FISHERIES RESEARCH BOARD OF CANADA

Translation Series No. 2672

Ecological investigations on Pleurobrachia pileus. 2. Laboratory investigations

by W. Greve

Original title: Ökologische Untersuchungen an Pleurobrachia pileus 2. Laboratoriumsuntersuchungen

From: Helgoländer wissenschaftliche Meeresuntersuchungen
(Helgoland scientific marine research), 23 :
141-164, 1972

Translated by the Translation Bureau(ES)
Multilingual Services Division
Department of the Secretary of State of Canada

Department of the Environment
Fisheries Research Board of Canada
Biological Station
St. John's, Nfld.

1973

36 pages typescript

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

MULTILINGUAL SERVICES
DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES SERVICES
MULTILINGUES

FRB 2672

TRANSLATED FROM – TRADUCTION DE German	INTO – EN English

AUTHOR – AUTEUR
Greve, W.

TITLE IN ENGLISH – TITRE ANGLAIS
Ecological investigations of Pleurobrachia pileus
2. Laboratory experiments

TITLE IN FOREIGN LANGUAGE (TRANSLITERATE FOREIGN CHARACTERS)
TITRE EN LANGUE ÉTRANGÈRE (TRANSCRIRE EN CARACTÈRES ROMAINS)
Ökologische Untersuchungen an Pleurobrachia pileus
2. Laboratoriumsuntersuchungen

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET, TRANSCRIRE EN CARACTÈRES ROMAINS.
Helgoländer wissenschaftliche Meeresuntersuchungen

REFERENCE IN ENGLISH – RÉFÉRENCE EN ANGLAIS
Helgoland scientific marine research

PUBLISHER – ÉDITEUR	DATE OF PUBLICATION DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL NUMÉROS DES PAGES DANS L'ORIGINAL
				141-164
PLACE OF PUBLICATION LIEU DE PUBLICATION	YEAR ANNÉE	VOLUME	ISSUE NO. NUMÉRO	NUMBER OF TYPED PAGES NOMBRE DE PAGES DACTYLOGRAPHIÉES
Helgoland, Germany	1972	23		36

REQUESTING DEPARTMENT / MINISTÈRE-CLIENT: Environment

TRANSLATION BUREAU NO. / NOTRE DOSSIER N°: 183127

BRANCH OR DIVISION / DIRECTION OU DIVISION: Biological Station

TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES): E.S.

PERSON REQUESTING / DEMANDÉ PAR: Dr. R. J. Miller
St. John's Nfld.

YOUR NUMBER / VOTRE DOSSIER N°: 183127

DATE OF REQUEST / DATE DE LA DEMANDE: Feb. 5, 1973

UNEDITED TRANSLATION
For information only
TRADUCTION NON REVISEE
Information seulement

SOS-200-10-6 (REV. 2/68)
7530-21-029-5333

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

MULTILINGUAL SERVICES DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES SERVICES MULTILINGUES

CLIENT'S NO. Nº DU CLIENT	DEPARTMENT MINISTÈRE	DIVISION/BRANCH DIVISION/DIRECTION	CITY VILLE
	Environment	Biological Station	St. John's Nfld.
BUREAU NO. Nº DU BUREAU	**LANGUAGE LANGUE**	**TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES)**	
183127	German	E.S.	JUL 18 1973

Reference: Greve, W.; Ökologische Untersuchungen an Pleurobrachia pileus. 2. Laboratoriumsuntersuchungen. Helgoländer wissenschaftliche Meeresuntersuchungen, 23 : 141-164 (1972).

Ecological investigations of Pleurobrachia pileus

2. Laboratory experiments

W. Greve

Helgoland Marine Biological Station, Germany

ABSTRACT: Ecological investigations on *Pleurobrachia pileus*. 2. Laboratory investigations. The tentaculate ctenophore *Pleurobrachia pileus* FABR. is one of the most abundant holoplanktonic invertebrates of the German Bight (North Sea). It has been successfully cultivated under laboratory conditions at Helgoland. Additional information was obtained on reproduction and relationships to abiotic and biotic environmental factors. *P. pileus* tolerated temperatures from − 1° to 26° C, and salinities from 12 ‰ to 45 ‰ S; in both cases the lower and upper limits may not represent the ultimate tolerance maximum. Temperature effects on rates of embryonic development, feeding, and growth were studied, as well as the interaction of turbulence and high seston content of sea water and their effects upon the behaviour of the ctenophore. *P. pileus* selects certain swimming organisms from a variety of possible food sources; it is well adapted to a life in detritus-rich habitats. Planktonic, nectonic and benthonic organisms have been used for testing interrelations to *P. pileus*. The patterns of these interrelationships are discussed.

The ctenophore Pleurobrachia pileus FABR. is one of the most common carnivorous holoplankters in the Heligoland Bight and other sea areas (BIGELOW 1928, FRASER 1970, GREVE 1971, HARTLAUB 1893, KÜNNE 1952). This species is suspected of being a great enemy of newly hatched pelagic fishes (FRASER 1970, LEBOUR 1922, 1923). This opinion is based on the report by LEBOUR who found several Clupea larvae in the pharynx of Pleurobrachia pileus and even observed the latter feeding on this type of prey. However, so far, FRASER's analyses of pharynx contents failed to support this point of view. As for the rate of food intake by Pleurobrachia pileus, only preliminary results have been reported by BISHOP (1968, 1969).

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After the development of new culture methods (GREVE 1968, 1970), it became possible to conduct long-term investigations under controlled conditions, aimed at the ecology of Pleurobrachia pileus, and performed in addition to the field investigations (GREVE 1971). The multitude of biotic and abiotic environmental factors that might exert an influence upon the population dynamics of Pleurobrachia pileus became apparent from our field investigations. Not only the organisms of the pelagic zone are in contact with this ctenophore but, on account of the aggregation of individuals close to the sediment observed in the region under investigation, the ben- p. 14 thos had also to be included in our studies. Hence, a great many factors whose ecological importance to Pleurobrachia pileus was still little known needed clarification. Therefore, the experiments led primarily to qualitative results; as far as possible, these were complemented by quantitative studies.

Material and methods

The Pleurobrachia pileus specimens used in our experiments were collected from plankton hauls near Helgoland. Prior to their use in the various tests, the ctenophores were kept for some time (1-4 weeks) either in a planktonkreisel* (GREVE 1968), phytoplankton-kreisel, or twin-cuvette

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*) Translator's note: "Kreisel" could have been translated in this case as "rotator" or "turbine"; however, since the term "planktonkreisel" has already been introduced into the English literature (see Fig. 1 from GREVE 1968, reproduced here) it has been retained throughout this translation.

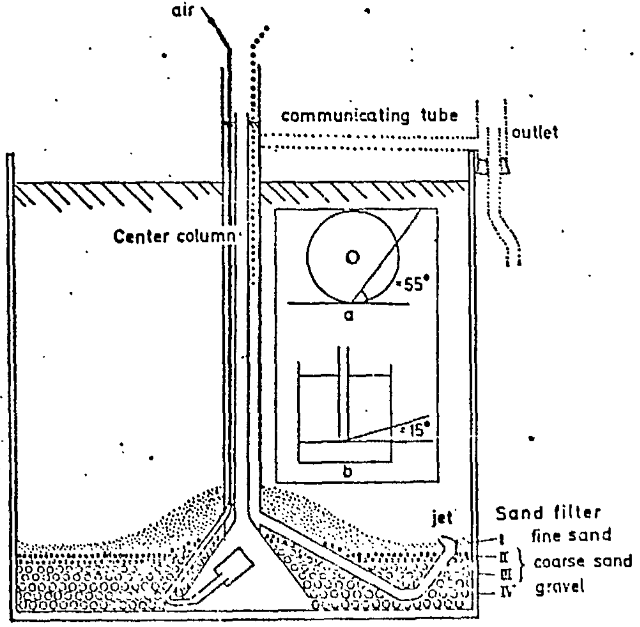
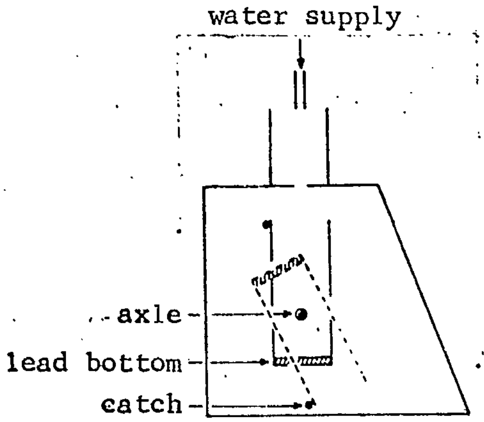


Fig. 1. Planktonkreisel, side view. Inset indicates directions of the jet outlet and the emerging water stream (a: top view, b: side view). The water stream keeps the culture medium in continuous rotation

(GREVE 1970), until it could safely be assumed that possible artifacts inflicted during the hauling process had been eliminated, so that all individuals used in our experiments had long tentacles. The ctenophores were so well fed before experiments began that continuous growth of the <u>Pleurobrachia pileus</u> could be registered.

The normal temperature during upkeep was 15°C, the salinity was 32‰ ± 1‰. For comparative tests with various temperatures, the experimental animals were given about a week to adjust to the test temperature selected. The light conditions were not under special control since preliminary tests had shown that even strongly fluctuating light intensities fail to affect the behavior of <u>Pleurobrachia pileus</u>. The even distribution of prey was nevertheless achieved since the methodically produced turbulence in the vessels took care of this. In one experiment designed to test the effect of ocean currents on ctenophores, turbulence was further enhanced with the help of a special device working from above the surface of the water. A simple automatic "ocean-current simulator" (Fig. 1) poured every 40 seconds 350 ml of water from a height of 30 cm into the test tank which, in this type of experiment, was always a phytoplankton-kreisel. Further details will be discussed as they come up in connection with each of the factors investigated.



<u>Fig. 1</u>: Ocean-current simulator.
The outermost contours indicate the shape of the protective spill box surrounding the water container which tips for unloading. The catch prevents the water container from overturning completely in that it stops the latter when it reaches the position marked by the broken lines.

from p.14

The larvae of diverse invertebrates, needed for feeding especially the young ctenophores, were procured either by collecting the naturally occurring forms from the plankton, or by artificial breeding of larvae. Although the latter mode of procuring food has been mentioned repeatedly in the literature (e.g., HAGMEIER 1930), the methods used have never been described. More recent reviews (e.g., HAUENSCHILD 1968) are practically limited to the brine shrimp *Artemia salina*, as far as animal food is concerned. However, with the cooperation of several experienced associates of the Biol. Station Helgoland, larvae of the following species could be bred in greater numbers: *Pomatoceros triqueter*, *Balanus balanoides*, *Crangon crangon*, *Archidoris* species, *Lacuna divaricata*, *Ascidiella scabra*, *Eupagurus bernhardus*, and other marine forms.

The investigation of interactions between populations was greatly influenced by their availability and the feasibility of upkeep, so that in some cases not the suspected ecological importance of a species, but the possibility of using its members in an experiment had to be the criterion of selection. One individual of each species to be investigated were placed with *Pleurobrachia pileus* in a small container so as to intensify the reciprocal actions of these representatives from both populations by such p.143 an enforcement of abnormally frequent contact. In the case of forms detrimental to adult *Pleurobrachia pileus*, planktonkreisels with a capacity of 5 liters could be used because these were usually larger animals which could thus be observed. Forms eaten by adult *Pleurobrachia pileus* could be watched in a twin-cuvette. This vessel combines the advantages of the planktonkreisel with the facilities for photographic control and makes it possible, furthermore, to distinguish between the natural mortality among the copepodan plankton offered as food, and the mortality rate caused by predation in identical bodies of water. Within 24 hours, the mortality rate of freshly caught and immediately offered copepods reached a mean value of 30%; this was used as basis for determining the destruction rate of copepods in experiments in which food shortage or mechanical failure made uninterrupted observations impossible. The rate of destruction of copepods by Pleurobrachia pileus thus determined corresponds closely to the rate of Copepoda consumption established in other experiments and calculated on the basis of pharyngeal content analyses (GREVE 1970).

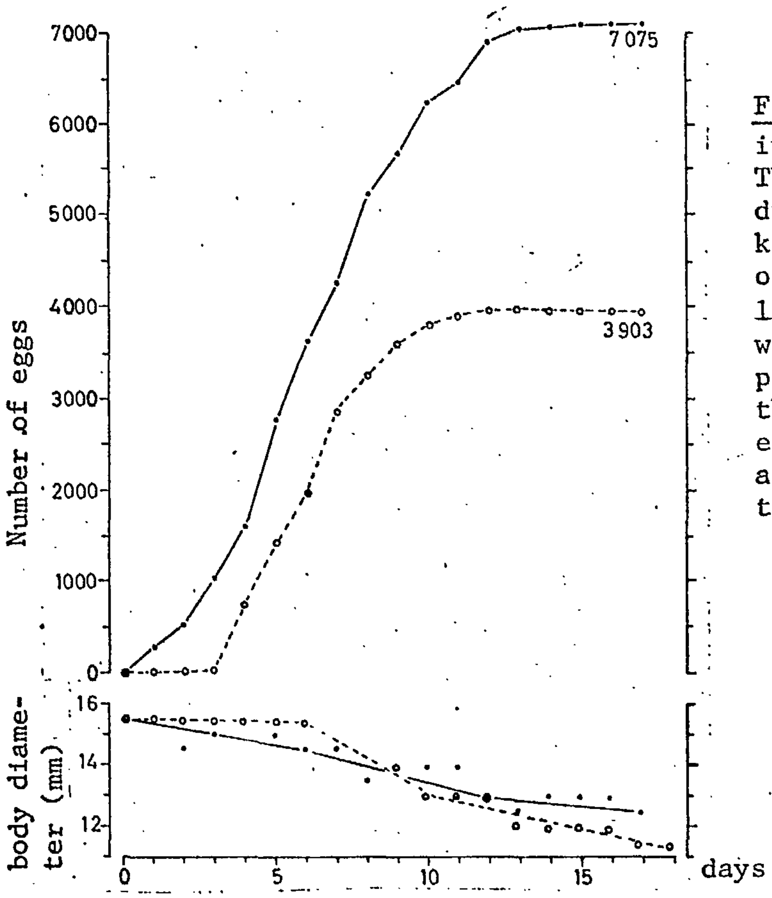
Experiments with newly hatched Pleurobrachia pileus were conducted in jars (250-1,000 ml) without special installations because, then, the offspring measures only 150 µm, which makes observation difficult. If necessary, the jars were aerated by gently introducing large air bubbles.

Results

The culture experiments with Pleurobrachia pileus made in preparation for the ecological investigations permitted a number of observations which are also of interest in regard to the ecology of this species. These include behavioral particularities (GREVE 1969), registration of growth p. 144
rates, length of generation (GREVE 1970), and observations on the reproductive rate of Pleurobrachia pileus. Fig.2 [p.7] shows the rate at which two individuals dropped their eggs. Each of the two ctenophores had a body diameter of 15.5 mm; both were artificially provoked into dropping their eggs by isolation in a Boveri dish (capacity 400 ml) (see GREVE 1970). Within two weeks they had dropped close to 4,000 and 7,000 eggs respectively. The sexual stimulation due to increased self-concentration enforced by the isolation in small containers served also as an indicator in determining the onset of sexual activity in well-fed individuals. Under

the conditions just described, the ctenophores reached maturity when they had attained a body diameter of approximately 5.5 mm. An earlier onset of sexual activity, e.g., the dissogeny described also in reference to Pleurobrachia pileus by REMANE (1956), could not be observed under our experimental conditions, nor during previous culture experiments. p. 145

Pleurobrachia pileus reacts euryplastic to all abiotic factors investigated. The temperature tolerance is already reflected in its natural distribution over annual isotherms ranging from 4°C to 21°C; occasionally, Pleurobrachia pileus has been observed also in waters of lower and higher temperatures. One method of establishing the range of tolerance of a population for each environmental factor consists of the LM 50/24 hrs. determinations, that is, the level at which 24 hours of exposure cause 50% mortality among the experimental animals. The tolerance of Pleurobrachia pileus for warm temperatures was determined in this manner in a planktonkreisel. Two experiments were performed, each with eight experimental animals which had been kept for several days at 23°C; the temperature was then raised daily by 1°C up to 26°C. At this level, four of the eight experimental animals succumbed within 24 hours in each experiment. At 24°C the ctenophores started already to swim frequently to the bottom. Under normal conditions, this reaction would bring Pleurobrachia pileus into lower and cooler strata, but under our experimental conditions they hit the bottom and ate grains of sand. Since body firmness was also diminished on account of the increased temperature, this behavior led to injuries of the animals in that they tumbled across the sand bottom due to the water current in the planktonkreisel; this additional hazard also contributed to the death of the ctenophores.



from p.144

Fig.2: Deposit of eggs and decrease in size of Pleurobrachia pileus. The curves relate to two individuals (1 = solid lines, 2 = broken lines), with an initial size of 6 mm which had increased to 15 mm by the time the experiment was started. No eggs were dropped 2 weeks prior to starting the experiment. The number of eggs deposited were subject to additive plotting. Experimental temperature 10°C.

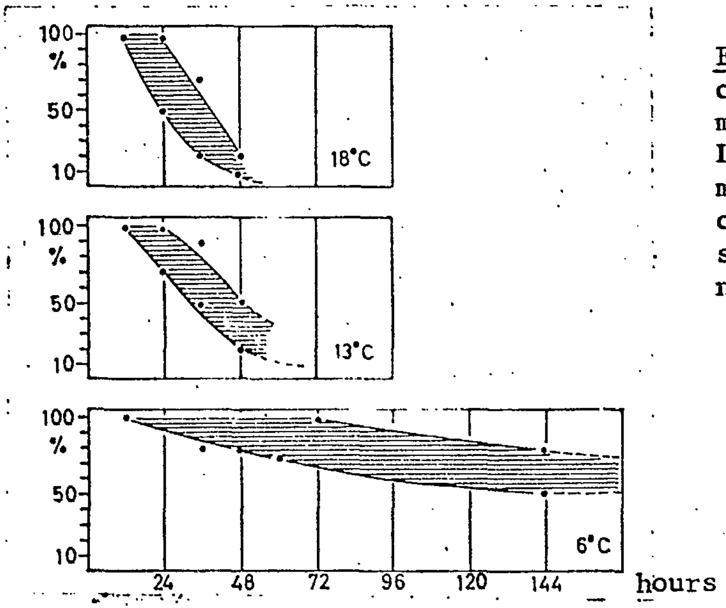


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Fig.3: Influence of temperature on the rate of embryonal development of Pleurobrachia pileus. Lined sections = eggs in developmental stages (two-cell to hatching); underneath = one-cell stage; above = hatched young ctenophores.

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The lower limit of temperature tolerance lies at the freezing point. PAGENSTECHER (in KRUMBACH 1926) reported the revival of frozen individuals after thawing out; however, confirmation of this statement has not been possible. All attempts of freezing Pleurobrachia pileus fast (within minutes) or slowly, with or without glycerin supplement, ended in the death of the experimental animals. However, temperatures down to the freezing point were tolerated for 24 hours without apparent damage, although beating of the combs decreases sharply at temperatures near 0°C so that the experimental animals sink to the bottom.

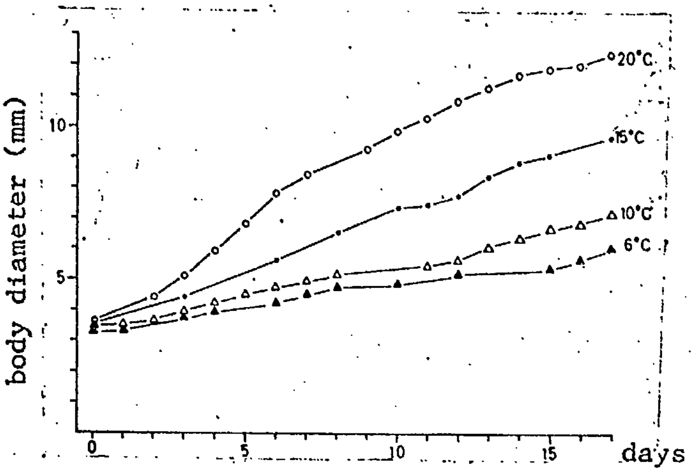

Fig.4: Growth rate of Pleurobrachia pileus at various temperatures. The individual values were rounded off to the nearest decimal. The growth values belong to the corresponding curves of the feeding rates plotted in Fig.5 (same symbols have been used).

Temperature not only determines the range of a species or population, but exerts also a decisive influence upon the speed of functional processes. It has been possible to investigate on several hundred eggs of Pleurobrachia pileus how much time embryonal development takes (Fig.3, p.7). In the two experiments conducted on this aspect, the eggs were dropped at a temperature of 12°C, while the experimental temperatures for embryonal development were 6°, 13°, and 18°C respectively. Transfer of the eggs into water with these experimental temperatures took place immediately after they had been dropped. Occasional checks were made to determine the proportion of eggs in their various stages of development (one cell, two cells, to unhatched young individual), and of free swimming young *Pleurobrachia pileus*. After six days the eggs became fungoid; in the experiments at 6°C, young animals had hatched from only 20% of the eggs at that time. The percentage of young individuals that hatched in the other experiments could be determined only for 48 hours after which time young ctenophores had hatched from 50% of the eggs in the 13°C, and 75% in the 18°C medium.

In addition to the influence of temperature upon the embryonic development of *Pleurobrachia pileus* we were able to observe also its effect upon the growth and feeding rates of adult individuals over a prolonged period of time (Fig.4, p.7; Fig.5, p.10). As experimental animals served *Pleurobrachia pileus* with a body diameter of approximately 3 mm, all caught on the same day in the Helgoland Roads and kept in one tank prior to experimentation, at which time they were transferred in groups of 2-10 individuals into twin-cuvettes with four different experimental temperatures p.147 (6°, 10°, 15° and 20°C). Control tests for all temperatures could not be made since the temperature of 6°C in one cuvette resulted in too high a mortality rate. The experimental animals were fed on Copepoda (about 90% *Acartia longiremis* and *Temora longicornis*; in one case, nauplii of the brine shrimp *Artemia salina* were offered as substitute food), which had been isolated from the daily plankton catches by filtration and short-term upkeep. Special care was taken that live prey was available in the cuvettes at all times, but not in too large numbers.

Photographs, taken in each case before and after feeding time, enabled us later to draw our conclusions as to the feeding rate of the ctenophores (see GREVE 1970). With this method it was also possible to measure the size of the experimental animals without disturbing them or injuring their tentacles. Unfortunately, in several control photos, the Pleurobrachia pileus conceal one another; this, the accumulation of copepods near the bottom, and failure of the photographic equipment rendered the data collected during the experimental period incomplete. However, the photographs taken sufficed to observe the activity of each individual so that it can be safely said that the d/l-values, that is, the destruction rate per predator (GREVE 1970), are free of errors which might have been introduced otherwise on account of succumbing individuals. The growth rates have also been corrected accordingly.

p. 148

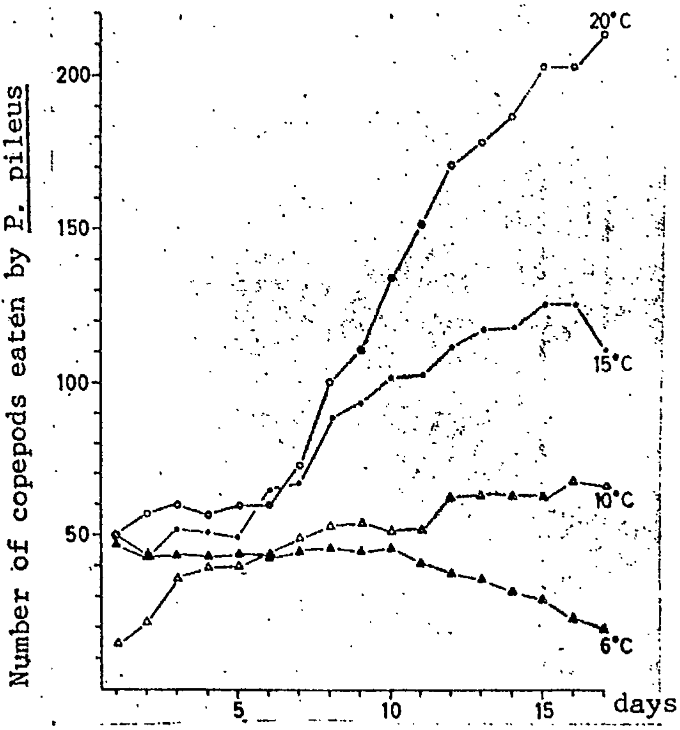

Fig. 5: Feeding rate of Pleurobrachia pileus at various temperatures. The individual values were rounded off to the nearest decimal. (Food intake = rate of copepods destroyed.) Each curve corresponds to the growth curves shown in the same order in Fig. 4.

from p.147

The slow rate of growth of Pleurobrachia pileus at 6°C contradicted the observation that, in the region under investigation, the largest individuals of this species are found during the cold season. Hence, the experiment was continued without daily photographic control (Fig. 6, p. 11). Within

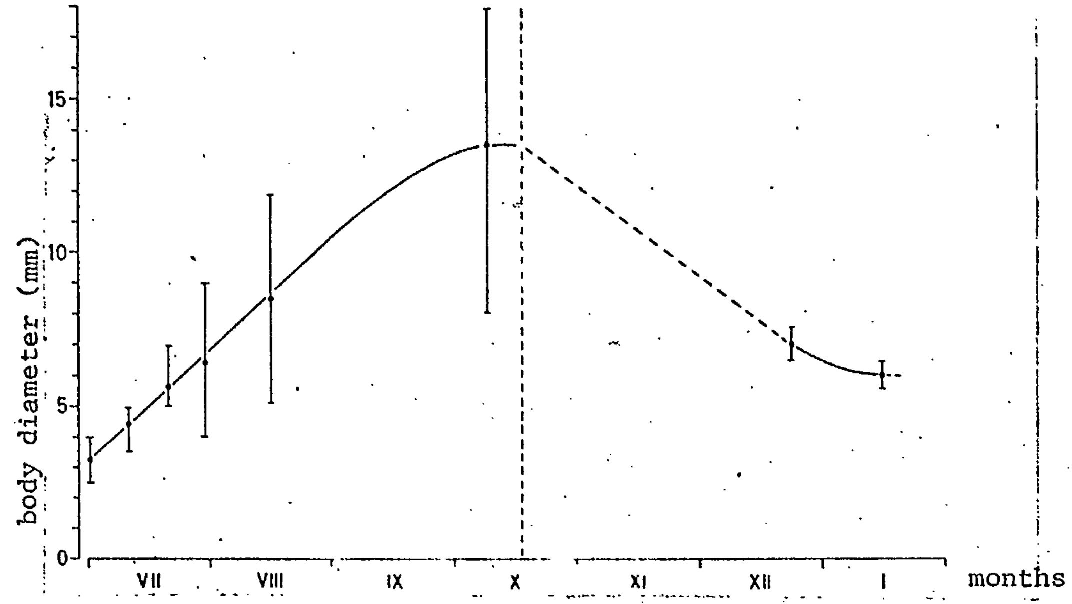

Fig. 6: Growth and emaciation of Pleurobrachia pileus at 6°C. Points plotted represent the mean diameter of three experimental animals with standard deviations; the vertical broken line marks the start of the hunger period.

three months, the experimental animals reached a body diameter (mean) of 13.5 mm (four of the seven individuals in this group succumbed at the end of the first month). The experimental animals whose history was, thus, a matter of record were subjected to a starvation test during which the temperature was constantly kept at 6°C. The smallest individuum died after marked emacication at the end of three months of starvation; The two larger ctenophores survived even a hunger period of four months.

A parallel test, conducted also in a planktonkreisel at 6°C, brought similar results. The three last survivors in a group of five Pleurobrachia pileus succumbed after a hunger period of three months. In other experiments we established that Pleurobrachia pileus is capable of resuming food intake and growth even after marked emacication.

Pleurobrachia pileus is euryhaline. In the Baltic Sea, adult individuals were found at a salinity of 7‰, and juveniles at 10 ‰ (MIELCK & KÜNNE

1935, KRUMBACH 1926, ACKEFORS 1969). Pleurobrachia pileus exists near Scotland in sea water with a salinity of 35‰ (FRASER 1970). However, this p. 149 wide a range of salinities cannot be tolerated without adaptation. If Pleurobrachia pileus is transferred from one medium into another in which salinity differs only by as little as 2-3‰, beating of the combs immediately changes in frequency, body gelatins become cloudy and, in some cases, mucus secretion occurs. The experimental animals either sink to the bottom or float on the surface of the water, and it takes often several hours before normal behavior is resumed.

Still other experiments were designed to determine the tolerance level of Pleurobrachia pileus to high salinities by gradually increasing the latter. For this purpose, the experimental animals were placed in planktonkreisels in which the water that evaporated on account of the constant aeration was not replaced by H_2O-supplementation (as is otherwise standard procedure). In this manner, the salinity increased to 45‰ within 3-4 weeks. This concentration was tolerated by Pleurobrachia pileus, although the experimental animals remained considerably smaller than the controls. The tolerance limit was not reached because feeding with live prey became increasingly difficult at such a high salinity.

Lower salinities of the water in the planktonkreisel were attained by the addition of rain water; in this manner, the experimental animals adjusted within one month to a salinity of 12‰ without showing any sign of damage. However, the observation reported by MIELCK & KÜNNE (1935) that the firmness of ctenophore bodies decreases considerably at such a low salinity could be confirmed in this experiment, which had also to be terminated before the lower tolerance limit was reached because none of the food organisms available could adjust fast enough to the low salinity to serve as actively swimming prey for the experimental animals.

HARDER (1952, 1968) reported that the population density of Pleurobrachia pileus and other plankton organisms increases at the interfaces of water layers. His findings could only partly be confirmed. Upon experimental production of salinity-(22‰/32‰ S) or temperature-interfaces ($14^{o}/18^{o}$C), aggregation was temporarily observed in all transition zones (water surface, halo- and/or thermocline, sediment surface); however, as soon as the experimental animals resumed their normal behavior, which had been upset by the manipulations during transfer, they were found to be fairly evenly distributed throughout the test vessel.

The existence of photosensory organs in ctenophores has, so far, not been established with certainty (HORRIDGE 1964). Even rapid changes in light intensity from almost complete darkness up to 60,000 lux* did not cause any photic reaction in Pleurobrachia pileus. However, the rising temperatures of the water in the test tanks due to the intensive illumination prompted the animals to swim to the bottom.

Natural ocean currents were imitated by attaching the ocean-current simulator (Fig. 1, p. 3) to a phytoplankton-kreisel. Not included in our experiments was the investigation of each component of the effect that ocean currents have on Pleurobrachia pileus (e.g., orbital course of water particles, tearing water masses, air bubbles that are torn into the water, fluctuations in pressure). The experiments conducted in a phytoplankton-kreisel over several days showed that the simulated ocean current has an influence on the depth selected by Pleurobrachia pileus which otherwise show a normal behavior (fishing with outstretched tentacles). In undisturbed water, the ctenophores aggregate near the surface; when the ocean-current simulator is in p. 150 action they prefer lower water levels. About 150 specimens of Pleurobrachia

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*) Translator's note: 1 lux = 1 lumen/m^{2}.

pileus were, during this experiment, subjected to the influence of the simulator after having been kept in the phytoplanktonkreisel for several days under normal water rotation. The vertical distribution of the ctenophores was registered with the help of photographs, while their behavior was directly observed. In addition to the immediate flight reaction of individuals surprised by a "breaker," a decrease in the length of the tentacles during the pursuit of prey has also been observed. When evaluating the photographs, all individuals visible in the first, second, third and fourth quarter of the total height of the phytoplankton-kreisel were counted. The percentage of distribution calculated from these counts served as the basis for the schematic presentation (Fig. 7). The latter clearly shows the temporary changes in the vertical distribution of Pleurobrachia pileus after the onset of turbulence. In addition to this temporary reaction, a lasting concentration of the ctenophores at sites less affected by the "ocean current" became apparent. The physiological principles of a prolonged effect of this nature on the part of ocean currents is still an unexplained ecological factor. However, the importance of this aspect is emphasized also by the fact that it takes at least half a day after ocean-current simulation is terminated before normal vertical distribution with distinct surface preference is restored (see also SCHÖNE 1970).

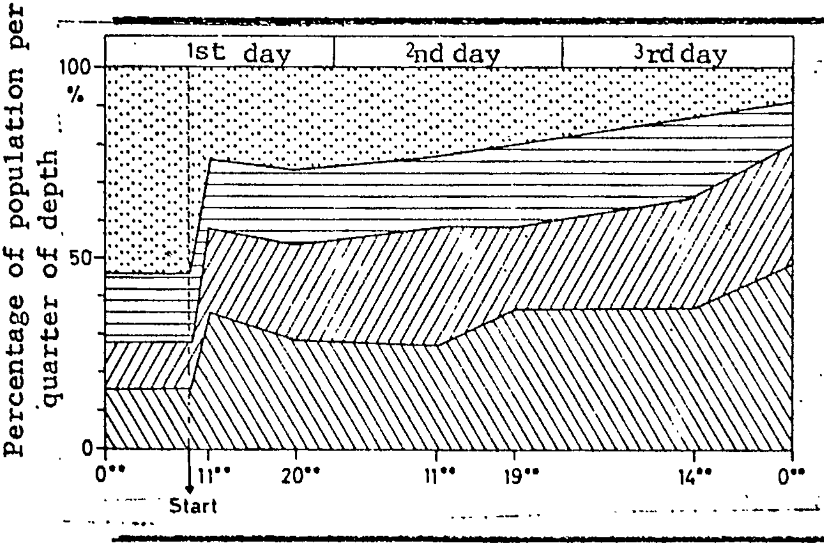

Fig. 7: Changes in the vertical distribution of Pleurobrachia pileus in the phyotoplanktonkreisel under the influence of simulated ocean current, expressed as percentage of total population present in each quarter of depth (1st quarter = top, followed by 2 and 3 = middle, and 4 = bottom).

Not only the ocean currents caused by surface turbulence but also the motions of the water caused by currents near the bottom exert a special influence on Pleurobrachia pileus (GREVE 1971). For example, experiments in a planktonkreisel showed that the duration of each bottom contact is determined by the speed at which the water rotates.

Passive individuals are reactivated by water motion. Furthermore, Pleurobrachia pileus drifting in the water are also carried by the ocean p.151 currents close to the benthos dwellers, some of which will eagerly consume the ctenophores. Such contacts become more frequent with increasing speed of the current, but the chance for successful catches diminishes because such short contacts rarely suffice to hold on to the ctenophores. To find out whether bottom contact as such has a detrimental effect on Pleurobrachia pileus with certain types of sediment, comparative studies were made of the effect elicited on the ctenophores by fine sand, coarse sand, gravel, and shell fragments. The uppermost layer of sand in the planktonkreisels was topped with one of these four types of sediment, and 10 ctenophores each were used in this 10-day experiment; frequent bottom contact was enforced by low levels and fast rotation of the water. However, the reaction of Pleurobrachia pileus to the various sediment types showed no important differences.

Pleurobrachia pileus is a neritic form, frequently found in seston-rich sea regions. We studied the influence of high seston contents on Pleurobrachia pileus in the phytoplankton-kreisel with the result that neither organic detritus nor diatoms in high concentration can notably disturb the ctenophores in their feeding activities. Keeping its tentacles only slightly shorter, Pleurobrachia pileus ate even the few copepods which, in addition to the inactively floating seston, had been placed into the vessel.

Upon subsequent autopsy, pharynx contents were found to be strictly of animal origin. If, instead of the organic seston, drift sand was introduced into the phytoplankton-kreisel, part of it adhered to the threadlike processes of Pleurobrachia pileus while sinking to the bottom. The ctenophores ate the sand, thereby increasing their weight so that they too sank; being thus exposed to the heavy sand drift near the bottom, some of the experimental animals were injured.

Even inorganic seston particles barely disturb the swimming and feeding activities of adult Pleurobrachia pileus. In experiments with $Fe_2(OH)_3$, a by-product of the treatment of sewage from a titanium plant near Helgoland (see also KAYSER 1969), and the "red sludge" which is a waste material resulting from aluminum production, we tested the original waste substances in solutions of up to 1 : 25,000 (ml or g of substance per liter of sea water). This test showed that the ctenophores in vessels without such artificial seston caught the copepods offered as food only slightly faster than those in test vessels in which these waste materials were kept in suspension.

The adaptability of Pleurobrachia pileus to life in seston-rich biotopes has been further supported by the results of another experiment which showed that the ctenophores concentrate on actively swimming prey while passive drifters of equal size are only rarely eaten. This experiment was conducted in a twin-cuvette, and the following organisms were offered consecutively in the order listed: 100 flatfish eggs (Solea vulgaris), 100 flatfish larvae (just hatched, 2.5 - 3.0 mm long), and 100 metanauplia of the brine shrimp Artemia salina (about 3 mm long). The behavior of the ctenophores (body diameter 12 mm) was under photographic as well as direct optical observation. Fig. 8 shows the changes in the concentration of food organisms during the experiment. The very actively swimming larger organisms were caught faster than the less active smaller ones. The selectivity with which Pleurobrachia pileus singles out the actively swimming forms as its food qualifies it particularly well for an existence amidst many seston particles.

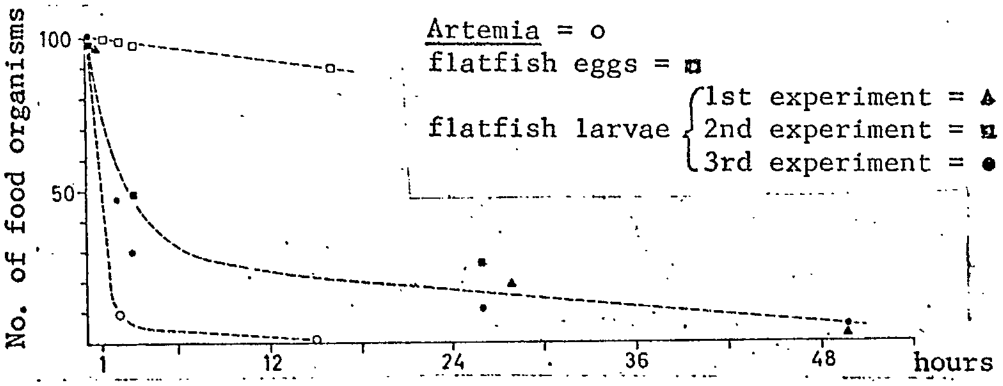

Fig. 8: Feeding rate of Pleurobrachia pileus as influenced by activeness and size of prey. Offered were eggs and larvae of the flatfish Solea vulgaris of fairly equal size, and young brine shrimps (Artemia salina, about 2.5 mm long). The more active and larger Artemia salina were eaten much faster by Pleurobrachia pileus than the less active fish larvae and fish eggs.

The ctenophores as holoplanktonic forms have, among the organisms p. 152 of their biotope, naturally a most intensive relationship with other holoplankters. The food of Pleurobrachia pileus consists according to BISHOP (1968, 1969), FRASER (1966, 1967, 1970), and LEBOUR (1922, 1923) of Copepoda and Cladocera. However, attempts of feeding newly hatched Pleurobrachia pileus with various pelagic copepods always failed since the representatives of the species involved (Calanus helgolandicus, Temora longicornis, Acartia longiremis) attacked the young animals. This observation was made during an experiment in which groups of 10 newly hatched Pleurobrachia pileus were placed for 48 hours together with 5 or with 20 copepods of the aforementioned species into small dishes with a capacity of 100 and 300 ml respectively. The results listed in Table 1 show that the ctenophores were in all cases harmed by the copepods.

Table 1: Harmful effect of three Copepoda species on newly hatched Pleurobrachia pileus. The values entered represent the number of survivors among the young ctenophores after 48 hrs. under these experimental conditions.

No. of copepods	Capacity of test vessel (ml)	Copepoda species			Control groups
		Calanus helgolandicus	Temora longicornis	Acartia longiremis	
20	100	0	0	0	10
20	300	0	0	3	10
5	100	1	0	9*	10
5	300	0	2	3	10

*) Three of the five experimental copepods in this vessel succumbed.

These results were complemented by observations on adult ctenophores. Not all organisms seized by their tentacles are eaten, and not every morsel of food entering the pharynx is being digested. If food supply is abundant, or if the ctenophores suffer indigestion, the entire pharynx content is often expelled. Frequently, an organism caught by the tentacle will tear off the prehensile processes, thus injuring the ctenophore. In experiments with an extremely high abundance of copepods, we observed that, in extreme cases, Pleurobrachia pileus emacicated and starved amidst this abundance of food since it cannot feed itself without tentacles, but these never had a chance to grow longer than 1.5 to 2 cm before they were again torn off. p. 153

Pleurobrachia pileus continuously regenerates lost tentacles (KRUMBACH 1926). It is not yet known how much time this process takes. In some instances, copepods were drawn by the tentacle contraction into the tentacular pouch and damaged the surrounding mesogloeal tissue from the inside, thus injuring the Pleurobrachia pileus so severely that they perished. BISHOP (1968, 1969), and GREVE (1970) reported on the amounts of copepods eaten by Pleurobrachia pileus. Another group of crustaceans among the plankton which might be of ecological importance to the neritic ctenophore are the Mysidacea. Of these, Mesopodopsis slabberi, Mysis mixta, and Praunus flexuosus have been investigated in some aspects of their relation to Pleurobrachia pileus. All three species are suitable as food for Pleurobrachia pileus; however, while Mesopodopsis slabberi of any age group can be captured by the ctenophore, are adult Praunus flexuosis and Mysis mixta nearly always able to tear away from its tentacles. Since the Mysidacea are longer than the pharynx of Pleurobrachia pileus, they are either kinked while being eaten, or they hang in part still out of the ctenophore's mouth while the first-ingested part of the body is already being digested; bit by bit, the entire worm is gradually fibrillated into the pharynx in this manner.

Feeding experiments with Mesopodopsis slabberi showed clearly that, due to their habit of remaining — in defiance of the current — optically orientated in one place, they come easily into contact with the tentacles of adult Pleurobrachia pileus. Furthermore, it is highly probable that this Mysidacea species also feeds on young ctenophores, or will at least harm them.

REMANE (1956) found in the pharynx of a young Pleurobrachia pileus a specimen of Sagitta setosa, the most frequent chaetognath in the Heligoland Bight. Despite the fact that, in this case, we might be dealing with an artifact created during the hauling process, it can be assumed that the Chaetognatha serve as food for juvenile as well as adult Pleurobrachia pi-

leus. Experiments with young *Sagitta setosa*, which are difficult to observe, and young *Pleurobrachia pileus* did not result in unequivocal findings. In the planktonkreisel showed the young individuals the same limited swimming activity as the adult *Sagitta setosa*. It was therefore possible to keep them together with adult *Pleurobrachia pileus* without great losses. Of special ecological importance to *Pleurobrachia pileus* are the other three ctenophore species found in the Heligoland Bight, as discussed elsewhere (GREVE 1970). Among these is *Beroe gracilis* the most important form because it has the greatest influence on the population dynamics of *Pleurobrachia pileus* since it feeds exclusively on the latter. This dietary specialization posed quite a problem in our investigations of the Beroida species since their experimental observation requires a constant supply of *Pleurobrachia pileus* in sufficient amounts to feed them. Long-term experiments could, therefore, be performed with only a few specimens. The life p.154
history of one of these experimental animals recorded for the time of its upkeep elucidates some of the aspects observable under these conditions, namely that of growth rate, feeding habits, and reproduction of *Beroe gracilis*. This particular specimen was caught in February 1968 in the Helgoland Roads; it was fed randomly at irregular intervals at 10 to 12°C until April 5, 1968, when registration commenced of the size of the individual, the number and mean size of *Pleurobrachia pileus* fed to it, the number of eggs dropped by *Boroe gracilis*, and the temperature of the medium. As far as conditions in the planktonkreisel permitted were the eggs removed with a pipette, and the counts made were entered as the nearest round figure. Only intact *Pleurobrachia pileus* were offered as food.

Boroe gracilis grows never larger than about 30 mm even with intensive feeding. The rate of food intake of this Beroida differed greatly during the time of observation, ranging from a minimum of 0.46 P. pileus daily (between April 5 and May 2, whereby the animal was still growing), and 8.4 P. pileus/day, the maximal intake between May 21 and June 6. The eggs were most often dropped 24 hrs. after food intake. During the phase of maximal food intake, Beroe gracilis dropped a total of 2,200 eggs, 600 of these on one day alone. The temperatures at which Beroe gracilis shed its eggs ranged from 5° to 20°C. The embryonic development could be observed at the same experimental temperatures.

Tomopteris helgolandicus is a holoplankter which is quite frequent along the coast of Helgoland. Its upkeep together with Pleurobrachia pileus established the actively swimming polychaete as a natural enemy of the ctenophore, devouring not only its tentacles but also chunks of tissue of injured individuals. Among the other holoplankters, found around Helgoland, are the Tintinnidae and Appendicularia possibly an important food source particularly for young Pleurobrachia pileus. However, due to technical difficulties, experimental clarification of this problem was not feasible.

Some species of the meroplanktonic Hydromedusae occur often in great numbers in the region under investigation. According to LEBOUR (1923) feed Cosmetira pilosella and Phialidium hemisphericum on Pleurobrachia pileus. To obtain proof of such interspecific relations, individuals of the species Bougainvillia britannica, Eutonina indicans, Nemopsis bachei, Obelia sp., Phialidium hemisphericum, Rathkea octopunctata, and Sarsia tubulosa were kept in a planktonkreisel together with Pleurobrachia pileus. The observations (in each case at least for one week) showed that only Eutonia indicans succeeded in catching and eating Pleurobrachia pileus. Phialidium hemisphericum and Rathkea octopunctata, while often holding on to Pleurobrachia pi-

leus during their plankton catches, have never been seen to eat them during this experiment.

According to the observations made so far (CARGO & SCHULZ 1967, HAGMEIER 1930) are several Scyphomedusae species of greater importance to the *Pleurobrachia pileus* population than the Hydromedusae. Experiments with *Aurelia aurita*, *Rhizostoma octopus*, *Cyanea lamarckii*, and *Chrysaora hysoscella* could be carried on for more than one week only in the case of the two first-mentioned species. The other two species, having longer tentacles, were upset in their feeding habits even in the large phytoplanktonkreisel. Adult ctenophores were not eaten by adult *Rhizostoma octopus* and *Aurelia aurita*. *Cyanea lamarckii* was seen to eat *Pleurobrachia pileus* in some of the experiments, but disabled more of the latter by its sting. *Pleurobrachia pileus* is not killed by the nematocystic poison, but shrivels p.15 up while discharging a cloud of mucus, and is temporarily paralyzed. *Chrysaora hysoscella* (diameter of umbrella = 40 mm) ate 4-10 *Pleurobrachia pileus* daily, each of these individuals having a body diameter of 10 mm. The aforementioned mucous discharge by *Pleurobrachia pileus* decreased the number of successful catches for the Scyphomedusae because their tentacles adhered to the surface of the mucus cloud and became easily detached. The interrelations between young individuals of all the species mentioned has not been investigated.

The neritic plankton is characterized by its high contents of larvae of the benthic invertebrates (THORSON 1946, GIERE 1968). Investigation of the reactions of individual species among these planktonic larvae was possible only to a limited extent. Feeding experiments with adult *Pleurobrachia pileus* showed that actively swimming larvae ranging in size from about 400 µm up to the largest forms in existence (e.g., the larvae of *Homarus* gammarus) are caught and eaten by the ctenophores. Adult Pleurobrachia pileus rarely bother to catch inactive larvae, particularly not the small ones (see also FRASER 1966, 1967, and BISHOP 1969); these seem to have greater importance for the juvenile stages of Pleurobrachia pileus. Culture experiments were successful only if the newly hatched Pleurobrachia pileus were fed on the larvae of tunicates and polychaetes (we used mainly the trochophores of Pomatoceros triqueter). However, veligers* and plutei* were as inadequate for raising Pleurobrachia pileus as the nauplii of Balanus balanoides.

Most fish larvae are also meroplankters. Experiments with eggs and larvae of the flatfish Solea vulgaris (Fig. 8, p. 17) had already shown that limited activeness inherent to certain forms or developmental stages can protect them from being eaten by the ctenophore. This could be confirmed in experiments with larvae of the rockfish Agonus cataphractus which are much more active swimmers. For this purpose, 30 newly hatched Agonus cataphractus larvae were placed into a planktonkreisel which already contained 4 Pleurobrachia pileus (body diameters = 8, 10, 10, and 12 mm). Only five minutes later 10 of the larvae had already landed in the pharynx of the ctenophores (0, 3, 3, 4). After 24 hrs. were 15 fish larvae missing, 20 after 48 hrs., 22 after 72 hrs., and 23 after 96 hrs. Two larvae died of injuries inflicted by the ctenophores, and five specimens of Agonus cataphractus survived this experiment. In a parallel test, two Pleurobrachia pileus (body diameters = 14 and 16 mm) ate within 24 hrs. 9, and in 48 hrs. all of the 11 Agonus cataphractus larvae placed with them in the same vessel. The temperature was kept at 10°C in both experiments.

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*) Translator's note: Veligers = larvae of mollusks; plutei = larvae of sea urchins, brittle stars, basket stars.

Feeding experiments with larvae of the sand eel Ammodytes sp. showed that herringlike larvae are also consumed by Pleurobrachia pileus. Unfortunately, larvae of Clupea harengus were not available.

Studies on adult fishes are often more difficult to conduct than experiments with larvae and invertebrates and had, therefore, to be limited to a few small-scale experiments and observations. The feeding habits of Cyclopterus lumpus as related to the ctenophores could be observed at the Aquarium of the Helgoland Biological Station. About 200 Pleurobrachia pileus, 30 Beroe individuals, and 30 Bolinopsis infundibulum were placed (from the top) in a tank with a capacity of approximately 1.5 m^3 occupied by a male specimen of Cyclopterus lumpus (about 40 cm long) which was fully adjusted to its surroundings and had been fed before on several occasions on ctenophores. As soon as the first of the above-mentioned ctenophores had come as close as 30 to 50 cm, the fish started up, taking direct aim at the prey. Recognition at this distance could be confimred p.156 in several observations. Apparently, the fish can distinguish between the ctenophore species from a distance of 2-5 cm, Cyclopterus lumpus consistently rejected Bolinopsis infundibulum. If the lobate ctenophore had nevertheless been swallowed accidentally along with a Pleurobrachia pileus individuum, both ctenophores were immediately ejected from the mouth. A special reaction to Beroe was not observed. The rate of food intake immediately upon feeding was 18 P.pileus/min.; several minutes later, we could register only 6-10 Pleurobrachia pileus as having been eaten by the fish within an equal period of time.

Additional experiments proved Centronotus gunnellus to be a ctenophore-eater, while Pleuronectis platessa, Gobius species, and Ctenolabrus species paid no attention to the Pleurobrachia pileus offered to them.

The vertical distribution of Pleurobrachia pileus revealed a marked preference for water layers near the bottom (GREVE 1971). This would indicate that the interactions between benthos and pelagic zone deserve increased attention in this connection. The vagile macrofauna of the benthos of the North Sea consists largely of decapod crustaceans. Underwater photography, dredgings, and diving expeditions in the investigated area showed Eupagurus bernhardus to be a particularly frequent benthos dweller. The ecological importance of this hermit crab has been studied along with that of Galathea squamifera, Carcinus maenas, Portunus holsatus, and Crangon crangon. One specimen of each of these species was placed in a separate planktonkreisel (capacity = 5 liters) together with 10 Pleurobrachia pileus. Once daily we checked how many of the ctenophores had been eaten and subsequently replenished the losses. If the rate of food intake of an experimental animal was particularly high, several checkups were made per day. In this manner, we arrived at the rates of food intake compiled in Table 2 [p.26].

The behavior of Eupagurus bernhardus during these experiments showed that this species has a particular talent for catching Pleurobrachia pileus. The crab mounted the higher pebbles in the planktonkreisel and stretched its antennae straight across the current. The tentacles of the ctenophores drifting by, come at least temporarily into contact with the antennae and are, thus, noted by Eupagurus bernhardus. On the other hand, stimulation of the tentacles evokes their contraction and, consequently, the ctenophore draws closer to the hermit crab which, at the same time, jumps in the direction of the contact with Pleurobrachia pileus, thereby spreading its legs far apart; after several such jumps the crab usually takes successfully hold of the ctenophore and, clutching it firmly to its belly, the crab then starts eating its victim. Excitation and searching motions can be triggered by only a few drops of juice extracted from dead *Pleurobrachia pileus*.

Table 2: *Pleurobrachia pileus* eaten by benthic enemies. The average daily feeding rate has been calculated on the basis of counts taken over the days indicated. Only intact individuals of *Pleurobrachia pileus* with a maximal diameter of 7-8 mm were offered as food to the hostile species listed here according to the amounts of daily food consumption.

from p.157

Species	Size of individual (measurements taken)	(mm)	Duration of experiment (days)	No. of ctenophores eaten daily (mean)
Metridium senile	Ø of oral disk	70	11	19.0
Carcinus maenas	width of carapace	41	7	13.7
Eupagurus bernhardus	carapace length x width	14 x 10	9	11.4
		10 x 8	9	6.3
		4 x 3	9	1.0
Sagartia sp.	radius of tentacles (Ø)	50	9	9.8
Portunus holsatus	width of carapace	32	5	7.8
Galathea squamifera	carapace, length x width	22 x 15	5	5.8
Alcyonium digitatum	2 colonies each	40 x 40 x 20	9	2.9
Centronotus gunnellus	length	120	2	2.0
Crangon crangon	length	36	8	0.6
Gobius flavescens	length	40	3	0.3
Urticina felina	Ø of oral disk	55	8	0.3
Pleuronectes platessa	length	60	9	0

Carcinus maenus also feeds eagerly on *Pleurobrachia pileus*. However, the process of capturing its prey is not as effective as in the case of *Eupagurus bernhardus* because of its short antennae. Of a more complex nature are the interactions of *Crangon crangon* and *Pleurobrachia pileus*: Small individuals of Pleurobrachia pileus are destroyed by adult Crangon crangon, p.156 cont'd but larger Pleurobrachia pileus (in one case observed, the ctenophore had a body diameter of 15 mm) eat Crangon crangon up to 20 mm long.

Of the sessile macrofauna of the benthos, only the coelenterates have been investigated. Smaller hydropolyps such as Podocoryne species which eat the eggs of ctenophores, as well as the large solitary polyps such as Metridium senile which eats adult Pleurobrachia pileus, may have a direct influence on the population dynamics of the latter. In the laboratory, p.157 some scyphopolyps show a normal development only if fed on ctenophores (CARGO & SCHULZ 1967). The results of our experiments with coelenterates are included in Table 2 [p.26].

Another benthic enemy of Pleurobrachia pileus was discovered on account of a chance observation: A spionid worm, dwelling in the sand filter in one of the planktonkreisels, held a ctenophore by its tentacles, pierced its prostomium into the victim, and ate it up within 20 hours.

Discussion

The multitude of experimental results and observations on the reactions of Pleurobrachia pileus to changes in abiotic environmental factors, and the interrelations between this ctenophore and the populations around it, reflect the complexity of ecological situations of this nature. Infer- p.158 ential judgement of conditions in the natural habitat on the basis of laboratory findings can therefore be made only to a very limited degree. At best, the growth and feeding rates established at various temperatures in the laboratory (Table 3, p.28) may allow comparative calculations of values for the natural habitat. The mean diameter of the Pleurobrachia pileus caught near Helgoland increased from 3.5 mm on May 13, 1968, to 7 mm on June 5, 1968. The mean temperature of the biotope at that time was 9°C.

Table 3: Growth rate and average rate of food intake (d/l*) of Pleurobrachia pileus at various temperatures.

Temperature (^{o}C)	No. of test animals	Diameter (mm) (mean) 1st day	Diameter (mm) (maximal) 21st day	No. of copepods eaten (d/l)
6	7	3,3	5,7	26,3
10	4	3,4	7,6	37,2
10	3	3,6	6,7	44,9
15	4	3,7	11,6	65,4
15	8	3,3	9,4	52,0
20	2	3,75	12,5	112,0
20	9	3,6	8,3	51,7

The Pleurobrachia pileus in the laboratory, which showed a similar increase in size at comparable temperatures, ate approximately 35 copepods per day. At a population density of 10 P. pileus/m^3 the corresponding daily rate of Copepoda destruction would amount to 350 copepods/m^3. This ratio is relatable to the abundance of ctenophores and copepods in June 1967 and 1968 (June 1967 = approximately 600 copepods/m^3 and 10 P.pileus/m^3; June 1968: about 3,700 copepods/m^3 and 2 P.pileus/m^3) (GREVE 1971). While this comparison cannot prove causality, it is indicative of a relationship. The vast number of factors not investigated does not allow additional conclusions.

Behavioral studies and field observations are necessary prerequisites for an evaluation of the composite aspects of the ecological interrelations between a population and its environment. This includes the occasional preference for strata close to the bottom shown by Pleurobrachia pileus in the region under investigation. As experiments with members of the predatory macrofauna of the benthos have shown, this behavior may be of fatal consequence to a great number of individuals of this population.

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*) Translator's note: Rate of destruction (of copepods) by 1 individual of P.pileus (see also text, p.10).

To clarify the actually existing interrelations between populations, it will be necessary to study, in great detail, the distribution throughout the strata immediately above the bottom of the sea.

The behavior of *Pleurobrachia pileus* and particularly its partiality for actively swimming forms as its prey permits a prognosis as to the composition of its food if we consider the availability of potential food organisms at any given time. FRASER (1966, 1967, 1970) examined the pharynx contents of *Pleurobrachia pileus* and found them to consist predominantly of Copepoda and Cladocera. His findings support our point of view despite the fact that the abundance of the various food organisms p.159 detected during his investigations was unknown. This makes it especially clear that the development of a population is not decided by the availability of suitable food as such, nor by the number of potential predators. It is much more important that characteristic behavior and other specific qualities selectively establish interactions between populations that match like a biological key would match a lock (as in the extreme case of *Pleurobrachia pileus* and *Beroe gracilis*).

To analyze the ecologic situation of a population, or make a prognosis of its development, the interrelations between all developmental stages of all populations involved will necessarily have to be taken into consideration. It has often been tried to illustrate these ecological relations; any attempt to present such complex relations calls necessarily for simplifications. For example, the model of the relations between a population and its environment used by PIMENTELL (1966) shows mainly how one relation connects to another. Correspondingly, an extremely simplified diagram is provided here to illustrate these relations in the case of *Pleu-*

robrachia pileus (Fig. 9). Populations having a direct relation with the one under investigation are arranged in a circle around it. Arrows point in the direction from the source of influence to the target. Only a few examples have been given of other populations and abiotic factors which, in turn, affect the development of the populations that form the circle, in this case in relation to Calanus. The inclusion of all secondary and tertiary relations, which are often of greater consequence than the primary ones, would by far exceed the scope of this diagram.

p.161

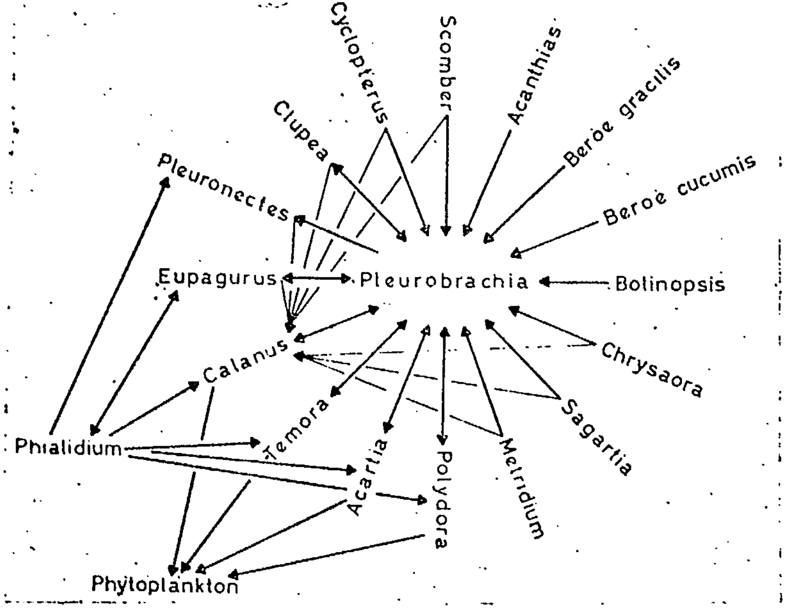

Fig. 9: Graphic presentation of some of the populations that have a direct or indirect relation with Pleurobrachia pileus. Inner circle = direct effect; lightly drawn arrows = indirect (secondary) effect on P. pileus through Calanus; outer circle (incomplete) = indirect effect of other factors. Arrows point in the direction of the target of the influence or detrimental effect exerted.

from p.15

p.161 cont'

A simple method for showing all established interactions between connected factors in the proper perspective exists in the form of a matrix. The populations and biotic factors shown in Fig. 9 have been compiled to such a matrix [Table 4, p.31]. Listed horizontally, the populations represent the source of an influence exerted upon the vertically-listed target populations. In what way the former affect the latter is expressed in a simplified manner by symbols (positive or negative). Since each of the populations is listed horizontally as well as vertically, this model of the ecosystem makes it possible to spot secondary as well as tertiary relations at a glance. The blank spaces in this matrix emphasize how much more information it can hold than the diagram (Fig.9) on which it is based.

Table 4: Interrelations between the populations shown in Fig.9, presented in the form of a matrix. Here, the symbols (+, -, 0) take the place of the arrows, their direction and emphasis (see text). p.16

source target	*Pleurobrachia*	*Beroe gracilis*	*Beroe cucumis*	*Bolinopsis*	*Chrysaora*	*Sagartia*	*Metridium*	*Polydora*	*Acartia*	*Temora*	*Calanus*	*Eupagurus*	*Pleuronectes*	*Clupea*	*Cyclopterus*	*Scomber*	*Acanthias*	*Phialidium*	„Phytoplankton"
Pleurobrachia	0	---	--	-	--	-	--	++ -	+++ -	++ -	+++ -	+ --	+	++ -	--	+ --	--	0	0
Beroe gracilis	+++										0								
Beroe cucumis	++										0								
Bolinopsis	0										+++								
Chrysaora	+										++								
Sagartia	+										++								
Metridium	+										++								
Polydora	-										0							-	+++
Acartia	--										0							--	+++
Temora	--										0							--	+++
Calanus	---	0	0	---	---	--	--	0	0	0	0	-	-	--	-	-	0	--	+++
Eupagurus	++ --										+							+ -	
Pleuronectes	+ -										+							-	
Clupea	+ --										++								
Cyclopterus	++										+								
Scomber	++ -										++								
Acanthias	+										0								
Phialidium	0										++	+ -	+						
„Phytoplankton"	0							---	---	---	---								

The disadvantage of this form of presentation is mainly that unspecific symbols are used which cannot transmit detailed information. To demonstrate this point, let us look at the particularly evident example of the interrelations between <u>Pleurobrachia pileus</u> and <u>Temora longicornis</u>: As our experiments have shown, <u>T. longicornis</u> has a decidedly damaging effect on young <u>P. pileus</u>, but these very same copepods are the main source of food for adult <u>P. pileus</u>. Hence, we must add to the triple symbol "+++" a single minus ("-") which applies, however, only to a certain age group of the ctenophore. On the other hand, we have learned that an extreme p.16 cont abundance of Temora may be detrimental even to adult individuals of P. pileus. Therefore, the age factor as well as the abundance of the populations involved should be incorporated in the symbols representing the interrelations between them in a matrix. p.162

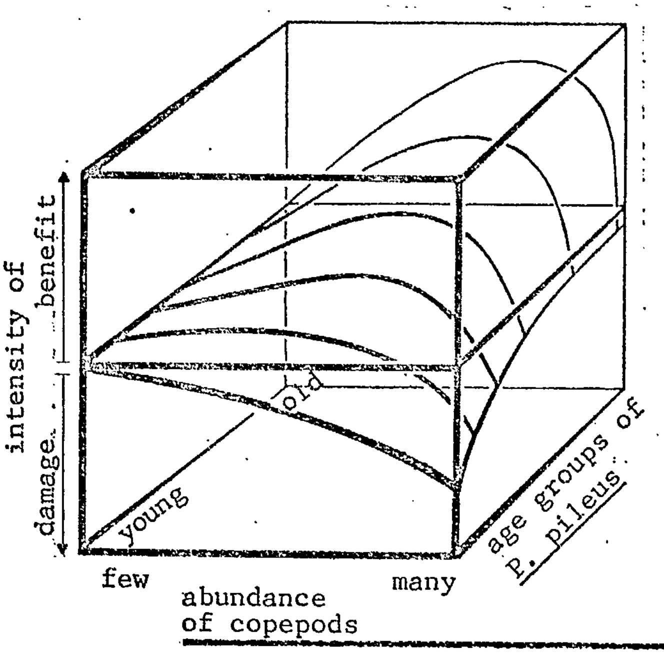

Fig. 10: Tridimensional model of the interrelations between Pleurobrachia pileus and adult copepods of one population. With increasing abundance of the copepod population its damaging effect upon young ctenophores increases as well (see also Table 1, p. 18), and so does its positive influence upon the adult ctenophores for which it is a source of food. If abundance is very high, the effect lies again below the level of indifference. from p.161

If the three aforementioned variables (degree of damage or benefit, abundance of the species identified as source of influence exerted, age group, etc., and the age groups of the target population) are linked with the three coordinates, a diagram can be designed as shown in Fig. 10, from which the biological effect of the influence-exerting species can be read off directly. For example (front left to right): The greater the numbers of adult copepods, the higher the losses among young Pleurobrachia pileus; (back left to right): Initially, the ecological conditions for adult Pleurobrachia pileus improve with increasing abundance of copepods up to a certain maximum beyond which even adult ctenophores will suffer losses; (right, front to back): The older the individuals of Pleurobrachia pileus, the less harmful is even a massive abundance of adult copepods. p.16 cont'

In connection with the matrix allows this schematic drawing a fairly extensive symbolization of biologic relations and can, thus, serve as preliminary step towards an analysis of the ecosystem which, in contrast to the model of food chains and similar diagrams, concentrates on the network of interrelations among populations. In what way additional dependencies (e.g., upon temperature) may be included has been described elsewhere (GREVE 1969). The degrees of damage or benefit indicated in this cube-shaped diagram represent a multitude of varying biological relations. However, this simplification seemed justified since it is the only way in which the sum of all factors that have an influence upon population dynamics can be included in a functional model. It is the result of one of the attempts called for by WATT (1966) who would like to see the descriptive presentation of ecological interrelations being replaced by the model which potentially lends itself for electronic data processing.

Summary

1. The tentaculate ctenophore Pleurobrachia pileus FABR. has been cultivated in the laboratory and subjected to ecological experiments. As culture and test vessels served the planktonkreisel, the phytoplanktonkreisel, and the twin-cuvette.

2. Mature Pleurobrachia pileus (body diameter 15 mm) deposited up to 7,000 eggs within two weeks; the smallest of the sexual active individuals measured 5.5. mm.

3. Temperature threshold experiments showed that Pleurobrachia pileus tolerates temperatures from -1° to 26°C; the most extreme salinities tolerated were 12‰ and 45‰ S, respectively; neither of these values represents the absolute tolerance limit.

4. The influence of environmental temperatures upon the rate of embryonal development of ctenophore eggs, as well as the rate of food intake and the growth rate have been studied at temperatures ranging from 6° to 20°C. Within this range, *Pleurobrachia pileus* — while developing normally — showed distinctly graded reactions to the varying temperatures.

5. Simulated ocean currents causes *Pleurobrachia pileus* to change p.163
its vertical distribution; the ctenophore avoids the surface turbulence.

6. Even a high concentration of seston in the medium has very little effect on the behavior of ctenophores hunting for food. They predominantly catch actively swimming organisms. Drift sand can have a damaging effect on *Pleurobrachia pileus*. Ferric hydroxide particles and other industrial waste matter did not disturb food intake of the ctenophore.

7. The interrelations between *Pleurobrachia pileus* and other holoplankters are, in part, of a very complex nature. For example, adult copepods are first enemies and later the food of the ctenophore, depending upon the age group of *P.pileus*.

8. Of the meroplanktonic forms are particularly some Scyphomedusae important enemies of *Pleurobrachia pileus*. The larvae of many benthic inverbrates serve as food especially for young individuals of *P.pileus*. Fish larvae are mainly eaten by *Pleurobrachia pileus* if they are active swimmers.

9. Fishes that are bottom dwellers and the vagile macrofauna of the benthos are, in part, enemies of *Pleurobrachia pileus*. *Cyclopterus lumpus* eagerly feeds on the ctenophore; *Eupagurus bernhardus* proved by its behavior that it is especially suited to catch *Pleurobrachia pileus*.

10. The schematic presentation illustrating the interrelations between *Pleurobrachia pileus* and its neighboring populations is suggested as a basic model for the analysis of the ecosystem.

Acknowledgments. The present paper is an abridged and edited part of the author's thesis (GREVE 1969) which has been updated by including the results of additional investigations. I wish to thank Prof. Dr. O. KINNE, Director of the Helgoland Biological Station, for suggesting these investigations, and for his assistance in all phases of this work. My thanks are due also to all coworkers at the Helgoland Biological Station for their cooperation and particularly to the technical staff without whose help many experiments would not have been possible. Miss M. HENGST deserves special thanks for assisting me in the evaluation of the experimental results. The investigations have, in part, been subsidized by the Deutsche Forschungsgemeinschaft [German Research Council].

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Address of the author: Dr. W. Greve
Biologische Anstalt Helgoland (Meeresstation)
2192 Helgoland
Federal Republic Germany