DISTRIBUTION, ABUNDANCE AND SOME POPULATION CHARACTERISTICS OF THE OCEAN QUAHOG, *ARCTICA ISLANDICA* (LINNAEUS, 1767), IN THE MECKLENBURG BIGHT (BALTIC SEA)

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ABSTRACT In the Mecklenburg Bight (western Baltic Sea), the ocean quahog, Arctica islandica, constitutes the most important species below the halocline. In 1999 a benthos survey at 95 stations in the Mecklenburg Bight showed a wide distribution of A. islandica at depths between 15.6 and 29.6 m. Mean abundance at these depths was 91 ind/m² with a biomass (AFDW) of 15 g/m². Maximum densities observed at these depths were 571 ind/m² and 120 g/m², respectively. The Mecklenburg Bight had an estimated colonized area of 5200 km² and a total annual production of 26500 t AFDW. In comparison to a data set of the 1960's, we found an increased quahog population. Ocean quahogs ranged from 1.5 to 64 mm in shell length and from 1 to 70 years of age. Growth was relatively slow for the first 40 years. Most (90%) individuals in the population measured <30 mm shell length, indicating strong recruitment in the Bight during the past decades. While the highest abundance (most juveniles) was observed in depths between 15 and 20 m, maximum biomass (due to adults) lay between 20 and 25 m. Probably the recruitment zone was displaced from below 20 m to 15–20 m depth in the last decades. Mean quahog wet meat yields was 18.3%. The individual ash free dry weight decreased significantly with increasing shell length from 14.3% (<10 mm) to 9.4% (>40 mm). All results were compared with data from populations in North Atlantic and adjacent waters.

KEY WORDS: Arctica islandica, ocean quahog, distribution, abundance, growth, size, meat yield, Baltic Sea, Mecklenburg Bight

INTRODUCTION

The ocean quahog, Arctica islandica, is an arctic-boreal species that occurs in North Atlantic and adjacent waters. In the North Sea region, the species' range extends into the Western Baltic Sea and reaches its eastern limit of distribution in the Arkona basin (von Oertzen and Schulz 1973). The largest populations reside in Kiel and Mecklenburg Bights. The ocean quahog is the largest bivalve in the Baltic Sea and lives for more than several decades (Arntz and Weber 1970, Brey et al. 1990). The long living species is an important indicator for environmental conditions. Beside salinity and sediment structure, oxygen concentration has a strong influence on the composition of Baltic Sea fauna and flora. Since the 1960's, oxygen deficiency below the halocline (16 to 20 m) has resulted in destruction of the bottom fauna of Mecklenburg Bight (Gosselck et al. 1987, Schulz 1968). Although A. islandica is highly resistant to oxygen depletion, the population is diminished by mortality caused by frequent and long lasting periods of anoxic conditions. In the deeper parts of Lübeck and Mecklenburg Bights a severe decrease of the Baltic Sea population of Arctica islandica has resulted during recent decades (Gosselck et al. 1987, Schulz 1968). Long living species like the ocean quahog (Arctica islandica) decreased in abundance and were replaced by communities of short living polychaetes (spionids, capitellids).

The geographical variability in growth rates of *A. islandica* is well documented for the North Sea and adjacent waters (Witbaard et al. 1999) and for US and Canadian east coasts (Kennish et al. 1994, Kraus et al. 1992, Murawski et al. 1982). Much is known about the reproduction, meat yield and age mostly for Atlantic populations off North America and Iceland coasts (e.g. Chaisson and Rowell 1985, Fritz 1991, Steingrimsson and Thorarinsdottir

Area of Investigation

The Mecklenburg Bight is part of the Belt Sea and belongs to the transition area between the North Sea and Baltic Sea (Fig. 1). It is connected with Kiel Bight via Fehmarnbelt and with Kattegat via the Belts. To the East, the Kadet trench crossing the Darsser rise connects it with the Baltic proper.

The location in the southwestern part of the Baltic with its relatively high salt content is decisive for benthic colonisation. Fauna and flora of the area are determined by hydrological and morphological factors, with salinity being the formative influence. Another important factor is the sediment structure, which is formed by residual sediments and mud.

During 1999 a macrozoobenthos survey was made in the Mecklenburg Bight. In total 95 stations were sampled between March and September (Fig. 1). The depth interval was 5 to 29.6 m. the sediment varied from fine sand at the shallowest stations to sand mixed with silt and clay at deepest stations. The sediment characteristics and current data within the area were published by Lange et al. (1991).

MATERIALS AND METHODS

Profiles of salinity were recorded throughout the water column using a CTD (conductivity/temperature/depth probe) system.

^{1995,} Thorarinsdottir and Einarsson 1996). Little is known about populations of this species in the vicinity of the Baltic Sea (Arntz and Weber 1970, Brey et al. 1990). The purpose of this study was to investigate the distribution, frequency and biomass of the recent population of *Arctica islandica* in Mecklenburg Bight as the first extensive study on the population characteristics of this important indicator species near its limit of distribution. A further aim was to compare these results with existing data from the 1960's compiled by Schulz (1969a) and to include an 11-year time series of one monitoring station.

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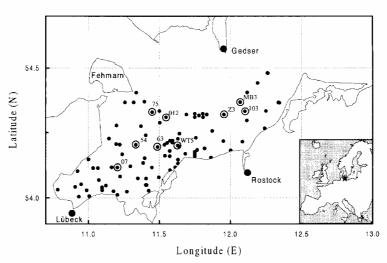


Figure 1. Investigation area with 95 stations in the Mecklenburg Bight (encircled stations refer to text and figures).

Samples for bottom water oxygen were taken with a 5 l water sampler (mounted on the CTD) at 0.5 m above the bottom and were determined with Winkler titration. Benthic samples were taken with a $0.1\ m^2$ Van Veen grab. At each station three parallels of grab samples were carried out. Due to sediment conditions grabs of different weights were used. The samples were sieved through a 1 mm screen and animals preserved with 4% formaldehyde in the field. For sorting in the laboratory, a stereo microscope with 10-40× magnification was used. A dredge haul (net mesh size 5 mm) was taken in order to obtain A. islandica specimens for the study of population size structure. For the characterisation of the habitats, i.e. assessment of sediment structure, epibenthos and current. an underwater video-system was used which was mounted on a sledge. The sledge was towed over the bottom by a drifting vessel at lowest possible speed (< 1 knot). The camera was installed on a pan and tilt head. Scaling was accomplished by four crossed laser beams projected into the picture. In addition bivalve siphon openings detectable at the sediment surface were counted to assess patchiness and distribution of adult (approximately >30 mm shell length) ocean quahogs.

At each station the shell length of all collected individuals of A. islandica were measured with a vernier calipers to the nearest 0.1 mm for the length-frequency distribution and the length-meat weight relationship. In total about 2300 specimens were measured. The valves and the wet meat of the specimens were weighed separately. Furthermore, the dry weight (DW) and ash free dry weight (AFDW) were determined to the nearest 0.01 mg. Because of very low weights, quahogs with shell lengths <3 mm were weighed in groups of 5 or 10 individuals sorted in size classes of 0.1 mm. Length-frequency distribution for each station was calculated for 10 mm size classes. The age of each A. islandica was estimated by measuring internal growth bands in the shell. This method is only applicable for specimens younger than 40 years (nearly all observed individuals are younger). For comparison and calibration, several shells were processed for observation of internal growth lines in acetate peels (see Ropes 1985).

The distribution map of the ocean quahog in the Mecklenburg Bight was made using Surfer (Win32) version 6.04 program of Golden Software Inc. The recent distribution was compared with the results from Schulz (1969a), whose data were transformed into the Surfer program to obtain a comparable map. Quahog distributional data from the monitoring station 12 of the Baltic Sea Research Institute Warnemuende and the Institute of Marine Research Kiel were used for the 11-year time series (1988–1999).

RESULTS

Bottom Water Variables

Salinity ranged between 7.5 and 22 psu in the water column. Bottom water salinity of areas inhabited by *Arctica islandica* varied between 12.5 and 22 psu in 1999. No oxygen deficiency was observed during our survey. Up to a depth of 16 m more than 7 mg/l were measured. Oxygen content decreased to a minimum of 4.5 mg/l only in the deepest parts of the Bight.

Distribution, Abundance and Biomass

In 1999 Arctica islandica was distributed between 15.6 and 29.6 m in the Mecklenburg Bight. Most stations within these depths were colonized (Fig. 2). Only in the deepest parts of the innermost area (Lübeck Bay) were no quahogs found. Furthermore, the outer Kadet trench with strong currents and stony substrates was not inhabited. The highest abundance was found in the south-eastern part of the Bight with a maximum of 571 ind./m² and an AFDW of 34 g/m² at station 103 (water depth 17.4 m). Thirty years ago (in the mid 1960's), A. islandica reached an abundance between 10 and 100 ind./m² with a maximum of 200 ind./m² in the central part of the Bight (Schulz 1969a) (Fig. 2). At depths below 20 m of the innermost area (Lübeck Bay), no A. islandica were found. The highest biomass (AFDW) was observed in deeper parts of the central Bight at station 54 (water depth 23 m) with 120 g/m² and an abundance of 236 ind./m 2 (Fig. 3). The Mecklenburg Bight had an estimated colonized area of 5200 km² within water depths of 15 and 30 m, a mean abundance of 91 ind./m2 and a biomass (AFDW) of 15 g/m². Based on these values, the whole population

Arctica islandica abundance ind./m² in 1999 Gedser 54.5 Fehmarn Latitude (N) Rostock 54.0 11.0 12.0 12.5 13.0 Longitude (E) Arctica islandica abundance ind./m2 in 1965 54.5 Latitude (N) Rostock 54.0 11.0 12.0 12.5 13.0

Longitude~(E) Figure 2. Distribution of Arctica islandica (ind./m²) in 1999 and during the investigation period in the mid 1960's of Schulz (1969a) (same scale for better comparison).

of the Bight was estimated at approximately 4.7E + 11 individuals with a biomass (AFDW) of 7.8E + 04 t (1.04E + 06 t wet weight).

In 1965 the mean abundance reached 20 ind./m². In the last 11 years the abundance of *A. islandica* at station 12 varied between 20 and 120 ind./m² (Fig 4). *A. islandica* occurred in mean density of 40 to 75 ind./m². However, due to patchy distribution of this species, the standard deviation was very high. The same was observed in 1999, when the highest abundance occurred with 120 ± 70 ind./m². Similarly, records by the video showed a similar patchy distribution of the quahog siphon openings. If only adults, specimens were taken into account, the average counts of openings were comparable with the estimated abundance by grabs at several stations. However, due to patchiness, the maximum abundance was much higher and ranged between 400 and 700 ind./m². Between these colonized centers, big patches of unsettled sediments were visible.

In this study the highest abundance was observed in depths between 15 and 20 m, whereas the maximum of biomass occurred

between 20 and 25 m (Fig. 5). With increasing water depth, the abundance decreased from an average of 155 ind./m 2 in 15-20 m, to 85 ind./m 2 in 20 to 25 m, and 35 ind./m 2 in 25 to 30 m, respectively. In comparison the biomass (AFDW) was low in both the 15 to 20 m, and 25 to 30 m interval (7–9 g/m 2), but averaged 28 g/m 2 at 20 to 25 m.

Population Structure, Meat Yield and Growth

During the benthos survey, shell lengths of Arctica islandica were between 1.5 and 64 mm (Fig. 6). Quahogs in the size class 0 to 10 mm composed 40% of the population. Particularly at shallower stations (15–20 m), the one- or two-year size classes (<10 mm) dominated. In deeper water (>20 m) individuals >20 mm were the dominant group. Generally only one size class dominated the population structure of an area. At shallow stations (stns WT5, MB3 and 103, see fig. 1 and 6) the most successful settlement took place during the last two years (the size class 0 to 10 mm domi-

Arctica islandica biomass AFDW in g/m² in 1999

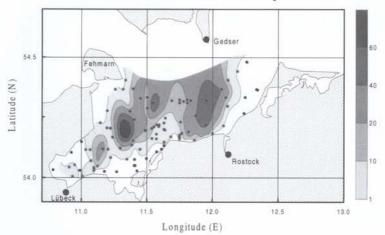


Figure 3. Biomass distribution of Arctica islandica (g AFDW/m2) in 1999.

nated with over 50%), whereas little or no recruitment was detected in stations deeper than 20 m. The dominant size class varied from 11 to 20 mm at stations 12 and Z3 via 21 to 30 mm at stations 63 and 07, to 31 to 40 mm at stations 75 and 54 (Fig. 6).

The wet meat yield (percentage of total wet weight) increased with increasing size up to shell length of 55 mm (Fig. 7). The mean meat yield of all individuals (1.5–55 mm) was 18.3% and varied between a minimum at 5% (2.7 mm shell length) and a maximum at 38% (47 mm shell length).

The organic content (all organic material of a quahog, i.e. meat, periostracum and ligamentum) was calculated as the relation of individual ash free dry weight to dry weight (Fig. 8). With increasing shell length a significant decrease in organic content was observed. The highest amount (14.3%) appeared in the shell size class <10 mm. The lowest organic content was 9.4% in the size class >40 mm. The mean organic content of DW of all individuals (1.5 to 55 mm shell lengths) ranged from 7.1% to 22.3% with a mean value of 11%.

Relationship between shell length and individual weight (meat

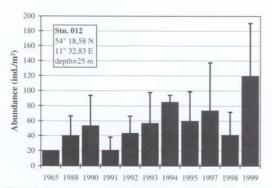


Figure 4. The development of mean abundance (± SD) of Arctica islandica at station 12 in the last 11 years in comparison with data of (Schulz 1969a) from the mid 1960's.

wet weight and ash free dry weight) is shown in Figure 9. In these graphs all measured specimens (1.5–64 mm) of all stations are included. The smallest meat wet weight was 0.095 mg at a shell length of 1.5 mm and the largest was 14.7 g at 64 mm (Fig. 9a). The average meat yield per unit shell length of *Arctica islandica* is indicated by the estimated mean regression line. Differences between the station means were not statistically significant. The ash free dry weight varied between 0.1 mg (1.9 mm in length) and 1.6 g (64 mm in length) (Fig. 9b). The estimated regression lines of the different populations (stations) did not differ significantly. The results indicate that quahogs throughout the Mecklenburg Bight approximately contained the same meat per unit shell length for the range of length considered.

Growth was estimated by measuring internal growth bands in the shell. The corresponding equation for the calculated best-fit regression lines for all included individuals (1.5 to 55 mm) given in Figure 10. The oldest measured specimen reached an age of

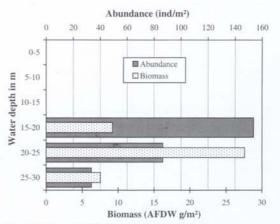


Figure 5. The vertical distribution of abundance (ind/m²) and biomass (AFDW g/m²) of Arctica islandica in 1999.

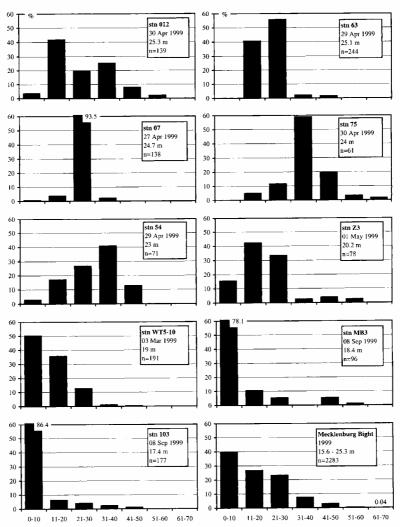


Figure 6. Shell length-frequency distribution for 10 mm size classes of Arctica islandica at several stations in depths between 17.4 m and 25.3 m in Mecklenburg Bight in 1999.

approximately 40 years. The largest and oldest specimen (64 mm) was not included because of difficulty of age estimation. After the equation, we got an age of app. 70 years.

DISCUSSION

The occurrence of Arctica islandica in the Mecklenburg Bight has been known since the last century when the first investigations on benthic fauna of the Baltic Sea took place (Boll 1852, Lenz 1875). While the main Baltic populations live in the Bay of Kiel and in parts of Sound and Belt, the distribution in the Mecklenburg Bight and the Arkona Basin represent the most eastern occurrence of this species in the Baltic Sea (von Oertzen and Schulz 1973). Due to the decreasing salinity in areas east of Mecklenburg Bight A. islandica has its natural limit of distribution there. Several in-

vestigations on biology and ecology of *A. islandica* of the Kiel Bay have been conducted (e.g. Arntz and Weber 1970, Brey et al. 1990, Oeschger and Storey 1993). However, information from the Mecklenburg Bight is very scarce (e.g. Al-Hissni 1989, Köhn 1989, Prena et al. 1997). Hagmeier (1930) observed a high biomass of *A. islandica* (195.1 g/m² fresh weight) in the Mecklenburg Bight during the 1920s, which is comparable with present biomass estimations. He found mostly adult specimens with juveniles scarcely occurring. The investigations of Schulz (1969a, b) at the end of the 1960s give the distribution pattern of *A. islandica* in the Mecklenburg Bight which was used for comparison with the present study. In the 1960s densities were low (20 ind./m² in mean). During the 1980s the abundance of the ocean quahog decreased in this region due to a long period of oxygen depletion (Gosselck et al. 1987,

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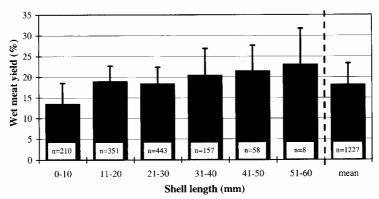


Figure 7. Mean wet meat yield in 10 mm size classes of Arctica islandica from the Mecklenburg Bight in 1999 (± SD).

Prena et al. 1997). In the inner part of the Lübeck Bay, in the 1980s no quahogs were found. In the early 1990s, the density of *A. islandica* increased in some regions of the Mecklenburg Bight (Al-Hissni 1989, Köhn 1989, Prena et al. 1997). Recently, a mean abundance of approximate 91 ind./m² in depths between 15 and 30 m occurred. The highest abundance was observed in the region between 15 and 20 m, whereas the maximum biomass occurred in deeper zones. Below the halocline, *A. islandica* is the most important species in the Mecklenburg Bight with respect to biomass. The mean biomass reached 15 g/m² AFDW (200 g/m² fresh weight). Brey et al. (1990) gave a P/B ration of 0.34 for populations in the Kiel Bay. If this ratio is applicable for the Mecklenburg Bight, the average annual production (AFDW) below the halocline amounts to 5.1 g/m². The total production of the Mecklenburg Bight is approximate 26500 t AFDW per year.

The different maximum zones for abundance and biomass are probably a result of recruitment failure in the deeper anoxic regions. In the deeper parts, oxygen depletion in late summer prevents the successful recruitment and growth of the juveniles, which settle mostly in summer and fall (Mann and Wolf 1983, von Oertzen 1972). The high biomass in the deep regions is based on adults (low numbers) that are able to survive critical times of oxygen depletion. Arctica islandica is one of the most tolerant species to oxygen deficiency and to hydrogen sulphide (von Oertzen and Schlungbaum 1972, Oeschger and Storey 1993, Theede et al. 1969). Nevertheless, Weigelt (1991) and Schulz (1969b) stated that possibly the high tolerance to oxygen deficiency is restricted to the adults, whereas the juveniles are more susceptible. Therefore, recruitment takes place only in favorable years. In the shallower zones (between 15 and 20 m), no major hypoxic episodes have been observed in the recent past (Matthäus et al. 1999). Although recruitment can take place in the shallower areas, conditions for growth are sub-optimal, probably due to the lower nutrition supply, lower salinity and higher temperature. The optimal temperature-range for fertilization, growth and survival of larvae and juveniles is 10° to 15°C (Landers 1976). Possibly the growing eutrophication of the western Baltic Sea explains the increased A. islandica population (see Arntz & Weber 1970, Persson 1987) and the displacement of the recruitment zone from below 20 m to the 15 to 20 m depth region.

The largest quahogs found were 64 mm long. In the 1960's Schulz (1969b) pointed out that only few specimens between 60 and 100 mm occurred in the central part of the Bight and juveniles

were only found around 18 m depth. In this study sizes above 70 mm were observed only as empty shells. The most frequent size classes were 1.5 to 30 mm which included >90% of the *A. islandica* population of the Mecklenburg Bight. This population structure is completely different from populations of the Atlantic Ocean, where the smaller size classes are mostly absent (e.g. Fritz 1991, Murawski et al. 1982, Thorarinsdottir and Einarsson 1996, Steingrimsson and Thorarinsdottir 1995). We attribute this to successful recruitment in the Mecklenburg Bight during the last 10 to 15 years. In contrast in Atlantic waters, ocean quahog populations have only sporadic recruitment and strong recruitment events occur only every twenty (or more) years (Murawski et al. 1982, Steingrimsson and Thorarinsdottir 1995).

The mean wet meat yield of *A. islandica* of 18.3% (5% to 38%) is similar to other reported values. For a population in the Kiel Bay, Arntz and Weber (1970) reported a percentage of 19.3 to 22.2 with minimum values in winter. The meat yield of *A. islandica* off Iceland coasts ranged between 17% and 40% and averaged 30% (Thorarinsdottir and Einarssson 1996). If only the smaller size classes (<40 mm) of quahogs off Iceland are considered, then the mean wet yield of approximately 20% is similar to the result of this study. The meat yield observed from grounds off the coast of the United States and Canada ranged between 20.7% and 23% (Bakal et al. 1978, Chaisson and Rowell 1985).

In the Mecklenburg Bight, the mean individual ash free dry weight of *A. islandica* decreased from 14.3% to 9.4% with increasing size classes. The increasing mean wet yield and the decreasing

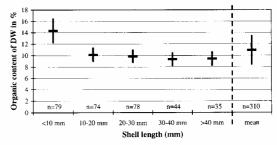


Figure 8. Mean individual percentage of ash free dry weight for different size classes of *Arctica islandica* from the Mecklenburg Bight in 1999 (± SD).

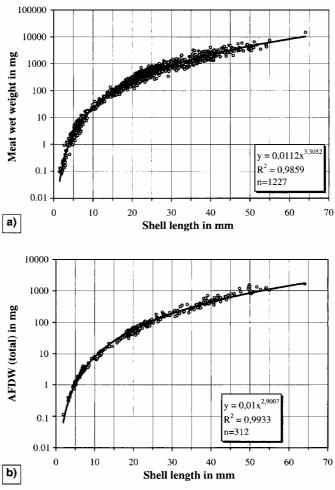


Figure 9. a) Estimated shell length-meat wet weight relationship for Arctica islandica, b) estimated shell length-ash free dry weight relationship for Arctica islandica. In these graphs all measured specimens of the whole Mecklenburg Bight populations are included. The corresponding equations for the calculated best fit regression lines is given in the figure.

ash free dry weight with increasing shell length indicate relatively higher water content of bigger quahogs. The length specific meat wet weight (shell-length to meat-weight relationship) in this study was similar to that reported for ocean quahogs off United States coasts. In the Mecklenburg Bight, the calculated meat wet weight for an individual of 95 mm shell length was 39 g. The meat wet weight of *A. islandica* off New York reported by Murawski et al. (1982) were 36 and 38 g and off New Jersey 37.9 and 51.3 g (Fritz 1991). The biggest meat wet weights of *A. islandica* ever reported (47.6, 55.5 and 70 g) were found off Iceland by Thorarinsdottir and Johannesson (1996). The calculated AFDW for an individual of 95 mm shell length reached 5.4 g.

Several authors reported on geographical differences in growth rates of *A. islandica* in its distribution area and between field and laboratory populations (e.g. Brey et al. 1990, Fritz 1991, Josefson et al. 1995, Kennish et al. 1994, Kraus et al. 1992, Steingrimsson

and Thorarinsdottir 1995, Witbaard 1996, Witbaard et al. 1999). Ocean quahogs are among the slowest growing and long-living marine bivalves (Murawski et al. 1982, Thompson et al. 1980). Growth rates for this species vary with respect to location (temperature, food supply, salinity, and abundance). Kraus et al. (1992) observed the fastest growth in the laboratory where A. islandica reached 54 mm from 9.6 mm within three years. In the laboratory the specimens grow to 37 mm within two years. In the field they need 26 to 33 years to achieve the same shell length. The comparison of the growth curve of the Mecklenburg Bight population with growth curves calculated by Witbaard et al. (1999) for 12 populations from the North Sea and adjacent waters shows similar growth increments for the first 40 years of life. For the first five years, the Mecklenburg Bight population had a growth rate very similar to populations of the Kattegat with approximate linear increase in size with age (Josefson et al. 1995). In comparison with 168 Zettler et al.

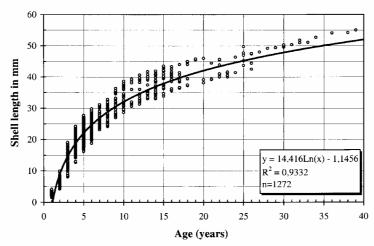


Figure 10. Growth curve of Arctica islandica from the Mecklenburg Bight for the first 40 years of life.

the growth rates of a Kiel Bay population calculated by Brey et al. (1990), the growth in the Mecklenburg Bight was slower. A. islandica in the Kiel Bay reached about 84 mm after 40 years; whereas, the specimens in the Mecklenburg Bight had a mean shell length of 52 mm in the same time. These differences are difficult to explain. The lower salinity may be one reason for the observed slower growth of quahogs in the Mecklenburg Bight. A possible further explanation might be that the Kiel Bay higher bottom currents (closer openings to the Small and Great Belt), enriched in suspended or re-suspended material, would supplement A. islandica, as a filter-feeder, with advective food supply (see Witbaard et al. 1999).

The present study shows the peculiarities of the ocean quahog in the Mecklenburg Bight near its eastern distributional boundary within the Baltic Sea. Further investigations must deal with the differences in observed growth rates of quahogs within the Baltic and adjacent waters. The comparative population dynamics of dif-

ferent water depths and/or sediment structure and the dispersion and settlement patterns of the larvae in this "border" area are of interest. Two of the main questions following this study are: Is the short life expectancy of quahogs in the Baltic due only to the salinity and which conditions cause the success of strong recruitment in its geographical distribution.

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LITERATURE CITED

Al-Hissni, Z. 1989. Saisonale und annuale Fluktuationen des Makrozoobenthos in der Lübecker und Mecklenburger Bucht in den Jahren 1985– 88. PhD Universität Rostock.

Arntz, W. E. & W. Weber. 1970. Cyprina islandica L. (Mollusca, Bivalvia) als Nahrung von Dorsch und Kliesche in der Kieler Bucht. Ber. Dt. Wiss. Komm. Meeresforsch. 21:193–209.

Bakal, A., W. F., Rathjen & J. Mendelsohn. 1978. Ocean quahog takes supply spotlight as surf clam dwindles. Food Product Development 12:70–78.

Boll, E. 1852. Cyprina islandica in der Ostsee (vor Niendorf) in Mecklenburg. Arch. Fr. Ver. Naturgesch. Mecklb. 6:p125.

Brey, T., W. E., Arntz, D., Pauly & H. Rumohr. 1990. Arctica (Cyprina) islandica in Kiel Bay (Western Baltic): growth, production and ecological significance. J. exp. mar. Biol. Ecol. 136:217–235.

Chaisson, D. R. & T. W. Rowell. 1985. Distribution, abundance, population structure, and meat yield of the ocean quahog (Arctica islandica) and Stimpson's surf clam (Spisula polynyma) on the Scotian Shelf and Georges Bank. Can. Ind. Rep. Fish. Aqu. Sci. 155:p134.

Fritz, L. W. 1991. Seasonal condition change, morphometrics, growth and

sex ratio of the ocean quahog, Arctica islandica (Linnaeus, 1767) off New Jersey, U.S.A. J. Shellfish Res. 10:79–88.

Gosselck, F., F., Doerschel & T. Doerschel. 1987. Further developments of macrozoobenthos in Lübeck Bay, following recolonisation in 1980/81. Int. Revue ges. Hydrobiol. 72:631–638.

Hagmeier, A. 1930. Die Bodenfauna der Ostsee im April 1929 nebst einigen Vergleichen mit April 1925 und Juli 1926. Ber. Dt. Wiss. Komm. Meeresforsch. 5:156–173.

Josefson, A. B., J. N., Jensen, T. G., Nielsen & B. Rasmussen. 1995. Growth parameters of a benthic suspension feeder along a depth gradient across the pycnocline in the southern Kattegat, Denmark. Mar. Ecol. Prog. Ser. 125:107–115.

Kennish, M. J., R. A., Lutz, J. A., Dobarro & L. W. Fritz. 1994. In situ growth rates of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the middle Atlantic Bight. *J. Shellfish Res.* 13:473–478.

Köhn, J. 1989. Zur Ökologie sandiger Böden der Mecklenburger Bucht. PhD Universität Rostock: 170pp.

Kraus, M. G., B. F., Beal, S. R., Chapman & L. McMartin. 1992. A comparison of growth rates in *Arctica islandica* (Linnaeus, 1767) between field and laboratory populations. J. Shellfish Res. 11:289–294.

- Landers, W. S. 1976. Reproduction and early development of the ocean quahog, *Arctica islandica*, in the laboratory. *Nautilus* 90:88–92.
- Lange, W., E. Mittelstaedt & H. Klein 1991. Strömungsdaten aus der Westlichen Ostsee. Meβergebnisse aus dem Zeitraum 1982 bis 1986 sowie historische Beobachtungen vom Feuerschiff "Fehmarnbelt". Dt. Hydrogr. Z. Erg. Heft Reihe B 24:1–129.
- Lenz, H. 1875. Die wirbellosen Thiere der Travemünder Bucht. Theil 1. Komm. wiss. Unters. disch. Meere Kiel: 1–24.
- Mann, R. & C. C. Wolf. 1983. Swimming behavior of larvae of the ocean quahog Arctica islandica in response to pressure and temperature. Mar. Ecol. Prog. Ser. 13:211–218.
- Matthäus, W., G. Nausch, H.U. Lass, K. Nagel & H. Siegel 1999. Hydrographisch-chemische Zustandseinschätzung der Ostsee 1998. Meereswiss. Ber. 35:69pp.
- Murawski, S. A., J. W., Ropes & F. M. Serchuk. 1982. Growth of the ocean quahog, Arctica islandica, in the mid-Atlantic bight. Fish. Bull. 80:21– 33.
- von Oertzen, J.-A. 1972. Cycles and rates of reproduction of six Baltic Sea bivalves of different zoogeographical origin. *Mar. Biol.* 14:143–149.
- von Oertzen, J.-A. & G. Schlungbaum. 1972. Experimentell-ökologische Untersuchungen über O₂-Mangel- und H₂S-resistenz an marinen Evertebraten der westlichen Ostsee. Beitr. Meereskd. 29:79–91.
- von Oertzen, J.-A. & S. Schulz. 1973. Beitrag zur geographischen Verbreitung und ökologischen Existenz von Bivalviern der Ostsee. Beitr. Meereskd. 32:75–88.
- Oeschger, R. & K. B. Storey. 1993. Impact of anoxia and hydrogen sulphide on the metabolism of Arctica islandica L. (Bivalvia). J. exp. mar. Biol. Ecol. 170:213–226.
- Persson, L.-E. 1987. Baltic eutrophication: A contribution to the discussion. *Ophelia* 27:31–42.
- Prena, J., F., Gosselck, V., Schroeren & J. Voss. 1997. Periodic and episodic benthos recruitment in southwest Mecklenburg Bay (western Baltic Sea). Helgol. Meeresunters. 51:1–21.

- Ropes, J. W. 1985. Modern methods used to age ocean bivalves. The Nautilus 99:53–57.
- Schulz, S. 1968. Rückgang des Benthos in der Lübecker Bucht. Monatsber. Dtsch. Akad. Wiss. Berlin 10:748–754.
- Schulz, S. 1969a. Benthos und Sediment in der Mecklenburger Bucht. Beitr. Meereskd. 24(25):15-55.
- Schulz, S. 1969b. Das Makrozoobenthos der südlichen Beltsee (Mecklenburger Bucht und angrenzende Seegebiete). Beitr. Meereskd. 26:21–46.
- Steingrimsson, S. A. & G. Thorarinsdottir. 1995. Age structure, growth and size at sexual maturity in ocean quahog, Arctica islandica (Mollusca: Bivalvia), off NW-Iceland. ICES Council Meeting K 54:1–11.
- Theede, H., A. Ponat, K. Hiroki & C. Schlieper. 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Mar. Biol.* 2:325–337.
- Thompson, I., D. S., Jones & D. Dreibelbis. 1980. Annual internal growth banding and life history of the ocean quahog Arctica islandica (Mollusca: Bivalvia). Mar. Biol. 57:25–34.
- Thorarinsdottir, G. & S. T. Einarsson. 1996. Distribution, abundance, population structure and meat yield of the ocean quahog, Arctica islandica, in Icelandic waters. J. Mar. Biol. Ass. UK 76:1107–1114.
- Thorarinsdottir, G. & G. Johannesson. 1996. Shell length-meat weight relationships of ocean quahog, Arctica islandica (Linnaeus, 1767), from Icelandic waters. J. Shellfish Res. 15:729–733.
- Weigelt, M. 1991. Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforsch* 33:197–224.
- Witbaard, R. 1996. Growth variations in Arctica islandica L. (Mollusca): a reflection of hydrography-related food supply. ICES J Mar Sci 53: 981–987
- Witbaard, R., G. C. A., Duineveld & P. A. W. J. de Wilde. 1999. Geographical differences in growth rates of Arctica islandica (Mollusca: Bivalvia) from the North Sea and adjacent waters. J. Mar. Biol. Ass. IIK 79:907–915