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A Tentative Field Experiment on Population Dynamics of macrobenthos in the Western Baltic*)

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Summary: In the scope of our investigations on the basic processes in a soft-bottom macrobenthos community, as a preliminary test, a series of five 1 m² metal boxes filled with sterilized sediment from the surrounding habitat was exposed in an enclosed area in the western Kiel Bight at a depth of 20 m from September 1972 until July 1975. The establishment and succession of the soft bottom association in the boxes was followed and compared to the association on the surrounding sea floor by monthly to bimonthly sampling by the diving group of SFB 95.

While the number of species increases continuously until a final level of about 20 per 0.1 m² is reached in January 1974, the values of total biomass (the starfish excluded) fluctuate seasonally being high in autumn and early winter and low in March and April. In a late experimental stage in January 1975, before or just in the beginning period of the regression of the bivalve populations, the association in the boxes (80 g wet wt./m²) has only reached 50% of the biomass of the assemblage outside where large long-lived and slowly growing bivalve species contribute 75% of macrobenthos weight. The data of total specimen number fluctuate widely due to oxygen deficiency in late 1973 followed by a high colonization activity by opportunistic spionid species immediately after.

According to the dominance in specimen numbers of the major taxononomic groups, three phases can be distinguisted: crustacea (mainly *Diastylis rathkei*) — sedentary polychaetes (spionids, *Pectinaria koreni*) — bivalves (*Abra alba*) together with errant polychaetes (*Nepthys spp.*).

In terms of biomass, however, there is an additional phase of echinoderm prevalence (*Asterias rubens*) during the last five months. The starfish obviously utilize the bivalve production to a high extent: between 94 and 75% mortality for the three most abundant bivalve species within six months.

For the last six months of the experiment, the net production of all bivalve species is calculated as 24 g wet wt./m², i.e. 0.61 g organic carbon of living tissue, most of which is produced by only three species (*Abra alba, Cardium fasciatum* and *Mya truncata*: 22 g wet wt/m².)

It is suggested that predators are of eminent importance in controlling succession and production of the new association. The effects of the experimental conditions on the findings is discussed, and a design for extended interdisciplinary in situ experiments to be carried out from 1976 on, based on the experiences of this first test, is presented.

Ein erstes Experiment zur Populationsdynamik von Makrobenthos in der Westlichen Ostsee (Zusammenfassung): Im Rahmen unserer Untersuchungen der grundlegenden Prozesse in einer makrobenthischen Weichbodengemeinschaft wurden als Vorversuch fünf je 1 m² große Metallkästen mit sterilisiertem Sediment aus dem umgebendeu Habitat beschickt und von September 1972 bis Juli 1975 in einem geschützten Versuchsgebiet im Westen der Kieler Bucht auf 20 m Wassertiefe aufgestellt. Es wurden Proben in Abständen von einem bis zwei Monaten durch die Tauchgruppe des SFB 95 entnommen und Formierung und Sukzession der Weichbodengemeinschaft in den Kästen verfolgt, vergleichend mit den Veränderungen in der Assoziation des Umfelds.

Während die Artenzahl ständig zunimmt bis auf ein Niveau von etwa 20/0,1 m² ab Januar 1974, zeigen die Werte der Biomasse (ohne Seesterne) jahreszeitliche Schwankungen; sie sind hoch im Herbst bis Frühwinter und niedrig im März und April. In einem späten Versuchsstadium (Januar 1975), noch vor oder gerade zu Beginn der Dezimierung der Muschelpopulationen, hat die Assoziation in den Kästen mit 80 g Lebendgewicht pro m² erst 50% der Biomasse der Gemeinschaft außerhalb erreicht, wo große langlebige und langsamwüchsige Muschelarten vorherrschen (75% des Makrobenthos-Gesamtgewichts). Die Werte für die Gesamt-Individuenzahl schwanken erheblich als Folge von Sauerstoffarmut Ende 1973 und der unmittelbar anschließenden Massenentwicklung von opportunistischen Spioniden-Arten.

Betrachtet man die Dominanzverhältnisse bezüglich der Individuenzahlen größerer taxonomischer Einheiten, so lassen sich drei Phasen voneinander unterscheiden: Crustacea (vor allem *Diastylis rathkei*) — Polychaeta-Sedentaria (Spioniden und *Pectinaria koreni*) — Bivalvia (*Abra alba*) mit erranten Polychaeten (*Nephthys spp.*). Bei der Dominanz nach Biomasse läßt sich während der letzten fünf Monate des Experiments zusätzlich eine vierte Phase erkennen, die der Echinodermen (*Asterias rubens*). Die Seesterne nutzen augenscheinlich einen hohen Anteil der Muschel-Produktion: Die Sterblichkeit innerhalb der letzten sechs Versuchsmonate liegt bei den drei häufigsten Bivalvia-Arten zwischen 94 und 75%. Die Nettoproduktion aller Muscheln beträgt für Januar bis Juli 1975 24 g Naßgewicht pro m² (= 0.61 g C_{org} lebendes Gewebe), davon werden 22 g Naßgewicht durch nur drei Arten produziert (*Abra alba, Cardium fasciatum, Mya truncata*). Es wird angenommen, daß räuberische Arten eine Schlüsselrolle bezüglich Sukzession und Produktion der neuen Gemeinschaft innehaben.

Die Auswirkungen der Versuchsbedingungen auf die Ergebnisse werden diskutiert, und es wird der Entwurf einer erweiterten interdisziplinären Anlage für Freilandexperimente vorgestellt, die — aufbauend auf den Erfahrungen aus diesem Vorversuch — ab 1976 in Angriff genommen werden.

Introduction

Long-term investigations on the biological processes in a shallow subtidal macrobenthos community are primarily complicated by 2 circumstances (in addition to the usual hydrographical instability of such areas):

(1) The difficulty in returning repeatedly to exactly the same position, especially in areas where depth and bottom sediments vary. Even with modern navigation techniques one can easily miss an exact position by 50 m, the result being the possible collection of samples from a different habitat.

(2) The second complication originates from the great complexity of systems already established, resulting in our failure to understand the fluctuations in the community structure. This difficulty can be overcome by reducing the number of possible interactions, that is by creating a more or less artificial habitat in which the number of the different ecological elements (for example the number of species or faunal groups) is considerably reduced. One way to investigate a simpler system is to culture one or several species in aquaria; but data from such observations do not necessarily apply to natural conditions because of the technical problems associated with the intended imitation of the natural environment (especially the food supply).

Another approach to the investigation of community processes under controlled conditions are in situ experiments on the sea bottom. By the exposure of sterile substrates a developing association can be studied from the very beginning through increasing stages of complexity and to a certain extent manipulated without inducing "unnatural" environmental conditions. This second way was chosen as a means to follow up the establishment and succession of a new zoobenthos association and the population dynamics of the most abundant species. The aim was to obtain precise data on benthic turnover and to gain a more comprehensive understanding of the mechanisms leading to the community changes observed in the natural environment.

A protected research area "Hausgarten" (fig. 1) was created in 1971 near the entrance of Eckernförde Bay — one and a half hours by ship from Kiel — as a location for field experiments of the "Joint Research Programme (SFB 95)". It concludes a depth range of 8—22 m and is situated on the northern slope of the major channel of Kiel Bight, where the environmental conditions are representative of large parts of Kiel Bight (ARNTZ, BRUNSWIG & SARNTHEIN, 1976).
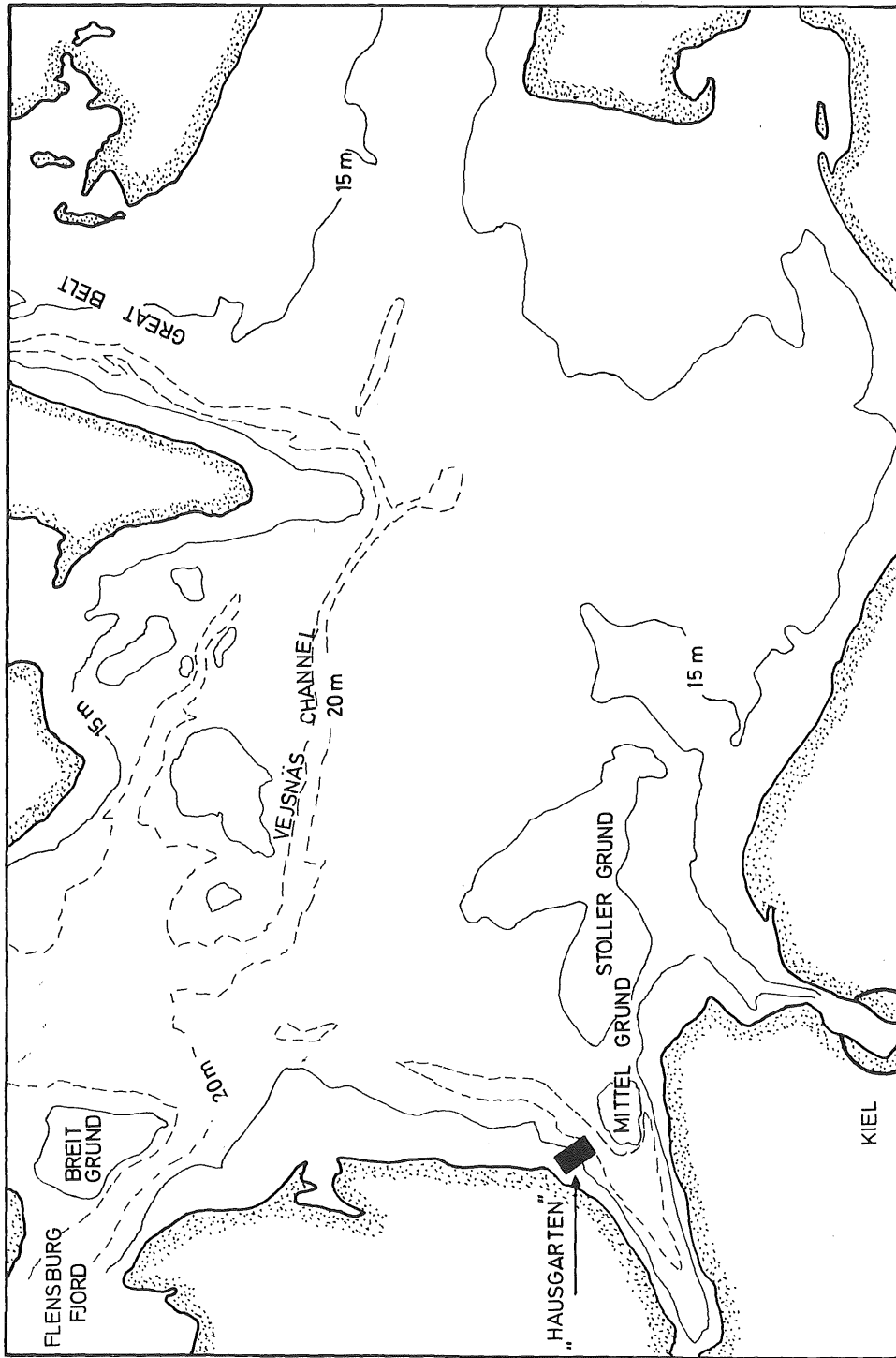
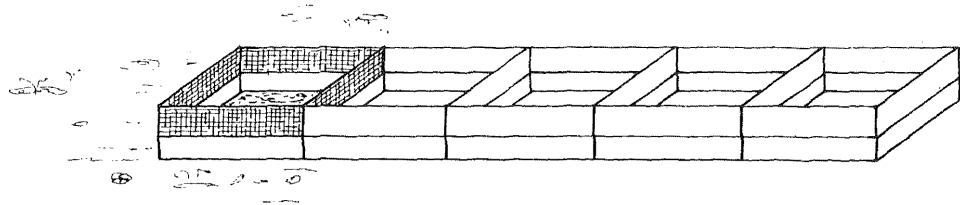Fig. 1: Kiel Bight and "Hausgarten" research area.

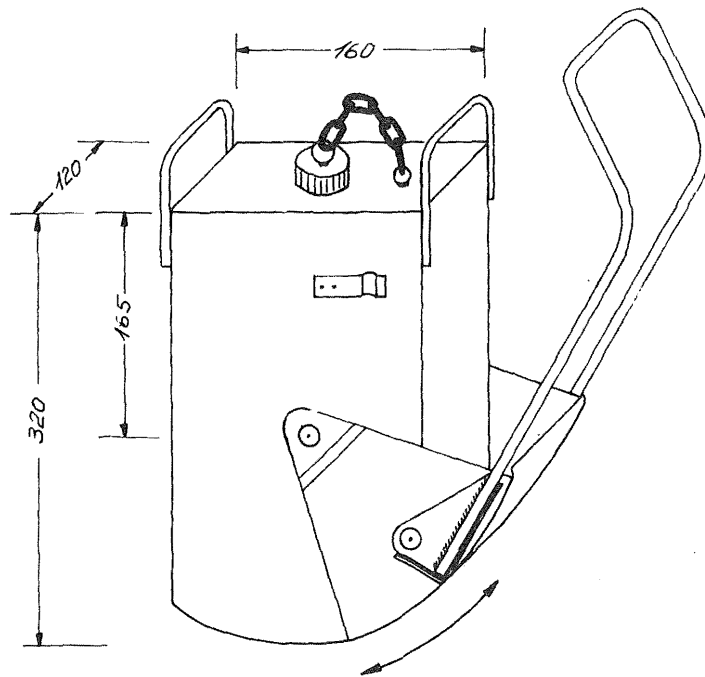Fig. 2: The "benthos boxes".

Fig. 3: The diver-operated corer. All distances are in millimetres.

Material and methods

Five open metal boxes (stainless steel, 1 m² area each, 60 cm high steel wall, the lower half being solid and the upper half meshed, cf. fig. 2) were exposed at a depth of 20 m where the natural sediment is muddy sand (WEFER, 1974). The benthos boxes were filled to a depth of 30 cm with sediment taken from the surrounding habitat and "sterilized" by air drying for several months. These sterile substrates were exposed in September and October 1972 — at a time when the concentration of meroplanktonic larvae in the plankton was still high (MARTENS, 1975).

For the first annual cycle, samples were taken from the boxes eight times at monthly or bimonthly intervals between June 1973 and May 1974. On each sampling date, one 192 cm² sample was collected from each box with a diver-operated mechanical corer (fig. 3). After another seven months, in January 1975, two boxes were completely emptied with a suction sampler for comparison of the associations in different containers and to provide more comprehensive material for size-frequency analyses of the most abundant species.

Then, on four occasions between March and July 1975, a 0.5 m² sample from one of the remaining full boxes was taken by the suction technique. All samples were washed over a 0.5 mm² screen and preserved in buffered formalin. After sorting, the mollusks were kept in alcohol to avoid dissolution of the shells. The macrofauna species were identified, and individual length and total wet weight were recorded.

The comparison of five replicate samples (table 1) does not show high variations. Regarding species numbers, two boxes (i.e. one out of ten possible combinations) differ somewhat from each other: $s_{box\ 1} > s_{box\ 3}$. There are some little differences concerning the biomass data (two-sided U-test after WILCOXON, MANN and WHITNEY; level of significance $\alpha < 0.20$ in each case): $b_{box\ 5} > b_{box\ 2,\ 3,\ 4}$ and $b_{box\ 1} > b_{box\ 2,\ 3}$. In no case do the density values differ from each other. Because of this fair agreement in the state of colonization between the individual containers, the five corer samples were combined in order to get sufficient data for the interpretation of succession.

Results

Succession

Species succession

If we consider the number of species per unit area, some final state is possibly reached in January 1974 (16 months after exposure). After then, the values per 0.1 m² keep between about 20 and 25.

The specimen number does apparently not reach a steady state during the whole period (fig. 4, above). The lower curve does not include the specimen number of the most dominant species. The cumacean *Diastylis rathkei* is the most abundant species during the first year. The decline of the curve in September and December 1973 is preceded by a period of several weeks of oxygen deficiency (VON BODUNGEN, 1975). This, together with the explosive increase of the populations of spionid worms (1973/74) and of *Abra alba* and *Nephthys spp.* (1975), leads to extreme fluctuations in abundance. The final values in 1975 hardly exceed those of December 1972.

The biomass values of the macrofauna are increasing continuously (fig. 4, below). In the second year of exposure the species dominating by weight are *Pectinaria koreni*, *Abra alba* and *Nephthys spp.* The biomass of *Asterias rubens* exceeds the weight of all other invertebrates by far from March 1975 onwards, while the rest of the fauna stays fairly constant in weight after January 1975.

Table 1

Comparison of species number (s), specimen number (n) and biomass (b) in 0.02 m² corer samples taken at the same date from the five benthos boxes, "Hausgarten", 20 m depth. Values in ( ): rank number among the five replicate samples; biomass: in $g \cdot 0,1 \, m^{-2}$

		VI/73	VII/73	IX/73	X/73	XII/73	I/74	IV/74	V/74	Sum	Average per sampling date	Sum of rank numbers
Box 1	s	5 (3.5)	11 (1)	6 (1)	7 (2)	3 (4)	15 (1)	8 (2.5)	7 (5)	23	7.8	20
	n	11 (4)	36 (2)	11 (1)	9 (4)	4 (4)	108 (1)	11 (4)	41 (3)	231	28.9	23
	b	7 (4)	23 (2)	19 (1)	23 (1)	4 (4)	66 (1)	21 (2)	38 (2)	201	25.1	17
box 2	s	5 (3.5)	10 (2)	4 (2.5)	4 (4.5)	3 (4)	9 (3)	4 (5)	9 (2)	21	6.0	26.5
	n	17 (2)	42 (1)	5 (4)	6 (5)	4 (4)	60 (2)	10 (5)	25 (4)	169	21.1	27
	b	8 (3)	26 (1)	8 (4)	7 (5)	6 (3)	16 (4)	15 (4)	16 (4)	102	12.8	28
box 3	s	4 (5)	8 (3)	3 (4.5)	5 (3)	5 (2)	4 (5)	5 (4)	11 (1)	17	5.6	27.5
	n	6 (5)	28 (3)	8 (2.5)	18 (2)	6 (2)	11 (5)	12 (3)	59 (1)	158	19.8	23.5
	b	6 (5)	16 (3)	9 (3)	10 (4)	9 (2)	11 (5)	12 (5)	23 (3)	106	13.3	30
box 4	s	6 (2)	4 (4)	3 (4.5)	4 (4.5)	3 (4)	11 (2)	11 (1)	8 (4)	18	6.3	26
	n	20 (1)	6 (4)	8 (2.5)	14 (3)	4 (4)	28 (3)	28 (1)	15 (5)	123	15.4	23.5
	b	10 (1)	9 (4)	7 (5)	11 (3)	3 (5)	25 (3)	33 (1)	11 (5)	109	13.6	26
box 5	s	7 (1)	1 (5)	4 (2.5)	8 (1)	6 (1)	7 (4)	8 (2.5)	8 (3)	18	6.1	20
	n	14 (3)	2 (5)	3 (5)	22 (1)	28 (1)	25 (4)	17 (2)	43 (2)	154	19.3	23
	b	9 (2)	6 (5)	12 (2)	21 (2)	38 (1)	43 (2)	20 (3)	59 (1)	208	26.0	16
Sum (box 1 to box 5)	s	10	14	11	14	17	19	15	18			
	n	68	114	35	69	46	232	78	183			
	b	40	80	55	72	60	161	101	147			
Average per box	s	5.4	6.8	4.0	5.6	4.0	9.2	7.2	8.6			
	n	13.6	22.8	7.0	13.8	9.2	46.4	15.6	36.6			
	b	8.0	16.0	11.0	14.4	12.0	32.2	20.2	29.4			
Coefficient of variation	s	21.1	61.9	30.5	12.0	35.3	45.1	38.6	17.7		32.⸱%	
	n	39.8	78.5	44.0	39.3	114.5	56.9	47.7	111.8		66.6%	
	b	19.8	53.9	48.5	49.4	149.5	69.7	39.8	66.1		62.1%	

$V\% = \dfrac{s}{\bar{x}} \cdot 100$

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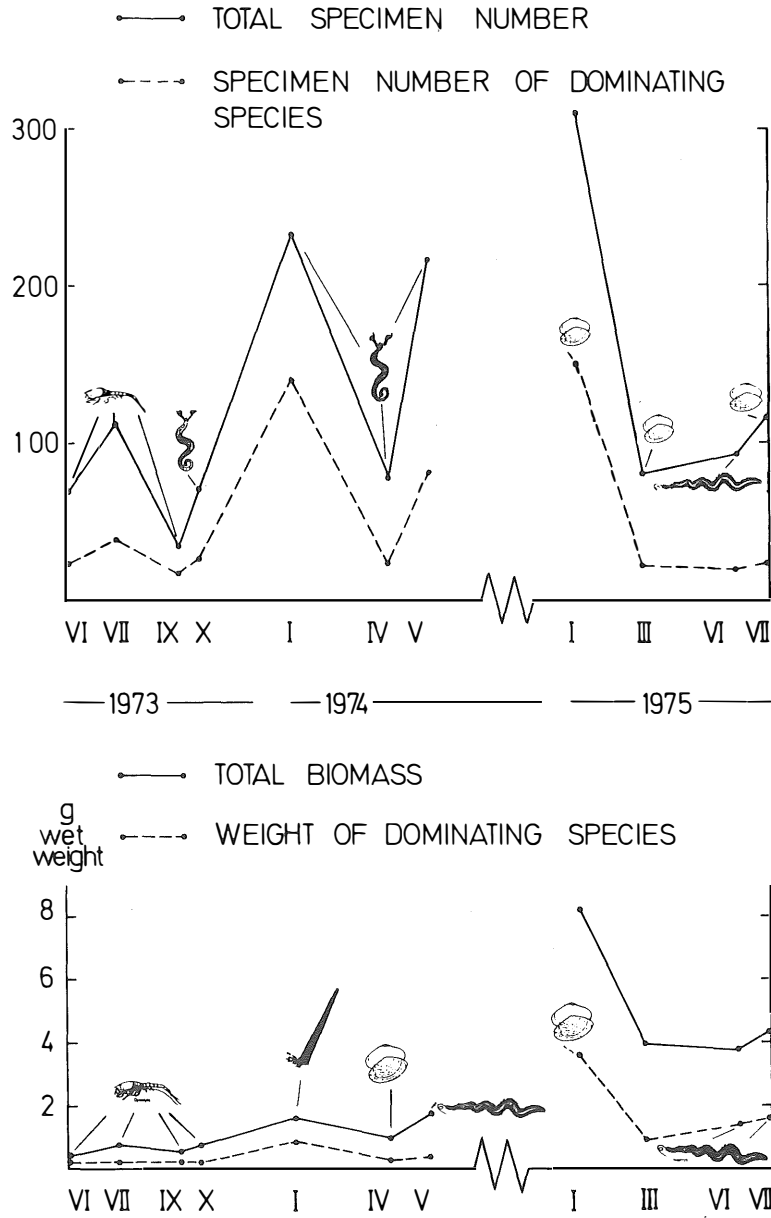
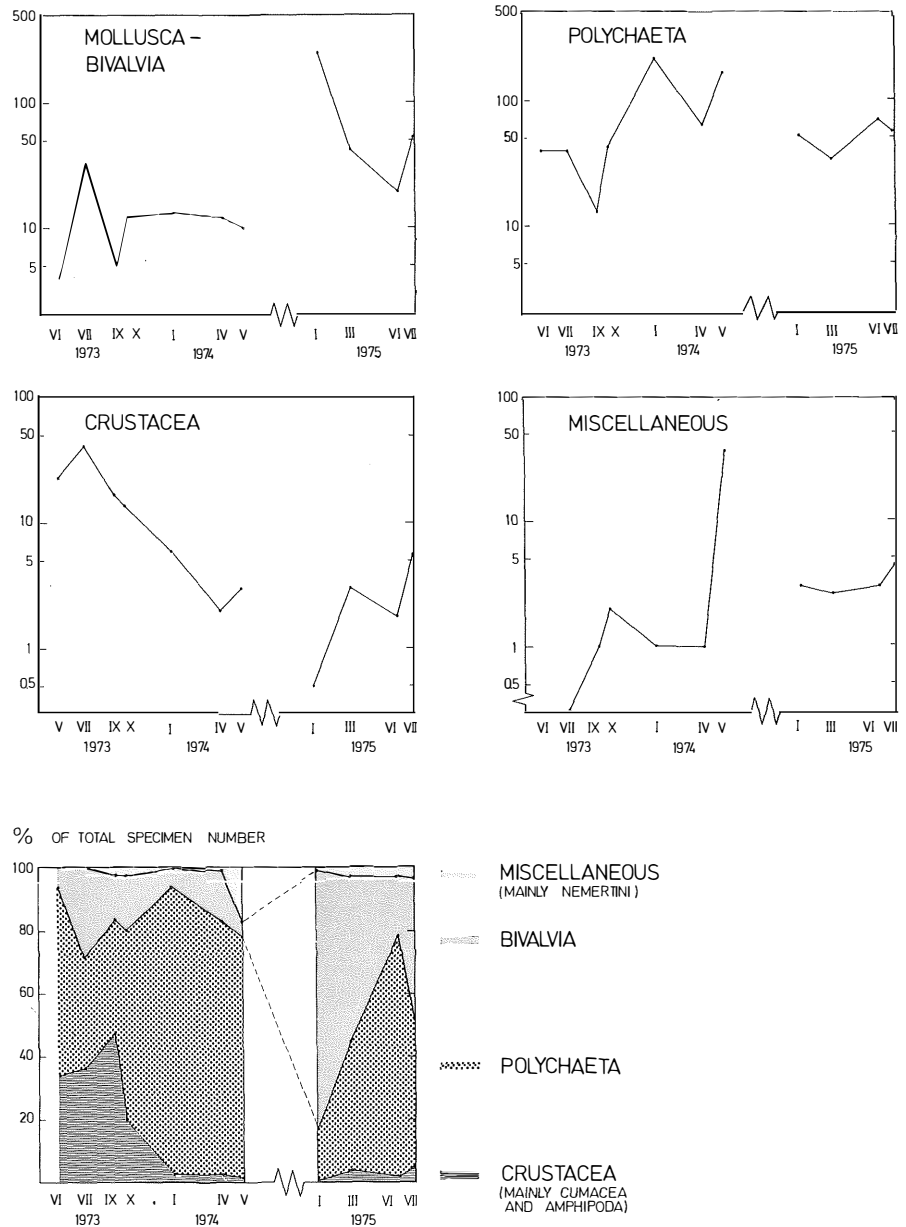Fig. 4: Variation in total specimen number and biomass, and sequence of dominating species (all values per 0.1 m²).

Fig. 5: Variation in specimen numbers of major taxonomic groups (n per 0.1 m²).
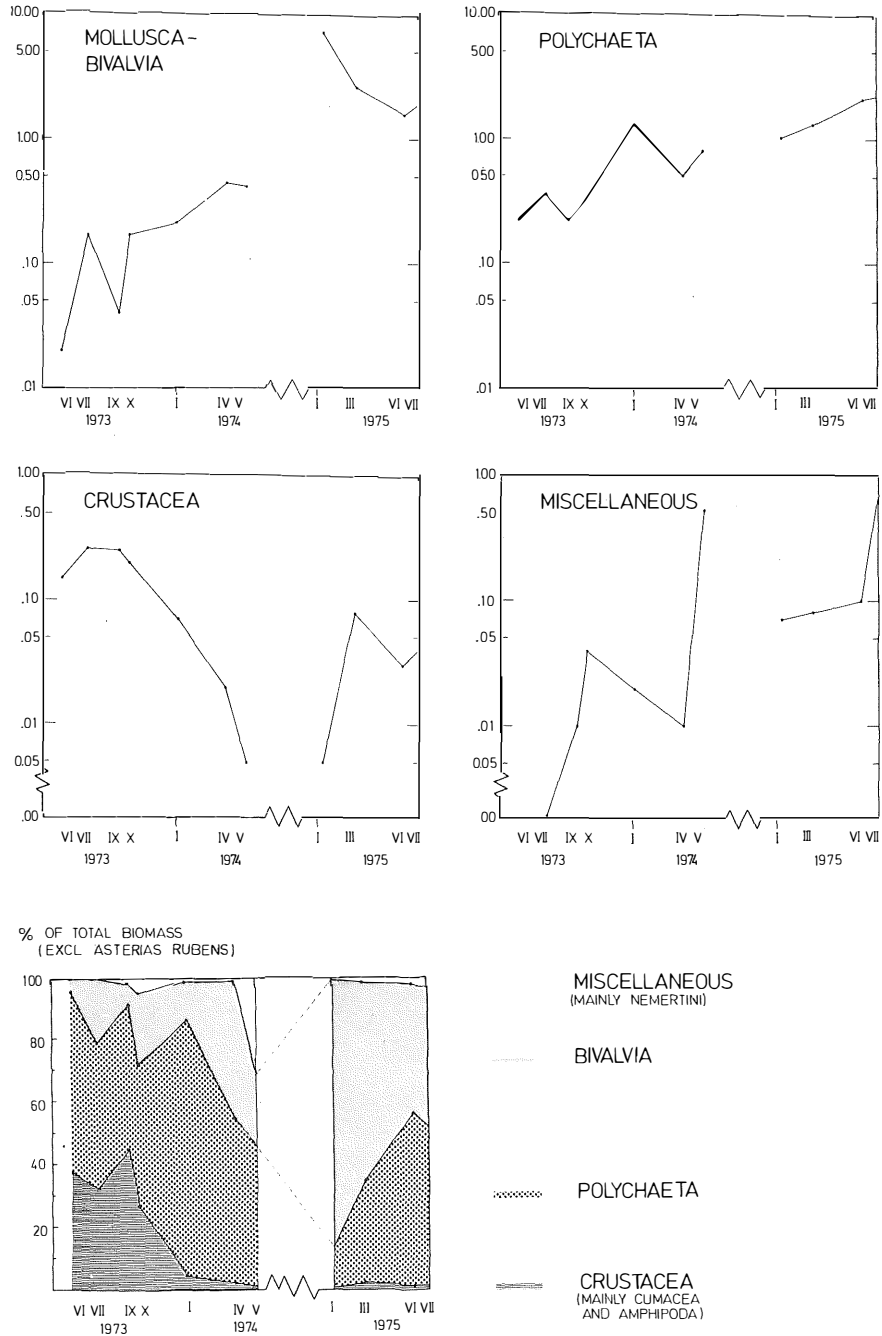
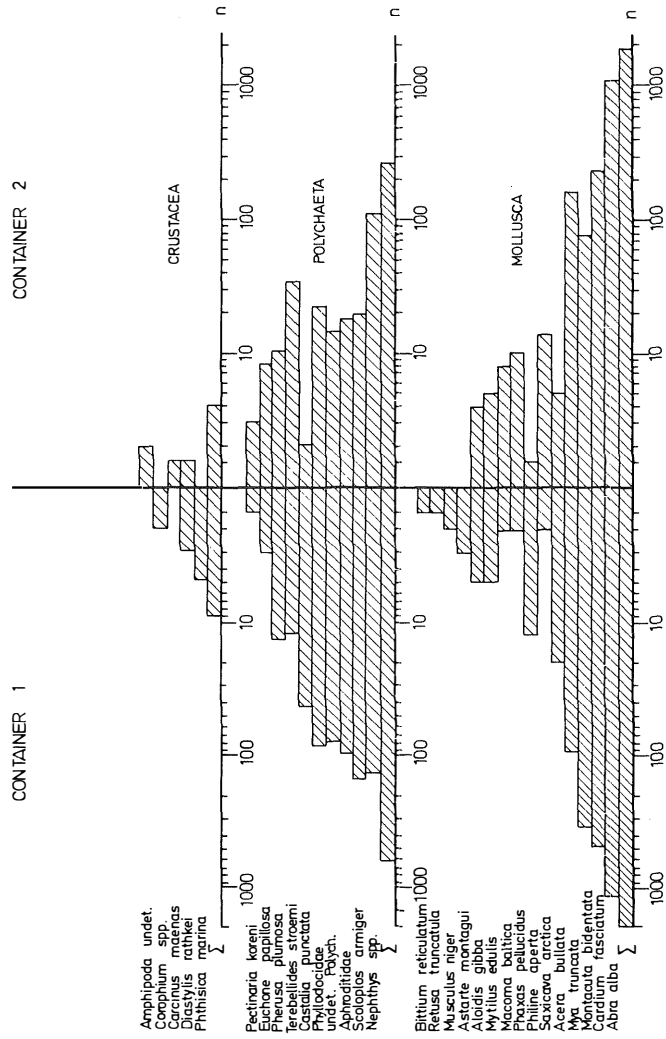Fig. 6: Biomass variation of major taxonomic groups (g wet wt. per 0.1 m²).

Fig. 7: Comparison of macrobenthos species pattern in two experiment containers after 15 months exposure (n/m⁻², "Hausgarten", 20 m).

Succession of faunal groups

For the numerical contribution of different faunal groups (fig. 5), we can distinguish several principally different phases: During the first year of the experiment, crustaceans (mainly the cumacean *Diastylis rathkei*) and polychaetes prevail. During the succeeding seven months, until May 1974, the polychaetes alone contribute the highest share to the total number. Their decrease in the following summer is preceded by a strong development of the nemertean populations. The polychaetes' numerical dominance is then taken over (until January 1975) by the bivalves. Simultaneously, starfish (*Asterias rubens*) appear in greater numbers and reach a peak of 8% of the total number during the following months, while the bivalve number decreases considerably until June (the increased occurrence of the starfish in 1975 reflects to some extent the change in sample size from 0.1 to 0.5 m²).

The change of biomass values within the different faunal groups exhibits a similar pattern of succession (fig. 6). As a major difference from the numerical data, during the last half year of the experiment, the biomass of the echinoderms (mainly *Asterias rubens*) increased to more than 70% of total biomass. This is due to the increase of the average individual weight from 0.5 to 2.1 g. In the same period, the mollusk biomass shows a reverse trend ($\alpha < 0.01$ for negative rank correlation after SPEARMAN) while their share of total number is increasing again between June and July, after a new spatfall in spring. The polychaete and nemertean biomass, however, seems to keep to a fairly constant value.

Final species pattern

The numerical faunal composition during the phase of *Abra alba* dominance (as in January 1975) is demonstrated in fig. 7. A surprisingly similar species pattern developed in both 1 m² boxes. Indeed, all of the more abundant species are common to both containers, and the rank order of the dominating species is nearly the same. Only the very rare species show greater deviations. The number of species in each container amounts to between 40 and 45.

Faunal comparison between boxes and surroundings

Between June 1973 and May 1974, three 0.02 m² corer samples were taken from the surrounding sea floor parallel to the samples from the boxes. In January and March 1975 larger reference samples from the surrounding area were taken (0.1 m² van Veen grab) according to the increased size of the box samples.

In summer 1973, the total number of specimens in the boxes amounted to about 20% of that of the natural sea bottom (table 2). This is mainly due to a greater abundance of the bivalves *Astarte spp.* and *Abra alba* as well as sedentary polychaetes. From September 1975 on, however (coinciding with the decrease of oxygen in the deeper water layers), there is a sudden development of spionids resulting finally in higher density values in the boxes in April and May 1974. Also in spring 1974 the group Errantia (mainly *Castalia punctata*) and various nemerteans are much more abundant in the experimental containers, while bivalves are present in significantly lower numbers.

In January 1975, from a comparison of the individual species' biomass, it can be seen that succession on the originally animal-free substrates during the phase of bivalve dominance — after a period of 28 months — has not resulted in an association similar to that in the field outside (fig. 8; the values of the surrounding area are extrapolated

Table 2

Faunal composition in the benthic boxes (A) and the surrounding area (B) — All values are the mean of two sampling dates (IX/73 — I/74: four dates) and refer to a 0.1 m² area.

A. *Benthos boxes*: Values from five 0.02 m² corer samples (VI/73 — V/74), from two 1 m² suction samples (I/75) and from one 0.5 m² suction sample (III/75).

B. *Surrounding area*: Values calculated from two 0.02 m² corer samples (VI/73 — V/74) and from two 0.1 m² van Veen grab samples (I—III/75)

Species or group	VI—VII/73 A	VI—VII/73 B	IX—I/74 A	IX—I/74 B	IV—V/74 A	IV—V/74 B	I—III/75 A	I—III/75 B
Polynoidae (mainly *Harmothoe sarsi*)	2.5	(4.6)	1.5	(9.1)	12.0	(0.3)	5.3	(0.0)
Phyllodocidae (*Anaitides mucosa, Eteone longa, Mysta barbata*)	3.0	(0.0)	3.5	(6.6)	7.0	(0.1)	3.1	(2.5)
Castalia punctata	3.5	(6.7)	5.0	(2.5)	14.0	(2.5)	1.2	(0.0)
Nephthys spp.	3.5	(21.3)	2.3	(12.5)	6.0	(6.5)	11.5	(4.0)
ERRANTIA, total	12.5+	(32.6+)	12.5+	(32.4+)	39.0+	(9.4+)	21.2+	(6.6+)
Scoloplos armiger	14.0	(35.5)	0.0	(10.9)	3.5	(11.7)	10.4	(6.0)
Spionidae	0.0	(21.3)	47.5	(5.9)	53.0	(0.1)	0.0	(0.5)
Pectinaria koreni	0.0	(0.0)	10.7	(22.5)	5.0	(4.5)	0.3	(58.0)
Terebellides stroemi	0.0	(23.7)	0.0	(0.9)	0.0	(0.3)	1.7	(2.1)
SEDENTARIA, total	14.0+	(183.5+)	60.5+	(53.5+)	62.0+	(21.4+)	14.3+	(76.6+)
Undet. Polychaeta	13.0	(9.3)	1.5	(4.1)	0.5	(2.3)	6.2	(3.0)
POLYCHAETA, total	39.5	(225.4)	74.5	(90.0)	101.5	(33.0)	41.8	(86.3)
Diastylis rathkei	31.0	(84.3)	8.5	(35.0)	2.0	(2.6)	0.8	(1.9)
Amphipoda	1.0	(1.6)	0.3	(0.0)	0.5	(4.0)	0.7	(2.5)
CRUSTACEA, total	32.0	(85.9)	9.5	(35.0)	2.5	(6.9)	1.9	(4.8)

Astarte spp.	1.0	(32.3)	0.7	(38.4)	0.5	(12.3)	0.3	(8.5)
Cyprina islandica	0.5	(0.0)	0.0	(5.9)	0.0	(1.5)	0.0	(4.0)
Montacuta bidentata	11.5	(14.3)	1.3	(78.4)	0.0	(37.0)	8.7	(50.0)
Cardium fasciatum	0.0	(5.9)	0.3	(0.9)	3.0	(2.0)	21.2	(7.0)
Abra alba	4.5	(65.6)	5.5	(110.0)	4.0	(14.0)	71.2	(96.0)
Macoma baltica	1.5	(0.9)	0.2	(0.9)	2.0	(12.5)	0.3	(0.4)
Macoma calcarea	0.0	(10.9)	0.0	(12.5)	0.0	(4.0)	0.0	(2.4)
Mya truncata	0.0	(12.5)	0.0	(6.6)	0.5	(2.6)	11.2	(4.4)
BIVALVIA, total	19.0	(151.5)	8.0	(257.6)	10.5	(89.5)	115.4	(188.9)
MOLLUSCA, total (incl. Gastropoda)	19.0	(151.5)	8.0	(257.6)	10.5	(89.5)	124.7	(194.7)
Asterias rubens	0.5	(0.0)	1.5	(0.0)	1.0	(0.0)	7.2	(1.1)
Ophiura albida	0.0	(5.0)	0.0	(5.9)	0.5	(4.0)	0.2	(12.0)
ECHINODERMATA, total	0.5	(5.0)	1.5	(5.9)	1.5	(4.1)	7.4	(13.1)
NEMERTINI, total	0.0	(2.5)	0.5	(1.6)	14.5	(1.3)	1.5	(4.6)
Other phyla (Anthozoa, Priapulida, Tunicata)	0.0	(1.8)	1.1	(3.4)	0.0	(1.4)	1.0	(3.5)
Total specimen number	91	(47)	96	(394)	130	(136)	179	(307)

from three 0.1 m² van Veen grab samples). In the boxes, many errant polychaetes, fast growing clams, and predatory species comprise a greater share, while in the field long-lived bivalves (the *Astarte* species, *Cyprina islandica*), mysids, *Ophiura albida* and also *Pectinaria koreni* exhibit a greater biomass. The total biomass of the macrobenthos outside the boxes (200 g/m²) is twice as high as that inside. 75% of the high biomass value of the natural sea bottom is due to the long-lived and slowly growing clams *Astarte borealis* (90 g/m²) and *Cyprina islandica* (60 g/m²). In contrast, fast growing and short-lived bivalves (*Abra alba* and *Cardium fasciatum* 31 g/m²) dominate inside the boxes, accompanied by a high starfish biomass (40 g/m²). These differences are also reflected in terms of specimen numbers.

Growth

Species succession in a soft bottom community is the result of many single processes influencing each other, such as (1) sequence and (2) density of spatfall, (3) elimination of the recruited animals by competition and grazing as well as (4) differences in specific and seasonal growth rates. Studies on the items (3) and (4) became possible only after we had started the 0.5 m² sample series. Despite the large sample size, growth estimation from length-frequency distributions was merely possible for a few of the most abundant species, as shown for *Abra alba*, *Cardium fasciatum* and *Mya truncata* for the final period in fig. 9. In January 1975, nearly all the specimens of *Abra alba* belong to only one age group, the recruits of 1974. In July, the first settled individuals of the new age group of 1975 have reached a length of about 1 mm and are retained by the 0.5 mm screen. Unfortunately the time of larval settlement ranges over seven months (from April until October) thus making the evaluation of growth and mortality rates very difficult. The 1974 age group of *Abra alba* shows a length increase from about 5 mm in January to about 8 mm in July (figs. 9 and 10). *Cardium fasciatum* grows much more slowly: from 1—2 mm to a length of 2—5 mm during the same period. In *Mya truncata*, where two or three age groups overlap, the growth rates cannot be determined by this material.

In fig. 10, the seasonal variation of individual weight is shown for the 1973 year class of *Abra alba*. Growth nearly ceases in winter and early spring and accelerates tremendously in the second half of the year. Only a few specimens reach an age of more than one year and over 12 mm in our boxes (the observed maximum values being 18 mm and over two years in Kiel Bay); this indicates intensive predation pressure on this species.

Mortality

From the density data ("total number") in fig. 9, a rapid decrease in population size (number and weight) in early 1975 is seen for the three species while the starfish population quadruples its weight. Until May, before the new year class of the bivalves appears in the samples, no more than 6% of the individuals of the *Abra alba* population present in January have survived. For *Cardium fasciatum*, the respective value is 9%. *Mya truncata*, which lives deeper in the sediment is not decimated to such a high extent (35% survival).

Bivalve Production

For the last period of the experiment, the graphical ALLEN method for production assessment (ALLEN, 1950) is applied on the data of density and length-frequency distribution for the three bivalves mentioned. For this first half of the year, the square metre pro-

MACROBENTHOS SPECIES PATTERN (BIOMASS) IN THE BENTHOS BOXES AND
SURROUNDING AREA
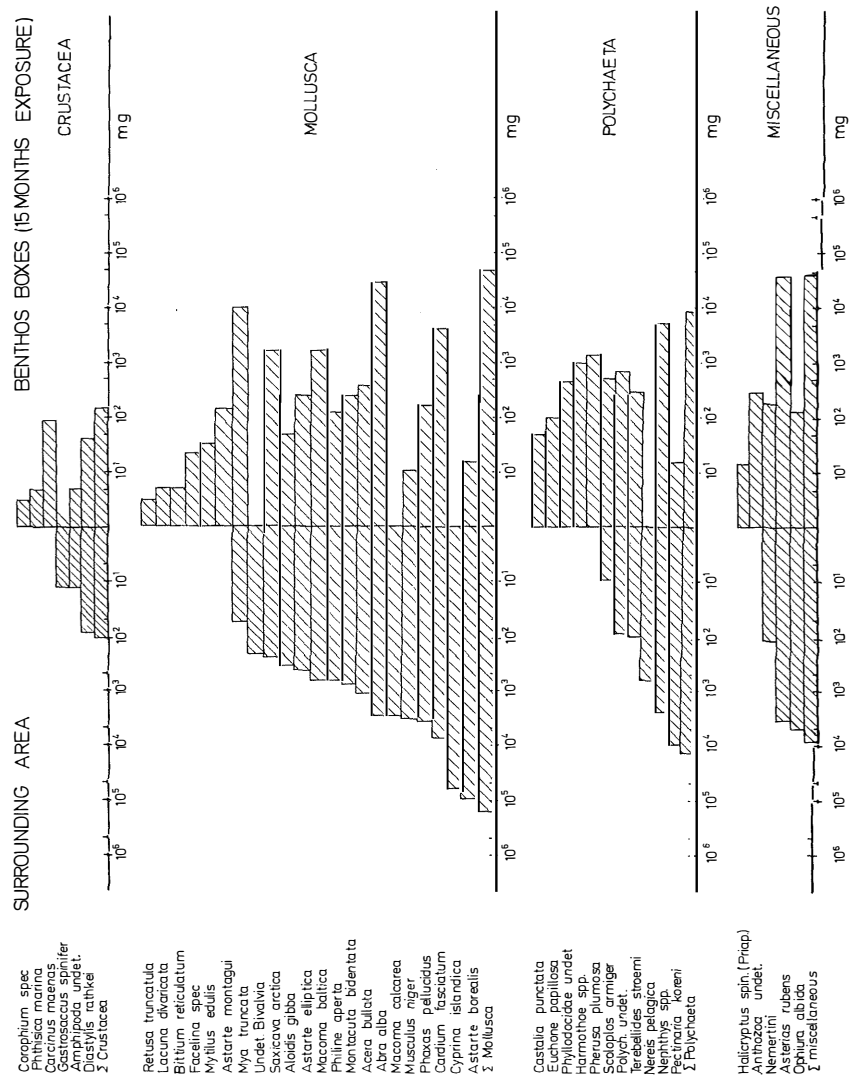mg/m², "HAUSGARTEN", 20m, JAN.
1975

Fig. 8: Macrobenthos species pattern (biomass) in the benthos boxes and surrounding area (mg/m²,
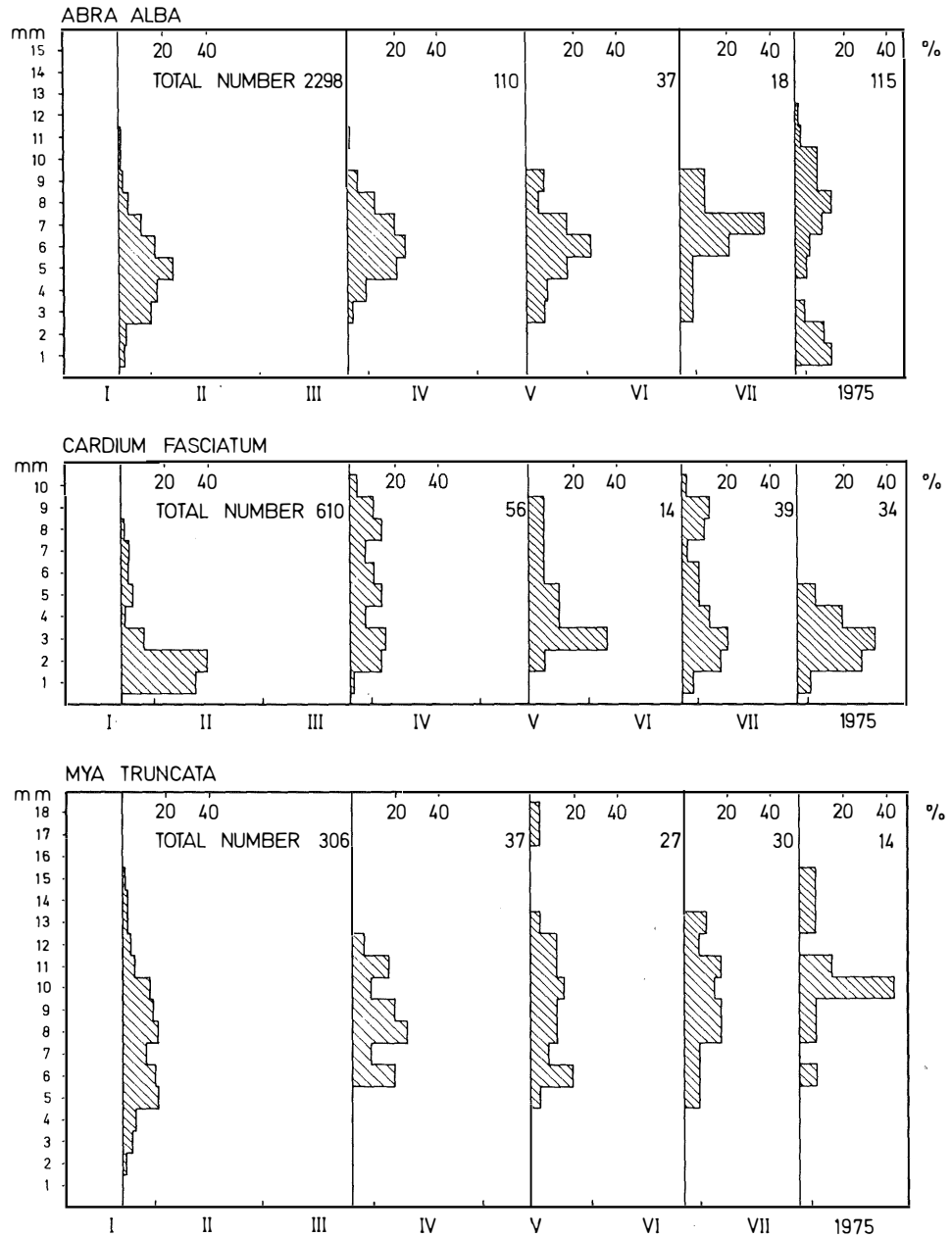"Hausgarten", 20 m, Jan. 1975)

ABRA ALBA

CARDIUM FASCIATUM

MYA TRUNCATA

Fig. 9: Length-frequency distribution of the most abundant bivales, 0.5 m² samples from benthos boxes (I/75:2 m²), 20 m depth.

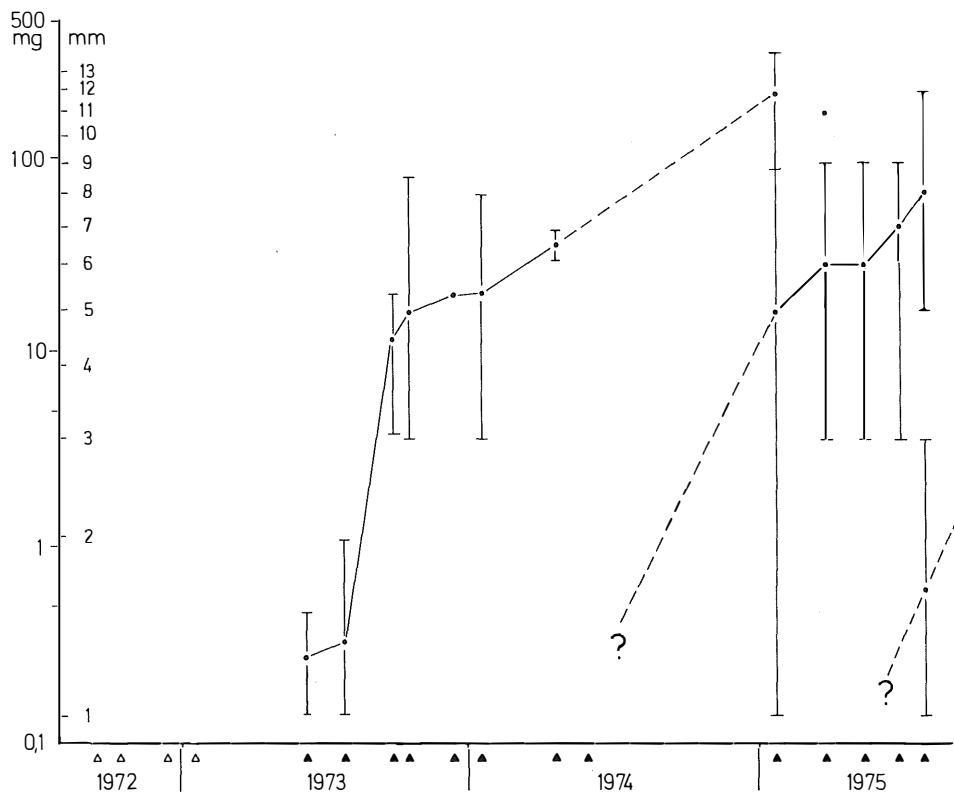Fig. 10: Albra alba, growth in benthos boxes, 20 m depth.

PROTECTED RESEARCH AREA

" HAUSGARTEN "

NN

5

10 DEPTH
m
15

20

8

10

12

14
16
18
20
22

BENTHOS EXPERIMENTAL AREA

0   100 200
m

↟ AREA BUOY

⬥ MOORING BUOY

TILL
LAG SEDIMENT (SAND & STONES)
MUDDY SAND
SANDY MUD

11 m ⊥

submerged substrate platforms
16 m ⊥

sensor platform

elevated small experimental
containers

19 m ⊥

small experimental
containers

algae retaining fence
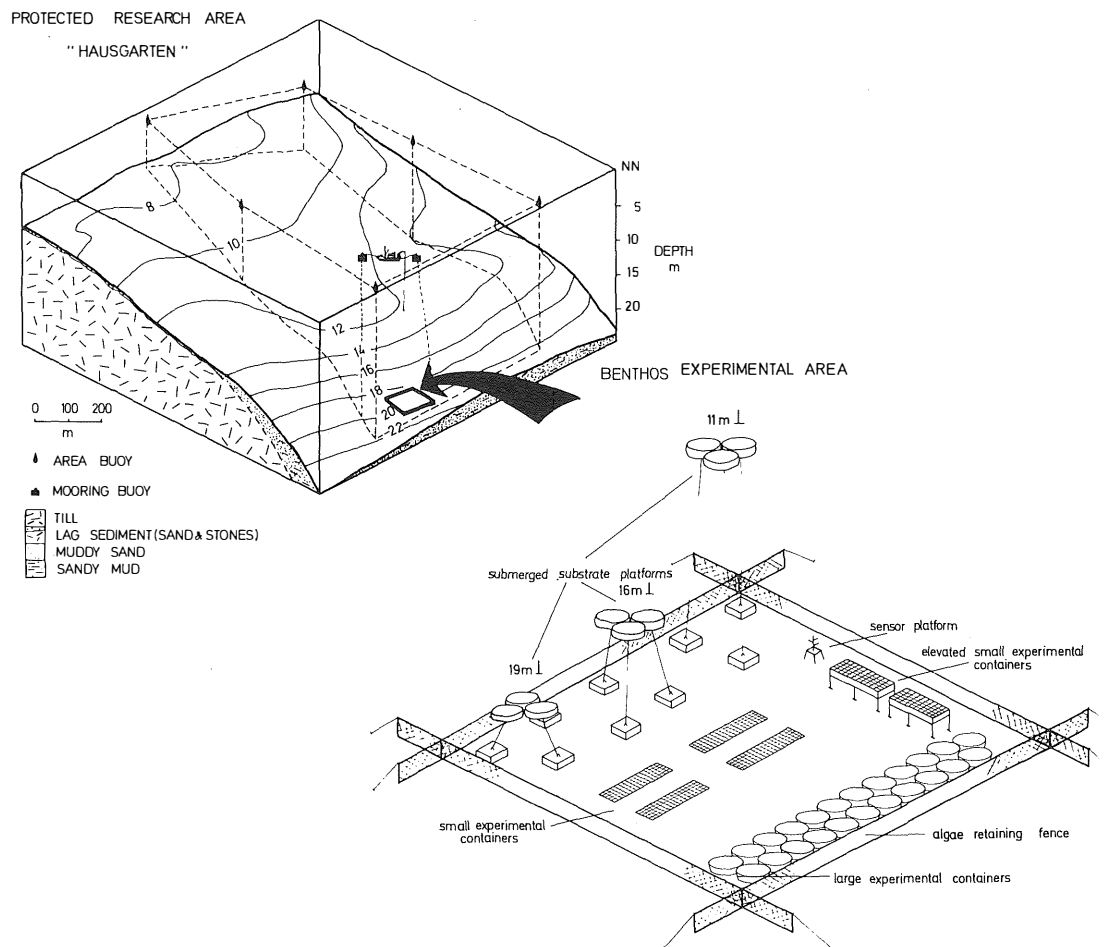
large experimental containers

Fig. 11: Protected research area "Hausgarten" and benthos experimental area.

duction of total wet weight amounted to 13 g for *Abra alba*, 6 g for *Mya truncata* and 3 g for *Cardium fasciatum*. The respective values of g carbon living tissue are 0.34 g, 0.15 g and 0.07 g (cf. BRUNSWIG, 1973). From these data and the weight proportion of the three species to total bivalve biomass, the total bivalve production for the first 6 months of the year can be estimated to be 24 g wet weight (0.61 g C living tissue).

Discussion

The succession observed in the boxes is apparently influenced by a different combination of ecofactors effective during subsequent periods, and by the experimental design itself.

During the initial periods of colonization the motility of the individual species is of utmost importance. This applies to the cumacean *Diastylis rathkei* and epibenthic polychaetes of the Errantia group (e.g. *Harmothoe sarsi*) which contribute a greater share to the fauna in the boxes, while Sedentaria and bivalves occur only in low numbers. Species without or with only a short pelagic stage of laval development, e.g. the three *Astarte* species and *Macoma calcarea*, are very rare on the artificial substrates.

The second phase (polychaete dominance) is the result of early colonization, high initial settling densities of the successful populations, and a fast growth of the recruits. Because of their longer life span and higher individual weight the bivalves catch up gradually, being the most important group at the beginning of the third phase. The decrease of the polychaetes before January 1975 might be due to the preceding increase in the nemertean populations.

The period of bivalve dominance is also quite short; the clams — mainly the thin-shelled, fast growing species — are probably severely decimated by *Asterias rubens*, which is known to prefer bivalves to other bottom invertebrates (THORSON, 1957; MEYER, 1976). There are no observations as to what extent flatfish predated on the clams. Generally the macrobenthos invertebrate predators (*Asterias rubens*, *Polynoidae*, various nemerteans, *Carcinus maenas*), scavengers (*Buccinum undatum*) and gobies are significantly more abundant in the boxes. The high concentration of predators which greatly influences the success of the other invertebrate species must be assumed to be the effect of a secondary hard bottom on the sea floor, as has also been shown by ARNTZ (1976) for a simultaneous cage experiment.

Another factor affecting succession is oxygen deficiency, occurring annually in late summer. The sharp decline of the biomass and density values in autumn 1973 is due to an extraordinarily low oxygen tension from August until October. It took the fauna of the neighbouring sea floor about nine months to regain normal levels of abundance.

As can be seen from the abundance data for *Abra alba*, *Pectinaria koreni*, and *Diastylis rathkei*, the differences in recruitment from year to year also influence succession. The low numbers of *Diastylis rathkei* in the containers during the second and third year presumably reflect both low recruitment and high mortality by predation.

A succession following the same pattern (Polychaeta — Mollusca — Echinodermata) was observed by ROSENBERG (1972, 1973), who studied the succession in a recovering macrobenthos community in a Swedish fjord, after the closure of a pulp mill. The different first phase described in this study (polychaetes tolerating pollution rather than crustaceans) might be explained by the fact that ROSENBERG's seabed was not yet in an unpolluted state at that time. The association needed about five years for full recovery; this is in good agreement with the results of the above experiments, that in spite

of a positive development the biomass of the fauna inside the boxes had only reached one half of the value outside after three years.

The total biomass fluctuates seasonally. The spatfall of the larvae in spring and summer as well as an accelerated individual growth of most species in the second half of the year due to higher water temperatures — result in maximum values of population weight in autumn and early winter. Afterwards, population growth is less than losses by predation which leads to minimum biomass data in March and April. —

Many problems concerning the structure and dynamics of Kiel Bight macrobenthos could not be examined by these provisional field experiments, but additional experimental work in the next years can now be based on some experience. A new set of experiments has been designed to answer more closely defined questions. We will concentrate on an experimental field within the protected research area of SFB 95 (fig. 11). This site of the experiment — again at 20 m depth — is surrounded by a fence to prevent large drifting algae from covering the containers. The "submerged substrate platforms" (SARNTHEIN & RICHTER, 1974; RICHTER, 1975) have been included in this area. A long-term study of colonization and succession in a bottom community will be undertaken in large benthos containers (1.5 m diameter), filled with sterile sediment from gravel pits corresponding to the grain size composition found at the respective water depth. Sampling will be carried out every two months (at shorter intervals during the first six months) for four years. Small containers (12 cm diameter), some dug into the sediment, others put on elevated platforms, will be used to clarify the events of initial colonization and early growth. Simultaneously we hope to get information on the growth of important mollusk species by implantation of tagged specimens. Parallel investigations on meiofauna and sediment chemistry will give us additional data on the quality of and changes in and above the sediment. Environmental parameters ($T^\circ C$, $S^0/_{00}$, O_2, light) will be recorded by sensors and hydrographic transects. We hope, that the Joint Research Programme will provide a substantial part of the data needed to determine the processes involved in the turnover of matter in the macrobenthos soft bottom community of the Western Baltic.

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