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EXPECTED BIOLOGICAL EFFECTS OF LONG-TERM CHANGES IN TEMPERATURES ON MARINE ECOSYSTEMS IN COASTAL WATERS AROUND THE NETHERLANDS

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INTRODUCTION

The extensive use of fossil fuel resources for energy production, causes an increasing accumulation of carbon dioxide in the atmosphere. From this accumulation and that of some other gaseous substances a rise of temperature of the earth's atmosphere can be predicted. However, no precise prediction on future climate development can be made.

This study, a compilation of existing literature, was carried out to assess the possible effects of an arbitrary rise in temperature during a period of 50-100 years. It is thought likely that the temperature will rise by more than 2^0 C in the near future. After consultation with the principal the following starting points for this study were taken: a rise in mean summer temperatures of +2 to $+4^0$ C and a change of winter temperatures of -2 to $+2^0$ C in the coming 50-100 years, compared with the mean summer and winter temperatures at present. In this study, biological effects of the assumed changes in coastal water temperatures will be discussed.

CHAPTER 1. TEMPERATURES OF DUTCH COASTAL WATERS

1.1. Long-term global changes in air temperature vs changes in Dutch coastal waters

Temperature measurements in the air as well as in Dutch coastal waters during the last 90-120 years are available. The changes over that period can be compared with global changes in air temperature to see if the Dutch coastal water temperatures ran parallel with the global ones.

Jones et al. (1986) published an assessment of global air temperature variations between 1861 and 1984 combined for 15 regions on land as well on sea. These data have been combined to produce comprehensive estimates of global mean air temperatures (Fig. 1). The results show only little trend before 1900, a clear warming till about 1940, a stabilization (or slight decrease) till the mid-seventies, followed by a rapid warming during the last 10 to 15 years.

They conclude that a long-term warming trend occurs. The overall change is in the right direction and of the correct magnitude, compared with the change expected from the CO_2 accumulation hypothesis. The relative stability of temperatures between 1940 and the mid-seventies presumes the existence of some compensatory factor.

In Dutch coastal waters long-term series of temperature measurement of surface waters are available from Den Helder-'t Horntje (from 1861-1980) and the Oosterschelde (from 1894-1980) (van der Hoeven 1982, 1983). Besides, long-term measurements from light vessels are available. In this investigation, measurements from the light vessels Noord Hinder (near the Belgian coast) and Haaks-Texel are used (van der Hoeven 1984). To straighten out variations in the mean yearly temperatures, means of groups of ten year have been calculated with standard error. The results are shown in Figs 2A, B and C.

In Fig. 2A (Den Helder-'t Horntje) two periods of temperature decrease can be distinguished, from 1861-1910 and 1941-1970. A warming occurred between 1910 and 1940 and during the seventies. In the Oosterschelde about the same temperature changes can be observed, but smaller, and with smaller standard errors. The results of the light vessel measurements (Fig. 2C) show a temperature decrease between 1890 and 1910, and for Haaks-Texel a decrease between 1951 and 1970. Thus, within the Netherlands coastal waters there is a very good agreement.

In the water temperatures there is no clear evidence of a steady trend of temperature increase from 1900 to 1980. In fact, at Den Helder-'t Horntje (Fig. 2A), mean temperature from 1860-1870 was slightly higher than from 1971-1980.

When a comparison is made between the change in global air temperature as determined by Jones et al. (1986) and the measurement in Dutch coastal waters as shown here, especially with the longest series Den Helder-'t Horntje (Fig. 2A), a significant difference is observed between 1860 and 1910 (little trend vs significant decrease), a correspondence occurs between 1910 and 1941, and a slight difference between 1931 and 1970 (stabilization vs slight, not significant decrease). And again a correspondence during the last 10 or 15 years (increase).

When air temperatures at De Bilt over the period 1880-1980 (Van Engelen 1983) are plotted in the same way as the sea water temperatures, results are obtained as given in Fig. 2B. A comparison with Fig. 2A (sea water temperatures at Den Helder-'t Horntje) shows a clear difference in the trend of temperature development over the period 1880-1910, but in the period 1910-1980 the trends are the same. This means that the temperature of the Dutch coastal waters is determined not only by air temperature, but also by hydrographic changes on the North Atlantic Ocean, for example the course of the Gulf Stream.

Thus, temperatures in Dutch coastal waters follow only partially both the global and the local air temperature change. However, both the recent warming up from 1970 and the lowering trend after 1940, as well as the rising trend between 1920 and 1940, as shown in the global air temperatures, are reflected in the coastal water temperatures.

1.2. Short-term changes and expected mean temperatures

In the region of the North Sea and the Wadden Sea and the Oosterschelde, where tidal currents prevent the development of summer stratification, the water follows the air temperature with a short time lag of 6 days for the Wadden Sea and 35 days for the North Sea. This means that the North Sea water usually will show an appreciable time lag with respect to seasonally meteorological conditions. The sea follows the annual trend more closely the shallower the water is. Also, the amplitudes are smaller where the water is deeper (Postma 1982).

Offshore water temperatures in the North Sea could be obtained from observations of light vessels. From two light vessels, Noord Hinder (off the Flemish coast) and Haaks-Texel (off the island of Texel), monthly temperatures were used over periods of 1971-1980 (Noord Hinder) and

1967-1977 (Haaks-Texel). Ten-year means + standard errors of all monthly temperatures are given in Fig. 3.

To indicate summer temperatures of coastal waters, the mean monthly temperatures of August (the warmest month) are taken, and the highest and lowest mean temperatures recorded during the 1971-1980 period are given as a measure of variation.

Sea water temperatures in relatively shallow and sheltered basins such as the Dutch Wadden Sea and the Oosterschelde will in summer as well in winter deviate from those of offshore coastal water. Since in the Wadden Sea and the Oosterschelde the amplitude is closer to that of the air, the area is warmer in spring and summer and colder in autumn and winter (Fig. 5). Mean monthly temperatures in the Oosterschelde basin in the period 1971-1980 are given in Fig. 4. Also, for the Wadden Sea, mean temperatures at Breezanddijk, near the Afsluitdijk, in the period 1971-1980 are shown.

The same method is applied as with the light vessel temperatures, but with other mean monthly temperatures taken for summer and winter temperatures because of a time lag in temperature development compared with coastal waters. Mean summer temperatures in the Oosterschelde, around 18.5° C in August, are somewhat higher than those of the Wadden Sea, around 17.5° C.

From observations of light vessels, mean temperature during winter months at Haaks-Texel are about 2° C lower than those at Noord Hinder. Generally, mean yearly temperatures at Noord Hinder are 0.6-0.8° C higher than at Haaks-Texel (Fig. 2C).

To indicate winter temperatures of coastal waters, the mean monthly temperature of February (the coldest month) are taken. February mean temperatures varied between 5 and 6° C (Haaks-Texel) and 7 and 8° C (Noord Hinder).

If mean winter temperatures were to rise by 2° C, mean temperatures would become ~7° C (Haaks-Texel) ~ 9° C (Noord Hinder). If mean winter temperatures were to decrease by 2°C, mean temperatures would become ~3°C (Haaks-Texel) to ~5° C (Noord Hinder).

The difference in mean winter temperatures between the Oosterschelde and the Wadden Sea is half of those of the light vessels: about 1°C. In the Oosterschelde mean February temperatures are around 3.5°C, and in the Wadden Sea around 2.5° C.

To get an impression of the variations in the coastal water temperatures, and the extreme temperatures which can occur in different locations, mean sea water temperatures and temperatures in the warmest summer month (August) and the coldest winter month (February) are given below:

Table 1
Summer (August) temperatures (monthly averages)

	period	mean temp.	extreme temp. range	standard deviation	n
Haaks-Texel	1948-1976	17.3	15.7-19.5	0.91	29
Noord Hinder	1948-1981	16.8	15.7-18.5	0.73	33
Wadden Sea	1951-1980	17.4	15.4-20.2	0.98	29
Oosterschelde	1951-1980	18.6	17.3-21.4	0.95	29
		Winter temperatures			
Haaks-Texel	1948-1976	4.6	-0.1-6.2	1.38	29
Noord Hinder	1948-1981	6.5	1.3-8.6	1.34	33
Wadden Sea	1951-1980	2.0	-1.1-5.0	1.58	29
Oosterschelde	1951-1980	2.9	-1.4-5.4	1.86	29

If mean summer temperatures were to rise by 2^0 C (or 4^0C), mean summer water temperatures in the Oosterschelde basin would become ~20.5^0 C and 22.5^0 C, respectively, and in the Wadden Sea ~19.5^0 C and 21.5^0 C (see horizontal lines in Fig. 4).

If winter mean temperatures were to rise by 2^0C, temperatures would become 5^0C in the Oosterschelde, and 4^0 C in the Wadden Sea. If mean winter temperatures were to decrease by 2^0 C mean temperatures would become ~1^0 C in the Oosterschelde basin and ~0^0 C in the Wadden Sea (see horizontal lines in Fig. 4).

The temperature of the Westerschelde water is influenced by the temperature of the river Scheldt and the temperature increase of water used for cooling of power stations and industry (Antwerp). The Grevelingen is a stagnant salt water lake, in which temperature differs from that of Dutch coastal waters.

Not only mean summer temperatures and mean winter temperatures are important for life in the Dutch coastal waters, but so are extreme temperatures in summer and winter. When the highest and the lowest mean monthly temperatures are plotted against the mean yearly temperature, a linear relation appears. The mean temperature of the coldest month clearly becomes higher when the mean year temperature rises. Also, but but less clearly, the mean temperature of the warmest month rises when the mean year temperature is higher. Generally, an alteration in the mean year temperature goes together with a considerable alteration in the mean winter temperature, and a lesser alteration in summer temperature.

The temperature of the water on the tidal flats at high tide can be higher or lower than the mean water temperature in the Oosterschelde or the Wadden Sea. Solar radiation during daytime warms up the shallow water on the tidal flats. During the night the reverse occurs and the water cools by losing radiant heat. The shift of the lunar tide through the day causes a pulse in the daily water temperature cycle with a period of about 2 weeks (14.76 days) and a variation of the daily mean temperature by the same period. This periodicity is caused by the fact that for one week tidal flats are emerged during the mid of the day and directly exposed to solar radiation and in the other submerged during

the day. The temperature of the water on the tidal flats at high tide differs from the mean temperature by 0.5° C with a standard deviation of ± 0.1°C (Vugts and Zimmerman 1975, 1985). In stagnant pools on dry tidal flats water temperature can rise to about 30° C (Kristensen 1957).

When the flats are emerged during the day and exposed to solar radiation, the sediment warms up. In spring and summer the surface temperature of the sediment often considerably surpasses the air temperature, whereas during autumn and winter the surface sediment generally stays below the maximum temperature of the air (de Wilde and Berghuis 1979, Fig. 6). According to these authors, temperatures up to 29° C have been measured on the surface of the sediment.

Results of a series of measurements of 17 months are given in Fig. 6. At a depth of 10 cm the temperature of the sediment is clearly less extreme than at the surface (Fig. 6). If the temperature of the coastal water were to rise 2 or 4°C, temperatures of emerged sediment would become higher because of a higher start temperature.

Temperature variations in the sediment differ clearly from those in the water column, and as a consequence the bottom fauna also lives in temperature ranges different from those in the water column.

When mean winter temperatures become lower, the probability occurs of an increasing number of days with ice. An appreciation of this will follow in chapter 6.2.

CHAPTER 2. EFFECTS OF TEMPERATURE ON ANIMALS

2.1. General effects

For many species of marine organisms the temperature range at which they occur in nature is relatively narrow: these animals are called stenothermal. They may be cold- or warm-limited or both. Other marine organisms have a much larger temperature range, living in coastal waters where fluctuations in temperature are much larger than in seas and oceans. They are called eurythermal organisms. Littoral organisms, except for seasonal transients, are in general eurythermal. Of these, sessile or hemisessile forms tend to be more eurytherm than vagil ones, and those with cosmopolitan distribution are usually more or less eurytherm. All over the world, typical eurytherm species appear to be fewer than stenotherm ones (Kinne 1963).

Many animals avoid critical temperatures by vertical and horizontal migration into more suitable conditions. The temperature range tolerated is often more restricted during the reproductive phase than during the asexual phase. In many species it is narrow during very early ontogenetic development, then increases somewhat and finally decreases again in the senile adult.

The upper limits of thermal tolerance of marine organisms are associated with both latitudinal and local variations in the environmental range experienced under natural conditions. The zone of tolerance of an organism is defined by an upper and a lower incipient lethal temperature, both of these values often being modifiable by

exposure to long-term changes in environmental temperature. Such acclimatory responses allow the organism to adjust the limits of its zone of tolerance until "ultimate" upper and lower incipient lethal temperatures are reached. At this stage injury to the whole organism or to its biochemical components is irreversible.

It is generally recognized that three distinct time phases can be distinguished in the response of any particular process in invertebrates to a change in environmental temperature: 1. First, there is a direct (acute) response of the physiological process to a change in temperature. This may be accompanied by an overshoot, followed by a period of stabilization which takes place over a period of minutes or hours. 2. Second, following longer-term exposure to changed temperature conditions lasting days or weeks, the organism may show an adjustment of its rate functions. When in response to temperature itself, this phenomenon is known as "thermal acclimation", whereas a compensatory adjustment in response to more complete seasonal changes in environmental conditions is distinguished as "seasonal acclimatization". 3. Third, long-term changes in environmental temperature operating over many generations favour the appearance of genetic variants adapted to the new thermal regime.

When the long-term changes in environmental temperature occur too fast or are too large, adaptation is not possible and death occurs.

2.2. Short-time temperature alterations

A lot of experimental work has been performed on short-term temperature alterations. Such experiments have been carried out with single animal species. From this type of experiments no predictions can be made on the effects of long-term temperature alterations (50-100 years). However, these experiments can give information about the survival of animals in the tidal zone, especially at high tide.

Precht (1973) and Prosser(1973) distinguish between different types of short-term adaptation to temperature of marine animals. Individuals of a given species of aquatic animals can be experimentally acclimated to several temperatures. The experimental determination of lethal temperatures provides a useful tool in assessing (1) inter- and intraspecific differences in temperature tolerance,(2) the physiological condition, (3) the status of acclimation to a given temperature.

Usually the mortality percentage is plotted as a function of time at each temperature, and the time to death of 50% of each group is plotted against exposure temperature. The median tolerance temperature (LD50) falls at longer times until, after about 48 hours, for most animals investigated, no further deaths occur; this lowest temperature causing deaths is the upper incipient lethal temperature. Data for cold death are treated similarly, and two lines are plotted, the incipient high and low lethal temperatures against acclimation temperature. The tolerance polygon obtained (Fig. 7) is fairly characteristic of a species.

The lethal temperature is influenced not only by acclimation temperature and genetic background, but also by diet, age, size, and environmental factors such as photoperiod, oxygen and salinity. When the

temperature is raised or lowered abruptly, most poikilotherms show an initial overshoot or a shock reaction, sometimes an undershoot on cooling. If an animal is kept at the altered temperature for many days, its rate functions often show some compensation, i.e. it becomes acclimated. Usually the acclimated rate lies between the first stabilized value and complete acclimation, i.e. there is partial compensation. In all patterns, the inactivation temperature or tolerance limit changes with acclimation.

Precht (1973) used results of rate function measurements at the two temperatures of acclimation only, and from the results obtained with many animal species distinguished 5 types of reaction on temperature change.

He distinguishes between compensations (types 1-3), no compensation (type 4) and "inverse" compensation (type 5). Type 3 represents the normal and most frequent case, namely partial compensation; type 1 represents overcompensation and type 2, perfect compensation resulting - after completion of acclimation - in constant rate functions.

Prosser (1973) not only used rate function measurements at acclimation temperatures, but measurements of stabilized rates over the entire temperature range as well. In this way additional evidence can be obtained regarding the nature of acclimation. Thus, Prosser (1973) distinguishes between four basic possibilities: pattern I: little or no temperature acclimation; pattern II: shift in position of rate curve without change in Q10 over the biological range of temperature; pattern III: change in Q10 (rotation) without shift in position of rate curves; and pattern IV: translation coupled with rotation.

According to Prosser (1973), change in position of a rate : temperature curve (translation) implies a change in activity (in the thermodynamic sense) of some enzyme system; change in slope (rotation) suggests a change in Q10 and hence in activation energy. Factors most likely to cause translation are: a change in enzyme concentrations, or in controlling conditions (salinity, pH, etc) or a change in relation among enzymes in series or parallel.

Factors most likely to change slope are: alteration of the enzymatic protein, a change in some cofactors, or a shift in control of a reaction to alternate enzymatic pathways. Acclimation to different temperatures may involve changes in orientation, migration and other behavioural aspects such as territorialism (size of territory) as well as biological rhythms.

According to Newell and Branch (1980), the responses of individual physiological processes to a change in temperature should fall into two main categories as far as the overall energy balance of the organism is concerned: 1. Those such as irrigation and feeding rates, involved in the acquisition of energy from the environment; 2. Those, such as metabolism (expressed as oxygen uptake), which are a measure of energy loss from the organism. In terms of energy conservation the organism would be expected to make compensatory adjustments to each of these groups of processes in such a way that maximal rates of energy gain are maintained, and energy loss is minimized in the face of a change in environmental conditions. They consider suspension feeders, because it

is rather difficult to quantify the feeding rate synchronously with oxygen consumption in other animal groups.

They distinguish three respose types: In response type 1, the clearance may be adjusted up to a point where rates coincide with the environmental temperature; at the same time the oxygen consumption, and hence metabolic energy losses, may be relatively reduced following a rise in environmental temperature. Example of an animal species with response type 1: Crepidula fornicata.

In response type 2 the clearance rate may be adjusted in response to a change in environmental temperature, but metabolic losses increase sharply with environmental temperature. Examples of animal species with response type 2: Ostrea edulis, Donax vittatus.

In response type 3 the energy input is inflexible and shows no adjustment in response to a change in environmental temperature, but there is a relative reduction of metabolism following warm acclimation. Examples of animal species with response type 3: Littorina littorea, Balanus sp.,Patella granularis, P. cochlear.

Many marine animal species, especially fish, can avoid critical temperatures by migration. Examples are young flounders and plaice, living in coastal areas in the tidal zone. During ebb tide they move from the flats into the tidal channels, and return with the flood during both day and night. In the Dutch Wadden Sea, the unfavourable temperature conditions on the flats in the warmer parts of the year suggest that this tidal migration is a forced escape behaviour of plaice and flounder from the feeding grounds. Maximum temperatures of 20^0 C to about 24^0 C have been found during daytime at low tide. The difference between day and night temperatures in summer ranged from 2-3^0 C during high tide and up to 6^0 C during low tide (van der Veer 1986, Balgzand, Dutch Wadden Sea).

Experimental research has shown (Waede 1954) that for plaice 28^0 C is fast lethal, and at 27^0 C they live only for 14 hours. For flounders a lethal temperature of 29^0 C was shown. If sea temperatures should rise 2^0 C, lethal temperatures for young plaice would be nearly reached; a temperature rise of 4^0 C would be lethal for young plaice, and a lethal temperature for young flounders would be approached. In fact, in the German Wadden Sea occasionally dead plaice have been found in periods of hot weather (Berghahn 1983). For young sole lethal temperatures are not reached in this temperature range (Fonds 1975).

CHAPTER 3. ZOOGEOGRAPHY AND ALTERATIONS CAUSED BY TEMPERATURE CHANGE IN THE PAST CENTURY

3.1. Zoogeography

The most important factors determining the geographical distribution of a given species are: 1. Historical factors which may or may not have provided a chance for a given species to come into contact with a given geographic area or habitat. 2. Abiotic factors, especially temperature and salinity which may or may not allow a species to establish itself

after contact has occurred. 3. If these factors are favourable, biotic factors tend to determine increasingly the ecological dynamics and hence the distribution of a species (Kinne 1963).

Considering temperature, the most obvious effect on animal distribution is exclusion of species from areas with unsuitable temperature conditions. Less obvious are effects of temperature on growth rates, length of life, reproductive capacity and intra- and interspecific dynamics.

Temperature not only affects the distribution of individual species; it will also determine the species composition of a community or an ecosystem. Gradual decreases or increases in temperatures over decades or centuries have repeatedly changed the species composition in vast areas of the earth. Whole faunas differ in their horizontal distribution, for example warm-water fauna of the shelf, Mediterranean-Atlantic fauna, Boreal fauna of the North Atlantic, Arctic fauna. Adaptation in an ecological sense may be defined as adjustments of living systems to one or more factors of their natural environment, which ultimately result in an increase in their capacity to survive, reproduce and compete.

Distinction is necessary between non-genetic adaptation involving non-genetic changes in the response mechanism - also known as acclimation or acclimatization - and genetic adaptation involving genetic changes in the response mechanism.

Non-genetic adaptations of individuals are not passed on as such to the next generation, but the ability to adapt and the mechanisms involved are evolutionary products. In this sense non-genetic and genetic adaptation represent different aspects of the same phenomenon. The principle of genetic adaptation is selection acting upon genetic variation.

The effect of temperature appears to be that of an ecological master factor, not ruling out appreciable secondary effects caused by other factors (Kinne 1963).

Distributional differences arise because organisms have varying tolerances for maximum and minimum temperatures and different optima as well. Such terms as "Boreal", "Lusitanian", "Arctic", "Caribbean", etc. are primarily names for temperature conditions. The relations between temperature and distribution of such groups are not simple, as indicated by the overlapping distributions of many organisms belonging to different groups. The control in one organism may be effected by the breeding season, in another by the survival of adults or larvae at the extreme; usually the distribution is a result of various combinations (Gunther 1957).

The mode of biological response to climatic events tends to be that of a population; the numbers change slowly or sharply in time and such changes manifest themselves most clearly in restricted areas such as spawning grounds. The places where some of the crucial biological mechanisms occur might be small in scale and particular in character, such as the western English Channel or the north-west coast of Ireland (Cushing and Dickson 1976).

3.2. Effects of temperature changes in the past century

Three examples will be treated here of the effect on marine faunal populations of climatic change going together with distinct changes in sea water temperature. First, the effect of the temperature rise in the North Sea and the N.E. Atlantic Ocean. Second, the effects of temperature rise and fall on the ecosystem of the Channel (Russell Cycle). Third, the effect of temporary temperature changes on the Peru anchovy fishery and the offshore ecosystem (El Nino).

3.2.1. North Sea and N.E. Atlantic

There were two trends in biological response to temperature rise in the North Sea and the N.E.Atlantic Ocean during the 1920-1960 period. First, subtropical animal species migrated to the north, to British waters, to the Faroe Islands and Iceland. Second, Boreal or Atlantic animal forms appeared at the Murmansk coast, Svalbard, N. and E. Iceland and W. Greenland. Both trends are thus widely apparent over the whole north Atlantic Ocean (Cushing and Dickson 1976).

The simplest response was probably the earlier to be recorded, the appearance of an exotic invader, the indicator species. In the waters around France and the British Isles an invasion of animals from more southerly waters took place. For example Physalia (Siphonophora) strandings in S.W. England became more frequent in the past hundred years. Another example of the manifestation of exotic invaders is the infrequent plague of Octopus vulgaris Lam. in the Southwest Channel, which is associated with the highest temperatures in the Western Channel.

A spread of benthic animals of more southern origin into the Murman Current took place from 1935 onwards, probably most in the late 1940s and early 1950s.Boreal (and one or two subtropical) animal at all depth ranges reached further north : Faroe Islands, Iceland, East and West Greenland, Jan Mayen and the Barentz Sea.

In the English Channel the spread of two competing species of coastal barnacles, Balanus balanoides L. and Chthalamus stellatus Poli has been followed. Between the 1920s and 1930s Balanus retreated eastward from the south coast of Cornwall; Chthalamus spread eastwards off the Island of Wight and southwards along the coast of Scotland. Between the 1930s and 1949 the eastward shift of the Boreal barnacle continued and the southern one replaced it (Crisp 1956). Between 1962 and 1965 such changes were reversed quite sharply (Cushing 1982).

Also Laminaria ochroleuca de la Pylae, a seaweed recorded in the Plymouth area in the late 1940s, had spread all over the south west by the early 1960s; it declined sharply between 1965 and 1975.

3.2.2. The Russell Cycle

In the English Channel close to Plymouth a detailed analysis of the macroplankton was made on changes in the ecosystem which had occurred

between 1925 and 1935, and were reversed between 1965 and 1979. The profound events were named the Russell Cycle.

There are five prominent components in the cycle: the magnitude of the winter phosphorus maximum; the quantity of fish larvae; the quantity of macroplankton; the presence or absence of the arrow worms Sagitta elegans Verrill and Sagitta setosa J. Muller, and the appearance and disappearance of a pilchard fishery. The occurrence of the Russell Cycle went together with a rise in mean temperature in the English Channel.

In all probability, hydrographic alterations, originating on the North Atlantic Ocean, occurred first and brought on the alteration of the factors mentioned above.

From the period 1903-1927 to the period 1928-1959 a rise in mean water temperature of 0.46° C was measured off Plymouth; at Seven Stones lighthouse between 1903 and 1959 a rise in temperature of about 0.5° C was measured. This was later followed by a reverse.

The first biological event in the Russell Cycle was the decline in herring recruitment between 1926 and 1930. At the same time, an increase in pilchard recruitment occurred (Fig. 8). Generally, a decrease of macroplankton occurred after 1930. After 1935 the numbers of non-clupeid fish larvae were much reduced. They increased by nearly an order of magnitude in 1965 and that increment was sustained and augmented by 1971. The decrement of the macroplankton in 1930 and the increment in 1970 would have been the consequence of increased and then decreased competition with the pilchards (Fig. 8). In 1962-1965 the first signs appeared of a reversal of the Russell Cycle, probably caused by a return to a former hydrographic situation preceding the onset of the Russell Cycle, which was accompanied by a lowering of temperature.

In 1970, the numbers of copepods returned to their previous level and the numbers of pilchard eggs declined in 1971 and 1973 (Fig. 8). Sagitta elegans and Aglantha digitalis reached their numbers of the 1920s only in 1987. The development in the 1930s find their mirror in the 1960s.

3.2.3. El Nino

A third example of the effect of a change in sea water temperature going together with a change in marine ecosystems is El Nino, a warm current off the coast of Peru which disrupt the anchoveta stock. El Nino relates to a warm current of transaequatorial origin which appears irregularly every five or ten years off the coast of Peru and is so called because it appears at Christmas or just after.

As with the Russell Cycle, hydrographic alterations occur first and the rise in water temperature and the biological alterations follow.

Typically, the warm current strengthens from the region between the Galapagos Isles and Ecuador and flows south along the Peruvian coast to between 5° S and 14° S between February and May. It stabilizes for a period, retreats in August, September and October, but strengthens again in the following January, February and March, regressing again in the southern spring after a total life of about 18 months. The longshore winds persist during the period of El Nino, and the warm water wells up

in the same way as the cooler water does in the normal season but it is much less productive by a factor of about three.

Between a "normal"year and the 1972 El Nino,a temperature difference occurred between 1.1°C and 2.2° C or even more.

The 1972-1973 El Nino started in February 1972, had stabilized by March and in August, September, October it retreated; it strengthened again in the following January, February and March and then died away in May 1973. During the regression in August-October 1972, the sea surface temperature was 1° C warmer than the average between 1925 and 1973.

When El Nino started in February 1972, the adult cormorants left Peru and the population declined sharply. The presence of exotic marine invaders as a result of the rise in temperature was recorded in some detail during this El Nino. They included animals native to the waters of Central America, Mexico and Southern California, but one remarkable exotic, the milkfish (Chanos chanos Kluntz),may have come from Indonesia. The 1976 El Nino was remarkable for its very dense blooms of the dinoflagellate Gymnodinium splendens, which produced a dense red tide. Large quantities of jelly fish, called malagua, were observed for the first time since 1917. Stocks of other pelagic fish rose as the stock of anchoveta declined (Cushing 1982).

The 1982-1983 El Nino was almost certainly the most intensely observed since 1891. In September 1983, the sea surface temperature was 2-3° C warmer than the average between 1925 and 1973, in March 1983 4-7°C warmer, and in May 1983 even 5-10° C warmer. Low phosphate and nitrate concentrations occurred, leading to a decrease in phytoplankton production by a factor of 15 and having an adverse effect on zooplankton production, fish, etc. Sardine (Sardinops sagax) undertook a massive migration to the south.

The population of the three guano birds, the cormorant (Phalacrocorax bougainvilli), the booby (Sula variegata) and the pelican (Pelecanus thagus), decreased from an estimated population of 6 million birds in March 1982 to 0.3 million in May 1983.

The strong warming up of the sea adjacent to the Peruvian coast led to the disappearance and replacement of typical species such as cabrilla (Palalabrax humeralis), cachema (Cynoscion analis), flatfish, pejerry (Odontesthes regia regia), lorna (Sciaena delicosa), jack mackerel (Scomber japonicus peruanus) and suco (Palalonchurus peruanis) by species of tropical waters such as dorado (Coryphaena hippurus), sierra (Scomberomorus maculatus sierra), skipjack (Katsuwonus pelamis), stingrays, mantas (Mobula lucasana) and shrimp. The landings of the traditional species decreased to about 40-80% of those for the corresponding period of normal years.

CHAPTER 4. A COMPARISON BETWEEN THE PRESENT BOTTOM FAUNAS IN THE WADDEN SEA AND BOTTOM FAUNAS LIVING AT DIFFERENT SEA WATER TEMPERATURES

4.1. A comparison with the present bottom faunas of the Seine estuary and the Gironde estuary

Effects of a possible rise in sea water temperature in coastal waters of 2^0 C or 4^0 C can also be investigated in another way. A comparison between regions with mean temperature differences of 2^0 C and 4^0 C with the Dutch Wadden Sea could give an indication what alterations in the marine fauna could be expected.

The mean yearly seawater temperature in the Marsdiep (Dutch Wadden Sea) is 10.1^0 C. In the Seine estuary, a mean yearly temperature of 12.2^0 C occurs (Desprez 1981). The difference of about 2^0 C is found the whole year round (Fig. 9 in Beukema and Desprez 1986). In the Gironde estuary (Le Verdon, S.W. France), a mean yearly seawater temperature of 13.8^0 C. is found (Bachelet 1979), nearly 4^0 C higher than that of the Marsdiep. Again such differences occur throughout the year.

The marine bottom fauna of the Dutch Wadden Sea has been listed by Wolff and Dankers (1983); an inventory of the marine fauna of the Seine estuary is given by Desprez (1981), and an inventory of that of the Gironde estuary has been made by Bachelet (1979).

A comparison will be attempted between the macrozoobenthos of these regions, on the basis of two assumptions. The first is that the knowledge of the number of macrozoobenthos species in the Wadden Sea is nearly complete, that the chance that new macrozoobenthos species are discovered in the Wadden Sea is small. The second assumption is that sampling is aselect, i.e. the chance that a Seine or Gironde sample contains macrozoobenthos species occurring in the Wadden Sea is the same as for species that do not. This is necessary because the number of species found in a restricted sampling programme, as in the Seine or Gironde estuary, is much smaller than the number of species known from the Wadden Sea. The species lists given by the two French authors are very incomplete. Hydrographical and geographical circumstances of French estuaries roughly correspond with those in the Dutch Wadden Sea.

For a comparison with a macrobenthic fauna living at a mean temperature of nearly 4^0 C higher than that of the Wadden Sea, the number of macrozoobenthos species belonging to 8 taxonomic groups from the Gironde estuary as given by Bachelet (1979: table 5) were compared with the number of Wadden Sea species belonging to the same taxonomic groups (Wolff and Dankers 1983). For each taxonomic group the number of species was noted that occurred in the Gironde estuary but not in the Wadden Sea. Totally, of the 8 taxonomic groups considered, 299 species are mentioned for the Wadden Sea and 37 for the Gironde estuary. Of the 37 species mentioned for the Gironde estuary, 11 (or 29.7% of the total) have not been found in the Wadden Sea (Table 2A).

Table 2A

A comparison between benthic animal species in the Gironde estuary and the Wadden Sea

Taxonomic group	Gironde number of sp.	Wadden Sea number of sp.	Number of Gironde sp. not found in Wadden Sea
Gastropoda	4	47	2
Bivalvia	4	35	0
Polychaeta	12	105	4
Mysidaceae	2	8	0
Cumaceae	2	5	2
Isopoda	4	14	2
Amphipoda	6	62	1
Decapoda	3	23	0
total	37	299	11

For a comparison with a macrobenthos fauna living at a mean temperature of 2^0 C higher than that of the Wadden Sea, the number of zoomacrobenthos species belonging to 5 taxonomic groups (Desprez 1981) were compared in the same way with the number of Wadden Sea species belonging to the same taxonomic groups (Wolff and Dankers 1983). For each taxonomic group the number of species was noted that occurred in the Seine estuary but not in the Wadden Sea. Totally, of the 5 taxonomic groups considered, 239 species are mentioned in the Wadden Sea and 59 in the Seine estuary. Of the 59 species mentioned to occur in the Seine estuary, 20, (or 13.5% of the total) are not found in the Wadden Sea (Table 2B).

Table 2B

A comparison between benthic animal species in the Seine estuary and the Wadden Sea

Taxonomic group	Seine number of sp.	Wadden Sea number of sp.	Number of Seine sp. not found in Wadden Sea
Bivalvia	6	35	1
Polychaeta	30	105	12
Isopoda	4	14	0
Amphipoda	17	62	7
Decapoda	2	23	0
total	59	239	20

When the differences in macrozoobenthos species between the Gironde estuary, the Seine estuary and the Wadden Sea are compared, the difference found between the Seine estuary and the Wadden Sea lies about halfway the difference found between the Gironde estuary and the Wadden Sea. This can be expected when temperature difference is the dominant factor in determining the occurrence of macrozoobenthos species.

An increase in the mean water temperature of Dutch coastal waters by 2^0 C or 4^0 C will probably result in an increase in the number of macrobenthos species by ~13 and 30%, respectively.

No information can be given on the possible rate of dispersal of macrobenthos in a northern direction. Neither is it possible to indicate which species would vanish if an increase in the mean coastal water temperature of 2^0 C or 4^0 C should occur.

4.2. A comparison with the Eemien mollusc bottom fauna

A comparison of the Wadden Sea bottom fauna with those living now at higher mean water temperatures can be made with a relatively recent geological period, the Eemien (the last interglacial).

During the Eemien a shallow sea, which may be compared with the present Wadden Sea (but somewhat deeper), existed in the western pat of the Netherlands. The members of the fossil fauna of mollusc shells are nearly all species that still occur in European coastal waters.

When the highest sea level was reached during the Eemien, a moderate climate reigned which was warmer than the present-day climate in the Netherlands. Mollusc species from the Eemien fauna are now dispersed along the Atlantic coast from Gibraltar to the Channel, and even in the

Mediterranean. The recent distribution of mollusc species that also occurred in the Eemien over various coastal regions is shown in Table 3 (Spaink 1958).

Table 3

Recent distribution of Eemian Lamellibranch species (from Spaink 1958)

North Sea	:	45 species - 34.6%
Mediterranean Sea	:	37 species - 28.5%
Atlantic coast from Scotland to Gibraltar	:	100 species - 76.9%
Norwegian coast up to Finmark	:	5 species - 3.8%

Van Straaten (1956) found a high similarity between the fossil Eemien mollusc fauna and the recent mollusc fauna of the Bay of Arcachon, near Bordeaux. Of the Dutch fossil Eemien fauna, 63.3% of the species are now found in Arcachon Bay.

The mean yearly seawater temperature in the Bay of Arcachon is 14.6° C, against the Wadden Sea (Marsdiep) 10.1° C, a difference of 4.5° C. The similarity of the bottom fauna of the Dutch Eemien and that of present-day Bay of Arcachon, and the difference between the Eemien fauna and that of the present Wadden Sea indicate that the Eemien Sea was warmer than the Wadden Sea at present. The temperature of the Eemien Sea during its warmest period is thought to have been 14-15° C on the basis of faunal comparison. The diatom assemblage of the Eemien has not been studied sufficiently intensively to make any independent estimation of the possible temperature of the Eemien Sea.

From these fossil records of the Eemien the conclusion may be drawn that an increase in the mean temperature of the Dutch coastal waters by ~4° C could result in a change in the bottom fauna which will probably become the same as the present-day bottom fauna in Arcachon Bay.

CHAPTER 5. POSSIBLE EFFECTS OF SEA TEMPERATURE INCREASE ON THE OCCURRENCE AND DISTRIBUTION OF SEA GRASS AND BENTHIC MACROALGAE

5.1. Sea grass

In the Dutch Wadden Sea large submerged "meadows" of sea grass (Zostera marina L) occurred in the period before 1931 (Polderman and Den Hartog 1975). In 1931, a "wasting disease" eliminated the sea grass, not only

in the Wadden Sea but all along the European and American Atlantic coasts. In the North Pacific coasts no "disease" occurred.

At first, the elimination of the sea grass was attributed to disease-causing organisms, e.g. Labyrinthula, a fungus-like organism. Afterwards, a correlation between the mass destruction of the Zostera in the 1930s and the changed temperature conditions was found, so that the higher water temperature generally may have weakened the sea grass, and therefore directly or indirectly contributed to its destruction. Indirectly, by weakening the Zostera plants so that the ever present bacteria, slime moulds, fungi, etc could complete the destruction.

Rasmussen (1973) found a close correlation in Danish waters between summer water temperature and the survival of Zostera marina. From 1897 to 1931, no mention is made in the literature of a decline in the amount of Zostera in Danish waters. This period is characterized by an average of 9.9 days with water temperatures over 20° C (Fig. 10). From 1931 to 1951, i.e. the period with the Zostera decline, the average number was 19.5, or nearly twice that of the former period. The winters from 1929-1930 to 1938-1939 had a very low number of days with negative temperatures; this mild period occurred directly before and at the beginning of the mass destruction. From 1952 to 1960 the average number was 16.1 warm days, from 1961 to 1966 3.2 warm days; in the latter period the sea grass stands everywhere began to increase rapidly. In the following period, from 1967, a warming of the water occurred. In the Dutch Wadden Sea, littoral stands of Zostera decreased strongly from 1965 on. In the first half of the seventies, further decrease occurred (Polderman and Den Hartog 1975).

There seems to be a rather precise correlation between fluctuations in the Zostera stands and water temperature. This implicates that Zostera marina must contain ecological races with among other things different temperature preferences. Ecological races of Zostera marina must be considered stenothermic.

If the mean temperature of the Dutch coastal waters increased by 2° C or 4° C, a disappearance of Zostera marina can be expected. The only way to get any recovery would then be the introduction of Zostera from southern regions, for example the Seine estuary or the Bay of Arcachon, where Zostera lives at higher temperatures. The chance that anything of the sort will happen without human interference is small, because of the large distance between the Zostera meadows of the Netherlands and other countries. Moreover, Zostera has heavy seeds which sink to the bottom and are not easily transported by the water.

Next to Zostera marina another sea grass species occurs in Dutch coastal waters: Zostera noltii Hornem. This species lives in the littoral zone on the tidal flats. Contrary to Zostera marina, this species has not been attacked by the "wasting disease" (Polderman and Den Hartog 1975); however, the litoral meadows have diminished in the last few decades. In the Dutch Wadden Sea and in the Oosterschelde Zostera noltii is now the most important sea grass. Because of its littoral habitat, ice in winter can cause heavy damage to Zostera noltii.

Far less is known of Zostera noltii than Zostera marina. As its

distribution occurs from the Tropic of Cancer to south Norway (Den Hartog 1970) various physiological races will exist, as is the case in Zostera marina. If Zostera noltii should vanish from the Dutch coastal waters as a result of an increase in the mean water temperature by 2° C or 4° C, southern forms could eventually take over, comparable with Zostera marina.

A discussion of the influence of a possible increase in the mean coastal water temperature by 2° C or 4° C on the growth of salt marsh plants during flooding at high tide is given by Brouns (1988).

5.2. Benthic macroalgae

In the Netherlands the distribution of benthic macroalgae is almost limited to artifical substrates, e.g. dyke foundations, quays, sluices, etc. Next to the availability of substrates, other factors are of importance, for example the clearness of the water.

Along the West Atlantic coasts of Europe many species of benthic macroalgae occur, and on the basis of mutual similarity in species composition at least five regions could be demarcated along the coast, two of which could be divided into provinces (Fig. 11A). A correlation between the temperature regime and the pattern of phytogeographic regions is evident, when the temperature isotherms in February and August are given (Fig. 11B). Van den Hoek (1982) distinguished 8 phytogeographical distribution groups.

Two types of temperature bound phytogeographic limits can be distinguished (van den Hoek 1979): 1. The limit set by the ability of the species to survive adverse temperatures in the unfavourable season, i.e. for "northern" species in the northern hemisphere to survive a high summer temperature in the south and for "southern" species to survive a low winter temperature in the north. This appeared to be the predominant type of temperature-bound phytogeographic limit. 2. The limit set by the ability of the species to grow and reproduce sufficiently in the favourable season, i.e. for "southern" species the ability to grow and reproduce sufficiently during the summer at their northern limit, and for "northern" species to grow and reproduce sufficiently during winter at their southern limit. All northern Arctic limits appeared to conform to this latter type. Only few southern limits belong to this category.

A temperature-bound limit is generally not a sharp line, but rather a transition area where a species becomes more and more restricted to a gradually more reduced number of stations along the coast where conditions are not insuperably adverse.

At present the North Sea belongs to the cold temperate Atlantic-Boreal region and the northeast lob of the Atlantic temperate group, which is relatively poor in species. South of the Straits of Dover is the Lusitania province of the warm temperate Mediterranean-Atlantic region, which is rich in species (van den Hoek 1975). This latter group consists of stenothermous species with a difference of 18-22° C between minimum and maximum lethal temperatures (mean monthly values) allowing growth and/or reproduction. The region is characterized by small annual temperature fluctuations with a difference of 2-6° C to 6-10° C between

mean February and August temperatures, and up to 16^0 C difference between extreme values.

The cold temperate Atlantic-Boreal region consists of comparatively eurythermous species with the capacity to bridge a difference of more than 20^0 C between the minimum and maximum lethal temperatures (expressed as mean monthly values). The species can bridge wide temperature spans and have wide geographic distributions. Although the majority of investigated boundaries on the Northeast Atlantic shores are growth and reproduction boundaries and comparatively few are lethal boundaries, the warm-temperate Mediterranean-Atlantic group possibly contains many species with a "northern lethal boundary" of 0 to 5^0 C.

The phytogeographic boundaries of a species are determined by the temperature responses of the boundary populations. Ideally, therefore, these temperature responses should be checked for boundary populations and several populations in the intervening part of the geographic range. For few of the species such complete sets of data are available (van den Hoek 1982a). If the mean temperature of the Dutch coastal waters should increase by 2^0 C or 4^0 C, there is a chance that a number of Lusitanian species will migrate into Dutch coastal waters. Because of uncertainies of temperature-bound limits of benthic algal species, as mentioned above, it is difficult to indicate which part of the Lusitanian algal flora would immigrate. Another difficulty is formed by the large difference between the artifical "rocks" of Dutch coastal waters and the natural rocky Channel coast of France and England. Also the differences in the turbidity of the water would add to the problem of predicting how many Lusitanian macroalgae species would immigrate into Dutch coastal waters.

Next to the macroalgae which are permanently fixed on rocks or hard substrates, there are macroalgae in Dutch coastal waters which initially grow fixed to for example cockle shells or other hard substrates, but later on are torn loose and float in the water, often forming a layer on the tidal flats. The most important are the green macroalgae genera Ulva and Enteromorpha. Eutrophication as well as temperature influences growth and biomass. Algae have a limited growth season, for Enteromorpha May-July, for Ulva from July to September. If the mean temperature of the Dutch coastal waters should rise by 2^0 C or 4^0 C, a broadening of the growth season of these algae can be expected, and a larger biomass during the peak of the growing season.

CHAPTER 6. POSSIBLE EFFECTS OF A DECREASE IN THE MEAN WINTER TEMPERATURE IN DUTCH COASTAL WATERS ON THE MACROZOOBENTHOS AND BIRD LIFE

6.1. Mortality of littoral macrozoobenthos in severe winters

The effect of a decrease in the mean coastal water temperature by 2 C^0 may be predicted from the known present-day effects of severe winters. If a decrease in the mean coastal water temperature should occur, such adverse conditions would last longer and occur more frequently.

Beukema et al. (1978) and Beukema (1979, 1985) followed the zoobenthic

population of a large tidal flat area in the Wadden Sea, the Balgzand (Fig. 12) from 1970 on.

The 1971 to 1977 period was characterized by prevailing mild westerly winds, the temperature did not drop below -10°C and only for less than 10 days per winter was the temperature below 0° C all day. All seven winters were milder than average. Such conditions will favour species that are susceptible to low temperatures. Such species are Nephtys hombergii and Lanice conchilega (Vermes) and Angulus tenuis (Lamellibranchiata). The first 2 species already show mortality at cold spells of only 8 days, when temperatures of -7° C/-10° C occur. Such cold spells are not exceptional and characteristic of winters of average severity in the Wadden Sea. The warmer the winter, the higher was the biomass of Nephtys at the end of the winters. Generally it may be stated that less extreme winter conditions in the Wadden Sea resulted in a higher species diversity and a relatively stable biomass in the macrozoobenthos (Beukema et al. 1978).

After a succession of 8 winters with temperatures above average, the 1979 winter was relatively severe in the Wadden Sea area. Mean air temperature during the winter months was about 3° C below the long-term average, and temperature remained below freezing point for 32 days. Total biomass of the macrozoobenthos on the Balgzand at the end of the 1979 winter was just within the range observed during the 8 preceding years, 73% of the year-long average. None of the 6 species with the highest contribution to benthic biomass showed particularly low biomass values at the end of the severe winter of 1979. However,the following species were either absent or scarce at the end of the 1979 winter at places where they had been numerous during the preceding years: the bivalves Angula tenuis,Abra tenuis, Mysella bidentata; the scale-worms Antinoella sarsi and Harmothoe lunulata, and the shrimp Crangon crangon. Also the polychaetous worms Lanice conchilega and Nephtys hombergii had vanished. The cockle Cerastoderma edule responded with a significant reduction in numbers and biomass.It is well known that in a severe winter a mass mortality occurs in Dutch coastal waters of North Sea bivalves such as Donax vittatus, Angulus fabula etc.

Most of the sensitive species are limited to the top 5 or 10 cm of the sediment or nearly so and are thus fully exposed to extreme temperatures. Among the 3 species studied in detail, Cerastoderma lives exclusively in the top few cm, Nephtys in by far the greater part between 0 and 10 cm and Lanice lives in sand tubes that extend to above the sediment surface. Animals that live more than about 10 cm below the sediment surface live under the same moderate temperature conditions as a sublittoral population, for example adult Arenicola marina, Mya arenaria, Scrobicularia plana, Nereis diversicolor.

However, though within species heavier losses were found at the higher intertidal levels, reduction of total macrobenthic biomass values after a severe winter was significant only at the lower intertidal levels (Fig. 12). This seeming paradox can be explained by the distribution patterns of the major sensitive species, living predominantly in the lower half of the intertidal. At the highest levels the sensitive species contributed only a few percent to total biomass and accordingly

biomass values were not significantly affected by the severity of the winter in areas above mean tide level (Beukema 1985).

The present climate in the Netherlands has 1 or 2 more or less severe winters per ten years. In the short term, a severe winter means real stress for the intertidal fauna. The number of species is reduced by about 20 percent by the extinction of some 6 species and in another 4 species abundance is reduced to a low level. At present, these reductions are of a short duration. Species richness is restored within 1 or 2 years, and reproductive success on tidal flats tends to be extremely good during the summer immediately following a severe winter.

However, very severe winters, as that of 1962-1963, can obliterate macrobenthos species for 2-6 years. In the Oosterschelde Nephtys cirrosa vanished till 1965, Sthenelais boa vanished till 1968 or later, Platynereis duvierilii vanished till 1969, and Cirratulus cirratus vanished definitively.

If the mean winter temperatures of Dutch coastal waters decreases by 2^0 C, it can be expected that the effects which are now caused by severe winters will be extended and more frequent. This means that species which are now annihilated in the tidal or shallow tidal zone in severe winters, but restored in following years with mild winters, could disappear definitively from the Dutch Wadden Sea.

In contrast to macrobenthos, which cannot move and escape from unfavourable conditions, many animal species can move to deeper water with a higher temperature in severe winters. Shrimps move further from the coast into deeper waters during cold spells. Fish, for example plaice, also move to deeper water offshore during severe cold. Many animal species can in this way escape from the direct effects of low water temperatures and cold spells.

A decrease in mean winter temperature of Dutch coastal waters by 2^0 C is likely to enhance the number of days per year that icefields occur, especially in the Dutch Wadden Sea and the Oosterschelde. This might affect the survival of many species of wading birds.

6.2. Ice cover and its consequences for bird life

In fresh water it is much easier to calculate and predict the number of days when ice floes are floating on the water than in coastal waters. Wessels (1984) made calculations on the effect of warming up of the water of the lower Rhine on the number of days with ice cover. He concluded that a temperature increase of 1^0 C would result in an annual decrease of 15 days with ice cover.

The formation of ice on sea is a much more complicated process; it is therefore not permitted to extrapolate the calculations performed for fresh water to sea water. In sea water not only the air and water temperature, but also the depth of the water, tidal currents, salinity etc have to be reckoned with: a temperature balance is necessary.

Ynsen (1974) mentions reasons why in the Wadden Sea ice forms much faster than could be expected from the influence of temperature alone. At low water and eastern, strong winds, the dry intertidal bottom cools off fast; at high tide the water cools off fast. With strong wind, waves

are formed which give enlargement of the water surface. All these factors promote rapid cooling and freezing. At low tide, currents carry off the ice from the flats, and it floats with the currents.

An increase in the number of days with ice cover will have a harmful effect on the survival of wintering birds, especially wader birds, in Dutch coastal waters. These waters, especially the Wadden Sea and the Oosterschelde, are very important to birds, not only to birds that stay in winter but also to migrating birds that pass in spring and autumn and stay to feed temporarily. A change in the composition of the macrobenthos could influence the numbers of migrating birds that stay temporarily in the Wadden Sea or Oosterschelde. For example, during severe frost periods cockles die in large numbers in the tidal zone, which deprives migrating birds of food in spring.

During the peak periods of migration in spring and autumn, 2-4 million birds are present per day in the Dutch Wadden Sea, i.e. half of the coastal birds that migrate in N.W. Europe. This illustrates the importance of Dutch coastal waters to bird life.

In winter, large numbers of wader birds stay in the Dutch Wadden Sea: about 200 000 Oystercatchers, 50 000 Curlews, 50 000 Knots, 20 000 Bar-tailed Godwits and 9000 Redshanks. Heavy mortality of birds can take place in winter in the Dutch coastal waters, especially in the Dutch Wadden Sea and the Oosterschelde. This takes place during periods of frost, often in combination with strong winds. If no frost occurs, but western and northern winds blow, a rise in the sea level along the Dutch coasts can occur of at least 0.5 m above the expected level. This means that the flats are not exposed or are exposed for a very short time, or that only a small area is exposed. Birds then have a restricted opportunity to feed on the tidal flats; they have to draw upon their reserves. When such a period is followed by a frost period, the upper tidal zone changes fast into a closed ice field, and besides most parts of the lower flats are rapidly covered with floes. Birds cannot reach the macrobenthos. This has resulted in heavy mortality among Oystercatchers (Swennen and Duiven 1983). Although 61.3% of the victims had abnormal deviations, all had an extremely low weight and had died by hypothermia as soon as the energy reserves were exhausted.

Redshanks appear particularly susceptible to severely cold spells. They become very emaciated and die of starvation after using some or all of their fat reserves. They regain condition rapidly when weather conditions improve (Beecroft and Clark 1986). This pattern occurs in many wader birds: they are, however, less susceptible than redshanks. Also, especially when strong winds blow, birds die from an inability to mobilize fat reserves fast enough to meet energy requirement during severe weather. In cold spells, Redshanks, Oystercatchers and Dunlins die in largest numbers (Davidson and Clark 1985).

A very gradual decrease in the mean winter temperature could stimulate the birds to shift wintering regions to the south. However, there are hardly any wintering regions or halting-places in more southern regions that can be compared with the Wadden Sea or the Oosterschelde.

SUMMARY AND CONCLUSIONS

- When air temperatures during the last 100-120 years, either on a global scale, or at De Bilt, are compared with temperatures of Dutch coastal waters during the last 90-120 years, the conclusion can be drawn that in the period 1860-1910 the trends show a clear difference, whilst from 1910 on trends are similar. This shows that the temperature of Dutch coastal waters is not only determined by air temperature, but also hydrographical alterations on the North Atlantic Ocean have a clear influence, for example alterations in the course of the Gulf Stream.
- During the past century, alterations in hydrography which went with sea water temperature changes involved alterations in local marine fauna during periods varying from 2 to 40 years. However, few observations have been made and a possible temperature effect could, if at all possible, only be determined in retrospect. A need exists for far more and more complete information on alterations of plankton, fish and macrobenthos before a possible effect of temperature alterations can be established.
- Experimental work on the adaptation of marine organisms to higher or lower temperatures and on lethal temperatures have been performed only over short periods (for some hours, at most for some weeks). No conclusions on adaptation over long periods of 50 or 100 years can be drawn from these results.
- The effect of an expected rise in temperature on the macrobenthos was investigated by a comparison of the Wadden Sea with the Seine estuary (mean year temperature 2^0 C higher) and with the Gironde estuary (mean year temperature 4^0 C higher). From this comparison the conclusion can be drawn that at a rise in temperature of 2^0 C an enrichment of 13% of the number of species will occur, and at a rise of 4^0 C an enrichment of 30% of the number of species. It is not possible to predict how many species of macrobenthos which now live in Dutch coastal waters would vanish as a result of the warming up of the water.
- In the warmest period of the Eemien, the mean yearly water temperature in the Eemien Sea was about $14\text{-}15^0$ C, compared with 10^0C for the Dutch Wadden Sea. All species of molluscs known from the Eemien still occur in Europe. As a large resemblance exists between the mollusc species of the Dutch Eemien and the recent ones of Arcachon Bay, this supports the conclusion based on the comparison of the macrobenthos of the Dutch Wadden Sea and the Gironde estuary.
- If an increase in the mean temperature of the water of the Dutch Wadden Sea of 2^0 C should occur, the lethal temperature of young plaice on the tidal flats in summer would nearly be reached; if an increase of 4^0 C should occur, the lethal temperature for young flounders would be approached. The lethal temperature for young sole will not be reached. For plaice (and perhaps other fish species) the "nursery" function of the Wadden Sea would be affected.
- The occurrence of eelgrass appears for a large part to be dependent on sea water temperature. The survival of Zostera marina decreases strongly with the increase in the number of days per year with water temperature above 20^0 C. A rise in the mean yearly sea temperature by 2^0

C or 4° C might eliminate the present Zostera marina populations. In all probability Zostera consists of various ecological races with different upper temperature limits. In view of the large distance between the Dutch coastal waters and southern regions where Zostera marina occurs, immigration, if possible, from southern populations would take a long time.

- If a rise in the mean sea water temperature occurs by 2° C or 4° C, there is a chance that benthic marine macroalgae with a Lusitanian distribution will immigrate to Dutch coastal waters. Benthic marine algae which belong to the warm-temperate Mediterranean-Atlantic group and the North-Eastern extension of the Amphiatlantic tropical warm-temperate groups are possibly involved here. As the Dutch dykes cannot be compared with the rocky Channel coast and the turbidity of the sea water is very different, it is difficult to predict a future development.
- A decrease in the mean winter temperature of coastal waters by 2° C will result in a greater number of days with ice cover because of longer frost periods. This will have an unfavourable effect on birds which stay in the coastal areas in winter, especially on those in the Wadden Sea and the Oosterschelde. This effect, however, cannot be quantified.
- Another effect of a decrease in the mean winter temperature of coastal waters by 2° C will be a strong decrease in the numbers of bottom-living invertebrate species in the lowest part of the tidal zone, some of which will perhaps vanish from this zone. These species now already show a heavy mortality in severe winters, but re-appear within one or more years.

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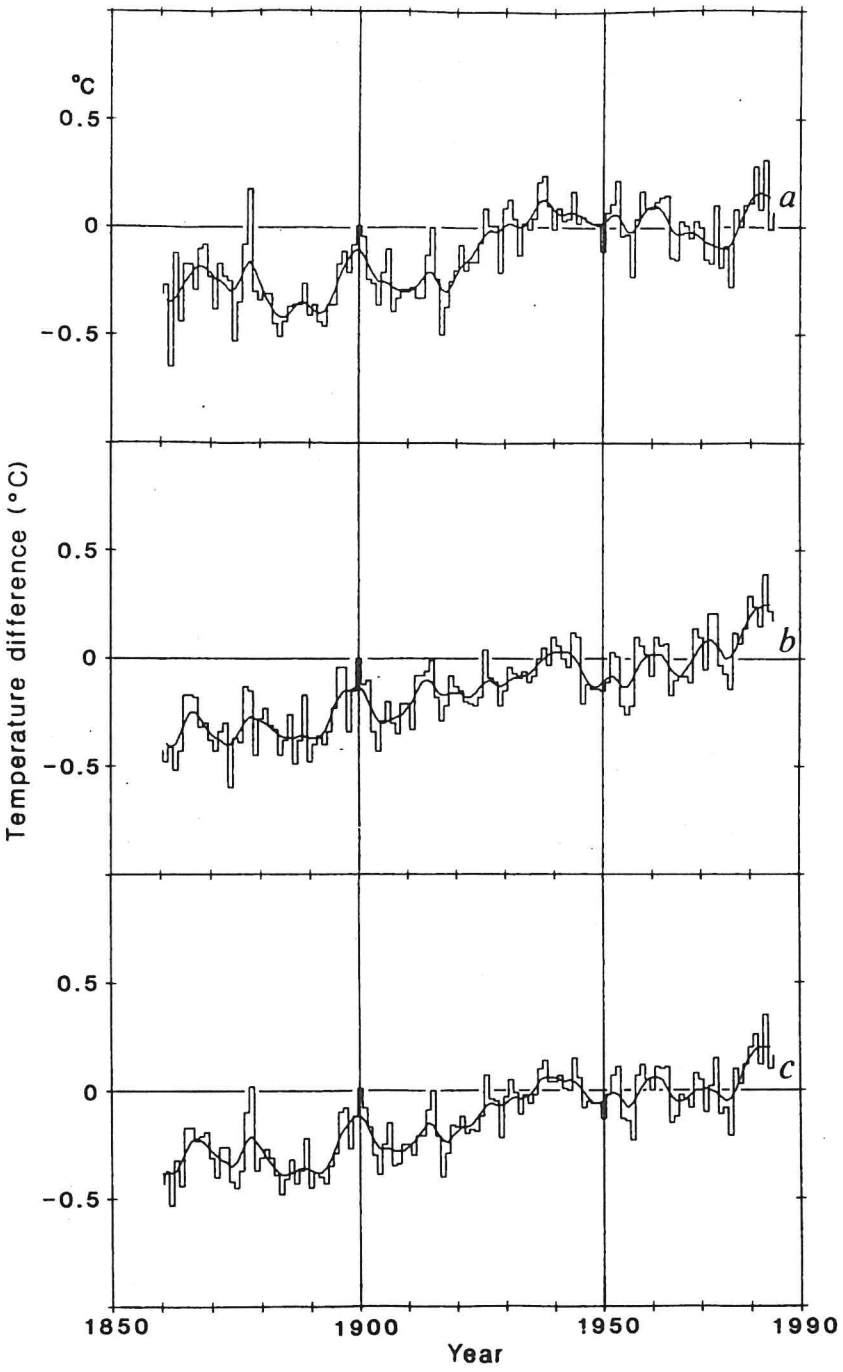

Fig. 1. Global (c) and hemispheric (Northern: a; Southern: b) annual mean air temperature variations since 1861, based on sea-surface air temperature data to represent the marine domain. Smooth curves show 10-yr gaussian filtered values. (From JONES *et al.* 1986)

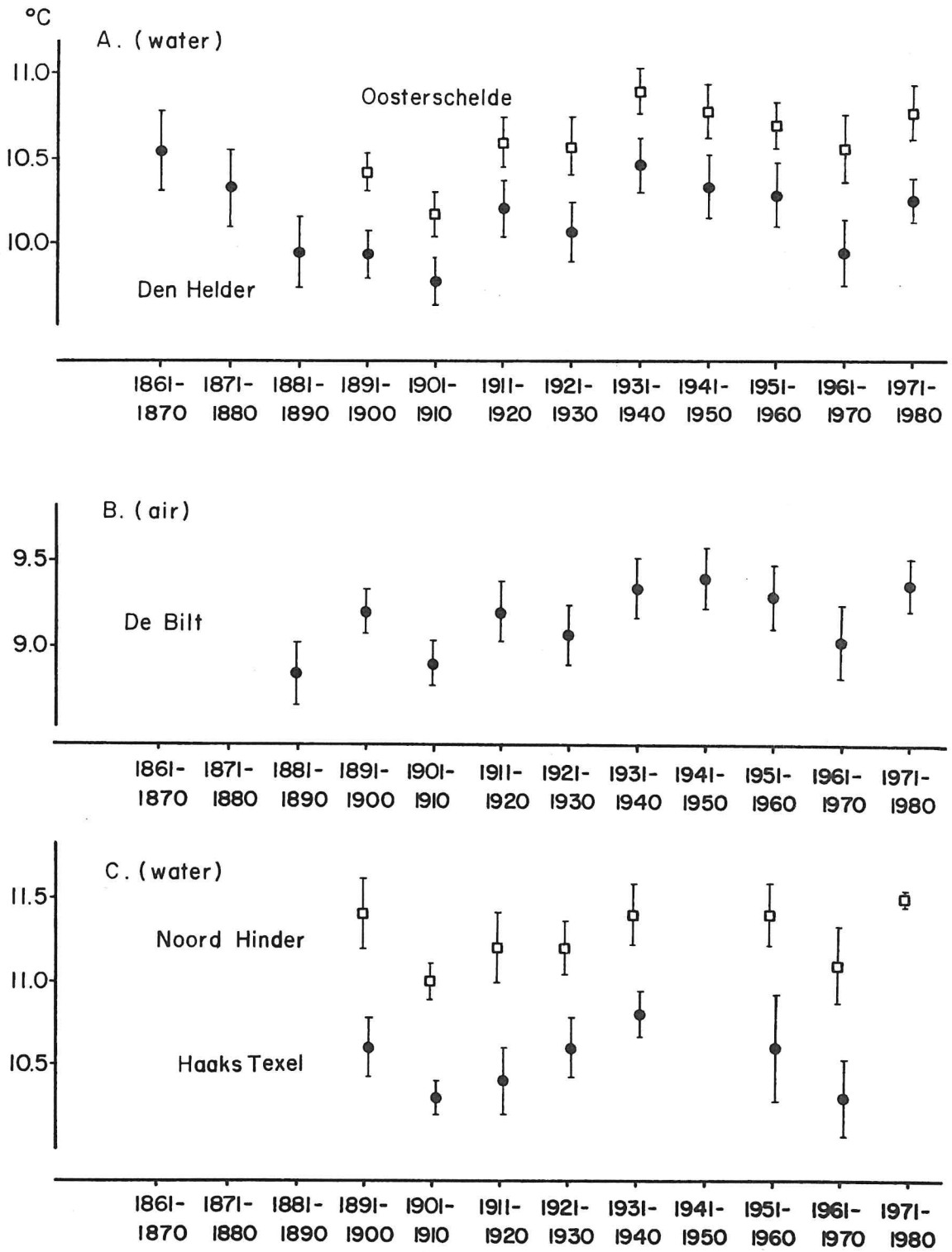

Fig. 2. Mean temperatures (10-yr averages with 1 s.e.) for various stations in the Netherlands: (a) water temperature at Den Helder (at the westernmost entrance of the Wadden Sea) and in the Eastern Scheldt (S.W. Netherlands); (b) air temperatures at De Bilt (central part of the Netherlands); (c) water temperature at 2 former light vessels, situated near the northern (Haaks Texel) and the southern (Noord Hinder) part of the Dutch mainland coast.

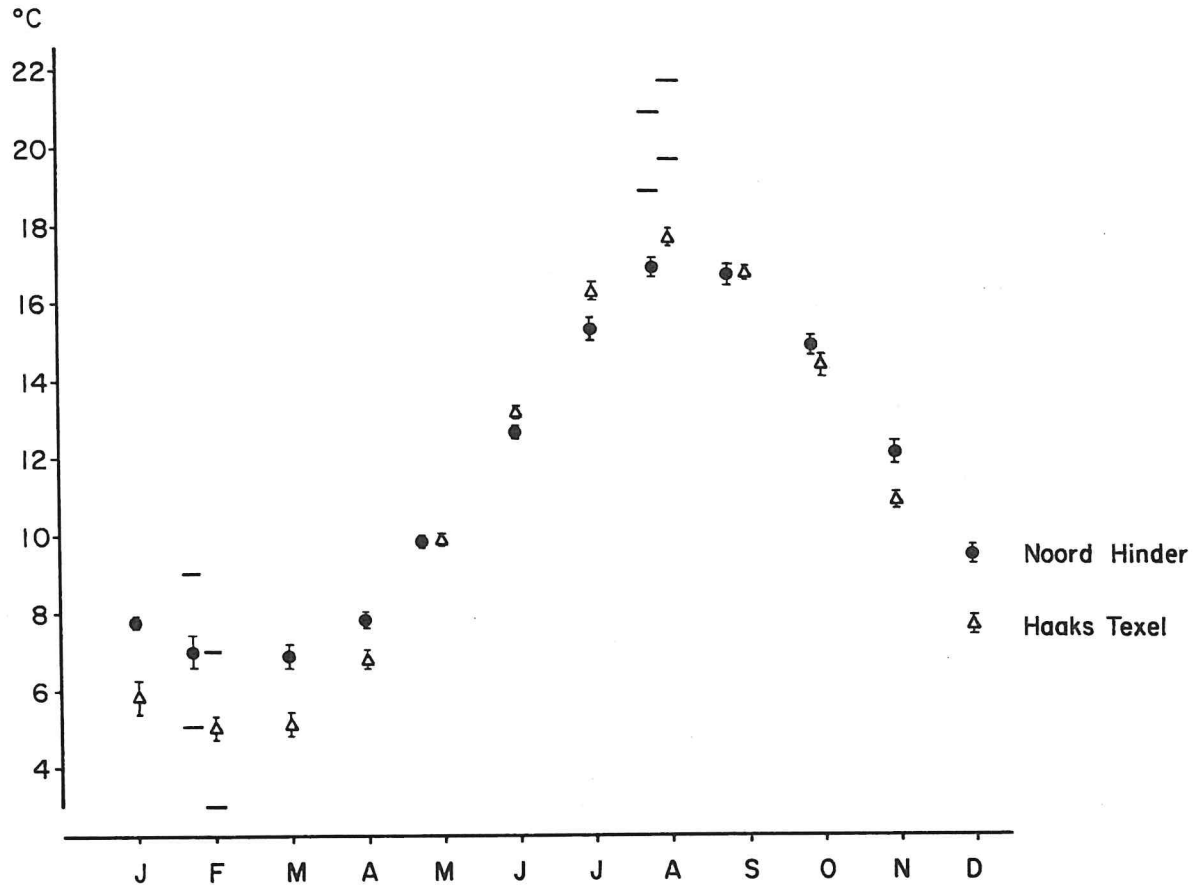

Fig. 3. Monthly averages with 1 s.e. for the 1967-1977 period of 2 former light vessels (compare Fig. 2c). The horizontal lines indicate the monthly averages after a rise of 2° or 4°C (summer) and after a rise or decline of 2°C (winter).

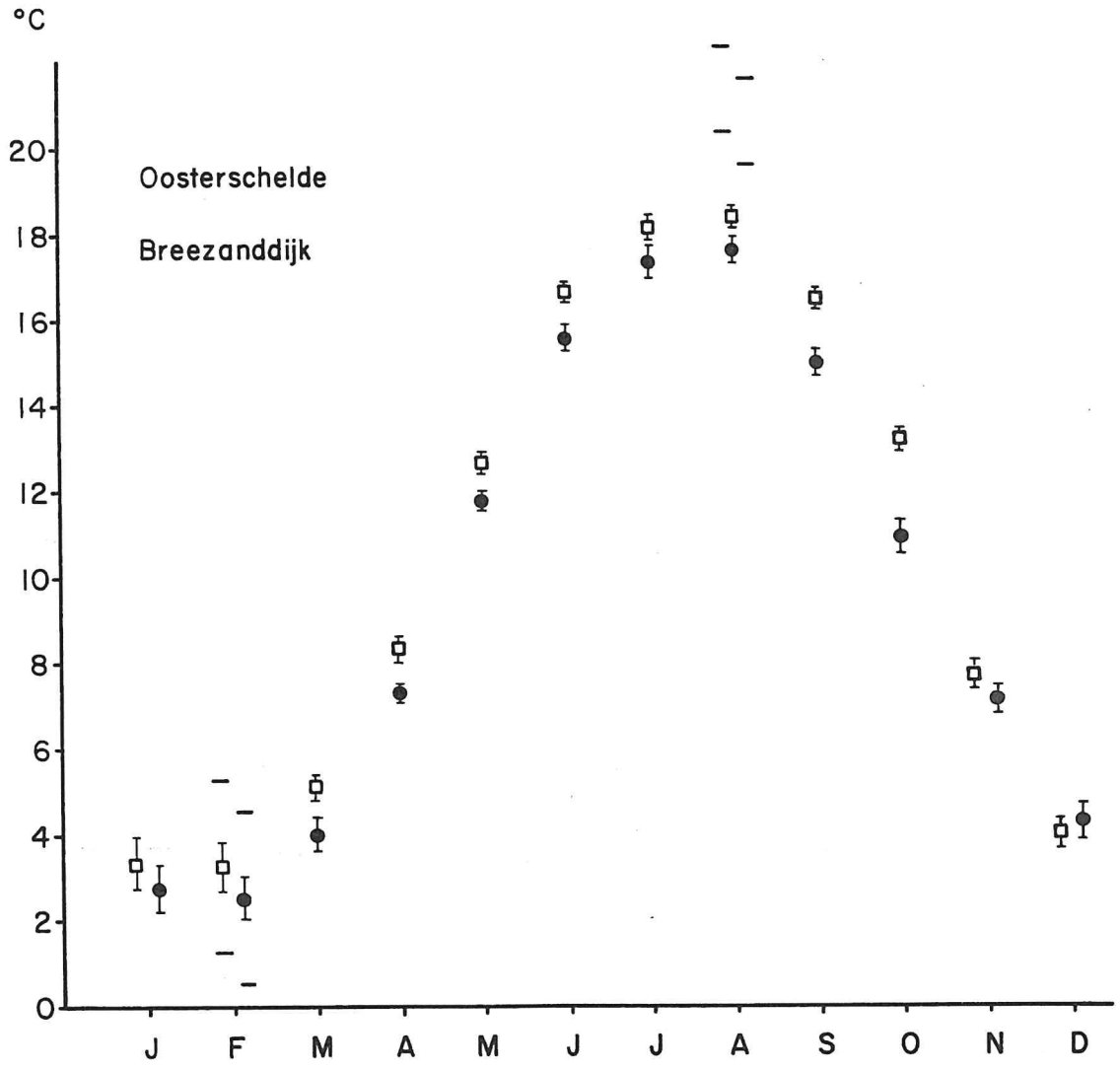

Fig. 4. Monthly average with 1 s.e. for the 1971-1980 period of 2 coastal stations, *viz.* Eastern Scheldt in the S.W. of the Netherlands (□) and Breezanddijk in the Wadden Sea in the N of the Netherlands (●). See Fig. 3 for meaning of horizontal lines.

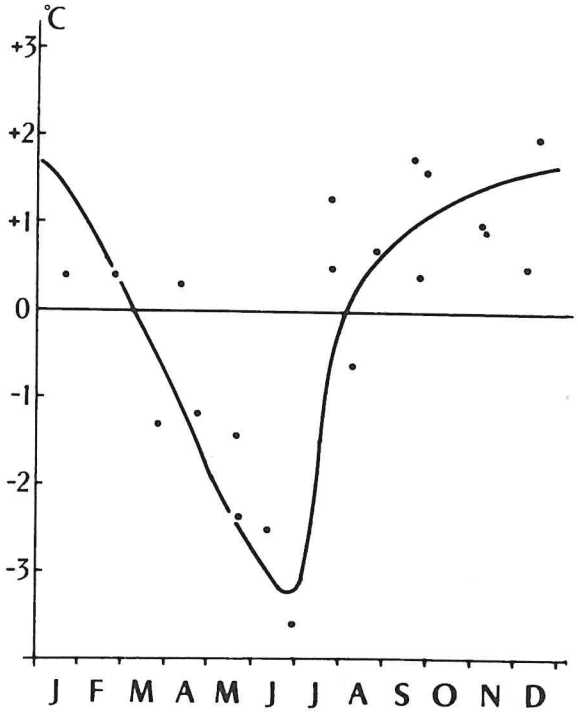

Fig. 5. Temperature differences between North Sea and Wadden Sea (Ameland watershed) in the course of a year. (From POSTMA, 1982)

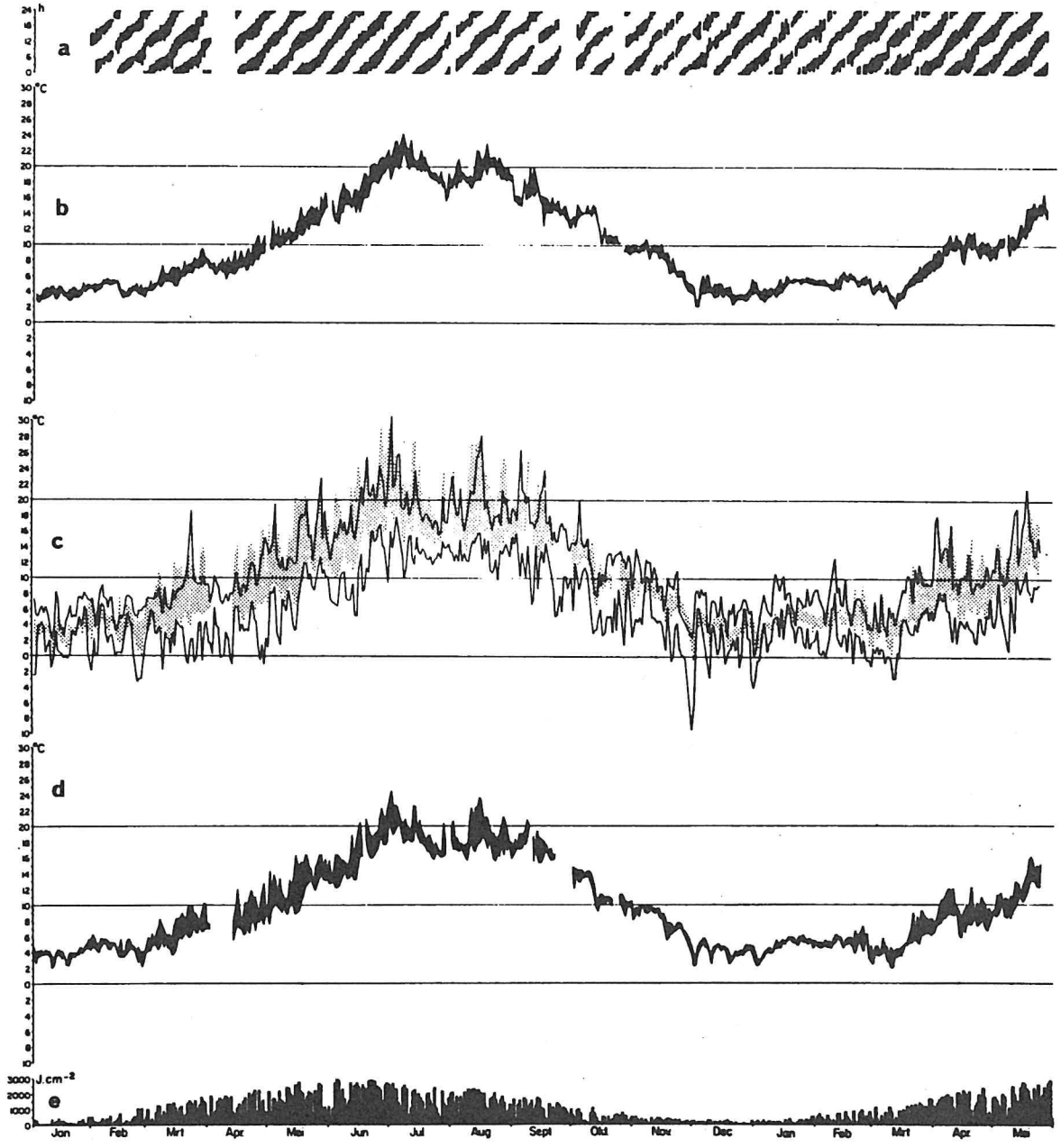

Fig. 6. Thermal regime from January 1983 to May 1974 of tidal mud-flats at the Marsdiep: a. tidal pattern of immersion at high tide (white) and exposure at low tide (black); b. range of maximum and minimum temperatures at high tide; c. maximum and minimum temperatures of air (lines) and surface sediment (shaded); d. range of maximum and minimum temperatures at a depth of 10 cm in the sediment; e. daily input of solar energy ($J \cdot cm^{-2}$).
(From DE WILDE & BERGHUIS, 1979)

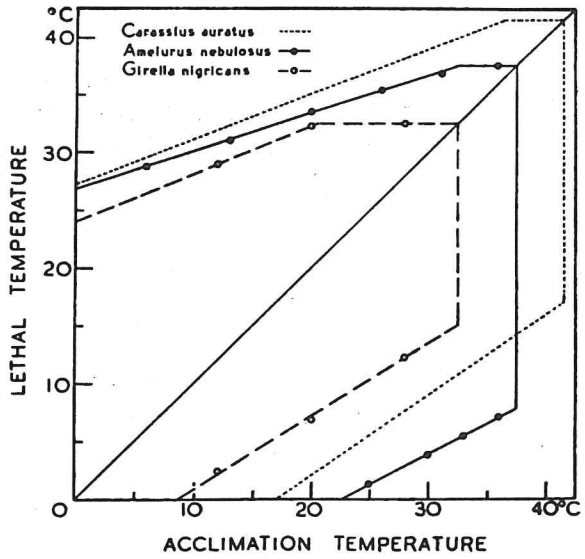

Fig. 7. Relation between median high lethal and low lethal temperatures as function of acclimation temperatures in three species of fish. Lethal temperature curves connected to provide tolerance polygons. (From PROSSER, 1973)

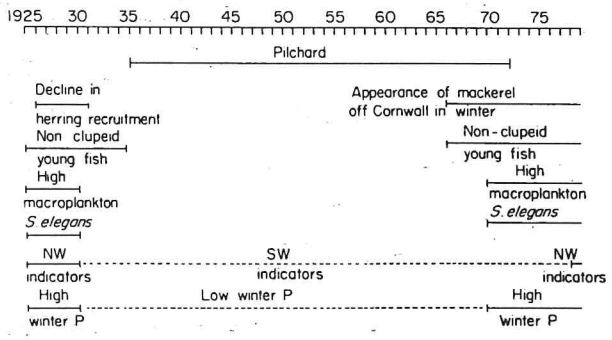

Fig. 8. Diagram summarizing the main changes described as the Russell cycle. (From CUSHING, 1982)

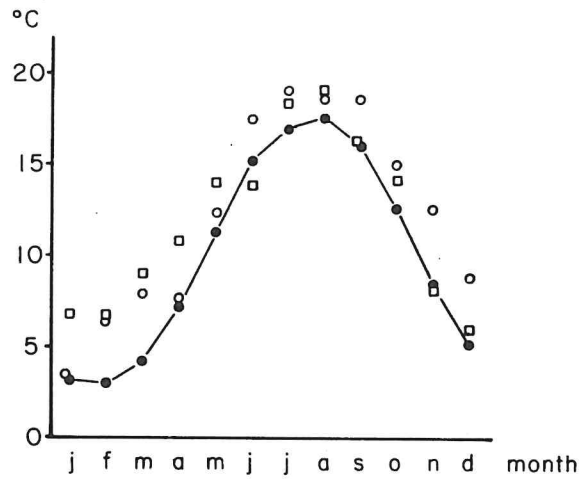

Fig. 9. Water temperatures in the westernmost part of the Wadden Sea (averages 1960-1980, o) and in the Seine estuary near Honfleur (o, 1982; □, 1983). (From BEUKEMA & DESPREZ, 1986)

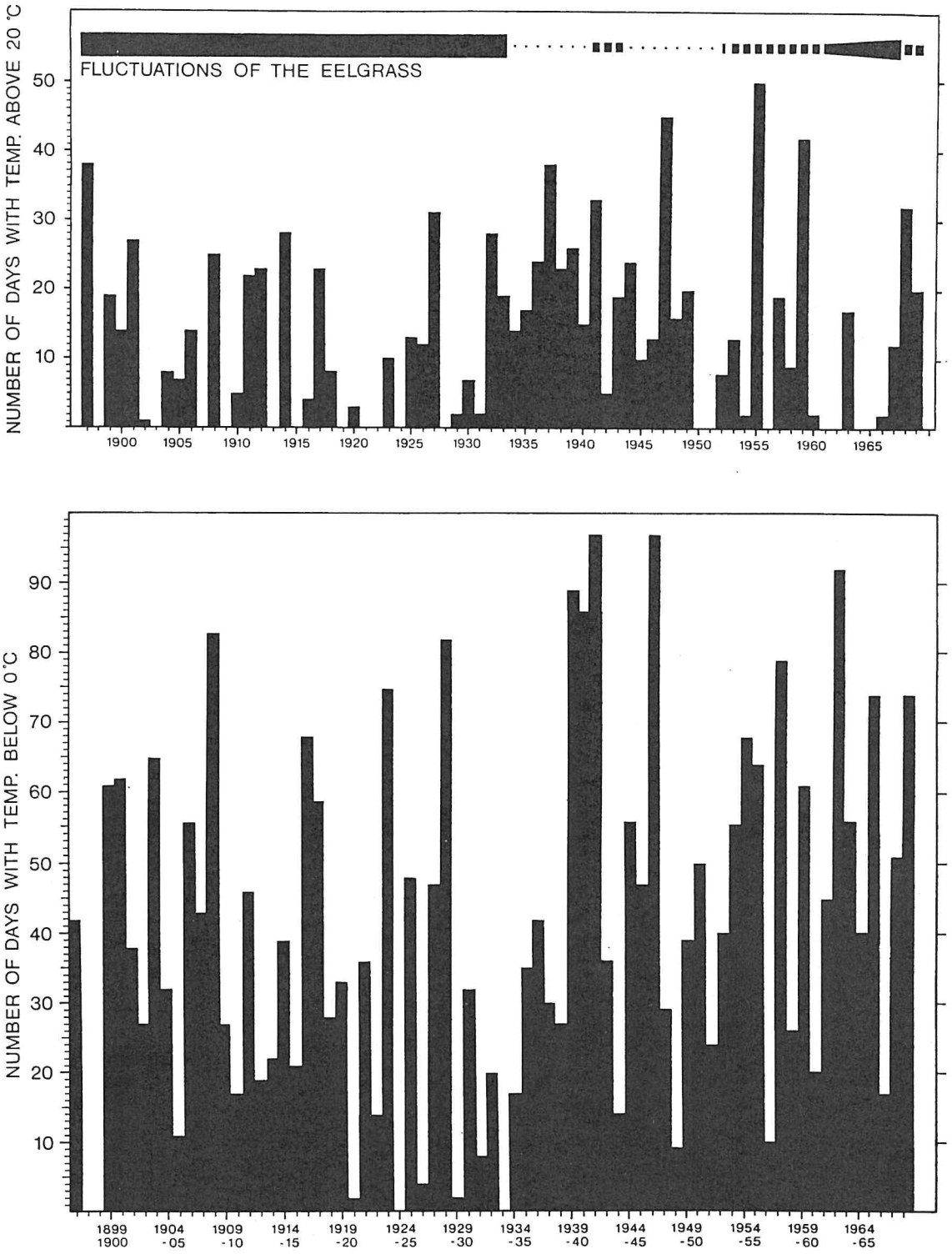

Fig. 10. Fluctuations in the eelgrass (*Zostera marina*) populations in the Isefjord area and partly in the remaining Danish waters (uppermost in the figure), and maximum and minimum surface water temperatures, 1897-1969, shown as the number of days with tempertures of ≥20°C, both based on daily measurements from Frederikssund, Roskilde Fjord. (From RASMUSSEN, 1973)

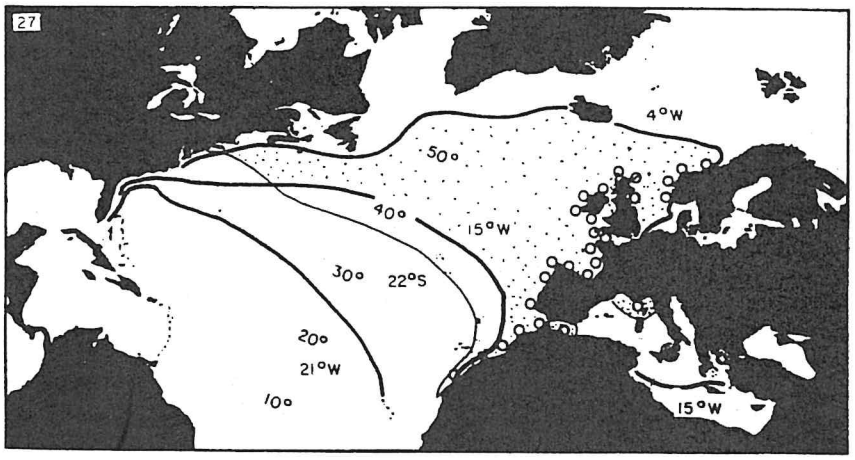

Fig. 11A. *Saccorhiza polychides*. Distribution in the north Atlantic Ocean. 8°S: 8°C summer isotherm. 4°W: 4°C winter isotherm. 23°S: 23°C summer isotherm. 21°W: 21°C winter isotherm. (From VAN DEN HOEK, 1982)

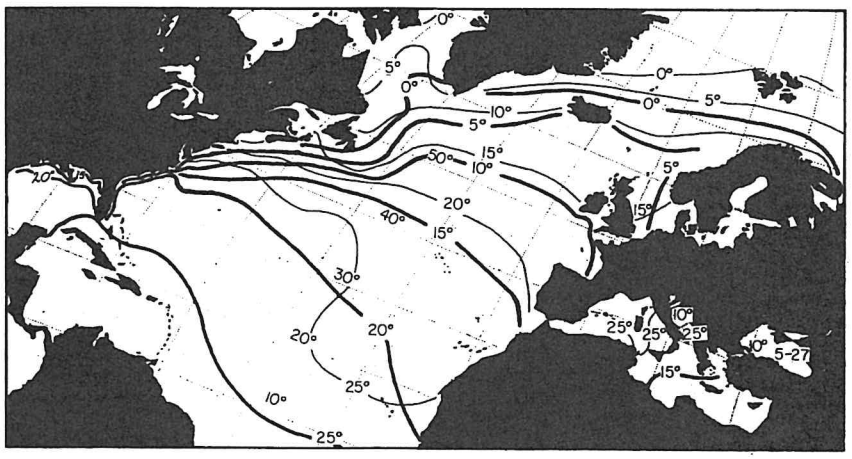

Fig. 11B. Surface temperatures in August and February of the northern Atlantic. Thin lines: surface temperatures in August; heavy lines: surface temperatures in February. (From VAN DEN HOEK, 1979)

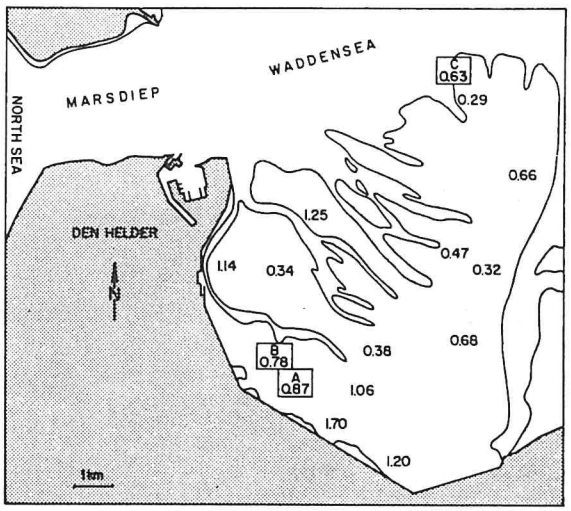

Fig. 12. Relative biomass values of macrozoobenthos at 15 sampling stations on the Balgzand, observed in March or early April 1979. Long-term (1971-1978) averages for each station taken as 1.00. (From BEUKEMA, 1979)