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Functional response of the euphausiid *Thysanoessa raschii* grazing on small diatoms and toxic dinoflagellates

by Sam McClatchie^{1,2}

ABSTRACT

The functional response of *T. raschii* feeding on monocultures of small phytoplankton at 0.4–14 $\mu\text{g pigment liter}^{-1}$ was determined using a time-series method in a large volume flow-through grazing system. A model-free robust regression procedure aided by graphical and statistical methods was used to compare Ivlev, Michaelis-Menten, linear, Disk equation and Holling type III models. Ivlev, Michaelis-Menten and Disk equation models were less preferable to a linear model because their parameters were highly correlated and could not be uniquely determined, although they appear to fit the data graphically. Holling type III model did not fit the data. A linear model both matched the model-free robust regression, and avoided problems of correlated parameters. No feeding threshold was detectable for the range of concentrations examined. *T. raschii* ingested the diatom *Chaetoceros gracilis* and both toxic and nontoxic clones of the dinoflagellate *Gonyaulax tamarensis* at the same rate at low concentrations (0.4–1.6 $\mu\text{g pigment liter}^{-1}$).

1. Introduction

The feeding ecology of krill³ has been increasingly studied in recent years, partly as a result of the interest in Antarctic krill (*Euphausia superba*) as a fisheries resource. Data collected to date have not provided an overall quantitative basis for predicting feeding rates of krill as a function of food concentration (functional response), food particle size and quality (selectivity), or the spatial and temporal distribution of food (patchiness).

Qualitative feeding studies on *T. raschii* indicate that it is omnivorous with a large component of phytoplankton and detritus in the diet. The well-developed mandibular molar (Ponomareva, 1976) and finely meshed feeding basket (7–8 μm , Berkes, 1976) suggest this krill is more herbivorous. Stomach contents of *T. raschii* from the Gulf of St. Lawrence showed high variability, being dominated by diatoms on one day and by

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3. The word krill is used to refer to euphausiids in general, consistent with standard usage in the multilingual dictionary of fish and fish products (OECD, 1968). The word is derived from Scandinavian terms for whale food (“krill” = Swedish; “storkrill” (big krill) and “smakrill” (small krill) = Norwegian) and should not be restricted to *Euphausia superba* alone, as it often is in popular usage. Although the term should be plural, this is violated for the sake of convenient units (e.g. $\text{ml krill}^{-1} \text{h}^{-1}$).

tintinnids and copepods the next. Dinoflagellates were uncommon, and much of the stomach contents were unidentifiable (Simard *et al.*, 1986). Sameoto (1980) reported that fewer than 5% of *T. raschii* in his samples from the Gulf of St. Lawrence contained the remains of copepods. He reported numerous different phytoplankton taxa ranging in size from 10 μm width to 15–80 μm length. Mauchline (1966) held the opinion that *T. raschii* fed both raptorially, and at the benthos upon detritus. Remains of copepods were common in the stomachs of *T. raschii* from June–August and October in the Clyde Sea, but were not as common as other components of the diet. Dinoflagellates were common in the guts during November. Mauchline inferred that detritus is the major dietary component of *T. raschii*. In this paper, I examine the functional response of herbivorously feeding krill.

The functional response is defined as the change in the attack-rate (or ingestion rate) per predator as a function of variation in prey density, for predators that search at random for a randomly distributed and homogeneous prey population (Solomon, 1949; Holling, 1959a, 1965; Hassell *et al.*, 1976). Several models of functional response have been described for invertebrate predators. The Holling type I model is characterized by a linear relationship between ingestion rate and prey concentration, up to an asymptotic maximum ingestion (Holling, 1959a). The disk equation (Holling, 1959b) and Ivlev responses (Ivlev, 1961) are characterized by a decreasing rate of change in ingestion rate as food density increases, and are the most common response among arthropod predators (Hassell *et al.*, 1976). The sigmoid type III response was thought to be more characteristic of vertebrate predators, and to imply learning to concentrate upon more abundant prey (Holling, 1965). However, Hassell *et al.* (1977) argued that sigmoid responses are more common in invertebrate predators than previously recognized, while Dunbrack and Giguere (1987) argued that the effects of foraging time and foraging velocity could combine to produce type III responses independent of learning. Dome shaped responses with reduced ingestion rates at high prey concentrations, attributed to interference or sensory adaptation of receptors, have also been described (Holling, 1961; Hassell *et al.*, 1976). Nonsaturating functional responses have been reported for the range of food concentrations predators are likely to experience in the field and can be considered a subset of the type I response (Conover, 1978; Huntley, 1981). Finally, on theoretical grounds, based on optimal foraging theory, Abrams (1982) demonstrated that when time spent foraging is incorporated in functional response models, complex functional responses can arise. He suggested that functional responses are more plastic than previously assumed, that they may have several accelerating and decelerating regions, and that the traditional type I, II and III typology may be inadequate to describe responses in the natural environment.

Five different functional response models have been applied to feeding in euphausiids. Parsons *et al.* (1967) applied a modified Ivlev model, incorporating a threshold concentration for zero ingestion, to describe the functional response of *Euphausia pacifica* feeding on mixed phytoplankton. Ohman (1984) fitted a type III model to

data for *E. pacifica* grazing on algal monocultures. A Holling type I model was used by Boyd *et al.* (1984) for *Euphausia superba* feeding on mixed phytoplankton, whereas Kato *et al.* (1982) described a dome-shaped response for *E. superba* ingesting natural phytoplankton. Samyshev and Lushev (1983) applied the Ivlev model to their data for *E. superba*. Stuart (1986) used a logistic model to describe the functional response of *Euphausia lucens* feeding on diatoms, copepods and anchovy larvae. To date, there have been no attempts to evaluate the appropriateness of different models for krill.

The concept of a feeding threshold has been applied in two different ways in studies of zooplankton feeding. Parsons *et al.* (1967) defined the feeding threshold as the food concentration below which no ingestion occurs, whereas Frost (1975) defined the threshold concentration in terms of the onset of maximum filtering effort (clearance rate).

The focus of this paper is on the nature of the functional response of the neritic boreal euphausiid *Thysanoessa raschii*. A time-series method using a large volume grazing system (McClatchie, 1986) is applied to estimate ingestion and clearance rates of *T. raschii* as a function of phytoplankton concentration. The phytoplankton used as food were monocultures of the diatom *Chaetoceros gracilis*, and the dinoflagellate *Gonyaulax tamarensis*. The question of whether a feeding threshold exists was addressed. A secondary aim was to compare feeding rates on both toxic and nontoxic clones of the dinoflagellate with rates measured on the smaller diatom at low food concentrations.

2. Experimental protocol

Adult *T. raschii* were collected at night in November 1984 at the deepest point (60 m) of Bedford Basin, a coastal inlet at the head of Halifax harbor (44° 42.3' N; 63° 39.2' W) using 10 minute tows with a 530 μm mesh 1 m diameter conical net. Grazing experiments were performed using algal monocultures in the flow-through grazing system described by McClatchie (1986). *C. gracilis* cells were 7 μm diameter, often occurring as pairs, but not in chains. *G. tamarensis* were about 35 μm diameter, single celled, and were bioluminescent with a diel periodicity. Food concentrations expressed as $\mu\text{g pigment l}^{-1}$ were the sum of chlorophyll and phaeopigments. Krill were acclimated to their food for 24 h prior to experiments by providing a declining time series of concentration similar to the experiments. The range of food concentrations experienced by the animals during acclimation was 0.85–0.01 $\mu\text{g pigment l}^{-1}$ for *G. tamarensis* and 8.5–0.1 $\mu\text{g pigment l}^{-1}$ for *C. gracilis*. *T. raschii* were acclimated to the nontoxic clone of *G. tamarensis* prior to measuring feeding rates on the toxic *G. tamarensis* on the assumption that 24 h exposure to the toxic algae might incapacitate the krill. Toxicity of the dinoflagellate clone was established using an assay based on the LD-50 for laboratory mice (Ives, 1985).

The light regime during all experiments was set to a diel cycle of 10:14 L/D.

Illumination was provided by two 40-W blue fluorescent tubes (Westinghouse F40B) mounted approximately 1 m above the grazing chamber. All experiments were run at night with the exception of the final experiment using toxic *G. tamarensis*. It is not known whether light affects the feeding rates of the krill. The dim blue light given by the fluorescent tubes was assumed preferable to white lights because krill did not show elevated swimming activity when these lights were switched on. Water temperature measured at the outflow from the grazing chamber was $6.5^{\circ} \pm 0.6^{\circ}\text{C}$ (mean \pm SD) for all experiments. Inflow temperature was $3.5^{\circ} \pm 0.5^{\circ}\text{C}$, indicating a 3°C warming while the water was in the grazing chamber. The density of animals was 1 krill (10 liters) $^{-1}$ in the 250 liter grazing chamber. Six experiments were run using the same animals, four using *C. gracilis* and two using *G. tamarensis* as food (one each with toxic and nontoxic clones). *G. tamarensis* cultures had been acclimated to a reverse diel cycle so that their period of maximum bioluminescence (scotophase) was during the day, and period of minimal bioluminescence (photophase) was at night (Ives, 1986). Sex of the krill was not determined. The mean dry weight of *T. raschii* used in these experiments (\pm SD) was 17.2 ± 5.3 mg dry wt.

3. Calculation of feeding rates

The duration of experiments was 4–10 h, but algal concentration was recorded every 60 s. Feeding rates were calculated from the difference over 10 min intervals between the predicted chlorophyll concentration due to the dilution rate of the algae and the observed chlorophyll concentration when krill were present. Ingestion rates (μg pigment krill $^{-1}$ min $^{-1}$) were calculated from

$$I = 1/N [((C_i - C_{i-1})/(t_i - t_{i-1})) - SC_x/v] \quad (1)$$

where C_i is pigment concentration (μg liter $^{-1}$) at time t_i , C_{i-1} is pigment concentration at time t_{i-1} , S is flow rate (liter min $^{-1}$), v is grazing chamber volume (liters), C_x is mean pigment concentration from t_{i-1} to t_i , and N is the number of krill in the grazing chamber (krill (250 liters) $^{-1}$).

Clearance rates (ml krill $^{-1}$ min $^{-1}$) were calculated from

$$F = (1000 I)/C_x. \quad (2)$$

4. Conversion of in vivo fluorescence to pigments

A pulse of phytoplankton was added to the grazing chamber in the absence of krill, and in vivo fluorescence logged as the phytoplankton concentration was diluted by an inflow of filtered seawater. At approximately 30-min intervals water was diverted through the filter array and samples drawn through Gelman GFC filters for analysis of extracted chlorophyll. Filters were frozen in the dark at -20°C and pigments extracted in 90% acetone for 24 h immediately prior to analysis (Strickland and Parsons, 1972).

5. Nonlinear parameter estimation

Five models were tested to determine their suitability for describing the functional feeding response of *T. raschii*. Two models incorporated a threshold feeding concentration; the Ivlev equation as modified by Parsons *et al.* (1967)

$$I = I_{\max} \cdot [1 - \exp(-\delta \cdot (P - p'))] \quad (3)$$

and the Michaelis-Menten equation as modified by Mullin *et al.* (1975)

$$I = I_{\max} \cdot (P - p') / [K_m + (P - p')] \quad (4)$$

No threshold concentration was incorporated in the remaining models which were the Disk equation (Holling, 1959b)

$$I = (a \cdot P) / (1 + a \cdot T_h \cdot P) \quad (5)$$

the Holling type III equation (Holling, 1959a)

$$I = (a \cdot P^2) / (1 + a \cdot T_h \cdot P^2) \quad (6)$$

and a linear model

$$I = c \cdot P + d. \quad (7)$$

I is ingestion rate ($\mu\text{g pigment krill}^{-1} \text{ min}^{-1}$), I_{\max} is the maximum (saturated) ingestion rate, δ is the initial slope, P is food concentration ($\mu\text{g pigment liter}^{-1}$), p' is the food concentration at which $I = 0$, K_m is a half saturation constant, a is the instantaneous attack rate ($\text{liters} \cdot \text{min}^{-1}$), T_h represents the handling time per prey item ($\text{min} \cdot \mu\text{g pigment}^{-1}$), c and d are constants. The models chosen were based on the attempts of earlier workers (Mullin *et al.*, 1975; Parsons *et al.*, 1967) to fit these particular equations to copepod and krill functional responses and determine whether threshold feeding behavior occurred.

A model-free smoothing procedure (robust locally weighted regression, henceforth LOWESS, Cleveland, 1979) was used to summarize the data and provide an objective fit against which the various models could be compared. Models were examined for high correlations between their parameters (Draper and Smith, 1981). Nonlinear regressions were performed using the Statistical Analysis System (SAS) NLIN procedure with the modified Gauss-Newton method (SAS Institute, 1985). The linear regression was performed with SAS REG procedure.

Analysis of covariance (SAS GLM procedure) was used to determine whether ingestion rates of *T. raschii* were different between the two dinoflagellate clones and *C. gracilis* at a given concentration. The procedure was run once including an interaction term in the model to test for homogeneity of slopes relating ingestion rate to pigment concentration in each taxon. When the result showed no difference in slopes ($F = 2.27$, $P = 0.107$), the data were pooled and difference in ingestion rate at a given concentration was tested.

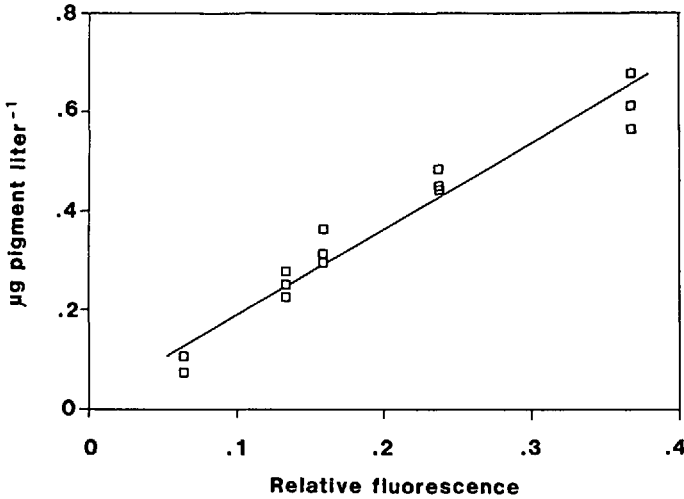


Figure 1. Regression relationship to predict total pigment concentration ($\mu\text{g liter}^{-1}$) from calibrated *in vivo* fluorescence for *Gonyaulax tamarensis* used in grazing experiments. Regression line is: P ($\mu\text{g liter}^{-1}$) = 1.735 (calibrated fluorescence) - 0.0157 ; $r^2 = 0.946$, $df = 1, 15$, $P < 0.001$.

6. Results

a. Conversion of in vivo fluorescence to pigments. Highly significant regressions allowed pigment concentration to be accurately predicted from fluorescence for both *G. tamarensis* (Fig. 1) and for *C. gracilis* (McClatchie, 1986).

b. Feeding rates on different species. At low food concentrations (0.4 – $1.6 \mu\text{g liter}^{-1}$) *T. raschii* fed on *C. gracilis* and *G. tamarensis* at rates that were not different, despite their difference in size. The analysis was restricted to low concentrations ($<1.6 \mu\text{g pigment l}^{-1}$) because experiments with dinoflagellates were run only at low concentrations. Analysis of covariance indicated that ingestion rates were not different between species or dinoflagellate clones at a given concentration ($P = 0.19$) (Table 1). The effect of cell concentration on ingestion rate was highly significant ($P < 0.0001$).

Table 1. Comparison of ingestion rates of *T. raschii* feeding on *C. gracilis*, and toxic and nontoxic clones of *G. tamarensis* at concentrations ranging from 0.4 – $1.6 \mu\text{g pigment liter}^{-1}$ using analysis of covariance.

Dependent variable: Ingestion rate			
Independent variables	<i>df</i>	<i>F</i>	Probability $>F$
Pigment concentration	1	94.5	0.0001
Species or clone	2	1.66	0.19

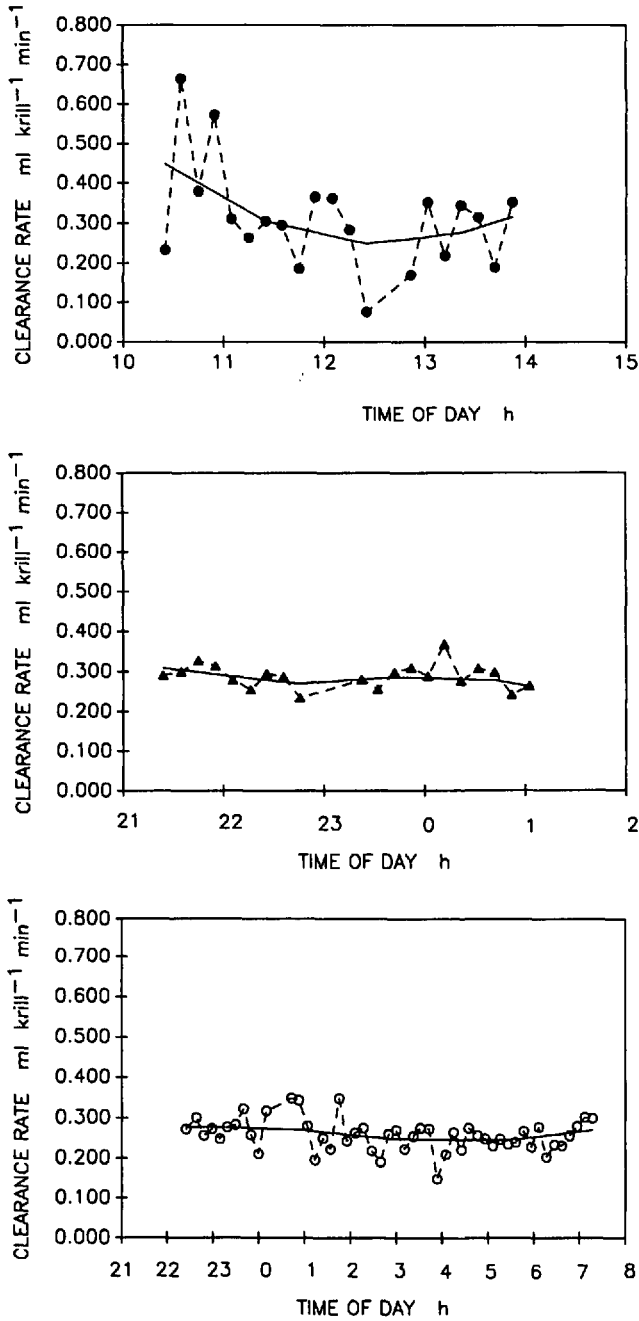


Figure 2. Time-series clearance rates (ml krill⁻¹ min⁻¹) for *T. raschii* grazing on (a) toxic *G. tamarensis*, (b) nontoxic *G. tamarensis*, (c) *C. gracilis*. Pigment concentrations ranged from 1.6–0.4 $\mu\text{g pigment liter}^{-1}$. Solid line is the robust locally weighted regression summarizing trend in the data. LOWESS parameters: $F = 0.075$, $n \text{ steps} = 2$, $\delta = 1$.

(Table 1). Each of the algae was offered as a monoculture rather than in mixtures and so no explicit test of selectivity can be made.

Time-series clearance rates (Fig. 2a) of *T. raschii* feeding on toxic *G. tamarensis* at concentrations of 0.4–1.6 $\mu\text{g pigment liter}^{-1}$ showed that clearance rate fluctuated between 0.1–0.7 $\text{ml krill}^{-1} \text{min}^{-1}$, with most values falling between 0.2–0.4 $\text{ml krill}^{-1} \text{min}^{-1}$. Clearance rates of *T. raschii* feeding on nontoxic *G. tamarensis* and *C. gracilis* also fluctuated with time (Fig. 2b, 2c), varying from 0.2–0.35 $\text{ml krill}^{-1} \text{min}^{-1}$. These values overlap with but are less variable than time-series clearance rates on toxic *G. tamarensis*. The LOWESS smooth showed no decline in clearance rate with time, in contrast to the clearance rates on toxic *G. tamarensis*. The higher variability of clearance rates on toxic *G. tamarensis* may have arisen from the greater bioluminescence of these cells which were in scotophase. The net effect of higher luminescence and greater toxicity was expected to depress clearance rates but no clear depression was measured. Although the smoothed fit to the data suggests an initial decline of clearance rate with time, this is the result of only two data points. This fact, and the failure of analysis of covariance to detect any difference in ingestion rates suggests feeding of *T. raschii* was not depressed on a time scale of 3–4 h when feeding on toxic *G. tamarensis*.

c. Model discrimination. All of the data were pooled to fit the functional response models. Examination of the residuals of all five models showed a pattern of increasing variance at higher pigment concentrations when untransformed variables were used. Transformation of the dependent variable could be used to stabilize the variance, but would complicate interpretation of the models. Consequently models were fitted in linear space and compared with the LOWESS fit to the data. This procedure and a simple graphical comparison of the models was used because it is statistically invalid to apply tests of significance (*F*-tests) to nonlinear models (Draper and Smith, 1981). An *F*-test was computed for the linear model only.

An *F*-test for the linear model showed that the linear fit was highly significant ($F = 590.5$, $P < 0.0001$, $r^2 = 0.64$, $df = 332$). The intercept of the linear model was not significantly different from zero ($P = 0.42$). The linear and Disk equation models were very close to the modified Ivlev and Michaelis-Menten curves (Fig. 3). The modified Ivlev and Michaelis-Menten models gave visually indistinguishable results. In contrast, the Holling type III model deviated from the other four, predicting a lower asymptote and a steeper initial slope. At concentrations ranging from 0.4–3.0 $\mu\text{g pigment liter}^{-1}$ the Holling type III model deviated from the data, predicting lower than observed values (Fig. 4). A comparison of the linear model with a LOWESS smooth fit showed quite close agreement (Fig. 5), particularly at the low pigment concentrations likely to be found for most of the year where *T. raschii* is abundant (Sameoto, 1976; Sargent *et al.*, 1985).

The fitted curve for clearance rates was calculated (Eq. 2) from ingestion rates

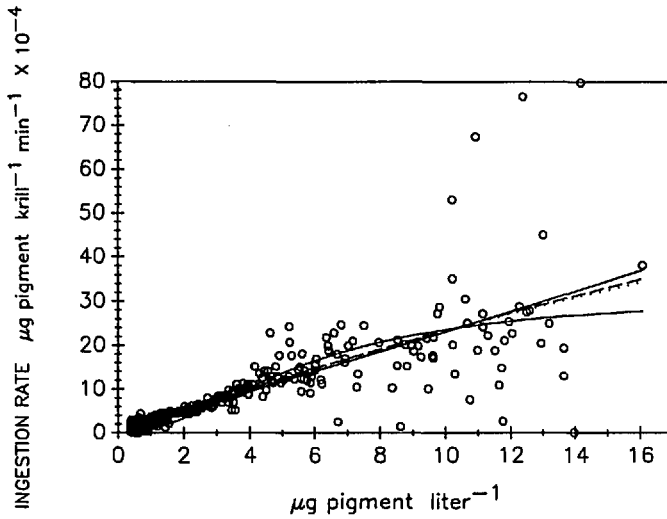


Figure 3. Functional response curve for ingestion rate of *T. raschii* (10^{-4} $\mu\text{g pigment krill}^{-1} \text{ min}^{-1}$) vs. mean pigment concentration ($\mu\text{g pigment liter}^{-1}$). \cdots = modified Ivlev model, $Y = 90.147 [1 - \exp[-0.03 (P - 0.054)]]$; $---$ = Disk equation, $Y = (2.646 P)/(1 + 2.646 \cdot 0.005 P)$; $- \cdot - \cdot$ = Holling type III model, $Y = (0.966 \cdot P^2)/(1 + 0.966 \cdot 0.032 \cdot P^2)$; $---$ = linear model, $Y = 2.276 P + 0.382$. $n = 333$. Data from all 6 experiments.

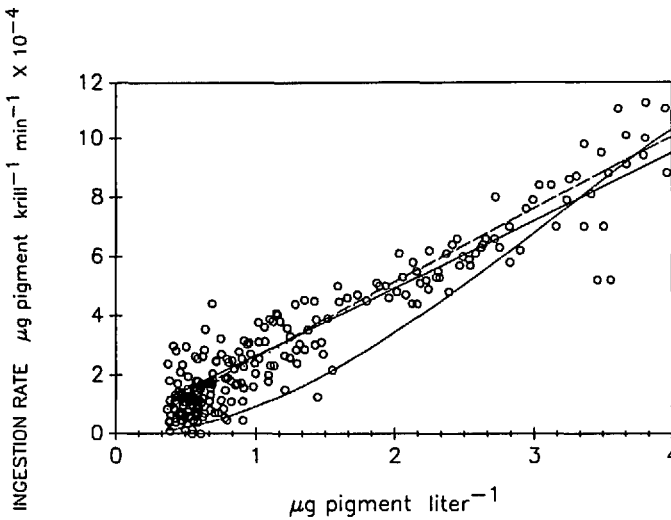


Figure 4. Functional response curve for ingestion rate of *T. raschii* (10^{-4} $\mu\text{g pigment krill}^{-1} \text{ min}^{-1}$) vs. mean pigment concentration ($\mu\text{g pigment liter}^{-1}$) over the concentration range expected in coastal waters. Symbols as in Figure 3. Data from all 6 experiments.

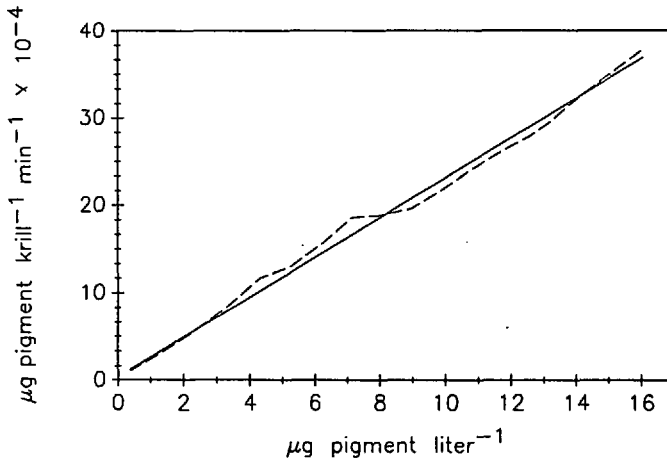


Figure 5. Comparison of linear model (solid line) fit to data in Figure 3 and a model-free smoothed curve estimated by locally weighted robust regression (LOWESS, dashed line). LOWESS parameters are the same as Figure 2.

fitted with the linear model (Eq. 7). The fit of predicted to observed clearance rates, was good in the range 1–4 $\mu\text{g pigment liter}^{-1}$ (Fig. 6). The variability in clearance rates observed at 0.4–1.0 $\mu\text{g pigment liter}^{-1}$ arises from the lack of averaging of clearance rates, such as occurs in conventional grazing experiments. The high frequency fluctuations in clearance rate that occur over time (Fig. 2), when measured every 10 min as in this study, produces the noise at low pigment concentrations.

If the correlation between any two parameters in a fitted model is greater than $|0.9|$, it is likely that more than one combination of these parameters will yield an equally

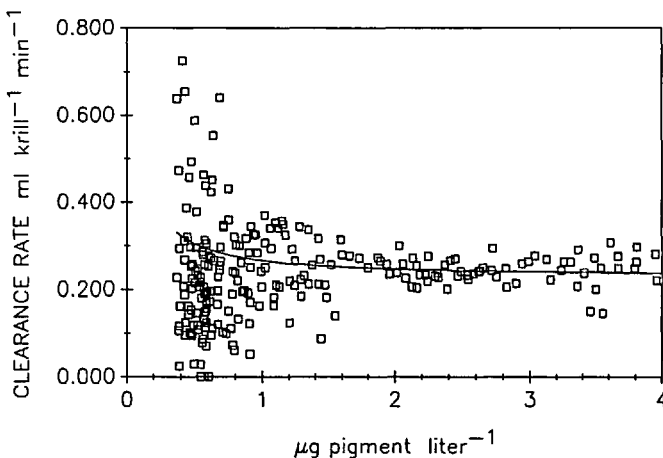


Figure 6. Functional response curve for clearance rate of *T. raschii* ($\text{ml krill}^{-1} \text{min}^{-1}$) vs. mean pigment concentration ($\mu\text{g liter}^{-1}$) derived from the linear model fit to ingestion rate data. Data from all 6 experiments.

Table 2. Partial correlation matrices for the parameters in the Ivlev, Michaelis-Menten, Disk equation, and Holling type III functional response models.

Ivlev	I_{\max}	δ	p'
I_{\max}	1.0	-0.99	-0.61
δ		1.0	0.63
Michaelis-Menten	I_{\max}	K_m	p'
I_{\max}	1.0	0.99	-0.62
K_m		1.0	-0.65
Disk equation	a	T_h	
a	1.0	-0.93	
Holling type III	a	T_h	
a	1.0	-0.29	

good fit to the data (Draper and Smith, 1981). In such cases, unique values of the parameters concerned cannot be obtained and the model should be regarded as ill-conditioned. Inspection of the partial correlation matrices (Table 2) for both the Ivlev and Michaelis-Menten models showed correlations between two parameters that exceed $|0.9|$. In the Ivlev model, the initial slope (δ) and maximum ration (I_{\max}) are highly negatively correlated (-0.99), whereas the half-saturation constant (K_m) and I_{\max} are highly positively correlated (0.99) in the Michaelis-Menten model. The Disk equation also showed a strong negative correlation (-0.93) between the attack rate (a) and handling time (T_h) parameters. In contrast, the correlation between the a and T_h parameters of the Holling type III model (-0.29) was low (Table 2). This problem does not arise with the linear model.

7. Discussion

The amount of data yielded by the time-series method permits statistical determination of the most appropriate model to describe the functional response curve, and to decide which, if any, of the models proposed by Frost (1975) and Mullin *et al.* (1975) are satisfactory. Conventional grazing experiments have not been satisfactory for this purpose, primarily because of a paucity of data. The time-series method also provides data on clearance rates that permits feeding activity to be monitored. The effect of suspected toxins, or other factors such as rapid changes in food concentration (McClatchie, 1986) can be determined. Previously this was only feasible using video observation of feeding appendages, since high speed cinematographic records are generally too short duration. The time series clearance rates also illustrate that clearance rate may not be constant as is assumed in grazing rate equations (McClatchie and Lewis, 1986).

Mathematically, the Ivlev, Michaelis-Menten and Disk equation models are ill-conditioned in that they show high correlation between their parameters. This means

that the values of the parameters cannot be uniquely determined. The Michaelis-Menten model is not useful to describe functional response data because the half-saturation constant (K_m) has no meaning out of the context of substrate kinetics. The interpretation of the parameters of the Ivlev curve (or the Disk equation) is more evident (Hassell *et al.*, 1976; McClatchie and Lewis, 1986). The Holling type III model can be rejected on the basis that the graphical fit to the data is poor. The linear model provides a good fit to the data, while avoiding the problems of high correlations between model parameters, and the interpretation of fitted parameters as behavioral elements. Its obvious limitation is that feeding rates cannot increase indefinitely, and must saturate at some level set by gut volume and gut passage time. Whether this level is reached in the field may depend on the food type and the acclimation of the animals.

Samyshev and Lushev (1983) predicted zero ingestion by *E. superba* at $0.04 \mu\text{g pigment liter}^{-1}$, allowing for the approximations involved in converting from dry weight to carbon to chlorophyll. The feeding threshold values estimated by Parsons *et al.* (1967) for *E. pacifica*, allowing for errors in conversion from cell volume to carbon and then to chlorophyll were approximately $1.2\text{--}2.6 \mu\text{g pigment liter}^{-1}$. Both these authors fitted Ivlev type curves. Using a linear model for a restricted range of concentrations, McClatchie (1986) predicted that *T. raschii* would cease ingestion at $0.25 \mu\text{g pigment liter}^{-1}$. The results presented here however yield an intercept from the linear model that is not significantly different from zero. The data do not show any concentration where ingestion ceases entirely within the range of concentrations examined. This suggests that *T. raschii* does not exhibit a feeding threshold when feeding on small phytoplankton, although the conclusion should be viewed cautiously since it is based on extrapolation to concentrations lower than $0.4 \mu\text{g pigment liter}^{-1}$. The data are consistent with the filmed and videotaped observations of copepod feeding and conventional grazing experiments which show that feeding and swimming are reduced at low concentrations but do not cease altogether (Frost, 1975, Price and Paffenhöfer, 1986b).

Conover (1978) suggested that the critical concentration for saturated ingestion rate depended upon the ambient concentration of food experienced by the animals, and that saturation kinetics rarely, if ever, applies to animals in the field. Phytoplankton concentrations as high as $7\text{--}8 \mu\text{g pigment liter}^{-1}$ occur only during the spring bloom in North Norwegian fjords where *T. raschii* is abundant (Falk-Petersen and Hopkins, 1981; Sargent *et al.*, 1985). Consequently it is likely that the functional response of *T. raschii* in nature would not saturate when krill are feeding on small cells at mean water column concentrations. Saturated feeding may occur in concentrated lenses of phytoplankton described by (Derenbach *et al.*, 1979), at oceanic fronts (Pingree *et al.*, 1975) or in the convergences of Langmuir circulations (Weller *et al.*, 1985).

Clearance rates reported in this study are low for zooplankters as large as *T. raschii*. For *C. gracilis* this is very likely because the food cells were small. While it is certain

that krill of several species do consume small cells (Parsons *et al.*, 1967; Lasker, 1966; Boyd *et al.*, 1984) they are probably not an optimum food size. In the case of *G. tamarensis* clones, bioluminescence of the cells (Ives, 1986) may have depressed clearance rates, although the cells were considerably larger than *C. gracilis*. Ingestion rates in copepods are depressed by highly luminescent dinoflagellate cultures (Esaias and Curl, 1972; White, 1979; Buskey *et al.*, 1983). Luminescence was equal in both dinoflagellate clones but the toxic clone was offered during the day (high luminescence phase), whereas the non-toxic clone was offered at night (low luminescence). I expected the combination of toxicity and bioluminescence to depress clearance rates, but this was not observed. Perhaps *T. raschii* is less sensitive than copepods to both toxicity and luminescence. Alternatively, because the effect was examined only over 3–4 h, clearance rates low, and the krill large relative to copepods, it is possible that insufficient toxin was ingested to elicit an acute physiological response.

Earlier experimental work on krill feeding, theoretical considerations, and the apparently equally good fit of several models to the data suggest caution when extrapolating laboratory functional responses to the environment. Ohman (1984) contrasted the functional response to *E. pacifica* feeding on diatoms (type II) with that on small copepods (type III). The implication is that the response of krill is not rigid and stereotypic but changes with prey type (ie., prey morphology, chemical composition or motility). Hassell (1978) summarized studies showing that the functional response of a predator can vary with prey type. Abrams (1982) argued that functional responses measured in the laboratory may differ from those in the field because of the difficulty of experimentally reproducing factors such as predation pressure which influence foraging time. These considerations, together with Abrams' (1982) demonstration of complex shaped functional responses suggest that it may be useful to adopt an empirical pragmatic approach in laboratory experiments. One way to do this would be to use robust regression (LOWESS) to characterize the functional response of krill fed natural mixtures of prey, rather than trying to fit variable data with models which may be inappropriate.

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