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Arctica (Cyprina) islandica in Kiel Bay (Western Baltic): growth, production and ecological significance

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Abstract: The growth of the ocean quahog *Arctica islandica* L. was investigated with data from two sites of Kiel Bay, Western Baltic. At the experimental site "Benthosgarten" (BG), length-increment data were obtained from a colonization experiment and from implanted and resampled clams. At the "Millionenviertel" site (MV), clams were caught by dredging. Length-increment data were obtained from annual growth bands formed at the surface of the shell. A Von Bertalanffy growth function was fitted to both data sets. Growth at the BG site ($K = 0.35$, $L_{\infty} = 60.6$ mm) was different from that at the MV site ($K = 0.07$, $L_{\infty} = 93.6$ mm). The BG site growth parameters are assumed to be strongly biased due to the experimental set-up. Growth of the MV site population is similar to Atlantic populations of *A. islandica* but maximum age and length are much smaller in Kiel Bay. The annual P/\bar{B} ratio of the MV site population was estimated to be 0.34, which results in an annual production of 15 g AFDW \cdot m⁻² in this particular area. Total annual production in Kiel Bay is estimated at \approx 11 000 t AFDW, \approx 40% of the estimated annual benthic community production. *A. islandica* is eaten mainly by cod *Gadus morhua*. During 1970–85, \approx 40% of the annual production of cod in Kiel Bay is estimated to have depended on this clam.

Key words: *Arctica islandica*; Baltic; Demersal fish; Secondary production

INTRODUCTION

The ocean quahog *Arctica islandica* L. is widely distributed through the boreal Atlantic and adjacent areas. In the Baltic, the Arkona Sea is the eastern limit of its distribution (Jagnow & Gosselck, 1987). *A. islandica* dominates the biomass of the benthic community below the halocline (\approx 15 m water depth) in Kiel Bay and is an important part of the diet of commercial fish species (Arntz, 1980). Growth and population dynamics of *A. islandica* have been examined recently by Thompson et al. (1980a,b), Murawski et al. (1982) and Sager & Sammler (1983) but no production estimates have been made. Therefore, the main objective of this paper is to discuss the ecological importance of *A. islandica* in Kiel Bay with respect to its biomass and annual production.

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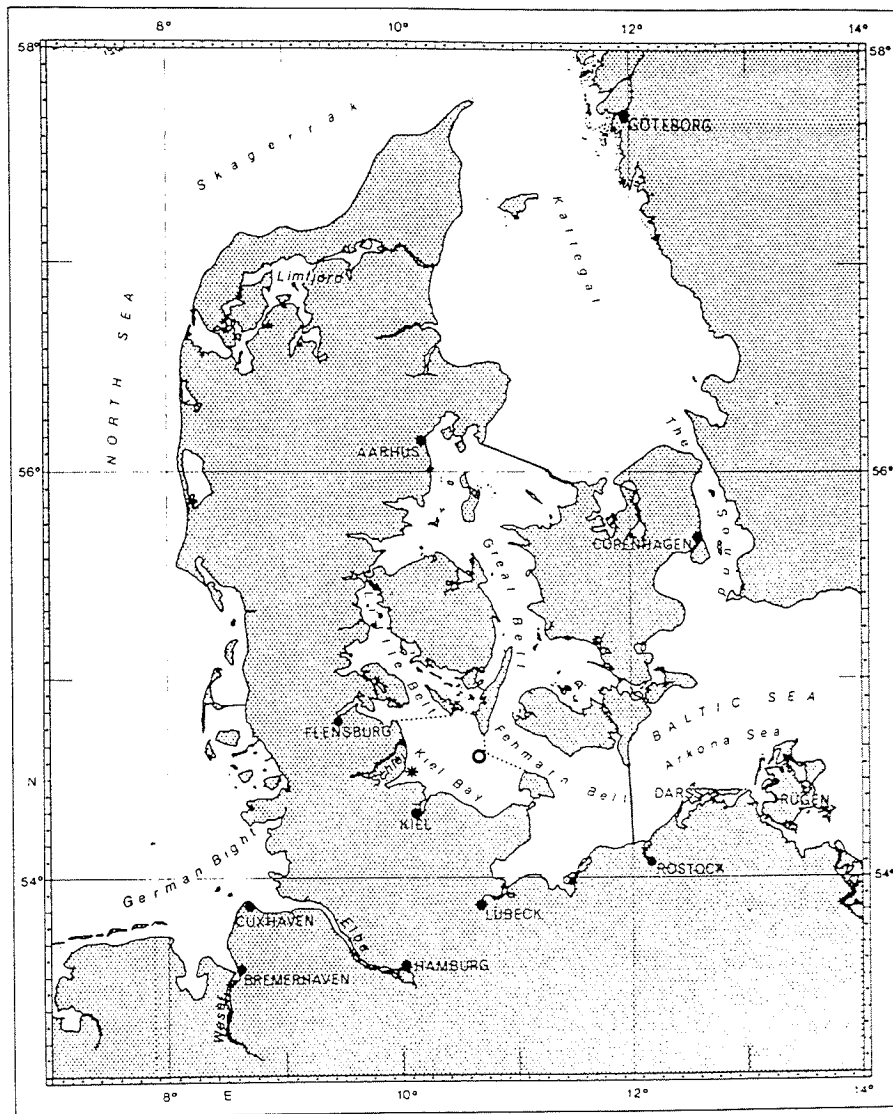


Fig. 1. Location of sampling sites in Kiel Bay; star, "Benthosgarten" (BG); circle, "Millionenviertel" (MV); solid lines, borders of ICES Subdivision 22.

METHODS

COLLECTION OF DATA ON GROWTH OF *A. ISLANDICA*

Data on *A. islandica* were available from two sites in Kiel Bay, from the experimental site "Benthosgarten" (BG) and from the site "Millionenviertel" (MV) in the northern part of Kiel Bay (Fig. 1).

The experimental set-up at the BG site has been described in detail by Rumohr & Arntz (1982). Large flower trays made of asbestos cement (40 cm high, with an upper diameter of 150 cm and a lower diameter of 46 cm) were filled with an artificial azoic sediment (washed fine sand + 18% clay), exposed at 20 m water depth and used both for a long-term experiment in benthic colonization and succession and for growth experiments in *A. islandica*. The length-frequency distributions of the *A. islandica* population, which developed in the trays between 15 December 1976 and 18 December 1978, are shown in Fig. 2. Clams sampled at the MV site were implanted in two additional trays on 15 December 1977 and were resampled 1 yr later, on 19 December 1978.

From the implanted clams and from samples taken from the colonized trays, we obtained three sets of length-increment data pairs (i.e., "tagging-recapture" data: L_1 at t_1 and L_2 at t_2) of *A. islandica*. The first of these was obtained from an additional tray, which received 27 individually marked clams of 45.5–59.5 mm length, i.e., 27 data pairs of L_1 and L_2 . The second set was obtained from another additional tray, which was subdivided into quarters and which received four different groups of *A. islandica* (Fig. 3). The examination of these resampled clams showed that most of them had formed one ridge-like growth mark on their shell during exposure. This mark was rather more distinct than older growth bands on the same shell. There was no significant difference ($P < 0.01$) between mean length at implantation and mean length at the growth mark in any of the four groups, i.e., the mark was formed just after implantation. 189 data pairs of L_1 and L_2 were obtained from these clams. The third set of length-increment data was obtained from the colonized trays. Many specimens sampled in 1978 from these containers also showed one distinct growth mark, which was not present in the 1977 samples. We included only specimens sampled in December 1978 to get an interval close to 1 yr between L_1 and L_2 . 38 length-increment data pairs were measured.

These three data sets were combined to a single set consisting of 254 length-increment data pairs. The interval $t_2 - t_1$ was set at 1 yr for all data.

From the natural *A. islandica* population at the MV site (20 m water depth), six dredge samples (10 × 10 mm mesh size) were taken between August 1978 and August 1979 (Fig. 4). Many smaller specimens found in these samples (≤ 55 mm length) showed external growth bands on their shell similar to those described by Murawski et al. (1982). The shell surface of larger specimens was in general dark brown or black, due to ferrous deposits, and external growth bands were not identifiable. Only in a very few individuals were we able to distinguish clearly more than four or five successive growth

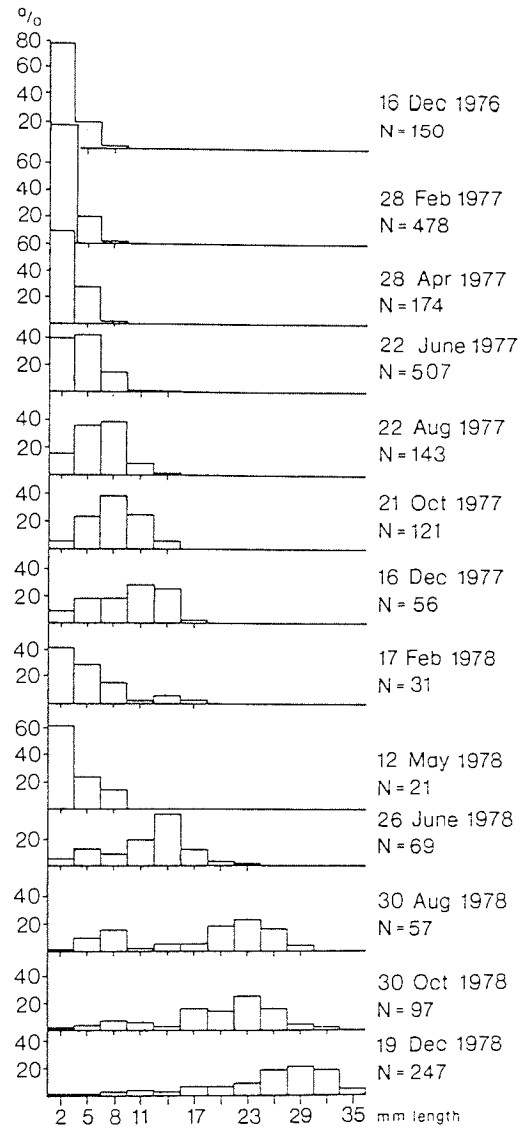


Fig. 2. Length-frequency samples of *A. islandica* from BG site.

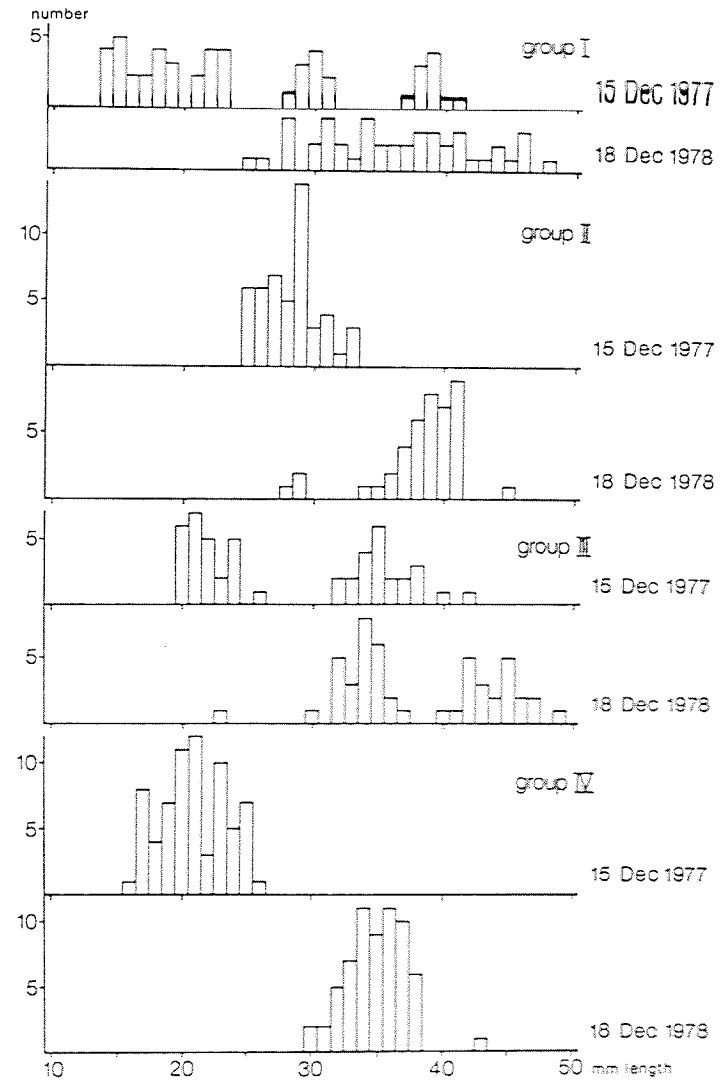


Fig. 3. Length-frequency samples of Groups I-IV of implanted *A. islandica* at implantation and at recapture.

bands, due to the poor definition of the bands and due to additional irregular marks (see Discussion). Therefore, we treated succeeding "length-at-growth band" data derived from single specimens not as length-at-age data but as length increments (see above for definition). Based on 142 individuals, we obtained 285 data pairs of L_1 and L_2 , segregated by intervals assumed to be annual.

To get an equal distribution of data over the whole length range available, both length increment data sets were re-arranged in length classes of 1 mm width with respect to L_1 , and average values for L_1 and L_2 were calculated for each length class (Tables I, II). This procedure was applied to reduce bias when using Fabens' method for the estimation of growth parameters (Chien & Chondrey, 1987, see below).

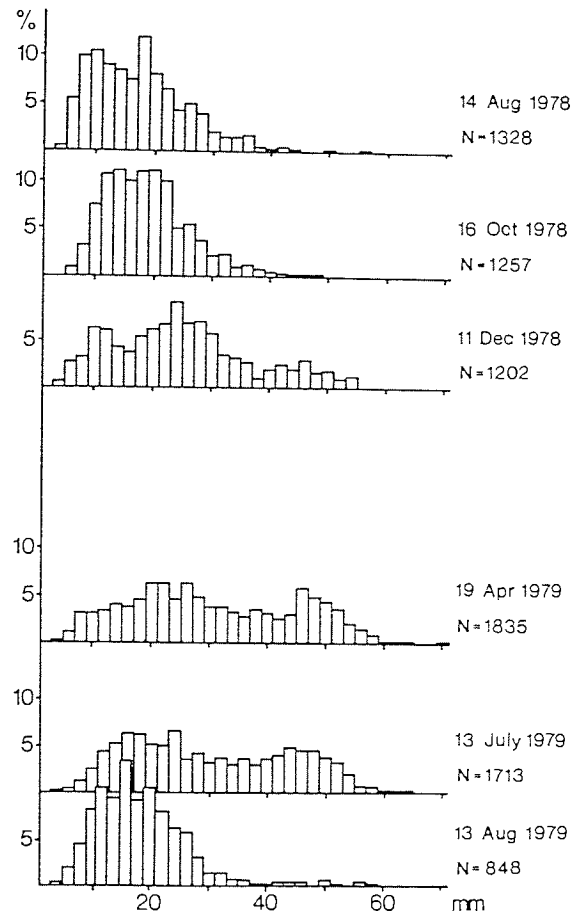


Fig. 4. Length-frequency samples of *A. islandica* from MV site.

TABLE I
Length-increment data of *A. islandica* from BG site: L_1 (mm) in December 1977. L_2 (mm) in December 1978.

Length class	Number of data	Mean L_1	Mean L_2
12	2	12.1	25.5
13	4	13.6	25.9
14	3	14.4	26.4
15	5	15.6	28.1
16	8	16.5	29.1
17	8	17.4	30.8
18	13	18.5	31.6
19	11	19.4	32.5
20	15	20.4	33.8
21	13	21.5	34.0
22	14	22.4	35.1
23	14	23.4	35.7
24	8	24.4	36.0
25	11	25.4	36.5
26	12	26.5	37.0
27	8	27.5	37.6
28	4	28.3	38.0
29	4	29.3	39.1
30	11	30.3	40.0
31	10	31.4	39.7
32	6	32.7	40.1
33	5	33.5	40.3
34	4	34.7	41.4
35	6	35.5	42.7
36	3	36.5	43.5
37	3	37.6	44.5
38	2	38.8	44.2
39	4	39.6	45.1
40	2	40.3	45.3
41	4	41.4	46.0
42	2	42.2	47.4
43	2	43.5	48.0
44	3	44.4	49.8
45	2	45.5	47.5
46	4	46.5	50.0
47	2	47.5	49.5
48	1	48.5	51.5
49	—	—	—
50	2	50.5	54.5
51	—	—	—
52	3	52.5	54.8
53	2	53.5	56.5
54	1	54.5	57.5
55	—	—	—
56	3	56.5	58.2
57	—	—	—
58	1	58.5	60.5
59	1	59.5	60.5

TABLE II

Length-increment data of *A. islandica* from MV site: L_1 (mm) in December 1977 (growth band n), L_2 (mm) in December 1978 (growth band $n + 1$).

Length class	Number of data	Mean L_1	Mean L_2
4	3	4.7	10.4
5	10	5.7	10.5
6	11	6.6	12.0
7	13	7.5	12.9
8	16	8.4	13.9
9	12	9.4	14.0
10	18	10.6	16.4
11	12	11.4	17.1
12	6	12.5	17.8
13	4	13.6	19.2
14	5	14.6	20.7
15	6	15.5	21.7
16	13	16.5	21.4
17	6	17.6	22.8
18	6	18.5	22.5
19	4	19.5	24.3
20	9	20.6	25.6
21	10	21.6	26.4
22	5	22.4	27.1
23	4	23.3	28.3
24	5	24.5	29.4
25	9	25.4	30.2
26	3	26.6	31.8
27	3	27.4	32.0
28	7	28.3	33.3
29	6	29.3	34.6
30	2	30.5	34.0
31	6	31.3	35.8
32	4	32.3	36.9
33	10	33.5	37.5
34	4	34.4	39.8
35	2	35.2	39.8
36	7	36.6	40.5
37	3	37.4	41.6
38	1	38.2	42.0
39	3	39.5	42.7
40	4	40.4	44.2
41	1	41.1	45.8
42	6	42.6	45.0
43	3	43.2	46.8
44	4	44.6	47.9
45	4	45.4	47.9
46	2	46.5	49.2
47	3	47.3	49.2
48	1	48.5	51.8
49	3	49.4	52.4
50	—	—	—
51	2	51.5	53.8
52	—	—	—
53	2	53.3	54.9
54	2	54.5	57.2

ESTIMATION OF GROWTH PARAMETERS

We limited our investigation of the growth of *A. islandica* in Kiel Bay to the Von Bertalanffy model (Von Bertalanffy, 1938) although there may be a growth function which would fit our data better (e.g., Sager & Sammler, 1983). We used this growth model because it leads to a straightforward method for the estimation of production (see below):

$$L_t = L_\infty * (1 - e^{-(K * (t - t_0))}). \quad (1)$$

To estimate the parameters K and L_∞ of this equation, we applied Fabens' iterative nonlinear least-square method (Fabens, 1965) to the length-increment data sets from both sites (Tables I, II). According to Sundberg (1984), this approach is superior to the methods introduced by Gulland & Holt (1959) and Munro (1982). As a control, we used the Walford plot (Walford, 1946) which can also be applied to tagging-recapture data when the interval between successive lengths is close to 1 yr (Ricker, 1975).

ESTIMATION OF ANNUAL P/\bar{B} RATIO AND PRODUCTION

P/\bar{B} ratio and production were estimated for the natural population at the MV site only. We were not able to separate the length-frequency samples of *A. islandica* into cohorts, hence methods of calculating production, which are based on age classes, could not be applied. We used two methods which both depend on the growth parameters and the length-frequency distribution of the population in question.

Method 1

Estimation of P/\bar{B} ratio via estimation of mortality in the steady-state population. Allen (1971) showed that in such a population total mortality Z is equal to the P/\bar{B} ratio if mortality can be described by a single negative exponential function, and if individual growth follows a Von Bertalanffy function. Z was calculated from a length-converted catch curve (Pauly, 1982–84). This curve consists of a plot of $\ln(N_i/\Delta t)$ against t_i , where N_i is the number of animals in the i -th length class, Δt is the time required to grow through this length class and t_i is the relative age of the midlength of length class i . All of these can be computed with a representative length-frequency sample and the growth-parameter values K and L_∞ of the Von Bertalanffy growth function. Z is estimated by a linear regression fitted to the right descending arm of the catch curve:

$$\ln(N_i/\Delta t) = a - b * t_i, \quad Z = -b. \quad (2)$$

If the right arm of the catch curve shows one or more distinct breaks, it is necessary to fit separate regression lines to the different regions of the catch curve. This will result in different estimates of Z for different length ranges of the population. The application of this method to bivalve populations has been described previously by Brey & Pauly (1986), Brey (1986) and Norte (1988).

Method 2

Production calculation via weight-specific growth rate (Method 3A of Crisp, 1984):

$$P = \sum N_i * w_i * G_i * \Delta t, \quad (3)$$

where N_i is the number of animals in the i -th length class, w_i is the mean individual weight in the i -th length class, G_i is the weight-specific growth rate of length class i and Δt is the sampling period.

Mean individual weight was derived from an equation relating length (mm) to AFDW (g), kindly provided by M. Weigelt, Hamburg, FRG:

$$\log(\text{AFDW}) = -5.0098 + 2.9300 * \log(\text{length}). \quad (4)$$

The weight-specific growth rate G_i was derived from the Von Bertalanffy growth-curve parameters K and L_∞ and the length-weight relationship (Crisp, 1984):

$$G_i = 2.9300 * K * (L_\infty - L_i) \cdot L_i^{-1}. \quad (5)$$

For both methods, we used the pooled dredge samples (Fig. 4) as a representative length-frequency sample of the *A. islandica* population at the MV site. Because the area these samples refer to is not known, we derived only an estimate of the annual P/\bar{B} ratio with both methods applied but no production figure.

Production was computed by means of the P/\bar{B} ratio and an estimate of average annual biomass. The long-term average of the biomass of *A. islandica* at the MV site is 44.4 g AFDW \cdot m⁻² (median: 1968–85, four stations, 174 values), the 95% CL values are 37.3 and 54.2 g AFDW \cdot m⁻².

For the conversion of measurements of height of *A. islandica* to length, we established an empirical length-height (mm) relationship:

$$\text{length} = 1.069 + 1.153 * \text{height}, \quad n = 35, r^2 = 0.996. \quad (6)$$

RESULTS

GROWTH OF *A. ISLANDICA*

The analysis of the length-increment data from the BG and MV sites led to quite different values of the parameters of the Von Bertalanffy growth function for both sites. Fabens' method as well as the Walford plot resulted in the following estimates \pm SE:

$$\text{BG: } K = 0.348 \pm 0.007 \cdot \text{yr}^{-1}, L_\infty = 60.6 \pm 0.5 \text{ mm}, r^2 = 0.989;$$

$$\text{MV: } K = 0.070 \pm 0.001 \cdot \text{yr}^{-1}, L_\infty = 93.6 \pm 1.3 \text{ mm}, r^2 = 0.998.$$

Fig. 5 shows the corresponding growth curves for both sites and Fig. 6 shows the plots of the residuals.

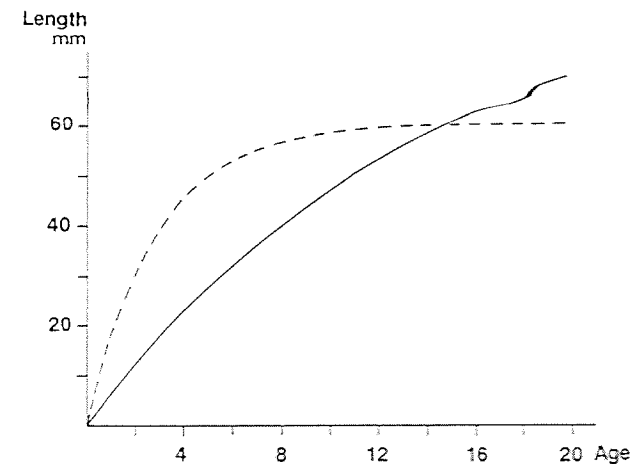


Fig. 5. Best-fitting Von Bertalanffy growth curves of *A. islandica* extrapolated to an age of 20 yr: stippled line, BG site ($K = 0.348$, $L_\infty = 60.6$ mm); solid line, MV site ($K = 0.070$, $L_\infty = 93.6$ mm).

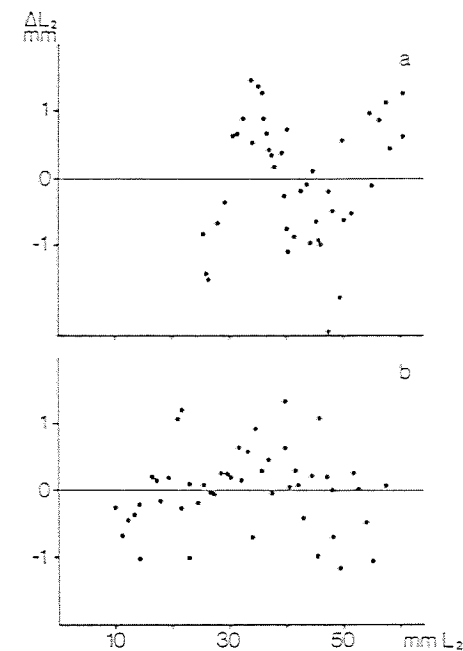


Fig. 6. Residuals of best-fitting Von Bertalanffy growth curves of *A. islandica*: a, BG site; b, MV site; $\Delta L_2 = L_2(\text{measured}) - L_2(\text{calculated})$.

MORTALITY, P/\bar{B} RATIO AND PRODUCTION AT MV SITE

Method 1

The length-converted catch curve for the *A. islandica* population at the MV site (Fig. 7) shows two distinct breaks in its descending arm at the relative ages of 7.5

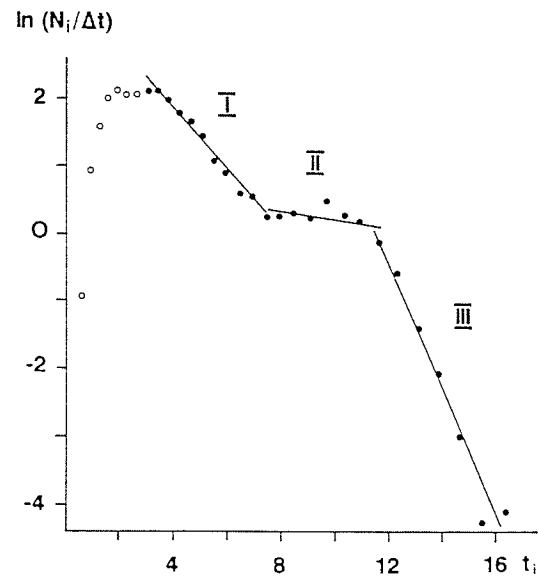


Fig. 7. Length-converted catch curve of *A. islandica* based on pooled length-frequency data (Fig. 4) and Von Bertalanffy growth curve. Dots: points included in calculation of Z : < 38 mm: $\ln(N_i/\Delta t) = 3.682 + 0.457 * t_i$ ($r^2 = 0.982$); 38–52 mm: $\ln(N_i/\Delta t) = 0.812 + 0.060 * t_i$ ($r^2 = 0.247$); > 52 mm: $\ln(N_i/\Delta t) = 10.614 + 0.923 * t_i$ ($r^2 = 0.962$).

(38 mm length) and 11.5 yr (52 mm length), which separate the population into three groups: Group I < 38 mm length, Group II 38–52 mm length and Group III > 52 mm length. Z was estimated at 0.457 for Group I, at 0.060 for Group II and at 0.923 for Group III by separate regression lines (Fig. 7). From the pooled length-frequency data and the length-weight regression (Equation 4), we calculated the distribution of biomass among the three groups of *A. islandica* at the MV site: Group I 36%, Group II 47% and Group III 17%, which is equal to 16.0, 20.9 and 7.5 g AFDW \cdot m $^{-2}$, respectively (total = 44.4 g AFDW \cdot m $^{-2}$). Annual production of the three groups is calculated at:

$$\text{Group I (< 38 mm): } P = 0.457 * 16.0 = 7.3 \text{ g AFDW} \cdot \text{m}^{-2}$$

$$\text{Group II (38–52 mm): } P = 0.060 * 20.9 = 1.3 \text{ g AFDW} \cdot \text{m}^{-2}$$

$$\text{Group III (> 52 mm): } P = 0.923 * 7.5 = 6.9 \text{ g AFDW} \cdot \text{m}^{-2}$$

The sum of these three values represents total annual production ($P = 15.5$ g AFDW \cdot m $^{-2} \cdot$ yr $^{-1}$) which leads to an overall annual P/\bar{B} ratio of 0.35.

Method 2

By means of the second approach, we derived an estimate of the annual P/\bar{B} ratio of 0.32. With the 1968–85 average biomass of 44.4 g AFDW \cdot m $^{-2}$, the annual production is calculated at:

$$P = 0.32 * 44.4 = 14.2 \text{ g AFDW} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}.$$

On the average, the annual P/\bar{B} ratio is estimated at 0.34 and the annual production at 15.1 g AFDW \cdot m $^{-2} \cdot$ yr $^{-1}$. With respect to the 95% CL values of \bar{B} , the limits of the annual production P are estimated at 12.7 and 18.4 g AFDW \cdot m $^{-2} \cdot$ yr $^{-1}$, respectively.

DISCUSSION

GROWTH OF *A. ISLANDICA*

The growth-curve parameters estimated here may be biased to some extent due to limitations of our data.

At the BG site, the annual length increment in *A. islandica* is twice as high in specimens of < 30 mm than at the MV site but this difference decreases with increasing length (≤ 44 mm). This observation could be explained by the experimental set-up at the BG site which may have provided different conditions to the different groups of clams. In general, the surface of the containers was ≈ 40 cm above the surrounding sediment. This situation may have offered an improved food supply as well as better oxygen conditions to all specimens. However, if the growth rate of *A. islandica* is density-dependent – as considered by Murawski et al. (1982) – the low biomass in the experimental trays during the colonization experiment may have offered very favourable conditions to the young colonizing clams, which could have led to rapid growth. On the other hand, the density of the implanted clams in the second additional tray was ≈ 120 ind \cdot m $^{-2}$, which is twice the average abundance at the MV site (see below). Additionally, the large implanted clams (> 45 mm) may have been affected negatively by the marking procedure.

The nonrandom distribution of the residuals (Fig. 6a) indicates systematic deviations of the length increments from the growth curve, which may be related to the different groups of clams included. Growth in these different groups may be better described by separate growth functions. Therefore, the BG site growth curve ($K = 0.348 \cdot \text{yr}^{-1}$, $L_{\infty} = 60.6$ mm) is assumed to be biased due to artificial conditions and is not used further below.

It is evident from these observations that the set-up of growth experiments may have significant effects on the experimental animals, which can result in a large change in growth in comparison to the natural population living in a particular area.

With respect to the MV site, the length-increment data (Table II) do not cover the whole length range of this population, for which representatives of ≤ 74 mm length can be found. However, the data included here are the best data available for *A. islandica* from Kiel Bay because it seems to be impossible to get reliable estimates of age for larger specimens. Even, the acetate peel technique (e.g., Ropes, 1984; Ropes et al., 1984) does not allow for accurate ageing in Baltic specimens because the internal growth lines are poorly defined (J. W. Ropes, pers. comm.). Additionally, there may be irregular lines caused by environmental factors such as anoxic conditions during summer. On the other hand, both methods led to identical growth parameter estimates with a correlation coefficient close to 1 and there were no systematic deviations in the residuals (Fig. 6b). So, the growth curve obtained for the MV population ($K = 0.07 \cdot \text{yr}^{-1}$, $L_{\infty} = 94$ mm) may be an accurate representation of the population growth curve, at least for clams of ≤ 55 mm length.

An unpublished analysis of clams sampled in an area south of the MV site in 1988 led to very similar growth parameter estimates ($K = 0.074 \cdot \text{yr}^{-1}$, $L_{\infty} = 91$ mm). Therefore, we suggest that the growth curve derived here for the MV site is representative for the greater part of Kiel Bay.

The comparison of the growth curve of the MV site population in Kiel Bay with growth curves calculated by Murawski et al. (1982) for a population in the Long Island

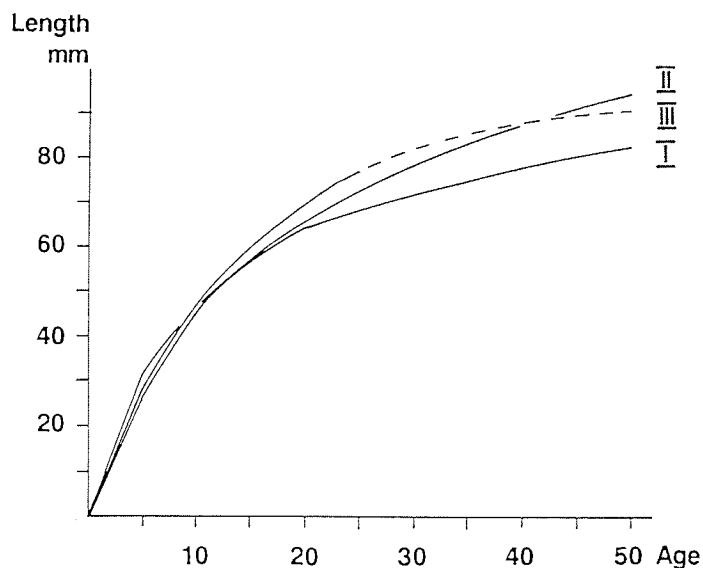


Fig. 8. Comparison of growth curves of *A. islandica* from different geographic sites: (I) Long Island Sound, New York, 53 m depth (Murawski et al., 1982): age < 20 yr: $L_t = 75.68 - 81.31 \cdot 0.9056^t$; age > 20 yr: $L_t = 104.95 \cdot (1 - e^{-0.020 \cdot (t - 27.66)})$. (II) Atlantic, different localities (Sager & Sammler, 1982; data from Thompson et al., 1980): Janoschek function with $L_{\infty} = 104.0$. (III) Kiel Bay, MV site (this paper): $L_t = 93.6 \cdot (1 - e^{-0.070 \cdot t})$, extrapolated to 50 yr.

Sound and Sager & Sammler (1983) for populations at different Atlantic locations (data from Thompson et al., 1980) shows quite similar growth increments for the first 20 yr of life (Fig. 8). After 25 yr of life, *A. islandica* would theoretically have grown to a mean length of 77 mm in Kiel Bay. However, the largest clam ever-recorded measured 74 mm. In contrast, individuals of the Atlantic populations may reach an age of > 100 yr and a length of > 100 mm (Thompson et al., 1980; Murawski et al., 1982). Modal age of the Middle Atlantic populations is 65–100 yr (Thompson et al., 1980) whereas in Kiel Bay modal age is < 10 yr. This may be due either to a physiological limit of size for this species in Kiel Bay, possibly related to the mesohaline environment with strong hydrographic fluctuations and periodic O_2 deficiency, or due to a higher mortality of *A. islandica* in this area.

MORTALITY, P/\bar{B} RATIO AND PRODUCTION

Although the length-frequency samples from the MV site (Fig. 4) indicate strong spatial heterogeneity, we assume the sum of all samples (8183 ind) to be representative for the part of the population of > 20 mm individual length. Therefore, the two breaks in the catch curve (Fig. 7) may be due either to changes in recruitment with time or to changes in mortality with age.

The observed breaks could be caused by an extraordinarily strong recruitment of one of the age classes of 8–10 yr of relative age. In this case, a single regression line would give a better approximation of Z and P/\bar{B} . It would be 0.41 for the whole population, which is slightly above the value estimated with separate regression lines (0.35). A strong recruitment ≈ 9 yr ago should be detectable in the long-term data set (1968–85) on *A. islandica*. In that year, abundance should be markedly higher and average individual weight should be lower than in previous years. During the following years, there should be a decrease in abundance and an increase in average weight. However, neither abundance (median: 53 ind $\cdot m^{-2}$; 95% CL values: 43 and 67 ind $\cdot m^{-2}$) nor average individual weight (median: 1.058 g AFDW; 95% CL values: 0.842 and 1.284 g AFDW) show any detectable trends during 1968–85.

If the breaks in the catch curve are due to age-related changes in mortality, then there are three distinct life stages with different mortality rates. Mortality is high in small specimens, low in specimens of medium size and high again in large specimens. Similar life-history patterns have been described for various benthic animals. In all of these cases, young animals suffered from predation and old animals from senility, whereas mortality of the medium aged part of the population was lowest because these animals were protected against predation, e.g., by deep burrows like the crustacean *Calocaris macandreae* (Buchanan & Warwick, 1974).

With respect to *A. islandica*, these changes in mortality may be related to a hypothesis developed by Arntz & Weber (1970) on the feeding of demersal fish on *A. islandica*. They assume that the important contribution of *A. islandica* to the food of cod and dab (see below) found in Kiel Bay in the 1960–70s, but not before World War II, is related to

the postwar increase in otter-board trawling. In the stomachs of the fish, the authors found, beside small clams (0-group) with shells, only the soft parts of larger clams but without the adductor muscle and the mantle edge. From a few experiments, Arntz & Weber (1970) conclude that not even adult cod are able to break the shell of *A. islandica*. Based on observations made by divers, they assume that the clams, which have very short siphons and live just below the sediment-water interface, are ploughed out of the sediment and damaged by the otter-boards, which makes the soft parts available for the demersal fish. The difference between the back-calculated average length of ingested clams (46 mm) and the average length of the population (≈ 25 mm) may indicate that the probability of being damaged by an otter-board is increasing with length for a single individual. In summary, the observed catch curve may be explained as follows. The mortality due to the ingestion of complete clams including shell decreases with age and the mortality due to otter-board damage increases with age. These two trends of opposite direction lead to a minimum in mortality at intermediate age.

Although our estimate of annual P/\bar{B} ratio (0.34) refers only to data from 1978/79 whereas the average annual biomass refers to data from 1968–85, we assume our estimate of production ($15 \text{ g AFDW} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) to be a reasonable long-term average because there are no trends in the biomass of *A. islandica* throughout 1968–85. However, during years with periods of O_2 depletion below the halocline in Kiel Bay, like 1981/82 (Weigelt & Rumohr, 1986), growth and production of *A. islandica* may be reduced seriously although this species is able to survive extended periods of O_2 deficiency (Dries & Theede, 1974). During years with very favourable abiotic conditions, production may be substantially higher than the long-term average.

We assume not only the growth function (see above) but also the estimate of the P/\bar{B} ratio from the MV site to be representative for Kiel Bay and usable for rough estimates of production in the whole area below the halocline (≈ 15 m water depth). The average biomass of *A. islandica* in this area is $\approx 18.4 \text{ g AFDW} \cdot \text{m}^{-2}$ (Arntz & Brunswig, 1975). With a P/\bar{B} ratio of 0.34, annual production would amount to $6.3 \text{ g AFDW} \cdot \text{m}^{-2}$ for the whole area. This area below the halocline is $\approx 1700 \text{ km}^2$ (Babenerd & Gerlach, 1987), so the total production of *A. islandica* in Kiel Bay is $\approx 10700 \text{ t AFDW} \cdot \text{yr}^{-1}$.

ECOLOGICAL SIGNIFICANCE OF *A. ISLANDICA* IN KIEL BAY

Below the halocline, *A. islandica* is the most important species in Kiel Bay with respect to biomass as well as production although the benthic community inhabiting this area is traditionally called the "*Abra alba* community" (Petersen, 1918). At the MV site, *A. islandica* shows the highest biomass ($44.4 \text{ g AFDW} \cdot \text{m}^{-2}$) and most likely the highest production ($15 \text{ g AFDW} \cdot \text{m}^{-2}$) of all macrobenthic species present.

In comparison, the second important bivalve species at the MV site, the bivalve *A. alba*, has a mean annual biomass of $1.6 \text{ g AFDW} \cdot \text{m}^{-2}$ and an annual production of $\approx 3.1 \text{ g AFDW} \cdot \text{m}^{-2}$ (Rainer, 1985; 1975–78).

For the whole area below the halocline (but with *A. islandica* excluded), Arntz &

Brunswig (1975) estimated an annual production of $\approx 8.6 \text{ g AFDW} \cdot \text{m}^{-2}$. With respect to our estimate of $\approx 6.3 \text{ g AFDW} \cdot \text{m}^{-2}$ annual production of *A. islandica*, this species would account for $\approx 40\%$ of the total annual community production.

Arntz (1973–1974, 1977, 1980) and Arntz & Weber (1970) investigated the feeding of several fish species on *A. islandica*. In terms of wet weight, *A. islandica* contributed 27.3% of total food intake of juvenile cod, 52.9% of adult cod, 14.1% of dab, 3.5% of whiting and 3.6% of plaice. These figures indicate that cod is an important predator of *A. islandica* in Kiel Bay.

During 1970–85, cod was one of the most important commercial fish species in ICES Subdivision 22, Western Baltic, which comprises the Belt Sea, Kiel Bay and Mecklenburg Bight (Fig. 1). According to Thurow (1973–74, 1982, 1984) and Sjöstrand & Weber (1988), the annual catch of cod in Subdivision 22 during 1970–85 was $\approx 28500 \text{ t}$ whereas the annual production was estimated to $\approx 35500 \text{ t}$. In 1985/86, the annual catch dropped to $\approx 12300 \text{ t}$, probably due to overexploitation of the stock. Simultaneously, the mean annual landing of cod at the FRG coast of the Baltic dropped from $\approx 8460 \text{ t}$ during 1970–85 to $\leq 2000 \text{ t}$ since 1986 (Anonymous, 1971–88).

$\approx 35500 \text{ t}$ wet wt of cod production are equivalent to $\approx 8400 \text{ t AFDW}$ (see Gerking, 1955, and Rumohr et al., 1987, for conversion factors). For a whole population of cod, we can assume a gross growth efficiency (production/food ingested) of $\approx 10\%$ (Edwards et al., 1972; Odum, 1972; Mann, 1978). Therefore, $\approx 84000 \text{ t AFDW}$ of food are required to produce $\approx 8400 \text{ t AFDW}$ of cod. So, the production of *A. islandica* in Kiel Bay ($\approx 10700 \text{ t}$) could contribute $\approx 13\%$ to the food required by cod in Subdivision 22 $\cdot \text{yr}^{-1}$.

It is difficult to estimate the amount of cod produced directly in Kiel Bay, because there is no information available about the spatial distribution of catches within Subdivision 22. However, with respect to the fact that Kiel Bay is $\approx 30\%$ of the area of Subdivision 22, we assume that $\approx 30\%$ of the cod production of Subdivision 22, i.e., $\approx 2500 \text{ t AFDW}$, is produced in Kiel Bay. If this holds true, the production of *A. islandica* is able to support at most $\approx 40\%$ of cod production in Kiel Bay. This figure is in good agreement with the portion of *A. islandica* in the stomach content of cod. The remaining $\approx 60\%$ of cod production depends on other benthic invertebrates and on various demersal and pelagic fish species, especially gobies and herring (Arntz, 1977).

Although these figures are only rough estimates, they indicate that the short food-chain *A. islandica* > *G. morhua* is an important component of the Western Baltic ecosystem, also from a commercial point of view. If the hypothesis of Arntz & Weber (1970) holds true that only otter-board trawling makes *A. islandica* available for cod, this food-chain is an artificial one which may be interpreted as a kind of self-fertilizing process in the demersal fisheries of Kiel Bay. However, a reinvestigation is required to evaluate the possible effects of the breakdown of the cod stock in 1985/86 and of the reduced fishery on the population dynamics of *A. islandica* in Kiel Bay.

REFERENCES

- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Can.*, Vol. 28, pp. 1573–1581.
- Anonymous, 1971–88. Die kleine Hochsee- und Küstenfischerei. *Fischerblatt*, Vols. 1971–88.
- Arntz, W.E., 1971. Die Nahrung der Kliesche (*Limanda limanda* (L.)) in der Kieler Bucht. *Ber. Dtsch. Wiss. Komm. Meeresforsch.*, Vol. 22, pp. 129–183.
- Arntz, W.E., 1973. Periodicity of diel food intake of cod *Gadus morhua* in the Kiel Bay. *Oikos*, Suppl. 15, pp. 138–145.
- Arntz, W.E., 1974. A contribution to the feeding ecology of juvenile cod (*Gadus morhua* L.) in the Western Baltic. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, Vol. 166, pp. 13–19.
- Arntz, W.E., 1977. The food of adult cod (*Gadus morhua* L.) in the Western Baltic. *Meeresforsch.*, Vol. 26, pp. 60–69.
- Arntz, W.E., 1980. Predation by demersal fish and its impact on the dynamics of macrobenthos. In: *Marine benthic dynamics*, edited by K.R. Tenore & B.C. Coull, University of South Carolina Press, Columbia, pp. 121–149.
- Arntz, W.E. & H. Rumohr, 1982. An experimental study of macrobenthic colonization and succession, and the importance of seasonal variation in temperate latitudes. *J. Exp. Mar. Biol. Ecol.*, Vol. 64, pp. 17–45.
- Arntz, W.E. & W. Weber, 1970. *Cyprina islandica* L. (Mollusca, Bivalvia) als Nahrung von Dorsch und Kliesche in der Kieler Bucht. *Ber. Dtsch. Wiss. Komm. Meeresforsch.*, Vol. 21, pp. 193–209.
- Babenerd, B. & S. Gerlach, 1987. Bathymetry and sediments of Kieler Bucht. In: *Seawater-sediment interactions in coastal waters*, edited by J. Rumohr et al., Springer, Berlin, pp. 16–31.
- Bertalanffy, L. von, 1938. A quantitative theory of organic growth. *Hum. Biol.*, Vol. 10, pp. 181–213.
- Brey, T., 1986. Estimation of annual P/B-ratio and production of marine benthic invertebrates from length-frequency data. *Ophelia*, Suppl. 4, pp. 45–54.
- Brey, T. & D. Pauly, 1986. Electronic length frequency analysis. A revised and expanded user's guide to ELEFAN 0, 1 and 2. *Ber. Inst. Meereskd. Kiel*, No. 149, pp. 1–76.
- Buchaman, J.B. & R.-M. Warwick, 1974. An estimate of benthic macrofauna production in the offshore mud of the Northumberland coast. *J. Mar. Biol. Assoc. U.K.*, Vol. 54, pp. 197–222.
- Chien, Y.-H. & R.E. Chondrey, 1987. Bias in estimation growth parameters using Fabens' mark-recapture procedure. *Asian Fish. Sci.*, Vol. 1, pp. 65–74.
- Crisp, D.J., 1984. Energy flow measurement. In: *Methods for the study of marine benthos*, IBP Handbook No. 16, edited by N.A. Holme & A.D. McIntyre, Oxford, second edition, pp. 284–372.
- Dries, R.-R. & H. Theede, 1974. Sauerstoffmangelresistenz mariner Bodensevertebraten aus der Westlichen Ostsee. *Mar. Biol.*, Vol. 25, pp. 327–333.
- Edwards, R.R.C., D.M. Finlayson & J.H. Steele, 1972. An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). *J. Exp. Mar. Biol. Ecol.*, Vol. 8, pp. 299–309.
- Fabens, A.J., 1965. Properties and fitting the Von Bertalanffy growth curve. *Growth*, Vol. 29, pp. 265–289.
- Gerking, S.D., 1955. Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. *Physiol. Zool.*, Vol. 28, pp. 267–282.
- Gulland, J.A. & S.J. Holt, 1959. Estimation of growth parameters for data at unequal time intervals. *J. Cons. Perm. Int. Explor. Mer*, Vol. 24, pp. 47–49.
- Jagnow, B. & F. Gosselck, 1987. [Bestimmungsschlüssel für die Gehäuseschnecken und Muscheln der Ostsee.] *Mitt. Zool. Mus. Berlin*, Vol. 63, pp. 191–268. [In German.]
- Mann, K.H., 1978. Estimating the food consumption of fish in nature. In: *Ecology of freshwater fish production*, edited by S.D. Gerking, Blackwell, Oxford, pp. 250–273.
- Monro, J.L., 1982. Estimation of the parameters of the Von Bertalanffy growth equation from recapture data at variable time intervals. *J. Cons. Int. Explor. Mer*, Vol. 40, pp. 199–200.
- Murawski, S.A., J.W. Ropes & F.M. Serchuck, 1982. Growth of the ocean quahog, *Arctica islandica*, in the Middle Atlantic Bight. *Fish. Bull.*, Vol. 80, pp. 21–34.
- Norte, A.G.C. del, 1988. Aspects of the growth, recruitment, mortality and reproduction of the scallop *Amusium pleuronectes* (L.) in the Lingayen gulf, Philippines. *Ophelia*, Vol. 29, pp. 153–168.
- Odum, E.P., 1971. *Fundamentals of ecology*. Saunders, Philadelphia, 574 pp.
- Pauly, D., 1982. Studying single-species dynamics in a multispecies context. In: *Theory and management of tropical fisheries*, edited by D. Pauly & G. Murphy, ICLARM Conf. Proc., Vol. 9, pp. 33–70.
- Pauly, D., 1983. Length-converted catch curves: a powerful tool for fisheries research in the tropics. Part 1. *Fishbyte*, Vol. 1, pp. 9–13.
- Pauly, D., 1984. Length-converted catch curves: a powerful tool for fisheries research in the tropics. Part 2. *Fishbyte*, Vol. 2, pp. 17–19.
- Petersen, G.G.J., 1918. The sea bottom and its production of fish food. *Rep. Dan. Biol. Stn.*, Vol. 25, pp. 1–82.
- Rainer, S.F., 1985. Population dynamics and production of the bivalve *Abra abra* and its implications for fisheries production. *Mar. Biol.*, Vol. 85, pp. 253–262.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, Vol. 191, 382p.
- Ropes, J.W., 1984. Procedures for preparing acetate peels and evidence validating the annual periodicity of growth lines formed in the shells of ocean quahogs *Arctica islandica*. *Mar. Fish. Rev.*, Vol. 46, pp. 27–35.
- Ropes, J.W., D.S. Jones, S.A. Murawski, F.M. Serchuk & A. Jerald, 1984. Documentation of annual growth lines in ocean quahogs *Arctica islandica* Linné. *Fish. Bull. NOAA*, Vol. 82, pp. 1–19.
- Rumohr, H., T. Brey & S. Ankar, 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. *Balt. Mar. Biol. Publ.*, No. 9, pp. 1–56.
- Rumohr, H. & W.E. Arntz, 1982. The "Benthosgarten", a new approach for the study of soft bottom communities. *Meeresforsch.*, Vol. 29, pp. 225–238.
- Sager, G. & R. Sammler, 1983. Mathematical investigations into the longevity of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Int. Rev. Gesamten Hydrobiol.*, Vol. 68, pp. 113–120.
- Sjöstrand, B. & W. Weber, 1988. A review on stock assessments of exploited fish stocks in the Baltic. ICES 1988 BAL/No. 47, 42 pp.
- Sundberg, P., 1984. A Monte Carlo study of three methods for estimating the parameters in the Von Bertalanffy growth equation. *J. Cons. Int. Explor. Mer*, Vol. 41, pp. 248–258.
- Thompson, I., D.S. Jones & D. Dreibeis, 1980. Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Mar. Biol.*, Vol. 57, pp. 25–34.
- Thompson, I., D.S. Jones & J.W. Ropes, 1980. Advanced age for sexual maturity in the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Mar. Biol.*, Vol. 57, pp. 35–39.
- Thurow, F., 1972. Kontingentierung in der Dorschfischerei der Ostsee? *Inf. Fischwirtsch.*, Vol. 20, p. 9.
- Thurow, F., 1974. Changes in population parameters of cod in the Baltic. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, Vol. 166, pp. 85–93.
- Thurow, F., 1982. Data used for the evaluation of "Growth production of the Baltic fish community", and some results thereof. *Veröff. Inst. Küsten- Binnenfisch. Hambg.*, No. 80, pp. 1–44.
- Thurow, F., 1984. Growth production of the Baltic fish community. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, Vol. 183, pp. 170–179.
- Walford, L.A., 1946. A new graphic method of describing the growth of animals. *Biol. Bull.*, Vol. 90, pp. 141–147.
- Weigelt, M. & H. Rumohr, 1986. Effects of wide-range oxygen depletion on benthic fauna and demersal fish in Kiel Bay 1981–1983. *Meeresforsch.*, Vol. 31, pp. 124–136.