Limnol. Oceanogr., 40(5), 1995, 947–955

Estimating the predatory impact of gelatinous zooplankton

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Abstract

We propose a new approach to assess the predatory impact of gelatinous zooplankton on their prey, in which information from field samples and laboratory experiments allows us to estimate predator ingestion rates from analyses of predator gut contents. The feasibility of this approach was tested in laboratory experiments with the ctenophore *Pleurobrachia bachei* feeding on adult stages of the copepods *Pseudocalanus newmani* and *Acartia longiremis*.

We developed a simple model of predator ingestion-egestion dynamics. The model assumes that predator clearance rates, F, and instantaneous egestion rates, ε, are constant over the range of prey concentrations appropriate to the field study. A series of experiments was designed to test the validity of these assumptions and to estimate values of the parameters F and ε for *Pleurobrachia* feeding on *Pseudocalanus* and *Acartia*. Results from these experiments indicate that the above assumptions are reasonable for these predator-prey pairs until prey concentrations exceed 60,000 prey m^{-3}. Ingestion rates are shown to be proportional to predator gut contents, with the slope of the relationship providing an estimate of the instantaneous egestion rate.

Provided that the model assumptions are met, this approach can be used to estimate the predatory impact of other planktivorous predators on more complex prey assemblages.

Two methods have been used to estimate the potential impact of gelatinous predators on their prey. The first method uses laboratory feeding experiments to determine the functional response of predators to varying concentrations of prey (Bishop 1968; Kremer 1979; Greene et al. 1986). Clearance rates (Gauld 1951; Frost 1972)—the volume of water cleared of prey per predator per unit time—are calculated as a measure of feeding effort. When combined with predator and prey abundance data from field samples adjusted by some quantitative measure of the spatial and temporal overlap between predator and prey populations (e.g. Williamson et al. 1989), these laboratory-derived feeding rates can be extrapolated to estimate predatory impact (PI) as follows (e.g. Reeve et al. 1978; Deason 1982; Swanberg and Båmstedt 1991);

$$\mathrm{PI} = F \times C \times P \quad (1)$$

where F is clearance rate, C is prey concentration, and P is predator concentration. (A list of notation is provided.) This method may yield inaccurate results because it is often difficult to determine the spatial overlap between patches of predators and their prey populations from samples collected with plankton tows (Williamson 1993). Also, due to the varying degrees of success in simulating field conditions in the laboratory (Reeve 1980), an alternative method, preferably one based on data collected from field samples, would be desirable to confirm the predatory impact estimated from laboratory feeding data.

The second method commonly used to assess the impact of planktivorous predators involves analyzing the gut contents of predators sampled in the field and using laboratory-derived gut passage times to estimate predator impact as follows (Reeve 1980; Kremer et al. 1986; Swanberg and Båmstedt 1990):

$$\mathrm{PI} = N \times G^{-1} \times P \quad (2)$$

where N is the number of prey in the predator's gut and G is gut passage time. This method has been criticized for a variety of reasons, ranging from problems associated with predator regurgitation of gut contents during sampling and preservation (Larson 1987) to inappropriate methods for determining gut passage times. For instance, most gut passage times are determined by starving a predator, feeding it a single type of prey, and then noting the time elapsed until it completely egests the prey from its gut (Reeve 1980; Sullivan and Reeve 1982). This approach assumes that the predator's egestion rate (the reciprocal of the gut passage time) is proportional to the number of prey in its gut. As will be shown, this assumption also implies that the instantaneous egestion rate remains constant over varying prey concentrations.

Acknowledgments

We gratefully acknowledge Jonathan Dushoff, Eli Meir, and Bruce Monger for help in developing models for interpreting our experimental results. Our thanks to Olga Ermakova and Jeff Cordell for help in identifying the species of copepods we used and to Lori Scanlon for help in the field. We are grateful to many members of the department of Ecology and Evolutionary Biology at Cornell University and also to Claudia Mills, Pat Kremer, and Hans Dam for their comments and suggested revisions. Last but not least, we thank the director and staff of the Friday Harbor Laboratories of the University of Washington for their help and for providing access to their exceptional facilities for experimental work.

This research was supported by the Office of Naval Research, the section of Ecology and Systematics at Cornell University, and the local chapter of Sigma Xi at Cornell University.

Notation

PI	Predatory impact, (prey ingested) volume^{-1}
I	Ingestion rate, (prey ingested) predator^{-1} time^{-1}
E	Egestion rate, (prey egested) predator^{-1} time^{-1}
F	Clearance rate, (volume cleared) predator^{-1} time^{-1}
C	Prey concentration, prey volume^{-1}
P	Predator concentration, predators volume^{-1}
N	Number of prey in gut
N^*	Number of prey in gut at steady state
G	Gut passage time
ε	Instantaneous egestion rate, (prey egested) (prey in gut)$^{-1}$ time^{-1}
m	Instantaneous prey mortality rate, time^{-1}
K	Constant of integration, prey predator^{-1}
τ	Duration of experiment, h
t	Time, h
t^*	Time to reach steady state, h
V	Volume of jar, liters

Due to the variety of potential error sources, it would be desirable to verify the assumptions of this second method under controlled laboratory conditions for each predator of interest. The objective of this paper is to illustrate a new approach for verifying the accuracy of this second method. The approach involves developing the following model based on a predator's ingestion and egestion dynamics (Fig. 1):

$$\frac{dN}{dt} = I - E \tag{3}$$

$$\frac{dN}{dt} = FC - \varepsilon N. \tag{4}$$

Integrating the above equations, we get

$$N_t = \int_0^t I\,dt - \int_0^t E\,dt \tag{5}$$

$$N_t = \int_0^t FC\,dt - \int_0^t \varepsilon N\,dt. \tag{6}$$

dN/dt is the rate of change of gut contents, I is the ingestion rate, E is the egestion rate, ε is the instantaneous egestion rate, and N_t is the number of prey in the gut at time t.

This model can be extrapolated to the field situation, assuming that the predator's ingestion-egestion dynamics are in steady state, with the rate of change in the gut contents of the predator equal to zero (Fig. 1). Under these conditions, Eq. 3 and 4 yield

$$I = E \tag{7}$$

$$I = FC = \varepsilon N^* \tag{8}$$

where N^* is the number of prey in the predator's gut (i.e. its gut contents) at steady state.

Laboratory experiments were conducted to test the model assumptions that clearance rate and instantaneous egestion rate are constant over varying prey densities. If these assumptions are valid, we can calculate the mean values of these two parameters from the experiments. Further, we can use the experiments to test the model's basic prediction—if F and ε remain constant over changing prey concentrations, then the ingestion rate and gut contents of the predator are related by a constant and are proportional to prey concentration (Eq. 8).

If the model's assumptions and basic prediction are verified in the laboratory, the model can be applied to field data on predator abundance and gut contents to estimate predatory impact and the prey concentration actually available to the predator:

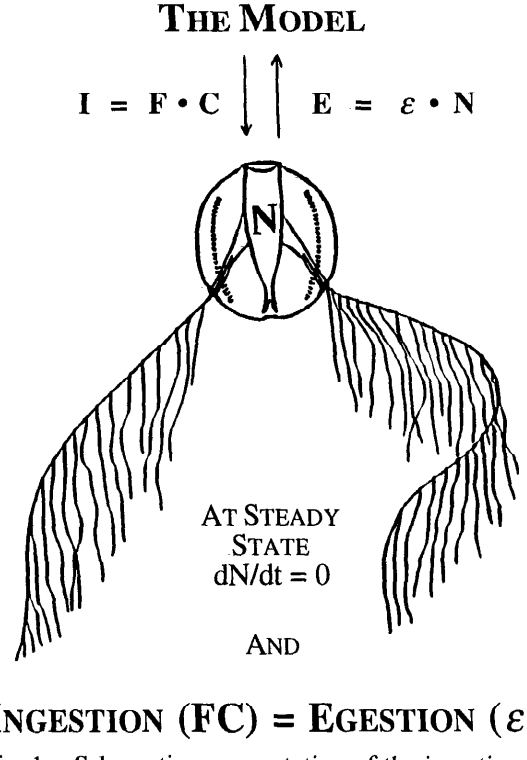

Fig. 1. Schematic representation of the ingestion and egestion feeding dynamics of the model predator, a ctenophore, at steady state.

$$PI = \varepsilon N^* \times P \tag{9}$$

$$C = \varepsilon N^*/F. \tag{10}$$

This latter estimate corresponds to the available prey concentration from the predator's perspective rather than that typically estimated by the investigator from plankton tows.

Methods

Collection and maintenance of experimental animals—Ctenophores (*Pleurobrachia bachei*) were hand-collected in plastic beakers from surface waters surrounding the floating breakwater at the Friday Harbor Laboratories (FHL) at Friday Harbor, Washington. They were kept in 15-liter plastic containers in a cold room at 12°C and fed daily with zooplankton collected from waters surrounding the breakwater. The water was changed daily by transferring the ctenophores to another bucket filled with fresh seawater. All ctenophores used in the experiments had an oral-aboral length of ~1 cm. *Pseudocalanus newmani* (Frost 1987) and *Acartia longiremis* were collected for the experiment by towing a 251-μm-mesh plankton net in San Juan Channel just adjacent to FHL. These prey species were kept in a 12°C cold room on a diet of the diatom *Thalassiosira weissflogii.*

Functional response experiments—Experiments with both prey types were set up with varying concentrations of prey and a single ctenophore in each 1-liter treatment jar. The ctenophores were starved for 12 h before the experiment to ensure that they had no prey in their guts. Eight replicates of jars with concentrations of 20, 40, 60, and 80 prey liter^{-1} and one control jar with no predators and a concentration of 20 prey liter^{-1} were prepared for the *P. newmani* experiment. A comparable setup, but without the 80 prey liter^{-1} jars, was prepared for the *A. longiremis* experiments. All jars were placed on a rotating wheel (3.5 rpm) to ensure that the prey did not settle to the bottom of each container. After 3 h, the ctenophore was removed from each jar, and the number of copepods present in its gut and the number of copepods remaining in each jar were counted. The 3-h duration was determined by conducting a series of experimental runs over varying lengths of time to establish when clearance rates and gut contents stabilized under the experimental conditions.

Predator clearance rates and prey instantaneous mortality rates for each of the two prey types were calculated from these experiments as follows (Gauld 1951; Frost 1972):

$$C_f = C_0 \exp(-m\tau) \tag{11}$$

$$F = \frac{Vm}{P} \tag{12}$$

where C_f is the final number of prey per jar, C_0 the initial number of prey per jar, m the instantaneous prey mortality rate, τ the duration of the experiment, V the volume of the jar, and P the predator concentration in the jar.

Predator instantaneous egestion rates for each of the two prey types were calculated by combining Eq. 4 and 11 to get

$$\frac{dN}{dt} = FC_0 \exp(-mt) - \varepsilon N \tag{13}$$

and then integrating over the duration of the experiment and solving for N:

$$N = \frac{FC_0}{\varepsilon - m}[\exp(-m\tau) - \exp(-\varepsilon\tau)]. \tag{14}$$

Using this equation, we can calculate ε, because N, F, C_0, m, and τ are known from the experiment.

Predator ingestion rates were calculated from experimental results

$$I = \frac{C_0 - C_f}{\tau}. \tag{15}$$

Estimating the time to reach steady state—In order to ascertain how effective this method would be in the field, one needs to estimate how long it would take a predator's gut contents to reach steady state after the predator enters a new prey patch.

Returning to Eq. 4, we can separate the variables to get

$$dt = \frac{dN}{FC - \varepsilon N}. \tag{16}$$

Integrating on both sides, we get

$$t + K' = -\frac{1}{\varepsilon}\ln\left(\frac{FC}{\varepsilon} - N\right) \tag{17}$$

where K' is the constant of integration.

Further, rearranging the variables and taking the exponential yields

$$N = \frac{FC}{\varepsilon} - K\exp(-\varepsilon t). \tag{18}$$

At $t = 0$, $N = 0$, and $\exp(-\varepsilon t) = 1$. Therefore, Eq. 18 is reduced to

$$\frac{FC}{\varepsilon} = K. \tag{19}$$

Substituting Eq. 19 into Eq. 18, we get

$$N = \frac{FC}{\varepsilon} - \frac{FC}{\varepsilon}\exp(-\varepsilon t). \tag{20}$$

Taking the natural logarithm and rearranging the variables will give us an estimate of the time to reach steady state:

$$t = \frac{-\ln[1 - (\varepsilon N/FC)]}{\varepsilon}. \tag{21}$$

By means of the above equation, we can approximate the amount of time for the predator's gut contents to reach at least 90% of its theoretical steady state value, given that $N^* = FC/\varepsilon$ at steady state (Eq. 8):

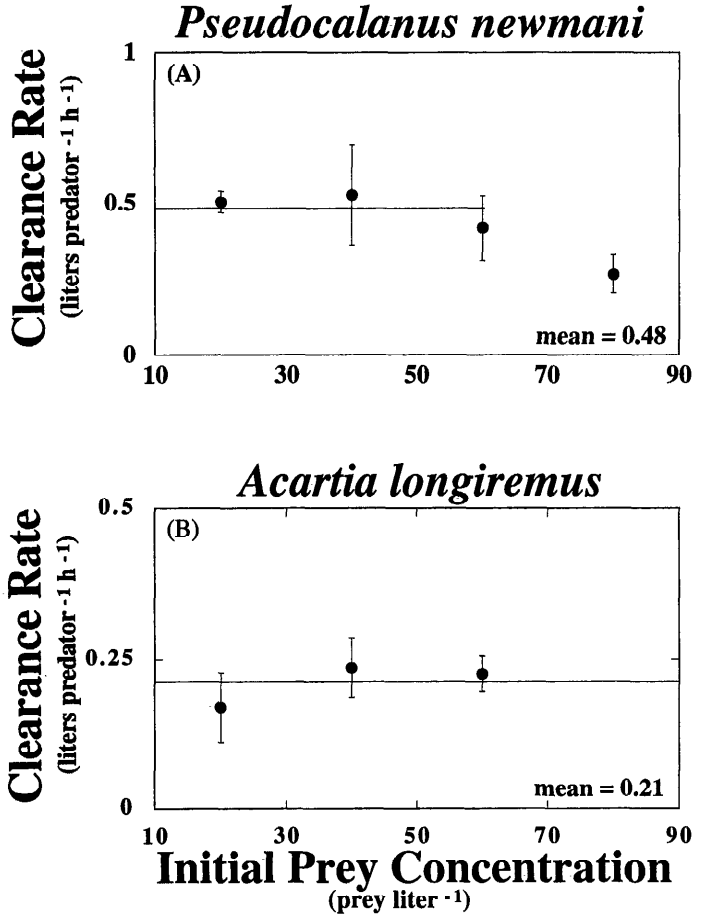

Fig. 2. Mean clearance rate values for *Pleurobrachia bachei* feeding on *P. newmani* and *A. longiremis*. The solid line in panel A indicates the average clearance rate values for 20–60 prey liter^{-1} and in panel B indicates the average clearance rate for all the prey concentrations, 20–60 prey liter^{-1}. There was no correlation seen for prey concentrations up to 60 prey liter^{-1} for the clearance rate values of *P. newmani* ($P > 0.35$, $r^2 = 0.04$). There was no correlation between the clearance rate and the initial prey concentrations for *A. longiremis* ($P > 0.13$, $r^2 = 0.11$). Each point represents the average of 8 replicates with 95% C.I. error bars.

$$t^* = \frac{-\ln(0.1)}{\varepsilon} \qquad (22)$$

where t^* is the time it takes to reach steady state. Similarly, we could estimate the amount of time to reach 50%, 70%, or any other value of the predator's steady state gut contents.

Because the recovery of copepods from all the control jars was 100%, no corrections were required for any of the above calculations.

Results

Clearance rate—Clearance rates were examined as functions of initial prey concentration. In the *Pseudocalanus* experiments, there was no correlation between clearance rate and initial prey concentration up to concentrations of 60 prey liter^{-1} (Fig. 2A). Adding results from the jars with initial prey concentrations of 80 prey liter^{-1} did result in a significant negative correlation ($P < 0.005$, $r^2 = 0.24$). These results suggest that clearance rates can be assumed constant up to concentrations of 60 prey liter^{-1} but not higher. The mean clearance rate on prey concentrations up to 60 prey liter^{-1} was 0.48 liter pred^{-1} h^{-1} (±0.07, 95% C.I.).

In the *Acartia* experiments, there was no correlation between clearance rate and initial prey concentration up to concentrations of 60 prey liter^{-1}. The mean clearance rate on prey concentrations up to 60 prey liter^{-1} was 0.21 liter pred^{-1} h^{-1} (±0.03, 95% C.I.) (Fig. 2B).

The clearance rates for *Acartia* were significantly lower than that observed for *Pseudocalanus* [Mann-Whitney test; H_0 is rejected at $\alpha = 0.05$, where $Z(-4.982) < \omega_{\alpha/2}(-1.6449)$].

Instantaneous egestion rate—Instantaneous egestion rates were also examined as functions of initial prey concentration. In the *Pseudocalanus* experiments, there was no correlation between instantaneous egestion rate and initial prey concentration (Fig. 3A). These results suggest that instantaneous egestion rates can be assumed constant over the range of prey concentrations used in these experiments. The mean instantaneous egestion rate on prey concentrations up to 60 prey liter^{-1} was 0.67 h^{-1} (±0.16, 95% C.I.).

In the *Acartia* experiments, there was no correlation between instantaneous egestion rate and initial prey concentration up to concentrations of 60 prey liter^{-1}. The mean instantaneous egestion rate on prey concentrations up to 60 prey liter^{-1} was 0.86 h^{-1} (±0.19, 95% C.I., Fig. 3B).

There was no significant difference between the instantaneous egestion rates for the two prey types. [Mann-Whitney test; H_0 accepted at $\alpha = 0.05$, where $Z_{\alpha/2}(-1.6449) < Z(-1.555) < Z_{1-\alpha/2}(1.6449)$.]

Gut contents—Gut contents also were examined as functions of initial prey concentration. For both the *Pseudocalanus* and *Acartia* experiments, there was a significant positive correlation between the number of prey in the gut and the initial prey concentration (Fig. 4). The regression equations for *Pseudocalanus* and *Acartia* were $y = 0.36x + 6.34$ and $y = 0.66x + 2.25$ where $P < 0.0002$ for both regressions.

Ingestion rate as a function of gut contents—*Pleurobrachia*'s ingestion rate and gut contents both vary proportionally with prey concentration. Hence, it is expected that they would vary proportionally with one another. This expectation is confirmed by the strong correlations in the functional regressions (Jensen 1986) between ingestion rate and gut contents observed for *Pleurobrachia* feeding on both *Pseudocalanus* and *Acartia* (Fig. 5). The slopes (*P. newmani*: $y = 0.44x + 4.58$; *A. longiremis*: $y = 0.89x + 0.76$) from each of these regressions provide a second estimate of *Pleurobrachia*'s instantaneous eges-

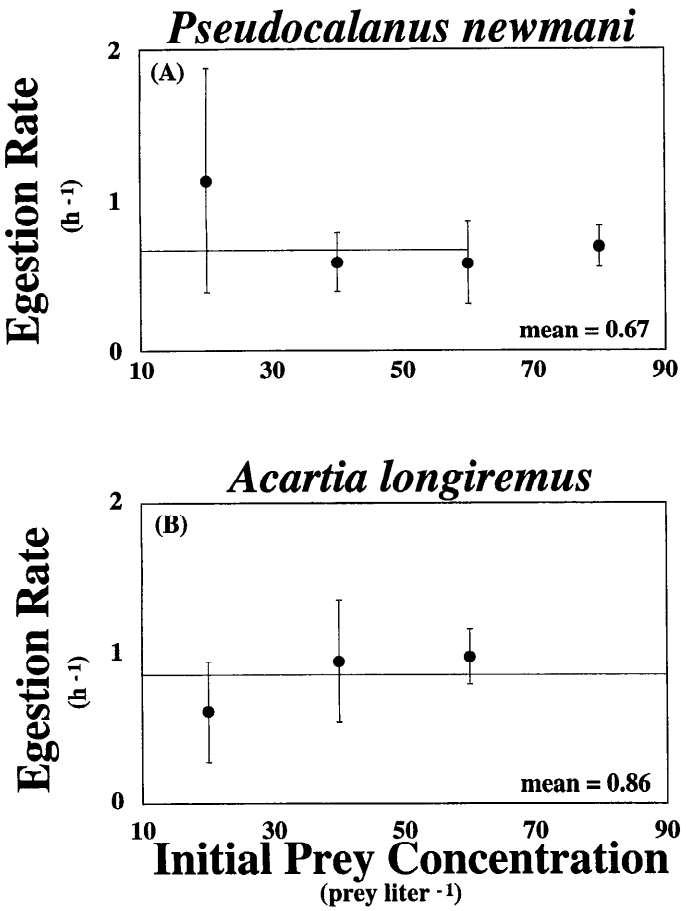

Fig. 3. Mean instantaneous egestion rates as a function of prey concentration for *Pleurobrachia bachei* feeding on *P. newmani* and *A. longiremis*. The solid lines indicate the average instantaneous egestion rates for prey concentrations up to 60 prey liter^{-1}. There was no correlation seen between the instantaneous egestion rate and initial prey concentration for either *P. newmani* ($P > 0.15$, $r^2 = 0.07$) or *A. longiremis* ($P > 0.13$, $r^2 = 0.10$). Each point represents the average of 8 replicates with 95% C.I. error bars.

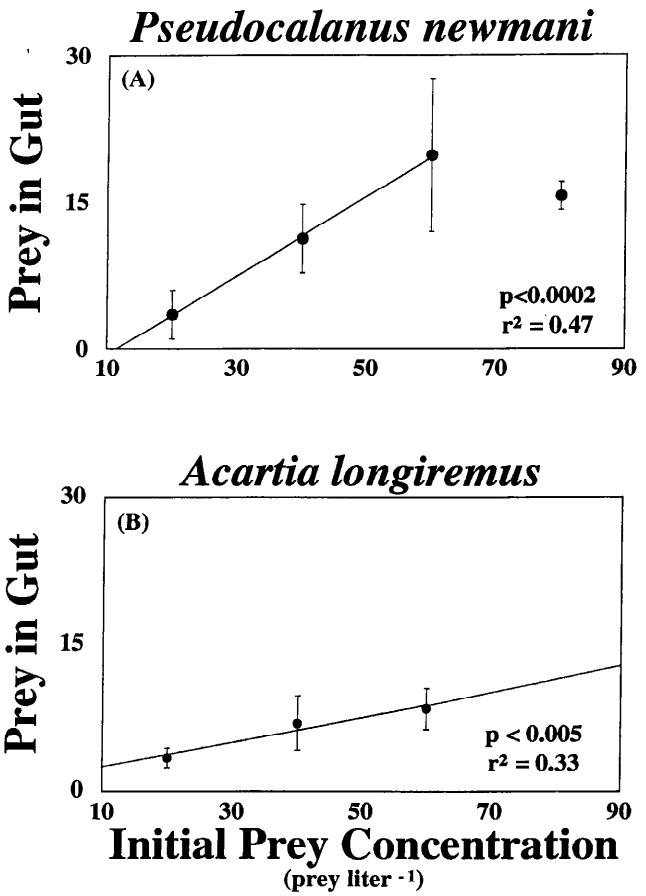

Fig. 4. Mean number of prey in gut as a function of prey concentration for *Pleurobrachia bachei* feeding on *P. newmani* and *A. longiremis*. The solid lines indicate the regression line between number of prey in the gut and initial prey concentration up to 60 prey liter^{-1}. There is a positive correlation seen for both *P. newmani* ($P < 0.0002$, $r^2 = 0.47$) and *A. longiremis* ($P < 0.005$, $r^2 = 0.33$). Each point represents the average of 8 replicates with 95% C.I. error bars.

tion rate on each prey species, where the instantaneous egestion rates for *Pseudocalanus* and *Acartia* are 0.44 h^{-1} and 0.89 h^{-1}. A *t*-test was run on each of the regression equations, and both were found to be significant ($P <$ 0.0002 for both *Pseudocalanus* and *Acartia*).

There is considerable variability in the value of ε at the lowest prey concentration of 20 prey liter^{-1}, especially in the *Pseudocalanus* experiments. At very low prey concentrations, there are only a few prey items in the gut. A change from one to two prey items results in a doubling of the gut contents, and this has a large effect on the estimated instantaneous egestion rate. At higher prey concentrations, there are more prey items in the gut, and an absolute change in the number of prey in the gut has a smaller effect on the estimated instantaneous egestion rate. Thus, greater variability in estimated instantaneous egestion rates is to be expected at lower prey concentrations.

Estimating the time to reach steady state—The instantaneous egestion rates estimated from the experiments for *Pseudocalanus* and *Acartia* were 0.67 h^{-1} and 0.86 h^{-1}, so we can use these values in Eq. 22 to estimate the time it takes *Pleurobrachia*'s gut contents to reach 90% of the steady state value. For *Pseudocalanus*, $t^* \approx 3.44$ h; for *Acartia*, $t^* \approx 2.67$ h.

Discussion

Clearance rates—Sullivan and Reeve (1982, p. 61) compared the two basic methods for estimating the predatory impact of ctenophores on copepods. They concluded that although it was heartening to find that the two approaches provided estimates that were within an order of magnitude of each other, "neither approach is the absolute by which the other should be tested, since both rely on inadequate data and make large assumptions."

The approach proposed here combines the features of

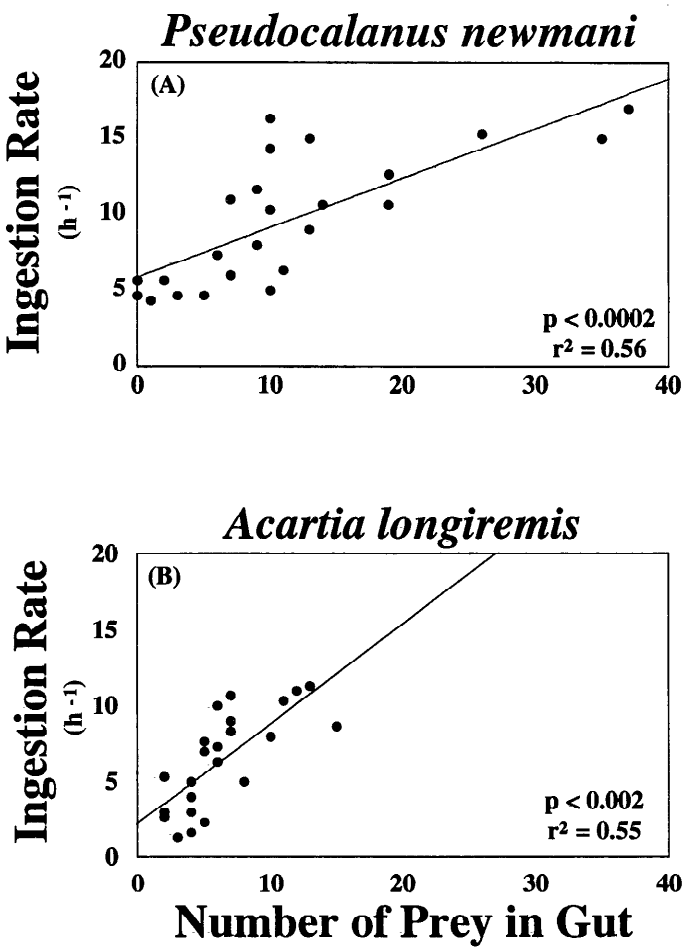

Fig. 5. Ingestion rate as a function of number of prey in the gut for *Pleurobrachia bachei* feeding on *P. newmani* and *A. longiremis*. The solid lines indicate the functional regression lines between number of prey in the gut and ingestion rates for prey concentrations up to 60 prey liter^{-1}. There is a positive correlation seen for both *P. newmani* ($P < 0.0002$, $r^2 = 0.56$) and *A. longiremis* ($P < 0.0002$, $r^2 = 0.55$). Each point represents the average of 8 replicates with 95% C.I. error bars.

both methods and thereby enables the investigator to look for internal consistencies in data derived from the laboratory and those derived from the field. If these data prove reasonably consistent, then it becomes possible to estimate not only predatory impact but also the prey concentrations actually available to predators in the field.

In this study, we tested the assumptions of the model underlying the proposed approach—namely, that both predator clearance rates and instantaneous egestion rates are constant over varying prey concentrations. We also examined the model's basic prediction that, at steady state, *Pleurobrachia*'s ingestion rate is linearly related to its gut contents.

Our finding that *Pleurobrachia*'s clearance rates remain constant with prey concentrations up to at least 60 prey liter^{-1} (=60,000 prey m^{-3}) is consistent with previous studies on tentaculate ctenophores. Greene et al. (1986) observed similar results in experiments with smaller (8 mm) *Pleurobrachia* feeding on *Pseudocalanus* and *Acartia*. Reeve et al. (1978) also observed similar results for 8-mm cydippid larvae of the lobate ctenophore, *Mnemiopsis mccradyi*, feeding on *Pseudocalanus minutus* and *Acartia tonsa*. In experiments with 30-mm lobate adults of the same species, Reeve et al. (1978) observed that clearance rates remained constant with prey concentrations up to 1,000 prey liter^{-1}. The functional responses of cydippid ctenophores and the cydippid larvae of lobate ctenophores start to saturate with increasing prey concentrations as handling times begin to accumulate and diminish the time available for tentacle deployment (Greene et al. 1986). Postlarval lobate ctenophores have no such constraint on their feeding capabilities, and there is little evidence for saturation of their functional response (Reeve et al. 1978).

The mean clearance rate determined in this study for 10-mm *Pleurobrachia* feeding on *A. longiremis* was 0.21 liter pred^{-1} h^{-1} (±0.03, 95% C.I.), comparable to the mean of 0.23 liter pred^{-1} h^{-1} (±0.012, 95% C.I.) found by Greene et al. (1986) for 8-mm *Pleurobrachia* feeding on *Acartia clausii*. The mean clearance rate determined for *Pleurobrachia* feeding on *P. newmani*, however, was slightly higher in this study, with a mean of 0.48 liter pred^{-1} h^{-1} (±0.07, 95% C.I.) compared to 0.34 pred^{-1} h^{-1} (±0.031, 95% C.I.) in the study by Greene et al. (1986). This difference could have arisen from different species of *Pseudocalanus* having been used. Unfortunately, this cannot be verified because the species of *Pseudocalanus* used in the Greene et al. study was not described at the time (Frost 1987).

Several studies have shown the potential importance of container size and shape on estimates of predation rates (Gibbons and Painting 1992; de Lafontaine and Leggett 1987; Luckingbill 1974). In order to avoid effects of predators and prey segregating in the experimental jars, we placed them on a rotating wheel. The 10-mm ctenophores fed normally in the 1-liter jars used in these experiments, and there was no evidence of tentacles retracting due to interactions with the sides of the jars. However, there may have been other factors that could affect clearance rates. One example is small-scale turbulence such as the surface shear created at the water–glass interface that may increase encounter rates if the prey move away from the shear zone (Marrasé et al. 1990). To look for such effects, we compared the clearance rate values of these experiments to those in experiments conducted by Greene et al. (1986), who used smaller (8 mm) *P. bachei* in larger experimental jars (3.785 liters). The clearance rates for the same prey species (*A. longiremis*) were comparable, as discussed above, which suggests that the effects of jar volume may be of lesser importance in our experimental design than when free-standing containers are used.

Egestion rates—In contrast to clearance rates, no previous efforts have been made to verify the assumption that instantaneous egestion rates are constant over varying prey concentrations. A number of studies (e.g. Reeve et al. 1978; Sullivan and Reeve 1982; Larson 1987) have used different methods of estimating ctenophore preda-

tion rates from their gut contents, but none have tested this assumption explicitly. This lack of rigorous testing is unfortunate because the assumption is critical to methods of estimating predator ingestion rates from analyses of their gut contents.

Here, a novel approach to estimate instantaneous egestion rates from laboratory experiments is introduced. In addition to enabling investigators to test the above assumptions, this approach also circumvents many of the problems associated with existing techniques for estimating gut passage rates. First, one can estimate egestion rates for predators without removing the prey and therefore without disturbing the animal as it feeds. Second, the egestion rates of predators which do not have transparent guts can also be determined. Finally, this approach avoids the need to run additional experiments to calculate gut passage rates. Only one set of experiments is required to calculate the values of the parameters F and ε for each predator-prey pair under a given set of experimental conditions.

Our results show that the ctenophore's instantaneous egestion rates are not correlated to changes in prey concentration for either of the two prey species. We conclude that egestion rates can be assumed constant over prey densities up to 60,000 prey m^{-3}, with a mean of 0.67 h^{-1} ($\pm$0.16, 95% C.I.) for *Pseudocalanus* and a mean of 0.86 h^{-1} ($\pm$0.19, 95% C.I.) for *Acartia* (Fig. 3).

Natural prey densities up to 10,000 m^{-3} for *Acartia* spp. in Biscayne Bay, Miami (Reeve et al. 1978), and up to 50,000 m^{-3} for *Pseudocalanus* spp. in Saanich Inlet, British Columbia (Reeve 1980), have been reported for these prey species. Thus, the prey densities used in these experiments are not unrealistic in terms of natural prey abundances, where ctenophores rarely encounter prey densities much higher than 60,000 prey m^{-3}.

As mentioned previously, the slopes from the regressions illustrated in Fig. 4 provide an additional estimate of *Pleurobrachia*'s instantaneous egestion rate on both prey species. It is heartening to find that the two different techniques used to estimate instantaneous egestion rates (i.e. direct calculations from experimental data and slopes from the regressions between ingestion rate and gut contents) give us comparable values. For the *Acartia* experiments, $\varepsilon = 0.86$ h^{-1} from direct calculation (Fig. 3) and $\varepsilon = 0.89$ h^{-1} from the regression slope (Fig. 5). On the other hand, for the *Pseudocalanus* experiments the estimates were further apart, with $\varepsilon = 0.67$ h^{-1} from direct calculation (Fig. 3) and $\varepsilon = 0.44$ h^{-1} from the regression slope (Fig. 5).

The discrepancy for the *Pseudocalanus* experiments may be explained by the amount of time it takes for the ctenophore's gut contents to reach steady state. All experiments were run for 3 h, and our calculations show that it takes *Pleurobrachia* ~3.4 and ~2.7 h to reach 90% of its steady state gut contents for *Pseudocalanus* and *Acartia*, respectively. Therefore, the ctenophore's gut contents may have not quite reached this steady state by the end of the *Pseudocalanus* experiments. In addition, there was considerably more variation in the *Pseudocalanus* data at 20 prey $liter^{-1}$, which was not observed in the data from the *Acartia* experiments. Both of these factors may have reduced the accuracy of the estimates for the instantaneous egestion rate on *Pseudocalanus*.

It is important to note that if we assume instantaneous egestion rate to be constant, it implies that the egestion rate is described by an exponential decay model (Dam et al. 1991). In other words, the egestion rate is a function of both the instantaneous egestion rate and the number of prey items in the gut. This result is characteristic of a batch reactor digestive system and in contrast to a steady-flow reactor system in which the egestion rate is a function of the instantaneous egestion rate alone (Penry and Jumars 1986). This model implies that food within the ctenophore's gut is processed in batch and that the digestive enzymes act on the whole volume of food in the gut (Penry and Jumars 1986). Examinations of the feces and gut contents of *Pleurobrachia* reveal that prey items are all digested together and not individually within the gut. These observations are consistent with the batch reactor type of digestive system and its associated exponential decay model.

Concluding remarks—Although the method developed here was based on a ctenophore species as the model predator, it is not restricted in its use to such predators and should be applicable to any predator-prey system that conforms to the assumptions of the underlying model.

If these assumptions are met, the model predicts that gut contents and ingestion rates are correlated to prey concentration and therefore correlated with one another. One particular study has hinted at the linear relationship between gut contents and prey concentrations. Sullivan and Reeve (1982, p. 63) showed that "a change in food availability with declining numbers of copepods is reflected in the ctenophore's gut contents." They examined the gut contents of predators kept in large (1,300 m^{-3}) mesocosoms over a period of 40 d during which no additional prey items were released. They did not directly correlate the gut contents with different prey concentrations. Our experiments, however, clearly demonstrate a positive correlation between gut contents and prey concentrations (Fig. 4), as would be predicted from the model given that clearance rates and egestion rates are constant over changing prey concentrations. Consequently, we also expected to find a positive correlation between ingestion rates and the number of prey items in the gut for both prey types, as was shown to be the case for *Pleurobrachia* feeding on both *Pseudocalanus* and *Acartia* (Fig. 5). The slopes of the regressions provide us with a simple means of estimating the instantaneous egestion rates of predators in the field.

It has been shown that the assumptions of the model are valid and that its predictions hold true, at least in the laboratory. It should be possible to extend this new approach to field studies, where investigators can estimate predatory impact by analyzing predator gut contents and combining these data with known laboratory measures of clearance rates and instantaneous egestion rates. Given that predators and prey are often patchily distributed and may also undergo extensive vertical migration patterns,

it is helpful to know how long a predator must be in a prey patch before its gut contents attain steady state. The calculations here show that it takes a predator starved for 12 h about 2.5–3.5 h to reach 90% of its steady state gut contents.

Before this method is used extensively in the field, however, experiments must be conducted to evaluate the influence of predator size and different prey types on the clearance and instantaneous egestion rate parameters. Previous experiments have shown that clearance rates are lower and digestion times longer for smaller size classes of predators (Reeve et al. 1978; Reeve 1980), as might be expected. These experiments were run with single prey species, and clearance rates and instantaneous egestion rates were evaluated independently. Since predator gut contents exhibit a wide diversity of prey (Sullivan and Reeve 1982; Larson 1987), it is necessary to run experiments to calculate different parameter values for each of the different prey types of interest. If we assume that the digestion of different prey species in the gut occurs independently, then mixed prey experiments should yield parameter values comparable to those from single prey experiments. If this is true, then parameter estimates from single prey experiments would be sufficient to convert predator gut content data to estimates of predatory impact. This prediction clearly needs to be tested under controlled laboratory conditions.

Ctenophores can be extremely important predators in the food chains of coastal (Reeve 1980) and open-ocean ecosystems (Swanberg and Båmstedt 1991). Larson (1987) has shown the large impact ctenophores can have as consumers of euphausiid eggs and larvae where they can compete with salmon and other juvenile fish for these same prey. Reeve et al. (1978) stated that ctenophores often act to balance the ecosystem by restraining an overabundance of copepods from virtually eliminating all phytoplankton from the water column. More recently, Travis (1993) has described the devastating effects of the ctenophore *Mnemiopsis leidyi*—a species introduced to the Black and Azov Seas through the ballast waters of ships. Fish catches dropped by an estimated 182,000 t in the Azov Sea alone, and predation by these ctenophores is believed to be the main cause of the decline. The ctenophores were found to have large quantities of zooplankton in their guts, including small crustaceans, as well as the eggs and larvae of fish. Consequently, ctenophore predation may result in both direct and indirect effects that can cascade throughout marine food chains and ultimately regulate the yield of commercially important fish stocks. Our understanding of the role ctenophores play in marine ecosystems requires that good, quantitative methods be developed to estimate their predatory impact.

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Submitted: 25 April 1994
Accepted: 6 October 1994
Amended: 27 February 1995