



Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Influence of spatial heterogeneity on the type of zooplankton functional response: A study based on field observations

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ARTICLE INFO

Available online 7 July 2008

Keywords:

Zooplankton feeding response
Holling's types
Calanus glacialis
Vertical distribution
Barents Sea

ABSTRACT

Mathematical models of plankton dynamics are sensitive to the choice of type of zooplankton functional response, i.e., to how the rate of intake of food varies with the food density. Conventionally, the conclusion on the actual type of functional response for a given zooplankton species is made based upon laboratory analysis on experimental feeding. In this paper, we show that such an approach can be too simplistic and misleading. Based on real ocean data obtained from three expeditions of R/V *Jan Mayen* in the Barents Sea in 2003–2005, we demonstrate that vertical heterogeneity in algal distribution as well as active vertical movement of herbivorous zooplankton can modify the type of trophic response completely. In particular, we found that the rate of average intake of algae by *Calanus glacialis* exhibits a Holling type III response, instead of Holling type I or II found previously in laboratory experiments. We argue that this conceptual discrepancy is due to the ability of the zooplankton to feed in layers with high algal density and to avoid depths with lower algal density. Since theoretical studies would predict enhancing in system stability in the case of Holling type III, our results may be of importance for understanding the main factors controlling plankton dynamics.

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1. Introduction

The dependence of zooplankton specific food intake rate (i.e., an amount of phytoplankton consumed per zooplankton biomass per unit of time) on algal density is known as zooplankton functional (or trophic) response. The available data reveal three basic types of such a response. In ecological literature they are known as Holling's trophic functions (Holling, 1959; Jeschke et al., 2004) and shown schematically in Fig. 1A–C. The simplest relationship (type I, Fig. 1A) is a direct proportionality between the algal density P and the rate of specific food intake $f(P)$; further $f(P)$ becomes constant for large P . Type II (Fig. 1B) shows a curvilinear growth of $f(P)$ which is concave downward and gets saturated for large P . Type III (Fig. 1C) is known as 'sigmoidal' response and characterized by an inflection point separating the concave part from the convex part of the curve. Note that in some cases a functional response can be more complicated and include a pronounced decrease of $f(P)$ for high algal densities (see Fig. 1D) due to intoxication processes (Gentleman et al., 2003). Sometimes

this type is referred in the literature as Holling type IV (Taylor, 1984).

The study of functional responses for different zooplankton species is not only a challenging problem of plankton biology but is of vital importance for mathematical modeling of plankton communities. The point is that the choice of an appropriate type of response becomes crucial when modeling a particular ecosystem. For example, Holling type III is often 'popular' among mathematical ecologists when one wishes to 'stabilize' the system at low algal density (e.g., Truscott and Brindley, 1994; Scheffer and De Boer, 1996; Bazykin, 1998; Hammer and Pitchford, 2005). Using an inappropriate type of response not only alters quantitative predictions of the model but may completely modify the system behavior and results in wrong conclusions.

The suggestion on the type of functional response for a particular zooplankton species is mostly based on results of laboratory experiments. In those experiments the rate of consumption of phytoplankton by zooplankton is measured while algal concentration P in the container is varied. Finally, by plotting $f(P)$ versus P , the conclusion about the appropriate type of trophic response can be made; the maximal uptake rate and the half-saturation constant can be estimated as well (e.g., DeMott, 1982; Hansen et al., 1990a).

However, a direct application of experimental results in the modeling is rather questionable. The point is that for a large

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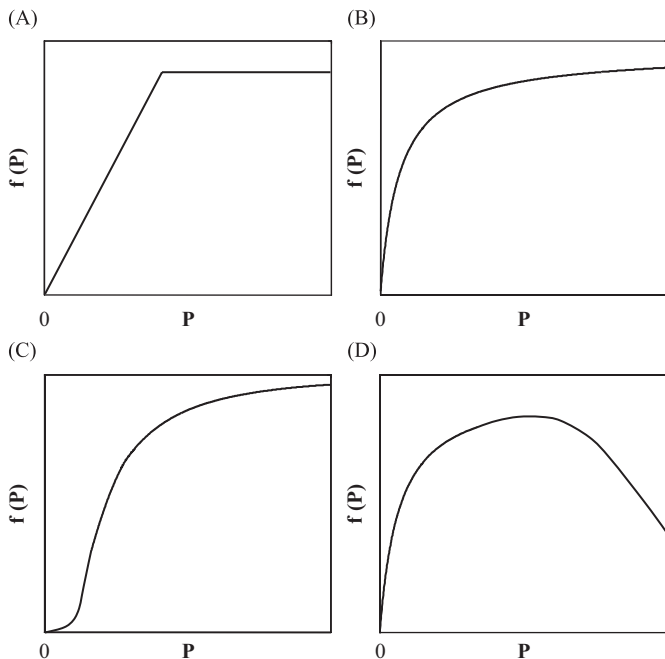


Fig. 1. Basic types of functional responses of zooplankton. The most frequent are: (A) Holling type I (linear response), (B) Holling type II ('hyperbolic' response), and (C) Holling type III ('sigmoidal' response). Type IV response (D) is less frequent and is called sometimes 'dome-shaped' (see Jeschke et al., 2004). Here P is the food concentration, $F(P)$ is the amount of food consumed per zooplankton biomass per unit of time.

number of models, the vertical distribution of phytoplankton is assumed to be homogeneous. Those models operate either with the total phytoplankton biomass P_{tot} in the photosynthetic layer (per unit surface) or with the average density \bar{P} obtained by dividing P_{tot} by the depth d of the layer. The rate E of the integral intake of phytoplankton by zooplankton in the whole layer is described by

$$E = f(P_{\text{tot}})Z_{\text{tot}}, \quad (1)$$

where Z_{tot} is the total biomass of zooplankton in the layer and $f(P)$ is the functional response found previously in the experiments (for the sake of simplicity, we consider only one dominant zooplankton species). It is well known, however, that the vertical distribution of plankton is highly heterogeneous (Raymont, 1980). Moreover, zooplanktoners are capable of performing vertical active displacement and concentrate within layers with abundant food (Vinogradov, 1970; Unstad and Tande, 1991; Pearre, 2003). As such, the use of (1) may lead to erroneous conclusions even if the experiments unambiguously tell us in favor of a given type of functional response $f(P)$.

In case we know the actual zooplankton and phytoplankton vertical distributions $Z(h)$ and $P(h)$, the integral intake rate E by zooplankton in the photosynthetic layer can be obtained by integration over the whole layer:

$$E = \int_0^d f(P(h))Z(h) dh. \quad (2)$$

We can rewrite (2) as

$$E = F_{\text{int}}Z_{\text{tot}} \quad \text{with} \quad F_{\text{int}} = \frac{\int_0^d f(P(h))Z(h) dh}{Z_{\text{tot}}}. \quad (3)$$

Here F_{int} is the average intake rate of zooplankton in the layer. We call F_{int} an average functional response of zooplankton. Note that F_{int} is not a function of P_{tot} in a strict mathematical sense since different vertical distributions of algae can have same values of

P_{tot} . In mathematics, such type of dependence is called a 'functional' (i.e., a function that takes functions as its argument), which is a function of $P(h)$ and $Z(h)$.

It is obvious that passing from the simple approach (1) to a more complex approach (3) renders a model much more complicated and often leads to analytically untreatable equations. As such, most conceptual plankton models use the approach based on (1). Note that this is quite reasonable in cases where the vertical distributions of plankton are homogeneous or close to homogeneous. However, for a highly heterogeneous plankton distribution (which is usually observed during algal blooms, see Herman, 1983; Eilertsen et al., 1989; Ohman, 1990) we may not be sure that such a simplification is acceptable.

In this paper, we show that the average functional zooplankton response F_{int} can exhibit different behavior compared to the functional response f obtained in laboratory experiments. Our research is based upon real ocean data on vertical plankton distribution. We plot the value of F_{int} against those of average chlorophyll densities \bar{P} in the whole layer. We show that the obtained graph can still be interpreted as a function $F_{\text{int}} = F_{\text{int}}(\bar{P})$, and, thus, be used for conceptual modeling of the ecosystem. However, the behavior of $F_{\text{int}}(\bar{P})$ shows a response of a different type compared to the one obtained in laboratory studies for *Calanus* spp. (Frost, 1972; Arashkevich and Drits, 1984; Hansen et al., 1990a). We argue that this conceptual discrepancy between the average F_{int} and the 'local' f functional responses is due to the ability of the zooplankton to feed in layers with high algal density and to avoid the depths with lower algal density as well as the depths with very high chlorophyll concentrations during blooms.

Thus, spatial heterogeneity of plankton in the water column as well as the ability of zooplankton to perform vertical movements lead to alteration of type of functional response for the zooplankton population as a whole. We discuss possible implications of our results for conceptual mathematical modeling of plankton communities.

2. Materials and methods

The observations were carried out at 10 stations in the central northern Barents Sea during three cruises of R/V *Jan Mayen* in July 2003 and 2004, and May 2005 (see Table 1). Depth-stratified sampling (Multinet, 180 μm mesh size, 0.25 m^2 mouth opening) was performed in order to investigate depth distribution and demography of *Calanus glacialis*. Samples were taken twice a day (at noon and midnight) from 100–50, 50–20, and 20–0 m, and preserved in buffered formaline (4% final concentration). All stages of *C. glacialis* were counted by using a dissecting microscope. Individual weights were measured in terms of carbon content for every copepodite stage with the help of a Leaman Lab 440 elemental analyzer.

Water samples for Chl *a* analysis were taken from 1, 5, 10, 20, 30, 40, 50, 60, 90, 120 m and, additionally, from the depth of fluorescence maximum. Hundred-ml subsamples were filtered on GF/F filters and extracted in methanol during 24 h in darkness at the room temperature (Holm-Hansen and Riemann, 1978). Chl *a* concentration was measured with a Turner Design AU-10 fluorometer calibrated with pure Chl *a* (Sigma, C6144). At every station we estimated the average chlorophyll concentration \bar{P} for the 0–20, 20–50, 50–100, and 0–100-m layers (Table 1) by using the trapezoidal method of numerical integration.

Feeding rate (R) in *C. glacialis* CI–CVI was assessed from gut fluorescence content and gut turnover time. For gut fluorescence analyses, copepods were collected midday and midnight with vertical hauls from 0–20, 20–50, and 50–100-m layers using a WP-2 net (0.25 m^2 mouth opening, 180 μm mesh size) with a

Table 1
Date, location, and Chl *a* concentrations at different stations

Date	Station no.	Latitude °N	Longitude °E	Depth (m)	Chl <i>a</i> max (depth m)	Chl <i>a</i> max (mg m ⁻³)	Chl <i>a</i> (mg m ⁻³) averaged over the layers			
							0–20 m	20–50 m	50–100 m	0–100 m
2003										
10.07	I	75° 32.1'	30° 16.6'	361	37	2.42	0.11	1.29	0.24	0.53
13.07	II	78° 13.9'	27° 19.2'	317	24	7.92	1.46	6.51	1.22	2.86
15.07	III	79° 02.6'	25° 41.5'	212	28	6.66	0.50	4.27	0.95	1.86
18.07	IV	77° 03.2'	29° 09.7'	229	10	2.24	2.06	0.69	0.09	0.66
2004										
23.07	VII	82° 24.9'	29° 26.2'	3500	0	0.86	0.36	0.10	0.07	0.14
27.07	X	79° 22.7'	28° 41.6'	300	20	2.96	1.28	1.00	0.63	0.87
2005										
20.05	XIV	81° 07.6'	16° 19.0'	2052	20	10.10	9.87	7.88	2.71	5.69
25.05	XVI	77° 08.4'	29° 56.7'	203	20	12.81	11.60	9.34	1.56	5.90
28.05	XVII	77° 25.7'	41° 02.8'	226	5	3.43	3.33	1.99	0.28	1.40
31.05	XVIII	75° 40.5'	31° 47.8'	343	10	4.43	4.18	3.16	2.95	3.26

non-filtering cod end. The copepods taken onboard were narcotized immediately with carbonic acid gas. For every analysis, from five (CV–CVI) to 30 (CI–CII) individuals were picked up under dissecting microscope and placed in methanol for pigment extraction. A further procedure was similar to that for Chl *a* analyses described above. The gut turnover time T was estimated from $T = (S_g/S_f)t_f$, where S_g and S_f are the gut and faecal pellet pigment content, respectively, and t_f is the time between two successive releases of faecal pellets. (For more detailed description of the methods see Pasternak et al., 2008.) The difference in day and night feeding was statistically insignificant (t -test, $P > 0.05$). We used day–night averaged values for given depth and station.

We divided the photosynthetic layer into the three following layers: $i = 1$, $0 < h < 20$ m; $i = 2$, $20 \text{ m} < h < 50$ m; $i = 3$, $50 \text{ m} < h < 100$ m. For every station and for each copepodite stage j ($j = \text{I–VI}$) we calculated the average functional zooplankton response $F_{\text{int},j}$ by applying a discrete version of (3):

$$F_{\text{int},j} = \frac{\sum_{i=1}^3 R_i^j \hat{Z}_i^j}{B_j \sum_{i=1}^3 \hat{Z}_i^j}, \quad (4)$$

where \hat{Z}_i^j is the abundance of zooplankton (inds. m⁻²) of copepodite stage j in water layer of number i ; R_i^j is the average ration of a zooplankter of stage j in layer i (i.e., the amount of chlorophyll consumed by an individual per day), and B_j is the average body weight (mg C) of individuals of stage j .

During the period investigated there was no difference in the shape of vertical profiles of day–night distribution of *C. glacialis*. We averaged the day–night data to obtain more precise values of abundance and biomass for a given depth. The lack of diel vertical migration in *C. glacialis* during periods of midnight sun in the Arctic has been well documented (for example, see Blackowiak-Samolic et al., 2006 and citations therein).

We estimated the average functional zooplankton response \bar{F}_{int} for the whole population of *C. glacialis* in the water column by averaging $F_{\text{int},j}$ over all six copepodite stages:

$$\bar{F}_{\text{int}} = \frac{\sum_{j=1}^6 F_{\text{int},j} B_j \sum_{i=1}^3 \hat{Z}_i^j}{\sum_{j=1}^6 B_j \sum_{i=1}^3 \hat{Z}_i^j}, \quad (5)$$

where the denominator gives the whole biomass of *Calanus* in the considered water column.

Finally, we plotted the values $F_{\text{int},j}$ and \bar{F}_{int} versus those of \bar{P} for all 10 stations.

We analyze the functional form of $\bar{F}_{\text{int}}(P)$ by applying the Akaike's information criterion (AIC) (Burnham and Anderson, 2002; Johnson and Omland, 2004). We considered different models (functions) for approximation of $\bar{F}_{\text{int}}(P)$ and the strength of support for each model was assessed by using Akaike weights.

3. Results

Table 1 shows the locations of the stations and the values of average chlorophyll concentrations \bar{P} in different layers for each station.

Fig. 2 represents the average functional zooplankton responses $F_{\text{int},j}$ obtained for all copepodite stages by applying (4) and plotted versus the values of \bar{P} . Fig. 2A shows the functional responses of stages IV–VI; Fig. 2B shows those of stages I–III. One can easily see that the patterns corresponding to the early (I–III) and late (IV–VI) copepodite stages show quite different behaviors.

While analyzing Fig. 2A, one can see that in case where chlorophyll densities are not large ($0 < \bar{P} < 4 \text{ Chl } a \text{ mg m}^{-3}$), the zooplankton functional response exhibits an increase which is more rapid than linear and looks concave upward. For high concentrations of algae (the two points corresponding to the highest \bar{P}), the intake rate generally shows a decrease. Note that these points correspond to phytoplankton blooms observed at stations XIV and XVI. The functional responses obtained for copepodite stages I–III (Fig. 2B) exhibit rather different behavior. For these stages, an increase in chlorophyll concentration results in a slight increase in $F_{\text{int},j}$ (for stages I and III) or is characterized by almost constant values of $F_{\text{int},j}$ (stage II). This can be explained by the fact that younger development stages reach the maximal feeding rate at lower food densities as compared with the older ones (Frost, 1974).

The average functional zooplankton response \bar{F}_{int} for the whole zooplankton population (obtained by averaging $F_{\text{int},j}$ over all stages j) is shown in Fig. 3. For low and intermediate algal densities, the plotted response looks concave upward. In terms of Holling's classification, it corresponds to Holling type III (before the inflection point). However, a visual comparison may not be considered as a solid argument in favor of the functional type III. As such, we apply further a powerful statistical criterion to support our suggestion.

We use AIC and Akaike weights (w_i) (Burnham and Anderson, 2002). AIC and w_i provide a reliable comparison of several

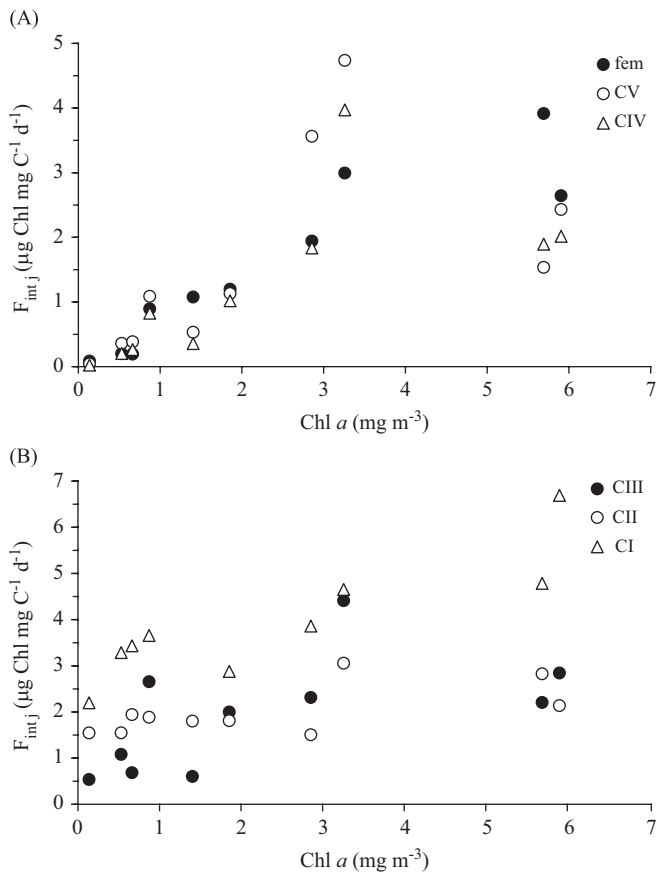


Fig. 2. Average functional responses $F_{int,j}$ of *Calanus* calculated from (4) for different copepodite stages: (A) responses of the late copepodite stages ($j = \text{IV-VI}$) and (B) responses of the early copepodite stages ($j = \text{I-III}$).

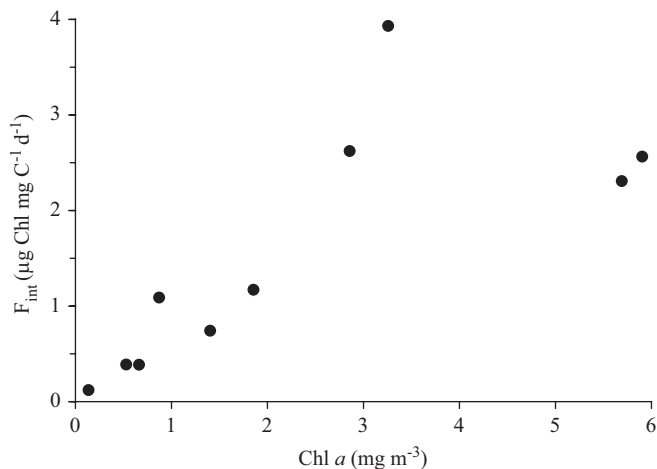


Fig. 3. The average functional response F_{int} of *Calanus* for the whole zooplankton population calculated by averaging $F_{int,j}$ over all copepodite stages.

functional fits for a given data set and are widely used in ecological research (Johnson and Omland, 2004). Here we concentrate our study on the average functional response F_{int} and on those of copepodite stages IV–VI. The contribution of the earlier copepodite stages (I–III) was found to be rather small due to the smallness of the total biomass of these stages.

In statistics, the fitting functions are often referred as ‘models’. Here we use models containing no more than two parameters. They are represented in Table 2 and include (1) linear dependence,

(2) quadratic parabola fit, (3) quadratic parabola fit with a linear term, (4) two-parametric Padé fit (Baker and Graves-Morris, 1996), (5) Ivlev (1961) response, and (6) trigonometric response (Fussmann and Blasius, 2005). Note that models (5) and (6) are concave downward functions, whereas models (2), (3), (4) are concave upward. Obviously, there exists an indefinite number of potential two-parametric models for the fit of F_{int} . Our particular choice of the above models is motivated by two reasons: mathematical simplicity of approximation (polynomial and Padé fits) and the use of functions in the modeling literature. The absence of saturation in some models for high P should not be considered here as an artifact since the current goal is to fit the feeding of zooplankton for intermediate chlorophyll densities.

We apply the small-sample version of AIC, which is called AIC_C (Johnson and Omland, 2004). To fit models’ parameters to the data sets we use the least-square method (LSM). Note that we did not include in our models’ list the ‘classical’ Mono response: $\alpha P/(1+\beta P)$ with $\beta \geq 0$, since LSM gives $\beta = 0$ for the data obtained. We did not include neither the ‘conventional’ sigmoid Holling III type parameterization $\alpha P^2/(1+\beta P^2)$, widely used in the modeling, since the estimated value of β is close to zero and the fit can be described by model (2). We rescale the values of AIC_C in the way that the model with the minimum information criterion has a value of zero: $\Delta_i = (AIC_C)_i - \min AIC_C$. Note that $\Delta_i < 2$ suggests a substantial evidence for a model, a model with $3 < \Delta_i < 7$ has substantially less support and a model with $\Delta_i > 9$ is very unlikely (Burnham and Anderson, 2002). Finally, we calculated the Akaike weights (w_i) which estimate the relative frequency at which a given model would be supported if the experiment were repeated many times (Burnham and Anderson, 2002). In case a model has the Akaike weight less than 0.01, this model may be rejected from consideration.

The values of Δ_i and w_i are shown in Table 2. One can see that concave upward behavior is most pronounced for copepodite stages IV and V and less pronounced for stage VI (we cannot reject completely the hypothesis on the linearity of the response for this stage). However, for the average feeding response F_{int} , the total Akaike weight of the linear and concave downward models is rather small (< 0.01), thus we can reject these models. The same conclusion can be drawn by considering Δ_i . In other words, the test confirms our initial suggestion on Holling type III for F_{int} . However, relatively close values of w_i for models (2)–(4) do not allow us to choose one of them as an ‘exact’ parameterization of F_{int} . In Fig. 4 we show fitting of F_{int} by the models from Table 2. We have calculated the standard errors (SE) for those fits, as well.

From Fig. 3 one can see that F_{int} shows a decrease for large chlorophyll densities (algal blooms events). This behavior would correspond to Holling type IV (Taylor, 1984). However, more data are needed to confirm this suggestion.

Note that previous laboratory experiments (see Arashkevich and Drits, 1984) on the functional response of *C. glacialis* have shown a linear response with a further saturation, i.e., Holling type I (see Fig. 1A). Similar results were obtained in experiments by Frost (1972) for *C. pacificus* and Hansen et al. (1990a) for *C. finmarchicus*. Thus, the laboratory experiments failed to describe the behavior of the zooplankton functional response that we have observed in the ocean.

To provide a possible insight into this apparent discrepancy, we analyzed the corresponding profiles of vertical distributions of phyto- and zooplankton. Fig. 5 shows vertical profiles for phytoplankton (left column), that of zooplankton (middle column), and abundances of different zooplankton stages (right column) for low, intermediate, and high values of \bar{P} .

At low chlorophyll concentrations (Fig. 5A, $\bar{P} = 0.87 \text{ Chl } a \text{ mg m}^{-3}$, Stn. X), the plankton distribution can be considered as slightly heterogeneous and laboratory experiments would provide

Table 2
Comparison of different fits ('models') of zooplankton functional response for low and intermediate chlorophyll concentrations ($0 < \bar{P} < 4 \text{ Chl } a \text{ mg m}^{-3}$)

Model	Number of parameters	Copepodite stage	AIC _c ^a	Δ_i^b	w_i^c
1. $f(P) = \alpha P$	1	CIV	4.034	13.005	0.001
		CV	5.225	16.067	<0.001
		Fem	-6.901	3.489	0.068
		Average	-1.285	9.731	0.004
2. $f(P) = \beta P^2$	1	CIV	-7.575	1.396	0.325
		CV	-10.842	0.000	0.766
		Fem	-10.390	0.000	0.388
		Average	-10.923	0.000	0.480
3. $f(P) = \alpha P + \beta P^2$	2	CIV	-1.981	6.990	0.020
		CV	-5.327	5.515	0.049
		Fem	-9.225	1.165	0.217
		Average	-7.630	3.362	0.089
4. $f(P) = \alpha P / (1 - \beta P)$ ($\beta > 0$)	2	CIV	-8.971	0.000	0.653
		CV	-8.004	2.838	0.185
		Fem	-9.732	0.658	0.280
		Average	-10.751	0.241	0.426
5. $f(P) = \alpha(1 - \exp(-\beta P))$	2	CIV	5.869	14.840	<0.001
		CV	8.595	19.437	<0.001
		Fem	-4.094	6.296	0.017
		Average	2.195	13.187	<0.001
6. $f(P) = \alpha \tanh(\beta P)$	2	CIV	5.249	14.220	<0.001
		CV	7.322	18.164	<0.001
		Fem	-5.308	5.082	0.031
		Average	0.6866	11.679	0.001

^a Akaike information criterion (the small sample version).

^b Difference between the model AIC_c and min AIC_c for a given model and stage.

^c Akaike weight, $w_i = \exp(-\Delta_i/2) / \sum_{k=1}^6 \exp(-\Delta_k/2)$.

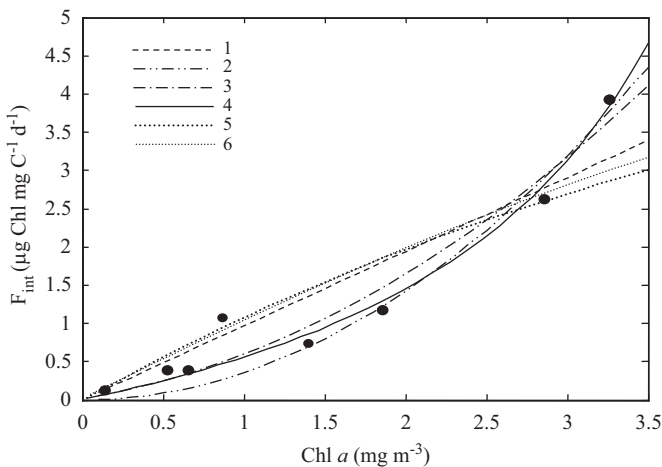


Fig. 4. Approximation of \bar{F}_{int} by the fitting functions ('models') from Table 2. The numbers of curves in the figure correspond to the numbers of models in Table 2. Estimation of models' parameters gives: (1) $\alpha = 0.96$, SE = 0.10; (2) $\beta = 0.96$, SE = 0.02; (3) $\alpha = 0.35$, SE = 0.21, $\beta = 0.23$, SE = 0.07; (4) $\alpha = 0.45$, SE = 0.01, $\beta = -0.19$, SE = 0.02; (5) $\alpha = 0.6$, SE = 0.20, $\beta = 0.2$, SE = 0.04; and (6) $\alpha = 5.35$, SE = 0.52, $\beta = 0.19$, SE = 0.07.

a reasonable prediction for the behavior of \bar{F}_{int} . For the intermediate concentrations (Fig. 5B, $\bar{P} = 2.86 \text{ Chl } a \text{ mg m}^{-3}$, Stn. II), the distribution of phytoplankton is highly heterogeneous. Rapid algal growth takes place in a relatively narrow layer and the zooplankton migrate to this layer and can feed at higher densities.

This effect results in a pronounced increase in \bar{F}_{int} . In case of an intense phytoplankton bloom (Fig. 5C, $\bar{P} = 5.9 \text{ Chl } a \text{ mg m}^{-3}$, Stn. XVI), the algal density is now too high and zooplankton avoid those layers and feed in other layers with lower concentration of chlorophyll. This leads to a pronounced decrease of \bar{F}_{int} . Note that such an avoidance of layers of high chlorophyll concentrations by zooplankton has been observed before in other marine systems (Ratkova et al., 1989). Obviously, the behavior of \bar{F}_{int} observed in Fig. 5B and C can hardly be predicted based only on results of laboratory experiments.

4. Discussion

There is growing evidence that the spatial non-homogeneity of predator–prey interactions would alter the functional response of predators (consumers) both in terrestrial and aquatic ecosystems (Michalski et al., 1997; Cosner et al., 1999; Jeschke et al., 2002). In this paper, we analyze how vertical heterogeneity in algal distribution as well as active vertical displacement of herbivorous zooplankton can modify the type of zooplankton trophic response. Our study was based on real ocean data on vertical plankton distribution.

We show that although the previous laboratory experiments (Frost, 1972; Arashkevich and Drits, 1984; Hansen et al., 1990a) tell us in favor of Holling types I and II responses for *Calanus* spp., the actual response of the whole *Calanus* population in the upper ocean layer exhibits a different pattern of behavior. In particular, when the concentration of chlorophyll is not very high, the rate of

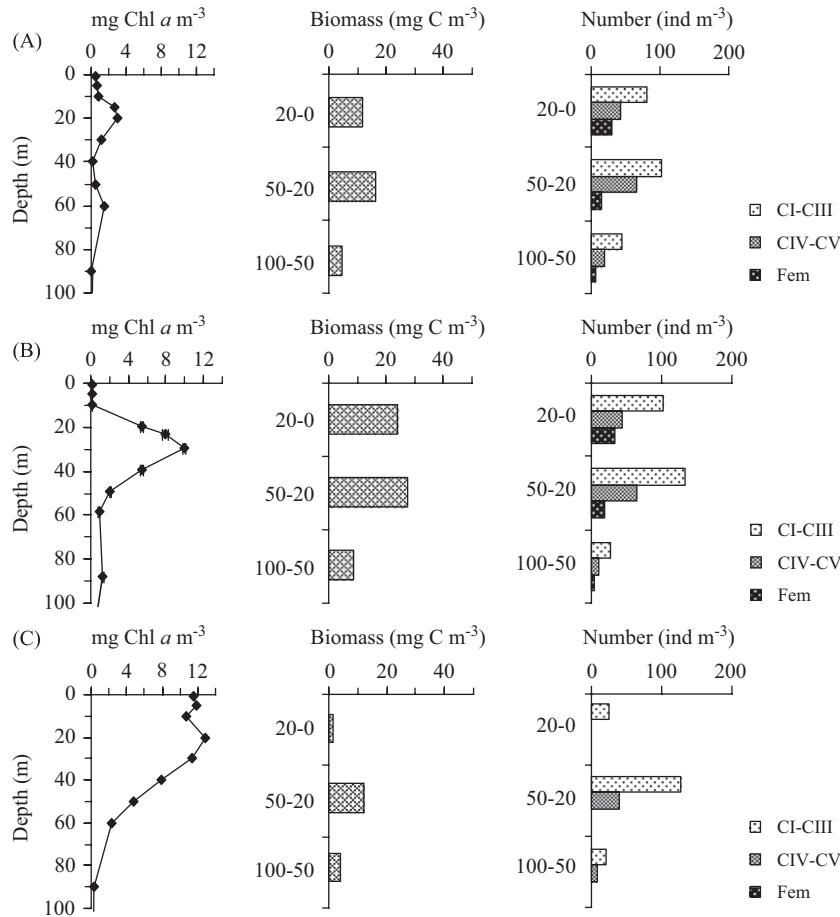


Fig. 5. Vertical profiles of day distributions of Chl *a* (left column), zooplankton (middle column), and abundance of different copepodite stages (right column) for low (A), intermediate (B), and high (C) chlorophyll concentrations integrated for a 100-m layer (\bar{P}); (A) Stn. X, $\bar{P} = 0.87$ Chl *a* mg m⁻³; (B) Stn. II, $\bar{P} = 2.86$ Chl *a* mg m⁻³; and (C) Stn. XVI, $\bar{P} = 5.90$ Chl *a* mg m⁻³.

average intake exhibits a Holling type III response, characterized by a concave upward function. The actual discrepancy between laboratory results and ocean data may be explained by a possibility of zooplankton selective feeding at depths with high algal density. This conclusion is in a good agreement with some previous data on the vertical distribution and feeding behavior of *Calanus* (Herman, 1983; Hansen et al., 1990b).

On the contrary, at very high algal densities (during plankton blooms) the rate of food intake by zooplankton would show a decrease. A decline in the predator intake rate for high prey densities was observed experimentally (e.g., Veldkamp and Jannasch, 1972; Łotocka, 2001); the main reason of the decline was considered to be an intoxication of the predator. Our study (cf. Fig. 5C) shows that along with possible processes of zooplankton intoxication, another mechanism is responsible for the drop in F_{int} . This is the avoidance by zooplankton of the layers of very high algal density. Unfortunately, the lack of the data corresponding to the range $3.5 \text{ Chl } a \text{ mg m}^{-3} < \bar{P} < 5.5 \text{ Chl } a \text{ mg m}^{-3}$ does not allow us to fulfill a complete analysis of F_{int} for large algal concentrations.

The fact that the average functional response of zooplankton becomes concave upward is of great importance for the system stability. Theoretical studies predict enhancing in stability in this case (Oaten and Murdoch, 1975; Bazykin, 1998). More precisely, stability takes place when the intake rate per predator at equilibrium shows a response more rapid than linear to an increase (or decrease) of prey density. As such, the reported

alteration of zooplankton functional response would provide some additional mechanisms of self-regulation in plankton communities. Those mechanisms have not been taken into account before. In particular, they can provide an explanation of resistance of aquatic ecosystems to nutrient enrichment. Spatial heterogeneity of plankton is now considered as a strong candidate for resolving the paradox of enrichment in eutrophic ecosystems (Rosenzweig, 1971; Gilpin, 1972; Jansen, 1995) and taking into account vertical migration of zooplankton may help resolving this paradox (Morozov et al., 2007).

However, for the feeding of herbivorous zooplankton, the use of Holling type III is sometimes criticized in literature (e.g., Scheffer and De Boer, 1996). The main reason to justify the choice of Holling type I or II, instead of the type III, is citing some experimental data on local functional responses (e.g., DeMott, 1982; Verity, 1991; Jeschke et al., 2004). We show that Holling type III still can occur in those systems as a result of complex spatial-temporal interactions. A direct interpretation of the laboratory experiments might be too simplistic.

Finally, our results show that for the ecosystem under study the average response of zooplankton defined by (3) may still be considered as a function of average phytoplankton density \bar{P} , i.e., $F_{\text{int}} \approx F_{\text{int}}(\bar{P})$. In other words, we can apply models based upon the conceptual approach (1) (i.e., models not taking into account explicitly the heterogeneity of vertical plankton distribution) by substituting the local trophic function f by the average response F_{int} . However, the behavior of $F_{\text{int}} = F_{\text{int}}(\bar{P})$ becomes rather

complex and the choice of parameterization for this function should be justified in every case. In particular, it can differ from the basic Holling's types.

5. Conclusions

In this paper, we demonstrate that spatial heterogeneity of vertical distribution of plankton in the ocean as well as selective feeding of zooplankton at depths with high algal densities (and avoiding those with lower algal density) may alter the type of zooplankton feeding response. In particular, the data obtained from expeditions in the Barents Sea show that the whole population of *Calanus glacialis* in the water column exhibits a Holling type III response, instead of responses of types I and II found previously in laboratory experiments. Thus, the conclusion on the type of feeding response for a zooplankton species made from a direct laboratory analysis can be too simplistic and misleading. Although this fact is of importance for the modeling of plankton communities (Holling type III would enhance stability in the system under study), it is rarely taken into account.

Our study leaves few questions open. The central question is: how often should we expect such an alteration of trophic response in plankton communities? For instance, should we expect such a phenomenon for shallow ecosystems as well? What zooplankton species would exhibit the observed pattern of behavior? What will be the influence of the diel vertical migration of zooplankton on the type of trophic response? We remind that in the ecosystem under study we did not observe patterns of diel vertical migrations; however, in other cases those patterns might play an important role. We plan to include those issues in our next studies.

Acknowledgments

This work was supported by the Norwegian Research Council Project no. 155936/700 (CABANERA) and the Russian Foundation for Basic Research (Project nos. 05-05-64686 and 07-04-00029).

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