A decline in the availability of oyster (induced by changes in water salinity) triggered the adoption of agriculture since the recourse was important as a buffer for times where naturally other resources were not available.

The Laziness of the Short-Distance Hunter: The Origins of Agriculture in Western Denmark

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"Oysters," said the Carpenter, "You've had a pleasant run! Shall we be trotting home again?"

But answer came there none—

And this was scarcely odd, because

They'd eaten every one.

Lewis Carroll,
The Walrus and the Carpenter

The Ertebølle Mesolithic culture of western Denmark resisted the advance of agriculture for over 1000 years. Marine resources were predominant in the Mesolithic diet. Oysters were a relatively minor resource but are argued to have played an important role by filling a gap in the resource cycle in late winter and spring. The appearance of agriculture coincides with a decrease in marine salinity, which caused a decline in oyster availability. Other marine resources may also have declined for the same reason. © 1984 Academic Press, Inc.

INTRODUCTION

Bandkeramik farmers reached north-central Germany by about 4500 B.C., but agriculture did not spread into Denmark until very much later, around 3200–3100 B.C. I have argued elsewhere (Rowley-Conwy 1983) that the nature of the local later Mesolithic may have been an important factor in this delay. The Ertebølle culture apparently consisted of permanently settled groups; coastal resources played a large part in their diet, and both group size and population density are likely to have been greater than for Mesolithic groups in central Europe. Foraging may thus have been as attractive as farming.

When farming does finally appear, however, it does so quite suddenly. This article will attempt to account for the spread of agriculture into the area of the Ertebølle culture of western Denmark.

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Marine resources were probably crucial to the Ertebølle. The rise in sea level during the 5th and 4th millennia B.C. allowed marine resources to penetrate down the eastern coast of Denmark, a process documented by radiocarbon dates for the spread of the salt-demanding oyster (Fig. 1). The ingress of increasingly saline water into the eastern Danish seas is the context within which the development of the Ertebølle shell middens should be viewed.

A relatively large, sedentary group would deplete local, nonmigratory plant and animal resources more than a smaller, more mobile group would. Local resources would be more intensively exploited (because of the larger exploiting population), and there would be no seasonal absence of the human group to allow the resources to recuperate. This would be likely to increase the role of the marine resources, most of which were migratory (various fish species, waterbirds, marine mammals). Unless predation levels were so high that total stocks were affected, the number of individuals of a migratory species captured in a given year would be unlikely to affect the number available next year. Mesolithic fishermen would be unable to exert much influence on the availability of cod, for example—stocks of this fish have not been threatened until this century.

By exploiting a migratory resource concentrated in one part of the annual range of that resource, a human group gains access to part of the productivity of a much wider area than that covered by the group's area of exploitation. Mass capture of migratory resources demands a suitable technology. There is evidence of such technology from Mesolithic Scandinavia, for example, the 30-m seine net from the Boreal period site of Antrea (Clark 1975:223), and the fish traps made of fixed stakes at the Ertebølle site of Tybrind Vig (Andersen 1980:20). Fixed installations continue "working" without human presence, requiring (after the initial construction) only maintenance and periodic emptying. Sedentary hunter-gatherers are better placed than nomads to maintain large, complex items of technology even if these are used on resources normally of secondary importance, because such items may be stored on the settlement. This is of great importance when it comes to facing unpredictable interannual fluctuations in resource availability, because normally minor strategies may be temporarily intensified to make up the shortfalls in other resources.

If large group size implies greater potential vulnerability, therefore, aspects of the technology and resource use of sedentary hunter-gatherers in turn provide greater security. This would have been a major factor enabling the Ertebølle economy to continue despite the proximity of farming cultures. It also implies that the final replacement of foraging by
farming may have been because of a decrease in the reliability and productivity of the Ertebølle resource spectrum. Evidence for this will be examined below.

**ERTEBØLLE RESOURCE RANKING**

Many resources are known to have been exploited in the Ertebølle. Wild pig, red deer, roe deer, and (in Jutland) aurochs and elk were the resident ungulates. Hazelnut shells are commonly found, and many other plant foods must also have been exploited. Marine resources include shellfish (principally oysters), many fish and bird species, and marine mammals. These were frequently exploited from temporary, special-purpose camps. As a first stage in the examination of the seasonal cycle of resource use, an attempt will be made to rank their productivity. The results of the following discussion are summarized in Table 1.

1. *Shellfish.* Three sets of comparative figures are known to the author. Present-day shell collectors in northern Australia collect at around 1000 kcal/hour (Meehan 1977). Perlman (1980) gives a range of 1.3–4 kg meat

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**Fig. 1.** Map showing the maximum extent of the Litorina transgression (solid line), after Iversen (1973: Fig. 37). Dotted line shows present coast. Radiocarbon dates for the earliest known occurrence of the oyster: 1. Brovst, 6560 ± 120 B.P. (K 1860) (Andersen 1969). 2. Norslund, 6420 ± 130 B.P. (K 993) (Andersen and Malmros 1980). 3. Stensballe, 6340 ± 130 B.P. (K 1222) (Tauber 1968). 4. Roskilde Fiord, 5660 ± 130 B.P. (K 1190) (Tauber 1968). At Brovst and Norslund, the oysters are on the earliest levels of settlements, while at Stensballe and Roskilde Fiord they are from the earliest levels of natural oyster beds.
TABLE 1
SUGGESTED POSSIBLE RETURN RATES FOR SOME MAJOR ERTEBØLLE RESOURCES

<table>
<thead>
<tr>
<th>Resource</th>
<th>Suggested return rate (kcal/hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shellfish</td>
<td>1000–2000</td>
</tr>
<tr>
<td>Acorns</td>
<td>Over 18,000</td>
</tr>
<tr>
<td>Hazelnuts</td>
<td>Over 20,000</td>
</tr>
<tr>
<td>Fruits</td>
<td>1000</td>
</tr>
<tr>
<td>Land mammals</td>
<td>Over 14,000?</td>
</tr>
<tr>
<td>Swans</td>
<td>Much higher than shellfish?</td>
</tr>
<tr>
<td>Ducks</td>
<td>Much higher than shellfish?</td>
</tr>
<tr>
<td>Small whales</td>
<td>Much higher than shellfish?</td>
</tr>
<tr>
<td>Fish</td>
<td>Much higher than shellfish?</td>
</tr>
</tbody>
</table>

per hour, which at 600 kcal/kg (Diem 1962:512) is about 800–2500 kcal/hour. For the Llanrhidian Sands in South Wales, Hancock and Urquhart (1966) state that the cockle beds are uncovered about 2½ hours after high water, indicating a collection time of about 7 hours. In this time, 100–150 kg may be collected. This is about 14–21 kg/hour. Meat is 20% of the total weight, so the hourly rate is about 2.9–4.3 kg meat. This represents about 1750–2600 kcal/hour. These three sets of figures are reassuringly close together.

2. Acorns were experimentally collected by Perlman (1980). They occurred mostly in high densities, above about 65–85 acorns/m². Collection rates of 50–100 per minute were attained. Acorns of Quercus robur weigh about 4 g each, of which 80% is edible. Perlman’s collection rate yields 200–400 g/minute, or 12,000–24,000 g/hour. The edible 80% amounts to about 9600–19,200 g/hour. At about 5000 kcal/kg (Baumhoff 1963:163), this is 48,000–96,000 kcal/hour. Perlman’s acorn densities are very high—experiments by the author produced about 18,000–28,000 kcal/hour in areas with 5–7 acorns/m². Whichever figures are most appropriate, return rates are very much higher than for shellfish.

3. Hazelnuts apparently have not been collected experimentally. If, however, 50–100 nuts can be collected per minute (as Perlman achieved with acorns), then a figure can be calculated. The kilocaloric value is 6700 kcal/kg (Diem 1962:506). There are about 400 nuts/kg, and about 40% of this by weight is edible. At Perlman’s acorn rate, 125–250 g nuts may be collected per minute, or 7500–15,000 g/hour. The edible 40% provides 3000–6000 g kernel/hour. This is a return rate of around 20,000–40,000 kcal/hour.

4. Fruits of various kinds have been collected by the author. Return rates vary around 500–3000 kcal/hour. The higher figures were obtained with modern cultivars. A figure of around 1000 kcal/hour seems the likely maximum for wild fruit.
5. Land mammals cannot be evaluated by experiment. We may, however, speculate about their approximate order of magnitude. Many Ertebølle faunas suggest a kill of about 50% pig, 30% red deer, and 20% roe deer. Annual culls of wild pig may be double those of deer (Taber 1961), suggesting on-the-hoof proportions of around 33% pig, 40% red deer, and 27% roe deer. Using Jochim’s (1976:107) average weights of about 135 kg for wild pig, 220 kg for red deer, and 35 kg for roe deer, the live biomass proportions can be calculated as 31% pig, 62% red deer, and 7% roe deer. Mellars (1975:49) gives biomass figures of 1000–2500 kg/km² for ungulates in mixed deciduous woodland. Given the calculated biomass proportions, Mellars’ upper figure suggests about 6 pig, 7 red deer, and 5 roe deer/km². His lower figure suggests about 2 pig, 3 red deer, and 2 roe deer/km².

Perlman (1980:277) shows that hunting success for modern Americans using firearms is directly proportional to animal density, and produces a graph to express the relationship (Fig. 2). We have no way of knowing what the Mesolithic success rate was. For lack of any more relevant information, Perlman’s figures are therefore used here, but it must be remembered in the following that Mesolithic success rates may have been very significantly lower.

The upper biomass figure of Mellars suggests some 18 animals/km² (47/mile²), for which Perlman’s graph suggests a kill rate of about 0.25 animal/hour. Mellars’ lower figure suggests some 7 animals/km² (18/mile²), giving a rate of around 0.075 animal/hour. Given the proportions in which the animals are calculated as occurring, one “average animal” weighs 140 kg. If 60% is edible, each “average animal” yields about 84 kg meat. The high rate of 0.25 animal/hour thus yields 21 kg meat/hour. The low rate of 0.075 animal/hour yields 6.3 kg meat/hour.

Fifty percent of the cull was wild pig (this is the assumed kill figure given at the start of the calculation). On the basis of this figure and Jochim’s animal weights (quoted above), about 48% of the cull was pork,
52% venison. Diem's (1962:510-511) average figure for pork is about 3000 kcal/kg, 1400 kcal/kg being given for venison. The high return rate of 21 kg meat/hour gives about 10 kg pork (= 30,000 kcal) and about 11 kg venison (= 15,400 kcal), totaling about 45,000 kcal/hour. The low rate of around 6.3 kg meat/hour gives about 3 kg pork (= 9000 kcal) and 3.3 kg venison (= 4600 kcal), totaling nearly 14,000 kcal/hour.

These calculations, suggesting a return rate of around 14,000-45,000 kcal/hour, have come through so many stages and have made so many assumptions that the figures are, in any direct sense, meaningless. What they do hint at, however, is that the return rate for ungulates might have been more similar to that for nuts and acorns than that for fruit and shellfish.

Other resources can scarcely be quantified even in this dubious manner. One approach is possible, however.

6. Swans. Whooper swans (Cygnus cygnus) weigh about 9 kg each (Møhl 1978:70). If 6 kg of this is edible, and if the kilocaloric value is the average of that for ducks and geese at around 3350 kcal/kg (Diem 1962:510-511), then each swan provides some 20,000 kcal. To equal the shellfish/fruit rate of about 1000 kcal/hour, one swan would have to be killed every 20 hours. To equal the higher rates (say around 20,000 kcal/hour), one swan per hour would be needed. We cannot know what the Ertebølle rate was, but ethnographic accounts of large kills (Storå 1968) suggest that high return rates could be achieved. The fauna from the Ertebølle site of Aggersund suggests that the site was a special-purpose camp for procuring swans (Møhl 1978).

7. Ducks. If each duck yields 2 kg edible meat of 3200 kcal/kg, then each duck provides 6000 kcal. One every 6 hours would equal the shellfish/fruit rate, while about three per hour would equal the 20,000 kcal/hour return rate. Once again, ethnographic records suggest that quite high return rates were feasible, and the Ertebølle site of Sølager was apparently a special-purpose camp concentrating on ducks (Skaarup 1973:77).

8. Small whales. Common porpoise (Phocaena phocaena) weigh about 65-80 kg, while the white-beaked dolphin (Lagenorhynchus albirostris) is rather larger. The average weight of the two common small whales of the Ertebølle might thus be around 110 kg, of which 65 kg might be meat. Because of the high fat content, the kilocaloric value is likely to be high, perhaps about that for seals of 4000 kcal/kg (Bailey 1978:47). Each “average small whale” therefore yields some 265,000 kcal. To equal the fruit/shellfish rate, one would have to be killed every 265 hours, while to attain the higher rate of 20,000 kcal/hour one would have to be killed every 13 hours. The whales leave the Baltic every winter in groups of 6-20, which in recent times were driven ashore in shallow bays (Dudok van Heel 1962). The location and faunal content of some Ertebølle sites suggest
that this sort of hunting took place in the Mesolithic as well (Rowley-Conwy 1980).

9. *Fish.* Evidence of varying quality suggests the existence of Ertebølle special-purpose camps at which cod, mackerel, and perhaps eels were important. The kilocalorie per kilogram values are: cod 800 [average of the values given by Diem (1962) and Daan (1975)]; mackerel 1880; and eels 1620 (Diem 1962). The average of these three values is 1430 kcal/kg, and if one `average fish` weighed 1 kg, of which 70% was edible, then it would yield about 1000 kcal. One of these per hour would equal the fruit/shellfish rate, 20 per hour the higher rate. Given the evidence for mass-capture technology (see above), there seems little doubt that quite high return rates could be achieved.

None of the above figures include processing or transport costs—it must be stressed that this is not an attempt to construct a formal optimal-foraging table. We cannot know how efficiently Ertebølle people could (for example) crack nuts, and little would be gained by introducing further uncertainties. The figures are tentative and often dubious, and should not be taken literally. What can be said with a moderate degree of confidence is that shellfish and fruits provided returns of a lower order of magnitude than the other resources.

**SEASONAL SCHEDULING AND THE ROLE OF THE OYSTER**

The tentative figures put forward above suggest that shellfish and fruits are likely to have been less attractive than most of the other available resources. This seems to be borne out by the archaeological evidence. Fruit stones are only occasionally found in Ertebølle contexts. Oysters have been calculated to have formed only a minor part of the Ertebølle diet, usually less than 10% at most (Bailey 1975; Clark 1975). This would seem reasonable in view of their low productivity per hour of work, and they have as a result been regarded as an occasional relish, or as a standby in times of starvation (Paludan-Müller 1978).

This is a reasonable conclusion except for one thing: Most known western Ertebølle coastal sites are made of oyster shells. Occasional use as relish or standby would hardly involve the sustained and regular exploitation necessary for the accumulation of the many large middens. There are no comparable mounds of fruit stones, for example. This suggests that some special effect is counteracting the ranking of resources according to average productivity, and this is most likely to be heavy seasonal usage of oysters to plug a gap in the resource cycle.

Use of continuously available local resources for this purpose is widely documented among recent sedentary hunters. The Ainu, for example, ignored locally resident deer for parts of the year, hunting them only when
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'J'F'M'A'M'J'J'A'S'O'N'D'

FIG. 3. Predicted seasons of exploitation of the major resources exploited by the western Ertebølle. All the animal resources are known to have been exploited in the Ertebølle, with the exception of grey seal pups.

other (migratory) resources were unavailable (Watanabe 1972). Shellfish were exploited during winter on the Northwest Coast, when other resources were relatively scarce (Drucker 1951); among the Tlingit this reached a peak in March when shellfish condition was best (Oberg 1973).

Many of the Ertebølle resources discussed above were only available seasonally, so it should be possible to predict the main season of oyster exploitation from a consideration of these resources (Fig. 3).

(1) Nuts and acorns would have been available in September and October. Storage of hazelnuts may have been more problematic than is sometimes supposed—if they are collected when thoroughly ripe, correctly dried, stored in a suitable container, covered with a layer of sand, and kept in a cool cellar, they may last until late March (Howes 1948). The unlikelihood of all these conditions being met in the Ertebølle would certainly raise the risk of spoilage before this.

(2) Fish. Cod and mackerel are available inshore in summer (Becker 1939; and personal experience). Eels may be taken at any time but are most concentrated and nutritious in autumn (Davies 1944).

(3) Small whales leave the Baltic in groups of 6–20 in December and early January, this being the main period of exploitation. They return in late spring, but are not nearly so attractive a resource at this time as they move singly or in pairs (Dudok van Heel 1962; Møhl 1970).

(4) Seals. Harp seals (Phoca groenlandica) are believed to have been available in the autumn. Grey seals (Halichoerus grypus) can be taken all year but mass in winter to breed. Hunting traditionally took place at the rookeries in February (Møhl 1970). No evidence of the exploitation of the rookeries is known before the Neolithic, however (Skaarup 1973).

(5) Migratory water birds. Some bird species are available in western
Denmark all year round, but the most useful for large-scale exploitation would have been the major concentrations of migratory water birds that overwinter in the area. These include various species of swans, geese, and ducks known to have been exploited in the Ertebølle. These birds leave Denmark during the spring, the exact time being determined by climatic conditions in individual years (Bruun and Singer 1970).

(6) *Ungulates* would have been at their most attractive in the early autumn. Red deer and wild pig rut during the autumn, and the males lose much condition during this period (de Nahlik 1974; Frädrich 1974). All ungulates lose weight during the winter, and in particular their fat contents decrease, so that the animals are least useful during late winter and spring (Speth and Spielmann 1983). Average fat contents of various resources are listed in Table 2. Speth and Spielmann, however, emphasize that the degree of seasonal variation makes an average figure valueless for ungulates—"the meat of wild ungulates at the low point in their annual cycle of condition probably ranged in fat content from as low as 0.9% to a maximum of about 1.5–2.0%" (Speth and Spielmann 1983:12). As a result, large amounts of lean meat would have to be eaten if nothing else was available—an active hunter would probably have to consume about 3.4–3.6 kg lean meat per day to satisfy bodily needs (Speth and Spielmann 1983:12).

The low fat content of ungulates in late winter and spring brings them down to the level of the oyster in this respect—the oyster shows little seasonal variation in fat content (Fig. 4), so the average listed in Table 2 is relevant to this time of year (in contrast to that for ungulates). It may well be that the oyster, despite its lower average kilocaloric and fat values, was more attractive in this season. It shows no significant loss of meat weight at this time, and the kilocaloric value of the meat declines only slightly (Fig. 5). If its late winter/spring kilocaloric value is taken as 800/kg fresh meat, then 2500 kcal can be attained from about 3.1 kg meat, rather less than Speth and Spielmann’s estimate of lean ungulate meat needed (see above). Bailey (1975,III:5) points out that the daily requirements of almost all nutritive substances can be obtained from far fewer oysters than would be necessary to produce 3.1 kg meat, so that a diet based on oysters would be a healthy one. Carbohydrate is also necessary in late winter and spring, as this diminishes the loss of body protein which can occur in a calorie-deficient diet (Speth and Spielmann 1983:12). Oysters contain significant quantities of carbohydrate (Table 2, Fig. 4), while ungulates do not.

It is not, of course, suggested that anyone ever actually lived solely on oysters and nothing else. It is, however, likely that the oyster formed a major part of the diet for two or three months in the year. Success in hunting ungulates would vary, while the oyster is so static as to be un-
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TABLE 2

FOOD VALUES PER 100 g OF SOME COMMON ERTEBØLLE RESOURCES

<table>
<thead>
<tr>
<th>Resource</th>
<th>kcal</th>
<th>Protein (g)</th>
<th>Fats (g)</th>
<th>Carbohydrates (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple</td>
<td>58</td>
<td>0.3</td>
<td>0.4</td>
<td>15.0</td>
</tr>
<tr>
<td>Blackberry</td>
<td>56</td>
<td>1.2</td>
<td>1.1</td>
<td>11.9</td>
</tr>
<tr>
<td>Cherry</td>
<td>60</td>
<td>1.1</td>
<td>0.4</td>
<td>14.6</td>
</tr>
<tr>
<td>Strawberry</td>
<td>37</td>
<td>0.8</td>
<td>0.6</td>
<td>8.1</td>
</tr>
<tr>
<td>Dandelion greens</td>
<td>44</td>
<td>2.7</td>
<td>0.7</td>
<td>8.8</td>
</tr>
<tr>
<td>Hazelnuts</td>
<td>671</td>
<td>12.7</td>
<td>60.9</td>
<td>18.0</td>
</tr>
<tr>
<td>Beef (medium fat)</td>
<td>330</td>
<td>23.0</td>
<td>26.0</td>
<td>0</td>
</tr>
<tr>
<td>Pork</td>
<td>302</td>
<td>18.6</td>
<td>24.3</td>
<td>0</td>
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<tr>
<td>Venison</td>
<td>139</td>
<td>20.0</td>
<td>6.0</td>
<td>0</td>
</tr>
<tr>
<td>Goose</td>
<td>349</td>
<td>16.4</td>
<td>31.5</td>
<td>0</td>
</tr>
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<td>Duck</td>
<td>321</td>
<td>16.0</td>
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<td>Cod</td>
<td>70</td>
<td>16.5</td>
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<td>0</td>
</tr>
<tr>
<td>Eel, fresh</td>
<td>162</td>
<td>18.6</td>
<td>9.1</td>
<td>0</td>
</tr>
<tr>
<td>Eel, smoked</td>
<td>325</td>
<td>18.6</td>
<td>27.8</td>
<td>0</td>
</tr>
<tr>
<td>Flounder</td>
<td>64</td>
<td>14.9</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>Herring</td>
<td>136</td>
<td>19.0</td>
<td>6–12</td>
<td>0</td>
</tr>
<tr>
<td>Mackerel</td>
<td>188</td>
<td>18.7</td>
<td>12.0</td>
<td>0</td>
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<tr>
<td>Pike</td>
<td>80</td>
<td>18.7</td>
<td>0.6</td>
<td>0</td>
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<tr>
<td>Cockle</td>
<td>48</td>
<td>11.0</td>
<td>0.3</td>
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<tr>
<td>Mussel</td>
<td>80</td>
<td>11.6</td>
<td>1.7</td>
<td>2.9</td>
</tr>
<tr>
<td>Oyster</td>
<td>59</td>
<td>9.4</td>
<td>1.9</td>
<td>5.9</td>
</tr>
</tbody>
</table>

Note. Figures from Diem (1962), except shellfish, after Bailey (1975).

* Average of three values. Brain, heart, kidneys, tongue, and tripe all have lower values.
* Average of three values. Brain, kidneys, and liver all have lower values.

This predictability had a major influence on settlement, and it is no coincidence that the suggested base camps (Rowley-Conwy 1983) are sometimes located immediately adjacent to natural oyster beds of Mesolithic date (Andersen 1976:36). The unusually low tides occurring...
Fig. 5. Annual variations in (a) weight of 100 fresh oyster meats, and (b) kcal in 100 g fresh oyster meat. a, Whitstable; b, Mersea; c, Ipswich; d, Burnham (all southeast England) for 1919 (and January 1920 for meat weights). e, Ytrepoll, Norway, September 1935–April 1937. a–d from Russell 1923: Tables I and II. e recalculated from Gaarder and Alvsaker 1941: Table 6.

during the spring would have uncovered more of these beds than normal, so making them more accessible.

If ungulates are at their worst in late winter and spring, therefore, the same is not true of oysters, which are often improving at this time of year. The condition index of oysters is determined by the formula

\[
\text{condition index} = \frac{\text{average dry weight of meat (g)}}{\text{average volume between shells (ml)}} \times 1000.
\]

Walne (1974) found that the oysters at Tal-y-Foel, North Wales (one of the coldest oyster habitats in Britain) on average increased their condition index during late winter and spring. Korringa (1957a) presents slightly different results from a single year in Holland, suggesting that condition declined slightly during the winter. Figures are also available for southern English oysters for the year 1961, a very poor oyster year (Walne 1970). These results are combined in Fig. 6, and show the index to average about 90 in March. Oysters with a value of 90–100 are regarded as average; an index of 80 indicates a lean animal, while one of 70 is very poor. Walne has published graphs of the Tal-y-Foel oysters’ average dry meat weight for 1968 and 1969, and they show meat weight increases in March of approx 10–20% over the February weights (Walne 1974: Fig. 35), as did some of the populations in Fig. 5.

Feeding and meat-weight increase begins when sea temperature is as
low as 7–8°C (Walne 1974). Present Danish sea temperatures suggest that the main period of oyster growth in waters off eastern Jutland would begin in late April (Fig. 7), were there any oysters present inshore today. The temperature during the Atlantic period was 2–3°C warmer than today, and sea temperature was correspondingly warmer as well (Iversen 1973). Furthermore, the inner area of fiords where the oysters grew would have been considerably warmer than the open sea (Nielsen 1938). These two factors would have served to move the start of the oyster growing season to an earlier point, so that more of its main period of growth fell within the period of suggested Ertebølle exploitation. This would add to its attractiveness.

The oyster loses weight and condition when it breeds in the summer (see Figs. 5 and 6). It does not breed until the sea reaches a temperature of 15–16°C (Korringa 1957b), now usually in June in Northwest European waters. In these waters a burst of plankton productivity occurs in the spring (Cushing 1975), so the oysters, feeding on this plankton but not yet expending nutrients in the form of reproductive products, are effectively storing up nutrients in a form exploitable by humans, just at the time they were needed in the western Ertebølle resource cycle.

The Ertebølle lean period is thus likely to have been the spring: February, March, and April (see Fig. 3). Oysters were available at this time but fruits were not. This, it is suggested, is the reason that most western Ertebølle coastal sites consist of oyster shells and not of fruit stones, although the two resources have similar return rates. Modern sedentary hunters show great variability in the economic activities of individuals at any one time, and yet certain major resources do provide the bulk of their foodstuffs in particular seasons. In the Ertebølle, oysters were
doubtless exploited on a casual basis throughout the year, and other activities would also have been carried out during the period of oyster exploitation. Despite this, the rarity and low return rates of alternative resources during the spring must have mitigated for the more frequent collection of oysters during the spring. Only in this way can the oyster’s low kilocaloric return rate and low contribution to the western Ertebølle diet as a whole be reconciled with the importance indicated for it by the consistent formation of large middens.

THE OYSTER DECLINE

The oyster is the classic shellfish of the Ertebølle. The decline of the oyster at the time of the first appearance of the Neolithic is a widely noted phenomenon—middens from the early and early middle Neolithic consist predominantly of the mussel (*Mytilus edulis*) as at Askø or the southern mound at Udbyhøj (Skaarup 1973), of the cockle (*Cerastoderma edule*) as at Norsminde (Andersen 1976), or of a mixture of the two as at Lyø (Christensen et al. 1978). Many sites covering the transition from Ertebølle to Neolithic show an abrupt change, contemporary with the transition, from densely packed oyster shells below to a more diffuse layer above (Fig. 8). This upper layer contains more charcoal and a lower

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**FIG. 7.** Average monthly temperature of surface seawater from three locations off eastern Denmark (data from Thomsen 1961). Recording points: 1, Anholt Nord; 2, Halsskov Rev; 3, Gedser Rev.
density of shell (Skaarup 1973). Contemporary with the start of the Neolithic, therefore, shellfish collection both switched species and declined in intensity. It will be argued below that this was due to a decline in marine salinity.

It has long been recognized that the oyster was at the limits of its salinity tolerance range during the Ertebølle. The oyster requires a minimum of about 23‰ (Yonge 1960), and will not grow in Danish inshore waters today (except in parts of the Limfjord) because the salinity is too low. In the early years of this century, Nordmann noted that oysters in Ertebølle middens showed a regular decline in size, being smaller to the southeast, i.e., away from the more saline North Sea. From this he concluded that the oyster was on the limits of its salinity tolerance in the Ertebølle period, as no other factor (e.g., temperature) could explain the size cline (Nordmann 1903). Nielsen has suggested that tidal action was the mechanism whereby more saline water entered the western Baltic. Tidal movement today is minimal, due to the present configuration of the North Sea bed, but in the Litorina period,
Even the innermost corners of the long fiords would be subject to high water exchange, so that these too would have had a higher salt content. Nutrition of marine organisms would improve, partly because the production of phytoplankton would increase because of the greater mixing of surface water with nutritionally enriched deeper water, and partly because e.g. mussels would flourish because of the increased water mixing. For the nutrition of the oyster, for example, high water exchange is of the greatest importance. (Nielsen 1938:341, my translation)

The innermost fiord areas would have been more suitable for oyster growth than the more open waters offshore, as the increased water mixing in the open sea would dissipate much of the solar energy received. The surface layer would therefore not be suitable for the growth of oyster larvae (Nielsen 1938). Therefore, "the real growth areas for oyster larvae were probably the inner parts of fiords" (Nielsen 1938:342, my translation). The tidal hypothesis is still accepted today (Aaris-Sørensen 1980), and evidence for tidal movement has been found in the form of a channel probably cut by tidal action at the Ertebølle site of Tybrind Vig (Andersen 1980:20).

The decline of the oyster does not coincide with the end of the period of the Litorina Sea. The Litorina Sea conventionally has a sequence of four transgressional peaks. This is based on classic studies such as those from Søborg, Ordrup, and Korup (Iversen 1937), Amager (Troels-Smith 1939), and Dyrholm (Troels-Smith 1942). The Ertebølle is contemporary with the third of these, the Late Atlantic transgression.

Three recent studies have succeeded in establishing continuous sea level curves for the Litorina Sea. Figure 9 combines the curves from Vedbæk (Christensen 1981), Blekinge (Berglund and Liljegren 1971), and Barsebäck (Digerfeldt 1975). The recent curves broadly agree with the classic studies of the 1940's and 1950's, so that

The sea level changes in the above places, and also at Søborg, Ordrup, Korup, Amager and Dyrholm, can apparently be fitted into one overall scheme, demonstrating an Early, a High, and an apparently complex Late Atlantic transgression . . . (Christensen 1981:106, my translation)

Christensen (1981:105) further points out that the period of highest sea level at Barsebäck has not been securely dated, so that it need not belong to the transgression to which it is allocated. Evidence from as far apart as Søborg, Vedbæk, and Blekinge (Fig. 8) shows that the most marked drop in sea level was in fact the regression (reaching a minimum just before 3000 B.C.) which followed the Late Atlantic transgression (Christensen 1981:105).

Salinity maxima occur at the times of the transgression maxima (Iversen 1937, Mikkelsen 1949:158). An important consequence of the Litorina Sea was the widening of the Kattegat (the entrance to the western Baltic); the northern tip of Jutland and the Swedish west coast
were submerged, and northern Jutland was broken up into a series of sounds and islands (Fig. 1). The transgression and regression phases would have alternately widened and narrowed the entrances through which the more saline tidal waters reached the Ertebølle areas.

It is suggested that the oyster decline occurred as the result of a major narrowing of these entrances. The classic Ertebølle runs from about 3800–3700 B.C. to about 3200–3100 B.C., and it is striking that the end of the accumulation of oyster middens coincides with the most marked drop in sea level. Two facts must be stressed: (1) The ingress of salt tidal water was crucial to the oyster (Nielsen 1938), and a drop in sea level and narrowing of the Kattegat would have diminished this ingress. (2) The oyster was already at the limits of its salinity tolerance during the Ertebølle (Nordmann 1903), when the Kattegat entrances were at their widest. These two facts make it probable that the narrowing of the Kattegat entrances reduced salinity to below the tolerance limits of the oyster.

**CONSEQUENCES OF THE OYSTER DECLINE**

The oyster was not eradicated by the fall in salinity. It lives today in the Kattegat below depths of 9–18 m, because sufficiently saline water, being heavier than fresher water, is found only at that depth (Nordmann 1903). If the fiords after 3200–3100 B.C. were no longer capable of supporting oysters, and if the lessening of tidal activity meant that oyster larvae were now better able to develop in open waters (see the quote from Nielsen, above), then the oysters would withdraw from their accessible locations in the fiords and occupy deeper areas in the open sea. Such a move might not take them very far offshore; however, while oysters might conceivably be collected occasionally from depths of up to a
few meters, it is virtually impossible that they could continue to form a major resource under such circumstances.

If the oyster played the important part argued for it above, then its removal from the resource spectrum would have been a serious blow to the Ertebølle. Other developments were probably also occurring. The higher salinity of the Ertebølle period would have led to an overall increase in marine productivity (Nielsen 1938). If tidal flow declined, basic estuarine productivity would also have declined. This might mean that other resources would also decrease at the time of the oyster decline. The oyster decline was therefore both a serious problem for the Ertebølle in itself and perhaps also the symptom of other problems less archaeologically visible.

Could other resources be intensified to plug the gap? Winter resources such as small whales or swans could be exploited more intensively and stored, but given the fluctuations in numbers of all migratory species, there would be years when this would not be sufficient. Whether the

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**Fig. 10.** Seasonal changes in dry meat weights and condition index of cockles from the Llanrhidian Sands, South Wales (after Hancock and Franklin 1972:Fig. 5).

**Fig. 11.** Seasonal variations in dry meat weight of mussels of standard lengths from the Conwy estuary, North Wales (after Dare and Edwards 1975:Fig. 1).
decline in salinity might lead to a decrease in the availability of these resources is uncertain, but it is at least possible that the decrease in basic marine productivity might have adverse effects on the productivity and/or reliability of these resources—and this just at the time when intensification would be needed.

Extra predation on the local ungulates could take place. They would, however, be at their worst in late winter and spring (see above). Oysters contain some carbohydrate (Table 2); ungulates contain none, and so could not be a complete substitute for the oyster. As stated above, the ungulates would probably already be under considerable hunting pressure. The possible removal of cuts of pork from Ringkloster (Rowley-Conwy, in preparation) testifies to the intensive exploitation of land mammals in the Ertebølle. The meat was presumably taken to the coastal base camps; Ringkloster was occupied mainly in the winter and spring, and lies 14 km from the coast.

The other shellfish species are not an adequate substitute for the oyster. Cockles are much more seasonal than the oyster. They lose much condition in the winter and are at their worst in spring. Biomass in spring may be half what it is in September (Milne and Dunnet 1972), and a given weight of shellfish may contain 50% more meat in July than in February (Hancock and Simpson 1962). Lowest weights are reached in April (Hancock and Franklin 1972; Fig. 10). There is no weight increase earlier in the spring, partly because the cockle is more truly intertidal than the oyster, spending more of its time not covered by water and so not feeding (Kristensen 1957), and partly because it is not dependent on so high a sea temperature as the oyster in order to breed. It therefore disperses its reproductive products from April onwards without going through a period of storage (Hancock and Simpson 1962). Mussels in the Conwy estuary of North Wales do not start to put on weight until April or even May under modern conditions (Fig. 11), and 32–48% of meat weight may be lost during the winter (Dare and Edwards 1975). Similar patterns have been noted for mussels in Holland (de Zwaan and Zandee 1972) and Poland (Drzycimski 1961). Fat and carbohydrate contents also decline (Dare and Edwards 1975; Fig. 12). These factors must be added to the generally smaller sizes of cockles and mussels, which makes their collection less efficient (Fig. 13), and it is probable that the decline in marine salinity that adversely affected the oyster would also have reduced the productivity of the other shellfish. Neither cockles nor mussels seem to be an adequate substitute for the oyster.

A combination of resources stored from the previous summer, autumn, and winter might solve the problem in some years. (There is no direct evidence for storage in the Ertebølle, but it would be interesting to know what the Ertebølle pottery was used for.) Interannual variations in the
availability of these resources, as well as the risks of spoilage, would all increase the occurrence of bad years. While the oyster was present, variations in the small whale or waterbird migrations earlier in the winter would not have been a severe problem; oyster collection could begin earlier in the year. It could also be extended later if a cold spring delayed the start of the growing season, or if for any reason fishing could not begin as early as usual.

With the oyster no longer available, shortage or spoilage of other resources would acquire a new significance. What would formerly have been an average year, with most or all other resources available, would become a more difficult year as more of these resources had to be procured and stored. What would formerly have been a more difficult year,
with one or more of the other resources not available in the usual quantity, could now be the cause of major hardship or disaster.

CONCLUSIONS: THE ARRIVAL OF AGRICULTURE

It is suggested that the foregoing is the background to the appearance of agriculture in western Denmark. All other things being equal, an ecological crisis of the sort described here would probably have resulted in a decline of the hunter-gatherer population, and possibly an increase in mobility. For the Ertebølle, all other things were not equal, because a fully fledged farming economy had existed not far to the south for well over 1000 radiocarbon years. Contact between farmers and foragers is documented by the finds of shoelast adzes of German Neolithic manufacture in Ertebølle contexts (Fischer 1982). Despite this contact, farming was not adopted until problems arose with the hunter-gatherer economy.

Akazawa (1982) has presented a similar argument for the spread of agriculture eastward across Japan. Central and eastern Honshu were densely settled by Jomon foragers, and a delay of several centuries occurred before cultivation spread to these areas. This spread of cultivation took place at the same time as a drop in sea level, which dried out many of the productive shallow bays from which a large part of the Jomon diet came.

It is clear that the particular reasons for the adoption of agriculture are specific to each local area and may not apply elsewhere. Ertebølle sites in eastern Denmark, for example, do not always show such a heavy degree of shellfish exploitation as do the sites in the more western areas discussed here. Marine resources were, however, very important (Aariss-Sørenson 1980). It would be interesting to know what effect a decrease in salinity might have had on these resources, and whether such a salinity decrease could have caused problems for this Mesolithic economy—agriculture appears here at the same time as in western Denmark.

Coastal Mesolithic groups thus seem to play an important role in hindering or helping the spread of agriculture. Long-term changes in resource availability would always have occurred in coastal economies; if a farming economy was available within a short distance when a resource deterioration took place, the adoption of farming was one of the possible options. The nature of the problems facing Mesolithic economies will of course be unique in each case, and ecological factors may have to be considered in some detail—in the present case, the decline in oyster availability does not seem a particularly serious problem until its role as a resource bridging the late winter/spring gap is appreciated. For this reason I feel that the economic evidence from settlement sites is a much
more powerful tool with which to examine the spread of farming than are artifactual or other conventional archaeological materials.

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