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The 1989 German Bight invasion of *Muggiaea atlantica*

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In July 1989 a population of *Muggiaea atlantica* invaded the German Bight where it reached abundances of up to 500 colonies m^{-3}, becoming a key population of great impact on the pelagic ecosystem. Predation on small copepods caused a lowering in the grazing pressure on phytoplankton, enabling the growth of the algal populations and a reduction of phosphates.

Key words: Siphonophore, invasion, predator control, top-down control, Helgoland Roads, German Bight, North Sea, systems ecology.

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Introduction

The introduction of new species by man often has disasterous consequences on the existing ecosystem, and it is becoming increasingly problematic to justify such introductions on an experimental basis. Indeed, in many countries there is a political control on bringing in new species to either open or tightly controlled habitats. In 1989 the immigration, or invasion, of *Muggiaea atlantica* Cunningham, 1892, into the German Bight provided an opportunity to investigate the natural introduction of a new species, starting at a time when the annual synoptic surveys were in progress by the Biologische Anstalt Helgoland (BAH). It was thus possible to follow closely the progress of the invasion and to use the existing BAH time series of plankton and hydrographic observations to compare the progress of events with what happened in earlier years.

Material and methods

The Biologische Anstalt Helgoland has been documenting the population processes in the German Bight since 1892. The only offshore marine station of the North Sea has employed at least one zooplanktologist since that time, with the exception of the war years. Although no permanent quantitative sampling series was produced, the qualitative and semi-quantitative reports give evidence for at least the presence or absence of taxonomic groups. Since 1974 sampling was converted into a quantitative time series of meso- and macrozooplankton samples being taken every second work day in the Helgoland Roads (positioned about 50 km off the coast between the two islands of Helgoland at 54°11′3″N, 7°54′0″E). Passing between the islands from a depth of up to 50 m to the south, or 30 m to the north, the tidal currents mix the water in the shallow, 6-m-deep passage between the islands. The mean residual current passes along the German Bight in a counter-clockwise direction. The river plumes of the Weser and Elbe reach as far as Helgoland. Thus, the samples taken may represent waters of coastal, estuarine, or stratified central North Sea water origin. Since 1980 an annual investigation of the biocoenotic (Möbius, 1877) development takes place by a quasisynoptic research cruise that is carried out every second week in July, sampling 75 stations in the German Bight. At this time primary carnivores (mainly *Pleurobrachia pileus*) are being succeeded by secondary carnivores (mainly *Beroe gracilis*) (Greve and Reiners, 1988). The sampling programme gives a signal of the annual ecosystem performance earlier in the year.

The macrozooplankton sampling was carried out with a 500-µm-mesh size CalCOFI net and mesozooplankton by a 150-µm-mesh Hydrobios plankton net both using oblique hauls and sampling approximately 100 and 0.6 m^3 of water, respectively. Each net was equipped with a current meter. Data on phytoplankton and phosphate from a time series starting in 1962 were provided by Hickel (pers. comm.). MABIS computer graphics (Greve and Reiners, 1989) were used for the visualization of the data.

Results

During a cruise from 10–14 July 1989 a population of *Muggiaea atlantica* was meaured in the German Bight which reached abundances of up to 91 colonies m^{-3}

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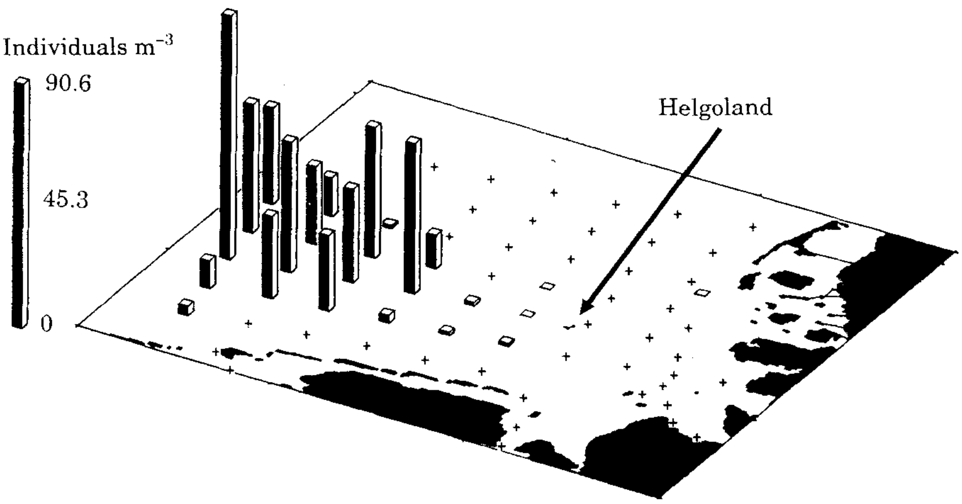

Figure 1. The distribution of *Muggiaea atlantica* at its detection in the German Bight 10–14 July 1989 (abundance: colonies m^{-3}); + shows none caught.

(Fig. 1). The maximum abundance was measured at the westerly deep-water stations, the number of colonies decreasing to the east and south. The siphonophore colonies were accompanied by eudoxids, indicating reproductive activity.

At the permanent plankton station "Helgoland Roads" the density of *Muggiaea atlantica* was monitored (Fig. 2). The abundance of *M. atlantica* reached levels of up to 500 siphonophore colonies m^{-3} (53 eudoxids m^{-3}) in August. The numbers then declined and since November 1989 this species was found in the plankton samples only at very low abundances.

The annual population dynamics pattern of copepods varied from the long-term mean in 1989 (Fig. 3). The values for the copepod abundances at the time of the maximum impact of *M. atlantica* were just outside the standard deviation of the 14 years measured prior to 1989.

At the time of the depressed copepod abundance the phytoplankton differed from the long-term mean, indicating the effect of a reduced grazing control (Fig. 4). The deviation from the mean was even more pronounced than in the copepods. In six out of the last eight measurements the phytoplankton abundance in 1989 lay outside the long-term (1962–1988) standard deviation. The production of phytoplankton requires nutrients. Of the last eight 1989 phosphate values, four lay outside the standard deviation of the 1962–1988 mean (Fig. 5). The comparison of the confidence intervals of medians indicates significant differences of each of the pairs ($p \leq 0.05$).

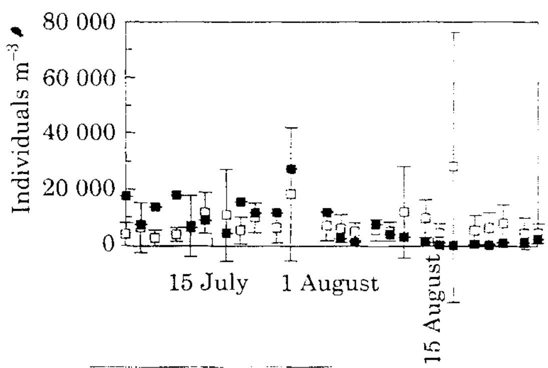

Figure 3. Small calanoid copepod abundance (ind. m^{-3}) 3 July to 30 August 1989. 1989 measurements (black); 1974–1988 mean (white), and standard deviation.

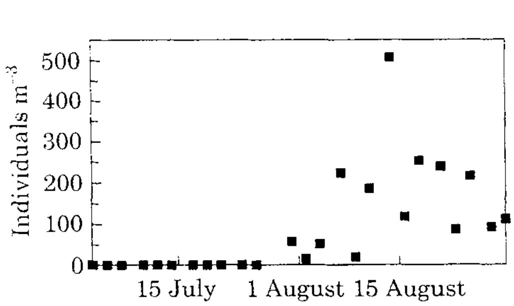

Figure 2. Abundance dynamics (colonies m^{-3}) of *Muggiaea atlantica* in the German Bight, measured at the station "Helgoland Roads" from 3 July to 30 August 1989.

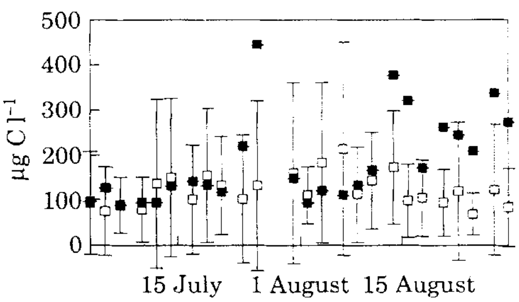

Figure 4. Phytoplankton abundance (µg C l^{-1}) 3 July to 30 August 1989. 1989 measurements (black); 1962–1988 mean (white), and standard deviations.

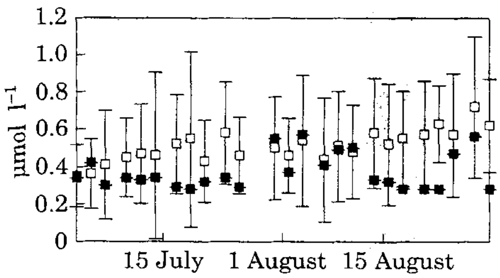

Figure 5. Phosphate concentration (µmol l^{-1}) 3 July to 30 August 1989. 1989 measurements (black); 1962–1988 mean (white), and standard deviation.

Discussion

Totton and Fraser (1955) did not count siphonophores as regular members of the North Sea fauna, but *M. atlantica* is a part of the Lusitanian plankton in the western part of the English Channel (Russell, 1934). This makes the 1989 siphonophore invasion an extraordinary event, which has implications, first, for the plankton dynamics of the German Bight in 1989, second, for the understanding of the regulatory processes functioning within the ecosystem, and, third, for the constancy of biocoenotic regimes in the southern North Sea, especially with respect to possible shifts in the fauna of the North Sea with the anticipated climatic changes.

1. Modifications in the plankton process pattern of the German Bight. From Purcell's (1982) investigations it is known that *M. atlantica* is a voracious predator on copepods; from her measurements a population of 100 colonies m^{-3} would require up to 2000 food items daily. As the mean copepod abundance (mainly *Pseudocalanus elongatus, Paracalanus minutus, Acartia clausi, Temora longicornis, Centropages typicus,* and *C. hamatus*) at the Helgoland Roads stations is given as 8000 ind. m^{-3} (Greve and Reiners, 1988), the demand of a population of up to 500 colonies of the siphonophore equals the available quantity of copepods. The resulting reduction in copepod abundance in 1989 confirms Purcell's results.
2. Improvements in the understanding of the regulatory processes. The "*M. atlantica* event" shows that the pelagic ecosystem in summer is modified by an excess predator control beyond that of chaetognaths and other groups that normally reduce the number of grazers to a lesser degree. By this disturbance of the equilibrium of the ecosystem a phytoplankton bloom occurs in the autumn since nutrient and light conditions are not limiting. The natural experiment of the invasion of a new predator species thus renders evidence for the "top-down" control of pelagic ecosystems, so supplementing the primary production resource limitations which are equally important. In ecosystems with ample nutrients autumn phytoplankton blooms may regularly depend on this trophic control system.
3. Expected modifications of the biocoenotic constancy. *M. atlantica* entered the German Bight at lower abundances than measured later at Helgoland, the growth conditions favouring the siphonophore. Thus, *M. atlantica* could live in the German Bight biocoenosis, but it did not survive the winter conditions or return in the years to follow. The reasons for its appearance and disappearance are not known but the ecological potential of the population must be further acknowledged, especially in the light of the predicted climatic changes (Dickinson, 1986). We have to face the possibility that *M. atlantica* can replace *P. pileus* as the dominant carnivore. Then, *Beroe gracilis* could no longer play its role as the controlling secondary carnivore and so support the biocoenotic equilibrium characteristic of the German Bight. Summer phytoplankton blooms and possible deep-water oxygen depletions, as experienced in the area earlier (Gerlach, 1990), could be the consequence.

The other populations of the pelagic ecosystem of the German Bight, which have also been sampled and counted during this period, showed no sign of irregular population processes. In *Sagitta setosa* and *S. elegans*, which are summer and fall populations, the low abundance in 1989 may well be related to the siphonophores as predators or competitors on the same food items.

The reasons for the *M. atlantica* invasion are not known. The salinity, usually indicating Atlantic water from the Channel or north of Scotland, did not increase significantly. Later, in 1989, Lindley *et al.* (1990) reported an extraordinary population of *Doliolum nationalis*, which was measured in CPR samples from October to December in central and south-easterly North Sea areas. This report includes personal observations of *D. nationalis* in the German Bight. The assumption of an increased inflow of Channel or Atlantic water is supported by the documented *Muggiaea atlantica* invasion of the German Bight. As no further observations from stations on the east coast of Great Britain have been reported, the origin of the population from the English Channel seems more plausible.

The ecologically significant appearance of *M. atlantica* in 1989 is reinforced by further records of the Helgoland Roads plankton. In 1987 the siphonophore was counted in eight samples at a maximum density of 0.37 colonies m^{-3}; 1988, four samples, 0.86 colonies m^{-3}; 1990, 12 samples, 0.32 colonies m^{-3}; 1991, one sample, 0.01 colonies m^{-3}; 1992, one sample, 0.01 colonies m^{-3}. The 1989 invasion seems to have been a unique event, with the possibility of future repetitions.

Acknowledgements

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