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In situ studies on the diurnal activity pattern of *Diastylis rathkei* (Cumacea, Crustacea) and its importance for the "hyperbenthos"

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KURZFASSUNG: **In-situ-Untersuchungen zum täglichen Aktivitätsrhythmus von *Diastylis rathkei* (Cumacea, Crustacea) und ihre Bedeutung für das „Hyperbenthos".** Es wurde bisher angenommen, das äußerst wichtige Fischnährtier *Diastylis rathkei* KRÖYER habe eine besonders hohe Bedeutung innerhalb der bodennahen Fauna, dem Hyperbenthos. Mit Hilfe des Unterwasserlaboratoriums (UWL) „Helgoland" wurden deshalb in situ die Vertikalwanderungen und das Aktivitätsmuster in Relation zum Lichtfaktor beobachtet. Parallele Untersuchungen zur Populationsdichte im Sediment einerseits und zum Erscheinen von *Diastylis rathkei* im Plankton andererseits beweisen, daß diese Cumacee niemals das Sediment verläßt, solange noch Licht vorhanden ist. Die Vertikalwanderungen beginnen etwa eine Stunde nach Sonnenuntergang, haben ihre maximale Intensität von ca. 22 bis 24 Uhr und enden um Mitternacht. Ein Fraß durch Fische oder andere Tiere konnte während dieser Phase nicht beobachtet werden. Diese Beobachtungen stehen im Gegensatz zu den Annahmen einiger anderer Autoren. Die von diesen benutzten Methoden werden kritisch diskutiert. Aus den vorliegenden Ergebnissen wird geschlossen, daß *Diastylis rathkei* überhaupt keine Bedeutung im „Hyperbenthos" hat. Die Existenz dieser Gemeinschaft in der westlichen Ostsee wird in Zweifel gezogen.

INTRODUCTION

In some recent studies conducted in Kiel Bay (Western Baltic Sea) (HESTHAGEN, 1973, BOYSEN, 1974, 1975a, b) the role of the so-called "hyperbenthos" for the energy cycle of the marine ecosystem has been regarded to be very important. BEYER (1958) defined the "hyperbenthos" as a community of originally benthic origin found in the near-bottom water. Other inhabitants of the same biotope (the "hyperbenthal") originating from the plankton he described as "tychobenthos". BOYSEN called both of them, independently of their origin, "hyperbenthos" and defined this as the community of the near-bottom water, whereas "nearbottom" is defined simply as the range covered by BEYER's epibenthic closing net.

ARNTZ (1971, 1974) found that a few benthic animals constitute the main component of the food of demersal fish in Kiel Bay. The cumacean *Diastylis rathkei* KRÖYER is obviously the most important fraction in the diet of dab (*Limanda limanda*

L.), cod (*Gadus morrhua* L.) and probably of many other fish species. Like other Diastylidae (cf. HALE, 1953; GRANGER, 1969, 1970; CHAMPALBERT & MACQUART-MOULIN, 1970) this crustacean is known for vertical migrations in the plankton. The true progress of this behaviour was totally unknown and has led to different, in many cases wrong, ideas about its extent, frequency and biological significance. HESTHAGEN and BOYSEN assumed the production of this prominent food organism to be formerly much underestimated due to its supposed semipelagic life in the "hyperbenthos". They tried to gain better information using BEYER's epibenthic closing net and presented findings on seasonal and even diurnal changes of *Diastylis rathkei*. Their results are compared with our own investigations on vertical migrations and responses to the light factor. They are critically disscussed with special reference to the methods employed.

MATERIAL AND METHODS

In August and October 1974 saturation dives in the underwaterlab "Helgoland" (UWL) were carried out by the authors. The missions took place at a depth of 15 m near Neustadt (Lübeck Bay, Western Baltic Sea). A total of 730 quantitative sediment samples representing an area of 100 cm^2 each was taken by means of diver operated box samplers. In this way 6524 specimens of *Diastylis rathkei* were sampled from the sediment. Additionally 1123 individuals were caught directly from the plankton by means of a hand operated net (mesh size: 1 mm). Sediment investigations on the diurnal activity pattern of *Diastylis rathkei* were carried out exclusively in August at Station I. Some more detailed information on the methods, the study site and sediment parameters is given by VALENTIN & ANGER (in press).

RESULTS

Quantitative bottom samples were taken at intervals of one to two hours over day and night. The comparison of the mean values is given in Figure 1: From sunset (20.00 h) until shortly before midnight a decline of population density was found in the sediment. Statistically significant differences (according to STUDENT's test) are indicated by * in the curve. A variance analysis of all values gathered from 0 to 18 hours did not show any significant difference during this period. Parallel observations on the behaviour of *Diastylis rathkei* were made in the pelagic environment from the sea floor (15–17 m depth) to 6 m above it. Swimming at higher levels was not possible for us in the state of nitrogen saturation. The results were as follows: During the whole investigation period of three weeks, a specimen of *Diastylis rathkei* was never observed in the water during day-time. The first swimming cumaceans appeared shortly after sunset (mostly at about 20.30 h) just above the bottom. When illuminated by a torch they immediately sank down to the sediment and dug themselves in. They behaved this way also during all daylight hours when dug out and stirred up by hand. These observations confirm the statement of ZIMMER (1941) that *Diastylis rathkei* normally shows strong negative reactions to light. This species lives during the day exclusively dug in the sediment and does not leave it as long there is any light.

During the observation period a maximum intensity of the pelagic phase in the activity of *Diastylis rathkei* was noted from about 22.00 to 23.00 h. Most specimens did not stay in the water layer very near the bottom, but were dispersed in the whole water column. Their reaction to light had also altered in the meantime. They now tended toward every light source. This held true also for specimens dug out and stirred up by hand; nevertheless no specimen left the sediment by itself when it was illuminated nor could it be observed that light (reflections) on the bottom attracted swimming animals to settle on it. Thus it follows that the sediment sampling at night was not disturbing and is to be regarded as fully quantitative.

The swarming activity declined from about 23.00 to 24.00 h. Shortly after midnight it had always finished; only a single specimen was observed in the water as late as 1.30 h. Later examinations showed a preponderance of male individuals in those samples taken in the pelagic environment, and of females in those of the sediment. The sex ratio in the latter was 56,2 % ♀♀ : 43,8 % ♂♂ and thus nearly identical with that found by KRÜGER (1940) in Kiel Bay (56,3 ♀♀ : 43,7 ♂♂). This ratio in our material is, according to a χ^2-test, significantly different from a hypothetical one of 50:50. This is in contrast to the ratio of 45 % ♀♀ : 55 % ♂♂ found in the plankton samples.

Since it was found that the nightly vertical migrations of *Diastylis rathkei* were made in the investigation period exclusively for moulting, the following facts can be discussed as causes for that remarkable difference: The seasonal moulting periodicity of the female fraction of the population seems to follow that of the males with a delay

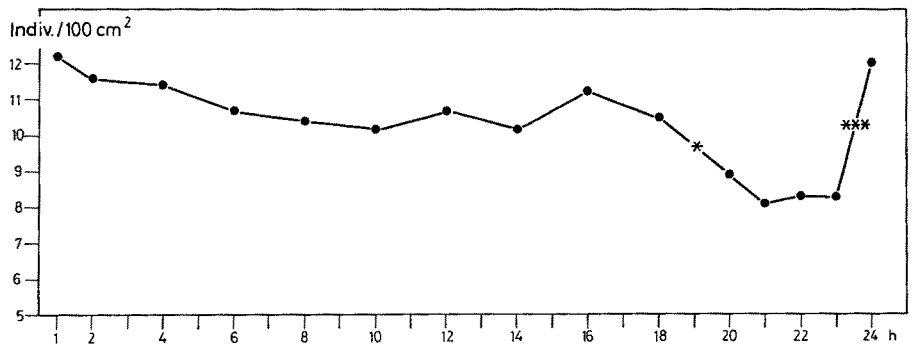

Fig. 1: Mean population density of *Diastylis rathkei* in the sediment during a 24 hour period

of several days and is probably less distinct (VALENTIN & ANGER, in press). Moreover, there is possibly a delay of the males within the daily periodicity: One night the plankton samples of the subperiods 20–22 h and 22–24 h were separately stored and examined. The sex ratio was reciprocal in these two samples the first one containing many more females, the second one more males. According to ZIMMER (1941) the females are worse swimmers than the males for anatomical reasons. Thus it is possible that most of the females leave the sediment sooner and return to it sooner, while the males swim higher and for a longer time above it and can thus be caught more easily

by divers. The noctural swarming could be observed with the distinctness described above only for about one week in August. Before and after that time it was much weaker but identical in all other respects.

The whole diurnal activity pattern of *Diastylis rathkei* can be summarized as follows: The species treated here is buried in the sediment as long as there is any light. According to sediment examinations, about 10–20 % of the population can take part in nightly migrations in the water. The first animals leave the sediment shortly after sunset, most of them about two hours later. The pelagic phase ends at about midnight, long before sunrise. It was never observed during the night investigations that *Diastylis rathkei* was eaten by fish or other enemies, although the authors spent many hours outside the UWL swimming and searching all over the study area.

DISCUSSION

In the present report results are presented which could hardly be obtained by methods other than saturation diving from a fixed underwater habitat. The complex biology of benthic animals which sometimes become planktonic was the subject of often sophisticated studies, but could be elucidated to only a very small extent. Only some additional, but partly erraneous information on *Diastylis rathkei* was gathered after the careful observations of FORSMAN (1938), KRÜGER (1940) and ZIMMER (1941). In particular the extensive investigations on the so-called "hyperbenthos" by HESTHAGEN (1973) and BOYSEN (1974, 1975a, b) must be subjected to a critical discussion. In their reports the importance of "hyperbenthic" animals for the marine ecosystem is stressed. It is stated that production estimates on the benthos are much too low because the "hyperbenthos" is not considered in studies using only the bottom sampler technique. High numbers of animals per volume unit water seem to show evidence that all marine scientists have overlooked a rich and particularly valuable biocoenosis above the sea floor. The most valuable food organism for demersal fish in Kiel Bay, *Diastylis rathkei,* is supposed by HESTHAGEN to be of great importance in the "hyperbenthos". Like BOYSEN he found high numbers in his epibenthic closing net throughout the day and night and in all seasons of the year. In this respect some remarks on the methods of sampling "hyperbenthos" are indispensable. BEYER's epibenthic closing net ranks beside that of MACER (1967) and a modification by POIRIER et al. (1969) as the most suitable one. The following facts are explicit in the work of BOYSEN (1974): It consists of a horizontal plankton net mounted on a sledge with sheet metal in front which ploughs the bottom and transports a high, fluctuating, principally unknown amount of sediment into the net. The sampler sinks uncontrolled into the bottom, depending on the sediment quality, towing speed and weather conditions; the ratio of animals taken up with sediment to those caught in the water cannot be determined. Starfish and large algae have to be removed from the samples before fixation. The difference between benthos and "hyperbenthos" is decided arbitrarily: algae belong to the former, amphipods and isopods to the latter, Polychaeta sedentaria to the former, Polychaeta errantia to the latter, etc. In HESTHAGEN's list of "hyperbenthic" animals the blind, sand-dwelling amphipod *Phoxocephalus*

holbölli KRÖYER occurs together with adult hermit crabs (*Eupagurus bernhardus* L.) and many other species living only in or on the sediment or in the phytal.

Thus it is obvious that results and numbers obtained by such a method have no meaning at all. Seasonal and geographical variations found in this way reflect – even more imperfectly – the same trends a dredge or a grab would show. Diurnal variations as found by HESTHAGEN are only produced by chance. Nevertheless this author discussed his randomly zigzag-shaped diurnal curves; peaks not usable in his hypotheses were referred to "by-catch of sediment". These examples of extensive, but worthless investigations are shown to illustrate misleading conclusions occurring in the literature. Thus it is stated by HESTHAGEN that *Diastylis rathkei* returns from the water to the sediment at dawn and is eaten at this time by demersal fish. It was noted in our study that the cumacean returns much sooner. Our own observations in combination with the results of ARNTZ (1971, 1974) on the feeding periodicity of dab and cod show that *Diastylis rathkei* is not eaten in the pelagic environment (during the night) but in the benthos (during the day). The numbers given by BOYSEN (1975b) also indicate indirectly the extremely low or even lacking significance of this species within the biotope he called "hyperbenthal": He could take samples at his station 6 (Howacht Bay) exclusively during night (this information is given only in BOYSEN, 1974) because it is situated in a military area. According to our results one would expect to find especially high numbers in this case. But they were even lower than in other comparable areas sampled by day.

A further observation given by VALENTIN & ANGER (in press) supports our view that *Diastylis rathkei* is an important food organism in the sediment and nowhere else: the numbers of individuals in the bottom sediment did not change during the short, but intensive pelagic activity period. During these few days nearly 60 % of the females and 70 % of the males within the population moulted in the water, but the population was not reduced. From August to October only weak swarming activity took place, but the population was markedly reduced – probably mainly by demersal fish. All these results, together with our direct observations in the natural environment, the short, rather infrequent swimming periods of *Diastylis rathkei*, its dispersal in the whole water column, and many biological notes in the literature make it most likely that almost 100 % of all specimens of this species caught by HESTHAGEN and BOYSEN by means of BEYER's epibenthic closing net were caught in the sediment as by any other dredge.

Conclusions made by these authors on other species and on the "hyperbenthos" itself are also doubtful. Except in the case of mysids and the sporadic occurrence of swimming benthic animals, the existence of a "hyperbenthos" in the Western Baltic Sea as it is described in the literature cited has to be rejected on the basis of our present knowledge.

The nocturnal swimming and drifting behaviour of *Diastylis rathkei* may have some adaptive significance, since it provides horizontal dispersion of an animal which is otherwise almost nonmotile throughout its life. In addition, the behaviour of the species results in an avoidance of predators during its most sensitive times of life: moulting, mating and hatching. Lack of protection against feeding activity of fish in

these periods would severely threaten the population and even the species *Diastylis rathkei.*

The coincidence of enemy inactivity and sensitive life stages is probably a biological mechanism similar to that described by THORSON (1953) for planktonic larvae and their predators during the settling phase. It is likely that some of our statements on *Diastylis rathkei* are largely valid also for other crustaceans.

SUMMARY

1. *Diastylis rathkei* KRÖYER exhibits negative phototaxis during the whole day. It never leaves the sediment as long there is any light.
2. The vertical migrations into the pelagic environment, as observed in August and October, start about one hour after sunset; they have their maximum intensity from about 22.00 h to 23.00 h and end at midnight. *Diastylis rathkei* reacts positively to light during this time.
3. Fishes and other predatory animals are almost inactive during this period. Population loss by predation is thus negligible or even lacking.
4. The literature on the "hyperbenthos" is critically discussed in relation to the method mostly employed, the use of BEYER's epibenthic closing net. This gear is not considered to be useful, and the results obtained by it are doubted.
5. *Diastylis rathkei* has no significance at all for the "hyperbenthos". The existence of this community in the Western Baltic Sea is doubted.

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LITERATURE CITED

ARNTZ, W. E., 1971. Biomasse und Produktion des Makrobenthos in den tieferen Teilen der Kieler Bucht im Jahre 1968. Kieler Meeresforsch. **27**, 36–72.

— 1974. Die Nahrung juveniler Dorsche *(Gadus morrhua)* in der Kieler Bucht. Ber. dt. wiss. Kommn. Meeresforsch. **23**, 97–120.

BEYER, F., 1958. A new, bottom-living Trachymedusa from the Oslofjord. Nytt Mag. Zool. **6**, 121–142.

BOYSEN, H. O., 1974. Quantitative Untersuchungen am Hyperbenthos der Kieler Bucht. Rep. Sonderforschungsbereich 95 Univ. Kiel **2**, 1–204.

— 1975a. Seasonal variations in abundance of hyperbenthic animals in the Kiel Bight. Merentutkimuslait. Julk. **239**, 206–212.

— 1975b. Das Hyperbenthos in der Kieler Bucht – Zusammensetzung, Jahresgang und Verbreitung. Ber. dt. wiss. Kommn. Meeresforsch. **24**, 151–171.

CHAMPELBERT, G. & MACQUART-MOULIN, C., 1970. Les Péracarides de l'hyponeuston nocturne du Golfe de Marseille. Cah. biol. mar. **11**, 1–29.

FORSMAN, B., 1938. Untersuchungen über die Cumaceen des Skageraks. Zool. Bidr. Upps. **18**, 1–356.

GRANGER, D., 1969. Variations journalières et saisonnières d'abondance des Cumacés à l'entrée de la Baie des Chaleurs en 1968. Rapp. Stn. Biol. mar. Grande-Rivière **1968**, 1–8.

— 1970. Distribution bathymétrique benthique et migrations verticales journalières des Cumacés a l'entrée de la Baie des Chaleurs en 1968 et 1969. Rapp. a. Minist. Ind. Comm. Serv. Biol. Quebec **1969**, 1–12.

HALE, H. M., 1953. Notes on distribution and night collecting with artificial light. Trans. Roy. Soc. S. Austr. **76**, 70–76.

HESTHAGEN, I. H., 1973. Diurnal and seasonal variations in the near-bottom fauna – the hyperbenthos – in one of the deeper channels of the Kieler Bucht (Western Baltic). Kieler Meeresforsch. **29**, 49–85.

KRÜGER, K., 1940. Zur Lebensgeschichte der Cumacee *Diastylis rathkei* (KRÖYER) in der westlichen Ostsee. Kieler Meeresforsch. **3**, 374–402.

MACER, C. T., 1967. A new bottom-plankton sampler. J. Cons. perm. int. Explor. Mer **31**, 158–163.

POIRIER, L., GRANGER, D., WEINSTEIN, M. & BRUNEL, P., 1969. Pêches hyperbenthiques et planctoniques quantitatives à l'entrée de la Baie des Chaleurs: Protocole et methodes en 1968. Rapp. Stn. Biol. mar. Grande-Rivière **1968**, 47–57.

THORSON, G., 1953. The influence of larval settlement upon the composition of marine level-bottom communities. Proc. 8th Pacif. Sci. Congr. **3A**, 1171–1176.

ZIMMER, C., 1933. Cumacea. Tierwelt Nord.-Ostsee **10**, 70–120.

— 1941. Cumacea. Bronn's Kl. Ordn. Tierreichs **5** (14), 1–222.

VALENTIN, C. & ANGER, K. In situ studies on the life cycle of *Diastylis rathkei* (Cumacea, Crustacea). Mar. Biol. (in press).

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