cues (Montgomery and Macdonald 1987; Janssen 1997). A reliance on such senses could explain the change in the swimming behavior of *A. annularis* at the lowest light intensity, which shifted to longer periods of motionless drift (Fig. 4). This behavior may allow a more "quiet" environment, which probably improves prey detectability by the lateral line. Nevertheless, the very small reactive distance in the lowest light level implies a severe constraint on the reactive volume, causing a sharp decline in feeding rate at $<1.5 \times 10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Fig. 3).

Of the three environmental factors measured in our Bongo net experiment (prey density, light, and flow), prey density was the main factor that determined the fish's functional response. The effect of flow, an important factor in visual zooplanktivory by diurnal fish (Hill and Grossman 1993; Kiflawi and Genin 1997), was not tested in the flume, nor was it resolved in the Bongo net experiment (Fig. 2C). It is therefore addressed in the text below, using a simple model originally developed for diurnal zooplanktivorous fish by Kiflawi

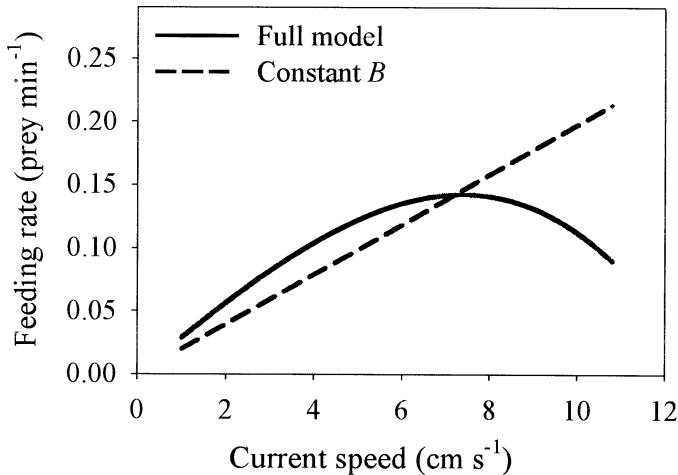


Fig. 5. Expected feeding rates vs. current speeds based on a complete model that accounts for the effect of current speed on the fish's reactive area (B) and a simplified model in which that area was considered constant (see "Discussion" section). Values of strike speed and distance are based on the flume experiment. In both models, feeding efficiency was assumed to be 50% and prey density 1 m^{-3} .

and Genin (1997). *A. annularis* and those diurnal fishes are similar in size, the habitat they occupy, and their striking single zooplankters in flowing water.

The observed capture of one prey every ~ 8 min, under the assumption that the handling time in the field was similar to that in the flume (2.3 s at most), indicated that search time was the main factor affecting the fish's feeding rate. Search time is a function of prey density, flow speed, and reactive distance (e.g., Aksnes and Utne 1997; Kiflawi and Genin 1997)

$$T_s = \frac{1}{DS_f B} \quad (3)$$

where D is the prey density (in prey cm^{-3}); S_f is the flow speed (in cm s^{-1}), and B is the reactive area projected on the plane perpendicular to the flow (in cm^2 ; fig. 5 in Kiflawi and Genin 1997). Under conditions of negligible handling time, the predation rate can be approximated as the inverse of T_s :

$$FR = aDS_f B \quad (4)$$

where a is the capture efficiency. The reactive area is a function of L_r , the reactive distance (in cm), and θ is the critical strike angle:

$$B = \pi[L_r \sin(\theta)]^2 \quad (5)$$

The relationships between L_r and light intensity were measured in the flume (Eq. 2). θ is a function of S_p , the ambient current speed, and S_a , the fish's strike speed (Kiflawi and Genin 1997):

$$\theta = \cos^{-1}(S_f S_a^{-1}) \quad (6)$$

In the flume, the strike distance changed very little in the range of natural light, which allowed us to use a constant strike distance (17.5 cm; expected under moonless night, 4.6

Table 2. The effect of environmental parameters on *A. annularis* feeding rate. The regression model ($F_{3,14} = 12.3$, $P < 0.001$, adjusted $r^2 = 0.66$) used prey flux, the fish's reactive distance, and strike angle to predict the flux of prey passing through the fish's reactive volume at the combinations of prey density, current speed, and light intensity observed in the field.

	β	$T_{(14)}$	P
Intercept		-1.50	0.15
Prey flux (prey $\text{m}^{-2} \text{s}^{-1}$)	0.98	5.25	0.001
Reactive volume (cm)	0.08	0.59	0.56
Strike angle ($^\circ$)	0.29	1.54	0.14

$\times 10^{-5} \text{ mol quanta m}^2 \text{ s}^{-1}$). The in situ strike speed was assumed to be similar to that observed in the flume (12.8 cm s^{-1}), and the density was kept constant (1 prey m^{-3}). Two versions of the model were used: a "complete" model (as described above) and a "simplified" model in which θ was kept constant at a value corresponding to the average current speed during our Bongo net runs (7.2 cm s^{-1}).

In the range of current speed $1\text{--}8.6 \text{ cm s}^{-1}$, the feeding rates predicted by the two models differed by $<15\%$ (Fig. 5). Hence, the current effect in this range is mostly through its direct linear effect on the flux of prey. The additional effect on strike angle becomes important only at higher speeds (Fig. 5), because of the narrowing down of the critical strike angle. The lack of apparent flow effect in the Bongo net experiment (Fig. 2C) was apparently because most of the data (14 of 18) were obtained under conditions of currents $<8.6 \text{ cm s}^{-1}$.

A multiple-regression analysis was used to assess the differential effects of prey flux, light, and predicted strike angle on of the observed feeding rates (FR) in the Bongo net experiment:

$$FR = a + bF + cF' + dF'' + \varepsilon \quad (7)$$

where F is the contribution of prey flux, F' is the contribution of light intensity (Eq. 2), and F'' is the contribution of current through its effect on strike angle (Eqs. 5, 6). The analysis (Table 2) indicates that the only significant contribution was that of flux ($\beta = 0.98$; $P < 0.001$), with a negligible contribution of the other two factors.

The lack of light and current effects in the in situ experiment implied a constant strike angle (θ) and distance (L_r) and, hence, a constant reactive area (B). Under conditions of $\theta = 55.8^\circ$ and $L_r = 19.2 \text{ cm}$, B was $\sim 800 \text{ cm}^2$. If we assume that the reactive areas of the three fish in the Bongo cage did not overlap, the fish captured $52\% \pm 34\%$ of the prey passing through their combined reactive area (0.24 m^2). This high value of predation efficiency is conservative, because overlapping reactive areas would have yielded lower values of per capita prey flux.

A. annularis is an efficient predator. Our findings indicate that vertical migration does not provide large zooplankton an efficient refuge from visual predation. If the predation by *A. annularis* is representative and if nocturnal planktivorous fish are abundant, one would expect migrating zooplankters to fine-tune their depth during the night on the basis of body size and lunar illumination.

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