#### CHAPTER 2

#### STRUCTURE AND VARIATION IN OYSTER SHELLS

In the introductory chapter the aims of the research project have been outlined together with the reasons for undertaking this particular study and for the methods used. A prerequisite of the study of oyster shells from archaeological sites is an understanding of the basic biology and life history of the species. This has been achieved through an extensive search of the existing literature on the subject. In this chapter on the structure and variation in oyster shells, the appearance of the shell, its composition and construction, the types of variation and the possible causes of them are discussed in some detail. The minimum requirements by way of habitat are also considered because variations in the immediate environment of an oyster may influence its shape and size.

## TYPICAL APPEARANCE OF THE OYSTER OSTREA EDULIS L

Most people would be able to recognise an oyster shell but few would be able to describe its typical appearance adequately. However, such a definition is necessary if the way in which oysters vary from the normal is to be examined. The solid shell is inequivalve, that is the two valves of which it is composed are unalike. The left valve on which the oyster originally settles, although it may turn over if it becomes free at a later stage, is generally convex or saucer shaped. The right (upper) valve is flat and sits within the left valve.

The two valves are joined by an internal dark brown ligament composed of a proteinaceous material called conchyolin that is attached to a triangular pit at the more pointed end of each valve. This is the oldest part of the shell. The outline of the shell tends to be distorted but is usually rounded with a length, at maturity in modern oysters, up to 10.16cm. The colour of the left valve can be fawn, yellow, pale green or brown with pink, green or purple markings. The right valve is grey-brown or brown, also with markings. There may be

a thick dark brown layer called the periostracum but this does not survive well in the archaeological record. The left valve is sculptured into a series of concentric ridges and deep radiating ribs and grooves. The right valve has concentric lines, perhaps radiating ribs and grooves and sometimes grey horn-like scales near or overlapping the margin of the shell.

The inside of the shell is typically white or pearly with sometimes patches of other colours. The adductor muscle, that is the strengthened area of shell where the muscle responsible for closing the shells is attached, is also usually white or nearly so. The outer shell margin of the left valve may have the appearance of being notched, or crenulate, where the radiating grooves make recesses in it (Lovell, 1884; Barrett and Yonge, 1958; Tebble, 1966; McMillan, 1968).

#### SHELL CONSTRUCTION

### Composition

The basic structural material of the oyster is a horny organic material called conchyolin which is impregnated with calcareous matter, except in the ligament. The shell is secreted by a fleshy part that envelopes the whole animal and is termed the mantle (Yonge, 1960).

### Formation of the shell

The mantle lobes are in continuous contact with the shell. They are flat and featureless except at the margins which are thickened by concentric and radial muscles and a pallial nerve. They are elaborated into three parallel folds. The large muscular fold controls the flow of water into and out of the shell. The middle fold has the functions normally associated with the head of other molluscs; it bears sensory tentacles. The outer fold is concerned with the formation of the shell which is the primary and original function of the mantle, not only at this outer fold but over its entire surface.

### The periostracum

Most bivalves have a shell composed of three layers. The periostracum is the thin, horn-like outer layer that is formed by the inner surface of the outer mantle fold. A transparent and elastic part of this periostracum at the shell margin remains in contact with the mantle throughout life, and allows the mantle to withdraw a short distance from the edge of the shell while remaining in contact. The periostracum is easily eroded.

### The prismatic layer

The two inner layers are thicker, and the conchyolin is calcified to a greater extent - the calcium being derived from solution in the surrounding water and incorporated in the organic matrix by use of the enzyme phosphotase. The outermost of these two layers consists of the more usual crystalline form of calcium carbonate, which is calcite, and is comprised of vertically-arranged prisms which give it the name prismatic layer. It is reduced and confined to the flat right valve where it forms flattened, horn-like scales although they actually only have 5 or 6% of organic matter. However, as they lack rigidity they allow for perfect marginal contact of the two valves of the oyster when it is closed by action of the adductor muscle. The prismatic layer is created by the outer surface of the outer mantle lobe (as opposed to the periostracum that is derived from the inner surface of the same fold).

## The nacreous layer

The third part of the shell is known as the nacreous layer and consists of horizontally-arranged plates of aragonite that are responsible for the iridescent, pearl-like sheen on the shell's inner surface. The nacreous layer is produced by the general surface of the mantle and remains always in contact with it, increasing in thickness continually and therefore is the only one of the layers capable of being repaired if the shell is damaged anywhere but at its margins.

### Rate of calcification

The rate of calcification is greater in the left cupped valve than in the right flat valve. Most of the left valve is composed of a subnacreous layer of calcite called calcite-ostracum which is arranged in horizontal sheets like the nacreous layer but not in such a regular way, therefore lacking any iridescent sheen. (Tsujii et al, 1958). Where the large adductor muscle is attached, the shell shows scars because of a localised strengthened form of shell called the hypostracum.

## Alteration of shape by chalky deposits

Oysters are unlike other bivalves in that they are able to alter the internal contours of their shell in two ways. One is the laying down of a type of padding referred to as "chalky deposits". These are opaque, porous white masses containing seawater and are essentially a less dense form of crystalline calcite-ostracum. They are frequently covered over by hard subnacreous material but contain only about one fifth of the shell material required for such normal subnacreous deposits.

# Alteration of shape by chambering

Secondly, oysters, especially the left valves of older specimens, exhibit a condition known as "chambering". Water or mud-filled chambers are enclosed within wide spaces between layers of subnacreous material. The condition is caused by shrinkage of the shell-forming mantle surface so that it becomes stretched taut across the deeper areas of the cupped valve. The shrinkage may be caused by dehydration of the tissues accompanying a transition to waters of higher salinity or as a result of body reduction following spawning. Under these two types of conditions (causing diminution of the body) the volume of the shell is also reduced by a rapid deposition of organic conchyolin which is later consolidated by the production of subnacreous material.

## Changes in shape with age

As the body of the oyster grows, so do the dimensions of the shell increase by addition of new material at the margins and by thickening overall. In early life the additions of shell resulting in greater diameter are regular. Growth is reduced but does not stop entirely in the lower temperatures of the winter months. Addition of new shell material is related more to the temperature of the seawater than the food supply.

Sometimes new shell in adult oysters is added rapidly in the form of light-coloured, fragile shoots of up to 10mm that are gradually strengthened by more material on the under surface. The shell shoots give rise to the typical series of concentric wavy ridges that appear on the outer surface of the valves.

#### TYPES OF VARIATION

## Documentary evidence for oyster shell variations

Yonge (1960) mentions that oysters growing in good conditions have a shell that is flat and evenly rounded. Yet it is known from a cursory examination of archaeological or modern oysters that the shape varies a great deal. To what can these differences be attributed, and what is the significance of these variations to the archaeologist in attempting to interpret the finds from a site? Tebble (1966) tells us that the oyster shell exhibits a degree of distortion depending on the shape of the surface to which it is attached and that a very great degree of variation in the shape of Ostrea edulis results from the ecological conditions under which separate populations or individuals are living. Thus the form of the archaeological shells may be a valuable indicator of the environment at the time of their growth.

The way in which an oyster shell reflects the habitat where it was bred has been acknowledged since antiquity. Pliny the Elder writes in his Natural History about the characteristic colours, consistencies and tastes of oysters from different countries (Pliny, XXII, chapter 21(6)), while the Roman poet Lucilius is reported to have said (Philpots, 1890):

"When I but see the oyster's shell,
I look and recognise the river, marsh or mud
Where it was raised."

Yonge (1960, 18) cites how Sir Anthony Carlisle in his Hunterian Oration of 1826 described the distinctive marks of an oyster that were liable to change, and form individual varieties reflecting the vissitudes of every location with regard to food, water depth, currents, tides and other influences. Yonge sums up by saying "that an experienced person can often tell from what bed any particular oyster has come".

## The significance of oyster shell variations

Taking into careful consideration the way in which oyster shells recovered during archaeological excavations may have altered in appearance from their original state, and bearing in mind the changes in all the factors influencing shell shape that might have occurred since their burial, the possibility exists to determine, at least in part, the kind of ecological and environmental conditions that prevailed when the oysters were growing. The exact nature of the macroscopic variations observed needs to be recorded and analysed.

The features that are most readily quantifiable in archaeological oyster shells are linear size, age, shape as a factor of size, evidence of encrusting or infesting organisms, and other marine mollusc species associated with the oyster shell deposits. Because there is a tendency for marine and littoral invertebrates to prefer different habitats, such as rocky in contrast to sedimentary substrates, or on the shore as opposed to an entirely sublittoral location, the evidence provided by oyster pests and other molluscs could be a useful indicator as to the type of location, if not the exact position, of the oyster beds being exploited.

### Variation in size

Age affects size. The older the oyster, the larger it grows until it reaches the stage where linear expansion is minimal and growth is mainly in thickness rather than diameter. In technical terms, bivalve growth curves are typically sigmoidal in shape, the initial exponential phase of growth being followed by a gradual decline as the animal ages. Environmental conditions play an important part in this general pattern of growth. Reduced growth rate may not be the result of great age but an effect of adverse food supply, temperature, substratum, salinity, light, depth turbity, population density or exposure to high energy environments (Rhoads and Lutz, 1980, 32-37).

Temperature is probably the most important influence because of its close relation to metabolic processes, availability and abundance of phytoplankton and the salinity of the water (Orton, 1928). Temperature directly affects growth rate and size. The temperature of seawater controls the rate of respiration in oysters; there is almost no demand for oxygen at zero temperatures. Oysters obtain inorganic salts from solution in the sea for increasing the calcareous parts of their shells. Material for the organic matrix is derived from food. When temperature is favourable, growth is related to the availability of food (Yonge, 1960, 104).

Three kinds of mineralogical variations in bivalve shells have been attributed to environmental controls, principally temperature. The first is the addition of calcite to shells in cooler water species. These tend to have more calcite than warmer water species of the same genus. For example, the Mytilinae show a strong positive correlation between calcite secretion and a species preference for cooler ambient temperatures.

Secondly, there is an increase in the whole-shell calcite-aragonite ratio among cooler water and higher salinity populations of species. In <a href="Mytilus edulis">Mytilus edulis</a> the calcite-aragonite ratio can be useful for assessing palaeotemperature.

Thirdly, there is an increase in the abundance of mineralogical aberrations, such as isolated patches of calcite within a largely aragonitic layer, which show a low but statistically negative correlation between their abundance and the open sea surface temperature (Rhoads and Lutz, 1980, 96).

Microgrowth increments are useful in recognising how seasonally variable environmental factors affect molluscan growth. For example, cockles from the Thames estuary stopped growing in sub-zero temperatures (Farrow, 1971). Closely-spaced growth increments were recorded in winter for Gemma gemma compared with widely-spaced microgrowth increments in the summer (Tevesz, 1972). Although the examination of the oyster shells in this thesis is on a macroscopic level, the instances described above serve to illustrate the importance of temperature on the shell growth of bivalves.

Depth of water is another important limiting factor in oyster shell growth. Intertidal populations are regularly exposed to air at low spring tides. Oysters cannot produce shell while out of water. In fact, some shell may be dissolved by the acidic metabolic byproducts of anaerobic respiration while the oyster keeps its valves tightly shut (Rhoads and Lutz, 1980, 125-128). Therefore the size of oysters in intertidal populations might compare unfavourably with that of sublittoral oysters which are constantly submerged.

Genetics will also be responsible for a certain amount of inherent size variation in a population of oysters. High proportions of abnormally small oysters may be found in modern populations. These oysters are called "dumps", clumps" or "stunters" in the oyster trade. They are small, thick-shelled and do not increase substantially in size even when transferred to more favourable conditions. A form of stunting occurred in the oyster beds of the Fal estuary in Cornwall in the 1920's (Orton, 1928) and it was concluded that these shells, which sometimes resembled Brazil nuts, were a genetic variant. This extreme form has now died out. Recent research work has been directed towards the use of this idea of genetic

strains to select for oysters that grow larger (Newkirk and Haley, 1982; Haley and Newkirk, 1982).

Environmental factors can be responsible for the size charcteristics of oyster populations. In the late 1950's stunted oysters again became prevalent in English oyster beds but these oysters were regular in shape and deep-heeled despite the fact that they rarely attained the required size of 65mm for marketing. The possible causes for stunting in this instance were investigated by Cole and Waugh (1959). Temperature and food supply were not thought to be unfavourable, as stunted oysters occurred mixed with normal ones. The effect of a strong current bearing a heavy load of silt and suspended sand constantly bombarding the shell-producing mantle edge was discounted since the oysters concerned were incapable of improvement when transferred to better conditions. It had already been shown that a strong current without mineral particles could be favourable for growth in some circumstances since it ensured full oxygenisation of the surrounding water and a continuous food supply (Korringa, 1956).

The effect of heavy infestation by the commonly occurring burrowing marine polychaete <u>Polydora</u> was taken into account. Elimination of <u>Polydora</u> had been shown in Holland to result in a marked improvement in shell growth rate (Korringa, 1951). Cole and Waugh agreed that from their own observations <u>Polydora</u> was capable of checking shell growth severely and that it might have played a major part in the production of stunted oysters, but the degree of involvement was difficult to ascertain (Cole and Hancock, 1956). However, not all stunted oysters were heavily affected by Polydora.

It was finally concluded that the high incidence of stunting was due to the introduction for relaying of Brittany oysters which, for reasons of cost-effectiveness, had been reared high on the shore. The relatively poor nutritional environment had resulted in a permanent check to their growth potential which could not be reversed. The situation on the English oyster beds, to which oysters of limited growth potential had been introduced, was made worse by the fact that dredged stunted oysters were returned to the water in the hope that they would eventually reach marketable size. The normal adults were removed. This unintended selection procedure meant that a disproportionate number of the population were stunters and the situation worsened from year to year. It was eventually recommended that stunted specimens should be sold off cheaply for cooking, or cast on the shore to bleach for cultch.

## Variation in shape

# Elongate and round oyster shells

Variation is also apparent in the shape of oyster shells. There are indications that the shape may vary according to the substrate on which the oyster is growing, the depth of water and the degree of competition for space from other oysters. Some research has been carried out with regard to bivalves in general and the substrates on which they live, and also on other species of oyster than the European flat oyster. The results of these observations may be applicable to Ostrea edulis. It is thought that thinner, longer oysters grow on softer substrates in crowded conditions. Heavy rounded shells are found on hard bottoms in deeper water where there is less competition for growing space. Examples of the two extremes of shape can be seen in Plate 2.1.

The Portuguese oyster, <u>Crassostrea angulata</u> (Lamarck), tends to be naturally oblong. A long narrow form lives on muddy intertidal beds. It is believed that in these conditions the mantle edge is extended upwards in the area most remote from the hinge, for feeding and respiration, taking advantage of clearer water than around the sides of the shell which lie more or less in the mud. Since the mantle edge is also responsible for shell growth, shell addition is at this more restricted area and upwards in direction. In deeper water the beds are thought to be less muddy with more regularity to the direction of currents so that the mantle can extend more uniformly around the

periphery of the shell, and new growth of shell is not confined to one area, with a resulting broader shell (Orton, 1936).

The American oyster, <u>Crassostrea virginica</u> Gmelin, tends naturally to be broadly oval in outline. In a report by Galtsoff and Luce (1930) we learn that one of the interesting peculiarities of American oysters living on soft mud is their inclination to grow vertically with the hinge end buried in the mud and the very sharp edges of the bills just above the mud. The heavier, narrow hinge end gradually sinks in the mud aided by slight vibrations of the soft medium caused by vigorous closing of the shells. Keeping itself above the mud and silt the oyster grows in length and develops into a long, sharp-edged specimen known as a "snapper" or "coon" oyster. It is not a race or mutation but a reaction to peculiar environmental conditions. Coon oysters broken apart and replanted on firm bottom change their form and develop into good-shaped oysters (Coker, 1907).

Oyster shells from heaps left by American Indians of the Pre-colonial period (pre 16th century) were compared with modern oysters by Lunz (1938) who stated that they were much larger than present forms that had decreased in size as the result of cultivation. But it was soon pointed out by Gunter (1938) that the shape factor had been overlooked. There were two basic shapes. On hard bottom with sufficient room oysters were known to grow almost as wide as long, with the long axis of growth curving to the right. Wild oysters from Karankawa Bay, Texas conformed to this type. Where oysters were crowded or grew on soft bottom the shells grew straight, upright and very long. The shell was thinner, and longer than wide. Commercial beds were more likely to yield rounded but smaller oysters. Coon oysters often grew in shallow waters where they were so frequently taken by hand that wading for oysters in some localities was called "cooning". This type of oyster would have been more easily available to the Indian than the rounded deep water forms. Well cultivated beds and some wild beds produced oysters of comparable size.

More recent work by Thayer (1975) has validated the principles involved in the observations of earlier workers. Adaptations of bivalves to soft bottoms involve one or more mechanisms. These include reduction of bulk density by the production of thinner shells with less ornamentation. The "iceberg" adaptation is where the partial submersion of the bivalve in the fluid surface mud adds buoyancy thereby allowing firmer underlying sediment to support it. The "snowshoe" adaptation means a flattening or other method of increasing the area of surface supported (the production of a broader bearing-surface). The last adaptation would be a reduction in size.

# Irregularities

Iregularities of shape can be caused by overcrowding. Many oyster spat may settle on the same hard object and, as they develop, compete with each other for growing space. Oysters which are not separated before they are three years old are likely to yield a proportion of flat or mis-shapen oysters (the "cripples" of the oyster trade) which will never recover sufficiently to make good market oysters (Cole, 1956).

## Variation in infestation

Not many of the pests which attack or infest oysters leave easily recogniseable evidence of their presence in archaeological shells. Only those organisms that burrowed into the shell leaving distinct marks, or those creatures that attached themselves by hard parts to the shells can provide evidence of encrustation and infestation. The types of organisms represented and the relative abundance of them will differ according to the local conditions in which the oysters were growing.

# Damage by the Polydora worms

The two most commonly occurring pests on oysters are the marine polychaete worms Polydora ciliata and Polydora hoplura which in the first instance create mud tubes in the crevices of the shells. P. ciliata is about 25mm long and the holes that it makes as it extends its burrow backwards into the shell are scattered over the general

surface of the shell. Heavy infection can render the shell friable but that is the sole extent of the damage. P. hoplura is twice as long (about 50mm) and does not bore but settles between the mantle and the shell at its margins. In reaction to this irritation, the oyster seals off the worm and mud, and forms a blister on the inner edge of the shell. The worm, its body bent double, cuts back through the shell as it grows causing the blister to be enlarged. The U-shaped channels and mud blisters are easy to distinguish from the borings of P. ciliata on the outer surface of the shell. In contrast to P. ciliata, P. hoplura poses a real threat to the well-being of the oyster which has difficulties closing the valves because of the blisters, and has to divert much energy to repairing the shell (Yonge, 1960).

The two species of <u>Polydora</u> have different habitat preferences. <u>P.</u> <u>hoplura</u> is found mostly in the southwest of England where it thrives in oysters on soft ground in still, warm conditions such as the head waters of creeks or inlets. <u>P. ciliata</u> has a wider distribution and is found predominantly on hard sandy or clay grounds, particularly in warm shallow water (Hancock, 1974; Cole, 1956).

## Cliona sponge borings

The sponge, Cliona celata, bores into oysters by dissolving the shell. In life it is identified by the numerous yellow pustules on the surface of the shell, but in archaeological specimens it is recognised by the honeycomb appearance of the shell. When severely attacked, the shells are easily crushed and are known as "rottenbacks" in some areas (Hancock, 1974; Cole, 1956). The disease is prevalent in the south and south-west of England.

### Predatory gastropods

Two species of mollusc bore straight through the shells of oysters, especially young ones with thin shells, in order to suck out the meat of the animal. Successful boring results in the death of the oyster but some oysters obviously withstand the attack by rapidly laying down new shell. Some of the mature Hamwic shells had boreholes that

had been sealed. The most common borer would have been the European rough tingle or sting winkle, Ocenebra erinacea (L.), although the dog whelk, Nucella lapillus (L.), may prey on oysters in the same way. Both are gastropods with a pointed shell, inhabit shallow water and feed with a long proboscis. At the end of the proboscis is a small mouth with a tongue-like radula armed with rows of teeth. The teeth penetrate the shell by using a rasping action.

The organisms that created holes in the shells at Hamwic are considered in more detail because more information was readily available about their habits and distribution than those of the encrusting organisms such as <a href="Pomatoceros triqueter">Pomatoceros triqueter</a>, <a href="Sabellid spp.">Sabellid spp.</a>, Bryozoa and Cirrepedia.

#### Variation of associated molluscs

Oyster shells from archaeological excavations are frequently found in association with other marine mollusc shells. These might include well-known edible species such as winkles, <u>Littorina littorea</u> (L.); whelks, <u>Buccinum undatum L.</u>; mussels, <u>Mytilus edulis L.</u>; and cockles, <u>Cerastoderma edule</u> (L.); as well as less familiar species such as dog whelks, <u>Nucella lapillus</u> (L.); flat or rough periwinkles, <u>Littorina</u> spp.; saddle oysters, <u>Anomia ephippium L.</u>; tellins, <u>Tellina spp.</u>; carpet shells, <u>Venerupis pullastra</u> (Montagu) and odd specimens of other non-edible mollusc.

Each species has its special habitat requirements. Their presence may therefore provide additional clues to the locations being exploited for shellfish. For example, winkles are generally very common between tide marks on rocks and weeds on rocky, stony or muddy beaches (Barrett and Yonge, 1958; McMillan, 1968; Graham, 1971). Whelks prefer to live on muddy gravel, sand or rocky shores at low water and below. Mussels occur from high in the intertidal zone to depths of a few fathoms attached by byssus threads to rocks and other hard objects within sheltered harbours and estuaries as well as rocky shores of the open coast (Tebble, 1966). Cockles generally occupy clean sand, muddy sand, mud or muddy gravel from mid-tide livel to

just below low water mark. They are common in sandy bays and river estuaries and can tolerate low salinities up to 20 parts per thousand. Dog whelks live on rocks, usually in the barnacle zone, sometimes with mussels, on all rocky shores except exposed ones from high water of neap tides downwards. Saddle oysters are always attached by a chalk-impregnated byssus to stones, rocks or shells from low water to about 80 fathoms. Carpet shells are also usually attached to a solid object by a byssus thread a few cwntimetres below the surface of substrates like sand, stony sand, muddy gravel or muddy sand at the base of rocks.

# SUITABLE HABITATS FOR OSTREA EDULIS L.

Having looked at the typical appearance of the European or flat oyster, the way it varies in size, shape and infestation, and the conditions which may influence these parameters, it is appropriate to consider the exact ecological requirements for a population of oysters. They have very specific needs depending on whether the oysters belong to a naturally-maintained breeding population or a population of oysters that have been relaid by man for fattening and improvement prior to marketing. The requirements for relaying fisheries are not so stringent. The main factors of importance are substrate, shelter, salinity and currents.

This type of oyster normally lives offshore from about low water to between 15 and 45 fathoms on firm, stable ground of stiff mud, rocks, muddy sand, muddy gravel with shells, hard silt or similar (Tebble, 1966). Clean sand is unsuitable because oysters would soon be covered by it, especially during high winds. Very soft mud provides similar problems of suffocation, but for relaying fisheries this type of substrate can be consolidated by adding gravel ballast, shells or sand, possibly over a layer of brushwood.

Shelter is vital for a breeding population to minimise the movement of the oysters themselves and also the surface of the substrate on which they are settled. It has been observed since early times that areas where freshwater entered the sea either from small streams or rivers enhanced the growth of oysters when compared with those of the open coast:

Oysters love freshwater and spots where numerous rivers discharge themselves into the sea; hence it is that pelagia (deep sea oysters) are of such small size and so few in number. Still, however, we do find them breeding among rocks and in places remote from the contact of freshwater, as in the neighbourhood of Grynium and of Myrina, for example.

(Pliny, XXXII, chap 21(6))

The preference is thought to be due to the fertilising effect of land drainage, and the fact that mud and silt brought down by rivers overlies or mixes with other material to form a favourable substrate for oysters. The salinity range tolerated by <u>O. edulis</u> is from 25 to 36 parts per thousand (open sea water around British coasts is about 34 to 35 parts per thousand) and this can be found in the middle and lower reaches of estuaries but not higher where constant fresh water input in rainy weather is too great. If the salinity is often reduced to 28 parts per thousand or below, then oysters do not thrive (Cole, 1956).

The tidal flow pattern and water currents are particularly significant to a breeding population. Minute shelled larvae are shed into the water during spawning and swim aimlessly in the upper levels of the water column for a period of 7 to 14 days, depending on temperature and food supply. When sufficiently developed, they sink and cement themselves as spat to a suitable hard object (known as cultch). During the free swimming period the larvae are at the mercy of tides and currents. Ideally, an area where the tidal ebb and flow are confined, and the water subsequently recirculated, is preferred. Such locations might include enclosed bays, estuaries or narrow straits between islands and the mainland. Oyster larvae from populations in other types of open situation, without this sort of tidal regime, could be dispersed great distances from the parent

stock and possibly fail to find a suitable substrate on which to settle.

In this chapter, the biology and life history of Ostrea edulis has been described to provide a background for understanding the variations likely to be encountered in oyster shells from archaeological deposits. In the next chapter, the methods devised for handling the material, recognising the relevant features and recording the variations are outlined. It gives details of the equipment required, suggests a suitable spreadsheet, describes how to measure and age shells, provides illustrations of infestation damage and encrustations, and gives an indication of the speed at which the details can be recorded from the shells.