

H.O. Fock · W. Greve

Analysis and interpretation of recurrent spatio-temporal patterns in zooplankton dynamics: a case study on *Noctiluca scintillans* (Dinophyceae) in the German Bight (North Sea)

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Abstract Data from the Helgoland Roads time series and from two series of quasi-synoptical zooplankton surveys in 1979 and 1984 were analysed with respect to recurrent patterns of dynamics of the dinoflagellate *Noctiluca scintillans*. Based on a Lotka–Volterra model, the patterns were interpreted in terms of potential interactions. The work was conducted as a comparative analysis consisting of spatial, temporal moving window correlations and cross-correlations. In a reverse of the principle of space-for-time substitution in ecosystem analysis, space-and-time concordance of results was applied to indicate the relevance of interactions in time and space. A time series model on intra-annual dynamics significantly reproduced the dynamics of *N. scintillans* in 1979 and 1984. Results indicate that the dynamics of *N. scintillans* populations were linked to the population dynamics of *Pleurobrachia pileus* (Ctenophora), *Sagitta* spp. (Chaetognatha), hydromedusae, especially *Rathkea octopunctata* and *Lizizia blondina*, and copepod nauplii. Evaluation of historical data sets from the Wadden Sea and the Bulletin Trimestrial series supported the statistical analysis. A food web model for the postulated relationships is discussed. The statistical method did not allow us to distinguish between predatory or competitive interactions.

Introduction

Modes of regulation in marine zooplankton communities are still a matter of debate. Whereas in freshwater

systems predictable interaction patterns can often be obtained, similar approaches have failed for marine plankton (Koslow 1983). Food limitation and quality, as for copepods (Daan 1989; Ianora et al. 1999), predation (Huntley and Hobson 1978; Greve and Reiners 1988; Kuipers et al. 1990; Greve 1994), individual life cycles (Verity and Smetacek 1996) and the complex interplay between the physical environment and biological components (Smetacek et al. 1984; Kiørboe 1991) have been discussed as important factors for marine plankton dynamics. In general, two approaches can be chosen to investigate interdependencies between plankton populations. Firstly, feeding and dietary requirements can be used to estimate daily consumption and fluxes between components either in the field or experimentally (e.g. Daan 1989; Frid et al. 1994; Purcell and White 1994). Secondly, interactions between populations can be deduced from fluctuations of abundance. Long-term analyses of trends (Koslow 1983; Cushing 1990, 1995), as well as intra-annual analyses of fluctuations (Huntley and Hobson 1978; Greve and Reiners 1988; Greve 1994), have been applied in this respect.

The neritic, non-toxic dinoflagellate *Noctiluca scintillans* (Macartney) Kofoid is globally distributed. During summer it is a dominant species in temperate seas, contributing considerably to zooplankton abundance (Kang et al. 1996; Jang and Kim 1998). It exhibits mass developments and enormous “red tides”, which upon descent can cause considerable damage to commercial fish farming and benthic fauna through oxygen depletion (Zevenboom 1994; Huang and Qi 1997) and potential ammonium toxicity (references in Smayda 1997). This species has long been known to inhabit the southern North Sea (Lauterborn 1894; Pratje 1925). In the German Bight during summer, the biomass of *N. scintillans* has been estimated at 10,000–25,000 t C (Uhlig and Sahling 1995).

It has often been attempted to link *N. scintillans* dynamics to eutrophication and nutrients, as previously shown for autotrophic dinoflagellates (Zevenboom 1994). On the other hand, *N. scintillans* has been char-

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H.O. Fock (✉) · W. Greve
Forschungsinstitut Senckenberg,
Notkestraße 31, 22607 Hamburg, Germany

Present address: H.O. Fock
Alfred-Wegener-Institute for Polar and Marine Research,
PO Box 120161, 27515 Bremerhaven, Germany
e-mail: hfock@awi-bremerhaven.de

acterised as voracious predator (Capriulo et al. 1991), with a diverse diet ranging from phytoplankton to copepods (Schaumann et al. 1988; Elbrächter and Qi 1998; Kiørboe and Titelman 1998; Nakamura 1998) and with different feeding modes (Uhlig and Sahling 1990; Shanks and Walters 1996; Elbrächter and Qi 1998; Tiselius and Kiørboe 1998). Recent results further suggest that *N. scintillans* is also coupled to the microbial food web (Brussard et al. 1995, 1996; Kirchner et al. 1996; Nayak et al. 2000).

The aforementioned literature mainly concentrates on feeding and bottom-up aspects the position of *N. scintillans* in the heterotrophic community, and, thus, possible top-down aspects of its regulation remain unclear. In the present study, we pursue two objectives. Firstly, an approach is developed to indirectly infer interactions between populations from their spatio-temporal dynamics in the field. This is a further advancement of the space-time concept of Greve and Reiners (1988) and the interaction concept of Fock (Fock and Reinke 1994; Fock 1996). Secondly, we exercise this approach with respect to *N. scintillans*.

Materials and methods

Zooplankton sampling and analysis

Time series data from 1975 to 1994 at Helgoland Roads (HR) and data from two series of quasi-synoptical surveys in the German Bight in the years 1979 and 1984 were used for this analysis (Fig. 1). In 1979 five cruises with a maximum of 30 stations were carried out from 23 April to 23 July (weeks 16, 19, 22, 25, 29). In 1984 five cruises were undertaken in 2-week intervals from 23 May to 17 July with a maximum of 73 stations (weeks 21, 23, 25, 27, 29).

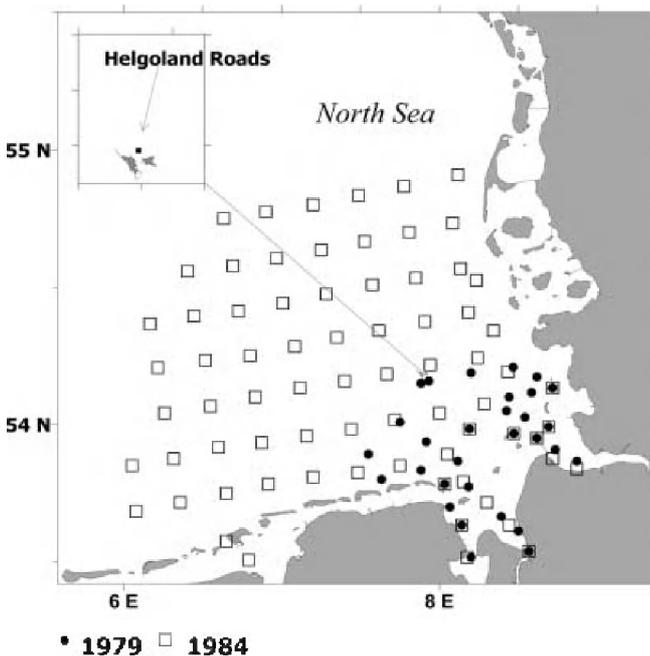


Fig. 1 Location of Helgoland Roads (*inset*) and sampling stations in the German Bight (*circles* 1979; *squares* 1984)

For the HR time series, starting in 1974 (see Greve and Reiners 1995), mesozooplankton was sampled three times a week by vertical hauls with a 150 μm plankton net, and macrozooplankton once a week by double-oblique hauls with a 500 μm CalCoFi (California Cooperative Oceanic Fisheries)-net. Weekly means were used for further calculations. During the 1979 survey sampling and analysis were the same as for the time series. In 1984 direct zooplankton counts were accomplished onboard. For this purpose the mesozooplankton sample was split. From the stirred and mixed sample a 3 ml aliquot was separated with a stempel pipette for microscope counting of smaller specimens (Projectina microscope, Heerbrugg, Switzerland). The macrozooplankton sample was poured into a transparent bowl and mounted onto a measuring table for eye counting of ctenophores and other larger specimens. Both samples were stored afterwards.

Salinity and temperature were measured with a WTW-191 conductometer.

Spatio-temporal dynamics

At any given location marine plankton populations depend on import (advection) and export processes (dispersion), plus local biological interactions with predominantly non-linear dynamics (Dubois 1976; Roughgarden 1997). In order to analyse such complex systems we first assume that it is applicable to choose a linear approach (Yodzis 2000). Secondly, we assume that spatial and temporal dynamics are linked, so that in a reverse of the principle of space-for-time substitution in ecosystem analysis (Pickett 1989) a concordance of spatial and temporal dynamics can be applied to indicate a functional feature. Thirdly, we assume that it is appropriate to analyse the system from the viewpoint of the target species rather than to define a framework for the dynamics of the whole system. This approach means that direct effects are of primary concern, although indirect effects are also important in pelagic systems (Yodzis 2000). Four steps are involved in the analysis of spatio-temporal dynamics: (1) outlining the analytical model in order to define and interpret the type of targeted pattern, (2) selection of variables, (3) analysis of spatio-temporal patterns and (4) validation.

The analytical Lotka–Volterra model

Lotka–Volterra (LV) models imply negative relationships between interacting populations. An LV-competition model (Keddy 1989) was adapted by including emigration and immigration terms (Levin 1974; Rose 1987), equivalent to a simple reaction–diffusion model (Tilman et al. 1997). The dynamics of the population N_i at a given location x can be described as:

$$\frac{dN_i}{dt} = \frac{rN_i}{K_i} (K_i - \alpha_{ii}N_i - \sum_j \alpha_{ij}N_j) + \sum_y D_{xy} - \sum_y D_{yx} \quad (1)$$

where K_i is the carrying capacity and r is the reproduction rate. D_{xy} is the advective term of N_i for all locations from y to x and D_{yx} is the corresponding dispersion term; α_{ij} is applied as a general interaction coefficient of population N_j on N_i , summarising both predation and competition effects (e.g. Fock and Reinke 1994). The intraspecific competition coefficient α_{ii} is by definition unity (Keddy 1989). K and D deserve special attention. In all analyses we treated K_i as a constant, as if all locations x belonged to the same water body with the same upper limit of population growth. In a synoptical survey the advective (D_{xy}) and dispersive (D_{yx}) processes become zero, since no movements occur if $dt=0$. For a time series the LV-model by means of negative relationships can be applied only if the D_{yx} and D_{xy} terms can be neglected. This can be achieved: (1) under the premise of perfect mixing (Lehman and Tilman 1997), so that import and export effects compensate each other within a short time (i.e. tidally mixed shallow seas), or (2) when the terms are minute compared to births and deaths (e.g. isolated fjords and ponds, see Aksnes et al. 1997). Extensive tidal stirring indicated by

the lack of stratified conditions in the area around Helgoland (see also Daan 1989; Frey 1990) is in support of the first condition. Regular stratification is known to occur only to the north-west of Helgoland.

Applying the LV-model to a synoptic survey, ideally no change over time occurs and dN_i/dt becomes zero at all locations x . Then following Eq. 1, N_i should have a negative spatial correlation with its interactor N_j at all locations x :

$$N_i \sim - \sum_j \alpha_{ij} N_j \quad (2)$$

Furthermore, it is assumed that the populations at the many locations x are not in phase, so that each location represents a different situation in the phase diagram of N_i and N_j . This follows from the population wave concept (Greve and Reiners 1988) and can be seen in the field (see Fig. 3). The spatial formulation of the LV-model requires no equilibrium condition. Instead, the time series must be analysed under the premise of equilibrium ($dN_i=0$). Interacting populations N_j are negatively related to N_i .

Variable selection

Potential interactors with *N. scintillans* were selected on the basis of two conditions. First, in line with the LV-model, negative time series correlations in the whole time series for the time window of interest were required, i.e. weeks 10–30, 20–30 and 20–40 (see Table 1). Secondly, from the negatively correlated species, a subset of species was chosen being sufficiently present in the spatial data sets. For this, the numbers of surveys were counted, in which the species were present at 50% or more of the stations during a single survey. Pearson correlation coefficients deliver peculiar results if >50% of a data matrix consist of zero entries (Bakus 1990).

Analysis of spatio-temporal patterns

The condition “ K_i =constant” was achieved with second-order partial correlations (SAS 1994), eliminating unwanted effects due to different water bodies. Salinity and temperature served as proxies for water body characteristics and were partialled out.

For spatial patterns partial Pearson moment correlations were applied. For the analysis of temporal patterns a moving window correlation (MWC) was applied, adopted from the moving window approach of Cornelius and Reynolds (1991). MWC provides information on short-term relationships. Calculations were carried

out for the years 1979 and 1984 and the whole series (1975–1994). For instance, a 3-week MWC starts in week 1 on data from weeks 1–3. The corresponding correlation coefficient is assigned to week 2, the midpoint of that period. Shifting the window 1 week forward, the subsequent correlation considers the next interval assigning the coefficient to week 3, and so on. Window lengths of 5 and 7 weeks for the MWC analysis cover the relevant time scales in zooplankton (20–30 days, see Krause and Radach 1980).

Following the principle of space-and-time concordance a strong spatio-temporal pattern (pattern of dynamics, POD) was indicated if both temporal [partial (pMWC) and unpartialled (MWC)] and the spatial correlations were negative at the same time. If only the two partial correlations were negative, the pattern was termed “weak”, with seasonal or advective signals probably masking the underlying pattern.

Validation

For validation we followed a meta-analytical line of thought. Dependent on the chosen scale and methodology (sampling, locations and grid, processing), in communities, multiple interactions have to be anticipated implying that not all relationships, though being relevant, appear to be statistically significant. The goal of meta-analysis is to identify relevant processes within a suite of related investigations even if the singular investigation shows no significance (see Mann 1990; Osenberg et al. 1999). In its simplest form this can be achieved by vote-counting of supporting findings (see Bärlocher 1999). Treating the results of the independent analysis steps as new dichotomous variables, with “yes”=“result/tendency as expected” versus “no”=“not as expected”, and applying vote-counting, we deduce that for five times “yes” in five trials, following a test on binomial probabilities (Zar 1996), the relevance level becomes $P < 0.05$ (first order failure). However, this does not indicate the feature’s strength.

Further findings from cross-correlations, modelling of intra- and inter-annual dynamics and investigation of historical data were evaluated.

Cross-correlations

Interacting populations are expected to have a specific cross-correlation (CCF) pattern within the same time window, for which the POD was detected. The CCF pattern indicates whether the negative MWC depends on the seasonal sequence of subsequent popula-

Table 1 Selection of taxa for the analysis of interactions with *Noctiluca scintillans*. Ranks derived from time series correlations, the most negative correlation receiving rank 1. Asterisks indicate selected species (O/h omnivorous and/or herbivorous feeding; C carnivorous feeding)

Rank	Taxon	Trophic status	Status in 10 spatial series expressed as number of surveys with occurrence at the stations 50%
1	<i>Amphiura filiformis</i> pluteus	O/h	3
2	Mitraria larvae	O/h	0
3	Actinotrocha larvae	O/h	0
4	Rotatoria	O/h	2
5*	<i>Rathkea octopunctata</i> and <i>Lizzia blondina</i> ^a	C	2 (total hydromedusae: 5)
6	<i>Alaurina composita</i>	C	1
7	<i>Frittilaria borealis</i>	O/h	1
8*	<i>Pleurobrachia pileus</i> ^b	C	10
9	Pilidium larvae	O/h	0
10*	<i>Sagitta</i> spp.	C	6
11	<i>Calanus helgolandicus</i>	O/h	2
12	<i>Steenstrupia nutans</i>	C	0
13	Polychaete larvae	O/h	0
14*	Copepod nauplii	O/h	10
15	Bivalve veliger	O/h	3

^aThe hydromedusae *R. octopunctata* and *L. blondina* were not separated in time series analysis until 1985

^bAdult and juvenile *P. pileus*

tions. A pure follow-up of subsequent populations is assumed to be one-directional with population A always increasing after the decline of population B, but never vice versa. This results in positive CCF values only in one direction of the time lag axis and negative values elsewhere. In turn, an interaction effect should lead to a sequence of opposite ups and downs at the times populations A and B disturb each other, noticeable by means of positive cross-correlations at both negative and positive time lags and negative correlations at t_0 . Consistent with the application of CCF in the analysis of transfer functions (Box and Jenkins 1976), the positive maxima define the time scale of interactions between populations. Similar approaches were chosen by Matthews and Bakke (1977) and Feigenbaum and Kelly (1984). Cross-correlations were checked for auto-correlation (STATISTICA, ver. 1995, StatSoft).

Analysis of intra- and inter-annual population dynamics

On the intra-annual level, time lags derived from the cross-correlation analysis were deployed for multiple regression models dealing with *N. scintillans* in 1979 and 1984 (MODEL procedure, SAS 1993). In accordance to Pace et al. (1998), each independent regressor was incorporated with only one single temporal component:

$$N_i = aN_{j1-t1} + bN_{j2-t2} + \dots + \text{const} \quad (3)$$

where N_{j1-t1} indicates the interacting population $j1$ at time lag $t1$. The coefficients a , b , ... do not refer to the α 's. Focussing on the impact of interacting populations, the model contained no auto-regressive term for the dependent variable, but one hypothesised food item. From the two potential food items, i.e. autotrophic flagellates and diatoms, tested by means of carbon content, flagellates proved to be twofold better predictors. Significance levels for the model results were estimated from the 99th percentile of a distribution of 1,000 correlation coefficients (r_R) between the *N. scintillans* time series and models with randomised, independent regressors of the same mean and variance as the original regressors (e.g. Carpenter et al. 1989; Heyen et al. 1998). In permutation tests, power increases only slightly after 199 runs (ter Braak and Smilauer 1998, p. 101). Significance was stated for $r_O > r_{R,99}$, corresponding to $P < 0.01$, with r_O being the coefficient between time series model and time series.

Secondly, on the inter-annual level, regressions were carried out for the time windows used for the variable selection, i.e. week 20–30 and week 20–40, in order to indicate whether the intra-annual relationships also become evident on the inter-annual scale.

Historical time series

Historical data sets for the coastal North Sea [Wadden Sea at Sylt 1947–1949 (Künne 1952), coast off Belgium 1903–1907] and the central North Sea (Germany 1903–1904) were employed for tabulated analysis of conjoint occurrences of the target species. The earlier series were obtained from the publication series Bulletin Trimestrial (Conseil permanent international pour l'Exploration de la Mer 1910). Data sets provided a semi-quantitative classification of abundance, which tentatively can be traced back to abundance according to Apstein (1903). However, due to uncertainties, with probably differing classification schemes between countries and cruises, data were redefined into the categories "rare" and "common". Taking into account the coastal character of *N. scintillans*, both for coastal and central North Sea data series adapted schemes were applied (see Table 5).

Results

Selection and description of the plankton variables

From the 15 most negatively related taxa (Table 1), four taxa were selected as being sufficiently present in the

spatial data sets, i.e. with five to ten counts satisfying the presence criterion in ten data sets: small hydromedusae, *Pleurobrachia pileus* (Ctenophora), *Sagitta* spp. (Chaetognatha) and copepod nauplii.

The unresolved taxon "hydromedusae" in the spatial series was resolved to *Rathkea octopunctata* and *Lizzia blondina* in the temporal analysis since they obtained a high correlation rank. Due to this compositional inconsistency only temporal analysis was carried out for hydromedusae. *P. pileus* was separated into two size-classes: juveniles (1 mm diameter) from the 150- μ m-net samples and adult specimens (1–25 mm diameter) from the 500- μ m-net samples. The genus *Sagitta* comprises *S. setosa* and *S. elegans* at HR. These were not distinguished in the early years of the analysis of HR zooplankton, so this taxon was treated on the genus level.

The year 1979 appeared to be the coldest in the 20-year record of HR zooplankton (see Fig. 2); 1984 was a medium year both for salinity and temperature.

Annual mean abundances for *Noctiluca scintillans* were high in 1979 and medium in 1984 (Fig. 2). This was the same for *Sagitta* spp., whereas *R. octopunctata* and *L. blondina* had low abundances in 1979 and 1984. Juvenile *P. pileus* reached high abundances in 1979 and 1981. Adult *P. pileus* reached high densities in 1984.

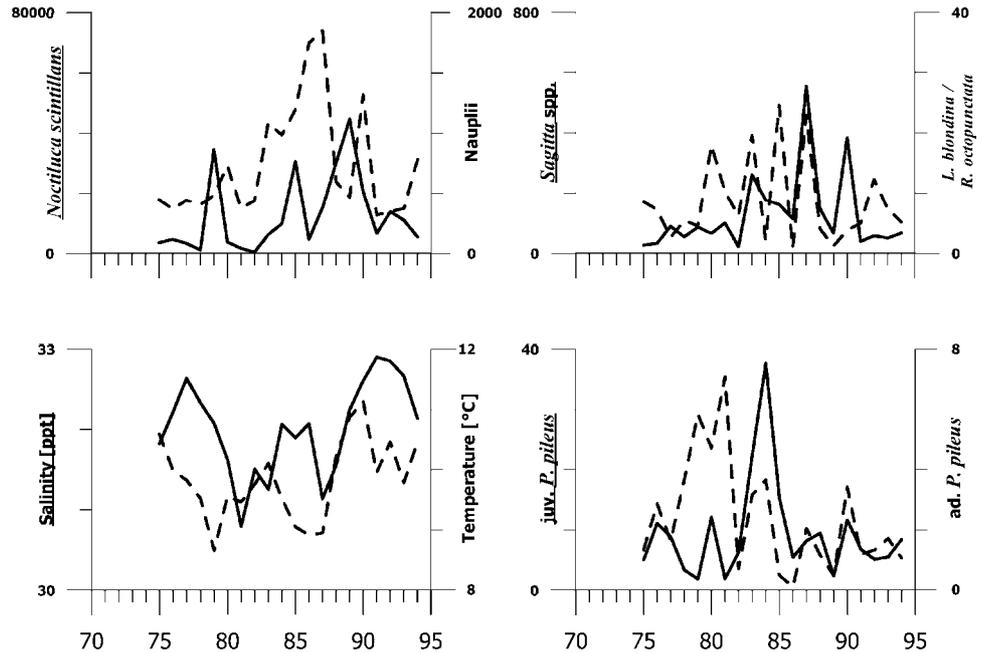
On the annual level, the abundance of *N. scintillans* at HR started to rise in 1979 in week 25 and in 1984 in week 26 (see Fig. 9). However, the spatial data (Fig. 3) reveal that before reaching Helgoland *N. scintillans* had already started its development in coastal waters in week 22 (see Uhlig and Sahling 1995). The population increase of *N. scintillans* in 1979 started in the northern and in 1984 in the southern part of the investigation area.

During the investigations a coastal thermohaline gradient was apparent with colder and more saline waters in the German Bight proper compared to warmer coastal waters with reduced salinity (Fig. 4).

Spatio-temporal correlations and detection of PODs

In the years 1979 and 1984, in each 10-week period (1–10, 11–20, ...), negative pMWCs could be found in relation to the dynamics of *N. scintillans*. Negative pMWCs in the first and fourth period could be attributed to *Sagitta* spp. (Fig. 5a), followed by juvenile *P. pileus* in periods 1–3 (Fig. 6a) and *L. blondina* and *R. octopunctata* in the second decade (Fig. 5b). Especially in 1979, adult *P. pileus* determined the mid-year phase (Fig. 6b). The pMWC plot for copepod nauplii (Fig. 7) showed several spikes, especially for 1979. In the 20-year plots, the negative pMWCs for *Sagitta* spp. were weak, whereas stronger negative pMWCs could be found for *P. pileus* (peaking around week 20), *L. blondina*/*R. octopunctata* (around week 33) and for copepod nauplii (around week 38). For *P. pileus* negative pMWCs at low and at high population levels can be distinguished. From these only the pMWCs at high population levels appear in the 20-year analysis, indicating strong relationships during

Fig. 2 Time series of annual means of selected species (ind. m⁻³), and salinity (ppt) and temperature (°C) at Helgoland Roads, 1975–1994. Solid lines refer to the left y-axis, broken lines refer to the right y-axis



the increase and weaker relationships during the decline of the *P. pileus* populations.

The results of the spatial correlations are summarised in Table 2. PODs between *N. scintillans* and copepod nauplii, juvenile and adult *P. pileus* are seen in 1979 in weeks 22–29. In 1984 patterns between *N. scintillans* and adult *P. pileus* and *Sagitta* spp. are seen in weeks 25–27. Weak PODs can be found between *N. scintillans* and nauplii in week 25 in 1979. In 1984 weak patterns can be found in week 23 between *N. scintillans* and juvenile *P. pileus* and in relation to *Sagitta* spp. The weak pattern for juvenile *P. pileus* corresponds to the weak pMWC and the weak cross-correlation function (see section “Validation”) at that time. No POD was found for nauplii in 1984. Weak patterns were temporally associated with the strong patterns, so for nauplii in 1979 and *Sagitta* spp. in 1984. It can be deduced from the extension of the PODs that the periods of potential interactions in relation to *N. scintillans* lasted for several weeks. However, temporal correlations indicated longer periods of interactions than the spatial correlations. For example, negative pMWCs were obtained in weeks 21 and 23 in 1984 for nauplii, whereas the positive spatial correlations deny a negative relationship at that time. This difference is possibly due to inconvenient realisation of the synoptical surveys. In turn, detecting relationships in the spatial data is a strong indication of PODs, since negative relationships in the spatial correlations were always accompanied by negative relationships in the time series analysis, but not vice versa.

Validation

Cross-correlations

All potential interactors delivered the requisite cross-correlation (CCF) patterns. The clearest signal, with

almost equal fringes at positive and negative lags, was obtained for juvenile *P. pileus* in 1979 and 1984 (Fig. 8). However, for 1984, the CCF pattern was found before the synoptical surveys started, i.e. weeks 5–21. In the period covered by synoptical surveys the CCF pattern could only be found after correcting for auto-correlation in weeks 16–32, supporting the indication of a rather weak POD at that time (Table 2). The pattern for adult *P. pileus* (Fig. 8), with a one-sided, strongly positive fringe, indicating seasonal succession and a weak arm attributed to potential interactions, is also typical for *Sagitta* spp., *L. blondina* and *R. octopunctata* and for nauplii. For *Sagitta* spp., the CCF pattern was found for weeks 20–40 (1979) and 22–40 (1984). For *L. blondina* and *R. octopunctata* the window was detected for weeks 9–27 (1979) and 8–25 (1984). Nauplii only showed a specific CCF pattern in 1979, between weeks 15 and 35, which is in good correspondence with the finding that no POD was indicated for 1984 (Table 2).

The time lags for *Sagitta* spp. in relation to *N. scintillans* were 8 weeks in 1979 and 9 weeks in 1984 (*N. scintillans* leading) and for *L. blondina*/*R. octopunctata* 5 weeks in both years. For nauplii the lag was 6 weeks in 1979.

Analysis of population dynamics of *N. scintillans*

Intra-annual dynamics

The time series model consisted of flagellates, juvenile and adult *P. pileus* and *Sagitta* spp. as independent regressors for both years. Lags were derived from the cross-correlation analysis (see Table 3). Flagellates were inserted at lag 2. Since nauplii behaved differently between 1979 and 1984, they were not inserted. It was

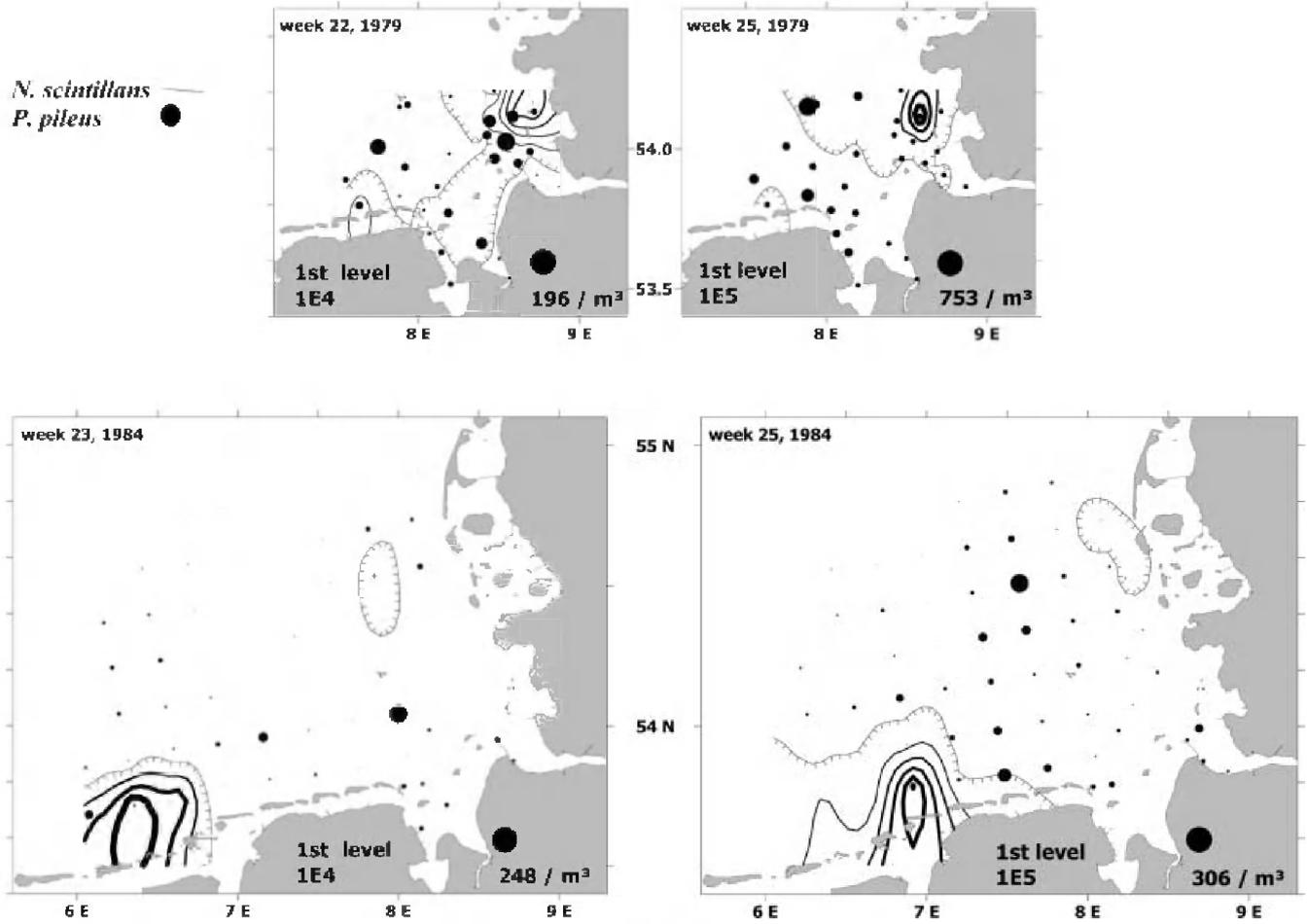


Fig. 3 Spatial distributions in 1979 and 1984 for *Noctiluca scintillans* (contour-lines) and *Pleurobrachia pileus* (circles), weeks denoted. For *N. scintillans* a value for the first contour level (hatching upward) is also noted; for *P. pileus* maximum values are noted (largest circles). Hatching upward for *N. scintillans*. All values in numbers of individuals per cubic metre

intended to keep the model as simple as possible in order to evaluate its principal behaviour.

In both years the main structure of the population dynamics was well fitted by the time series model (Fig. 9). In 1979 one major peak was modelled in accordance with the mass development from weeks 24 to 30. Two minor peaks were produced in the time series model, while abundance of *N. scintillans* was low in the time series.

In 1984 the model indicated three peaks during summer, which corresponds well with the actual

Fig. 4 Spatial distribution of sea surface salinity (SSS, ppt) and sea surface temperature (SST, °C) in the German Bight, June 1984

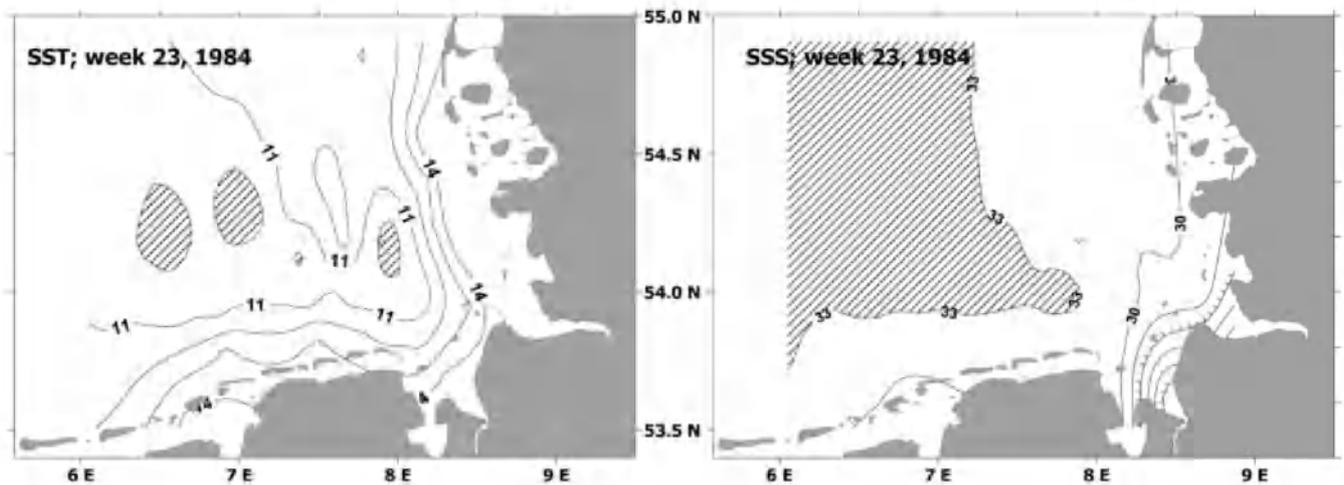
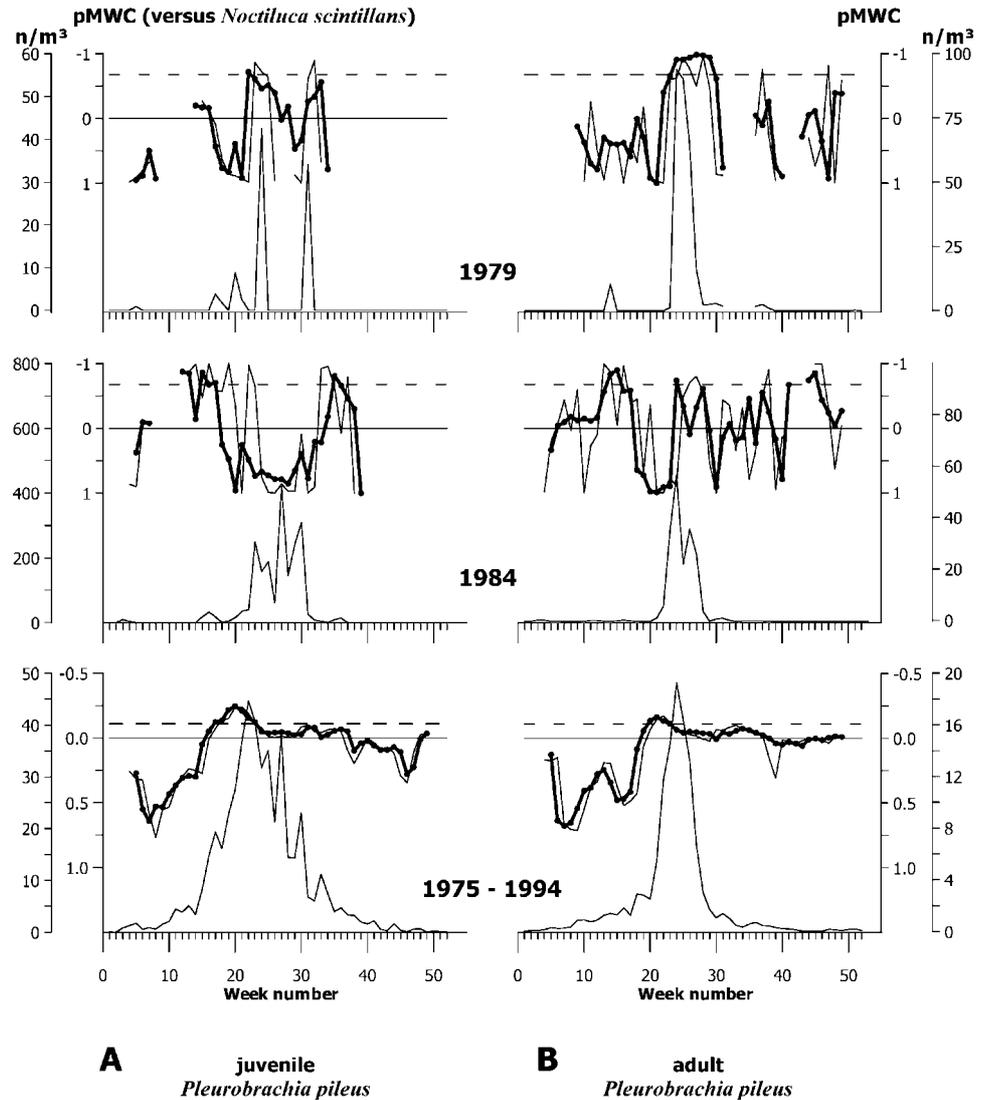


Fig. 5a, b Partialled moving window correlations (*pMWC*) with *Noctiluca scintillans* (*y*-axis: *inner scale*) and abundance (*y*-axis: *outer scale*) in 1979, 1984 and a 20-year mean: *Sagitta* spp. (a) and *Lizzia blondina*/*Rathkea octopunctata* (b). Note that negative *pMWC*s appear above the zero level. Only negative phases of *pMWC*s were considered in the analysis (*broken horizontal line* at $P=0.1$; *thin line* 5 week *pMWC*; *thick line* 7-week *pMWC*)



abundance pattern of *N. scintillans*. Again, in early spring and autumn, minor abundance peaks were found in the model, while *N. scintillans* was at a low abundance then.

Concerning the spring and autumn peaks, we assume that a better fit would have been obtained, especially for spring, if more seasonally diversified regressors had been incorporated in the model.

The coefficients of determination were 0.91 in 1979 and 0.36 (model 1) in 1984. This could be raised to 0.49 in 1984 (model 2) by inserting juvenile *P. pileus* and *Sagitta* spp. at lag 1 instead of lag 2 and at lag 2 instead of lag 9, respectively. The empirical improvement lies in a better match of the first peaks for both series, which then occur in the same week due to juvenile *P. pileus*, and a better match of the two series in the declining phase of the *N. scintillans* population due to *Sagitta* spp. However, the second model produced an extremely negative abundance value for week 24. The r_D values were 0.96 in 1979 and 0.6 in 1984. The r_{R-99} values were

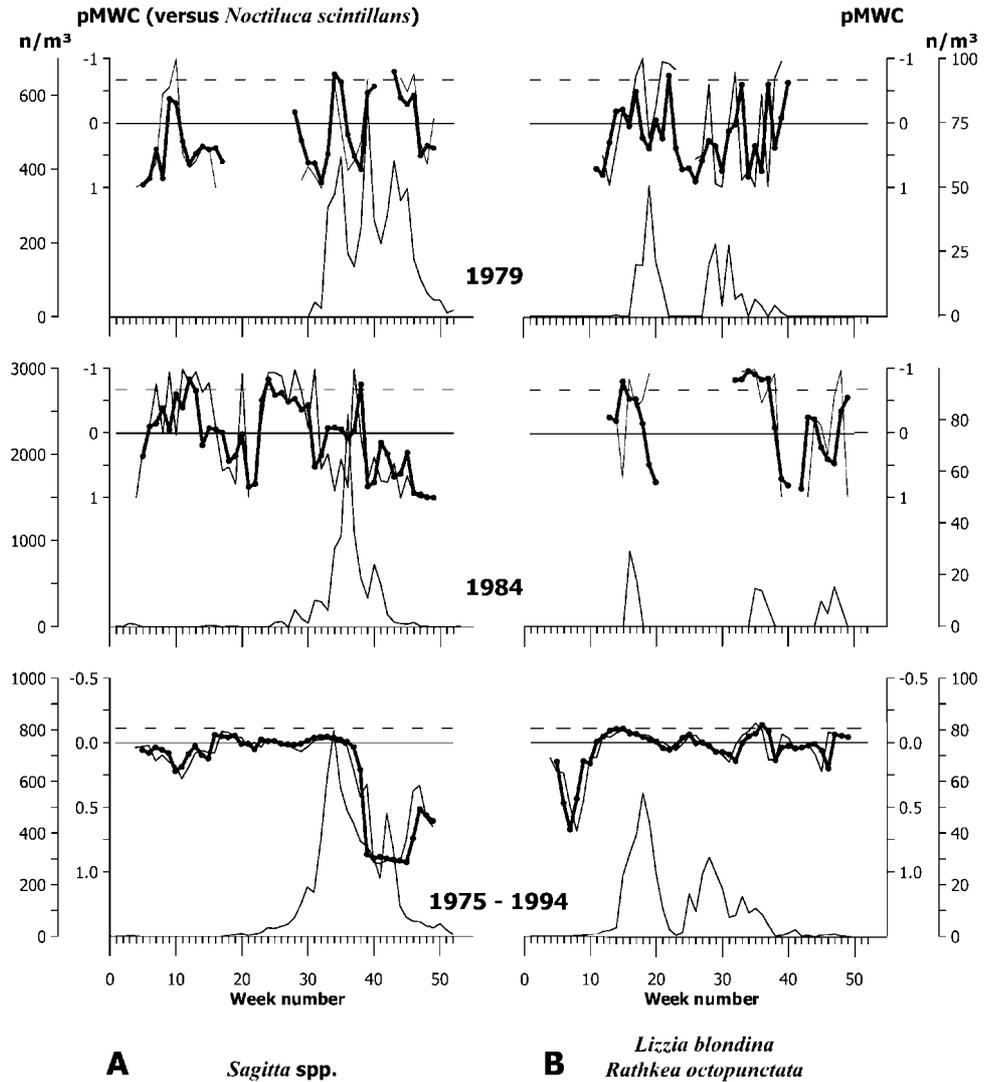
0.47 in 1979 and 0.24 in 1984, indicating significance of the applied time series models.

Additionally inserted water temperature (SST) at lags 0–3 had minor effects and accounted only for ca. 1% of the explained variability. In accordance with the CCF patterns, the values for the significant parameter estimates were positive (adult *P. pileus*, see Table 3). Adult *P. pileus* had a significant effect in both years. *Sagitta* spp. had no significant effects. The effects of flagellates and juvenile *P. pileus* differed between the years.

Inter-annual dynamics

The inter-annual analysis on a 10 year basis (Table 4) led to less precise results than the intra-annual analysis. Only flagellates in the 20–30 week period showed a significant effect; *Sagitta* spp. and *P. pileus* were negatively related to *N. scintillans*, which is in accordance with the correlation analysis for 1979 and 1984.

Fig. 6a, b Partialled moving window correlations ($pMWC$) with *Noctiluca scintillans* (y -axis: inner scale) and abundance (y -axis: outer scale) in 1979, 1984 and a 20-year mean: juvenile *Pleurobrachia pileus* (a) and adult *P. pileus* (b). For explanations see Fig. 5 legend



Historical data sets

The analysis of historical tables reveals that combinations of high abundances of *N. scintillans* together with high abundances of *P. pileus* and *P. pileus* plus *Sagitta* spp., respectively, were rare. This result becomes significant considering all the Wadden Sea data together (Table 5, $n=32$, $P=0.01$) and all of the early ICES data (Table 5, $n=124$, $P=0.03$), supporting the view of a negative relationship between these populations. It is noteworthy that in the historical data sets very early (February) and late (October–December) conjoint findings were recorded for both species.

Discussion and conclusions

Only the cumulative evidence by means of vote-counting of the intermediate results from MWCs, spatial and cross-correlations, as well as the fair reproduction of intra-annual dynamics by means of regression and the

cross-tabulation of findings in historical data sets, gives a strong indication that interactions occur between *Noctiluca scintillans*, *Pleurobrachia pileus*, *Sagitta* spp., nauplii and hydromedusae, the latter two with some reservation since nauplii yielded a result only for 1979 and the group “hydromedusae” resemble an unknown taxonomic composition. However, due to a lack of direct observations this interpretation remains a postulate. Earlier work also indicated a relationship between *N. scintillans* and *P. pileus* (Heyen et al. 1998).

Methodological considerations

For the simple correlations we assumed they would be linked spatially and temporarily in terms of space-and-time concordance. Spatial patterns were applied as indicators of interactions between *Pleurobrachia* and its prey by Suthers and Frank (1990). Negative spatial correlations were also used to indicate interactions between copepods and protozoa (Barquero et al. 1998),

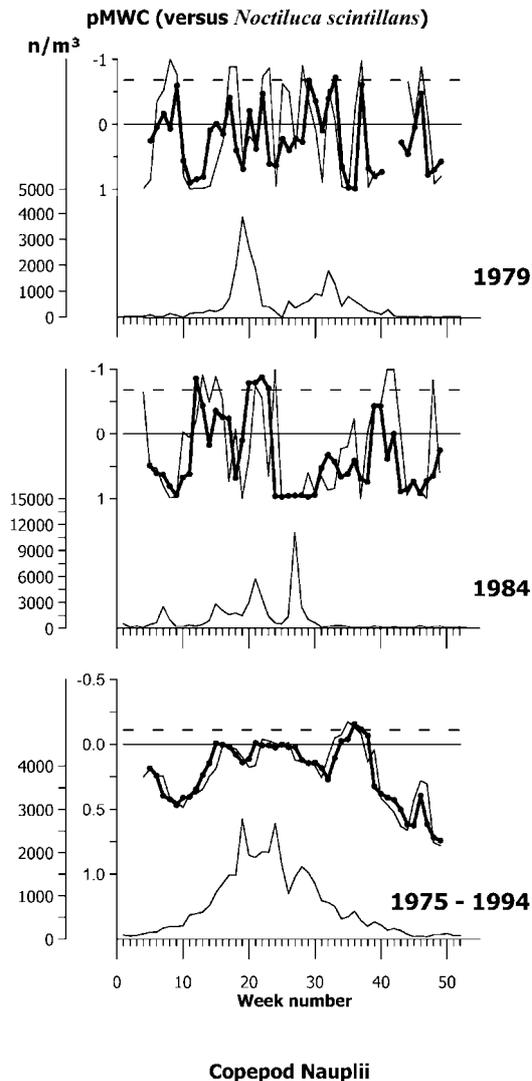


Fig. 7 Partialled moving window correlations (*pMWC*) with *Noctiluca scintillans* (*y*-axis: *inner scale*) and abundance (*y*-axis: *outer scale*) in 1979, 1984 and a 20-year mean: copepod nauplii. For explanations see Fig. 5 legend

krill and copepods (Atkinson et al. 1999) and between *P. pileus* and its predator, *Beroe* sp. (Båmstedt 1998).

The application of the LV-model was essential in order to interpret the observed PODs in terms of interactions. LV-models can be applied in two different ways, i.e. at a local equilibrium or globally (Haydon and Lloyd 1999). In this case, for data with large variability, the global formulation of the LV-model was applied. Thus, it was presumed that the true dynamics of the system are represented adequately by the LV-model. As a consequence, the simplicity of the linear terms of the LV-model needs to be considered carefully (Haydon and Lloyd 1999). Proof of the applicability of this type of linear model was given by Dubois (1976), by showing that, from a different type of predation model, LV-models can be derived. Combining evidence from Greene et al. (1986) and Kremer (1979) justifies the

formulation $\alpha \times N_i \times N_j$ for the predator-prey effect involving *Pleurobrachia*, i.e. the formulation used in the LV-model (actually N_i was factored out). Linear correlations on time series, in order to indicate interactions on inter-annual level, have been applied by Kovalev and Piontkovski (1998) and, on intra-annual level for gelatinous plankton, by Lucas et al. (1997) and Feigenbaum and Kelly (1984). Roff et al. (1988) stressed that, though being simple, these analyses have an indicative value for determining significant relationships in a complex web of zooplankton interactions. In conclusion, the linear approach appears applicable.

In turn, the analytical LV-models have limitations. They are inappropriate to analyse fluxes within communities, since fluxes can also be found without negative correlations (e.g. Daan 1989). They do not allow deduction of the type of interaction between the populations, either competition or predation. Both types of interactions appear in the statistical analysis with the same negative effect, i.e. sign.

Implications for community regulation

PODs and negative *pMWC*s were not indicated continuously throughout the year, but temporarily. This can be understood as a seasonally and periodically differentiated impact of predators. This interpretation is in accordance with the findings of Purcell and White (1994), who showed that clearance rates of gelatinous predators reached rather short-term maxima. Frid et al. (1994) and Enomoto (1956) also stressed the seasonal aspect of predator impact. Indirect evidence for a rather seasonal predator influence can be obtained from the model results of Gaedke (1990), who could not apply maximum predation rates of *N. scintillans* on *Acartia* eggs throughout the whole model run.

Wiafe and Frid (1996) discussed biological predator-prey interactions in homogeneous water columns as an important force in short-term structuring of plankton communities, at times when predators become very abundant. This is in accordance with the negative moving correlations with *N. scintillans* during the growth phase of *P. pileus* populations.

Implications for the dynamics of *N. scintillans*

The postulated relationships between *P. pileus*, *Sagitta* spp., hydromedusae, and nauplii are further discussed in terms of community interactions with *N. scintillans* and the prey spectra of the species considered.

N. scintillans

Negative community effects of *N. scintillans*, by means of an exclusive relationship to mesozooplankton and *Sagitta* spp. in particular, have already been discussed

Table 2 Indication of congruent patterns for spatial and temporal correlations [*bold* strong patterns of dynamics (POD – all correlations negative); *italic* weak PODs; *No value* no value was available, due to only *zero entries* in the respective data matrices, otherwise the presence criterion was not met (see “Materials and methods”); +, positive correlation]. For abundances see Figs. 5, 6 and 7. *Superscripts* indicate for which type of MWC the result was

obtained, if not explicitly mentioned negative results were obtained in all MWCs but best value taken (explanations see “Materials and methods”). For additional 3-week pMWCs, only temperature effects were partialled out. *, **, *** significance levels $P < 0.1, 0.05$ and 0.01 , respectively (*np* unpartialled correlation; *p* partial correlation)

Time	<i>Noctiluca</i> –copepod nauplii	<i>Noctiluca</i> –juv. <i>Pleurobrachia</i>	<i>Noctiluca</i> –adult <i>Pleurobrachia</i>	<i>Noctiluca</i> – <i>Sagitta</i>
1979				
Week 16				
MWC – np	+	-0.10	+	No value (zero entries)
pMWC	+	-0.16	+	+
Spatial correlation – p	+	No value (zero entries)	+	-0.07
Week 19				
MWC – np	+	+	+	
pMWC	+	+	-0.18 ^{w5}	
Spatial correlation	+	No value (zero entries)	+	+
Week 22				
MWC – np	-0.53	-0.39 ^{w3}	+	No value (zero entries)
pMWC	-0.47	-0.72*	-0.40	No value (zero entries)
Spatial correlation – p	-0.04	+	+	No value
Week 25				
MWC – np	+	-0.29	-0.28	No value (zero entries)
pMWC	-0.63 ^{w5}	-0.51	-0.91**	No value (zero entries)
Spatial correlation – p	-0.18	-0.05	-0.18	No value (zero entries)
Week 29				
MWC – np	-0.67*	-0.46	-0.09	-0.68*
pMWC	-0.67*	+	-0.94***	+
Spatial correlation – p	+		-0.27	No value
1984				
Week 21				
MWC – np	-0.47	+	+	-0.48
pMWC	-0.79*	+	+	+
Spatial correlation – p	+	+	+	+
Week 23				
MWC – np	-0.85**	+	+	+
pMWC	-0.71*	-0.65 ^{w5}	+	-0.51
Spatial correlation – p	+	-0.03	+	-0.22*
Week 25				
MWC – np	-0.93 ^{w3}	+	-0.26	-0.40^{w5}
pMWC	+	+	-0.34	-0.59*
Spatial correlation – p	+	+	-0.17	-0.12
Week 27				
MWC – np	+	+	-0.15	-0.18
pMWC	+	+	-0.33	-0.49
Spatial correlation – p	+	+	-0.12	+
Week 29				
MWC – np	+	-0.82 ^{w3}	+	-0.38
pMWC	+	+	+	-0.37
Spatial correlation – p	+	+	+	No value

by Russel (1936) for the English Channel. Similar conclusions were drawn by Le Fèvre and Grall (1970) for the same area, by Cataletto et al. (1995) for the Adriatic Sea and by Nayak et al. (2000) for Indian waters. Top-down regulation was considered important for the distribution of *N. scintillans* in the Bay of Sydney (Murray

and Suthers 1999), where populations develop off the coast and not near-shore as in the German Bight. Huang et al. (1996) discussed a “grey incidence” of factors, i.e. a multi-factorial influence of several variables on the increase of abundance of *N. scintillans* in the Chinese Sea, of which zooplankton density was the most important

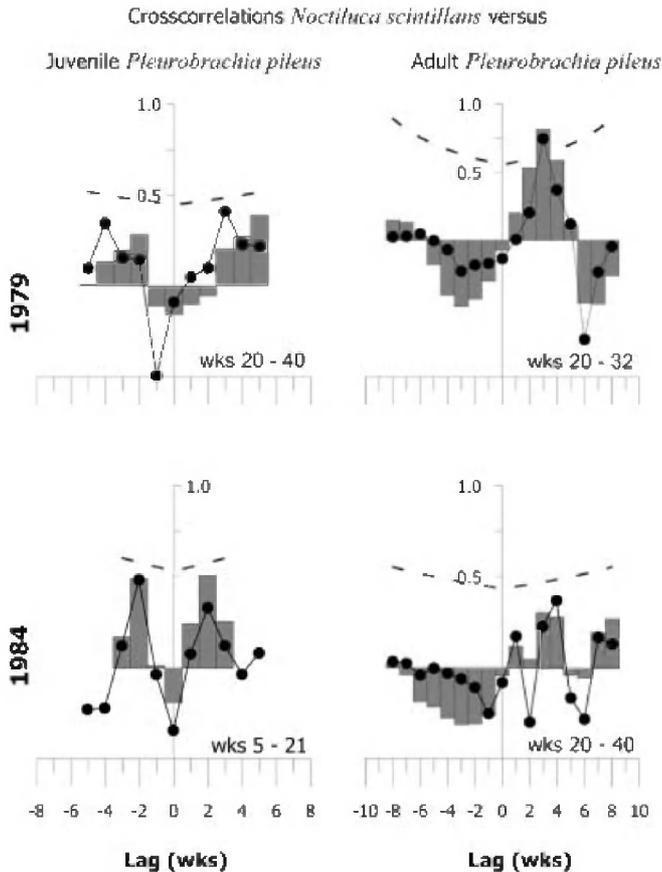


Fig. 8 Cross-correlation patterns for juvenile and adult *Pleurobrachia pileus* versus *Noctiluca scintillans*. Based on weekly values, time period of each year is also noted [bar notation raw data; line/dot notation based on data corrected for first order auto-correlation by subtracting the linear function $a + b \times \text{lag}_{-1}(x)$]. Significance level ($2n^{-0.5}$; n = number of data pairs) indicated by broken line

factor in terms of r^2 (which they phrase “relation degree”). In contrast to the situation in the German Bight, water temperatures $>29^\circ\text{C}$ terminate the annual *Noctiluca*-bloom in that area (Huang and Qi 1992; Huang and Qi 1997). Re-analysing data from Kovalev and Piontkovski (1998), a significant negative inter-annual correlation between *N. scintillans* and *Pleurobrachia bachei* in the Black Sea can be obtained. The presumably

Table 3 Parameter estimates for intra-annual time series modelling. Model 1 in 1984 with lags derived from the cross-correlation analysis, model 2 improved empirically. Graphic results presented in Fig. 9. Dependent variable is abundance of *Noctiluca scintillans*. *, **, *** significance levels $P < 0.05$, < 0.01 , < 0.001 , respectively

Parameter	Model 1		Model 2	
	Estimate	Lag (weeks)	Estimate	Lag (weeks)
1979				
Adult <i>Pleurobrachia pileus</i>	4,832.4***	3		
Juvenile <i>P. pileus</i>	3,433.7***	5		
<i>Sagitta</i> spp.	-2.1	8		
Flagellates	7.3	2		
1984				
Adult <i>P. pileus</i>	1,314***	4	2,472***	4
Juvenile <i>P. pileus</i>	-71.5	2	-232.4***	1
<i>Sagitta</i> spp.	-7.5	9	-11.3	2
Flagellates	737.5***	2	912.1***	2

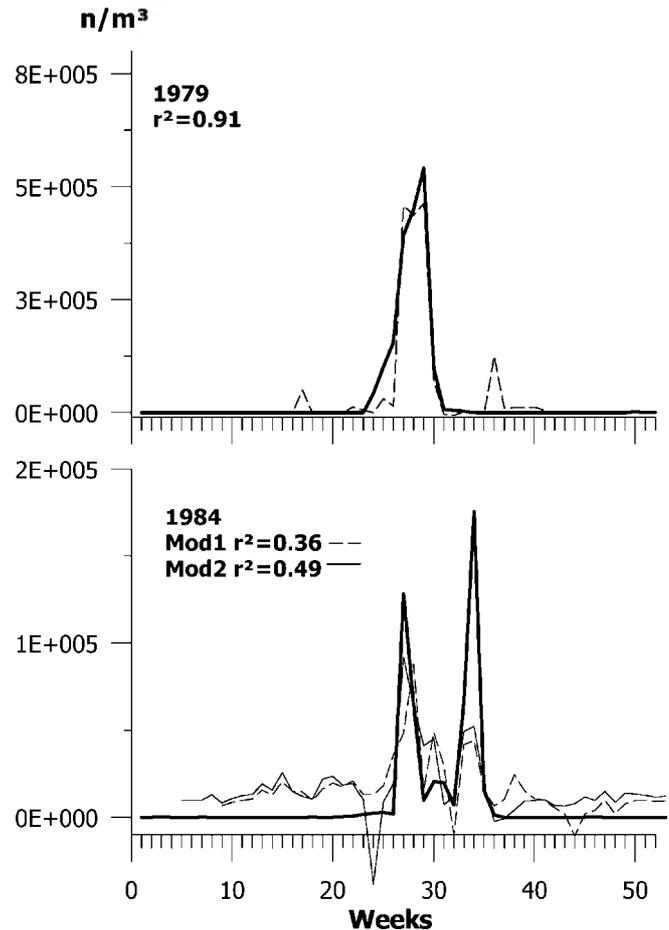


Fig. 9 Time series model (broken line and thin solid line model 1 and 2, respectively, in 1984) and actual abundance pattern (thick line) for *Noctiluca scintillans* in 1979 and 1984. Determination coefficients indicate degree of model fit

important role of *N. scintillans* in transferring organic matter through the food web and, thus, to serve as prey was discussed for the southern North Sea (prey for hydromedusae: Schaumann et al. 1988) and the Black Sea (Petipa et al. 1970). *N. scintillans* was found among prey items for hydromedusae (Daan 1989), and for *Calanus* spp., fish larvae, etc. (Petipa 1960; Porumb 1992). Under experimental conditions feeding on *N. scintillans* was

Table 4 Inter-annual multiple linear regression (1975–1985). Flagellate data only available until 1985. Except for flagellates (mg C m⁻³) abundances in number of individuals per cubic metre. Dependent variable is abundance of *Noctiluca scintillans* (n.s. not significant)

Parameter	Estimate	P
Weeks 20–40		
Intercept	2,380	n.s.
Flagellates	347.3	n.s.
<i>Sagitta</i> spp.	-0.8	n.s.
Adult <i>Pleurobrachia puleus</i>	-531.2	n.s.
Total model	$r^2=0.36$	n.s.
Weeks 20–30		
Intercept	8,658	n.s.
Flagellates	753.1	$P<0.05$
<i>Sagitta</i> spp.	-608.9	n.s.
Adult <i>P. puleus</i>	-303.8	n.s.
Total model	$r^2=0.71$	$P<0.05$

Table 5 Cross-tabulation of conjoint occurrences for *Noctiluca scintillans*, *Pleurobrachius puleus* and *Sagitta* spp from historical data sets. Data derived from Künne (1952) and the Bulletin Tri-mestrial series (e.g. Conseil permanent international pour l'Exploration de la Mer 1910). Occurrences for *N. scintillans* in rows, for *P. puleus* and *P. puleus* plus *Sagitta* spp. in columns. Abundances were originally classified into four (rare, not common, common, very common) or five density categories (*rr* rarissimus; *r* rarus; + nec communis nec rarus; *c* communis; *cc* valde communis) and redefined into two categories for the purpose of comparison, i.e. rare and common. German Wadden Sea (*rare*=rare to not common, *common*=common and very common), Belgish ICES Area (*rare*=*rr* to *r*, *common*=+ to *cc*), German ICES Area (*rare*=*rr*, *common*=*r* to *cc*); combinations with zero occurrences not included

	<i>P. puleus</i>	
German Wadden Sea, May–July 1947–1949	Rare	Common
<i>N. scintillans</i>		
Rare	5	5
Common	7	0
German Wadden Sea, October–December 1947–1949	Rare	Common
<i>N. scintillans</i>		
Rare	7	3
Common	5	0
Belgish ICES Area 1903, 1904, 1907 ^a	<i>P. puleus</i> + <i>Sagitta</i> sp.	Common
<i>N. scintillans</i>		
Rare	42	31
Common	12	3
German ICES Area 1903, 1904 ^b	Rare	Common
<i>N. scintillans</i>		
Rare	8	20
Common	5	3

^aStations B1–B8, B10–B11 in August 1903, February 1904, May 1904 and May 1907

^bStations DN (beginning and end), DN1–DN6, DN13–DN15, in August 1903, February 1904 and May 1904

found for the calanoid copepods *Acartia clausi*, *Temora longicornis* and *Calanus helgolandicus* (all stage CVI, Greve, unpublished data) and for decapod larvae (Lehto et al. 1998; Sulkin et al. 1998).

In turn, the prey spectrum of *N. scintillans* includes naupliar stages N1 and N2 (Greve, unpublished data). Evidence for naupliar prey (Thomas 1979; Sazhina 1996) and especially copepod egg prey (Sekiguchi and Kato 1976; Kimor 1979; Daan 1987; Sazhina 1996; Quevedo et al. 1999) underlines that *N. scintillans* preferentially consumes less mobile prey (Daan 1987). Predation on fish eggs is known to have a considerable environmental impact (Enomoto 1956; Hattori 1962). The fact that cannibalism was observed (Pratje 1925) and latex spheres were adsorbed (Kiørboe and Titelman 1998) indicates that immobile globular particles of a wide size range and consistency belong to the prey spectrum.

Sagitta spp. and *P. puleus*

Both, *Sagitta* spp. and *P. puleus* feed on a wide range of potential items and seem to utilise most plankton without clear selection (Pearre 1974, 1981; Reeve and Walter 1978; Feigenbaum and Maris 1984). Båmstedt (1998) showed that *P. puleus* intensified feeding on larger size classes of prey. Phytoplankton remains were found in the gut of *P. puleus*, but were assigned to food of formerly ingested copepod prey items (Hirota 1974). According to Petipa et al. (1970) *P. puleus* also preys upon *Sagitta* spp., which would support the complexity of

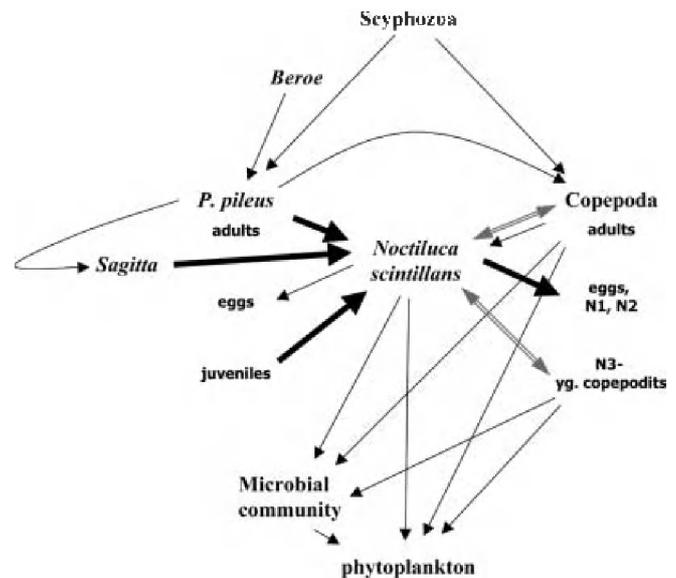


Fig. 10 Hypothetical food web related to *Noctiluca scintillans* (single-pointed arrows feeding relationships; double-pointed arrows potential competition; bold arrows potential interactions described in the "Discussion"). For copepods, eggs and early naupliar stages are summarised into one category, although only naupliar stages were investigated. Exemplary references for thin arrows: microbial community–*Noctiluca* (Kirchner et al. 1996) microbial community–copepods (Hansen et al. 1993; Nakamura and Turner 1997), phytoplankton–*Noctiluca* (Enomoto 1956; Kiørboe and Titelman 1998), *Pleurobrachia*–*Beroe* (Greve 1981), ctenophores–scyphozoa (Feigenbaum and Kelly 1984; Kopacz 1994), copepods–scyphozoa (Lucas et al. 1997)

interactions in natural food webs, with the postulated low level of statistical significance as discussed before.

Øresland (1987) reported a slight selectivity toward copepods for *S. setosa*, whereas *S. elegans* was found to be non-selective. As for *P. pileus*, a preference for larger prey items exists (Øresland 1987). Even phytoplankton and protozoans contribute markedly to the diet of Chaetognatha (Pearre 1974; Alvarez Cadena 1993). Generally, the diet determined by gut contents directly reflected the present composition of the ambient plankton community and did not indicate enhanced selectivity (Reeve and Walter 1978; Alvarez Cadena 1993).

Putting things together

Assembling findings from this analysis and the literature and taking into account the high predation capability of *N. scintillans*, presumably on all kinds of eggs, and the limited selectivity evidenced by *Sagitta* spp. and *P. pileus* enables us to develop a hypothetical framework of interactions in relation to this dinoflagellate (Fig. 10). A suite of inverse relationships appears, i.e. *N. scintillans* can affect populations of interacting species by cutting down their egg numbers and, in turn, is subject to predation by their juveniles and adults. Additionally, competition may occur where diet spectra overlap. This interpretation leads to the conclusion that the analysed relationships are indirect as far as egg predation is concerned. Hence, one of our basic assumptions, i.e. that we could detect direct relationships, was probably to some degree erroneous.

Furthermore, it appears that the community anticipated to be relevant in *Noctiluca*-dynamics comprises more populations than were investigated in this analysis, including mega-plankton such scyphomedusae. This could explain the failure of the inter-annual regression analysis (Table 4) to produce significant results for the parameters, because the suite of parameters was not quite complete.

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