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Predation efficiency in visual and tactile zooplanktivores

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Abstract

Gelatinous zooplanktivores (medusae, siphonophores, and ctenophores) and visual zooplanktivores (fish) interact through competition, predation, and commensalism. In the search for key factors governing the outcome of competition, we examined the instantaneous predation efficiency and its light dependency. The visual predator *Gobiusculus flavescens* and the tactile predator *Bolinopsis infundibulum* were used as experimental models for the two predation modes. The predation rate of *G. flavescens* was adequately described by Holling's curvilinear disc equation, and that of *B. infundibulum* was proportional to prey density. However, because of superfluous feeding, the feeding rate of *B. infundibulum* differed from the predation rate and approached the asymptotic limitation at high prey levels. The predation rate was reduced for *G. flavescens* at irradiances <5–10 μmol photons m^{-2} s^{-1}, whereas light had no significant impact on the feeding pattern of *B. infundibulum.* Provided sufficient light, the predation rate of *G. flavescens* was several orders of magnitude higher than that of *B. infundibulum.* These results are consistent with the results of other studies, which suggests that the maximum clearance rate (C_{max}) of visual and tactile predators is described by the power functions $C_{max} = 3.42 \times 10^{-7} L^{2.94}$ and $C_{max} = 6.02 \times 10^{-8} L^{1.77}$, respectively, where L is the length of the organisms in centimeters. We conclude that visual predation is most efficient at high visibility and low prey densities. As visibility decreases and prey density increases, the competitive efficiency of tactile predators increases.

Medusae, siphonophores, and ctenophores are voracious predators of zooplankton in marine ecosystems. Episodic and more persistent aggregations of gelatinous predators have been frequently reported (Graham et al. 2001). Competing for similar resources, gelatinous planktivores may reduce fish production and constrain harvest (Purcell and Arai 2001). Some ecosystems have converted from supporting viable commercial fisheries to hosting exceptional numbers of gelatinous planktivores and few fishes (Mills 2001). Numerous studies have investigated the causal factors for these remarkable blooms—for example, environmental degradation (Arai 2001), climate changes (Brodeur et al. 1999), overfishing (Daskalov 2002), and the introduction of alien species (Kideys 2002).

Most gelatinous zooplanktivores are characterized by high feeding, growth, and reproductive rates, as well as restricted predation (Alldredge 1984). From this perspective, it is not surprising that these animals are frequently dominant zooplanktivores. Indeed, one might wonder how planktivorous fish are able to compete with gelatinous planktivores. We addressed the question with a comparative study of the instantaneous predation efficiency for visual and tactile predators. Specifically, the functional responses (i.e., predation rate vs. prey density) of the visual zooplanktivore *Gobiusculus flavescens* (a fish) and the tactile zooplanktivore *Bolinopsis infundibulum* (a ctenophore) were examined. A literature review of predation efficiency in visual and tactile zooplanktivores indicated that these two animals can be considered as representative models of the two predation modes. Eiane et al. (1999) hypothesized that tactile predators, which are adapted to feed continuously, should increase their competitive efficiency relative to visual predators as visibility decreases. Accordingly, the influence of ambient light on predation efficiency was measured, to reveal how the two predation modes were affected.

Materials and methods

Measurements of predation rate in G. flavescens—Adult *G. flavescens* were collected from the littoral zone (1–4-m depth) of Raunefjorden, western Norway (60°13N, 5°16E), using a beach seine. On the basis of a criterion of similar size (total length; 4.00 ± 0.05 cm, $n = 7$), seven males were selected for the experiments. These individuals were separated, each in a 20×10^{-3} m^3 aquarium. To adapt them to the experimental conditions, the fish were isolated for 7 d prior to conducting the experiments. All experiments were done at constant temperature (12°C). Incoming seawater was purified through two separate filters (Hytrex 2 cartridge filters, 10 and 0.2 μm), to prevent the introduction of prey or optically disturbing particles. Light was provided by five halogen lamps directed at a linen tent. The linen cloth assured diffuse light conditions within the tent, where a square experimental aquarium ($50 \times 24 \times 27$ cm) was placed. Light intensity was measured with a planar LI-COR Quantum cosine-sensor, with an average difference in illumination of ±10% per trial.

Air, gently stirring the water, was provided through a hose connected to an oxygen pump. The hose was positioned to minimize the variance in flow-field within the aquarium. *Artemia* nauplii (2 mm) were added to the aquarium before the fish, which allowed the flow to create an even distribution of prey. A fish was transferred from its original aquarium to the experimental aquarium using a landing net. Observations were started immediately after the transfer, and the observer, using a computer, registered each prey captured. The software noted the point in time for each predation event. After

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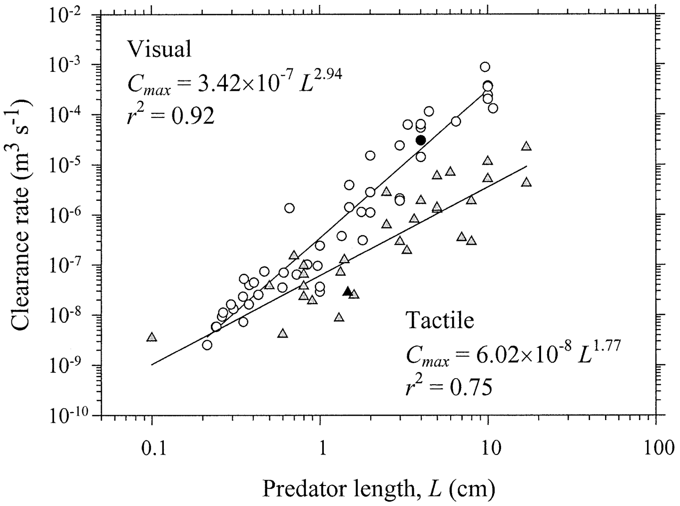

Fig. 1. Clearance rate (in m^3 s^{-1}) vs. length (in cm) for visual (circles; $n = 48$) and tactile (triangles; $n = 31$) zooplanktivores (Tables 1, 2). Filled circles and triangles represent our experiments on *G. flavescens* and *B. infundibulum,* respectively. Both axes are log$_{10}$-transformed, and the curves were fitted by linear regression on the log$_{10}$-transformed data.

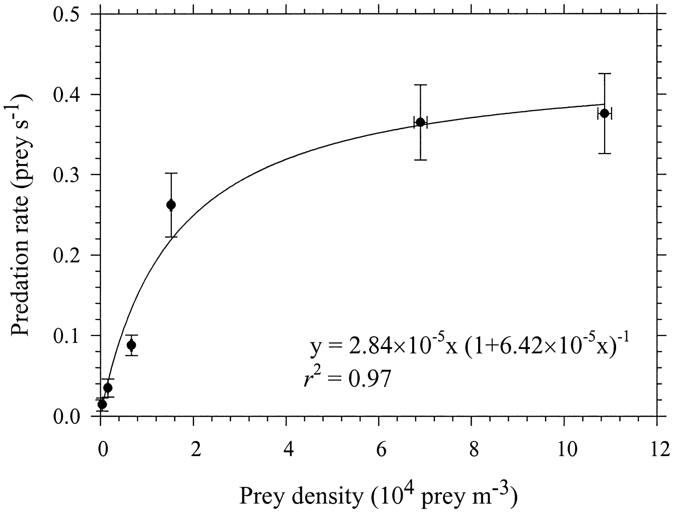

Fig. 2. Mean values (±SE) of predation rate (in prey s^{-1}) vs. prey density (in prey m^{-3}) for *G. flavescens* ($n = 7$). Holling's disc equation was fitted by nonlinear regression (ordinary least squares; Quasi Newton method).

10 min, when the experiment was completed, the fish was removed in the same manner as it had been introduced. The aquarium was emptied and cleaned after each trial. The fishes were not fed between experiments, to maintain a strong level of hunger.

The experiment was split in two parts, for both *G. flavescens* and *B. infundibulum* (see next section for details). The first measured how the predation rate varied with prey density (0.5, 2, 8, 20, 80, and 120 × 10^3 m^{-3}), keeping light intensity constant (30 μmol photons m^{-2} s^{-1}). The second revealed how the predation rate varied with light intensity (0, 0.1, 1, 4, 12, and 30 μmol photons m^{-2} s^{-1}), keeping the prey density constant (20 × 10^3 m^{-3}).

Measurements of predation rate in B. infundibulum—Specimens of *B. infundibulum* were collected from Raunefjorden with a 90-μm mesh, 0.5-m diameter WP-2 net. A large plastic bag was attached at the cod end, to mitigate damage to the ctenophores. On the basis of equal size (total length including lobes, 1.47 ± 0.07 cm; $n = 7$) and physical condition (no ruptures or damages to body tissue), seven individuals were selected for the experiments. Between each trial, the ctenophores were kept in separate 3 × 10^{-4} m^3 containers. Water was replaced every 24 h, to prevent the accumulation of waste-products. The experiments were conducted at constant temperature (12°C), with conditions identical to those described for *G. flavescens.* In addition to the linen tent previously described, a dark chamber of light-impenetrable cloth was constructed. These two habitats were used simultaneously during the second part of the experiment (feeding at various light intensities, see previous section). The first part of the experiment, feeding at various prey densities, was conducted in complete darkness. The experiments occurred in separate round jars with a capacity of 5 × 10^{-3} m^3. Because turbulence could have easily damaged these ctenophores, the water was not mechanically stirred in any of the experiments with *B. infundibulum.* Ctenophores were transferred between the containers and jars using a small plastic beaker. *Artemia* nauplii (8, 20, 80, 200, 400, and 800 × 10^3 m^{-3} in part 1 and 150 × 10^3 m^{-3} in part 2) were introduced before the ctenophores. The trials lasted for 6 h in the first part and 3 h in the second. The feeding behavior was observed for 5 min once every hour, using a red light. No aggregation of nauplii was apparent.

After each trial, ctenophores were removed, and water was sieved through a 30-μm mesh. Each experimental jar was flushed with excess water, to assure a complete transfer of prey. The filtered prey were counted. At high prey densities (e.g., 400 and 800 × 10^3 m^{-3}), the ctenophores lost boli of captured, but still not digested, prey to the bottom. The number of nauplii in each bolus was quantified with a light microscope. Predation was defined as prey capture, whereas feeding involved the actual ingestion of prey items. Although the numbers listed as ''predation rate'' include nauplii in boli, figures on ''feeding rate'' exclude them.

Fitting of the functional response curves—The Holling type II curvilinear functional response (disc equation) was fitted to the predation rate measurements of *G. flavescens* by means of the nonlinear regression

$$f = \frac{aN}{(1 + ahN)} \tag{1}$$

where f is the feeding rate (number of prey eaten per second), N is the prey density (prey m^{-3}), h is the handling time (pursuit, capture, and consumption of one prey item, in s), and a is the ''encounter rate kernel'' (m^3 s^{-1}). When the handling time approaches zero, the above equation reduces to the Holling type I linear functional response:

$$f = aN \tag{2}$$

This expression was fitted to the predation rate measure-

Table 1. Clearance rates of particulate-feeding visual planktivores (fish) feeding on crustaceans ($n = 48$). Data are from studies where feeding was not light-limited. Predator sizes are total/standard length (mm). Prey size range: 0.05–7.73 mm.

Predator species	Predator size (mm)	Prey type	Clearance rate ($m^3\ s^{-1}$)	Source
Perca fluviatilis	96.7	*Daphnia magna*	8.60×10^{-4}	Bergman 1988
Gymnocephalus cernua	107.7	*D. magna*	1.30×10^{-4}	Bergman 1988
Oncorhynchus tshawytscha	65	*Artemia salina*	7.10×10^{-5}	Gregory and Northcote 1993
Achirus lineatus larvae	2.13	Zooplankton*	2.50×10^{-9}	Houde and Schekter 1980
A. lineatus larvae	2.40	Zooplankton*	5.80×10^{-9}	Houde and Schekter 1980
A. lineatus larvae	2.61	Zooplankton*	9.20×10^{-9}	Houde and Schekter 1980
A. lineatus larvae	3.05	Zooplankton*	1.30×10^{-8}	Houde and Schekter 1980
A. lineatus larvae	3.48	Zooplankton*	2.30×10^{-8}	Houde and Schekter 1980
A. lineatus larvae	3.80	Zooplankton*	3.90×10^{-8}	Houde and Schekter 1980
Anchoa mitchilli larvae	3.50	Zooplankton*	7.20×10^{-9}	Houde and Schekter 1980
A. mitchilli larvae	3.78	Zooplankton*	1.60×10^{-8}	Houde and Schekter 1980
A. mitchilli larvae	4.30	Zooplankton*	2.50×10^{-8}	Houde and Schekter 1980
A. mitchilli larvae	6.09	Zooplankton*	6.90×10^{-8}	Houde and Schekter 1980
A. mitchilli larvae	7.28	Zooplankton*	6.30×10^{-8}	Houde and Schekter 1980
A. mitchilli larvae	8.41	Zooplankton*	1.00×10^{-7}	Houde and Schekter 1980
Archosargus rhomboidalis larvae	2.42	Zooplankton*	5.80×19^{-9}	Houde and Schekter 1980
A. rhomboidalis larvae	2.65	Zooplankton*	1.10×10^{-8}	Houde and Schekter 1980
A. rhomboidalis larvae	2.95	Zooplankton*	1.60×10^{-8}	Houde and Schekter 1980
A. rhomboidalis larvae	3.53	Zooplankton*	5.20×10^{-8}	Houde and Schekter 1980
A. rhomboidalis larvae	4.05	Zooplankton*	4.40×10^{-8}	Houde and Schekter 1980
A. rhomboidalis larvae	4.68	Zooplankton*	7.30×10^{-8}	Houde and Schekter 1980
Engraulis capensis	100.4	*Calanoides carinatus*	2.40×10^{-4}	James and Findlay 1989
E. capensis	100.4	*C. carinatus*	3.70×10^{-4}	James and Findlay 1989
E. capensis	100.4	*Artemia salina*	2.00×10^{-4}	James and Findlay 1989
E. capensis	100.4	*A. salina*	3.50×10^{-4}	James and Findlay 1989
Stizostedion vitreum larvae	9.7	Zooplankton*	9.43×10^{-8}	Johnston and Mathias 1994
S. vitreum larvae	18.0	Zooplankton*	3.07×10^{-7}	Johnson and Mathias 1994
Alosa pseudoharengus	10	*Artemia* sp.	2.85×10^{-8}	Miller et al. 1992
A. pseudoharengus	20	*Artemia* sp.	2.80×10^{-6}	Miller et al. 1992
A. pseudoharengus	30	*Artemia* sp.	2.10×10^{-6}	Miller et al. 1992
A. pseudoharengus	40	*Artemia* sp.	5.40×10^{-5}	Miller et al. 1992
Coregonus hoyi	10	*Artemia* sp.	2.40×10^{-7}	Miller et al. 1992
C. hoyi	15	*Artemia* sp.	3.90×10^{-6}	Miller et al. 1992
C. hoyi	20	*Artemia* sp.	1.50×10^{-5}	Miller et al. 1992
C. hoyi	30	*Artemia* sp.	2.40×10^{-5}	Miller et al. 1992
C. hoyi	40	*Artemia* sp.	6.30×10^{-5}	Miller et al. 1992
Perca flavescens	10	*Artemia* sp.	3.60×10^{-8}	Miller et al. 1992
P. flavescens	15	*Artemia* sp.	1.40×10^{-6}	Miller et al. 1992
P. flavescens	20	*Artemia* sp.	1.10×10^{-6}	Miller et al. 1992
P. flavescens	30	*Artemia* sp.	1.90×10^{-6}	Miller et al. 1992
P. flavescens	40	*Artemia* sp.	1.40×10^{-5}	Miller et al. 1992
Clupea harengus larvae	13.5	Zooplankton*	3.75×10^{-7}	Munk 1992
C. harengus larvae	17.7	Zooplankton*	1.13×10^{-6}	Munk 1992
C. harengus larvae	33.5	Zooplankton*	6.21×10^{-5}	Munk 1992
C. harengus larvae	44.8	Zooplankton*	1.13×10^{-4}	Munk 1992
Gadus morhua larvae	6.6	*Acartia tonsa*	1.35×10^{-6}	Munk 1995
Archosargus rhomboidalis larvae	5.98	Zooplankton*	3.47×10^{-8}	Stepien 1976
Gobiusculus flavescens	40.0	*Artemia* sp.	3.03×10^{-5}	Present study

* More than one prey species, in a mixed diet.

ments of *B. infundibulum* by means of linear regression. The unit of the parameter a corresponds to that of clearance rate ($m^3\ s^{-1}$). For responses of type I, a equals the clearance rate, whereas, for type II, it represents a maximum clearance rate at low prey densities.

Literature review of feeding studies—Maximum clearance rate (a in the above equations) was obtained from 22 published studies on the feeding rate in visual and tactile zooplanktivores (Tables 1, 2). This parameter was explicitly estimated in some studies but had to be calculated in others from reported feeding rates and prey densities. $C_{\max}$ denotes the maximum clearance rates obtained from this review. The power function

$$C_{\max} = cL^{b} \qquad (3)$$

Table 2. Clearance rates of tactile (gelatinous) planktivores feeding on crustaceans ($n = 31$). Medusa sizes are bell diameters, and ctenophore sizes are total length/diameter (cydippids) and total length including lobes (lobates). Prey size range: 0.09–3.20 mm. C: order Cydippida, L: order Lobata.

Predator species	Predator size (mm)	Prey type	Clearance rate ($m^3\ s^{-1}$)	Source
Ctenophora				
Pleurobrachia bachei^{C}	9	*Pseudocalanus minutus*	1.89×10^{-8}	Bishop 1968
Bolinopsis infundibulum^{L}	16	*P. minutus*	2.44×10^{-8}	Bishop 1968
Pleurobrachia rhodopis^{C}	1	*Acartia clausii*	3.47×10^{-9}	Buecher and Gasser 1998
P. rhodopis^{C}	5	*A. clausii*	3.76×10^{-8}	Buecher and Gasser 1998
Pleurobrachia pileus^{C}	13.3	*Calanus finmarchicus*	7.06×10^{-8}	Båmstedt 1998
P. bachei^{C}	8	*Pseudocalanus* sp.	9.66×10^{-8}	Greene et al. 1986
P. bachei^{C}	8	*A. clausii*	6.44×10^{-8}	Greene et al. 1986
Bolinopsis vitrea^{L}	7	Zooplankton*	1.50×10^{-7}	Kremer et al. 1986
B. vitrea^{L}	36.5	Zooplankton*	8.10×10^{-7}	Kremer et al. 1986
Mnemiopsis mccradyi^{L}	8	Zooplankton*	2.31×10^{-8}	Reeve et al. 1978
M. mccradyi^{L}	30	Zooplankton*	2.89×10^{-7}	Reeve et al. 1978
M. mccradyi^{L}	70	Zooplankton*	3.47×10^{-7}	Reeve et al. 1978
P. bachei^{C}	6	Zooplankton*	4.11×10^{-9}	Reeve et al. 1978
B. infundibulum^{L}	13	Zooplankton*	8.56×10^{-9}	Reeve 1980
B. infundibulum^{L}	14.7	*Artemia* sp.	2.80×10^{-8}	Present study
Cnidaria				
Aurelia aurita	33	Zooplankton*	1.90×10^{-7}	Båmstedt 1990
A. aurita	80	Zooplankton*	2.90×10^{-7}	Båmstedt 1990
A. aurita	60	Zooplankton*	6.94×10^{-6}	Båmstedt et al. 1994
Cyanea capillata	50	Zooplankton*	1.28×10^{-6}	Båmstedt et al. 1994
C. capillata	80	Zooplankton*	1.88×10^{-6}	Båmstedt et al. 1994
C. capillata	25	*Paracalanus indicus*	6.27×10^{-7}	Fancett and Jenkins 1988
C. capillata	50	*P. indicus*	1.39×10^{-6}	Fancett and Jenkins 1988
C. capillata	100	*P. indicus*	5.20×10^{-6}	Fancett and Jenkins 1988
Pseudorhiza haeckeli	25	*P. indicus*	2.78×10^{-6}	Fancett and Jenkins 1988
P. haeckeli	50	*P. indicus*	5.88×10^{-6}	Fancett and Jenkins 1988
P. haeckeli	100	*P. indicus*	1.14×10^{-5}	Fancett and Jenkins 1988
A. aurita	170	Zooplankton*	4.20×10^{-6}	Martinussen and Båmstedt 1995
C. capillata	170	Zooplankton*	2.20×10^{-5}	Martinussen and Båmstedt 1995
Pelagia noctiluca	8	*Artemia* sp.	3.70×10^{-8}	Morand et al. 1987
P. noctiluca	14	*Artemia* sp.	1.25×10^{-7}	Morand et al. 1987
P. noctiluca	40	*Artemia* sp.	1.91×10^{-6}	Morand et al. 1987

* More than one prey species, in a mixed diet.

where c and b are constants, and L (in cm) reported length of the organism, was fitted to the data (Fig. 1). When converting from length to dry weight (DW, mg), we applied the power function

$$\mathrm{DW} = dL^{e} \tag{4}$$

For fish, ctenophores, and medusae, d and e were approximated by 5.62×10^{-4} and 3.09 (Pepin 1995), 0.127 and 2.17 (Kremer et al. 1986), and 0.002 and 2.90 (Båmstedt 1990), respectively.

Results

Predation rate—Holling's disc equation (Eq. 1) adequately described the functional response of *G. flavescens* to prey density (Fig. 2). The predation rate was high at low prey densities but soon became plateous because of handling limitation. The predation rate of *B. infundibulum* was proportional to prey density (Fig. 3). In other words, within the boundaries of the experiment, saturation (in terms of predation) was not obtained for the ctenophores. However, the occurrence of mucus-entangled prey (in boli) added a complication to our results. As a consequence, we separated the event of predation from feeding. Because boli were observed only at nominal prey densities of 4×10^{5} and 8×10^{5} prey m^{-3}, complete ingestion was assumed at the four lower prey levels. When adjusting the predation rate for prey lost in boli (Table 3), a feeding rate adequately described by Holling's disc equation (Eq. 1) was apparent (Fig. 3).

Parameter estimates—Estimates of the maximum clearance rate (a, in $m^3\ s^{-1}$) and handling time (b, in s) were obtained for *G. flavescens* by fitting Holling's disc equation (Eq. 1) to the predation rate measurements. Calculations per fish were made to indicate individual variance (Table 4). For *B. infundibulum,* the clearance rate was given by the rate of increase (a in Eq. 2) for each predation rate curve (Table 4). Estimates of handling time were obtained by fitting Holling's

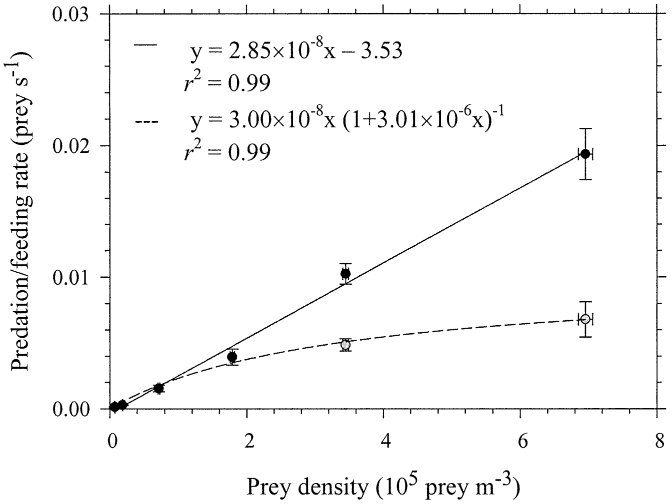

Fig. 3. Mean values (±SE) of predation (solid line) and feeding (dashed line) rates (in prey s^{-1}) vs. prey density (in prey m^{-3}) for *B. infundibulum* ($n = 7$). The curves were fitted by linear and nonlinear regression (ordinary least squares; Quasi Newton method), respectively.

disc equation (Eq. 1) to the feeding rate measurements (Table 4).

The mean value of the clearance rate for *G. flavescens* ($3.03 \pm 0.46 \times 10^{-5}$ m^3 s^{-1}) was ~3 orders of magnitude higher than that for *B. infundibulum* ($2.87 \pm 0.27 \times 10^{-8}$ m^3 s^{-1}). A concomitant pattern was revealed for mean values of handling time, with the estimate for *G. flavescens* (2.56 ± 0.42 s $prey^{-1}$) being substantially lower than that for *B. infundibulum* ($1.52 \pm 0.28 \times 10^2$ s $prey^{-1}$).

Predation rate and light dependency—The predation rate was reduced for *G. flavescens* at irradiances <5–10 μmol photons m^{-2} s^{-1}, which suggests light limitation in the visual foraging process (Fig. 4). No significant difference in predation rate was detected for *B. infundibulum* when it was exposed to light (30 μmol photons m^{-2} s^{-1}) and completely dark conditions (*t*-test, $P > 0.05$, df = 6). Mean predation rates (±SE) were $2.36 \times 10^{-3} \pm 3.31 \times 10^{-4}$ and $2.36 \times 10^{-3} \pm 4.13 \times 10^{-4}$ prey s^{-1}, respectively.

Table 3. Individual estimates of predation (No. of prey $predator^{-1}$ $experiment^{-1}$), prey in boli (no. of prey $predator^{-1}$ $experiment^{-1}$), and feeding (% of predation) for *B. infundibulum* ($n = 7$). The duration of the experiment was 6 h.

Predation (No. of prey)	No. of prey in boli	Feeding (% of predation)
Nominal prey density 4×10^5 m^{-3}		
170	94	44.7
188	88	53.2
267	156	41.6
188	93	50.5
228	138	39.5
290	129	55.5
217	115	47.0
Nominal prey density 8×10^5 m^{-3}		
385	266	30.9
376	274	27.1
356	243	31.7
469	418	10.9
259	120	53.7
606	343	43.4
474	235	50.4

Table 4. Estimated clearance rate (m^3 s^{-1}) and handling time (s) for *G. flavescens* ($n = 7$) and *B. infundibulum* ($n = 7$), obtained using nonlinear and linear regression (see text for details).

Organism and clearance rate (m^3 s^{-1})	Handling time (s)
G. flavescens	
4.08×10^{-5}	3.11
2.16×10^{-5}	1.91
1.66×10^{-5}	4.43
1.88×10^{-5}	3.43
2.04×10^{-5}	1.63
4.22×10^{-5}	1.56
5.17×10^{-5}	1.83
B. infundibulum	
2.52×10^{-8}	1.51×10^{2}
2.55×10^{-8}	1.12×10^{2}
2.46×10^{-8}	1.46×10^{2}
3.24×10^{-8}	2.36×10^{2}
1.72×10^{-8}	1.15×10^{2}
4.36×10^{-8}	4.60×10^{1}
3.26×10^{-8}	2.59×10^{2}

Discussion

Even though the predatory impact of visual and tactile planktivores has been well documented, comparative studies of their relative predation potentials have rarely been done

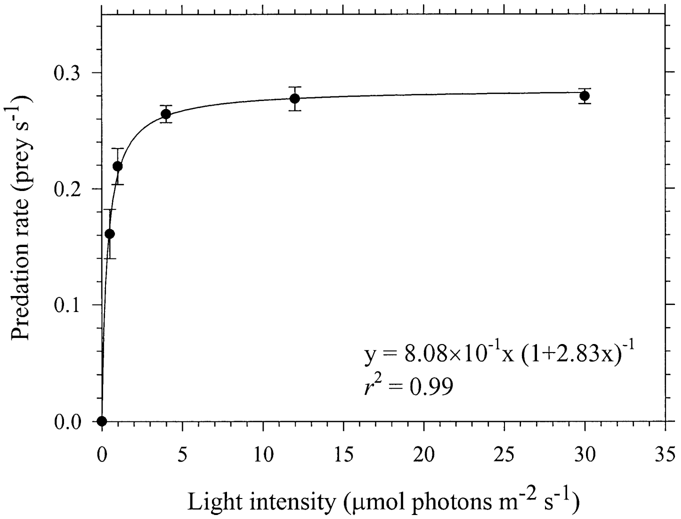

Fig. 4. Mean values (±SE) of predation rate (in prey s^{-1}) vs. light intensity (in μmol photons m^{-2} s^{-1}) for *G. flavescens* ($n = 7$). The curve was fitted by nonlinear regression (ordinary least squares; Quasi Newton method).

(but see Cowan and Houde 1993). Our experiments on *G. flavescens* and *B. infundibulum* revealed two characteristic differences. First, the predation rate at low prey densities is substantially higher for *G. flavescens* than for *B. infundibulum.* The three order of magnitude difference in maximum clearance rate was partly due to the larger size of *G. flavescens* (4.0 vs. 1.5 cm) but agreed with the general difference found for visual and tactile planktivores (Fig. 1). Second, although the predation rate for *B. infundibulum* was proportional to prey density, that of *G. flavescens* was plateous at fairly low prey levels (Fig. 2 and 3). It is a common feature for ctenophores to obtain linear predation rates (Reeve and Walter 1978). However, at high prey densities, prey are killed but not eaten by *B. infundibulum.* Thus, the feeding rate of *B. infundibulum* also reached satiation. This phenomenon has been observed for lobate ctenophores in previous studies (Reeve and Walter 1978; Kremer 1979) but has seldom been recognized for its importance in, for example, energy budgets.

The predation rate for *G. flavescens* is reduced at irradiances $<5–10\ \mu$mol photons $m^{-2}\ s^{-1}$, a value that is in agreement with the results that Utne (1997) obtained for reaction distance. The predation rate for *B. infundibulum* was independent of light, which suggests more flexibility in foraging patterns and habitat choice. This outcome was not unexpected, considering that ctenophores lack a photosensory apparatus (Graham et al. 2001). In total darkness, *G. flavescens* ceased feeding. Thus, somewhere $<0.1\ \mu$mol photons $m^{-2}\ s^{-1}$, *B. infundibulum* is more efficient than *G. flavescens* at all prey densities.

Gelatinous planktivores are considered to be voracious predators. However, compared with planktivorous fish, their instantaneous predation rates are, in fact, low. When combining our results on clearance rate with data from existing literature, we found that $C_{max} = 3.42 \times 10^{-7} L^{2.94}$ ($r^2 = 0.92$) for fish and $C_{max} = 6.02 \times 10^{-8} L^{1.77}$ ($r^2 = 0.75$) for gelatinous planktivores (Fig. 1). The different exponents of the C_{max} versus L relations may reflect a three-dimensional search image of visual predators (the exponent is 2.94) and a two-dimensional sensory area of tactile predators (the exponent is 1.77). Hence, large visual planktivores have substantially higher maximum clearance rates than tactile planktivores of comparable length (L, in cm). Despite the higher water content of gelatinous planktivores, this picture is more or less retained when size is expressed as dry weight (DW, in mg). Under the assumption of the relationships presented in ''Materials and methods,'' we found $C_{max} = 4.86 \times 10^{-7}$ $DW^{0.95}$ ($r^2 = 0.92$) for fish and $C_{max} = 1.22 \times 10^{-8}$ $DW^{0.76}$ ($r^2 = 0.60$) for gelatinous planktivores. The relations suggest that C_{max} increases almost proportionally to DW for visual predators and to $DW^{3/4}$ for tactile predators.

Our experiments on *G. flavescens* and *B. infundibulum* have suggested that both prey density and visibility influence the competition between visual and tactile planktivores. Tactile planktivores gain competitive efficiency, relative to visual planktivores, with increasing prey density (Figs. 2 and 3). In addition, visual planktivores lose competitive efficiency with decreasing visibility (Fig. 4), because predation by *B. infundibulum* is unaffected by the light regime. Thus, our findings seem to be consistent with the suggestion of Eiane et al. (1999) that the visibility regime affects competition between visual and tactile planktivores.

References

ALLDREDGE, A. L. 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers, p. 407–433. *In* M. J. R. Fasham [ed.], Flows of energy and materials in marine ecosystems: Theory and practice. Plenum.

ARAI, M. N. 2001. Pelagic coelenterates and eutrophication: A review. Hydrobiologia **451:** 69–87.

BÅMSTEDT, U. 1990. Trophodynamics of the scyphomedusae *Aurelia aurita.* Predation rate in relation to abundance, size and type of prey organism. J. Plankton Res. **12:** 215–229.

———. 1998. Trophodynamics of *Pleurobrachia pileus* (Ctenophora, Cydippida) and ctenophore summer occurrence off the Norwegian north-west coast. Sarsia **83:** 169–181.

———, M. B. MARTINUSSEN, AND S. MATSAKIS. 1994. Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata,* in western Norway. ICES J. Mar. Sci. **51:** 369–382.

BERGMAN, E. 1988. Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua,* under different environmental conditions. J. Anim. Ecol. **57:** 443–453.

BISHOP, J. W. 1968. A comparative study of feeding rates of tentaculate ctenophores. Ecology **49:** 996–997.

BRODEUR, R. D., C. E. MILLS, J. E. OVERLAND, G. E. WALTERS, AND J. D. SCHUMACHER. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish. Oceanogr. **8:** 296–306.

BUECHER, E., AND B. GASSER. 1998. Estimation of predatory impact of *Pleurobrachia rhodopis* (cydippid ctenophore) in the northwestern Mediterranean Sea: *In situ* observations and laboratory experiments. J. Plankton Res. **20:** 631–651.

COWAN, J. H., JR., AND E. D. HOUDE. 1993. Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Mar. Ecol. Prog. Ser. **95:** 55–65.

DASKALOV, G. M. 2002. Overfishing drives atrophic cascade in the Black Sea. Mar. Ecol. Prog. Ser. **225:** 53–63.

EIANE, K., D. L. AKSNES, E. BAGØIEN, AND S. KAARTVEDT. 1999. Fish or jellies—a question of visibility? Limnol. Oceanogr. **44:** 1352–1357.

FANCETT, M. S., AND G. P. JENKINS. 1988. Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. J. Exp. Mar. Biol. Ecol. **116:** 63–77.

GRAHAM, W. M., F. PAGÈS, AND W. M. HAMNER. 2001. A physical context for gelatinous zooplankton aggregations: A review. Hydrobiologia **451:** 199–212.

GREENE, C. H., M. R. LANDRY, AND B. C. MONGER. 1986. Foraging behavior and prey selection by the ambush entangling predator *Pleurobrachia bachei.* Ecology **67:** 1493–1501.

GREGORY, R. S., AND T. G. NORTHCOTE. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can. J. Fish. Aquat. Sci. **50:** 233–240.

HOUDE, E. D., AND R. C. SCHEKTER. 1980. Feeding by marine fish larvae: Developmental and functional responses. Environ. Biol. Fish. **5:** 315–334.

JAMES, A. G., AND K. P. FINDLAY. 1989. Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis.* Mar. Ecol. Prog. Ser. **50:** 275–294.

JOHNSTON, T. A., AND J. A. MATHIAS. 1994. The effects of temperature on feeding in zooplanktivorous walleye, *Stizostedion vitreum,* larvae. Environ. Biol. Fish. **40:** 189–198.

KIDEYS, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science **297:** 1482–1484.

KREMER, P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries **2:** 97–105.

———, M. R. REEVE, AND M. A. SYMS. 1986. The nutritional ecology of the ctenophore *Bolinopsis vitrea*: Comparisons with *Mnemiopsis mccradyi* from the same region. J. Plankton Res. **8:** 1197–1208.

MARTINUSSEN, M. B., AND U. BÅMSTEDT. 1995. Diet, estimated daily food ration and predator impact by the scyphozoan jellyfishes *Aurelia aurita* and *Cyanea capillata,* p. 127–145. *In* H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas [eds.], Ecology of fjords and coastal waters. Elsevier.

MILLER, T. J., L. B. CROWDER, J. A. RICE, AND F. P. BINKOWSKI. 1992. Body size and the ontogeny of the functional response in fishes. Can. J. Fish. Aquat. Sci. **49:** 805–812.

MILLS, C. E. 2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? Hydrobiologia **451:** 55–68.

MORAND, P., C. CARRÈ, AND D. C. BIGGS. 1987. Feeding and metabolism of the jellyfish *Pelagia noctiluca* (scyphomedusae, semaeostomae). J. Plankton Res. **9:** 651–665.

MUNK, P. 1992. Foraging behaviour and prey size spectra of larval herring *Clupea harengus.* Mar. Ecol. Prog. Ser. **80:** 149–158.

———. 1995. Foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and hunger. Mar. Biol. **122:** 205–212.

PEPIN, P. 1995. An analysis of the length-weight relationship of larval fish: Limitations of the general allometric model. Fish. Bull. **93:** 419–426.

PURCELL, J. E., AND M. N. ARAI. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. Hydrobiologia **451:** 27–44.

REEVE, M. R. 1980. Comparative experimental studies on the feeding of chaetognaths and ctenophores. J. Plankton Res. **2:** 381–393.

———, AND M. A. WALTER. 1978. Nutritional ecology of ctenophores—a review of recent research. Adv. Mar. Biol. **15:** 249–287.

———, ———, AND T. IKEDA. 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. Limnol. Oceanogr. **23:** 740–751.

STEPIEN, W. P., JR. 1976. Feeding of laboratory-reared larvae of the sea bream *Archosargus rhomboidalis* (Sparidae). Mar. Biol. **38:** 1–16.

UTNE, A. C. W. 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens.* J. Fish Biol. **50:** 926–938.

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