

# Macrozoobenthos on an intertidal mudflat in the Danish Wadden Sea: comparisons of surveys made in the 1930s, 1940s and 1980s

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**ABSTRACT:** To assess whether long-term faunal changes have occurred on intertidal flats in the Danish Wadden Sea, results of faunal surveys in the Skallingen area during the 1930s, 1940s and 1980s were compared. Since the earlier studies, two species have disappeared (*Scrobicularia plana* and *Petricola pholadiformis*) and two have invaded the area (*Tharyx killariensis* and *Ensis americanus*). This is, however, not a local event as species changes have occurred on a larger scale (Wadden Sea region). Comparison of abundance data did not provide evidence of changes from the 1930s until the 1980s. Spatio-temporal fluctuations in two dominant species, the mudsnail *Hydrobia ulvae* and the cockle *Cerastoderma edule* chosen for closer examination, could be explained by natural processes. Growth data on cockles from the 1930s and the 1980s matched perfectly. During both periods, cockles showed a much lower growth rate than generally reported from the Wadden Sea, while at the same time they occurred at high densities ( $> 2000 \text{ ind} \cdot \text{m}^{-2}$ ). Intraspecific competition among cockles is suspected as being a major cause of the low growth rates. Estimates of secondary production and P/B-ratios of cockles were also in general agreement during the 1930s and the 1980s when corrected for differences in the age structure of the cockle populations. With the possible exception of *Mytilus edulis*, which according to some observations has extended its range along the low-water line, the present comparison failed to demonstrate long-term faunal changes caused by increased eutrophication. This results is expected to be representative for intertidal flats not exposed to direct impacts from terrestrial run-offs and waste-water discharges.

## INTRODUCTION

The Dutch-German-Danish Wadden Sea area is important for a variety of species including shorebirds, fish, shrimps and crabs because of its high benthic productivity. Being an area of international significance to migrating birds and stocks of North Sea fish, there is a growing concern regarding possible threats to this particular ecosystem. Like several other near-coastal areas the Wadden Sea has been increasingly exposed to human activities with possible resulting detrimental effects on the benthos. Loading by nutrients and organic substrates from terrestrial run-offs and waste-water discharges, in particular, have been reported to influence the macrozoobenthos (Essink & Beukema, 1986; Madsen & Jensen, 1987; Beukema, 1989, 1991; Esselink et al., 1989). Furthermore, dredging activities and fishery on mussels, cockles and shrimps have either directly (through overexploitation) or indirectly (through the effects of fishing equipment on the sea bottom) been considered detrimental to the benthic community (Reise, 1982; Vlas,

1987; van der Veer et al. 1985). In subtidal areas of the German Wadden Sea, considerable faunal changes have occurred during the last 60 years that are mainly attributable to human activities (Riesen & Reise, 1982; Reise & Schubert, 1987). While faunal impoverishment has often been reported to follow prolonged and severe eutrophication in near-coastal sublittoral areas, this would not be a predictable effect on the intertidal fauna because of mixing by tidal currents. Accordingly, studies in the Dutch Wadden Sea have shown an increase in the abundance and secondary production of several intertidal flat species during the last 20 years to be a result of eutrophication (Beukema & Cadeé, 1986; Beukema, 1989, 1991). During the same period, the concentration of phytoplankton and the primary production of the microphytobenthos in the Dutch Wadden Sea have almost doubled (Cadeé, 1984, 1986a, b).

Although the utilization of the Danish Wadden Sea has, until quite recently, been less intensive compared with the Dutch and German parts, it nonetheless receives large amounts of nutrients and organic substrates from terrestrial sources (Henriksen et al., 1984). So far, no studies of long-term faunal changes in the Danish Wadden Sea have been reported. In an attempt to assess whether faunal changes have occurred on tidal flats in the Danish Wadden Sea, and to what extent such changes have been generated by human activities, I compared the results of two earlier faunal investigations with a more recent one. The tidal flats on the east coast of Skallingen (the northern part of the Danish Wadden Sea) were investigated during the early 1930s by Thamdrup (1935). In the 1940s Smidt (1951) performed a more extensive faunal survey in this area, and I sampled the fauna at Skallingen from 1982 to 1985. Since the study area is not under direct influence from any sewage outlet or polluted terrestrial run-off, any long-term faunal changes ought to reflect either natural processes or effects of a more general human impact on the ecosystem. Data on species composition and abundance of the macrofauna are compared. Furthermore, two dominant macrofaunal species, *Hydrobia ulvae* (Prosobranchia) and *Cerastoderma edule* (Bivalvia), are examined in more detail with respect to population dynamics (both species) and growth and secondary production (*C. edule*). These species each represent a separate part of the ecosystem, being a deposit-feeder and a suspension-feeder, respectively. Furthermore, *H. ulvae* dominates the upper intertidal zone whereas *C. edule* dominates the lower zone (Thamdrup, 1935).

#### AREA AND METHODS

The macrozoobenthos on the tidal flat east of the Skallingen peninsula in the northern part of the Danish Wadden Sea (55°30'N, 8°18'E, Fig. 1) has been examined previously by Thamdrup (1935) and Smidt (1951). During the period from 1982 until 1985, I quantitatively sampled the benthos along an intertidal transect in the vicinity of Thamdrup's "Fernsprechhaus-linie" (Fig. 1). Details on sampling procedures can be found elsewhere (Thamdrup, 1935; Smidt, 1951; Jensen & Jensen, 1985; Jensen, 1992). Small samples taken by Thamdrup (1935) were sieved through a 0.9 mm sieve, whereas Smidt (1951) used a 1 mm sieve for those samples reported here. I used a mesh size of 0.5 mm for small samples (21 cm<sup>2</sup>) and 1 mm for larger samples (143 cm<sup>2</sup>). Data on the quantitative occurrence of the macrobenthos have been read from Figures in Thamdrup (1935, p. 75–97) and from Table 18 in Smidt (1951). The shell lengths of cockles were taken from Figure 25, p. 75 in Thamdrup (1935) and Figure 34, p. 80 in Smidt (1951).

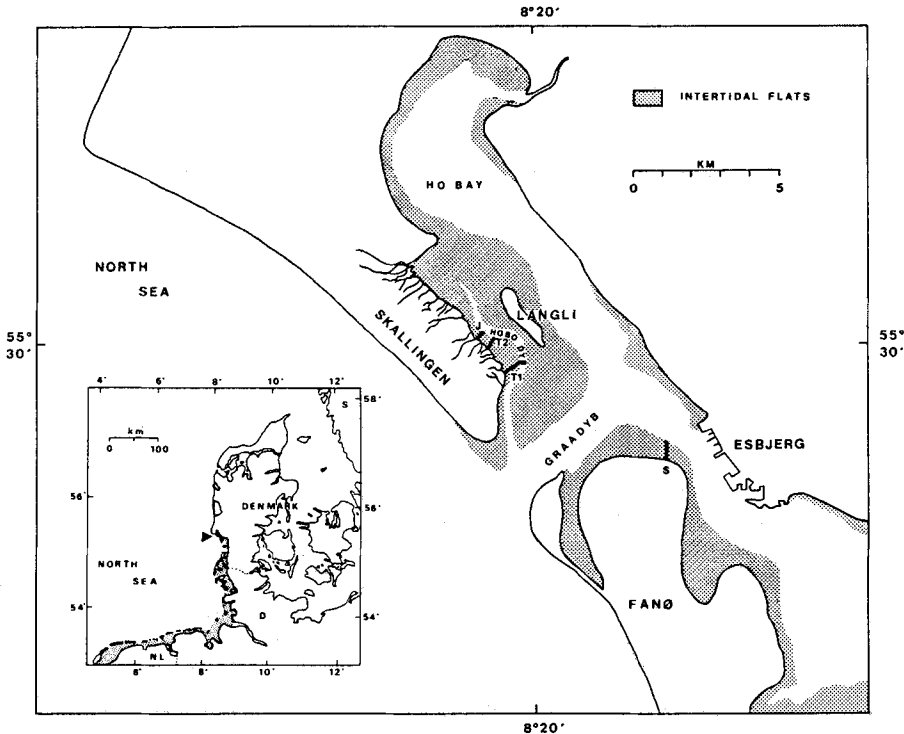


Fig. 1. Map of the northern part of the Danish Wadden Sea area showing the location of the studied transect (J) and those transects studied by Thamdrup (1935) (T1: "Buhnen-Linie"; T2: "Fernsprechhaus-linie") and Smidt (1951) (S)

Benthic samples were collected along two 500-m-long transects (Thamdrup, 1935; Smidt, 1951) and along one 400-m-long transect (1982–85) from the high-water line (HWL) to the low-water line (LWL). The transect used in 1982–85 was similar to the "Buhnen-linie" (Thamdrup, 1935) with respect to sediment composition. In the upper half of the intertidal flat the sediment was dominated by fine sand grains (mean grain size about 180  $\mu\text{m}$  and silt content below 2%) while the substratum was muddier at the lower flat (mean grain size about 130  $\mu\text{m}$  and silt content near 30%, St. 300 m) (1982–85, Jensen, 1992). The "Fernsprechhaus-linie" was a pure sand-flat with coarse sand grains (200–500  $\mu\text{m}$ ) as the dominant sediment fraction (Thamdrup, 1935). Smidt (1951) collected samples along the same transects as were used by Thamdrup. There are no remarks in Smidt (1951) concerning sediment composition when he collected samples in August 1942. The tidal range in this area is about 1.5 m.

Available data on densities and length of cockles (Figs 3 and 4) during the 1930s and the 1980s were used to calculate a rough estimate of secondary production during the two periods. The mean weights of cockles were estimated from their mean lengths using the following length-weight equation:  $\ln W = -5.61 + 3.15 \ln L$  ( $W$  in mg flesh ADW;  $L$  in mm), obtained from formaldehyde preserved specimens collected in October 1984 at St.

300 m (Jensen, in prep.). The secondary production between two dates  $t_1$  and  $t_2$  (separated by one year) is calculated as the product of the mean weight increment ( $\Delta w$ ) and the number of individuals living between  $t_1$  and  $t_2$ . To give the possible range in production, three estimates are calculated, assuming: (1) that the number of cockles growing between  $t_1$  and  $t_2$  is equal to the mean density at  $t_1$  and  $t_2$  (mean estimate); (2) that all cockles living at  $t_1$  survived until immediately before  $t_2$  (maximum estimate); (3) that only those present at  $t_2$  lived during the whole period (minimum estimate). The mean estimate of production is also used to calculate the P/B-ratio.

## RESULTS

### Macrozoobenthos at Skallingen in the 1930s, 1940s and 1980s

The macrozoobenthic species living on the intertidal flat at Skallingen are dominated by typical members of the '*Macoma balthica*' community (Table 1). Most of the species show characteristic distributional patterns along the intertidal gradient. Species such as *Pygospio elegans*, *Hydrobia ulvae* and *Corophium volutator* generally attain their highest numbers in the upper intertidal zone, whereas species like *Cerastoderma edule* and *Mya arenaria* increase in abundance in an off-shore direction. *Mytilus edulis* occurs in beds along the low-water line. During both faunal surveys in the 1930s and in the 1980s, cockles were the most important species quantitatively on the lower shore, whereas *H. ulvae* dominated on the upper shore.

**Losses.** Two species were recorded only during the 1930s (*Scrobicularia plana* and *Petricola pholadiformis*) and one species was observed only in the 1940s (*Cirratulus cirratus*) (Table 1). As this latter species was represented by a few juvenile individuals only, I will consider its occurrence as accidental. However, the absence of species from samples does not necessarily indicate that they have vanished from the area. I did not find *S. plana* or *P. pholadiformis* even though I have sampled regularly in this area for 3 years. *P. pholadiformis* was observed for the first time in the Skallingen area in 1905; it was common from 1910 and onwards (Jensen & Spärck, 1934, cit. by Thamdrup, 1935), but was observed only once by Thamdrup (1935). *S. plana* occurred in low densities during the 1930s on silty substrata (Thamdrup, 1935).

**Gains.** Three species (*Polydora ligni*, *Tharyx killariensis* and *Corophium arenarium*) were not mentioned in the earlier studies but were found during the surveys in 1982 and 1983. (It is assumed that both *Capitella capitata* and *Heteromastus filiformis* were included in Capitellidae and that *Eteone longa* and *Anaitides maculata* were included in Phyllodocidae in the data reported by Smidt, 1951). *P. ligni* might have been overlooked during the earlier surveys although Smidt (1951) found *P. ligni* from nearby localities. *T. killariensis* is identical to the species which hitherto has been described as *Tharyx marioni* sensu Farke, 1979 (M. E. Petersen pers. comm.). The genus *Tharyx* has recently been redescribed and restricted by Blake (1991). *T. killariensis* occurs in high densities at the lower intertidal flat on sites with a high silt-content. I have recorded maximum densities of 30 000 ind · m<sup>-2</sup> (March 1983). *C. arenarium* was described in 1937 by Crawford (Crawford, 1937) but was not mentioned by Smidt (1951). However, Stock (1952) found *C. arenarium* in Ho Bugt in 1952. Therefore, it is probable that the species was confused with *Corophium volutator* during the earlier surveys.

Changed abundance. *Nereis diversicolor*, *Scoloplos armiger* and members of the family Capitellidae were recorded in maximum densities in 1982–83, being more than 100 % higher than those reported in the earlier investigations. The presence of high numbers of juveniles, i. e. those individuals retained on a 0.5 mm mesh but not on sieves with larger mesh sizes, could contribute to the observed density differences. The high numbers of spat of *C. edule* and *M. balthica* both in 1942 and in 1982 followed severe winters in 1941/42 and 1981/82, respectively. In 1982 and 1983 the abundance of *C. volutator* was low on the intertidal flat compared with its abundance during the previous surveys. However, this species is subject to great spatiotemporal fluctuations. It was observed at high densities in tidal creeks at Skallingen in 1982 and 1983 (own obs.).

Temporal and spatial variation in population dynamics and growth

*Hydrobia ulvae*. The interannual variation in the abundance of *H. ulvae* is large. Samples taken in July during the period from 1931 to 1934 in the upper tidal zone showed a variation from 5000 to almost 50 000 ind · m<sup>-2</sup> (Fig. 2). Within one year I found a variation of the same magnitude (from 15 000 to 65 000 ind · m<sup>-2</sup>). Observations by Thamdrup (1935) suggest that *H. ulvae* is limited to the upper part of the intertidal flat. However, the distributional pattern reported by Smidt (1951) from an intertidal flat in the northern part of Fanø showed their presence in the lower intertidal zone, also. From monthly data on abundance of *H. ulvae* along the intertidal gradient at Skallingen, 1982–83, it appears that for peak density at each site there is a successive progression in a landward direction starting at station 300 m (Fig. 2). This pattern is presumably due to a settlement of *H. ulvae* in the lower intertidal zone followed by a net landward migration.

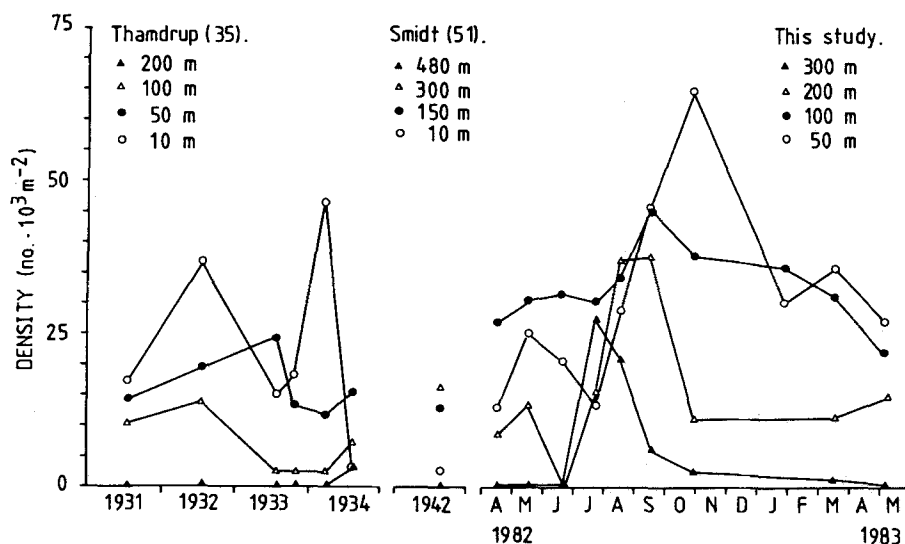


Fig. 2. Seasonal and long-term patterns in density (no. · m<sup>-2</sup>) of *Hydrobia ulvae* at Skallingen (symbols indicate sampling positions in metres from the MHWL)

Table 1. Macrobenthic species at Skallingen during the 1930s, the 1940s and the 1980s. All values are maximum numbers ( $\text{ind} \cdot \text{m}^{-2}$ ) along the transects for July or August. Ranges given for data from the 1930s and the 1980s denote the lowest and the highest maximum density registered in July during the study periods. If only a single value is indicated it represents the maximum numbers mentioned by the author. Juv.: 0-group; adu.: 1-year and older; "-": not mentioned; obs: observed

	Thamdrup, July 1931-35		Smidt, August 1942		Jensen, July 1982-83
	Transect 1	Transect 2	Transect 1	Transect 2	
<b>Oligochaeta</b>					
<i>Tubificoides benedeni</i>	-	-	-	-	4000-9000
Oligochaeta sp.	-	-	6200	2500	2000-12000
<b>Polychaeta</b>					
<i>Phyllodocidae</i>					
<i>Eteone longa</i>	-	-	-	-	440-520
<i>Anaitides maculata</i>	-	-	-	-	0-140
<i>Nereis diversicolor</i>	100-280	30-70	500	530	2000-3800
<i>Nephtys hombergi</i>	90	7-13	30	0	50
<i>Scoloplos armiger</i>	100	370-460	4900	1700	1600-15000
<i>Polydora ligni</i>	-	-	-	-	670-1200
<i>Pygospio elegans</i>	15000-20000	6000	2300	5600	3400-22000
<i>Cirratulus cirratus</i>	-	-	200	0	0
<i>Tharyx killariensis</i>	-	-	-	-	1300-5000
<i>Capitellidae</i>					
<i>Capitella capitata</i>	-	-	-	-	260-9000
<i>Heteromastus filiformis</i>	40	0	-	-	620-880
<i>Arenicola marina</i>	25-100	38	14	34	30-31
<i>Pectinaria koreni</i>	-	-	300	0	0
<i>Lanice conchilega</i>	obs.	-	70	0	0-50
<b>Gastropoda</b>					
<i>Hydrobia ulvae</i>	16000-37000	350-1000	16000	10000	5800-31000
<i>Littorina littorea</i> *	7-70	obs.	-	-	10-16
<i>Retusa obtusa</i>	-	-	250	170	50-90
<b>Bivalvia</b>					
<i>Cerastoderma edule</i> juv.	few - 2700	few - 250	72000	64000	300-62000
adu.	1300-4700	250-1500	70	0	0-4300
<i>Macoma balthica</i> juv.	300-5700	230	55000	23000	0-2650
adu.	350-1000	75	700	530	1100-1200
<i>Mya arenaria</i> juv.	110	0	8800	0	0-17000
adu.	13-20	0-13	0	0	30-50
<i>Scrobicularia plana</i>	60	0	0	0	0
<i>Mytilus edulis</i>	beds	no beds	beds	-	beds
<i>Petricola pholadiformis</i>	obs.	0	0	0	0
<b>Crustacea</b>					
<i>Corophium volutator</i>	1000-3200	300-1100	9200	17400	200-440
<i>Corophium arenarium</i>	-	-	-	-	100-1700
<i>Bathyporeia</i> spp.	obs.	obs.	0	200	0
<b>Nemertina</b>					
Nemertini sp.	-	-	100	100	50-260

\* Data from the mudflat (not mussel-beds)

Both Smidt (1951) and Reise (1987) observed that juveniles of *H. ulvae* occurred predominantly in the lower tidal zone. The natural variation in the quantity of larvae and the time of settlement may cause interannual differences in their distributional pattern. Thus, the peak density along a tidal gradient does not necessarily occur at the same site in a certain month each year. For example, severe winters may reduce the survival of *H. ulvae* disproportionately in the upper intertidal zone compared with the lower zone (Smidt, 1951). This could be an explanation for the distributions observed in 1942 and again in spring 1982 compared with the distribution in the 1930s. From September 1982 and onwards, the distribution along the intertidal gradient was similar to the distribution observed by Thamdrup (1935). As Thamdrup apparently missed the juveniles during the sampling in July because they could pass through his sieve, he would probably not detect individuals present in the lower intertidal zone. However, he does mention that among snails found on the lower flat a higher fraction belonged to the 0-group. Difference in mesh sizes may also explain the higher densities observed during the 1980s than during earlier investigations. The cause of the landward migration of *H. ulvae* is probably the presence of dense populations of large diatoms on the upper shore, these being important food items for *H. ulvae* (Jensen, 1980). Individual mudsnails move faster on substrata with poor food than on substrata rich in food items. This mechanism may gradually cause an accumulation of snails on sites with dense populations of diatoms (Jensen, 1980). In conclusion, there is no evidence that the abundance pattern of *H. ulvae* has changed since the 1930s.

*Cerastoderma edule*. In the years 1931 to 1935, two year classes of cockles (1928 and 1929) dominated the population of cockles at Skallingen (Thamdrup, 1935). During my study from 1982 until 1985, only one year class of cockles occurred (Jensen, 1992). This year class settled in July 1982 and it was exterminated during the winter 1984–85. Together, these investigations provide data on abundance and growth of cockles from their settlement until six years old (Figs 3 and 4).

In July 1982, the density of juvenile cockles was about  $35\,000\text{ ind}\cdot\text{m}^{-2}$  at St. 200 m and St. 300 m from the shoreline. Due to predation by juvenile crabs, the densities declined rapidly during August and September (Jensen & Jensen, 1985). After this time, there was a more gradual reduction in densities. In autumn 1984 the numbers at the lower sites varied from 2000 to 3000  $\text{ind}\cdot\text{m}^{-2}$ . Thamdrup (1935) found densities of cockles older than 2 years in the range of 2000 to 4500  $\text{ind}\cdot\text{m}^{-2}$  in the lower tidal zone. The densities of cockles along the "Fernsprechhaus-linie" were much lower than those along the "Bühnen-linie" (Thamdrup, 1935).

Data on lengths of cockles from their settlement until an age of 2 years (Jensen, 1992) have been combined with data provided by Thamdrup (1935) on the temporal variation in mean lengths of year class 1928 during 1931 to 1935 (3 to 6 years old) (Fig. 4). These sets of data agree quite well. Two- and six-year-old cockles on this mudflat reached maximum mean lengths of 18.4 and 22.5 mm, respectively. In comparison, a low-density population of cockles from the north coast of Fanø reached a mean shell length of about 27 mm after only two years (Fig. 1 and Smidt, 1951). This is more in accordance with growth patterns reported by other authors (Orton, 1926; Kreger, 1940; Kristensen, 1957). In addition, high growth rates in cockles were observed on the same transect in 1989. Cockles collected in October 1989 had reached a mean length of 30.3 mm after three growing seasons (St. 300 m). This difference in growth rates of cockles from the same

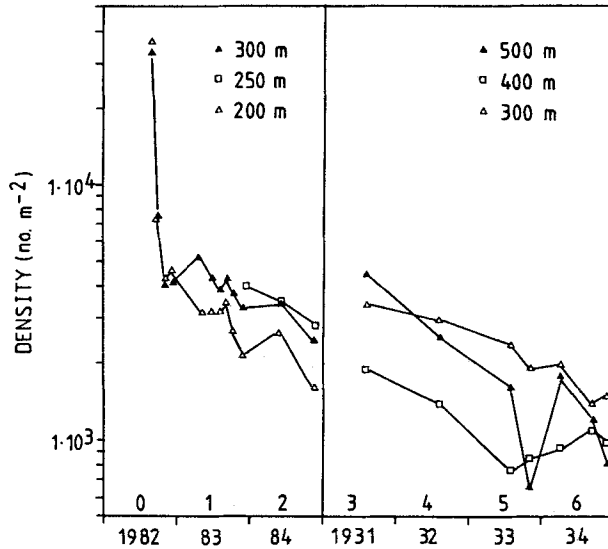


Fig. 3. Density ( $\text{no. m}^{-2}$ ) of *Cerastoderma edule* at Skallingen during 1982–84 (0- to 2-yr-old cockles) and 1931–34 (3- to 6-yr-old cockles). The transect studied in the 1930s was  $\approx 500$  m-long, while the one studied in 1980s was  $\approx 400$  m-long. (Symbols indicate sampling positions in metres from MHWL)

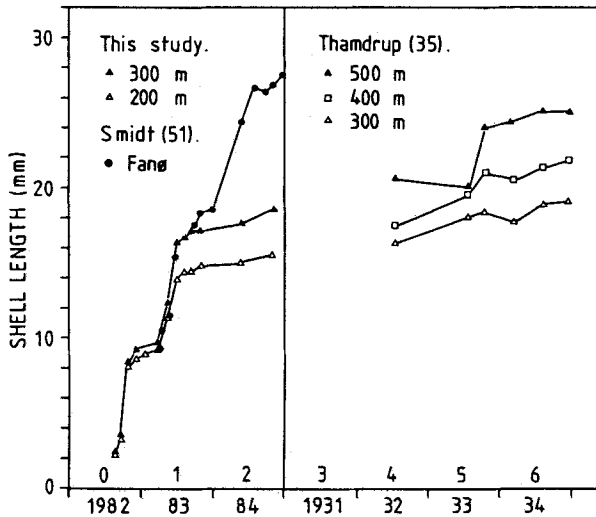


Fig. 4. Mean shell length of cockles during 1982–84 (0- to 2-yr-old cockles) and 1932–34 (4- to 6-yr-old cockles). In addition, length data (1- and 2-yr-old cockles in 1946, Fig. 34, Smidt, 1951) from a cockle population on the north coast of Fanø (Fig. 1) are plotted. Densities of the Skallingen populations can be read from Figure 3. The population at Fanø reached a maximum density of  $\approx 500$   $\text{ind} \cdot \text{m}^{-2}$  (June 1946, Smidt, 1951, p. 83)



Table 2. Estimates of average biomass, annual secondary production and P/B-ratios of cockles during 1932–33 (St. 300 m and St. 400 m) and 1983–84 (St. 200 m and St. 300 m) at Skallingen

	Biomass (g ADW m <sup>-2</sup> )		Production (g ADW m <sup>-2</sup> )	P/B
	July 32	July 33		
1932–33				
300 m	68.5	78.3	24.8 (22.3–27.3)	0.34
400 m	40.9	33.6	15.8 (11.2–20.4)	0.42
	May 83	May 84		
1983–84				
200 m	24.0	45.7	27.9 (25.4–30.3)	0.80
300 m	41.3	102.5	74.4 (69.2–85.7)	1.04

Table 3. Estimates of average biomass, secondary production and P/B-ratios of cockles during the period from May to October in 1983 and 1984 (St. 200 m and St. 300 m) at Skallingen

	Biomass (g ADW m <sup>-2</sup> )		Production (g ADW m <sup>-2</sup> )	P/B
	May 83	Oct 83		
1983				
200 m	24.0	36.3	24.3 (19.7–28.8)	0.81
300 m	41.3	89.5	66.1 (57.6–74.6)	1.01
	May 84	Oct 84		
1984				
200 m	45.7	31.6	6.4 (4.7–8.1)	0.17
300 m	102.5	86.4	15.1 (12.6–17.6)	0.16

locality is probably a result of density-dependent growth regulation in cockles because fewer than 32 ind · m<sup>-2</sup> were present in 1989 (Jensen, 1992, and in prep.).

Data on density and growth of cockles have been combined to estimate annual secondary production at two stations in 1932–33 and 1983–84 (Table 2). From this it appears that the production was higher in 1983–84 than in 1932–33, suggesting a higher production of food items (phytoplankton). P/B ratios seem to support this. However, it should be noted that the cockles from 1932–33 were older than those from 1983–84. A comparison of the secondary production during the periods May to October 1983 and 1984 confirms that productivity decreases with the age of cockles (Table 3). For this reason, the present data would not support less food production during the 1930s than during the 1980s.

#### DISCUSSION

Two species appear to have vanished from the Skallingen area since the 1930s, namely *Petricola pholadiformis* and *Scrobicularia plana*, and one has emerged, namely *Tharyx killariensis*. In addition, *Ensis americanus* (previously misidentified as *Ensis*

*directus*; see van Urk, 1987), has recently been reported from the Hobo-Dybb tidal area (Rasmussen, unpublished). Two of these species (*P. pholadiformis* and *E. americanus*) are exotic species as originally they were immigrants from USA. *P. pholadiformis* was already on the decline during the 1930s (Thamdrup, 1935). Lack of specific adaptations to new environments with respect to abiotic factors or disease agents (e.g. local parasite community) may eventually cause the local extinction of foreign species. The two new species (*T. killariensis* and *E. americanus*) were first observed during the late 1960s and 1970s (Farke, 1979; Essink, 1985; Reise, 1985; Swennen et al., 1985). The decline in *S. plana* seems to be a widespread phenomenon as it has also been reported to have disappeared from other regions of the Wadden Sea (Essink et al., 1991; Reise, 1982). However, increased numbers have been reported from some Dutch areas (Beukema & Cadeé, 1986). Presently, there are no clues as to these opposite trends in occurrence (Essink et al., 1991).

Two deposit-feeding groups of polychaetes (*Scoloplos armiger* and Capitellidae) and one omnivorous polychaete (*Nereis diversicolor*) showed considerably higher densities in the early 1980s than previously registered. Part of this increase could be due to higher numbers of juveniles during the latest survey because of the smaller mesh size used. On the other hand, increased numbers of these species have also been reported from the tidal flats near Sylt and from the Dutch Wadden Sea (Reise et al., 1989; Beukema, 1989).

The abundance patterns and dynamics of populations of *Hydrobia ulvae* and *Cerastoderma edule* were similar during the surveys in the 1930s and the early 1980s. In addition, the growth pattern of cockles followed the same trajectory during these periods. In both periods, cockles exhibited extremely low growth rates. This has been interpreted as a result of a negative density-dependent mechanism, probably as a result of food competition (Jensen, 1992 and in prep.). The growth data of cockles strongly support great similarity during the early 1930s and 1980s in terms of environmental conditions. Assuming that eutrophication and, in turn, increased primary production would enhance growth rates in suspension-feeders from intertidal flats, as shown in *Macoma balthica* (Beukema & Cadeé, 1986, 1991), the present results suggest that the same amount of food was available to cockles in the 1930s and 1980s. This is also largely corroborated by the estimates of secondary production. Considering the age of cockles living from July 1932 to July 1933, they exhibited a high secondary production. The P/B ratios also support the suggestion that cockles from the 1930s were at least as productive as those from the 1980s.

The present faunal comparison does not suggest that major alterations in faunal structure and function occurred during the period from the 1930s to the 1980s on the studied mudflat. Nonetheless, intercontinental shipping is the ultimate cause of the appearance of some new species in the present ecosystem. Apart from this, variability caused by natural processes may explain most of the observed differences in densities. However, it remains possible that the increased numbers in three polychaete groups could be a result of increased eutrophication (Beukema, 1991).

No long-term studies of primary production have been conducted in the Danish Wadden Sea. The Hobo-Dybb tidal area is supplied directly with coastal water from the Graadyb tidal inlet. Henriksen et al. (1984) have measured levels of phytoplankton production in Graadyb that exceed measurements in the tidal inlet Marsdiep in the western Dutch Wadden Sea from the mid-1970s (Henriksen et al., 1984). However, later

reports from the Marsdiep area indicate an increase by a factor 2 in phytoplankton production from the mid 1970s until the early 1980s (Cadeé, 1986b) due to increased supplies of phosphate. Thus, phytoplankton production reached comparable high levels in the tidal inlet of Marsdiep and Graadyb in the early 1980s. The high phytoplankton production in Graadyb is a result of high nutrient supplies from the river Varde Å and from the city of Esbjerg (Henriksen et al., 1984; Pejrup et al., 1990). As these supplies have increased since the faunal investigations during the 1930s and 1940s due to the use of fertilizers in agriculture and increased amounts of sewage discharge, it seems reasonable to assume that the phytoplankton production also has increased. Faunal studies from the western Dutch Wadden Sea have indicated long-term trends of increasing biomass, densities and growth rates of several intertidal flat species in response to the increased primary production since 1970 (Beukema, 1991). However, a study from the eastern Dutch Wadden Sea failed to detect long-term faunal trends despite increased eutrophication (de Jonge & Essink, 1991). To consider why the present study failed to detect any such changes, a few shortcomings should be mentioned. For example, data in Table 1 are strongly simplified as spatiotemporal fluctuations are ignored. In fact, most species are subject to large fluctuations in abundance due to natural processes. The conclusions arrived at are also based on subjective interpretations rather than on rigorous statistical tests. It is possible that the years of comparison are atypical and therefore fail to reveal any long-term trends overriding the multitude of factors otherwise influencing the benthos. The approach adopted by comparing more detailed abundance data in two dominant invertebrates, *H. ulvae* and *C. edule*, and growth data of cockles, summarising data for longer periods than those in Table 1, albeit in a few species only, is more likely to reveal real trends.

The question remains as to whether other species not examined in detail could have responded to increased eutrophication. Remarks on the distribution of mussels (*Mytilus edulis*) during the 1930s (Thamdrup, 1935) and 1940s (Smidt, 1951) and my own observations during the 1980s suggest that this species has extended its range along the Hobo-Dyb channel. There were mussel beds along the low-water line in the 1980s at the studied transect. However, Figure 2 in Thamdrup (1935) and comments by Smidt (1951) suggest that during their studies mussels were more or less restricted to the southern edge of the Hobo-Dyb tidal channel. Mussels might therefore have taken advantage of the higher primary production in this area. Expansion of mussel beds along the low-water line has also been reported from the German area (Reise et al., 1989).

The two transects studied by Thamdrup (1935) exhibited different faunal compositions. In the 1930s, the transect named "Fernsprechhaus-linie" was more sandy and homogeneous along the tidal gradient than the other transect ("Buhnen-linie"). The transect studied during 1982–85 was almost identical to the "Buhnen-linie" with respect to sediment and faunal composition, though it was situated closer to the "Fernsprechhaus-linie". Spread of mussel beds since the 1930s along the Hobo-Dyb tidal channel could have caused increased sedimentation on the lee-side of the mussel beds, and in turn could have brought about a change in faunal composition.

According to Dankers & Koelemaij (1989), mussels often occur in such densities that they influence the whole ecosystem. In some years they may filter the entire water volume every few days. Thus, they may influence the amount of food available for other organisms. The high densities of cockles as reported here would suggest that they also

might influence the phytoplankton biomass. Other studies support the idea that dense assemblages of suspension-feeding organisms may exert some control on the phytoplankton biomass and primary production (Cloern, 1982; Officer et al., 1982). In addition, it has been experimentally demonstrated that high densities of cockles may reduce the settlement of their own larvae (André & Rosenberg, 1991) as well as *Macoma balthica* larvae (Jensen, 1985). Furthermore, the burrowing and ploughing habits of cockles have detrimental effects on some species (Reise, 1983; Jensen, 1985). Therefore, both cockles and mussels may be key organisms in this particular ecosystem through their functional (regarding energy flow) and structural importance. Interannual variability in the numbers of these two species may cause variability in other species. In particular, other suspension-feeding organisms may suffer from food depletion due to high densities of either mussels or cockles. In other words, cockles and mussels may control the response of other organisms to increased eutrophication.

In conclusion, the present comparison failed to detect any major faunal changes caused by human impact since the 1930s. However, the limitation of the approach adopted has to be recognized. The comparison is based upon macrobenthic data collected from a single locality. Furthermore, the study area is situated far from any terrestrial run-offs and waste water discharges. Any changes, therefore, would at most reflect possible effects of a generally increased nutrient loading and, in turn, increase in primary production. Comparison of macrozoobenthic data from a larger area through a sequence of years would produce a more comprehensive picture.

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