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## **Invertebrate predator control in a coastal marine ecosystem: the significance of *Beroe gracilis* (Ctenophora)**

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### **Abstract**

The early summer dynamics of major zooplankton populations in Helgoland Bight are discussed on the basis of the GILLBRICHT extension of LIEBIG's law of the minimum. On the basis of monofactorial control of population dynamics, copepod decline in June is caused by predation of *Pleurobrachia pileus*, phytoplankton never being at levels which would starve copepods. Copepod recovery is correlated with the control of *Pleurobrachia pileus* by *Beroe gracilis*, an exclusive predator on this tentaculate ctenophore. By controlling copepods before they can seriously deteriorate the phytoplankton standing stock, high phytoplankton summer levels are possible which characterize the rich ecosystem of Helgoland Bight.

### **Introduction**

"The total environment influences the development of a species or population, but normally one factor only influences *de facto* the system at any moment." (GILLBRICHT 1969). GILLBRICHT's extension of LIEBIG's "law of the minimum" permits a more simple view of the ecosystem as a whole than multiple process oriented ecosystem models. It is thus possible to select factors accordingly, trying to focus on the momentarily dominant system control mechanisms for ongoing research. This approach towards the identification of the more important system components is supported by problems due to anthropogenic stress on the system as identified during the last EMBS on Helgoland (KINNE 1980).

### **System description**

Information on Helgoland Bight has been provided in a series of recent publications. LUCHT and GILLBRICHT (1978) described a general pattern of the nutrient dynamics. HAGMEIER (1978) provided long-term data on phytoplankton dynamics and nutrients. LÜNING (1979) in his investigations on benthic algae provided light measurements which combine information on light and turbidity. Growth conditions in the sea are better characterized by available light than by surface illumination values. RACHOR (1980) and GREVE and REINERS (1980) provided information on benthos and zooplankton.

On the basis of these publications a scheme of some basic parameter dynamics in Helgoland Bight has been established (Figure 1).

The annual dynamics of growth conditions for phytoplankton are characterized by low temperatures until late April and a constant increase of available energy for primary production until July. Nutrients do not limit growth during the early summer period. This conforms with LÜNING's data on *Laminaria* summer growth (LÜNING 1979).

Phytoplankton accordingly increases in biomass from March to August. A qualitative change from diatoms to flagellates should be mentioned in this respect. Of course, the data used here are mean dynamics over 12 years, and statistic treatment hides the decrease in biomass correlated with the May propagation of calanoid copepods. Yet, the level of phytoplankton does not drop below 20 to 30 microgram carbon, an order of magnitude above starvation level to copepods. In 1979, the year when zooplankton data are available (Fig. 2), the minimum values measured at Helgoland Roads (MANGELSDORF and TREUTNER 1980) were at a level of 40 microgram carbon  $\cdot$  l $^{-1}$ . This value is probably below the mean as low values are normally found at this location; HAGMEIER (1978) showed an increase in phytoplankton biomass with decreasing salinity.

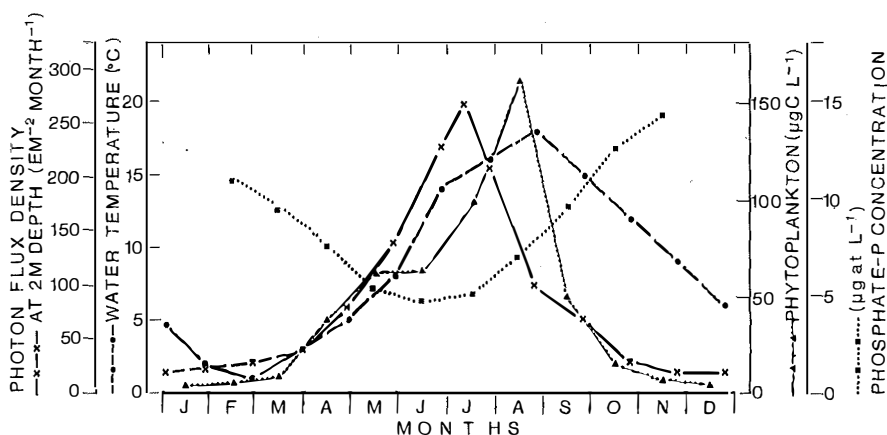


Figure 1

Annual dynamics of environmental parameters at Helgoland Roads. Light and temperature after LÜNING (1979), phosphate-P after LUCHT and GILLBRICHT (1978), phytoplankton-C after HAGMEIER (1978). Data represent different years or multiannual means.

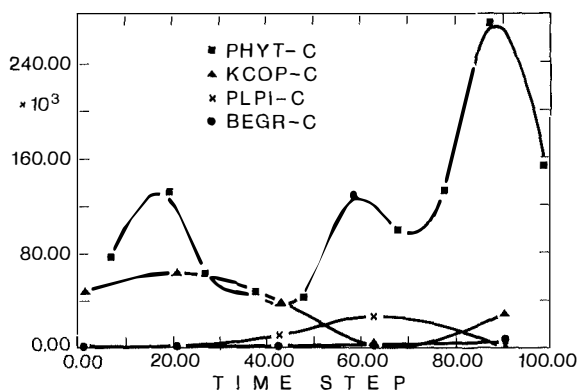


Figure 2

Early summer dynamics of plankton populations in Helgoland Bight 1979. PHYT-C: phytoplankton carbon at Helgoland Roads after MANGELSDORF and TREUTNER (1980), KCOP-C: Small copepod carbon mean of 30 stations in Helgoland Bight after GREVE and REINERS (1980), PLPI-C: *Pleurobrachia pileus* carbon and BEGR-C: *Beroe gracilis* carbon (same origin as copepod carbon)

The number of copepods decreases during a period characterized by phytoplankton carbon values, which would provide a trophic basis to herbivorous organisms. If according to GILLBRICHT's extension of LIEBIG's law one factor only influences the copepod population *de facto* at this period, the mortality due to predatorial impact on the copepod population must be taken into account as another possibility of population control.

*Pleurobrachia pileus* is well known as a voracious predator on copepods (FRASER 1970, GREVE 1972). The increase in the population of *P. pileus* correlates with the decrease in the population of copepods. The decrease in the number of *P. pileus* corresponds to a recovery of the population of copepods.

An explanation of the decrease in the population of *P. pileus* again requires information on the control mechanisms governing this process. *P. pileus* is known to have a high starvation resistance (up to three months have been measured, GREVE 1972), and the level of possible prey to *P. pileus* was only close to starvation level. Biochemical proofs of starvation could not be measured *in situ* (HOEGER, personal communication).

Therefore if "one factor only influences *de facto*" the population it may well be *Beroe gracilis*, which controls the tentaculate ctenophore in Helgoland Bight. The population decline of *P. pileus* is correlated in the form of a prey predator system with the population incline of *B. gracilis*.

The information on the system as described in Figures 1 and 2 is complemented by further available information. The dynamics of ctenophores in Helgoland Bight as measured by GREVE and KINNE (1971) have shown a strong tendency for ctenophores to gather close to the sea bottom; therefore the pelagic benthic interactions in a system with high biomass levels of macrobenthos must be considered (RACHOR 1980). This fact, the uncertainty as to the level of copepods predated upon by fish, the insufficiency of food as assumed by MARTENS 1981, and the possible effects of parasites and diseases make it impossible to be sure that thinking on the lines of GILLBRICHT's proposed law has led to causal analysis, yet it has helped to focus upon a working hypothesis which can be falsified by further investigations.

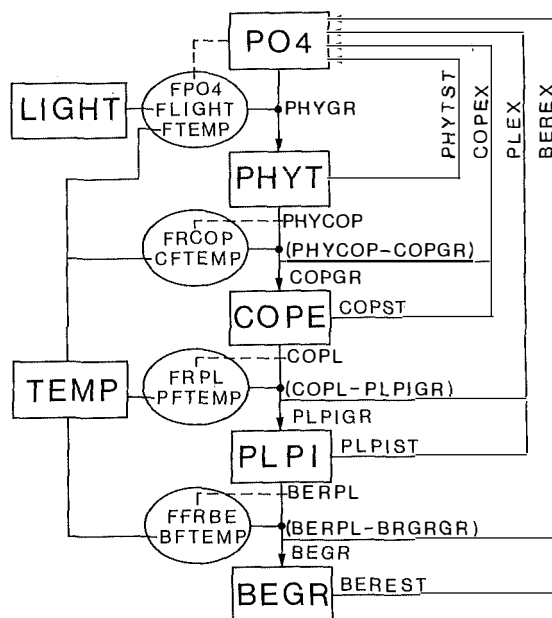
One test is the correlation of processes assumed to be linked. The correlation coefficient of copepods and *P. pileus* is  $-0.97$ ; *P. pileus* and *B. gracilis* have a correlation coefficient of only  $-0.77$  though it is known that *P. pileus* is the only food of *B. gracilis*. The correlation of the decline in phytoplankton in May/June at the time of maximum copepod abundance was not calculated because of the different origin of the measurements.

Another test is the comparison of the orders of magnitude of the trophic levels to be dealt with. Again, phytoplankton is beyond comparison, but copepods ( $62 \mu\text{g Carbon} \cdot \text{l}^{-1}$ ), *P. pileus* ( $27 \mu\text{g Carbon} \cdot \text{l}^{-1}$ ) and *B. gracilis* ( $7 \mu\text{g Carbon} \cdot \text{l}^{-1}$ ) decrease in their maxima inversely to their trophic levels, transferring a high proportion of the biomass to each higher level and thereby displaying a dominant relationship between populations.

A mathematical model of the system synthesized from information such as feeding, utilization and growth rates may further validate the logic consistency of a hypothesis. Such a model was developed.

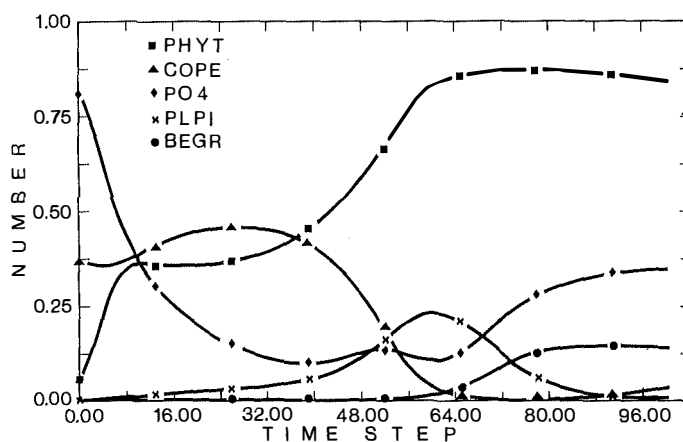
The simulation model (Figure 3) consists of two driving variables (light, temperature), five state variables (phosphate-phosphorus, phytoplankton-phosphorus, copepod-phosphorus, *P. pileus*-phosphorus, and *B. gracilis*-phosphorus) and 14 non-linear and several linear functional relationships of the variables. State variables and non-linear

rates were programmed using SLP-functions, providing linear relationships between set data points. The program was written in FORTRAN using the BAHSIM simulation control package (KARTHEUS and GREVE, in prep.).



**Figure 3**

Flow chart of simulation model. Driving variables: LIGHT=light and TEMP=temperature taken from Figure 1. State variables: PO4 = Phosphate-P, PHYT = phytoplankton-P, COPE = copepod-P, PLPI = *Pleurobrachia pileus*-P, BEGR = *Beroe gracilis*-P. Each calculation considers the nutritional status, the temperature dependency and the trophic conditions in determining growth, excretion and mortality due to starvation (see text)



**Figure 4**

Simulated dynamics of main status variables. Expressed as relative abundance. PHYT: phytoplankton-P, COPE: copepod-P, PLPI: *Pleurobrachia pileus*-P, BEGR = *Beroe gracilis*-P. Initial conditions according to measured values see figure 1,2

Detailing of all simulation solutions to describe the full behavior of the simulation model was not possible. One example (Figure 4) shows that the dynamics measured *in situ* are in the range of the possible solutions. Therefore the relationships incorporated into the simulation model may suffice to interpret the *in situ* dynamics.

### Discussion

On the basis of this evidence supporting the hypothesis that the dynamics of copepods in Helgoland Bight are predator controlled by *P.pileus*, which again is controlled by *B. gracilis* during the period under consideration, the systems significance of the ctenophore populations must be accepted.

We may then ask: what are the systems impacts of ctenophore control? *P.pileus* feeds on copepods at the time of increasing predation pressure of copepods on phytoplankton, thereby reestablishing primary production before long-time low phytoplankton levels could be caused by copepod populations. The same type of control has to be assumed for *P.pileus* which could establish long-lasting control of copepods during starvation. *Beroe gracilis* prevents this. This highly specialized predator has a high starvation resistance and maintains control beyond the period investigated. FRASER (1970) describes a coastal ecosystem with *Pleurobrachia pileus* but without *Beroe gracilis*. In this system the period of high abundance of *P.pileus* is much further extended than in Helgoland Bight. A comparative investigation of the systems ecology of ctenophores in ecosystems with or without *Beroe* populations as given by GREVE et al. (1976) could augment the understanding of coastal marine ecosystems. Other populations may, of course equally well take over the role of controlling the tentaculate ctenophores. This is known from the hydromedusa *Aequorea* (NEEDLER ARAI, personal communication) and the scyphomedusa *Chrysaora* (CARGO, personal communication).

Extended ctenophore control on copepods has been investigated recently *in situ* and in experimental biological oceanography. MOUNTFORD (1980) describes the impact of lobate ctenophores on a coastal ecosystem, and GRICE et al. (1980) describe large plankton bag experiments in which ctenophore control occurred. The fact that this ctenophore control did not occur in the surrounding waters supports the importance of predator control of ctenophore populations by commonly-known herbivores such as large copepods and euphausiids. These feed unselectively on juvenile ctenophores, thereby hindering the development of further adults (GREVE 1977). Plankton bags, if started during the day, exclude such vertical migrants and their predator control capacity. Therefore the system may then be controlled by ctenophores. GREVE et al. (1980) have suggested that the behavior of the system is instable, which may be ascribed to inverse trophic interactions. These in turn may be derived from an ecological development along the lines of the mathematical theory of ecological catastrophe as set out by JONES (1977). In this theory the composition of phytoplankton is of key importance as discussed in detail by PARSONS (1979). Changes in the diatom flagellate ratio under anthropogenic stress of the system as measured by O'CONNOR et al. (1978) and experimentally investigated by PARSONS et al. (1978) may shift the stability properties of coastal systems towards ctenophore control. FISHER (1976) suggests similar changes for the North Sea. *Beroe gracilis* may provide a good indicator species for such system changes.

The areas where *Beroe gracilis* has been found until today (Helgoland Bight: KÜNNE 1939, Bristol Channel and Lancaster Bay: GREVE et al. 1976) are highly productive areas. Helgoland Bight is characterized by the wadden sea system along the coast, which is of special importance to fishery (NELLEN 1978). The role of ctenophores in

supporting the high level of phytoplankton input into this system by controlling copepods and maintaining nutrients within the pelagic system may be important for the functioning of the wadden sea system.

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