THÜNEN

GELATINOUS ZOOPLANKTON SYSTEMS ECOLOGY
IN GERMAN BIGHT

by

Wulf Greve, Frank Reiners and Jutta Willführ-Nast
Biologische Anstalt Helgoland, Notkestraße 31, D-22607 Hamburg, Germany

Abstract

German Bight (North Sea) is one of the most productive marine areas. The annual cycle supports the development of key populations of carnivores and secondary carnivores. Most of these are gelatinous zooplankton. A continuous plankton investigation since 1974 enables the determination of the means and variances of these populations, the abundance and the timing of population processes and their functional relationship to prey and predator populations within the system. The abundance of predators at any trophic level limits the development of the prey populations. The availability of prey cannot be accounted for in the limitation of growth of the predators at any trophic level. A model was derived for the annual shift in the localization of the key control parameter from the abiotic parameters to primary producers, herbivores, carnivores and secondary carnivores, including the chitinous populations but excluding vertebrates for which comparable information was not available.

Introduction

The success of a population depends on the fit of the ecological niche with the actual environment experienced by the developmental stages during their reproduction and growth period.

(1) $P_{t+1} = P_t * N / N_{opt}$

(The development of a population [P] is a function of the fit of the current conditions [N] with the optimal ecological niche requirements [N_{opt}]).

In plants Justus von Liebig (1840) realized the "law of the minimum", the fact that growth is controlled by the least fit of the niche, though this latter phrase was not defined at that time. Liebig thus helped to improve the growth conditions in fields which were otherwise grazer-, and pest-controlled. His detections on nutrient kinetics further influenced the early planktologists who strongly favoured phytoplankton and nutrients as measures of ecosystem performance.

Findings such as the Lotka (1925) and Volterra (1926) equations on the interaction of prey and predator, the definition of the ecological niche theorem of Elton (1927) in the twenties of this century did not influence biological oceanography too much, though the facts (e.g. Hardy, 1924) were basically known. The attempt of the "food chain research group", (Strickland, 1965) to extend our vision at least into a functional view of the marine world created a linear scale, according to which comparative measurements could be made. With the improvement of network analysis in marine ecology (Wulff *et al.*, 1989; Cohen *et al.*, 1990), the marine ecosystem theorem regained its multi-dimensionality and brought back the awareness of the functional importance of the knots of the "food web", depending on the specific populations. Accordingly, the application of Liebig's law on any dimension of the ecological niche of all populations is required. That is: "The minimal chance to avoid a predator is equally important as the minimal availability of nutrients". The acceptance of this theorem leads to changes in the investigative strategies. Instead of the aggregation of population data into "zooplankton biomass" to be measured on the basis of the "replacement-volume" or calculated "copepod carbon", the specific population abundance, preferentially in developmental stages, will deliver the best information for analytical marine plankton process investigations which have the potential to lead to predictive models. When Greve realized that twenty years ago (Greve, 1971), measurements on the meso- and makrozooplankton populations were started at the position "Helgoland Roads" in the south east of the North Sea (Figure 1) which have hence been continued.
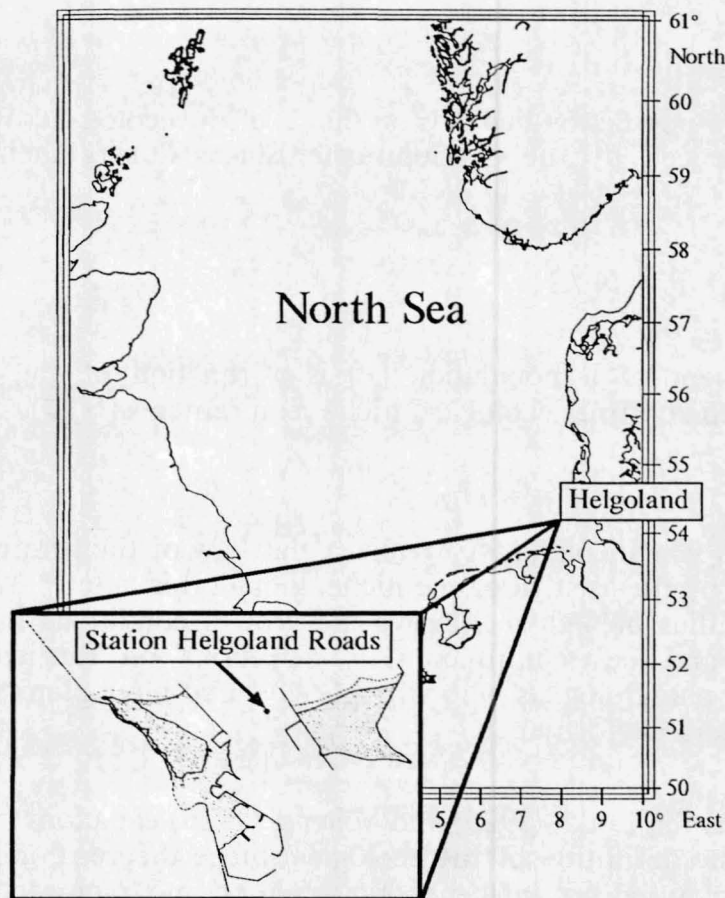
Figure 1: Location of the Station "Helgoland Roads" in the German Bight, North Sea

Materials and methods

These samples which are collected every second workday (Greve and Reiners, 1988) in accordance with a daily series on the physical data, nutrients and phytoplankton that started in 1962, provide the material for this investigation. From these series data on some key plankton parameters at the time of the building up of the holoplanktonic trophic layers have been selected.

In reality this information is imbedded into a rich biocoenotic information material, composed of nearly as many meroplanktonic populations, including carnivorous hydro- and scyphomedusae, decapod-larvae, and fish larvae as well as polychaete-, echinoderm-, balanoid- and other larvae as well as the full spectrum of holoplanktonic species including e.g. larvaceans, chaetognaths, and others, which play a role in the ecosystem regulation and which had to be neglected in this study, concentrating on two ctenophore-species and their prey. Within these limitations it was investigated which part of the ecological niche was most limiting, the lack of food, or the presence of predators.

The first 16-year period (1975 to 1990) was selected to visualize the three-month periods within which the replacement of the food-population by the predator population usually occurs. The three-month period shifts with the trophic level from April to June in the phytoplankton-copepod system, from May to July in the copepod-*Pleurobrachia*

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system, from June to August in the *Pleurobrachia-Beroe* system. This choice was applicable in the majority of years.

The exceptions are discussed.The measured values were converted into graphs, using a SPLINE function (Späth, 1973).

Three displays were then chosen from the MABIS-menu (Greve and Reiners, 1989):
- a qualitative representation dimensioning the figures as to the maximum values in each figure,
- a quantitative representation scaled after the maximum values measured,
- a phase-plane graph, defining the direct qualitative interrelationships of the pairs of interacting populations during the three-month period.


Results

Starting with the populations whose trophic relationship is best known, *Beroe gracilis* feeds exclusively on *Pleurobrachia pileus* in German Bight; we see that the expected sequence of a prey-predator relationship is to be seen in almost every year (Figures 2, 3, 4). The exception in 1989 is part of the foreward shift of the population development of *Pleurobrachia pileus* in the last years, following very mild winters. The abundances in these years did not reach the levels measured earlier, as seen. The typical prey-predator cycle is seen in 1980, only, while 1984 and 1985 visualize the shift of biomass of the predator to the prey.

1976 decouples the population processes, permitting predator growth in the absence of prey, visualizing the fact that the measurements at Helgoland Roads indicate regional processes which may have their interaction zones in remote areas, becoming evident in the measurements as signals only (see Greve and Reiners, 1988).

Figures 5, 6, 7 equally represent the populations of small calanoid copepods (*Pseudocalanus, Paracalanus, Acartia, Temora, Centropages* etc.) and one of their major predators *Pleurobrachia pileus*. Again, the qualitative population dynamics supports the prey-predator relationship in 12 out of 16 years. The exceptions, 1977 and the years at the end of the last decade mostly coincide with anomalies in the *Pleurobrachia-Beroe* relationships. Other years, 1984, 1986, are in accordance with the prey-predator system requirements (decrease or reduced growth of prey at high abundances of predators).

The phase plane displays proper prey-predator cycles in the years 1975, 1978, 1980, 1981, 1982, 1983, 1984, 1985, and 1987. Given the argument of a forward shift in the late eighties and impacts of remote population proscesses to be measured at "Helgoland Roads" as indicator signals only, the copepod-*Pleurobrachia* relationship is even more pronounced than the *Pleurobrachia-Beroe* system.

The phytoplankton-copepod system is not part of the pelagic evertebrate story. But as the data were available from the BAH (Hickel, personal communication), the study was extended this level further down.

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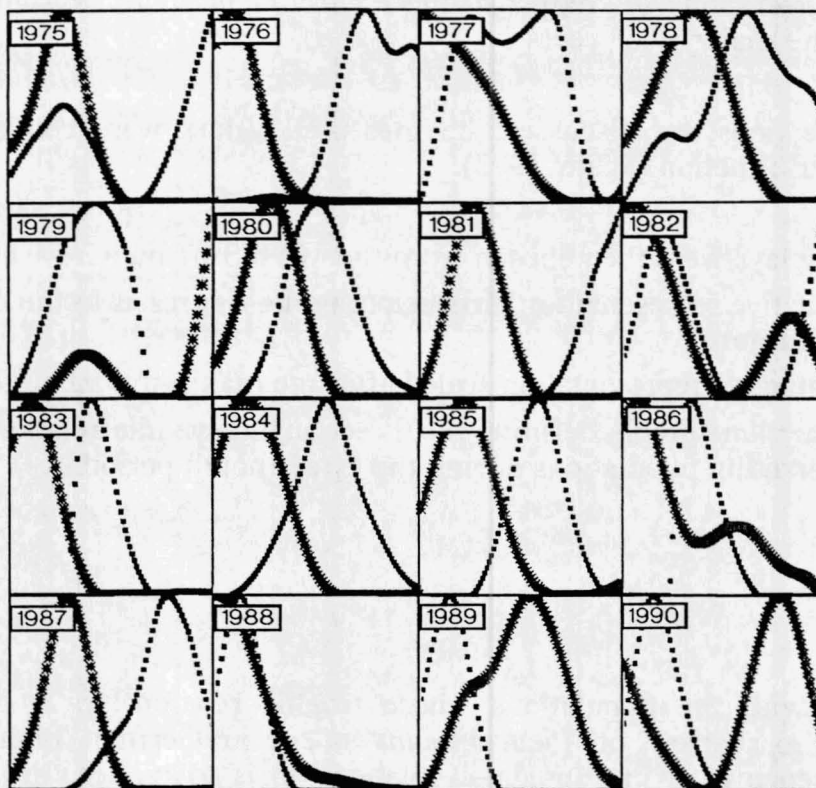
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Figure 2
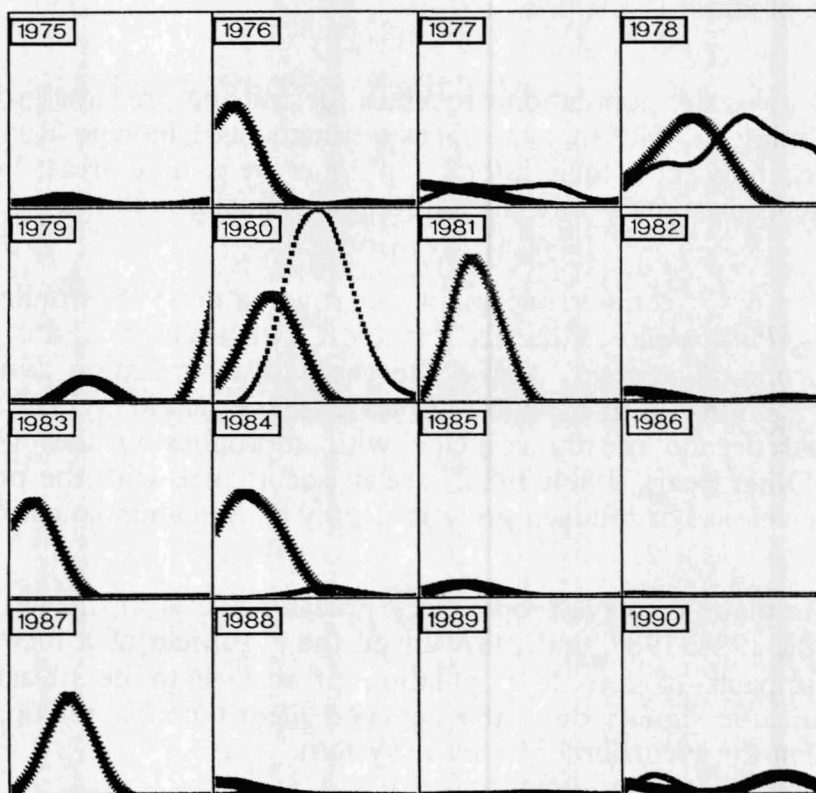
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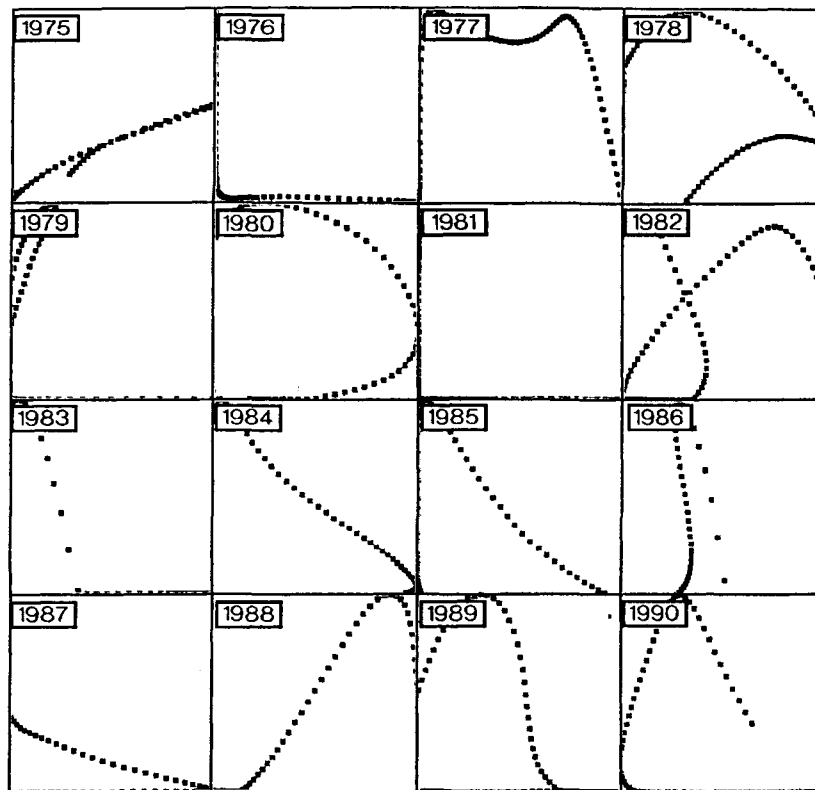
Figure 3

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Figure 4

Figures 2, 3, and 4: The population dynamics of *Pleurobrachia pileus* (*thick line*) and *Beroe gracilis* (thin line) in the months June, July and August of the years 1975 to 1990 at Helgoland Roads (abundance maxima, Ind. * m^{-3}: 69.3 *Pleurobrachia pileus*, 3.1 *Beroe gracilis*, 4: phase plane representation, x: *Pleurobrachia pileus*, y: *Beroe gracilis* [see text])
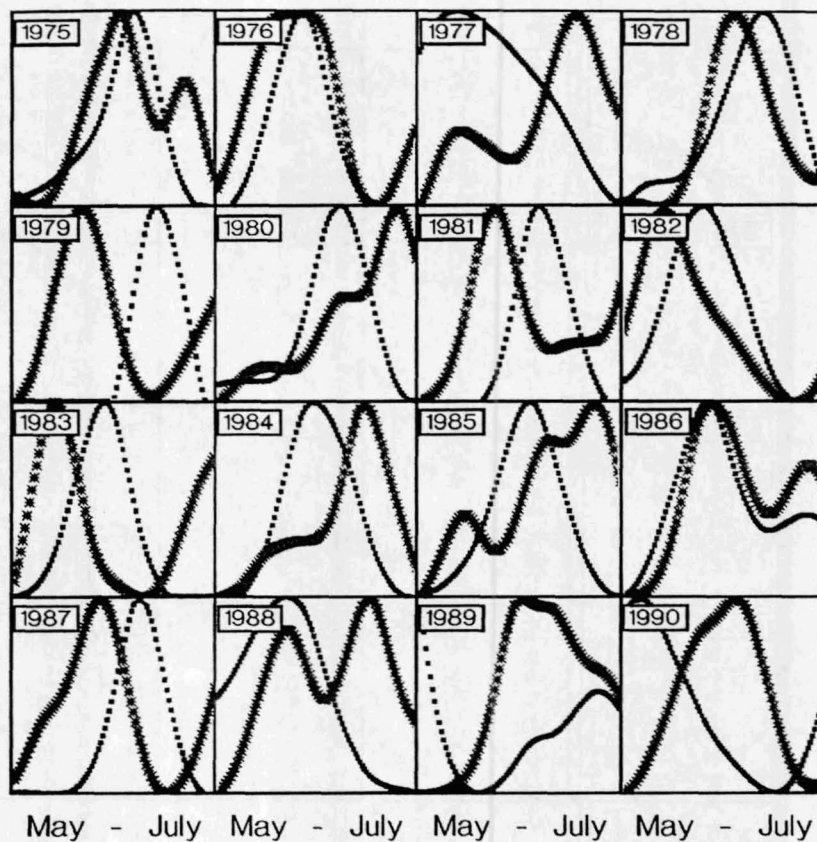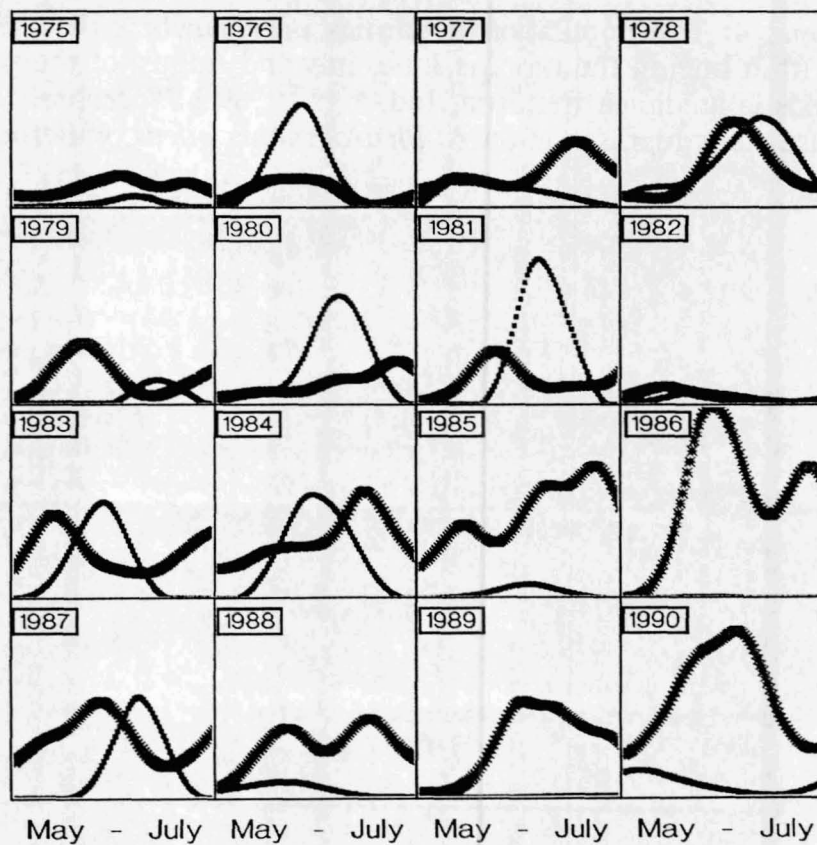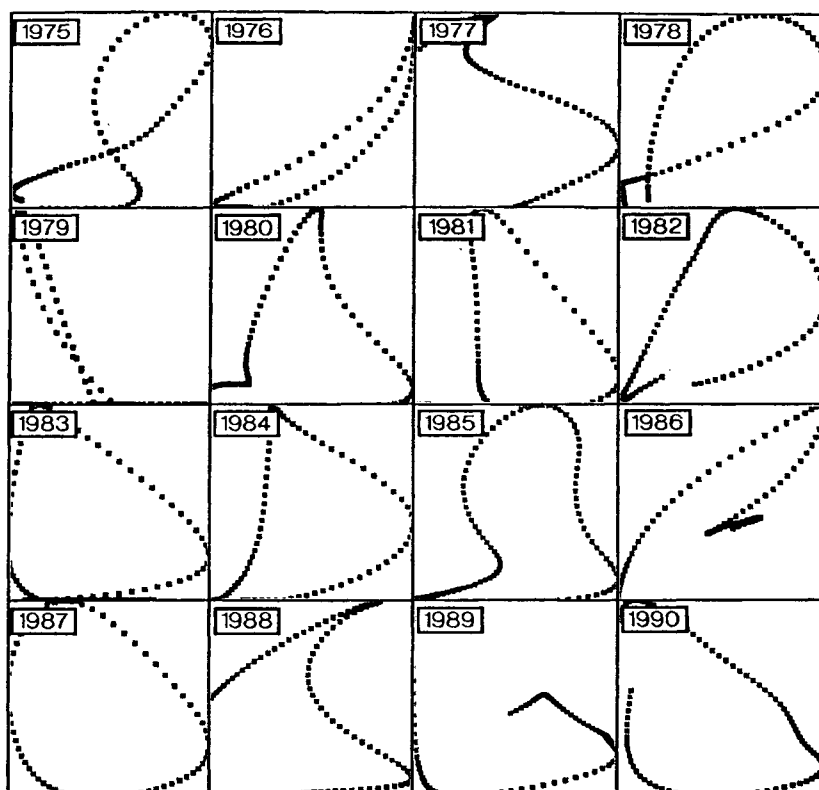
Figure 5

Figure 6

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Figure 7

Figures 5, 6, and 7: The population dynamics of small calanoid copepods (thick line) and *Pleurobrachia pileus* (thin line) in the months May, June and July of the years 1975 to 1990 at Helgoland Roads (abundance maxima, Ind. * m^{-3}: 44.9 to 37355 small calanoid copepods, 69.3 *Pleurobrachia pileus*, 7: phase plane representation, x: copepods, y: *Pleurobrachia pileus* [see text])
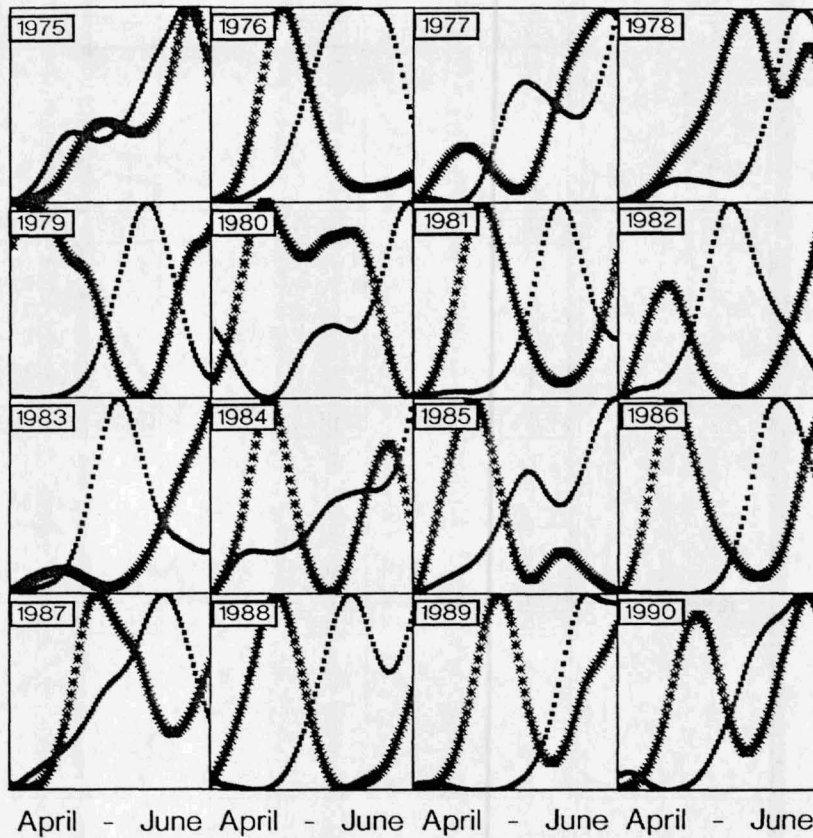
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Figure 8
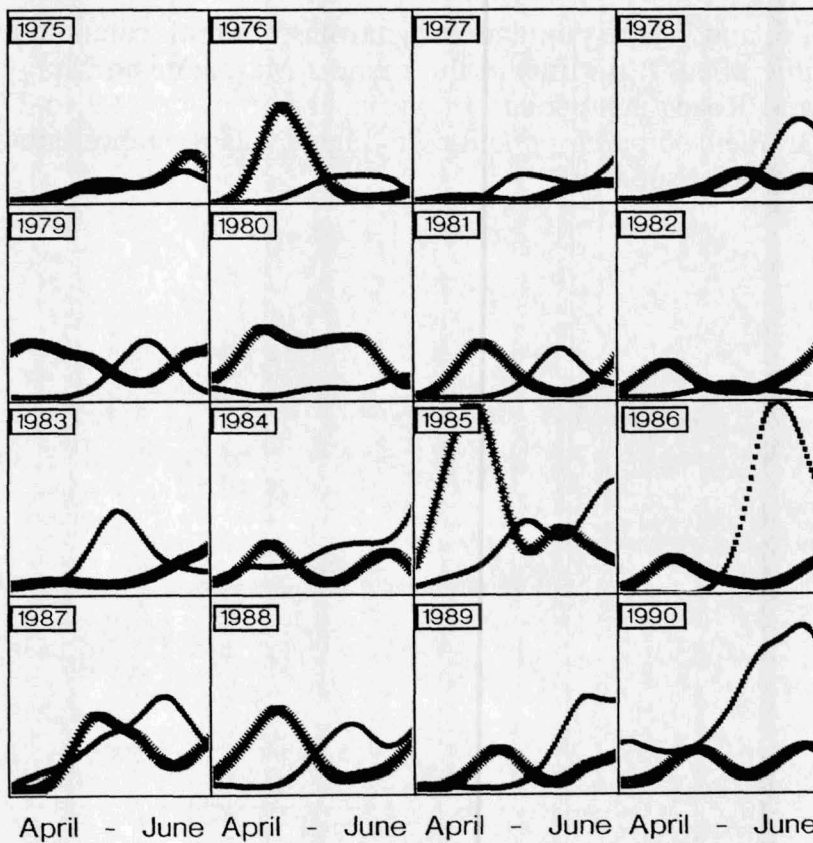

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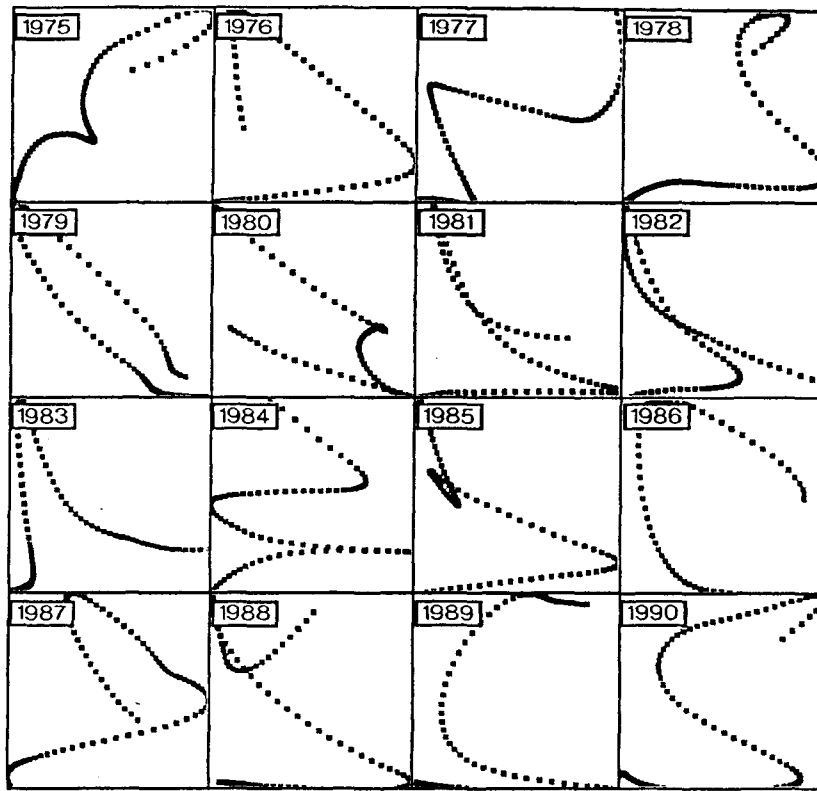
Figure 9

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Figure 10

Figures 8, 9, and 10: The population dynamics of phytoplankton (thick line) and small calanoid copepods (thin line) in the months April, May and June of the years 1975 to 1990 at Helgoland Roads (abundance maxima, $\mu g\ C * L^{-1}$: 0.9 to 488.2 phytoplankton, Ind. $* m^{-3}$: 44.9 to 37355 small calanoid copepods, 10: phase plane representation, x: phytoplankton, y: small calanoid copepods [see text])

Again, we see some correspondence of high grazer values with the reduction or growth limitation of food (Figures 8, 9, 10). This can be seen in the years 1976, 1977, 1978, 1979, 1980, 1981, 1982, 1983, 1984, 1985, 1986, 1987, 1988, 1989, and 1990, in 15 out of 16 cases. The phase portrait regularly displays the x to y transformation, but also deviations from this basic pattern.

Discussion

All pairs of prey and predator investigated here are obviously linked in their population processes. The phase - diagram clearly displays the change of the relationships from a prey dominance to a predator dominance.

According to this rule, each time the predator reduces the prey, which on the other hand provides a trophic basis for successful growth. The general statement of Huntley and Lopez (1992) that copepod populations are predator-controlled and not food-limited, cannot be decided on the basis of these measurements, yet, the predator control theory is confirmed.

The marine pelagic ecosystem is still regarded by some scientists as a "food chain" of phytoplankton, copepods, and fish. This model has been replaced by many scientists [e.g. Greve (1981) and Fedra (1981)] with a more realistic concept, which is confirmed in this investigation to be of general validity.

In the German Bight, nutrient limitation is not seen at any time of the year (Radach and Bohle-Carbonell, 1990). Therefore, the annual growth limitation (according to Liebig's law) must be the light. This limitation ends with the beginning of spring. From then on, phytoplankton seems to be grazing-controlled. The level of phytoplankton never reaches minima for a long period, so copepods should be able to survive unless they are predated upon by predators, in spring this seems to be *Pleurobrachia pileus*. The tentaculate ctenophore itself is predator-controlled by *Beroe gracilis*.

This control pattern may be aggregated in form of a model (Figure 11), assigning a certain time of the year to each prime control function.

This model indicates the change in the priority measurements for documenting the parameters which successively form the key control populations.

This is basically known since the beginning of this century (see Hardy, 1924) and has been confirmed many times. Yet, the resilience of the "food chain myth" is admirable (especially as our scientific referee system is assumed to be functional). For example, Fransz *et al.* (1991) in a review on the North Sea zooplankton research, omit any reference to the trophic pattern of the spring and summer plankton.
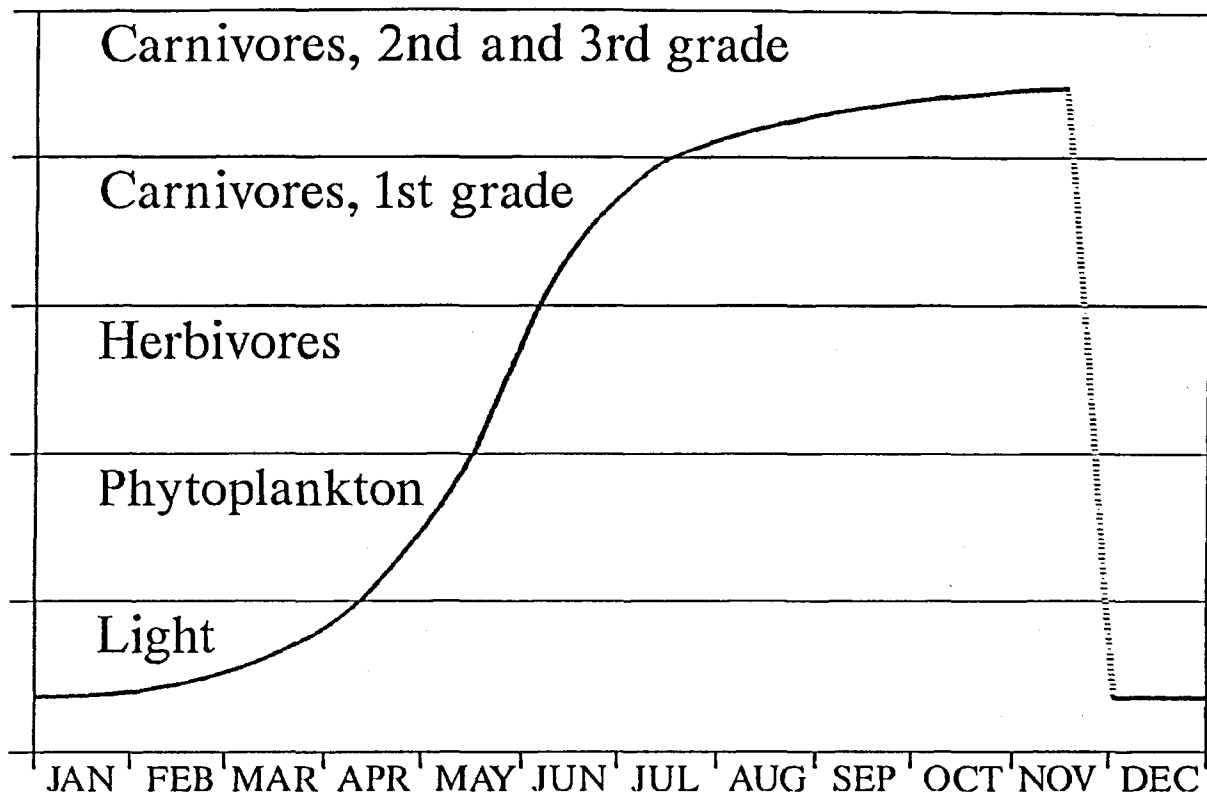
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Figure 11: Model of the annual shift of the key control parameter in the
German Bight pelagic ecosystem (for details, see text)

Kuhn (1967) characterizes the scientific revolution on the basis of the paradigmatic changes occurring. So we will have to lean back and wait for the paradigmatic change to happen as no further evidence is needed for the assumption that the marine pelagic ecosystem is as much production- and predator-controlled as any other ecosystem and that evertebrate carnivores which are among the most potent predators have to be measured in any study trying to budget the ecosystem processes.

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