Long-term, predation-based control of a central-west North Sea zooplankton community

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Long-term monitoring of the zooplankton community at a station 5.5 miles from the English coast in the central-west North Sea has been performed since 1968. Analyses of these data have revealed an inverse relationship between annual total zooplankton abundance and the position of the Gulf Stream North Wall (GSNW). This long-term relationship is opposite to the long-term positive association observed between the GSNW and total zooplankton abundances throughout most of the oceanic NE Atlantic region and the northern and central North Sea using Continuous Plankton Recorder data.

This study investigates the mechanism behind the inverse relationship with the GSNW, focussing on the importance of zooplankton predators in influencing long-term changes in the zooplankton community of the central-west North Sea. The results suggest that the dominant zooplankton predator *Sagitta elegans* plays a key role in mediating spring copepod population growth rates and thus their maximum and overall productivity during any one particular year. In turn, the abundance of *Sagitta* during the spring appears to be related to climatic factors. The implications of this on the zooplankton community are discussed.

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Introduction

The importance of zooplankton as secondary producers in the marine ecosystem, and thus their potential influence on fish stocks, has been the primary reason why researchers have attempted to determine how their long-term dynamics are influenced by climatic (e.g. Taylor, 1995; Fromentin and Planque, 1996), and/or anthropogenic factors (Greve et al., 1996).

Previous evidence has suggested that zooplankton dynamics across the NE Atlantic and North Sea region are principally controlled by processes occurring during the spring (e.g. Dickson et al., 1988), which set in train the dynamics of the rest of the seasonal cycle. In the North Sea, long-term trends in zooplankton are influenced by the (weather-driven) timing of the stratification of the water column and the resulting spring bloom (e.g. Dickson et al., 1988). Further research found that long-term zooplankton trends throughout most of the North Sea and NE Atlantic regions were related to long-term changes in the Gulf

Stream North Wall (GSNW) (Taylor and Stephens, 1980; Taylor et al., 1992; Taylor, 1995, 1996). In NW Europe, northerly positions of the GSNW are related to warmer/wetter weather (Topliss, 1997), and to increased zooplankton productivity across the NE Atlantic and in the northern and central-eastern North Sea (Figure 1). However, such relationships were absent from those areas of the North Sea and Irish Sea which lack a coupling between productivity and wind-induced mixing of the water column. This suggested that changes in the GSNW were associated with changes in the timing and intensity of the spring bloom (in a development of the model of Dickson et al., 1988). These associations were considered to be further evidence of a climatic connection spanning the North Atlantic, and suggested that the long-term trends in plankton (or at least those recorded by the Continuous Plankton Recorder (CPR) device) were predominantly externally driven rather than controlled through trophic interactions (Taylor et al., 1992).

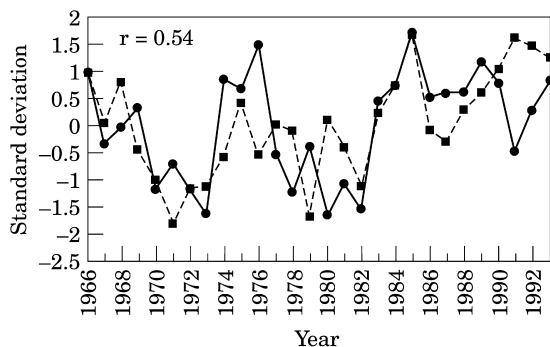In the central-west North Sea, monthly zooplankton sampling by the Dove Marine Laboratory at a single station

Figure 1. Standardized time series plot showing the relationship between the position of the GSNW (- - ■ - -) and total copepods in CPR area B2 (northwest North Sea) over the 1966 to 1993 period (—●—). Adapted from Taylor (1995).

has been performed since 1968 (Roff *et al.*, 1988). Long-term zooplankton trends observed in this series have been found to be dissimilar to those observed from the CPR data in other North Sea regions (Huliselan, 1995; Clark and Frid, 2001). Furthermore, Frid and Huliselan (1996) observed that total zooplankton abundances in the Dove series over the 1969 to 1992 period were negatively related to the GSNW, contrary to those observed in the northern and central-eastern North Sea regions (Figure 1) by Taylor (1995). Such disparate observations are not due to differences in sampling methods, as the relative interannual fluctuations in zooplankton abundance and community structure observed in the Dove series are comparable to those in the CPR series for an area centred on the Dove zooplankton station (Clark and Frid, 2001). Previous studies (e.g. Austen *et al.*, 1991; Evans and Edwards, 1993), on the Dove series have suggested that long-term plankton trends in the central-west North Sea were predominantly influenced by environmental factors, yet more recent investigations have proposed that biotic factors are more important in affecting long-term zooplankton dynamics in this region (Roff *et al.*, 1988; Frid *et al.*, 1994; Huliselan, 1995; Frid and Huliselan, 1996). A number of processes influence the growth rate and development of zooplankton populations. While many studies have focussed on the processes, which influence zooplankton "birth" rates, fewer studies have addressed the importance of zooplankton "death" on zooplankton dynamics (Ohman and Wood, 1995), and this is especially true for examinations of the long-term dynamics of zooplankton populations. This is based on the incorrect assumption that marine plankton communities are purely bottom-up rather than top-down controlled systems (Ohman and Wood, 1995). Yet studies of some zooplankton communities suggest that even at conservative levels of predation, predators are able to control the dynamics (Steele and Henderson, 1992) and the population growth rates of some zooplankton populations (Davis, 1984b; Ohman, 1986; Frid *et al.*, 1994; Ohman and Wood, 1995; Sullivan and Meise,

1996). This study presents analyses of the Dove zooplankton series (1969–1996), focussing on the month to month and interannual relationships of the predators and omnivores within the zooplankton community. A mechanism is proposed as to how long-term interannual fluctuations in zooplankton abundance might be influenced by predation, and why changes in the latitude of the GSNW might be related to long-term zooplankton trends.

Methods

Dove Marine Laboratory time series

Zooplankton sampling by the Dove Marine Laboratory was initiated at a station approx. 5.5 n miles east of Blyth on the Northumberland coast at $55°07'$N $01°20'$W in August 1968. Sampling has taken place on a monthly basis except in 1989 when no samples were taken. Sampling consisted of four vertical hauls from 50 m to the surface (water depth approximately 54 m), which were pooled, using a 200 μm meshed WP2 net (UNESCO, 1968) with a mouth diameter of 0.56 m.

In addition, to enable a more accurate quantification of larger, but rarer zooplankton taxa, a 10 min horizontal trawl at approximately 30 m depth was taken using a 1 mm meshed WP3 net with a 1 m mouth diameter (UNESCO, 1968). On return to the laboratory, zooplanktons were identified to species level where possible, and abundances were determined. The abundance of each taxon was derived, according to its size, from either the WP2 or the WP3 net (see Evans and Edwards, 1993 for rationale). Certain taxa were further subdivided into sexes, or were categorized as juveniles and adults.

Initial data manipulations

Monthly data from the Dove zooplankton data covered the period 1969–1996 (excepting 1989). Due to the large number of taxonomic entities recorded in the Dove series (89 entities), only those predator and omnivore taxa, which represented at least 2% of the total zooplankton community *in any one monthly sample*, were used in the following analyses [a total of 46 taxa (see Table 1 for taxa list)]. Predators were considered to be those zooplankton species which were known to be carnivorous, whereas omnivores were those taxa, which were predominantly herbivorous zooplankton, but could include those taxa, which were opportunistic feeders, consuming both plant and animal materials.

Relationships between zooplankton and the GSNW

Correlation analysis was employed to examine long-term relationships between taxa and the position of the GSNW. For all taxa, abundances were $\log_{10} + 1$-transformed. Due to the problem of autocorrelation inherent in time series data (Jassby and Powell, 1990), additional post correlational

Table 1. Abundances of omnivorous and predatory zooplankton taxa taken from the 27-year Dove zooplankton series and representing at least 2% of the total community in any one monthly sample. For each taxa, the correlations between the GSNW and the mean annual abundance of each taxa are given. All probability values are corrected for serial correlation. Only those probabilities significant at less than $p \leq 0.05$ are included, significant correlations after correction are in bold. Global $p = 0.026$.

Trophic level	Taxa	Mean abundance (per m³)	Correlation coefficient (r) and probability value (p)
Omnivore	*Pseudocalanus/Paracalanus/Microcalanus*	963.17	**−0.61, p = 0.006**
Omnivore	*Oithona similis*	930.18	**−0.45, p = 0.033**
Omnivore	*Acartia* spp. juveniles	760.92	−0.24
Omnivore	*Evadne nordmanni*	439.85	−0.15
Omnivore	*Acartia clausi*	327.98	0.02
Omnivore	*Temora longicornis*	323.57	**−0.47, p = 0.018**
Omnivore	*Acartia longiremis*	161.86	−0.38
Omnivore	*Pseudocalanus elongatus* adults	155.33	−0.14
Omnivore	*Oikopleura diocia*	86.48	−0.17
Omnivore	Bivalve larvae	73.45	−0.31
Omnivore	*Calanus* spp. juveniles	66.19	−0.15
Omnivore	Cirripeda larvae	63.25	−0.10
Omnivore	Ophioplutei larvae	45.93	0.14
Omnivore	Gastropoda larvae	38.54	**−0.54, p = 0.023**
Omnivore	*Fritillaria borealis*	37.35	0.053
Omnivore	Polychaeta juveniles	33.27	0.09
Omnivore	*Paracalanus parvus*	33.18	−0.08
Omnivore	*Podon* spp.	31.82	−0.28
Omnivore	*Euphausiid* spp. nauplii	24.65	−0.06
Omnivore	*Centropages hamatus*	22.07	0.12
Omnivore	*Centropages* spp. juveniles	18.49	0.06
Omnivore	Euphausiid spp. juveniles	17.59	−0.16
Omnivore	Bryozoan juveniles	9.73	−0.30
Omnivore	*Microcalanus pusillus*	8.5	0.16
Omnivore	*Microsetella norvegica*	5.88	−0.22
Omnivore	Echinoderm larvae	5.7	−0.15
Omnivore	Echinoplutei larvae	4.95	−0.07
Omnivore	*Calanus* spp. males	4.84	−0.04
Omnivore	*Centropages typicus*	3.93	−0.03
Omnivore	*Tomopteris helgolandica*	1.76	−0.32
Omnivore	*Calanus helgolandicus* females	1.47	0.07
Omnivore	Phoronid larvae	1.44	0.20
Omnivore	Anomuran larvae	1.09	0.19
Omnivore	*Calanus finmarchicus* females	0.97	0.36
Omnivore	*Tigriopus* spp.	0.23	0.45, p = 0.106
Omnivore	*Oncaea venusta*	0.11	**0.47, p = 0.022**
Predator	*Sagitta elegans*	13.09	0.17
Predator	*Aglantha digitale*	5.02	0.02
Predator	Jellyfish larvae	3.06	−0.07
Predator	*Themisto gaudichaudi*	1.09	0.10
Predator	*Corycaeus anglicus*	0.64	0.20
Predator	Fish larvae	0.27	−0.06
Predator	*Thysanoessa raschi*	0.26	−0.05
Predator	*Nanomia cara*	0.11	−0.18
Predator	*Nyctiphanes couchi*	0.05	−0.03
Predator	*Thysanoessa inermis*	0.05	0.36

corrections were employed to compensate for this. Thus, the number of degrees of freedom used for testing the significance of correlations between taxa and potential forcing factors was reduced according to the method of Quenouille (1952), which calculates the effective number of independent observations (E) as follows:

$$E = \frac{N}{(1 + 2r_1 r_1' + 2r_2 r_2')}$$

where N is the number of points in each of the two time series; r_1 and r_1' are the one-point lag autocorrelations of each time series; r_2 and r_2' are the two-point lag autocorrelations of each time series. Additionally, to give an indication of the probability of spurious correlations in the data, for each table of independent tests, a global significance level was calculated based on the number of significant correlations (prior to the tests for autocorrelation).

Predator–prey relationships over the seasonal cycle

The seasonal cycle of omnivores and predators were compared between low zooplankton years [defined as years where the mean annual total zooplankton abundance was more than 0.5 standard deviation below the long-term mean (Table 2)], and high zooplankton years [defined as years where the mean annual total zooplankton abundance was more than 0.5 standard deviation above the long-term mean (Table 2)]. From these plots, differences in the seasonal cycle between low and high abundance years, and possible relationships between the predators and omnivores were investigated.

Long-term predator–prey relationships

The dominant zooplankton predator in the central-west North Sea zooplankton system (as observed in the Dove zooplankton series) is the chaetognath *Sagitta elegans* Verrill (Table 1). As such, the investigations of predator–prey relationships within the zooplankton community dealt primarily with this predatory species. Those factors, which influence spring omnivore population growth rates, such as predation are likely to moderate the overall annual productivity during that year. Thus, the examination of predator–prey relationships concentrated on the ability of *Sagitta* to moderate the annual maximum omnivore productivity through regulation of their population growth rate during the spring. Thus, the presence of long-term relationships between mean spring (February to April) *Sagitta* abundances and the maximum abundance of each omnivorous taxa over the 27-year time series were explored using correlation analysis. All significance tests were corrected for autocorrelation using the formula of Que-nouille (1952), and a global significance level was calculated based on the number of significant correlations present.

Relationships between spring *Sagitta* and environmental factors

The main periods of *Sagitta* recruitment are said by Feigenbaum and Maris (1984) to coincide with sharp increases in the abundance of *Pseudocalanus* nauplii (the main prey item of young chaetognaths), which would be expected to be greater with increased spring phytoplankton productivity (Feigenbaum and Maris, 1984). Thus, in order to establish whether spring *Sagitta* abundances were related to spring phytoplankton or weather, standardized time series of $\log_{10}$ February–April *Sagitta* abundances were plotted alongside standardized February–April values of air temperatures and daily sun duration taken at nearby Tynemouth (obtained from the British Atmospheric Data Centre), the annual mean position of the GSNW, and mean February–April phytoplankton index data from the CPR survey for the central-west North Sea.

Table 2. Low and high zooplankton years in the 27-year Dove zooplankton series. See text for definitions.

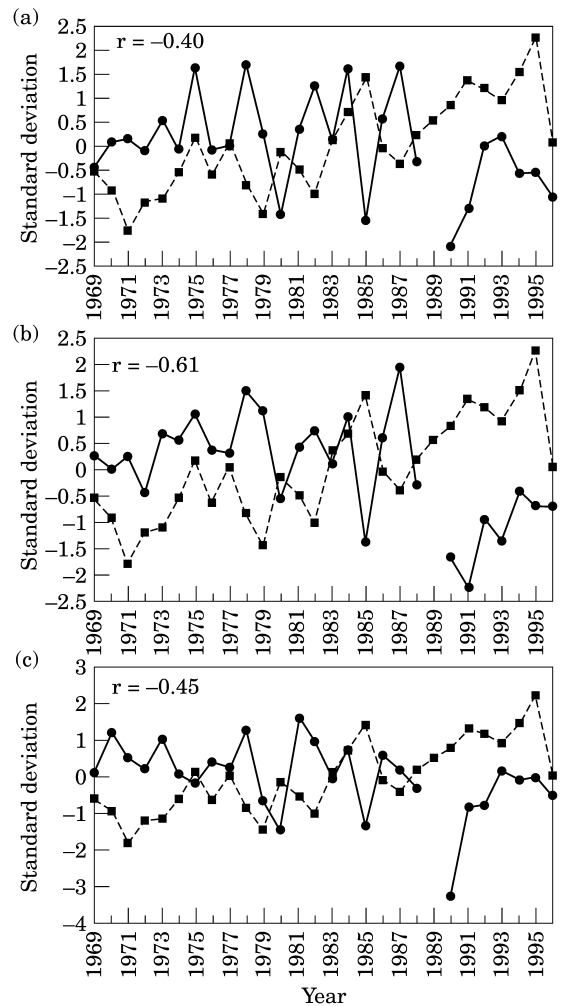| Low zooplankton abundance years	High zooplankton abundance years
1980	1973
1985	1975
1990	1978
1991	1982
1994	1984
1995	1986
1996	1987

Figure 2. Standardized time series plot showing the relationship between the position of the GSNW (- -■- -) and the abundance of (a) total zooplankton (—●—), (b) *Pseudocalanus/Paracalanus/ Microcalanus* (—●—), (c) *O. similis* (—●—), taken from the 27-year Dove zooplankton series.

Results

Over the 1969 to 1996 period, long-term trends in total zooplankton abundance were negatively correlated with the GSNW (r = −0.4, p = 0.046; Figure 2a), confirming the analyses of Frid and Huliselan (1996). Of the 46 taxa examined, long-term trends in four taxa were negatively related to the GSNW, and one taxon was positively related (Table 1). The strongest relationship observed with the GSNW was with the most dominant taxonomic group, the *Pseudocalanus/Paracalanus/Microcalanus* group (r = −0.61, p = 0.006; Figure 2b). The second most abundance taxa, *Oithona similis*, was also significantly negatively associated with the GSNW (r = −0.41, p = 0.03; Figure 2c). Together, these two taxa make up 40% of the total zooplankton abundance observed in the Dove series (Table 1).

On average, the spring omnivore increase began in March and continued until June, followed by a steady decline in abundance until the winter nadir from December to February (Figure 3). Omnivore abundances during the winter and early spring showed no relationship to maximum omnivore abundances during that year (Figure 4). Only by May did omnivore abundances bear any significant relationship to the maximum annual abundance attained. There was also a significant correlation between the difference in the abundance of the total omnivores from February to April (i.e. their increase in abundance over this period), and their maximum annual abundance (r = −0.45, p = 0.02). Thus, smaller differences in abundance (indicating higher rates of omnivore population growth from February to April), were related to a higher maximum abundance attained during that particular year, suggesting that the rate of increase during these months was critical in determining the maximum annual abundance reached.

From February to April, predator abundances were relatively low, and only started to increase after the increase in omnivore abundance (Figure 5). Except during May, when gelatinous zooplankton dominated (Figure 5), *S. elegans* Verrill (Chaetognatha) was the dominant predator in the zooplankton community, and from February to April this taxa made up 73% of total predator abundances (Table 3).
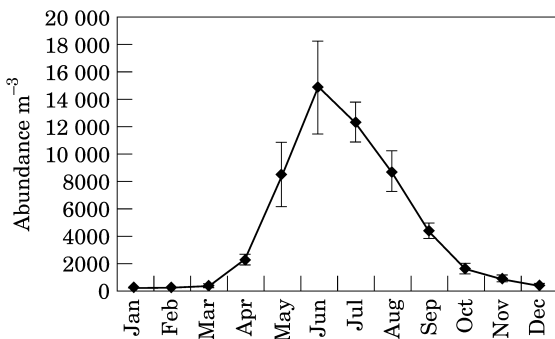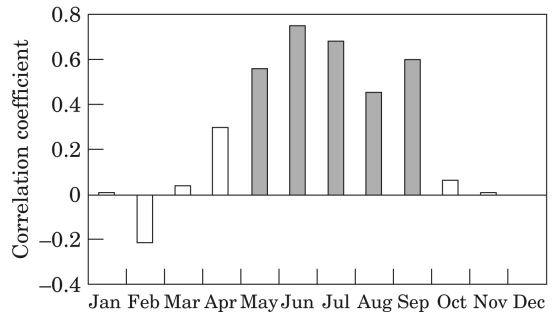
Figure 4. Correlation coefficients calculated over the 27-year Dove zooplankton series between the total omnivore abundance for each month and the maximum abundance during the year. Grey bars indicate those months with correlations significant at p ≤ 0.05.

Month to month and long-term predator–prey relationships

During high zooplankton abundance years, the rate of omnivore increase from February to the end of April was greater than that during low abundance years (Figure 6a), leading to an overall higher peak of abundance in the summer. During these high abundance years, predator abundances during the spring omnivore increase from February to April were relatively low (Figure 6a). Conversely, during years with higher spring predator abundance, the rate of omnivore increase from February to April was lower, leading to an overall reduced abundance. Based on the observations in Feigenbaum and Maris (1984) that North Sea *Sagitta* are able to consume 2.04 prey items per day, and on the abundance of *Sagitta* observed in March during low and high zooplankton abundance years, this equates to 5.93% of the omnivore community consumed in March during low abundance years against 1.34% of the omnivore community consumed during March in high abundance years. As omnivore abundances from November to February in both low and high abundance years were similar, the differences later on in the seasonal cycle do not arise from differences during the early part of the year, supporting the conclusion that abundances during the winter are unrelated to those during the summer.

Figure 3. Mean monthly abundance of total omnivores over the 27-year Dove zooplankton series. Error bars denote standard errors.
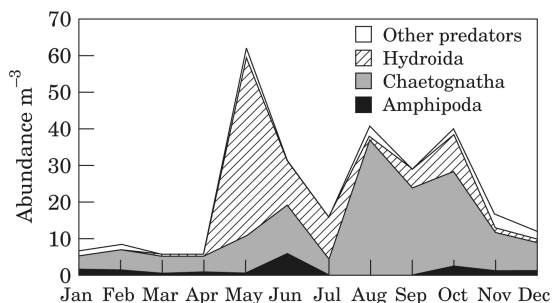
Figure 5. Area plot constructed from the mean monthly abundances of the main zooplankton predators over the 27-year Dove zooplankton series. For legend see figure.

Table 3. Proportions of zooplankton predators in the 27-year Dove zooplankton series from February to April.

Taxa	Predator mean abundance (per m^3)	Percentage proportion
Chaetognatha	4.76	72.93
Amphipoda	0.71	10.86
Hydroida	0.41	6.3
Copepoda	0.38	5.8
Euphausiacea	0.17	2.56
Fish	0.10	1.54
Siphonophora	0.0005	0.008

Similar patterns were observed in the relationship between the dominant two taxa (the *Pseudocalanus/Paracalanus/Microcalanus* group and *O. similis*) with the main predator *Sagitta*. For *Pseudocalanus/Paracalanus/Microcalanus*, the spring increase occurs during March and April (Figure 6b), whilst for *O. similis*, the increase occurs during February to April (Figure 6c). In both of these taxa, when the rate of population growth during the spring was low, *Sagitta* abundances were higher during winter, and vice versa (Figure 6b, c).

Over the 27-year series, there was a significant inverse relationship between the mean spring total predator (February–April) abundance and mean summer omnivore (June–August) abundance (r = −0.40, p = 0.046; Figure 7a). This relationship was especially strong during the 1974–1990 period, although 1980 had a lower omnivore abundance than would be expected given the numbers of predators present. Significant negative correlations (Table 4) were also observed between the spring (February–April) abundance of *Sagitta* and the maximum annual abundance of the *Pseudocalanus/Paracalanus/Microcalanus* juveniles (r = −0.45, p = 0.018; Figure 7b), *Calanus* spp. juveniles (r = 0.55, p = 0.006), gastropod larvae (r = −0.44, p = 0.023), euphausiid nauplii (r = −0.42, p = 0.03) and *Oithona* spp. (r = −0.41, p = 0.041; Figure 7c). *Calanus finmarchicus* was the only taxon to show a positive relationship between spring *Sagitta* abundances and its maximum abundance during the year (Table 4).

Environmental control during the spring

Spring *Sagitta* abundances (February–April) were low from the start of the Dove series until 1980 (excepting a peak in 1977), as was noted by Evans and Edwards (1993). Following this, there was a gradual increase in *Sagitta* abundances until 1983 (Figure 8a–d). These spring *Sagitta* abundances were found to be significantly related to a number of environmental variables over the entire 27-year time series. Positive associations were present between *Sagitta* and mean spring Tynemouth air temperature (Figure 8a), mean spring Tynemouth sunshine (Figure 8b), the GSNW (Figure 8c) and mean spring C2 phytoplankton index (Figure 8d). However, before 1977,
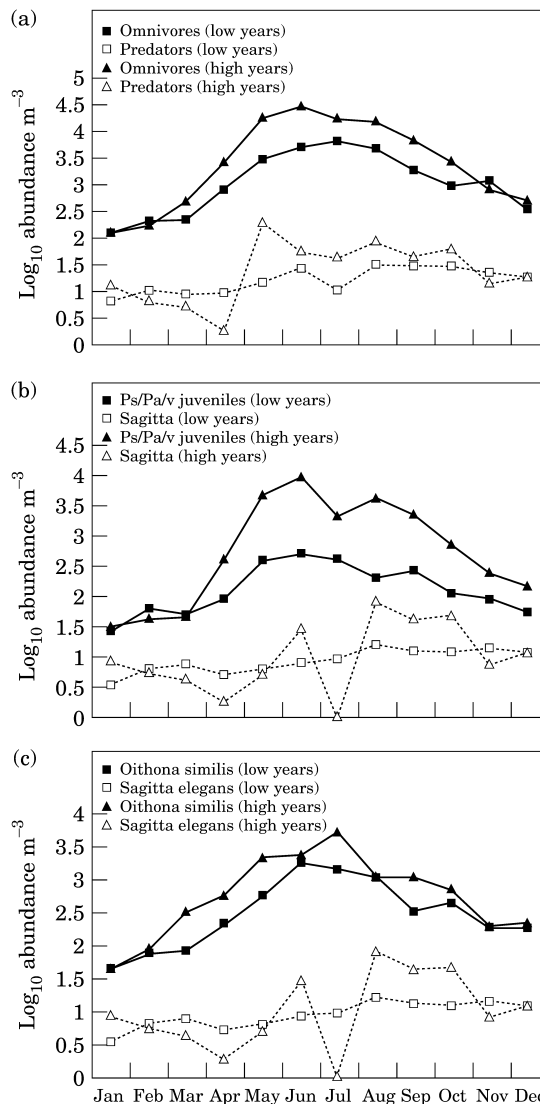

Figure 6. Mean monthly log$_{10}$-abundance in the 27-year Dove zooplankton series of (a) total omnivores and total predators, (b) *Pseudocalanus/Paracalanus/Microcalanus* and *S. elegans*, and (c) *O. similis* and *S. elegans*, during low and high zooplankton years. For legend see figure.

due to the low spring *Sagitta* abundances, there was no response to fluctuations in these environmental variables, although the peak in *Sagitta* during 1977 did coincide with peaks in sunshine and temperature.

Discussion

Previous studies by Roff *et al.* (1988) in the central-west North Sea suggested that the standing stock of zooplankton over the winter governed their maximum abundance the following year. However, this study has shown that over the whole series, there was no relationship between the
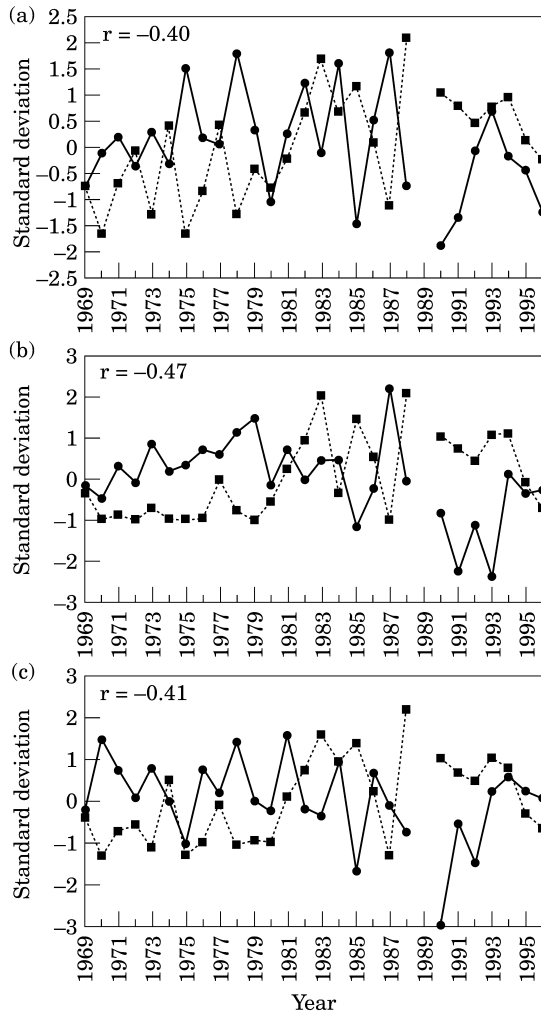
Figure 7. Standardized time series plot taken from the 27-year Dove zooplankton data, showing the relationship between (a) mean May–August total omnivore abundances (—●—) and mean February–April total predator abundances (- -■- -), (b) mean June–July *Pseudocalanus/Paracalanus/Microcalanus* abundances (—●—) and mean March–April *S. elegans* abundances (- -■- -), and (c) mean June–August *O. similis* abundances (—●—) and February–April *S. elegans* abundances (- -■- -).

Table 4. Results of correlation analysis calculated between mean spring *Sagitta* abundances (February to April) and the maximum abundance of omnivores during the same year. Only those probability values less than p ≤ 0.05 before correction for autocorrelation are included, significant correlations after correction are in bold. Data from the 27-year Dove zooplankton series. Global p = 0.008.

Taxa	Correlation coefficient
Acartia clausi	0.06
Acartia longicornis	−0.01
Acartia spp. juveniles	−0.35
Anomuran larvae	−0.01
Bivalve larvae	−0.20
Bryozoan larvae	−0.08
Calanus finmarchicus	**0.55, p = 0.006**
Calanus helgolandicus	0.24
Calanus spp. Juveniles	**−0.44, p = 0.021**
Calanus spp. males	0.29
Centropages hamatus	0.02
Centropages spp. juveniles	−0.03
Centropages typicus	−0.07
Cirripede larvae	0.03
Echinoderm larvae	−0.33
Echinoplutei larvae	−0.09
Euphausiid spp. larvae	−0.03
Euphausiid spp. nauplii	**−0.42, p = 0.03**
Evadne nordmanni	0.09
Fritillaria borealis	−0.26
Gastropod larvae	**−0.44, p = 0.023**
Microsetella norvegica	0.01
Microcalanus pusillus	−0.19
Oikopleura diocia	−0.11
Oithona similis	**−0.41, p = 0.041**
Oncaea venusta	0.08
Ophioplutei larvae	−0.22
Paracalanus parvus	−0.09
Phoronid larvae	0.01
Podon spp.	0.12
Polychaete larvae	−0.09
Pseudocalanus/Paracalanus/ Microcalanus juveniles	**−0.45, p = 0.018**
Pseudocalanus elongatus adults	0.01
Temora longicornis	−0.16
Tigriopus spp.	0.18
Tomopteris helgolandica	−0.07

standing stock of omnivores during the winter months, and peak omnivore abundances the following summer. In addition, omnivore abundances observed in January and February during low zooplankton years were similar to those observed during high zooplankton years. Thus, it appears that those processes occurring during the spring are crucial in determining the annual abundance and productivity of zooplankton in the central-west North Sea.

Sagitta has often been cited as a predator of copepod populations (Oresland, 1985; Conway and Williams, 1986; Alvarez-Cadena, 1993; Sullivan and Meise, 1996) and limitation of *Pseudocalanus* population growth and the interannual variability in the abundance of predators such as *Sagitta* was related to the annual mortality of *Pseudocalanus* in Dabob Bay, Washington (Ohman, 1986). Certainly we have shown that there are large differences in the percentage of the standing stock that are removed during low and high abundance years. This study has also shown that the peak annual abundances of four omnivorous taxa, of which two, *Pseudocalanus/Paracalanus/Microcalanus* and *O. similis*, are the most numerically dominant taxa recorded in the Dove series, were inversely related to spring *Sagitta* abundances. This suggests that predation upon these taxa by *Sagitta* was limiting their spring population growth and hence their annual maximum abundances and productivity. These four omnivorous taxa
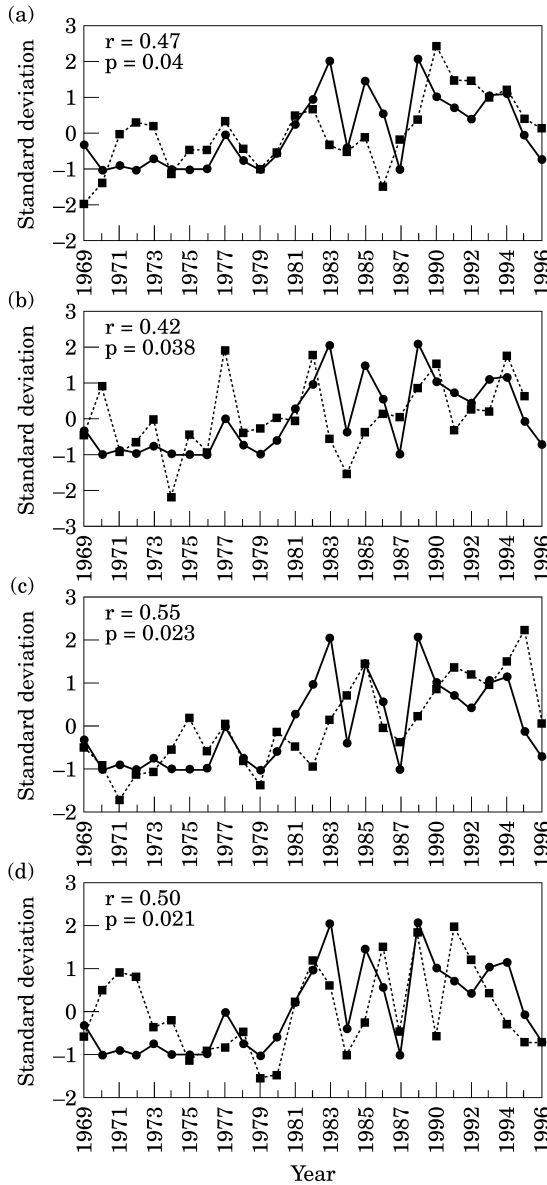
(a)

(b)

(c)

(d)

Figure 8. Standardized time series plot from the 27-year Dove series of (a) *S. elegans* (— ◆ —) and Tynemouth air temperatures (--■--). (b) *S. elegans* (— ◆ —) and Tynemouth sunshine (--■--). (c) *S. elegans* (— ◆ —) and the GSNW (--■--). (d) *S. elegans* (— ◆ —) and CPR phytoplankton index (area C2) (--■--).
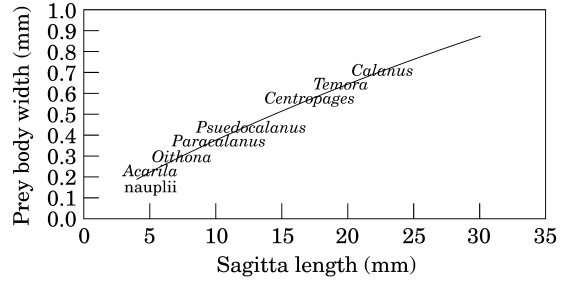

Figure 9. Relationship between length of *S. elegans* and maximum prey body width. Derived from Feigenbaum and Maris, 1984.

response. However, there is a relationship between the size of a *Sagitta* individual and the size of prey taken (Figure 9; Feigenbaum and Maris, 1984).

It would be expected that only juvenile *Sagitta* (stages I and II) individuals below approximately 15 mm length (Huliselan, 1995) would prey upon those omnivorous taxa identified in Table 4 (Feigenbaum and Maris, 1984). Larger omnivores, such as adult *Calanus* would not be expected to be consumed by juvenile *Sagitta*, although they could be consumed by those individuals greater than 15 mm length (Figure 9).

Given that small copepods are the principle target of predation by *Sagitta*, it might be expected that other small sized copepod taxa would be influenced by such predation. Yet at the population level, each taxon is likely to have a different susceptibility to control by predation, based on its life-history characteristics. For example, the *Pseudocalanus/Paracalanus/Microcalanus* group shows the strongest evidence of control by *Sagitta* (Table 4). It is known that *Pseudocalanus* at least does have a relatively low rate of population growth due to its low fecundity (Corkett and McLaren, 1978), which is limited by water temperatures rather than food supply (McLaren, 1965; Davis, 1984a). Therefore, it would be expected that this taxa would be relatively more sensitive to predation. The copepod *Acartia clausi*, on the other hand, might also be expected to be vulnerable to predation given its similar size to *Pseudocalanus*. Yet, due to its high reproductive rate (Colebrook, 1982) *A. clausi* will be relatively unaffected by predation, and thus it displays no relationship to the abundance of *Sagitta*.

Therefore, it is suggested that predation by *Sagitta* on the omnivores plays an important role in controlling the long-term dynamics of the coastal central-west North Sea zooplankton community, and as a result, this inverts the relationship which is observed between copepod abundances and the GSNW. The suggestion that predation reverses the sign of the relationship with the climatic variable (the GSNW) is also supported by the fact that the *Pseudocalanus/Paracalanus/Microcalanus* group were the taxa most strongly limited by *Sagitta*, and which also presented the strongest inverse relationship to the GSNW (Table 4). Conversely, those taxa, which were not related to *Sagitta* abundances, either due to their size, or due to high

could all be classified as small or medium sized (<2 mm length) copepods (Nicholas and Frid, 1999). Larger taxa (e.g. *Centropages* spp.) were found to show no such relationship to spring *Sagitta* abundances (Nicholas and Frid, 1999). Chaetognaths are ambush predators, sensing prey through vibrations (Feigenbaum and Maris, 1984). As such, they will prey upon whatever they encounter in the water column and emit the signals to trigger an attack

reproductive rates, were less influenced by predation and do not exhibit such a negative relationship with the GSNW.

Increased *Sagitta* abundances during the spring were related to higher spring temperatures and more northerly positions of the GSNW (Figure 8). Why *Sagitta* should show any relationship to climate is unclear. Although temperature is known to be linked to the growth rate and generation time of *Sagitta* (Oresland, 1985, 1986), food is more important to its fecundity and therefore its over-all abundance (Feigenbaum and Maris, 1984). However, Feigenbaum and Maris (1984) did note that the periods of recruitment of a new *Sagitta* cohort coincided with sharp increases in the abundances of *Pseudocalanus* nauplii (which are the main food source of young *Sagitta*; Baier and Purcell, 1997). Yet, as mature chaetognaths do not feed on small prey, and thus cannot detect their presence (Feigenbaum and Maris, 1984), it is more likely that the reproductive timing of *Sagitta* was related to the abundance of adult and larger prey items (which are consumed by mature chaetognaths; Feigenbaum and Maris, 1984).

It is proposed that the mechanism influencing the long-term control of the zooplankton system in the central-west North Sea ultimately functions through the presence of particular weather conditions during the spring. Northerly GSNW years produced suitable weather conditions to induce a spring bloom and increase the abundance of suitable prey for *Sagitta* (Figure 10a). This resulted in a new cohort of *Sagitta*, which was then able to reduce the growth rate of the small spring copepod population in proportion to their abundance, effectively inverting the signal of climate observed in the Dove zooplankton time series. Conversely, those weather patterns associated with southerly GSNW years resulted in a delayed spring bloom and a reduced fecundity of *Sagitta*. This smaller *Sagitta* population was then less able to restrict the population growth of the small copepods, resulting in a relatively higher rate of population growth (Figure 10b).

Although not considered in detail here, as high abundance years show an increased predator abundance during the summer months (Figure 6a), it appears, as originally suggested by Roff *et al.* (1988), that there are two main groups of predators present. There are those that regulate omnivore abundance through limiting the rate of population growth in the spring (i.e. *Sagitta*), and there are those other predators which follow omnivore abundances (e.g. fish larvae and *Pleurobrachia pileus* (Frid *et al.*, 1994; Nicholas and Frid, 1999)). The abundance of this latter group responds to the abundance of the omnivores (i.e. their food source), and these summer predators do not tend to have such a strong effect on omnivore abundance, as the established summer omnivore population and summer water temperatures allow a high omnivore reproductive rate (food availability permitting). In contrast, during the increase in copepod abundance during the spring, lower water temperatures and lower standing stocks mean that populations are more vulnerable to predation. Baier and
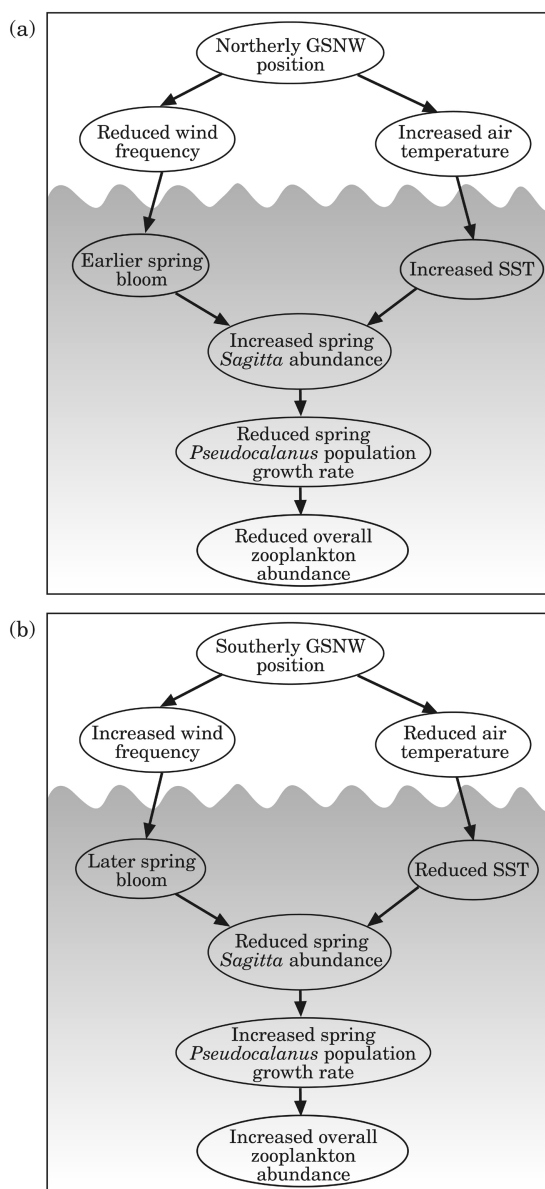

Figure 10. Conceptual model of the associations between the GSNW and the central-west North Sea copepod community through predation by *Sagitta*, during (a) northerly GSNW and (b) southerly GSNW. See text for details.

Purcell (1997) and Kehayias *et al.* (1996) have shown that chaetognath predation has the greatest effect during periods of low copepod reproduction.

In previous analysis of the Dove zooplankton series, Evans and Edwards (1993) observed a marked change in zooplankton species composition between 1979 and 1980, and suggested that the species most responsible for the observed change was *Sagitta*. Spring *Sagitta* abundances around 1980 did increase markedly at this time (Figure 8).

Other work has put forward chaetognaths as being sensitive to climatic shifts, and as indicators of changes in water temperature (Southward, 1980), and the timing of the increase in spring *Sagitta* abundances does coincide with the nadir in zooplankton abundances. As remarked by Roff *et al.* (1988), the interannual dynamics of zooplankton are highly complex, and during years when spring *Sagitta* abundances are low, other factors such as water temperature, food, or the standing stock of omnivores surviving the winter may be more important in influencing the seasonal zooplankton dynamics during that year. In addition, it is also likely that for those taxa with a relatively slow growth rate, reduction of the winter standing stock due to predation (as suggested by Roff *et al.*, 1988; Frid *et al.*, 1994; Nicholas and Frid, 1999), may also influence the productivity of these taxa the following year. However, previous studies have suggested that despite *Sagitta* being the dominant predator observed during the winter and spring period, other predators (e.g. *Themisto* spp.; fish larvae) are more voracious and may have a higher impact on copepod stocks (Frid *et al.*, 1994; Nicholas and Frid, 1999).

Sullivan and Meise (1996) noted that, on Georges Bank, *Sagitta* preferred the shallower well-mixed areas of the Bank, and as such, predation by *Sagitta* may be confined to shallower, well-mixed or coastal areas of the North Sea. Although the results presented in this study have focussed on the data collected from a single sampling station (i.e. the Dove series), as the relative interannual fluctuations in CPR data over the central-west North Sea region show similar long-term trends to the Dove series (Clark and Frid, 2001), the mechanism proposed here could operate over a wide area of the central North Sea. However, further analysis of CPR data is required to determine in which areas of the North Sea, chaetognaths might have the potential to influence copepod populations.

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