AN ECOLOGICAL INTERPRETATION OF MESOLITHIC SHELLFISH REMAINS ON THE ISLAND OF ORONSAY, INNER HEBRIDES

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SUMMARY

The island of Oronsay in the Inner Hebrides contains five Late Mesolithic shell middens. This research uses ecological investigations on limpets (Patella spp.), periwinkles (Littorina littorea L.) and dogwhelks (Nucella lapillus L.) from the present Oronsay coast to aid an interpretation of the shellfish collection strategies of the Mesolithic hunter-gatherer populations, and to establish the relative importance of the three shellfish species in their diet.

Section A is devoted to ecological examinations of contemporary limpets, periwinkles and dogwhelks, and in Section B this information is applied to the midden shellfish. In chapter 1 an examination is made of previous research into selected aspects of the ecology of the three species, which forms a necessary basis for the present research. In each species an examination is made into studies concerning population dynamics (reproduction and mortality), the distribution of the animals over the shore, growth, and the physiological ecology of body and shell development. Chapter 2 examines seasonal meat weight changes (ie body weights) in animals from an area of the present Oronsay coast at different tidal levels over a full year. For chapter 3 further fieldwork was carried out around the Oronsay coastline to examine the difference in population structure of the three species in varying coastal environments, and at different tidal levels. Attention was paid to variations in size in each of the species, and their relative proportions between sample sites. An examination was also made of shape distribution of limpets at different tidal levels. Chapter 4 makes comparisons between present Oronsay coastal environments and those of the Mesolithic, with relation to coastal morphology and exposure, and sea temperature, to assess the validity of using contemporary data to interpret activities on Mesolithic Oronsay.

Section B begins with a brief synopsis of the main approaches that have previously been adopted in midden studies. Chapter 6 then uses information gained in chapter 3 to explain the size distribution of each species in the middens, the shape distribution of the midden limpets, and the relative proportions of the three species, in terms of the collection strategies of the midden dwellers. Interactions between the human predators and the shellfish populations will be reflected in the size-frequency structure of the midden shellfish from the base to the top of the middens. From sample columns in each midden an assessment is made of the intensity and periodicity of exploitation, and of the relative importance of each of the three shellfish species. Chapter 7 uses data from chapter 2 to reconstruct the relative proportions of meat weight provided by each shellfish species in the middens. Account is taken both of shellfish size, tidal position, and the varying amounts of meat which may have been obtained at different seasons.

Seasonal changes in body weight are demonstrated in limpets, periwinkles and dogwhelks from the present Oronsay coast, which are related to their reproductive cycles and feeding intensities. When this information is applied to the midden shells, at each possible collection season limpets are shown to provide around 90% of the shellfish meat weight.

On the modern coast the relative proportions of the three species vary greatly from different shore environments, yet in the middens there is a much greater uniformity in the relative numbers of the three species. There are no major changes in species composition or size upward through the middens, and it is argued that this indicates a fairly low intensity, regular exploitation.

INTRODUCTION

The island of Oronsay in the Inner Hebrides contains five Mesolithic shell middens composed mainly of limpets (Patella species) with some periwinkles (Littorina littorea) and dogwhelks (Nucella lapillus). These remains have been analysed to gain an understanding of the collection strategies of the Mesolithic hunter-gatherers, and to establish the relative proportions of these three shellfish species in their diet.

Oronsay is situated approximately 30 kilometres to the west of the Scottish Mainland at a latitude of 56° North (Mellars 1978:371) (figure 1). It has a land area of 5.8 square kilometres, much of which is covered by windblown sand and peat accumulation. In the centre of the island Beinn Oronsay rises to 92.6 m O.D. During the higher sea level of the later Mesolithic it is probable that the land area was reduced to less than 4 square kilometres (Andrews 1981; Jardine 1977; Mellars 1978) (figure 2). Some metres to the north of Oronsay lies the larger island of Colonsay (figure 2). The two islands are separated by 'the Strand', an expanse of sand which is covered by the sea at every high tide. Some 10 to 12 kilometres to the southeast of Oronsay lie the islands of Islay and Jura (figure 1).

Figure 2 shows the locations of the five Mesolithic shell middens. These are shown in plates 1 to 5. Table 1 shows that the radiocarbon dates range from 4,240 ± 80 bc to 3,200 ± 380 bc and indicate a chronological overlap in occupation of the middens. All except Priory Midden are on the east coast. Caisteal nan Gillean I (CNG I) and Cnoc Sligeach were identified in the 19th century and excavated between 1879 and 1913 (Anderson 1898; Bishop 1914; Grieve 1885), whereas Caisteal nan Gillean II (CNG II), Cnoc Coig and the Priory Midden were identified by Dr P.A. Mellars during a programme of excavations throughout the 1970's. It does, however, appear that part of Cnoc Coig was also excavated in the early 20th century under the names of 'Drum Harstell' and 'Cnoc Riach' (Mellars 1981).

Although shellfish, especially limpets, are the most obvious features of these middens, they also contain other residue reflecting the activities of these hunter-gatherers. Fish bones and otoliths, seal, deer and bird bones, hazelnuts, stone, bone and antler tools, hearths and postholes all feature in these shell mounds (Anderson 1898; Bishop 1914; Grieve 1885; Mellars 1983; Mellars and Payne 1971; Mellars and Wilkinson 1980; Nolan 1984; Grigson 1981). It is, however, because of the alkaline conditions provided by the shells that most of these other objects remain.

Limpets are conical shellfish with rough ribbed shells which fit tightly onto the substratum (plate 6). On Oronsay there are presently two species, Patella vulgata and Patella aspera, the latter living on the lower part of the shore in areas of moderate exposure, only existing higher up on very exposed coasts. Patella vulgata exists throughout the intertidal range. Patella are herbivores, feeding on algae and fucoids. Both species are probably present in the middens though it is impossible to distinguish between them from the prehistoric shells.

Periwinkles (which are also referred to throughout this text as winkles) are snail-like animals again existing throughout the tidal range and are grazers, feeding upon algae and detritus. Dogwhelks (also referred to as whelks) also exist over the whole tidal range and are carnivores, feeding largely upon barnacles and mussels. Plate 7 shows the difference between periwinkles and dogwhelks. The former are black or dark brown and the latter varying shades of white/brown or yellow/white, and with a channel in the front of the aperture, termed the siphonal canal, through which they extrude a proboscis to drill the shells of their prey.

An essential prerequisite to an interpretation of the midden shellfish is an understanding of the ecology of the three species, and a full appreciation of the dynamic interrelationships of the coastal ecosystem. Only once armed with contemporary ecological data is it possible to suggest anything about the use to which Mesolithic peoples put their coastal resources. This data is not readily available, so specific ecological surveys have been conducted upon Oronsay to provide a basis for interpreting the midden shellfish. Thus, Section 'A' is devoted to the ecological research and in Section 'B' this information is applied to the midden shellfish.

Section 'A' begins with a brief synopsis of the current state of knowledge on aspects of the present day ecology of the three species that form the basis for the present research. The two main themes of this research are then examined in chapters 2 and 3. Any reliable estimation of the amount of meat provided by the midden shellfish must take account of both seasonal alterations in flesh composition and varying proportions of meat in animals of different sizes.

> 'Accurate archaeological reconstruction of the amount of mollusc meat originally collected at a site presupposes, among other things, good experimental data on populations of living molluscs. ....One might expect, moreover, experiments on live molluscs to fall in the province of the marine biologist. But the latter have dealt very little with mollusc weight, apparently because the problem is so messy.... At present, then, it would seem that archaeologists must generate their own shellfish data if they wish to reconstruct believable prehistoric mollusc meat weights'.
> (Koloseike 1969:150)

This is still true today. Thus, chapter 2 examines the changing flesh weight of limpets, periwinkles and dogwhelks during six surveys on Oronsay throughout 1980.

The second main theme of this research is the examination of the shellfish population in the middens as an indicator of human collection strategies. Again this is not possible without a knowledge of the population structure of an uncropped population, so the deviations from this may be observed in the middens. Thus, chapter 3 tells of a survey of the Oronsay coastline conducted in 1981 to look at changing species population structure in different coastal habitats.

Chapter 4 then assesses the reliability of using the modern Oronsay shoreline as a basis for an interpretation of Mesolithic shellfish exploitation.

Section 'B' applies the above data to the midden material. It begins with a brief assessment of previous shell midden studies, where the analytical trends may be applicable to an interpretation of the Oronsay middens. The size, shape, and relative proportions of the midden shells are then examined in chapter 6, and suggestions are made concerning the possible collection strategies of the Mesolithic gatherers.

Finally, chapter 7 uses data obtained in chapter 2 to calculate the relative proportions of meat weight provided by each of the three shellfish species in the middens. Account is taken of both shellfish size and the possibility of collection at different seasons, when the three species provide varying proportions of flesh.

TABLE 1 : Radiocarbon dates for Oronsay shell middens

Midden	Level	Date bc
Cnoc Coig	Upper	3,545 ± 75
	Upper	3,480 ± 130
	Lower	3,695 ± 80
	Lower	3,585 ± 140
Premidden	Upper	3,700 ± 60
	Lower	3,725 ± 60
Caisteal nan Gillean I	Upper	3,500 ± 50
	Upper	3,535 ± 50
	Middle	4,085 ± 70
	Lower	4,240 ± 80
	Lower	4,170 ± 80
Caisteal nan Gillean II	Upper	3,200 ± 380
	Lower	3,500 ± 140
	Lower	3,510 ± 65
Cnoc Sligeach	Upper	3,476 ± 159
Priory	Upper	3,520 ± 50
	Upper	3,560 ± 50
	Middle	3,767 ± 50
	Lower	3,875 ± 50
	Lower	3,920 ± 50

(From Mellars 1983)

SECTION A

CHAPTER 1 : ECOLOGICAL BACKGROUND TO LIMPETS, PERIWINKLES AND DOGWHELKS

A. INTRODUCTION TO COASTAL ECOLOGY

1. Zonation

Marine coastal zonation refers to the distribution of intertidal organisms vertically and horizontally over the shore. 'Intertidal zonation of organisms is thought to be maintained by the differing responses of organisms to changes in physical and biotic factors which vary from low to high intertidal areas' (Petraitus 1982:207). '...the distribution of any organism between tidemarks tends to be due to several factors working together rather than to a single isolated cause...' (Stephenson 1942:220). Factors such as tidal position, degrees of exposure to waves and sun, biological habitat and coastal morphology all combine to affect the ultimate distribution of species over the shore. This chapter will examine these factors and their influence upon the distribution of limpets, periwinkles and dogwhelks over the shore.

Throughout the thesis reference will be made to certain zonation features which require initial definition. On the seashore, conditions will vary from one position to another; they become wetter or drier, more or less exposed, more or less steeply sloping, and so on. All such changes influence the distribution, composition and abundance of intertidal organisms. To describe the interrelationships between these species, and between the species and their environment, requires a framework or classification system. There are a number of such systems (for a review see Lewis 1964) but the one chosen here is a combination of that developed by Stephenson and Stephenson (1949) and the modification of this made by Lewis 1964) and utilized by Crapp (1973).

This system relies largely on the Stephenson and Stephenson scheme for the following reasons. Their zones are easily recognized on the shore, and this scheme is universally applicable, being based on the idea that certain types of organisms characterize approximately the same levels on all rocky shores. The problems summarized by Lewis (1964) do not hinder the use of this system for the present study because it is not purely biological in scope. The ultimate aim is archaeological interpretation broadly applicable to the seashore, so the Stephensonian method benefits greatly from its generalized simplicity. Certain of Lewis's modifications are also incorporated.

Three coastal zones are recognized:

1. LITTORAL FRINGE. On the upper shore, this arid zone is transitional between land and sea, being wetted by waves only at spring tides and/or during heavy seas. A small number of species inhabit this zone; these are mainly of the *Littorina* genus (*L. neritoides* and *L. saxatilis*), and a few species of algae and lichens, especially *Verrucaria maura*. At the very high level the change from shore to land may take place over many metres, especially on exposed headlands, and the various lichens may mingle considerably.

2. EULITTORAL ZONE (or mid littoral). Being on the middle shore this is the most fully intertidal zone, at least part of which is covered and uncovered each day. There are many more species adapted to this dynamic habitat, containing a variety of specialized microhabitats. The upper limit is marked by the ending of large masses of barnacles (commonly termed 'the barnacle line', see plate 8). In shelter *Pelvetia canaliculata* often replaces the upper belt of barnacles. This zone is often distinguishable into two subzones, in the upper of which there are denser barnacle clusters, the barnacle being the dominant, or near dominant species, the other important species often being *Patella vulgata*. In the lower subzone the barnacles are of much less significance, and there are more algae, especially the class *Rhodophyceae* and *Himanthalia*. On some shores barnacles are subordinated by mussels and red algae.

3. SUBLITTORAL ZONE. This zone is uncovered at spring tides but not generally at neaps. In very exposed situations it may only be uncovered at the lowest spring tide in calm weather. The area is exposed to the air for only a short period of time and rarely, if ever, dries out. Kelp are the dominant species, and the top of the zone is marked by the upper level of *Laminaria*.

This scheme makes many generalizations yet provides an adequate framework for the development of ideas concerning archaeological coastal exploitation. Variations in zonation as a result of exposure, aspect and coastal morphology will be discussed in future chapters.

It is often necessary to describe an exact tidal position with a greater degree of precision. This may be done by relating the state of the tide to the extent of tidal range. Spring and neap tides occur on approximately fortnightly intervals which relate to lunar cycles. At maximum spring tide the sea moves over its fullest tidal range, from low down the sublittoral to high up the littoral fringe, and on maximum neap tides the movement is usually only within the eulittoral zone.

Around the period of the equinoxes (March and September) the rise of spring tides is higher, and the fall lower, than at other times. In winter, the morning high spring tides are higher and the succeeding low tides lower than the night tides; in summer, the contrary occurs. The greatest spring tides occur after a full moon in winter, but after a new moon in summer (Orton 1929).

For any area of the British coast on any day the extent of tidal movement is known, related to selected datum points. Using this system any area of coastline may be divided into the following vertical divisions:

Mean High Water Spring Tides	(MHWS)
Mean High Water Neap Tides	(MHWN)
Mean Low Water Neap Tides	(MLWN)
Mean Low Water Spring Tides	(MLWS)
Mean (Mid) Tide Level	(MTL)

Extreme High Water Spring Tides (EHWS)
Extreme High Water Neap Tides (EHWN)
Extreme Low Water Neap Tides (ELWN)
Extreme Low Water Spring Tides (ELWS)

In future these will be referred to by the initials. Because of the variations in spring and neap tides over the year, these values refer to average high and low water heights of these tides. The values refer only to the theoretical level of the sea.

These levels may be generally related to the zonation pattern outlined above, although this relationship varies from shore to shore. For instance in extreme shelter the littoral fringe is very narrow and does not extend above MHWS, but with increased wave action the zone becomes higher and wider and may lie entirely above MHWS, being wetted only by splash. The upper part of the eulittoral zone is often centred around MHWN or MTL, and the lower component around MLWN, though again variations depend on exposure and shore morphology, as steeper slopes will induce more splash. The top of the Laminaria zone may be around MLWS on very sheltered shores or just above MLWN in extreme exposure.

2. Limpets

There are three species of limpets in the British Isles: Patella vulgata (Linnaeus), the common limpet, Patella aspera (Lamarck) (= P. athletica Bean) and Patella intermedia (Jeffreys) (= P. depressa, Pennant). Patella intermedia does not occur north of Anglesey in north Wales, so will not be considered.

It is probable that these are three separate species as accepted by Bowman and Lewis (1977), Ebling et al (1962), Eslick (1940), Evans (1947a, 1947b, 1953), Gaffney (1980), Lewis and Bowman (1975), Orton (1946) and Orton et al (1956), and not a single species as claimed by Powell (1973). Gaffney (1980) provides electrophoretic evidence which demonstrates the distinctions of the three species. He considers that the enzymes revealed on the electrophoretic records are sufficiently distinct between P. vulgata, P. aspera and P. intermedia for these to be recognized as three separate species. Six enzymes were used, although discrimination between the three species could usually be achieved by a single enzyme.

Evans (1953), analysing limpets from the south coast of England, considered that there were transitional individuals between the three British species, and between P. vulgata and the Mediterranean form P. coerulea. He claimed that intermediate characteristics were evident in shell form: 'The writer is firmly convinced of the existence of "transitional" or "intermediate" shell types. Some show a mixture of characteristics on the external surface; these are difficult to describe and are only apparent to the experienced observer' (Evans 1953:364). He also considers there to be intermediately shaped pluricuspid teeth and transitional divisions within radula-length categories. Evans speculates on the reasons for these transitional forms and considers that if cross-breeding between the three British Patella species does occur it is not of major importance. Instead, he considers, the main differences may result from stages in the emergence of discrete species from a P. vulgata-like root stock.

Evans' observations, conducted on a large sample, are not in doubt, but these variations need not represent intermediate forms between different species. He admits that there is much variability in these characteristics, so all the observed differences may be accounted for by natural variation strictly within the three separate species.

Gaffney's (1980) evidence rules out both hybridization and incomplete speciation, indicating the distinctiveness of the three British species. Although he discovered limpets that looked intermediate and could not, morphologically, be placed in a definite species, they could be easily classified on the basis of their electrophoretic profiles. There were no electrophoretically intermediate or hybrid individuals.

It is often possible to distinguish between P. vulgata and P. asperaon the shore. Table 2 specifies the main differences. Sometimes it is necessary to go to the extent of examining the marginal tentacles of

TABLE 2 : SPECIES CHARACTERISTICS OF PATELLA VULGATA AND PATELLA ASPERA (after Campbell 1976, Ebling *et al* 1962, Fretter and Graham 1976, and based on personal observations)

SPECIES	SHELL	FOOT COLOUR	MARGINAL TENTACLES OF THE MANTLE	SHAPE OF PLURICUSPID TEETH	RADULA LENGTH
PATELLA VULGATA	Grey or whitish internal head scar (spatula) and orange or yellow internal ribs showing against a dark grey ground. Nacre increases with size and tends to hide the original colour.	Dark grey, ochre or a yellow orange mixture. Colours not as clear as in *P. aspera*, the dark pigment masks clarity.	Universally translucent.	Cusps arrow-shaped and middle teeth largest.	Length of radula depends on species, length of shell and tidal level. Once a correlation is made for length of shell and level (see Ebling *et al* 1962), the main radula length for *P. vulgata* is greater.
PATELLA ASPERA	Orange internal head scar and white or pale straw ribs against a bluish or purple nacreous ground. The greater degree of nacreous sheen gives shell interior a distinctive porcellanous appearance.	Ranges from very pale grey, through shades of cream to orange, colours clearer than in *P. vulgata*.	Either opaque white or with opaque white central band.	Cusps spear-headed and either the two outer cusps are nearly equal in length or the outer one is longer.	

the mantle, the shape of the pluricuspid teeth and measuring the radula length (Ebling et al 1962) because there can be variations in the colour of the internal shell head scar and foot.

There are certain important differences in lifestyle between P. aspera and P. vulgata. Their geographical ranges overlap from the Mediterranean to north-eastern Scotland, but from here to northern Norway P. vulgata is the sole limpet species. P. aspera is mainly found on exposed shores and at lower tidal levels, living on rocks from the shallow sublittoral to around MLWN. It may extend higher up shores which remain wet due to splash, and it also exists in upper shore rockpools. P. vulgata occurs on the majority of rocky shores from the most exposed to the most sheltered, occurring from the sublittoral zone to between MHWN and MHWS (Fretter and Graham 1976). The upper limbs are higher in more exposed or shady situations where there is increased wetness, and lower in sheltered or bright habitats where the rocks are dryer. Limpets on the lower shore have a more flattened appearance, whilst those inhabiting the upper shore are more conical. P. aspera are therefore always flattened, whereas P. vulgata may be flattened or conical (Ebling et al 1962; Fretter and Graham 1976; Jones et al 1979; Moore 1934; Orton 1928a, 1928b, 1933; Punt 1968).

It is sometimes possible to distinguish the shell of Patella aspera where the flesh has recently been removed, because of a slight orange interior apex with pale blue iridescence around this (pers. comm. Dr J.D. Fish). This colouration is not, however, always present in freshly killed limpets, and is certainly not evident in midden shells. The only idea we may have therefore of the extent of Patella aspera in the Mesolithic shellfish population is from estimations of degrees of exposure.

Limpets are browsers, feeding on all types of algae (Fretter and Graham 1976). Microscopic young algae is grazed and larger fucoids are trimmed at the edges. Optimum environments for growth are where each limpet has adequate food and is not impeded by competition from other species or other limpets (Fischer-Piette 1948; Jones 1948; Lewis and Bowman 1975).

P. vulgata is a protandrous hermaphrodite. A detailed summary of early studies in this subject is given by Orton (1928b). Orton et al (1956:161) note '...the smaller sizes of limpet in which sex can be determined are almost entirely male, while the larger sizes are predominantly female'. In samples from Aberdeen, Millport, Port St. Mary, Trevone and Plymouth, individuals less than 10 mm shell length were nearly all neuter (a total of 419 were neuter and 13 were male), but between 16 mm and 25 mm shell length, at all localities, there were at least 90% males. Around 40 mm shell length the two sexes were approximately equal in number, while 60-70% of limpets of 60 mm were female (Orton et al 1956:161).

Confirmation of this pattern comes from Blackmore (1969a) working at Robin Hood's Bay. Using age groupings he concluded that the first year P. vulgata were neuter, the second year male and the third year largely male with some female. After the third year females formed an increasingly greater proportion of the population, and by the fourth year there were about equal numbers of males and females. The fact that in both studies there were some males in the oldest age group suggests that some male limpets never change sex. In neither study was there evidence to suggest that the greater incidence of females within the larger size groups may be a result of differential growth rate between the two sexes.

Ballantine (PhD thesis, 1961, quoted in Thompson 1979), studying four diverse populations, noted that first year P. vulgata were immature, and in the third year they were all males. Females appeared at four years old, and about half the males changed to females between three and six years old. These results differ to those of Blackmore where there was an earlier appearance of females.

It was thought that there was no sex change in P. aspera (Dodd 1956; Fretter and Graham 1976) but Thompson (1979) has produced evidence to indicate that P. aspera is in fact a protandrous hermaphrodite like P. vulgata. In Bantry Bay P. aspera were neuter below a shell length of 13 mm to 20 mm and female P. aspera were not found at lengths below 18 mm. The proportion of male P. aspera was greatest at lengths of around 20 mm, where they comprised about 60% of the overall population and nearly 100% of the mature limpets. The proportion of females steadily increased from 18 mm to 55 mm shell length, ultimately comprising 40% of the overall population or nearly 70% of the mature limpets.

When converted by Thompson into age groupings this sample reveals that all the limpets were immature in their first year, but the proportion of immature individuals then declined, reaching zero in five year old limpets. Males were first evident in two year old limpets forming 7% of the total, but the proportion increased to 78% in the five year old animals. Females first appeared in three year old limpets and reached 47% of the total population in six year olds.

Although there is a slight variation in timing of maturation and sex changes, both P. vulgata and P. aspera exhibit a general developmental pattern. In both species the first year old limpets are immature, the proportion of these then declines and males are first evident in either the second or third years. Females then appear in either three or four year old limpets and are the dominant sex for the older limpet populations.

Although the indications are that P. aspera is a protandrous hermaphrodite it is possible that these changes could be due to a later maturation, faster growth rate, and longer life in females. For conclusive proof of sex change oogenesis must be observed in animals known to be, or to have been, male. This has been done for P. vulgata and P. coerulea but has not yet been attempted for P. aspera (Thompson 1979).

The ability to spawn successfully and for spat to settle and develop on the shore governs the geographical distribution of P. vulgata and P. aspera (Bowman and Lewis 1977; Vader 1975). The northern limits of P. vulgata occur in north Norway (Fretter and Graham 1976; Vader 1975). Vader notes a northward extension of this species on the island of Skjervøy between 1933 and 1973. During this period the only environmental factor known to have changed is sea temperature, which has become warmer. This supports the idea of increased recruitment failure with latitude (Bowman and Lewis 1977). The same authors suggest that the lower temperatures may cause incomplete gonad development in some years, thus causing spawning failure. A one year study (Bowman and Lewis 1977) showed that in 1974 gonads ripened 6 to 8 weeks earlier in north Norway than at Robin Hood's Bay in north Yorkshire, so this could indicate an adaption to cooler conditions thus avoiding incomplete gonad development. Further research is required here, but on present evidence it seems that the effects of low temperature on newly settled spat is the main deciding factor in the northward extension of P. vulgata.

In northern Norway P. vulgata is the only limpet present, yet it is joined in south-western Norway and north-eastern Scotland by P. aspera, and in north Wales by P. intermedia. Continuing southwards, P. vulgata becomes progressively subordinated by these two species towards its southern limit in south-west Portugal, and also has to compete with P. coerulea and P. lusitanica (Bowman and Lewis 1977). In south-western France P. vulgata is mainly restricted to tidal levels above the other species (Evans 1957), which indicates that it suffers increasingly from competition towards its southern limits. Other Patella species living at lower tidal levels are better able to tolerate the high temperatures. Throughout its range P. aspera occurs at low tidal levels, so it has an advantage, in the avoidance of desiccation, over P. vulgata. Near the southern limit of their range all Patella species avoid the open rocks more exposed to the sun, and concentrate at lower tidal levels and in damp microhabitats. These microhabitats, suitable for spat settlement, become rarer nearer the southern limits.

Patella species therefore exist within environmental tolerance limits governed by extremes of temperature, and the associated factors of desiccation, reproductive success and spat settlement, and competition.

3. Periwinkles and dogwhelks

> 'The common periwinkle, Littorina littorea (L.), is found where conditions are favourable around the entire British coastline except perhaps in the Isles of Scilly..... It is rare or absent on shifting substrata of shingle and unconsolidated sand, does not appear to favour rocks of chalk and limestone or shores exposed to the full force of storm waves...., and is most abundant on sheltered stony or rocky

> beaches. Periwinkles are often taken in the dredge below tide marks...., and it is probable that some individuals are permanently submerged throughout life. L. littorea is, nevertheless, characteristically intertidal in habit'.
> Smith and Newell 1955:35)

> 'The common Dog-Whelk of North Atlantic rocky shores, Nucella lapillus (Gastropoda : Muricidae), is a slow-moving carnivorous snail feeding mainly on barnacles and mussels. There is no planktonic dispersal phase in the life cycle and as the species is usually restricted to the intertidal zone and does not crawl over sand or mud it has formed innumerable, discrete, breeding units around coasts'
> (Crothers 1977a:181)

Dogwhelks are commonly referred to as Nucella lapillus, though in older literature 'Nucella' is replaced by either 'Purpura' or 'Thais'. Both periwinkles and dogwhelks have a wide geographical distribution. Moore (1936) reports Cooke's study of dogwhelk distribution. On the east side of the Atlantic the dogwhelk extends from the west coast of Spain and Portugal along the coasts of France, the British Isles, Belgium and Norway to the Murmansk coast and to one locality, its extreme northern limit, in Novaya Zemlaya (a large island dividing the Barents Sea and Kara Sea, northern Russia). It is absent from the Mediterranean, the Baltic and the White Sea, Spitzbergen and Jan Mayen Island, but occurs in the Faroe Islands and on the west and south coasts of Iceland. It is absent from the east coast of Greenland, and possibly also from the west coast. In North America it extends from the southern coast of Newfoundland to around New York.

No such detailed distribution study has been attempted for periwinkles. Bigelow and Rathbun (1903) tell how the species was introduced into Nova Scotia and New England in the 1850's. Campbell (1976) gives the species' very general distribution as the Mediterranean, Atlantic, English Channel, North Sea and western Baltic.

Both these snails inhabit the major part of the intertidal zone though only rarely do they extend above EHWN. Both have been recorded as occurring sublittorally, though in very low densities. The lower mid tide zone is most favoured. Being mobile species their distributions are not constant, though definite patterns do exist. Unlike limpets there are no morphological changes vertically up the shore, but dogwhelks do show morphological differences on different coasts. On most exposed shores dogwhelks are relatively short with a large aperture, and on most sheltered shores they are larger and the aperture is smaller.

Periwinkles are browsing omnivores (Hayes 1929; Williams 1964), feeding mainly when covered by the tide or in damp situations (Newell 1958a; Williams 1964). They will eat virtually any species of algae and any attached diatoms and other microscopic organisms. Dogwhelks are carnivorous and eat mainly barnacles and mussels (Bayne and Scullard 1978b; Connell 1961a, 1961b; Feare 1970a; Hughes 1972; Largen 1967a, 1967b; Moore 1936, 1938b; Morgan 1972a, 1972b).

An examination will now be made of aspects of seashore ecology applicable to an understanding of the exploitation of intertidal communities as part of the seasonal round of a gatherer-hunter population. Most emphasis is placed upon the value of limpets as an exploitable resource, but consideration is also given to both periwinkles and dogwhelks.

B. LIMPET POPULATION DYNAMICS

1. Reproduction and Recruitment

In any ecological study involving species population dynamics, the period of reproduction, and the timing of subsequent developmental stages, form a vital cornerstone to population structure at any moment in time. Table 3 indicates spawning times at different localities in the British Isles. The work of Orton et al (1956) shows that spawning usually occurs between September and late November. Subsidiary spawning may take place at any time between September and June. From around January to June the gonads pass into a resting phase, and from June the gonads develop prior to spawning.

The 'mean gonad index' of Orton et al (1956) has been used by others to monitor the reproductive cycle (Blackmore 1969a; Bowman and Lewis 1977; Lewis and Bowman 1975; Thompson 1979, 1980). Stage five represents a fully ripe gonad condition and below stage one the individual is in neuter state. Thus the index rises as gonads develop prior to spawning, and falls again once spawning has occurred. Neuter stages are never present during the period of maximum ripeness, nor are stages four and five present when the index is at its lowest.

Observations by Bowman and Lewis (1977) at Robin Hood's Bay between 1969 and 1974 have shown that (except for 1974) the level of maximum ripeness has been relatively constant at around level four, but its timing has varied by up to six weeks. For most years there was a sharp spawning fall in the index in October or November, followed by a steady decline into the resting phase. In 1969 and 1973 there were small index falls in September, then a re-ripening, and main spawnings occurred some weeks later.

Also in Robin Hood's Bay, Blackmore (1969a) records slight variation in the stages of sexual development over the two study years of 1965 and 1966. The emergence from the spent (neuter) condition began during the summer (August 1965, July 1966) and the larger limpets reached a peak of sexual maturity around three months later (November 1965, September 1966). As with the observations of Bowman and Lewis

TABLE 3 : THE SPAWNING PERIOD OF PATELLA VULGATA AT SEVERAL LOCALITIES

Location	Reference	Year	Date spawning began	Date most of sample spawned
Aberdeen	Orton, Southward, Dodd (1956)	1947	9 Sept to 17 Oct	19 Jan 1948
		1948	7 Sept to 10 Oct	6 Dec
St. Andrews		1948	17 Sept to 18 Oct	2 Nov
		1952	21 Sept to 27 Sept	4 Oct
Millport, Isle of Cumbrae		1947	1 Oct to 18 Oct	9 Dec
		1948	30 Sept to 2 Nov	2 Nov
		1949	10 Aug to 3 Sept	24 Nov
Port St.Mary		1947	6 Oct to 22 Oct	20 Nov
Isle of Man		1948	24 Sept to 13 Oct	13 Oct
		1949	5 Sept to 17 Oct	23 Oct
Trevone, N. Cornwall		1947	17 Sept to 11 Oct	14 Nov
		1948	30 Aug to 13 Oct	13 Oct
		1949	10 Sept to 19 Sept	4 Nov
Plymouth		1947	6 Oct to 3 Nov	16 Feb 1949
		1948	1 Sept to 14 Oct	21 Dec
		1949	12 Oct to 27 Oct	27 Oct
Bantry Bay	Thompson (1980)	1972	27 Sept	22 Nov
S.W. Ireland		1973	31 Dec	25 Feb 1974

(1977) maximum ripeness remained at level four. After spawning the population regressed to the spent condition over a period of three to six months, where it would remain until the beginning of the next cycle of sexual development. No difference in sexual development was discovered between low and high shore limpets. The reproductive cycle of limpets at Robin Hood's Bay has therefore been documented for 1965, 1966 and between 1969 and 1974, over which time most spawning has occurred between September and November.

On the eastern Scottish coast Jones et al (1979) found that there were 'good' and 'bad' years in terms of gonad production. For instance in two years no animals were observed with gonad indices greater than stage two, yet in another two years they reached stage five. They postulate that these variations could be due to the quality of feeding conditions in the spring.

Bowman and Lewis (1977) consider that once the majority of gonads have reached maximum ripeness, spawning is triggered by onshore gales and heavy seas. There is a good relationship between such conditions and spawning time over the whole study period. Although limpets are physiologically prepared for spawning at around the same time every year, the actual event is governed by the weather. For instance Bowman and Lewis note that the winter of 1972/1973 was remarkably storm-free, so a severe gale in April 1973 produced the only 100% neuter condition in seven years.

Orton et al (1956) observed the main period of spawning at Trevone in 1947 to be between 21st October and 4th November, by which time 80% of P.vulgata had spawned. This coincided with some very strong winds. At Port St. Mary in the same year the main spawning period was from 22nd to 25th of October when the wind was again strong. At St. Andrews in 1952 high winds between 21st and 27th of September meant that the whole population was spent by 4th October. In 1948 at Trevone most spawning occurred between 24th September and 13th October, a period of almost continuously high winds in this area. At Plymouth, however, winds were less and spawning occurred gradually over a longer period.

In Bantry Bay Thompson (1980) has shown that between 1972 and 1974 there has been a yearly variation in the main period of spawning intensity depending on the occurrence of storms. In 1972 the spawning pattern at Robin Hood's Bay and Bantry Bay was almost identical, with spawning occurring between late September and mid November. In 1973 the patterns were quite different. At both locations there was a small index drop during September gales, but at Robin Hood's Bay this was followed by the main spawning in early October, and in Bantry Bay this did not occur until early in 1974.

It seems that spawning is synchronous throughout a population during storms, yet in calmer weather spawning is more gradual throughout the population. If the weather is very calm it may not occur until a stormy stimuli is provided. The spawning stimuli of rough seas would be enhanced during neap tides, when the smaller tidal range and slower movement would prolong this influence on the limpet habitat.

The reproductive cycle of P. aspera has been studied in much less detail than that of P. vulgata, but certain features are nevertheless clear. In general P. aspera mature and ripen one or two months before P. vulgata. Maturation of the gonads begins in May-June and spawning occurs around late September or early October (Orton 1946; Orton et al 1956; Thompson 1980). As in P. vulgata spawning appears to be triggered by gales. Thompson (1980) shows this to be the case in Bantry Bay during 1972 and 1973. In 1972 this population was fully mature by early September but did not spawn until the first strong storm at the end of October.

Settlement

The free-swimming limpet spat settle on the shore when they reach a length of around 0.2 mm (Smith 1935), and experiments by Dodd (1957) indicate that settlement occurs ten days after fertilization. Limpets of this size are not easy to study on the shore, so data on the first month or so of limpet life are very tenuous. About six weeks after spawning the spat, still less than 1 mm in length, become more easily detectable on the shore.

The extent of settlement on any part of the shore is governed by four main factors: the physical nature of the site, the presence and density of other species, the density of existing limpets, and temperatures just after spawning.

Limpets on the upper shore have to withstand longer periods out of the water, so desiccation effects are more pronounced. By the time the young are large enough to be seen, those on the upper shore are generally restricted to wetter, more hospitable microhabitats such as crevices in the rocks (Lewis and Bowman 1975) and pools (Jones 1948; Orton 1929). It seems unlikely that these locations are selected by limpets in the settling stage when tidally submerged, so we may assume that this distribution reflects early mortality of spat that settle on open, more quickly-drying surfaces. On the lower shore, also, some habitats are more favourable than others, with the open rock surfaces being drier and more exposed to wave action than more sheltered depressions. Thus at both high and low shore levels when the spat first become visible on the shore they are clustered in more favourable areas, and thinly distributed or non-existent on drier, more exposed, rock surfaces.

The presence and density of other species also affects the survival chances of the newly settled spat. Observations by Lewis and Bowman (1975) on the more visible 1-2 mm juveniles indicates that the presence of a light density of mussels, barnacles and algae provides an ideal habitat for spat settlement. The damp sheltered patches between and within mussel colonies are the most highly favoured habitats, though for these to exist the colonies must not be too dense. Areas with more than about 70% continuous mussel cover usually have a low limpet density (Lewis and Bowman 1975:171). A light, scattered and patchy barnacle cover also provides a degree of dampness favourable to spat settlement, though the moisture retention value of such areas is not usually as high as with a broken mussel cover. A high density barnacle cover inhibits settlement. Limited amounts of *Fucus*, especially during the initial stages of colonization, reduce desiccation in the mid and upper shore levels and assist settlement, but a heavy perennial cover has either a screening or dislodging effect.

The influence of other species on spat settlement is therefore two-fold; a light covering of mussels, barnacles or Fucus provides shelter and a moister microhabitat for settlement, yet competition for space inhibits settlement when the species cover becomes too dense. The creation of favourable habitats is of greater importance on the upper shore where desiccation effects are more pronounced. These microhabitats are not stable over long periods of time, due to continually changing species population structures. The effects of this dynamic environment are given detailed consideration below in an examination of limpet distribution patterns on the shore.

The presence of other limpets may hinder spat settlement. Lewis and Bowman (1975) removed a patch of existing limpets and observed that spat settlement was much greater than in an adjacent control area. They conclude, along with Branch (1971) studying South African limpets, that the browsing of adult limpets destroys juveniles less than 1.5 to 2 mm in length.

Bowman and Lewis (1977) produce evidence to indicate that low air temperatures in the first few weeks of spat settlement can cause high mortality. At Robin Hood's Bay during the three seasons of poor settlement (1967/ 1968, 1971/1972 and 1972/1973) frosts occurred within four or five weeks of spawning. Frosts during the planktonic phase would have no effect on the spat, the critical period would be around, and just after, the period of settlement. In the four good settlement seasons at Robin Hood's Bay there was only one (1970/1971) with a slight frost, and this occurred on a night of high spring tides which protected the shore over the crucial time. Bowman and Lewis (1977) consider it improbable that severe frosts could cause complete recruitment failure, because some spat would be more sheltered. Rarely, if ever, do all limpets on a portion of shoreline spawn on the same day, and along an irregular shoreline the spawning stimulus of onshore waves would not affect every part of the beach at the same time.

Recruitment success is therefore dependent upon the chance interval between spawning-storms and frosts. For the highest probability of successful settlement the following sequence is beneficial: early ripening of gonads, followed by heavy seas as soon as the gonads ripen to promote spawning around late September or early October, and a period of a few frost-free weeks after settlement. Of these the latter is the most important, but the preceding events enhance the benefits of this frost-free period. Bowman and Lewis (1977:805) consider '...desiccation to be the predictable factor setting the initial distribution pattern, and frost mortality the main but irregular event that reduces the numbers of spat within this pattern'. They show how sites on the upper shore suffer less from frost-induced spat mortality than lower sites. This is probably because on the higher shore sites spat which have survived early desiccation because of their protected positions are also somewhat protected from frost. The lower shore spat on more open, damper sites are less subject to desiccation but more likely to suffer frost mortality. At very low levels the short period of emersion would provide protection against desiccation and frost.

Further south the effect of frost on spat is either lessened or of no importance. Here the effects of desiccation increase, so increased insolation reduces the number of protected microhabitats suitable for survival of newly settled spat in the autumn, and increases the death rate by desiccation of those that survive into the next summer.

Both Bowman and Lewis (1977) and Thompson (1979) consider that substantial variation in recruitment success can exist on any one site, but when all the survey results from different spat settlement habitats on a shore are combined there is little evidence of widespread annual fluctuations in recruitment.

2. Mortality

The only serious attempts at relating mortality to population structure are those of Lewis and Bowman (1975) and Thompson (1980), with mention being made of the problem by Feare (1971b), Lewis (1954) and Thompson (1979). An assessment of mortality rates is only possible after an understanding of migration patterns. 'The main difficulty in assessing mortality is that individuals may migrate away from the marked site but do not necessarily die' (Thompson 1980:182). Careful marking of individuals can help overcome this, though there is always scope for error in that the mark may be removed or covered in algae, or the individual may migrate to an area where it is not found. Such errors may be minimized in larger limpets, but an assessment of juvenile mortality is open to more problems. This is inextricably bound up with the recruitment process, and is complicated by differences between populations in the time of emergence, and also immigration and emigration.

Both Lewis and Bowman (1975) and Thompson (1980) note a relationship between specific types of sites and limpet life-spans. It appears that on wet sites, where spat settle directly onto the shore where they are to develop (termed direct settlement sites), there are a large number of settling spat and also high mortality of both spat and juveniles. On dry sites however, where spat do not settle directly but migrate in from damper microhabitats (termed late emergence sites), there are a smaller number of juveniles, and a lower mortality rate. This pattern is explained by the death of newly settled spat on the drier areas. Development of the surviving spat takes place in favourable microhabitats, from which they emerge when they are able to stand the rigours of this environment; hence the relatively low juvenile mortality. In areas of direct settlement the effects of desiccation and/or frost occur over a longer period of time than simply the first few hours after spat settlement, hence the higher juvenile mortality.

It is reasonable to assume that for the young limpet the most dangerous time is when it moves from its initial damp habitat to its drier adult home. It is now more likely to suffer from desiccation and frost. Experiments at Robin Hood's Bay (Lewis and Bowman 1975) have shown that following direct settlement on low level bare rock sites, mortality was initially high and then decreased, until by the third year the population had stabilized. At the other extreme a dry, high level barnacle site did not reach a peak in juvenile numbers until the end of the second year, after which time mortality was much more gradual than in the former site.

There is a relationship between growth rate and mortality, the highest mortality occurring where growth is fast or moderately fast, that is on low shore bare rocks or among the damp scattered mid-shore mussel and barnacle patches. In the faster growth, direct settlement, higher mortality site the maximum life-span is only 4 to 5 years, whereas in the site of slower growth, late emergence and lower juvenile mortality, the maximum age is around 9 years, though some individuals on this site may have lived to 12 or 15 years (Lewis and Bowman 1975:185)

There are a number of possible causes of post-juvenile mortality. Desiccation is still effective, though to a much lesser extent than for younger limpets. In a study of South African limpets Branch (1974) considers that mortality in old limpets may result from their inability to repair the edge of the shell. They therefore cannot then maintain a close fit with the rock, and they become vulnerable to predation and desiccation. Mechanical destruction by movement of boulders and stones during storms has been observed (Lewis and Bowman 1975). Biological agencies may also cause mortality. For instance in the case of heavy mussel settlement all but the largest limpets would succumb to either the weight of attached mussels or the lack of grazing space. Lewis and Bowman observed a few empty limpet shells firmly held by over-grazing barnacles. This could only occur when the limpets were alive, and then encroached upon by a fast-growing barnacle colony. The same authors also report limpet declines after invasions of Asterias (Common Starfish) on the lower shore. Although the dogwhelk (Nucella lapillus) preys mainly upon mussels and barnacles (Barnett 1979; Bayne and Scullard 1978; Largen 1967a) it will very occasionally kill a limpet. Thompson (1980) reports finding limpet shells drilled by the dogwhelk. (Dogwhelks drill through the shell, using both chemical and mechanical means, then devour the contents.)

Feare (1971b) reports how limpets are commonly taken by oystercatchers (Haematopus ostralegus). In fact this is the main limpet predator. His studies at Robin Hood's Bay indicate the methods employed by the oystercatchers to remove limpets from the rock. The birds pecked at the margin of the shell with the closed bill. This usually knocked P. vulgata off the rock, but the shell of P. aspera frequently broke, and the bird then inserted the bill into the fracture and levered the limpet off the rock. Once the limpet had been dislodged it was carried a short distance to a site where it could be supported while the bird cut around the adductor muscle (the muscle attaching the animal to the shell). Feare noted that the attacks were not aimed evenly around the edge of the shell, most were directed at the anterior end. The probable reason for this is that the adductor muscle is horse-shoe shaped, with the open end at the anterior, so this probably has the weakest hold on the rock. Oystercatcher attacks were more likely to be successful here than attacks elsewhere on the shell, though it is not known whether the birds go for the anterior, or whether it is simply these attacks that are successful. The latter is more likely as often it is not possible to tell one end from another.

Limpets on bare rock appeared to be more difficult for the birds to dislodge than limpets in pools. This is because in the latter habitat the limpets do not have to clamp down hard to avoid desiccation. Both on bare rock and in pools P. aspera was easier to dislodge than P. vulgata, probably reflecting the fact that the former species is concentrated at low tide level and in pools so again need not clamp down so tightly.

Feare discovered that the oystercatchers were selective about which limpets they chose to attack. There was a tendency to take the largest available limpets, and to take more P. aspera than P. vulgata. This is probably because large limpets gave the birds optimum return for the amount of energy expended, and P. aspera were easier to remove than P. vulgata.

The influence of oystercatchers on the limpet population will tend to be local and random, though if flocks concentrate on one area of shore the effects can be pronounced. Lewis and Bowman (1975:185) mention one marked site in a known oystercatcher feeding area which lost 81% of its limpets in the two months following the seasonal reappearance of the birds.

Limpet mortality is still not fully understood, especially in the youngest individuals. The various physical and biological agencies operate very locally and are extremely variable.

C. THE DISTRIBUTION OF LIMPETS OVER THE SHORE

There are three important factors which have a direct bearing on the distribution of limpets over the shore. Firstly there are the two interrelated features of degrees of exposure and the strict tidal zonation of P. vulgata and P. aspera on the shore, and secondly there are the effects of desiccation on limpets at different tidal levels. Thirdly there is the extent to which the animals move around the shore.

1. Exposure and the influence of tidal level

Exposure to wind and waves varies from coast to coast and between areas of differing morphology on the same small section of shore. 'Wave action on the shore varies greatly even over quite small distances. Some shores are almost landlocked, so sheltered that no waves larger than ripples ever reach them, while others are buffeted on most days by great rollers on the breaking swell from storms far out to sea. Every kind of intermediate condition exists between these extremes' (Ballantine 1961:1). A variety of attempts have been made to measure degrees of exposure. Moore (1935) used the number of days per hundred days in which any wind blew into the area over more than three miles of sea, and Southward (1953) measured splash heights above known tidal levels under varying wind conditions. Ballantine (1961) developed an exposure scale based upon the presence, absence and interrelationships between different organisms on the shore, using the principle that different species require different degrees of protection from the physical environment. This has been developed and altered by others to suit different geographical areas (Crapp 1973; Crothers 1976; Dalby et al 1978; Lewis 1964; Thompson 1979, 1980). An exposure scale has also been developed, and widely applied, using the dogwhelk (Nucella lapillus). This is based upon the ratio of aperture length to total length, the ratio being smaller in areas of greater exposure (Andrews 1981; Crothers 1973, 1974, 1975a, 1975b, 1976, 1977a, 1979, 1980). The detailed mechanisms, merits and faults of these systems are not of immediate concern here; what is of relevance is the effects of these varying exposure gradings upon patterns of limpet distribution and abundance.

In examining the tidal positions occupied by P. vulgata and P. aspera some authors have made subjective references to exposure such as 'very exposed' or 'very sheltered' (for example Ebling et al 1962; Evans 1947a, 1947b, Lewis 1954, Orton 1929) whilst others have attempted to quantify exposure (for example Crapp 1973; Crisp and Southward 1958; Crothers 1976, Dalby et al 1978; Lewis 1964; Little and Smith 1980; Moyse and Nelson-Smith 1963; Thompson 1979, 1980).

Reports on the tidal limits of the two species indicate that there is variation in the vertical extent of both species from different areas of coastline. Table 4 summarizes these limits. It will be seen that there are variations in both lower and upper limits. These are due largely to degrees of exposure and the height of the splash-line, especially at the upper limit. Both exposure and a higher splash-line means that limpets can exist higher up the shore and still avoid desiccation. A higher splash-line may be the result of greater exposure, a steeper shoreline, or a combination of both.

In the majority of works mentioned in table 4 the authors note variations in the upper limits with exposure. For instance at Dale in Pembrokeshire Moyse and Nelson-Smith (1963) note how, on the more sheltered shores P. vulgata is scarce on open rocks above MHWN, but extends higher in areas of greater exposure. In the Plymouth region Evans (1947b) observed that P. vulgata occurs only to just below MHWN on sheltered shores, and those southward facing slopes more open to drying by the sun, yet as splash height increases P. vulgata are common to above EHWS.

Patella aspera is more numerous on exposed shores and is rarely found in shelter. Fretter and Graham (1976:28) quote it as constituting around 90% of the limpet population in heavily wave-beaten situations. At Dale the few specimens seen on sheltered and very sheltered shores existed only in rockpools (Moyse and Nelson-Smith 1963). Its upper limit rises with increased exposure. Around Plymouth it almost reached MTL on very exposed shores, yet on sheltered reefs it only extended to MLWN (Evans 1947b). In Bantry Bay Crapp (1973) recorded

TABLE 4 : VERTICAL TIDAL EXTENSIONS OF PATELLA VULGATA AND PATELLA ASPERA FROM DIFFERENT LOCATIONS ON THE COASTLINES OF THE BRITISH ISLES

AUTHOR	LOCATION	SPECIES	LOWER LIMIT	UPPER LIMIT (not including rockpools)
Crapp 1973	Bantry Bay	*P. asp.*		MLWN-sheltered, MHWS-exposed
Ebling *et al* 1962	Lough Ine	*P. asp.*	Shallow sublittoral	Sublittoral fringe
Evans 1947a	Cardigan Bay	*P. asp.*	ELWS	MLWN to MTL
Evans 1947b	Plymouth	*P. asp.*	ELW	MLWN to MTL
Fretter and Graham 1976	Generally	*P. asp.*	Sublittoral-ELW	Below MLWN
Moyse and Nelson-Smith 1963	Dale, Pembs.	*P. asp.*		MHWN - exposed
Southward and Orton 1954	Plymouth	*P. asp.*		MHWN
Crothers 1976	Somerset	*P. vulg.*	MLWS to MLWN	
Blackmore 1969a	Robin Hood's Bay	*P. vulg.*	MLWS	Just below MHWS
Das and Seshappa 1948	Cullercouts	*P. vulg.*	LWS	Just above HWS
Ebling *et al* 1962	Lough Ine	*P. vulg.*	Shallow sublittoral	Between MHWN and MHWS
Evans 1947a	Cardigan Bay	*P. vulg.*	ELWS	MHWS to above EHWS
Evans 1947b	Plymouth	*P. vulg.*	MLWS-ELWS	MHWN-EHWS
Fretter and Graham 1976	Generally	*P. vulg.*	ELWS	MHWN-MHWS
Little and Smith 1980	Severn Est.	*P. vulg.*	Just above MLWS	Just below MHWS
Moyse and Nelson-Smith 1963	Dale, Pembs.	*P. vulg.*	MLWS	MHWN
Southward 1953	Port St.Mary Isle of Man	*P. vulg.*	Just above MLWS	
Southward and Orton 1954	Plymouth	*P. vulg.*	Below MLWN	Below MHWS

it as being the dominant limpet on extremely exposed and very exposed shores where it was found to MHWS, and in rockpools at all upper levels. On more sheltered shores it existed only below MLWN.

Lower tidal limits are less directly affected by exposure, depending more upon competition between the two species, though no-one has tested the extent of competition by removing P. aspera and seeing if P. vulgata does extend further down the shore. Thompson (1979, 1980), Crapp (1973) and Fretter and Graham (1976) are of the opinion that P. vulgata will extend lower on less exposed shores than on the more exposed shores where P. aspera is more common and extends higher. P. aspera occurs down to ELWS and below into the shallow sublittoral.

Patella aspera has a much more well-defined vertical range than P. vulgata. For P. aspera the centre of this range may be defined as low shore in extreme exposure (Thompson 1979, 1980). 'The centre of the range for a limpet may be envisaged as that habitat where favourable environmental conditions and reduced interspecific competition permit the species to achieve maximum growth and fecundity' (Thompson 1980:210). Patella vulgata has no such central range, instead occupying a much wider area of shore. Thompson (1980) considers that the nearest it gets to a central range is MLWN in moderate shelter, as here growth rates are greatest, and there is high juvenile mortality so those that do survive have high growth and fecundity.

2. Desiccation

Desiccation plays a very important role in the vertical distribution of the two species. Davies (1969) has shown that for any body size, P. aspera loses water by desiccation at a faster rate than P. vulgata, and low level P. vulgata loses water faster than high level P. vulgata. He has also shown that high level P. vulgata had a greater tolerance to water-loss than low level P. vulgata, which in turn had a greater tolerance than P. aspera. The percentage water-loss at which all three groups survived was 24% for P. aspera, 44% for low level P. vulgata, and 60% for high level P. vulgata; whereas the percentage water-loss causing 100% mortality was 40%, 55-60% and 65% for the same three groups respectively. Within P. vulgata this represents an adaptation to the drier high-tide environment. The increased water-loss and lowest tolerance to any water-loss of P. aspera are probably the most important factors governing the upper tidal limit of this species.

With increased tidal level, the amount of desiccation experienced increases, whilst the time available for recovery decreases. The upper limit of limpet distribution on the shore is most likely therefore to be determined by an interplay between the amount of desiccation experienced and the time taken to recover when covered by the tide. For example, a limpet which had lost water equal to 20% of its body weight would need to be covered by the tide for about three and a half hours for full recovery (Davies 1969:303).

When the factors of speed of desiccation, tolerance to water-loss, size of limpet, and recovery time are all considered it may be seen that high tide P. vulgata live within more closely confined ecological limits than do low level P. vulgata or P. aspera. Out of these two low tide species the latter is generally more ecologically constricted than the former. However, if exposure to wave action is considered, increased exposure favours P. aspera over P. vulgata, especially at the lower levels. In greater shelter P. aspera is not protected from desiccation at mid and high tide levels, while at low levels the more flexible P. vulgata grows faster and replaces P. aspera (Thompson 1980).

3. Movements and migration around the shore

After the occurrence of spat settlement, emergence and migration from the settlement sites takes place at different times in different habitats. Little work has been done on this apart from brief observations by Bowman and Lewis (1977) and Lewis and Bowman (1975) in Britain, and Branch (1975) in South Africa. In drier sites measurements by Bowman and Lewis show an decrease in juveniles throughout the first year, suggesting that individuals most susceptible to desiccation are eliminated very soon after settlement. In the lower wetter sites most desiccation mortality appears to be delayed until well into the first year, when numbers may fall by up to 60% during summer and autumn. In the drier areas migration from settlement sites occurs in the first year, and it may be assumed that in lower sites there is a much broader pattern of spat settlement, so such migration periods are of less significance. In South Africa Branch noted substantial mortality of newly settled Patella granularis that had settled at MTL and below within two days, leaving only a few specimens at low level and in moist cracks. As their tolerance increased they were seen to move upshore to the drier areas.

The movement of older animals is easier to determine. Such movements are of two types; firstly there are small feeding excursions from the home base, and secondly there are sometimes migrations of longer distance to establish a new home base.

It has long been realized that most limpets return to a definable position after feeding excursions (Boyden and Zeldis 1979; Cook et al 1969; Davis 1970; Hartnoll and Wright 1977; Jones 1948; Lewis 1954; Orton 1928b, 1929, Punt 1968). At the home base the shell is often moulded to the contours of the rock partly by growing around the natural rock and partly through movements which, especially on softer rocks, create a limpet-shaped ring in the rocks into which it sits. This snug fit reduces water-loss. Orton (1929) and Jones (1948) concluded that, although some foraging occurred when the limpets were uncovered in conditions of shade or humidity, most took place when they were immersed at high water. Their conclusions were confirmed by observations on Oronsay. Experiments by Hartnoll and Wright (1977) on two sites at the Isle of Man showed that during darkness there was no significant movement, irrespective of tidal position. In daylight limpets began to forage when immersed. As soon as they got regularly wet by the incoming waves they began to move. They were at the maximum distance from home around the time of high water, and then returned home one or two hours before the area was uncovered again. On average only three quarters of the population fed at any one time. The greatest distance reached from the home base was 1.21 metres, and the mean distance was 0.41 ± 0.09 metres (Hartnoll and Wright 1977: 807).

Limpets in different areas have been observed feeding at different times. Orton (1929) summarizes the results of a number of observers, giving a variety of feeding times. Hartnoll and Wright report the experiments of Funke showing that movement is predominantly at night when limpets were uncovered at low tide, and they summarize the work of others on different limpet species, all with varying times of feeding. The only unifying feature is that there is one relatively long period of feeding each day, and to avoid desiccation feeding is either done during immersion or by night, and occasionally both. In a very detailed study of New Zealand limpets Boyden and Zeldis (1979) found that there was increased feeding with increased wave action, during both day and night.

Cook et al (1969), Davis (1970) and Punt (1968) examine the mechanisms by which limpets can return to their homes after a feeding excursion. These mechanisms need not concern us here, except to note that they probably involve the use of both chemical trails and some form of topographic memory on the part of the limpet.

Migrations to a new area of rock have been noted by Jones (1948), Lewis (1954), Lewis and Bowman (1975), Orton (1929) and Thompson (1980) to be most common on smooth damp surfaces. On uneven surfaces or amongst thick barnacles the limpet shell often grows to fit the contours of the rock, so must return to the same home base. If an area is cleared adjacent to an uneven surface, recolonizaton will take place, but not to such an extent as on more even, smoother rocks. At Port St. Mary, Jones (1948) cleared an area of shore and noted how, after 16 months, movement from the adjacent rock into the strip had been much greater from bare rock, particularly where there was scattered Fucus, than from barnacle areas. At Bantry Bay Thompson records how, at two wet low level sites (MLWN), very few limpets remained on a single home for a full year, and there was much movement within, and in and out of, the marked metre squares. In drier habitats there was less migration, and at two such sites (MHWN and MTL) over 50% of limpets remained in one place for the full year (Thompson 1980:183). The MTL site was on bare rock bordering fucoids, indicating that it is not just large numbers of barnacles, but the dryness of the habitat that limits limpet movement.

Lewis and Bowman noticed that in a barnacle area a majority of marked individuals remained in the same few metres of shore for 1 to 3 years. When space was made available by clearance, re-population did occur, especially when there were adjacent populations in clefts and pools. There was sufficient movement from the barnacle area to restore the original density in less than a year. Length-frequency analysis of the migrants indicated that they were of the same general size/age structure as the original population prior to clearing.

Lewis and Bowman were the first to note the high degree of migrant activity in May and June. On a few very humid days in these months most limpets had their shells raised from the rock surface, and many were seen to move when the tide was out. This remains unexplained.

In his studies of high tide limpet movement on a breakwater at Aberystwyth Lewis (1954) records significant migrations. This is a smooth hard surface where there are few visible home-scars. On this fairly steep shoreline there is enough splash to make this a damp habitat. Distinct vertical migrations were observed, with movements downwards in spring and upwards in autumn. Lewis interprets this as an avoidance of the more intense desiccation effects of summer. In this way the limpets are, during their wanderings, keeping themselves in approximately the same type of habitat with relation to desiccation effects. He also notes a marked upwards movement of smaller limpets from levels below the breakwater, presumably where they settled.

At Aberystwyth movements occurred in all directions. This dispersion was not a slow gradual process, but occurred in sudden 'dashes' of possibly several metres. The situation on this breakwater is a unique study in that the habitat differs from the average rocky coast. Such vertical movements have not been observed on other shores (which does not, of course, mean that they do not occur). The ease of movement over such a uniform surface is in many respects atypical, so care must be taken when applying these results to the natural shore.

Damp, smooth rocky shores do seem to provide for the highest degrees of limpet movement. Here it is less important for them to return to their home-scar because desiccation effects are less pronounced. At Port St. Mary, Jones (1948) marked 182 limpets on a smooth flat limestone rock just below MHWN. Most limpets were large, with a mean length of 40 mm, and were not scattered evenly over the rock, but occurred in clumps of from 10-30 individuals. In most cases there was a distinctly scarred home base, indicating that the animal had occupied the same place for some time. There was, however, much movement. Every week some limpets had moved, and after 6 months only 9 of the original 182 were still in their original areas. Most limpets only moved a few yards, but one animal moved 30 yards down the shore (Jones 1948:66) There was no obvious directional movement.

The main value of this experiment is that no clearance was involved. Providing cleared areas into which migrating limpets can move is certainly valuable to show the extent of migration. Such experiments are also relevant in that in any clearance by man there would be a replenishment of stocks providing there were adjacent uncleared areas. When interpreting natural populations it is interesting to see that, even when there is no mass clearance, there is still movement, though this is less in areas of dense barnacle cover, very uneven surfaces, and dry areas.

Conclusions

A variety of complex interrelating factors govern the zonation pattern of limpets. Exposure and desiccation tolerance affect both the vertical extent of occupation and the relative proportions of Patella vulgata and Patella aspera on a shore. The emergence from settlement sites and the migration of adults to another area are significant factors in changing zonation patterns over time, yet feeding excursions usually result in the limpets returning to a home base.

D. GROWTH IN LIMPETS

It is evident from a variety of studies that all limpets do not grow at a uniform rate (Blackmore 1969a; Choquet 1968; Fischer-Piette 1948; Hatton 1938; Jones 1948; Lewis and Bowman 1975; Orton 1928a, 1928b; Russell 1909; Thompson 1979, 1980). A number of factors have been shown to affect growth rates, and these will now be individually examined.

1. Growth rate in limpets of varying size

When studying the growth rates of Patella vulgata around Boulogne Choquet (1968) concluded that growth is more rapid in smaller individuals. He periodically measured marked limpets from the lower shore amidst patches of Fucus serratus at Crèche. Figure 3 shows the results. Curves A, B and C represent the growth of three groups of limpets of 10 mm, 13 mm and 15 mm shell length respectively. It may be seen that individuals of 10 mm reach an average of 26 mm after one year, and 39 mm after two years. Curves B and C are parallel to A for the first year of the experiment. Table 5 shows the similarity in growth rate of these three size groupings. Figure 3 and table 5 demonstrate that limpets over 15 mm show progressively less annual growth. For instance, individuals of 38 mm reach an average 42 mm after one year, and 45 mm after two years.

TABLE 5 : AVERAGE LENGTHS, AFTER 1 AND 2 YEARS, OF LIMPETS MARKED IN SUMMER (after Choquet 1968)

Initial length	10	13	15	21	25	31	38	41
Length after 1 year	26	30	30.5	36	38	40	42	44
Increase after 1 year	16	17	15.5	15	13	9	4	3
Length after 2 years	39	40	41	43	44	45	45	46.5
Increase after 2 years	13	10	10.5	7	6	5	3	2.5

At Robin Hood's Bay Blackmore (1969a) also noticed a reduction in growth rate with size. He examined growth rate after settlement beginning in 1964. In 1965 the first year limpets had increased by 2 mm per month, the second years by 1.5 mm per month, and the third years by 1.2 mm per month. After five years he found identification of the component populations impossible.

Russell (1909) observed that in limpets at Gourock the rate of growth decreased with increased size. He concludes that between 10 and 25 mm shell length there is a gradual and uniform reduction in the rate of growth. Between 25 and 30 mm there is a sudden fall in the growth rate to little more than half what it was at 20-25 mm. There is then another gradual decrease up to a length of around 50 mm.

2. Seasonal growth

Choquet (1968) discovered distinct seasonal growth patterns at Crèche. Figure 3 curves A to H show that there are active growth periods from spring to early summer and in early autumn. There is slower growth during the later summer and a noticeable decrease during the winter. Even amongst the largest limpets there is still some winter growth, though it is barely perceptible. During the course of the next annual cycle similar variations are evident, but the total growth is less in the second year.

In Plymouth Orton (1928b) obtained similar results to those of Boulogne. In limpets up to 25 mm he found growth to be continuous throughout the year, being fast in spring, slower in mid-summer, fast again in autumn and very slow in winter. In older animals he noted that growth may stop in the winter. In Devon he observed regular shell growth from February to June followed by a reduction of growth in July and early August, and a resumption of growth at the end of August continuing through the autumn (Orton 1928a).

Blackmore (1969a) documented seasonal growth at Robin Hood's Bay of limpets directly after settlement from 1964 through to 1966. During the first six months after settlement (around January) growth was steady and relatively slow (0.40 mm per month in 1965 and 0.55 mm per month in 1966). By June the mean shell length was around 4 mm. Between June and October these first year limpets showed a marked increase in growth rate (1.28 mm per month in 1965 and 2 mm per month in 1966). After October the growth rate was again reduced to give a mean length by December of 9.5 mm, 11.5 mm and 9.8 mm in 1964, 1965 and 1966 respectively (table 6). Growth continued at a reduced rate throughout the winter at 0.13 mm per month in 1964-65 and 0.12 mm per month in 1965-66. After April the growth rate again increased. By the end of the second year these two populations had mean shell lengths of 17.8 mm and 16.7 mm respectively (table 6).

Russell (1909) found increased summer growth at Gourock. First year limpets were found to increase by 3 mm per month between June and August, 2.2 mm per month during September, 1.1 mm during October, 0.6 mm during November and 0.7 mm during December. The same general pattern was followed by second year limpets though at a reduced rate.

Southward and Southward (1978) monitored the re-colonization of the West Cornish coast after the ecological holocaust caused by the Torrey Canyon oil spillage and the subsequent application of toxic dispersants in 1967. They discovered that, by the second year, the 1967-68 settlement of spat had reached 12 to 14 mm shell length, and that they reached 40 mm by their third year, after which time there was virtually no growth. This study is, however, atypical as it records growth after virtual habitat destruction. The authors note that once fucoids became established initial growth was more rapid. Indeed, the development of fucoids probably explains the fast growth of these limpets after their second year.

3. The effects of temperature upon limpet growth

From the above observations on growth patterns, especially those in the winter, it will become clear that geographical location affects growth. It is highly probable that temperature is the controlling variable here. Table 6 shows that Robin Hood's Bay, in the relatively cool north-east of England, has much lower growth than other sites in milder areas. Here mean winter temperatures may fall to around 5°C or below for up to 3 months (Feare 1970a:7). It is probable that winter

TABLE 6 : LIMPET GROWTH MEASURED FROM DIRECTLY AFTER SETTLEMENT

REFERENCE	LOCATION	SETTLEMENT DATE	SIZE AT END OF FIRST YEAR (MM)	SIZE AT END OF SECOND YEAR (MM)	SIZE AT END OF THIRD YEAR (MM)
Blackmore (1969a)	Robin Hood's Bay, N.E. England	1964	9.8	17.8	25 (ie original 1964 group)
		1965	11.5	16.7	
		1966	9.8		
Orton (1928b)	Plymouth	1912	26-35	53	
		1913	11-27	47-49	
Southward and Southward (1978)	Cornwall (after oil spillage so atypical situation)	1967-8		12-14	40
Choquet (1968)	Boulogne area		12-19	30-33	40-43
Russell (1909)	Gourock, S.W. Scotland			*c.* 38	*c.* 43-45

temperatures are more important than those of summer in restricting growth. Fischer-Piette (1941) and Hatton (1938) report growth to be very regular throughout the year in Brittany, with only a slight reduction in winter. Here the average winter water temperature does not go below 10°C (Choquet 1968:458). In the Boulogne area it falls to around 6°C, and here Choquet reports reduced growth rate in winter. Orton (1928b) reports a similar pattern of seasonal growth for Plymouth, where the sea temperature falls to around 8°C in winter (Choquet 1968:458). Both of these sites show a greater winter growth than Robin Hood's Bay. It is interesting to note that during 1912 Orton found limpet growth at Plymouth to be unusually great, and this coincided with an unusually warm year.

4. The effects of biological habitat upon limpet growth

One of the major controls on limpet growth is the biological habitat in which they live. An increase in food and low competition results in larger limpets, whereas reduced food supply and high competition cause the limpets to be smaller (Choquet 1968; Fischer-Piette 1948; Jones 1948; Lewis and Bowman 1975; Orton 1928b; Thompson 1979, 1980).

There appears to be a relationship between barnacle and seaweed density, exposure, and population density and size of limpets. Jones (1948) working at Port St. Mary demonstrated that the largest mean sizes occur on either exposed bare rock or on semi-exposed rock with a thin *Fucus* cover. Sheltered rocks with a thin *Ascophyllum* cover contain limpets of a smaller mean size, and exposed barnacle-covered rocks have the smallest limpets. These smallest individuals attain the highest density, while the larger limpets on the bare rock and under thick fucoids attain a lower density. In this study no mention is made of tidal level.

Jones considers that the limpets amongst barnacles have reduced feeding space so growth and maximum size are low. On bare smooth rock the density is low to medium, and freedom of movement is greater, so the feeding area and average sizes are large. Although these surfaces seem bare they do contain considerable food potential in the form of algal sporelings and diatoms. Amongst thick fucoids, with few barnacles, the density is usually low and the potential food plentiful, so the average size is reasonably high. Feeding area is probably restricted by the fucoid stems, so there is less available food than on bare rocks, with adjacent algae and fucoids.

Thompson (1980) relates variations in limpet size to biological habitat, exposure and tidal level in Bantry Bay. The most striking relationship here is on very sheltered shores at MTL where the largest animals were found on bare rock patches with some fucoid cover. On rocks with very dense fucoid cover, on bare dry rocks, and among barnacles also at MTL, mean lengths were smaller. The smallest mean size was found in limpets living among mussels and patches of densely packed barnacles.

Lewis and Bowman (1975) note significant differences in the size of limpets from the two extreme habitats of barnacle encrustation and bare rock and near *Fucus*. Mean length was between 19-21 mm in the former and 28-33 mm in the latter. When related to age these values become even more significant, because they are reached by 6 to 8 year old limpets in the barnacle areas and 3 to 4 year olds on the bare rock and near *Fucus*.

Figure 4 summarizes the growth rates in ten different habitat types at Robin Hood's Bay (Lewis and Bowman 1975). This clearly demonstrates the most favourable habitats, curves a to e being bare rock and curves f to j being barnacle dominated. It will be seen that a limpet of 20 mm shell length may be 2 or 3 years old if living in an optimum environment, yet 4 to 5 or 6 years old if living in a slow growth habitat.

Figure 5 shows the different growth rates of limpets on rock with *Fucus serratus* (curve A) and with barnacles (curve B) at two sites near Boulogne (Choquet 1968). It may be seen that growth is faster amongst the fucoids and is especially noticeable in summer and autumn. Choquet believes this is because of the availability of a constant food source at site A. He considers that limpets adjacent to fucoids have the greatest potential for growth. Fischer-Piette (1948) comes to the same conclusion from examinations of limpet growth rates in the St. Malo-Dinard area of Brittany.

The importance of food availability to limpet growth is demonstrated by Orton (1928b). Table 6 shows how there was rapid limpet growth on the new wharf at the Great Western Railway docks at Plymouth. Orton attributes this rapid growth to the ready availability of food (as well as to unusually warm weather in 1912 as mentioned above). The piles provided an optimal grazing environment.

After the Torrey Canyon oil spillage and the total habitat destruction caused by the use of toxic dispersants there was very rapid growth of limpets between their second and third years (table 6). Southward and Southward (1978) attribute this to the large quantity of available fucoids. Crapp (1971) monitored limpet populations after an oil spillage at Milford Haven, and found that directly after the death of the majority of limpets there was very high spat settlement followed by a period of extremely rapid growth. Crapp attributes this to the reduction of competition for food and space from other limpets, and the beneficial effect of a newly developed fucoid cover.

When comparing the growth rates of Patella vulgata and Patella aspera Thompson (1980) found that the latter were much less variable, probably reflecting their more restricted shore distribution. Figure 6 shows how a 20 mm long Patella vulgata may be between 1 and 6 years old, yet a Patella aspera of the same length would be between about 2 and 5 years old.

5. An example of limpet population structure

Length-frequency limpet population structure is considered by Lewis and Bowman (1975) with relation to biological habitats at different tidal levels. They emphasize that these are 'typical' situations based upon observations over four years, and are hypothetical in that they must assume a constant and average recruitment level for several consecutive seasons, and do not take account of possible varying mortality (see figure 7).

In most instances, at low tidal level there is a slight increase in the maximum length in any one habitat. The greatest variations occur between the two extreme habitats, high level barnacles and low level bare rock or near Fucus. The larger sizes on the right of these latter two diagrams are a result of fast growth in these favourable habitats. The probable explanation for the tri-modal pattern of one of the bare rock low level alternatives is very fast growth, low density and a short life-span. This is a rarer pattern than the other alternative where there are about 4 to 6 generations and size ranges greatly overlap. On high level bare rock the occurrence of juveniles depends entirely upon the presence of a suitable spat settlement niche, such as a damp crack in close proximity, from which the young can migrate. The high level bare rock area may receive its population by migration from lower levels, which results in a bias to older larger limpets. Both alternatives are shown.

In the barnacle areas patterns are generally unimodal due to the reduced growth rate, which tends to an overlap in length range of each year class. High tide dry barnacle areas are the least productive biological zones for limpet development, where the maximum size is smaller than elsewhere, irrespective of age. This results in an accumulation of the upper size categories. Where mussels are present with the barnacles the microhabitat remains moister and more favourable, resulting in more younger limpets and a slightly greater growth rate and maximum size. On the upper shore growth rates are slower and survival rates higher than in mid-tide levels, thus explaining the greater proportions of medium-sized limpets at these levels.

6. Are variations in shell growth evident from growth-rings?

Deith (1982) experimented to discover if seasonal growth rings could be used to age limpets, and concluded that they could not. The variations in growth within and between years, and the continued winter growth, mean that there is no annual marker from which to assess the remainder of shell growth. She concludes:

> 'If the variations both within and between shells are as great as this pilot study indicates, the value of growth-line analysis as a technique for assessing seasonality in this species is very limited. In fact, it offers no unambiguous information additional to what can be inferred from the surface topography of the shell'.
>
> (Deith 1982:31)

Conclusions

The extent of limpet growth is dependent on a number of factors:

1. Growth is more rapid in smaller than larger limpets, regardless of geographical location.

2. There are seasonal variations in growth rate which appear to vary with geographical location. Around Boulogne (Choquet 1968) and Plymouth (Orton 1928b) there were spurts of growth in spring and autumn with a reduction in mid-summer, and at Gourock Russell (1909) observed an increase in spring and early summer but he does not record any increase in autumn. At Robin Hood's Bay in north-eastern England growth was relatively even throughout the spring and summer, with no noticeable mid-summer reduction (Blackmore 1969a). It is possible that the active growth spurts only occur in warmer areas, though further measurements are required to substantiate this.

   Evidence to date indicates that reduced winter temperatures restrict growth. There is little slowing of growth in Brittany (Fischer-Piette 1941; Hatton 1938) where the winter temperature does not drop below 10°C (Choquet 1968). Around Boulogne and Plymouth it falls to about 6°C and 8°C respectively, and there is slower winter growth (Choquet 1968; Orton 1928b). All these sites show faster winter growth than Robin Hood's Bay.

3. The seasonal fluctuations in growth affect the age/size structure of the limpet population. Table 6 shows that at the end of each year limpets at Robin Hood's Bay are smaller than in other areas. (Limpets at Cornwall are also relatively small in their second year but this concerns recovery after total habitat destruction,

so is atypical.) Table 6 demonstrates that there is slower growth at Robin Hood's Bay especially in the winter. Although the data suggests that temperature is an important factor in growth, it must not be viewed in isolation. Localized biological habitats also affect growth rates. From this it must be concluded that it is only possible to reconstruct the very approximate age of limpets from their shell size.

4. Varying biological habitats cause varying growth rates. A plentiful supply of food and minimal competition provide the optimum growth habitat. These are either on bare rock (where there are in fact many small algae) (Jones 1948; Lewis and Bowman 1975; Thompson 1980), or amidst fucoids (Choquet 1968; Fischer-Piette 1948), or ideally on bare rock adjacent to fucoids. The larger fucoids are grazed by the adult limpets but they are not conducive to settlement of young limpets. At the other extreme, a dense barnacle cover restricts limpet growth (Choquet 1968; Fischer-Piette 1948; Jones 1948; Lewis and Bowman 1975; Thompson 1979, 1980).

Thus, taking these variations into account, it is evident that it is only possible to get an approximate idea of limpet age from the size of the animal. The more that is known about the area inhabited by the limpets, the more accurate this prediction may be. Deith (1982) has concluded that it is not possible to use growth-rings to age limpets.

E. THE PHYSIOLOGICAL ECOLOGY OF LIMPET BODY AND SHELL DEVELOPMENT

Throughout the thesis reference will be made to relationships between the flesh and shell of limpets. To allow these relationships to be placed in perspective a basic knowledge is required of the physiological ecology of both body and shell development. Attention will be focussed on two areas: the physiological differences separating low and high shore P. vulgata and P. aspera, and the development of the shell.

1. Physiological differences within Patella

Metabolic differences have been investigated both between low level and high level P. vulgata and between low level P. vulgata and P. aspera (Davies 1966, 1967, 1969, 1970). Metabolic rate is a good indicator of internal state during environmental change because it reflects all energy transformations taking place within the animal.

Davies (1966) concludes that there is very little difference in the respiratory rate of the three limpet groups in January, but in July low level P. vulgata and P. aspera have a greater respiration rate than high level P. vulgata. This latter group has essentially the same respiratory rate in January as in July, but in both low level P. vulgata and P. aspera the respiratory rate is higher during July than in January. 'It is apparent therefore that the summer differences between the L.W. P. vulgata and P. aspera, and H.W. P. vulgata were brought out by the increase in respiratory rate of the former, whilst the rate of H.W. P. vulgata did not change from the low winter level' (Davies 1966:654).

This pattern is probably a result of temperature acclimatisation. In winter, the environmental temperatures of the three groups are quite similar, hence the similar respiration rate. In summer, however, high level P. vulgata are subjected to higher temperatures (due to a longer period of time subject to direct insolation), so it is possible that the low respiration rate is a response to this.

P. aspera was found to have a lower heat tolerance than P. vulgata. Whereas P. aspera showed the beginnings of heat stress at 30°C and heat coma at 35°C, P. vulgata respired freely at 30°C and had a slower but nevertheless regular respiratory uptake at 35°C (Davies 1966:652). High shore limpets have had body temperatures of 36.8°C on a hot day (Davies 1970:1076). Although this is below the lethal limit of 42°C determined by Evans (1948) and 41.5°C determined by Grainger (1975), Davies considers that on a very hot day the lethal temperature could be reached. When examining body temperatures for a whole tidal cycle (ie from high tide to high tide), Davies (1970:1074) calculated a mean temperature of 24.5°C for high level limpets and 13.6°C for low level animals. This was done on a hot day, the difference would be less in cooler temperatures.

Although such temperature acclimatisation may be one explanation for the differences in respiration rate, Davies (1966) considers that if it was the only important factor the respiration rate of all three groups in summer might be expected to be lower than in winter. He believes that the availability of food is another important factor. At high levels there is less available food than at lower levels, both because of the reduced fucoid density and as limpets feed mainly when covered by the tide. To test this idea populations of P. vulgata living in areas with abundant algae were compared with populations living on bare rock at the same tidal level (Davies 1967). In both March and July (the two sample months) at both high and mid shore level, those limpets living in close proximity to algae had the greater rate of respiration. Also, going from low, through mid to high tide populations there was a successive decrease in respiration rate as time available for feeding decreased.

Due to the fact that limpets from higher levels are subjected to higher temperatures, food would be metabolized at an increased rate, and the total amount oxidized during one tidal cycle would be greater. The low respiration rate is therefore an adaptation to conserve energy.

Proof that the observed metabolic changes are phenotypic adaptations to specific environments and not genotypic selection was obtained by Davies (1967) by moving high shore *P. vulgata* to low levels and vice versa. After three months a complete reversal of the interpopulation differences had occurred, with the transplanted high level *P. vulgata* increasing their respiration rate and the transplanted low level *P. vulgata* decreasing theirs.

Such a compensatory mechanism is probably absent in *P. aspera*. Davies (1967) postulates that a *P. aspera* living on the upper shore would be unable to limit its metabolic expenditure, and might starve in the summer by oxidizing its assimilated metabolites faster than they could be replenished by feeding.

It seems that much of the metabolic change may be related to the reproductive cycle. In November the respiratory rate of low level limpets of both species decreases, thus making it lower than high level *P. vulgata* (Davies1967). It is around this period that most limpet populations have just completed spawning. This is accompanied by a general loss in body weight (Blackmore 1969b; Jones *et al* 1979) so the reduction in respiration rate must reflect this general slowing down of bodily functions. Sometime around January the metabolic rate of both low level *P. vulgata* and *P. aspera* began to increase, probably because of an increase in growth during the spring (Davies 1967). It is still not clear why this does not occur in the high shore *P. vulgata* though it is probably a response to the more rigorous environmental conditions of this habitat.

It appears therefore that physiological differences within *P. vulgata* are phenotypic adaptations to specific environments. It is probable that low level *P. vulgata* exhibit the 'normal' metabolic behaviour and the upper shore individuals are adapted to suit their more specialized environment. *P. vulgata* is therefore a fairly flexible, adaptable species. *P. aspera* is not so adaptable, and consequently occupies a more restricted tidal range.

2. Shell development

Limpet shells are more conical at upper shore levels and more depressed at lower shore levels (Ebling et al 1962; Fretter and Graham 1976; Jones et al 1979; Moore 1934; Orton 1928a, 1928b, 1933; Punt 1968; Russell 1909). There are a number of possible factors which may act separately, or together, to produce the observed shapes. It is possible that the physical action of holding tightly to the substratum causes certain limpets to become more conical than others. The exact reason for this tighter grip in some limpets is uncertain. It probably has to do with an avoidance of desiccation and/or as a protection against rough seas and strong currents.

Orton (1933) and Moore (1934) consider that upper shore limpets would be more subject to desiccation, and to avoid this would clamp down tightly to the substratum. This would result in a shell of elevated form as the adductor muscle, attaching the body to the shell, would be continually pulling downwards, so when the shell grew it would grow upwards. Limpets not adhering so tightly to the rocks, such as those at low tide, would be allowed to grow in a more outward direction.

Some limpets exhibit a shelf in the shell representing a changed angle of growth. Moore (1934) discovered that no shelf is produced when flatter low level limpets were moved to a permanently wet habitat, but when high tide limpets were put in such a situation a shelf developed. The reason, he suggests, is that the animal would now relax its muscle and grow in more extended form. After a period of time, however, the shells of many animals returned to their original angle of growth. The reason for this remains unclear.

Desiccation factors, as mentioned above, will be greater on the upper shore. Limpets lose water between the edge of the shell and the substratum, so in a more conical shell there is a lower proportion of the animal available for potential desiccation.

Ebling et al (1962) suggest that, as well as exposure to air, wave action would also cause limpets to hold on tightly. They noted that P. aspera on a rock sill, although permanently submerged, were subject to strong currents, and hence had a fairly tall shell.

In a study of South African Patella species Branch and Marsh (1978) have established a relationship between tenacity of limpets and wave action. When the six species studied were ranked according to severity of the wave action normally experienced, thus P. cochlear, P. argenvillei, P. granularis, P. granatina, P. longicosta and P. oculus, it was discovered that tenacity is highest in the first two, intermediate in P. longicosta and progressively lower in P. granularis, P. granatina and P. oculus. Except for P. longicosta, which has a relatively high tenacity, this sequence is the same as would be predicted from the wave action experienced by each species. It does seem, therefore, that in these South African limpets at least, tenacity is generally greater in areas of greater exposure.

When considering the shape of these limpets the same authors found no relationship between shell shape and exposure or tenacity. In considering the drag effect (ie the resistance of the shell to the flow of water around it, which is governed by the shell shape), they noticed that both P. cochlear and P. argenvillei occur in wave beaten areas and have the highest tenacities but have, respectively, the lowest and highest drag values, with the former having a flattened shell and the latter a conical one. In South African limpets therefore, although there is a relationship between tenacity and exposure, no such relationship exists between tenacity or exposure and shell shape.

Grenon and Walker (1981) found no significant difference between the tenacity of low or high level P. vulgata on both exposed or sheltered shores. Their experiments do not, however, rule out the possibility of a relationship between position on the shore and either tenacity or shell shape. There are two main reasons for this.

Firstly, unlike Branch and Marsh who did their tenacity experiments directly on the shore, Grenon and Walker removed the limpets to the laboratory. This could have produced error. On studying a different aspect of limpet behaviour Boyden and Zeldis (1979:759) note how limpets are 'upset by removal from the shore'. Feare (1971b) observed that limpets on drier areas were harder for oystercatchers to prise off than those in wetter areas, especially in pools. The reason, he considered, was that the former were clamped down harder to avoid desiccation. After removing thousands of Oronsay and Colonsay limpets it seems that, on a subjective judgement, those on the lower shore and in pools were easier to remove.

Secondly, even if further experiments support the idea that there are no such differences in tenacity, we need not discard the idea of tidal position governing shell shape, because the shape differences may not be due to the actual power of tenacity at any one period in time, but instead may result from the amount of time the limpet spends clamped to the rock. Higher tide limpets need to be securely fixed to the substratum for longer than those at lower levels, hence when growing they are more likely to grow upwards than to spread outwards. Indeed Grenon and Walker did note that there is increased tenacity when the limpets are uncovered by the tide, when there is a change from aquatic to aerial respiration.

To date there has been no thorough examination of the relationship between tidal position, degrees of exposure, tenacity and shell shape for British Patella, and until such a comprehensive study is done we will be no further towards understanding the role of exposure in governing shell shape.

When considering the present evidence it seems that the tenacity with which limpets clamp onto the substratum, and/or the amount of time they spend clamped down, are important in determining shell shape. We cannot draw particularly close parallels between South African and British limpets because of great differences in behaviour and habitat, especially with regard to the number and zonation of species and the interactions between them. (For relevant information on South African limpets, see Branch 1971, 1975, 1976; Branch and Marsh 1978.)

The results of Branch and Marsh (1978), indicating a relationship between tenacity and wave action yet no relationship between shell shape and wave action, requires testing on British coasts. The experiments of Grenon and Walker (1978) require duplication on the shore itself, yet the fact that they also found no relationship between shell shape and wave action does indicate that perhaps the amount of time out of water is the key factor, with extremes of exposure perhaps affecting shell shape in certain localities. If degree of exposure was the factor of overriding importance we should see much more variation in shell shape from any one tidal position. Patella aspera exist on the most exposed coasts, yet are just as flat as P. vulgata on sheltered shores.

More attention should be given to the idea of Punt (1969) who suggested that high shore limpet shells may be more conical to allow for the storage of water to overcome the dry period. Also, the simple fact that conical shells present a smaller area of shell margin for potential desiccation has been overlooked in much of the literature.

F. PERIWINKLE AND DOGWHELK POPULATION DYNAMICS

1. Reproduction in periwinkles

Periwinkles lay egg capsules, usually over 200 at a time, into the sea from whence the embryo, as free-swimming veliger larvae, hatches after between 6 days (Hayes 1929:46) or 12 to 14 days (Fish 1979:173) probably depending on temperature. Breeding occurs over a longer period than for Patella, and different observers have recorded seeing evidence of breeding activity over all the later winter to early summer months.

Moore (1937) quotes Linke who considers that most spawning occurs in March, April and May, though sometimes there may be some spawning as early as January and as late as June. He also notes that eggs have been found in the plankton in November. Moore's own observations indicate that at localities around Plymouth spawning began around the beginning of December and was complete sometime between mid-March and mid-April. Fully ripe males were first discovered in the beginning of January, but would have been capable of copulation before becoming fully ripe. By early February all males were fully ripe, and in May a few spent ones were found. Tattersall (1920) observed the breeding season to be from January to June in Ireland, with a maximum in April and early May; and at Millport Elmhirst (1923) gives the spawning season as from January to July and occasionally August. Hayes (1929) records the main spawning period as from April to July in certain Canadian waters. In his experiments he had noted copulation at the end of July, though these were few, most individuals copulating earlier in the season. Lebour, quoted in Fish (1972) found egg capsules in plankton at all times of the year at Plymouth, but considered them to be most abundant in February and March. At Craig-Yr-Wylfa, near Aberystwyth, Williams (1964) recorded maximum spawning in March. In the Dyfi estuary egg capsules were seen to appear in large numbers in December or January and remain abundant until the end of May, though they were found occasionally until November (Fish 1979). Unpublished work by Maghraby reported in Smith and Newell (1955) notes that during 1953, three-weekly plankton hauls offshore from Whitstable revealed that eggs were present throughout the whole winter. They were scarce in January but became common in February and abundant in April and May.

It seems therefore that periwinkles are capable of breeding at any time of the year but, depending upon locality, this seems to occur from January to June with maximum release in February to April. Prior to spawning, the population matures rapidly over a few weeks, compared to dogwhelks (below) who mature over a much longer period. At Craig-Yr-Wylfa there were 38.3% mature periwinkles in December, 59.4% in January, 72.8% in February and 88.9% in March (Williams 1964:426). After spawning the population remained spent until they began to mature in the following autumn. This is in contrast to dogwhelks who begin to mature again almost immediately but the process is a slow one. At Craig-Yr-Wylfa periwinkles from the upper shore were found to mature faster than those from the lower shore (Williams 1964). This is in contrast to limpets whose rate of maturation does not vary over the shore (Blackmore 1969a).

The length of time between egg hatching and larval settlement is not known, but it is probably just a few weeks. Williams (1964) considers planktonic life of periwinkles to be about 4 or 5 weeks. As with spawning, there is considerable variation in records of the times of settlement. Elmhirst (1923) noted abundant young on the shore at Millport in April, but Moore (1937) could find none at Trevol on May 17th 1935. At the next visit, however, on July 1st young were abundant. At Drake's Island in 1936 no young were found on April 21st, but were present, though only in small quantities, on May 19th. In this same year there were only a few young at Trevol on June 2nd. Moore therefore considers that the main period of settlement is from the end of May to the end of June. At Craig-Yr-Wylfa Williams (1964) records settlement occurring in July in 1961 and mid-August in 1962. In his study of two contrasting populations in Cardigan Bay, one beneath the rocky headland at Craig-Yr-Wylfa, the other in the more sheltered Dyfi estuary, Fish (1972) recorded settlement in the former during July 1969 and 1970, and June 1971, and in the latter during

March 1970 and February 1971. Total records for the Craig-Yr-Wylfa population therefore span five years and settlement ranges from June to mid-August.

A number of factors have been suggested as trigger mechanisms for spawning. Smith and Newell (1955) consider that although periwinkles are potentially capable of breeding all the year round, maximum ovulation occurs when rising spring or early summer temperatures reach some critical level. Spring tides are related to lunar cycles, and a number of ideas have been put forward relating main periods of spawning to these cycles (Alifierakis and Berry 1980; Fish 1979; Grahame 1975).

From laboratory experiments Grahame (1975:195) noted that there was an indication of maximum spawning at about the time of full moon spring tides, but concluded: 'While it seems that there may be a lunar/tidal rhythm in spawning, this remains obscure'. His laboratory experiments did not, however, simulate tidal movements, so clear results on this cycle could not be expected.

Both Alifierakis and Berry, and Fish, conducting independent experiments (neither referencing the other's work), concluded that there is a lunar/tidal cyclic rhythm to spawning. The former relied on laboratory experiments simulating tidal movements experienced at the site of collection on the Firth of Forth, and the latter collected samples from the sea water at Ynyslas in the Dyfi estuary.

Alifierakis and Berry consider their results clearly indicate that periwinkles release far more eggs at spring tides than at neaps, especially during the height of the breeding season. This occurred in the laboratory even though the animals did not experience either the moon itself or the associated spring/neap changes in tidal range (in the experiments tidal amplitude was constant). During the 6.5 lunar months of the season (early January to mid-July) periods about new and full moon comprised 39.3% of days in the season but yielded 58.5% of the egg capsules, whereas the remaining 60.7% of the days in periods near half-moons yielded only 41.4% of the capsules (Alifierakis and Berry 1980:305).

As a control Alifierakis and Berry kept some female periwinkles immersed permanently in sea water. The total amount of egg capsules released was only about 25% of those from the tidal regime, and there was no relationship between egg release and new or full moon. In fact 81.8% of all capsules were released in the 60.7% of the days that fell in other parts of the lunar cycle (Alifierakis and Berry 1980:305).

Their results indicate that the semi-diurnal rise and fall of tides across the mid-shore area serves as a timing or counting cue for fortnightly increases in egg release, even when they cannot see the moon phases or experience changing tidal amplitude. Launching eggs on a spring tide means a greater potential dispersal. Animals with a more distinct high shore zonation, such as Littorina neritoides and Littorina melanostoma have a much more pronounced fortnightly rhythm (Alifierakis and Berry 1980). Living lower on the shore L. littorea is not so reliant on such a strict cycle.

From regular investigations into the abundance of egg capsules in the plankton around Ynyslas Fish (1979) discovered that while there is often some small increase in numbers before the new or full moon, sharp increases occur afterwards. He suggests that this peak in density is more closely related to the timing of the moon than the height of the tide. This would agree with the timing cue suggested by Alifierakis and Berry.

Periwinkles seem therefore to be capable of breeding over the whole year but, depending on locality, do so mainly between January and June or July, with most egg capsules being released between February and April. Williams (1964) concludes that the Craig-Yr-Wylfa populations mature when temperatures are at their seasonal lowest, and spawn in greatest numbers when temperatures begin to rise. It is probable that sea temperature also governs the duration of embryonic development (Fish 1979). Tattersall (1920) and Hayes (1929) suggest a period of 6 days for the eggs to hatch yet do not mention temperature. During laboratory experiments Fish (1979) recorded hatching after 17 days at

5°C and 6 days at 15°C. Under the temperature regime of the intertidal waters over the spawning period (4-8°C) he suggests hatching would take place after about 12 to 14 days.

2. Shore settlement of periwinkle spat

Settlement on the shore would occur after a few weeks, but exactly where this settlement occurs is still open to doubt. Because periwinkles are a mobile species this is not as significant as with limpets, but nevertheless there are contrasting observations. Williams' (1964) survey of Craig-Yr-Wylfa revealed many very small periwinkles scattered throughout the entire vertical range of the species, but Smith and Newell (1955) suggest that juveniles settle out of the plankton sublittorally, and recruitment is due to a continual upshore migration of very small periwinkles.

3. Periwinkle mortality

To the author's knowledge there is only one mention of predation on periwinkles, and this is by crows (Clegg 1972). Presumably they are also eaten by oystercatchers, though from his extensive observations Feare (1970a, 1971b) makes no mention of this. For some unknown reason periwinkles are not eaten by dogwhelks, who will tackle virtually any other mollusc (Morgan 1972a, 1972b). Out of the three shellfish species in the present study, only periwinkles are now collected on a large scale by man (Crowley 1973).

4. Reproduction in dogwhelks

Maturing and adult dogwhelks aggregate in clefts and pools in October-November and do not emerge from their non-feeding winter groupings until the egg capsules have been laid in April-May (Feare 1970b). Moore (1938a) quotes Pelseneer as observing the main period of laying to be around April. At Robin Hood's Bay Feare (1970b) records a second spawning in July-August, which had been preceded by a brief period of aggregation. Garstang (in Moore 1938a) has also recorded a second spawning period, this time around September.

Unlike periwinkles or limpets these capsules are laid directly onto the shore, and the young hatch directly as tiny snails without any intermediate planktonic stage. The opportunity therefore exists for genetic isolation of populations. The capsules are laid in clefts and pools between MLWS and MTL, the majority at the lower levels (Feare 1970a). At Robin Hood's Bay Feare (1970a:5) found that in clefts acting as freshwater drainage channels at MTL only 27% hatched, but where capsules were permanently immersed in sea water 100% hatched. In situations which dried at low water there was a variation in hatching success between 0% at MTL and 57% at MLWN. The eggs hatch after about 4 months (Moore 1938b:67).

Sperm development within the males is a slow process (Feare 1970b), beginning in February and not reaching a peak until the following December-January. Some ripe sperm is available at other times of the year as indicated by the occasional second spawnings. Moore (1938a) notes that around Plymouth egg capsules are found throughout the year, though the main spawning season is around the spring. In females new ova begin to develop immediately after spawning in April/May and, as in males, such a development is a slow process so again some ova are ripe at other times (Feare 1970b).

Temperature has been shown to play an important part in spawning times. Experiments by Largen (1967b:212-213) indicate that a mean of 9°C is the approximate minimum water temperature at which spawning occurs, and that the stimulus for oviposition is a rise in mean water temperature through 9-10°C. This could explain some differing observations concerning reproductive behaviour. Moore (1938a) quotes a number of cases where spawning is said to be from January to April. These are however of a southern distribution and so a slightly earlier start to spawning may be expected. Also Kostitzine (in Feare 1970b) has reported a much shorter developmental period for dogwhelks at Roscoff in Brittany than observed by Feare at Robin Hood's Bay, though they both spawned around the same time. This difference could again be due to temperature, but Feare (1970b) considers that exposure may also be important. He has observed that the spending of six months in non-feeding winter aggregations is a characteristic of exposed shore populations. The difference in duration of gonad development between Roscoff and Robin Hood's Bay may therefore be related to the degree of exposure rather than latitude.

5. Dogwhelk mortality

Mortality of dogwhelks due to predation by birds is sporadic and localized. Predation by the herring gull, purple sandpiper and rock pipit have all been reported (Berry and Crothers 1968) but the main predator is probably the oystercatcher (Feare 1971b). Observations by Feare at Robin Hood's Bay indicate that oystercatchers prey on dogwhelks only during the autumn and spring when they are moving into and out of their winter aggregations, though this could just be a local phenomenon. In this area at least, limpets were the favoured species, dogwhelks only being taken occasionally. The dogwhelk shells were not smashed but the main part of the body was removed through the aperture.

The main predator on dogwhelks appears to be crabs (Currey and Hughes 1982; Ebling et al 1964; Feare 1970a; Hughes and Elner 1979; Kitching et al 1966), and this is of a much more selective nature. Dogwhelks on sheltered shores are longer and have a smaller aperture than those from exposed shores which are more squat. There are many more crabs on sheltered shores, and it has been suggested that the shape difference is at least partly a selective mechanism against crab predation (Currey and Hughes 1982; Hughes and Elner 1979; Kitching et al 1966). Experiments by Hughes and Elner indicate that exposed shore dogwhelks living in the virtual absence of shore crabs are much more vulnerable to attack than sheltered shore dogwhelks. Those on exposed shores have a larger foot for greater adhesion on wave-swept rocks, but these are less able to exclude the chelae of attacking crabs. The narrower mouth of sheltered shore dogwhelks excludes the crab chelae, and the shells are thicker and more robust (Hughes and Elner 1979; Kitching et al 1966). Hughes and Elner found that these attributes were even more pronounced in a sublittoral fringe population of dogwhelks vulnerable to predation by the more powerful edible crab. They also established that there was a marked decrease in attack success rate as shell height increased for both sheltered and exposed shore dogwhelks, yet sheltered shore individuals were attacked less successfully than those exposed shore dogwhelks of similar height. Very few dogwhelks of 20-23 mm shell length were successfully attacked, and none beyond 27 mm could be broken (Hughes and Elner 1979:75). Experiments by these authors have shown that crabs will attack all dogwhelks encountered but quickly reject those that do not break.

Conclusions

Spawning in dogwhelks does therefore occur over a shorter more well-defined period than in periwinkles, though the main period of egg release is slightly earlier in periwinkles. Much investigation has gone into trigger mechanisms for spawning in periwinkles but, except for the influence of temperature, the problem has not been considered for dogwhelks. Trigger mechanisms are, however, not nearly so important in dogwhelks as they are not reliant on tides to disperse larvae. In periwinkles gonad development is rapid and occurs during the winter when growth is minimal, whilst in dogwhelks growth stops at maturity. In dogwhelks the gonad takes over twelve months to complete its development, whereas periwinkles mature rapidly just prior to spawning.

Virtually no work has been done on periwinkle mortality, yet it is probable that birds and man are the main predators. Bird predation on both periwinkles and dogwhelks is random and localized, depending on the bird distributions. Crabs have been shown to be a major predator of dogwhelks, which have morphological adaptations to reduce this threat.

G. THE DISTRIBUTION OF PERIWINKLES AND DOGWHELKS OVER THE SHORE

1. The effects of tidal level on periwinkle distributions

As with limpets a number of interrelating factors govern the distribution of periwinkles on the shore. The distribution is not, however, so specific with relation to exposure, shell size and shape, strict tidal level and biological habitat as is the case for limpets, periwinkles being a mobile species. This factor means that they can be found in much larger concentrations at any one period in time because they are not reliant on one fairly stationary food source. Despite their mobility and, as will be seen below, sometimes because of it, periwinkles do exhibit zonation patterns which require explanation. 'Motile species present a special problem since it is conceivable that it could reach all areas throughout the intertidal zone. Yet many motile intertidal species often appear in greater abundance at a particular intertidal height' (Petraitis 1982:207).

Periwinkles are most numerous at mid-tide level, and only occasionally are they found in any quantity above MHWN and below ELWS. Between these limits there is much local variation in abundance (Crapp 1973; Crothers 1976; Evans 1947a, 1947b; Gendron 1977; Lewis 1954; Moore 1937, 1940; Moyse and Nelson-Smith 1963; Newell 1958a, 1958b; Smith and Newell 1955; Williams 1964). From these observations, and from those made on the coasts of Oronsay and Colonsay, it seems that the optimum zone is between MLWN and MTL, depending on local conditions. Periwinkles do require wetting at every tide, and where they occur above MHWN the effective levels are raised by splash (Moore 1940). Smith and Newell (1955) note that they are often taken in the dredge below tide marks. Gendron (1977) obtained subtidal periwinkles by diving at Woods Hole, Massachusetts, USA, and Hylleberg and Christensen (1978:193) recorded many down to a depth of 0.5 m below sublittoral, and a few around 8 m depth.

Because they feed on decaying fucoids and various detritus which tends to collect in gullies, pools and on sheltered shores, these areas are favoured over more exposed coasts (Crapp 1973; Crisp and Southward 1958; Crothers 1976; Evans 1947a; Moyse and Nelson-Smith 1963; Newell

1958a). Where food is available on the shore above MTL the periwinkles' range is extended. This occurs around Aberystwyth so periwinkles are common among weed as high as MHWN (Evans 1947a). At Yealm in Devon where the upper shore was stony with little algal growth, periwinkles were very scarce above MLWN, yet at nearby locations with more algae they occurred up to MHWN (Moore 1940).

Within these limits a number of distributional patterns are evident which appear to be common features to a number of coastlines. In contrast to limpets, periwinkle zonation results more from movements around the shore than from initial settlement and mortality.

Limpets either develop or die where they settle on the shore, and only later may move a short distance to a new home base. The exact settlement pattern of periwinkle larvae on the shore is open to debate. Settlement may occur on the sea bottom below low water mark (Smith and Newell 1955) or intertidally (Williams 1964). Taking into account both reports, and also that of Moore (1940) describing variations in the distribution of young periwinkles on shores around Plymouth, it may be concluded that both direct settlement and movement of very young periwinkles upshore seem to occur. Reasons for these variations are not known but it may be due to varying tidal currents, degrees of wave action capable of moving the young periwinkles, or the morphology of the coast.

At Whitstable relatively few periwinkles survive beyond their second year on the upper part of the beach (Smith and Newell 1955), but at the lower part (which in this survey was only just below MTL) there were greater numbers of older larger animals. Moore (1940) also records this around Plymouth where in the four sites studied the largest periwinkles occurred at the middle and lower tidal levels. At Craig-Yr-Wylfa the largest individuals were at the lowest levels (LWS) (Williams 1964), as they were at Woods Hole, Massachusetts (Gendron 1977).

Smith and Newell suggest their presence here may be due to better survival conditions at this level, or to a movement upshore of older animals from below lower water mark. They dismiss the idea of downshore movement of animals previously living higher up the beach because all these larger periwinkles are covered in barnacles. Williams (1964) found no evidence of a downshore migration or of differential mortality over the shore. He considers that only in the lower areas, where conditions are optimal, can periwinkles attain maximum size. Hayes (1929) conducted experiments which showed that animals at low tide level grew much more rapidly than those at higher levels, and from this he concludes that immersion is a more important factor in growth than is warmth and sunlight during exposure.

There are local habitat variations on the shore which favour periwinkle distribution. On the Oronsay and Colonsay coasts pools of standing water, clumps of algae and sheltered crevices, often contained large groups of periwinkles, especially around mid to low level areas of the shore (chapter 3). Smith and Newell (1955) also found this at Whitstable as did Evans (1947a) in Cardigan Bay. It does not, however, seem that periwinkles will move over large distances to locate a favourable wet environment. At Whitstable observations on periwinkle movements by Smith and Newell show that although wet places are more favoured, periwinkles do not move up and down the beach to find them, but seek them within the bounds of their own particular beach horizons. They noted that the pattern of distribution of the adult periwinkles is substantially constant at all times of year despite variations in the distribution of surface water.

At Whitstable it was seen that the adult zonation pattern is achieved at the end of the first year, and after this distributional patterns of adults remain substantially constant (Smith and Newell 1955). There are however some movements around the shore, but if these were purely random this constant pattern of zonation would be upset.

2. Movements of periwinkles around the shore

A number of studies have been made of these movements; for a review see Newell (1979) and the details may be found in Newell (1958a, 1958b), Gendron (1977) and Petraitis (1981). From these it may be concluded that movements are related mainly to feeding activity, and also an avoidance of desiccation. Individuals move over relatively short distances and are guided by geotactic responses (mainly on angled surfaces), phototactic responses (mainly on flat surfaces) and an attraction to the direction of wave action. The majority of movements involve an outward and a return journey, so the periwinkle maintains the same general level on the shore. For movement to occur the periwinkle must first be agitated by the waves. In the absence of stimulation they are inactive and simply cling to the nearest available surface.

Variations in activity with season do not seem to be particularly pronounced, at least in observations of British periwinkles. From November to March they show less movement, becoming inactive when the light intensity and temperature are low (Newell 1958a). Experiments by Newell (1958a:236) show that at temperatures between 6°C and 8°C periwinkles become inactive even when illuminated at light intensities sufficient to promote crawling at higher temperatures. From November to March air and sea temperatures at Whitstable are usually below 8°C.

Gendron (1977) interprets distributional patterns on the shore at Woods Hole, Massachusetts, as indicative of a general migration downshore in the winter and upshore in the spring. His evidence is a decrease in the density of snails at his upper station between October and January and an increase between March and May. Despite these apparent seasonal shifts, there was no evidence of any significant shift in the zone of maximum density of any of the size classes between October and January. It is suggested (Gendron 1977; Newell 1979) that seaward winter migrations by gastropods may minimize exposure to sub-freezing temperatures. The effect of temperature extremes decreases at lower levels, so periwinkles from these lower levels would not have to migrate. Gendron only found evidence of seasonal changes in density among upper shore periwinkles.

Although such seasonal migration is a distinct possibility, it is not the only response that may account for the observed changes in density. Indeed Williams (1964) found no evidence of downshore migration at Craig-Yr-Wylfa. Periwinkles tend to occur in clusters and it may be that there was an alteration in local conditions favouring a cluster, perhaps even horizontally along the shore, during the winter months. Specific density distribution studies related to habitat are required to solve this problem. On present evidence seasonal migrations are possible but remain unproven. Possibly they are more pronounced in areas of lower winter temperatures, where upper shore periwinkles move downshore in the winter to minimize the effects of low temperatures.

3. The effects of tidal level on dogwhelk distributions

'At all times of the year the dispersion of dogwhelks on the shore presented a striking non-random appearance' (Feare 1970a:4). It favours shores of intermediate exposure, and in extreme exposure is scarce and confined to crevices (Evans 1947b; Moyse and Nelson-Smith 1963). It is most abundant around the lower middle shore (Crothers 1976), though it can exist up to EHWN where increased splash and a food supply allow (Evans 1947b; Moore 1938b). The lower level of abundance is around MLWN-MLWS (Evans 1947b) though Moore (1936:84) reports very large specimens, up to 63 mm shell length, from depths of around 10 fathoms. Hughes (1972) records highest densities at low tide level for a Nova Scotian population, and these densities are maintained to a depth of 1.5 m below low spring tide level. With increased depth the population thinned out, with only occasional individuals existing at 4 m below MLWS. At another Nova Scotian site at least half the population were sublittoral, yet at another there was no sublittoral extension, probably because of a lack of food (Hughes 1972).

The main factor governing intertidal distribution is the presence of a food source. Dogwhelks are carnivorous and eat mainly barnacles, either Balanus balanoides or Chthamalus stellatus(Bayne and Scullard 1978b; Connell 1961a, 1961b; Feare 1970a; Largen 1967a, 1967b; Moore 1936, 1938b; Morgan 1972a, 1972b) and Mytilus (Bayne and Scullard 1978b; Hughes 1972; Largen 1967a, 1967b; Moore 1936, 1938b; Morgan 1972a, 1972b), and sometimes other species, such as Cerastoderma edule (Kitching et al 1966; Morgan 1972a, 1972b), Gibbula (Moore 1938b), Patella vulgata (Moore 1938b), Patella intermedia (Largen 1967a) and even other dogwhelks (Moore 1938b), depending on availability.

Shells are bored by the dogwhelk (Bayne and Scullard 1978b; Fretter and Graham 1962; Largen 1967a), yet in barnacles the valves are usually forced apart (Largen 1967a; Moore 1938b) presumably because this provides the least resistance. Largen (1967a) records occasional instances of barnacles being drilled.

There are reports of both a selection of species and size of prey by dogwhelks. In some situations observers consider that barnacles are the preferred food (Barnett 1979; Connell 1961a; Moore 1938b) and in others mussels appear to be selected (Hughes 1972; Kitching et al 1966; Moore 1936; Morgan 1972b). Within these there often appears to be some size selection. For instance Bayne and Scullard (1978b) and Largen (1967a) note a preference for medium sized mussels and Connell (1961a) has demonstrated a preference for larger barnacles.

Though specializing in two main species, it appears that dogwhelks are 'capable of successfully attacking almost any shelled species of suitable size, with which it comes in contact' (Largen 1967a:125). Dogwhelks will concentrate on the species (usually either barnacles or mussels) that is most readily available on the shore, except where the distribution of this species has recently changed. If the favoured prey declines, and is replaced by another, dogwhelks are often slow to change to the new species. Moore (1938b) reports observations of Fischer-Piette on a shore initially dominated by barnacles, on which fed the dogwhelks. Barnacles declined and there was an increase in mussels. Dogwhelks only changed diet when they were forced to, and their first attempts to penetrate the mussels were very clumsy. After a time their feeding became more efficient and most mussels were destroyed, so barnacles returned, and the dogwhelks were slow to return to their original diet. It may therefore be the case that on an area of shore large clusters of either barnacles or mussels may be totally ignored by the dogwhelks.

The importance of prey availability on dogwhelk distribution is emphasized by Morgan (1972a, 1972b) when studying an isolated dogwhelk community at Old Den in the Humber estuary. At one time barnacles were plentiful and were the main food of the dogwhelks, but then they vanished (probably due to a severe winter and increased sediment accumulations) and the dogwhelks had to change their diet. The only possible alternative was the cockle (periwinkles were present but not eaten). Although these were widely distributed, the topographic arrangement of sediment between rocks allowed for this exploitation, as cockles inhabited the sediment and dogwhelks lived on the rocks. A number of dogwhelks clustered around one cockle, so the distribution pattern was one of small widely scattered groups of dogwhelks. When feeding on barnacles they were much more evenly distributed over the barnacle-covered rocks. When barnacles gradually recolonized, so the diet was changed once again. 'Features such as these clearly show that Nucella is a successful and very versatile intertidal species' (Morgan 1972b:272).

4. Movements of dogwhelks around the shore

The majority of dogwhelk movements around the shore are associated with food. Morgan (1972b) observed dogwhelks moving deliberately towards barnacles, yet when these supplies were scarce there was a wide dispersal around the shore. Where a prey species is thinly dispersed it becomes inaccessible to the predator unless that predator is itself able to search a wide area. 'Powers of dispersal are of considerable survival value to predators resident in areas with a fluctuating food supply; not only are dispersive predators more likely to locate fresh resources of food, but they are also more likely to locate the thinly scattered prey that remains' (Morgan 1972b:270). Such fluctuations in predator and prey produce varying densities of both, because in such a situation the over-exploitation of prey is almost inevitable. Such density fluctuations are, however, local in nature; over the shore as a whole densities will remain substantially the same.

As well as being distributed on the shore with relation to their prey, dogwhelks also exhibit an as yet little understood aggregation behaviour. The collection in sheltered habitats such as crevices and pools usually on the lower shore during the winter has been noted by Moore (1938b) and Feare (1970a, 1970b, 1971a). Marking experiments (Feare 1971a) have shown that adults spent more time in these breeding groups than juveniles who were there mainly for protection. Adults did not feed for the whole period (October-November to April-May) but juveniles fed in calm weather. It is probable that protection against winter storms and low temperatures is a major reason for this behaviour in both adults and juveniles. Largen (1967b:209) showed that movement and feeding were greatly reduced below 5°C. Although low temperatures did not affect the dogwhelks holding-power, once disturbed they were unable to regain a foothold. Thus, such winter groupings reduce the chance of dislodgement. These winter aggregations occur in all but the most sheltered beaches (Feare 1970a, 1971a).

Most egg capsules are laid in the aggregation sites, and the young will move up from these during the first summer (Feare 1970a). All individuals do not breed at exactly the same time so '...there are always some at low levels, some at high levels, and others either moving up or down' (Berry and Crothers 1968:9).

Summer aggregations have also been noted, but only by Feare (1971a) at Robin Hood's Bay. These only occurred on exposed shores, and they were found to contain from 20 to 500 dogwhelks. Feare has shown experimentally that dislodgement is harder when dogwhelks are in groups. Dogwhelks were more dispersed on sheltered shores, whereas the area of Robin Hood's Bay where summer groupings occurred was relatively flat and exposed. On a nearby exposed pitted coast dogwhelks were distributed in twos and threes in the pits. Here these provided necessary shelter, thus obviating the need for summer aggregations. Unlike the winter groupings, those in summer were more fluid with a greater movement in and out of individuals of all sizes. The position of the group was also seen to move around the shore (Feare 1971a).

5. Desiccation tolerance in dogwhelks

Desiccation tolerance has been shown to be of some importance in governing dogwhelk zonation patterns on the shore (Boyle et al 1979; Coombs 1973a). Coombs demonstrates how desiccation tolerance varies with age. Young dogwhelks are actually more tolerant to fluid loss than older animals, yet they lose water more rapidly, so the overall effect is that they are unable to live as high up the shore as larger dogwhelks. They tend to remain below MTL or in moist microhabitats. Dogwhelks that may accidentally stray to areas that are too dry will become comatose, the foot is relaxed and they fall off (Coombs 1973a). When uncovered by the tide dogwhelks avoid desiccation because of sea water trapped in the mantle cavity (Boyle et al 1979; Coombs 1973a).

Conclusions : Comparative distributions of periwinkles and dogwhelks

Both species are most abundant around the lower middle shore, and both exist sublittorally in small numbers, these generally being very large individuals. Within the intertidal zone periwinkles usually cluster in protection where food is available. The largest individuals occur at the lowest levels, and these tend to exist individually on the rocks and not in clusters. In periwinkles the general zonation pattern is established by the time the animal reaches one year old. Dogwhelks usually cluster in winter, but are generally distributed over the rocks in summer, the exact distribution being governed by the dispersal of their prey. On more exposed shores summer aggregations may also occur. There is no pattern of size distribution with level except the occasional large individual in the sublittoral.

Although the distribution pattern of adult periwinkles remains substantially constant at all times of year, within the general levels there are some movements related to feeding. When they are not actually feeding on material in or close to their home, the periwinkles go on feeding excursions when covered by the tide, and usually return to the same part of the beach. They are generally inactive in winter, yet it is possible that in cold areas upper shore periwinkles may move downshore in the winter months. Dogwhelks do not need to go on such regular feeding jaunts. They move from one prey to the next, and remain in position whether covered or uncovered by the tide.

H. GROWTH IN PERIWINKLES AND DOGWHELKS

1. Periwinkles

Periwinkle growth has been much less intensively studied than that of limpets. Nevertheless it is evident that, as with limpets, growth rate varies with season and age (Fish 1972; Moore 1937; Williams 1964). Figure 8 expresses the results of Williams (1964) from Craig-Yr-Wylfa. The smaller periwinkles grow faster than the older ones, and once they reach a size of around 20 mm shell length, growth is substantially reduced. (The minimum size collected on Oronsay was 18 mm shell length.) The smallest animals (A') show very little growth from December 1961 to March 1962, yet the larger group (A) show no growth at all from October to May. Williams explains this by reference to temperature and sexual activity. Sexual maturity in this population was reached at a size of about 12 mm shell length, so the longer period of no growth in population A corresponds to the period of maximum sexual activity. At this time of year all the food reserves are used for gamete production. The smaller periwinkles are not sexually mature and they stop growth when the temperature is below about 8°C (Williams 1964:419). It will be seen that population B have a shorter period of no growth than population A. Williams considers this to be due to the fact that the inhibitory effect on growth of sexual activity is far more pronounced in animals maturing for the first time than for the second or third time (pers. comm. Dr E. Williams).

The trend of reduced growth with increased age is clear from figure 8. Hayes (1927, 1929) has demonstrated that under favourable conditions small periwinkles can double their length in less than 2 months. Williams considers that animals over a shell length of around 19 mm (over 3 years old) grow only very slowly (pers. comm.).

As with limpets it appears that age-size relationships vary with location. Table 7 demonstrates the differences between three localities. Craig-Yr-Wylfa and Whitstable show very similar growth-age

TABLE 7 : PERIWINKLE GROWTH MEASURED FROM DIRECTLY AFTER SETTLEMENT

REFERENCE	LOCATION	SIZE AT END OF FIRST YEAR (MM)	SIZE AT END OF SECOND YEAR (MM)	SIZE AT END OF THIRD YEAR (MM)	SIZE AT END OF FOURTH YEAR (MM)
Williams (1964)	Craig-Yr-Wylfa, West Wales	8-9	13-14	15.5-16.5	17.5
Smith and Newell (1955)	Whitstable, South England	11-12	13-16	>17	
Moore (1937)	Plymouth region	*c.*17	*c.*22	*c.*25	*c.*27

relationships, yet Plymouth has much faster growth. Perhaps this is due to sea temperatures at the time of the survey (1935-36) and/or differences in habitat.

Thus it seems that young periwinkles grow faster than older ones, and the length of the winter no-growth period depends upon temperature and sexual maturity. Moore (1937) and Williams (1964) agree that sexual maturity is reached at between 15 and 18 months, which would be at a length of about 12 mm at Craig-Yr-Wylfa, or not until around 19 mm at Plymouth (pers. comm. Dr E. Williams). Fish (1972) agrees that it is usual for sexual maturity to be reached at around 12 mm.

2. Dogwhelks

In comparison with studies on the body and shell development of limpets and periwinkles, very little has been done concerning certain aspects of this study area for dogwhelks. Nearly all the work has concentrated on variations in shell morphology.

Both feeding and growth cease in winter as a direct response to low temperatures. Movement and feeding activity become very much reduced below 5°C, and at 3°C the animals are inactive (Feare 1970a:6; Largen 1967b:209). At Robin Hood's Bay during the winters of 1965-66, 1966-67 and 1967-68, the mean monthly temperatures fell to 5°C or below in three, one and two months respectively, and the shell lengths in the following April were 5.4 mm, 9.3 mm and 7.2 mm (Feare 1970a:7). Bayne and Scullard (1978a) have shown that respiration is lower in winter during the period of inactivity. This, they conclude, is due to the combined effects of reduced temperature and reduced feeding activity.

From October to March Largen (1967b) found little or no shell growth, and considers maximum growth to occur in the summer. He found feeding rate increased with increased temperature up to a maximum at around 20°C. Feare (1970a) agrees that the main growth period is from June to November. Laboratory experiments by Crothers (1980) show that growth varies with season and is fastest in spring and summer. Hughes (1972) concludes that growth occurs in spurts, and that some animals began growth at the end of April and all had ceased by October. Different dogwhelks began and ceased growth at all stages within the growth period, the total annual growth taking anywhere from 1 to 5 months for completion. Crothers (1977b, 1980) also discovered variations in growth rate between individual dogwhelks. In laboratory experiments some grew faster than others during the first few months, and thereafter became the largest and healthiest individuals. Crothers considers this pattern to be genetic, because the young developed to be the same size and shape as their parents.

With such variations in growth rate it is difficult to relate age to size. Indeed, in the published studies virtually no mention is made of specific sizes at specific ages. Moore (1938a:60) found that around Plymouth dogwhelks reached a length of 10 to 15 mm at the end of their first year, then increased by another 11 mm in their second year, then a slower growth rate in their third year brought them to a size of around 29 mm. Most workers have concluded that sexual maturity is reached after 2.5 to 3 years, which in the case of Plymouth occurred at a length of 25 to 29 mm. Hughes (1972:363) found that sexual maturity was attained at 16 mm and 20 mm shell lengths in two Nova Scotian populations, which was also at an age of around 2.5 years.

Moore (1938a) considers that variations in growth rate at different sites are reflected in the size at which maturity is reached. At a site with what he considers to be a fast growth rate, maturity was reached at a length of 28.7 mm, yet at a site of slower growth rate maturity was reached at 19.9 mm shell length. With such variations it is not possible to relate age to size with any degree of accuracy. The situation is further complicated by variations in length with exposure and by genetic variations in growth (Crothers 1977b, 1980).

Moore (1936, 1938a) suggested that growth stops at maturity when the shell lip thickens, and a row of 'teeth' are then deposited on the margin of the lip. There is general agreement that growth stops at maturity and that teeth form on the thickened lip (Cowell and Crothers 1970; Crothers 1971, 1980) although Feare (1970a) reports slight growth after maturity in some dogwhelks. Tooth formation occurs after prolonged cessation of growth, which may be at maturity or, if growth is temporarily halted, prior to this (Cowell and Crothers 1970; Crothers 1971; Feare 1970a). A period of no growth is probably due to starvation which may result from dislodgement and transportation away from the food source, or a long cold winter where there is a long period of total inactivity. The fact that Cowell and Crothers discovered that the frequency of these starved animals is greatest on exposed shores, where there is much food, indicates that rough conditions are an important inhibitor of feeding, presumably washing the dogwhelks from their prey.

There do therefore seem to be variations in growth between different locations, yet there are also genetic variations within the same population. Growth has been shown to be seasonal and often, though not always, to stop at maturity at around 2.5 years old.

Conclusions

Both species show variations in seasonal activity. Both have minimum temperatures below which they will not feed - for periwinkles it is between around 6 to 8°C (Williams 1964:419) and for dogwhelks around 3 to 5°C (Largen 1967b:209) - and both show reduced winter growth. In dogwhelks, growth generally stops at maturity which is reached after 2.5 to 3 years (Moore 1936:60; Crothers 1980:183). In periwinkles, growth continues after maturity is reached, which occurs around 17 to 18 months after settlement, though at a slower rate (pers. comm. Dr E. Williams). In dogwhelks, most growth occurs in summer and happens in spurts (Hughes 1972). Varying growth patterns between individual dogwhelks probably indicate genetic variability (Crothers 1977b, 1980).

I. THE PHYSIOLOGICAL ECOLOGY OF PERIWINKLE AND DOGWHELK SHELL DEVELOPMENT

Studies of shell shape are far more numerous for dogwhelks than periwinkles. This is because dogwhelks show distinct genetic variations between shores, whereas the free-swimming larvae of periwinkles prevent such genetic isolation. Nevertheless, the small amount of effort expended on studying periwinkle shell development does indicate the need for further research.

1. Periwinkles

Shell shape in periwinkles shows very little variation from one area to another, probably because of the pelagic larvae, the young being distributed in the sea and not usually returning to the same area of shore (Moore 1937). Despite this, a slight difference in shell morphology has been recorded by Hylleberg and Christensen (1977). At Limfjord in Denmark they found that periwinkles of a given length increase in shell weight from shelter to exposure. At sheltered sites they do not need thicker shells, so the authors suggest that it is advantageous for the animals to have a larger visceral mass and a larger foot securing better adhesion and longer feeding periods. With increased exposure, so a thicker shell becomes more necessary. Hylleberg and Christensen suggest that, because young periwinkles are not likely to settle on the same beach as their parents, so they must possess a high degree of genetic polymorphism, allowing them to adapt, during development, to either an exposed or a sheltered shore.

In absolute contrast to the results of Hylleberg and Christensen, Currey and Hughes (1982) found no correlation between the shell strength of periwinkles and exposure to waves, from three sites on the Anglesey coast. Dudley (1980) has, however, shown that periwinkle shells from two sides of Cape Cod, Massachusetts, are noticeably different in thickness, the shells from the northern side being thinner. The average 16% more thickness in the shells from the south side means that these shells are much stronger. Dudley considers that this may be part of a general trend whereby there is a gradient of shell thickness from north to south, shells from the tropics being thicker to avoid crab predation which is more intense in these areas. It could also be that the northern shores of Cape Cod are colder, and colder waters appear to inhibit calcification in molluscs (Dudley 1980). This explanation does not require a genetic difference between the two populations, it simply reflects a temperature dependent biochemical process. In fact genetic differences between periwinkle populations are unlikely because of larval dispersal, and in North America they are a recently introduced species (Bigelow and Rathbun 1909) and would probably not have had time to undergo genetic differentiation.

It does therefore seem that there are slight variations in the thickness of periwinkle shells in some geographical areas. The reasons for this are unclear. The ideas of Hylleberg and Christensen (1977) require further investigation, though subsequent work has shown that such a relationship between exposure and shell thickness does not occur in some other areas (Currey and Hughes 1982). It has been demonstrated above that limpet shell shape, and associated physiological attributes, are not determined until they begin to develop on either high or low shores. A similar genetic fluidity may be present in periwinkles, causing these geographical variations. At present the reasons for these variations are far from clear. Many more studies of periwinkle shell thickness are required and these should be related to exposure, biological environment, degrees of predation and sea current strength and direction.

2. Dogwhelks

The fact that dogwhelks have no planktonic larval stage means that spatially isolated populations may have undergone some local genetic adaptation. Berry and Crothers (1968) and Hoxmark (1970) report how around Roscoff in Brittany on exposed shores the chromosome number is 13, and on sheltered shores 18, while intermediate shores have intermediate chromosome numbers. Hoxmark also discovered chromosome number variation on the Norwegian coast, though there was not the strict relationship to exposure noted for Roscoff. On the Norwegian coast n = 13 was dominant in all localities, so the variation could be due to other ecological conditions as well as exposure, or it could be a gradation of different chromosome forms from north to south. The former explanation is more likely as Crothers (1975a) notes how n = 13 is the main genotype on the coast of southern England.

On a number of coastlines there are quantifiable changes in dogwhelk shape with exposure as measured by length divided by aperture length (Andrews 1981; Crothers 1973, 1974, 1975a, 1975b, 1977a, 1979, 1980; Crothers and Cowell 1979; Dalby _et al_ 1978; Kitching _et al_ 1966; Moore 1936). Cooke (1895) writes:

> 'Forms occurring in very exposed situations, ... are stunted, with a short spire and relatively large mouth, the latter being developed in order to increase the power of adherence to the rock, and consequently of resistance to wave force. On the other hand shells occurring in sheltered situations, ... are comparatively of great size, with well-developed .... spire and a mouth small in proportion to the area of shell surface'.
>
> (In Crothers 1973:319)

Crothers (1973) quantified the relationship between dogwhelk shape and exposure for Pembrokeshire, and in further studies discovered that this relationship held true for the southern coasts of Devon and Cornwall (1975a), the Channel Islands and northwest France (1975b), Portugal, Spain and the Bay of Biscay coast of France (1977a) and Norway (Crothers and Cowell 1979). Andrews (1981) has also found the relationship to be true of dogwhelks around the Oronsay coast.

There are areas where the relationship between dogwhelk shape and exposure is weak or non-existent. In the Bristol Channel (Crothers 1974) there is an elongated form which neither correlates with the pattern seen in Pembrokeshire nor shows any other clear relationship with exposure. Also, populations from the eastern end of the English Channel do not show this relationship, though those from the west do (Crothers 1975a). The populations in the Bristol Channel and eastern English Channel do not show the same variation from the 'normal' exposure-shell shape relationships. Despite the positive relationship for Norway, Crothers (1979) found that this was not the case in Shetland. Although the relationship holds for many west coast sites, on the east coast the elongated form usually associated with sheltered shores is found on all but the most exposed shores.

Both the existence of a relationship between shell form and degree of exposure in many areas, and the lack of a relationship in others, points to genetic differences existing between different populations of dogwhelks. The situation is compounded by the differential predatory effect of shore crabs. Kitching et al (1966:126) state that 'two strong selective influences - wave action and predation - favour and probably completely account for the present distribution of the two types of Nucella'. The shorter dogwhelk with the larger foot is afforded more foothold and a reduced area of shell to be washed from the rocks. There seems no reason why, on purely exposure-gradient grounds, this form should not also exist on sheltered shores. Perhaps therefore it is selection against crab predation that has caused the small-mouthed elongated shell to develop on sheltered shores where crabs predominate.

Due to their differing shapes these two shell forms have differential attributes. There are more functional apical whorls in sheltered shore dogwhelks to accommodate the longer, thinner body, and these sheltered shore animals produce thicker shells. 'The thicker walls leave less room for the animal inside or, conversely, smaller animals produce thicker shells' (Currey and Hughes 1982:54). In both forms the weight of shell per gram of dry tissue (SPG) increases with shell length as the animal progresses from juvenile to early adult, but it declines thereafter as shell length increases. At all shell heights the SPG of sheltered shore dogwhelks was 1.7 times that of those from the exposed shore, while the SPG of sublittoral fringe animals was 1.5 times that of the sheltered shore dogwhelks and 2.5 times that of the exposed shore dogwhelks (Hughes and Elner 1979:74). The implications of these results for Oronsay dogwhelk exploitation are discussed below (chapter 7).

Conclusions

Hylleberg and Christensen (1977) claim that periwinkles exhibit variations in shell thickness in Limfjord, and Dudley (1980) also records this around Cape Cod. Currey and Hughes (1982), however, found no differences around Anglesey. This phenomenon remains inadequately explained.

Whereas the pelagic larval stage in periwinkle development makes genetic differences unlikely, the lack of this stage in dogwhelks has resulted in genetic and morphological differences between populations. These animals show quantifiable changes in shell shape and thickness related to differing patterns of exposure and predation.

CHAPTER 2 : SEASONAL MEAT WEIGHT CHANGES IN LIMPETS, PERIWINKLES AND DOGWHELKS

INTRODUCTION

Seasonal changes in body weight have been recorded for a variety of intertidal species (Ansell et al 1964; Blackmore 1969a, 1969b; Grahame 1973; Hughes 1972; Hylleberg and Christensen 1977; Jones et al 1979; Koloseike 1969; Williams 1970). These changes have been shown to be related to the reproductive cycle in limpets (Blackmore 1969a, 1969b; Jones et al 1979), periwinkles (Grahame 1973; Williams 1970) and dogwhelks (Moore 1938a). Rate of feeding has also been suggested as a cause of changing seasonal body weights in limpets (Blackmore 1969b; Jones et al 1979), periwinkles (Williams 1964) and dogwhelks (Moore 1938a).

Despite this body of evidence it is still necessary to systematically collect contemporary data on meat weight changes in the three species. Published studies will provide comparisons, but they are not adequate to allow a reconstruction of the seasonally varying meat values of limpets, periwinkles and dogwhelks for the Mesolithic gatherers of Oronsay. Koloseike (1969:150) states:

> 'Accurate archaeological reconstruction of the amount of mollusc meat originally collected at a site presupposes, among other things, good experimental data on populations of living molluscs. .... One might expect .... experiments on living molluscs to fall in the province of the marine biologist. But the latter have dealt very little with mollusc weight, apparently because the problem is so messy .... At present, then, it would seem that archaeologists must generate their own shellfish data if they wish to reconstruct believable prehistoric mollusc meat weights'.

Three questions require to be answered for limpets, periwinkles and dogwhelks from the present survey. Are there significant seasonal differences in body weight (referred to here as meat weight) within each species? What may cause these variations? What are the different relative meat to shell weight values of animals of differing sizes and from different tidal positions? Only when such questions are answered will we be able to attempt to consider the possible meat values represented by the midden deposits.

A. DATA COLLECTION FOR AN EXAMINATION OF SEASONAL CHANGES IN MEAT WEIGHTS

At two-monthly intervals from January to November 1980 an ecological survey was conducted on two areas of coastline, one on the east of Oronsay below Cnoc Coig midden, and the other on the west coast of Colonsay below Dun Challain (figures 2 and 9). The aim was to collect limpets, periwinkles and dogwhelks from specific tidal levels to establish if there was any seasonal change in meat weight values over the year.

1. Techniques of shellfish collection

The main sampling area was on the east coast of Oronsay below Cnoc Coig midden. Figure 9 and plates 9 to 14 show this to be an area of low rock skerries interspersed with sand. It has been classed as sheltered by Andrews (1981) using the non-biological exposure measurements of maximum fetch and frequency of wind from the direction of maximum fetch.

Figure 9 shows that the area has been divided into tidal levels. This was done with reference to Admiralty tide tables, assistance from the Institute of Oceanographic Sciences and observations on the shore at times specified by the above. Table 8 shows the Admiralty tide tables indicating the height, date and time of maximum and minimum spring tides for 1980. These have been corrected from Ullapool to Scalasaig (on Colonsay) according to the specifications of the Institute of Oceanographic Sciences. For each study month the times of spring and neap tides were obtained from the Institute of Oceanographic Sciences, so observations on the shore at relevant times allowed the shore to be divided into tidal levels as described in chapter 1.

The different collection zones are shown in figure 9. Low shore limpets, periwinkles and dogwhelks were collected from between ELWS to just below MLWN, and upper shore animals from MTL (midway between MLWN and MHWN) to MHWS. At the times of ELWS which, during the collecting months were March and September (table 8), it would be possible for gatherers to reach other skerries which could not be reached without

TABLE 8 : PREDICTED SPRING TIDES FOR 1980, AND COLLECTION DATES

	MINIMUM LOW TIDE (M)			MAXIMUM HIGH TIDE (M)			SAMPLE DATES*	
MONTH	HEIGHT	DAY	HOUR	HEIGHT	DAY	HOUR	ORONSAY	COLONSAY
JANUARY	0.338	20	13 to 14	4.254	19	6 to 7	JANUARY 19 and 20	-
FEBRUARY	-0.105	19	14 to 15	4.405	18	6 to 7		
MARCH	-0.891	18	12 to 13	4.148	17	5 to 6		
APRIL	-0.310	1	12 to 13	4.130	12	5 to 6	MARCH 29	28
APRIL	-0.296	16	12 to 13	4.178	16	5 to 6		
MAY	0.287	1	12 to 13	3.599	31	18 to 19		
MAY	0.321	29	11 to 12	3.661	30	18 to 19	JUNE 1	MAY 31
JUNE	0.374	12	11 to 12	3.871	14	18 to 19		
JULY	0.295	30	1 to 2	4.075	30	19 to 20	JULY 27	28
AUGUST	0.083	29	1 to 2	4.310	27	18 to 19		
SEPTEMBER	0.094	24/5	24 to 1	4.606	25	18 to 19	SEPTEMBER 24 and 25	26
OCTOBER	-0.099	24/5	24 to 1	4.389	23	17 to 18		
NOVEMBER	0.385	23/4	24 to 1	4.623	22	17 to 18	NOVEMBER 23	22
DECEMBER	0.634	6	23 to 24	3.990	10	6 to 7		

* Note - this denotes the collection from the low shore only, upper tide animals may have been collected on adjacent days

swimming or by boat at MLWS. One such skerry can be seen as being the most seaward in plates 9, 11 and 14. This was not included in the present sample area.

Table 8 shows that all collections were done within three days of maximum lowest spring tide for that month. There is very little difference in tidal heights over this period of time. Obviously collections were not done at night but on the corresponding daytime lowest tide. The lower shore was sampled on the closest day possible to the lowest tide, and the upper shore on adjacent days.

Plate 9 shows the upper shore in the foreground, with the tide standing at MLWS (on June 1st). The person is standing just below the level reached at MLWN. Note the lowness of the rocks, a factor greatly aiding collection. This plate also shows the decrease in fucoids above MHWN. The skerry in the foreground in plate 10 has its upper part at MHWN. Beyond this are high tide rocks not included in the survey. In plate 11 the water is just above MLWS. This view incorporates much of the low shore collecting zone up to around MLWN. Plate 12 shows the water at MLWN. Plate 13 is a close view of one of the low shore skerries with the water at very slightly above MLWS. Note the denser fucoid cover in comparison to the upper shore zone in plates 9 and 10. Due to the height of such skerries as shown in plate 13, the collection of low tide species was restricted to the lower portion of the rock. In plate 14 the water is at MLWN and the person standing at just below MHWN.

Table 9 summarizes the areas of shore that were sampled. In future these will be referred to by abbreviations, which are also given in this table.

When collecting the shellfish a deliberate attempt was made to gather animals of varying sizes above the minimum size of 18-19 mm shell length for limpets, 18 mm for periwinkles and 20 mm for dogwhelks. There are very few midden limpets below 19 mm, for reasons discussed in chapter 6. This was therefore chosen as the lower size limit. It was easy to recognize limpets of this size on the shore, yet when in doubt pre-set calipers were placed over the animal. Some limpets

TABLE 9 : AREAS OF SHORE AND SPECIES SAMPLED

SAMPLE AREA AND SPECIES	ABBREVIATIONS
Oronsay low shore limpets	OLL
Oronsay high shore limpets	OHL
Colonsay low shore limpets	CLL
Colonsay high shore limpets	CHL
Oronsay low shore periwinkles	OLP
Oronsay high shore periwinkles	OHP
Colonsay periwinkles	CP
Oronsay low shore dogwhelks	OLD
Oronsay high shore dogwhelks	OHD
Colonsay low shore dogwhelks	CLD

between 18-19 mm were also included when there were not enough of the smaller animals of the desired size. The middens also contain hardly any periwinkles below 18 mm (chapter 6) so these were not sampled from the modern shore. It is not possible to tell the exact size of the midden dogwhelks because the shells are generally broken, yet it is unlikely that many are below 20 mm (chapter 6).

Periwinkles and dogwhelks were simply picked off the rocks, but limpets had to be prised off with a penknife. If caught unaware they were easy to remove, but often they became aware of imminent doom and clamped down tightly to the rocks. In this case they could be removed either by a sharp sliding motion with the knife, or by gently inserting the knife under the shell and giving a slight twist. The former method was found to be best for the larger limpets and the latter for the smaller. Any that were broken were discarded.

More animals were collected than were actually needed for processing, to allow for discards due to death or damage that may occur after collection. The numbers required for processing are given in table 10 along with the main reasons for choosing these specific sample sizes.

When deciding on sample size a number of variables had to be considered. Enough samples must be taken to allow for any variations within the sample area. For instance there must be an adequate coverage of all size ranges such that any results are not reliant on just a few individuals of a specific size. Periwinkles and dogwhelks show relatively less size variation than do limpets, so their sample size may be smaller. Koloseike states:

> 'Unfortunately for the experimenter, molluscs exhibit large inter-specimen variation. .... Because they are not carbon copies of each other, numerous specimens must be taken at any given time and collection point in order to establish an accurate average meat/shell ratio and a reasonable measure of deviation from this average. In general, the more specimens taken the closer the sample ratio is to that of the actual mollusc population. But the processing of large numbers of specimens is also costly in time and effort'.
> (Koloseike 1969:150)

TABLE 10 : PRINCIPAL REASONS FOR SAMPLE-SIZE SELECTION

SAMPLE	SAMPLE SIZE PER COLLECTION	MAIN FACTORS GOVERNING SAMPLE SIZE
OLL	120	Most numerous type in the middens, with relatively great size and shape variations. Any larger sample would drastically reduce stocks after the first few visits.
OHL	90	Any larger sample would drastically reduce stocks after the first few visits.
CLL, CHL	55	Any larger sample would drastically reduce stocks after the first few visits, especially of CHL. Samples only required for comparison with Oronsay.
OLP, OHP, CP, OLD OHD, CLD	45	OHD relatively scarce. Less size variation than limpets. Dogwhelks especially cannot be regarded as a major food resource in the middens.

This latter point is an important one. Processing is extremely time-consuming, so a balance must be sought between obtaining a representative sample size and working within constraints of time.

Another consideration must be the total number of individuals on the shore. Within the specified sample area there had to be enough individuals remaining for the sixth visit. This was one of the main restrictions upon the number of high shore limpets from both Oronsay and Colonsay. Another consideration is the relative importance of the different species with regards to an interpretation of the midden material. The predominance of low shore limpets in the middens means that special attention should be paid to these on the modern shore (chapter 6).

2. Specific collection areas

Oronsay low tide

This extends from ELWS to just below MLWN. Figure 9 and plates 9, 11 and 13 show it to comprise low rock skerries interspersed with sand. The skerries between ELWS and MLWS contain thick masses of *Laminaria saccharina*, *Laminaria digitata* and *Fucus serratus*, with some *Fucus vesiculosus*, *Arthrocladia villosa*, *Ascophyllum nodosum* and *Ulva lactuca*. Rocks higher up the shore contain higher proportions of *Fucus vesiculosus* and *Ascophyllum nodosum* and also large amounts of *Fucus serratus*.

The distributions of limpets, periwinkles and dogwhelks with relation to fucoids and barnacles are discussed in chapter 3. Here it is sufficient to note that as a general rule the largest limpets can be found adjacent to and under the fucoids and on bare rock (inhabited by microscopic algae) and the smaller limpets are also found on bare rock and amongst the barnacles. Periwinkles occur in occasional clusters of numerous individuals (sometimes many hundreds) anywhere where detritus accumulates such as in cracks and under older fucoids. They also occur individually on the rocks, usually on or adjacent to fucoids. There are more periwinkles occurring individually at the lowest tidal levels. Dogwhelks feed on barnacles and so they are found in greatest concentrations where their prey are most dense. Thus the three main habitat types, fucoids, barnacles and bare rock, provide the desired variety of sizes within the three shellfish species.

Specimens were only collected from the lower parts of the rocks and up to 0.5 m below the water surface. Collection was begun an hour before maximum low tide in the upper part of the zone, then the lowest part was sampled at the time of maximum low tide. Table 8 shows that sample dates were either on, or close to, the days of lowest spring tide. Within three days either side of this date there is very little difference in the tidal height.

Oronsay high tide

This extends from MTL to MHWS (Figure 9 and plates 9, 10 and 14). No samples were taken from rockpools in this area, only from the open rock. Fucoid cover is less dense above MHWN where there is more dry bare rock and lichens, especially Xanthoria parientina (plate 9). There are concentrations of Pelvetia canaliculata and Fucus spiralis, and around MTL Fucus vesiculosus. Many rocks have heavy barnacle encrustation.

The collection of variously sized limpets proved to be more difficult than on the lower shore. The habitats of the upper shore are much less diverse, and consequently so are the quantities of different sized limpets. Due to the lack of damp sheltered habitats for spat settlement (chapter 3) there are much fewer small limpets in this zone. Detailed searching was necessary to locate enough smaller individuals.

Periwinkles occurred largely in clusters of small animals, in contrast to the larger more isolated individuals on the lower shore. Dogwhelks were again found feeding on the barnacles, though in a much lower density than on the lower shore. Neither dogwhelks nor periwinkles occurred in any quantity above MHWN, most being between this level and MTL.

Colonsay collection area

This is on the very exposed western Colonsay coast below Dun Challain (figure 2, plates 15, 16, 17 and 18). Sample sizes are smaller (table 10) and provide a contrast to the sheltered eastern Oronsay coast. As on Oronsay the area was divided into low and high shore, the former being from ELWS to MTL and the latter from MTL to MHWS. Plates 15 and 16 are of the lower shore, plate 17 looks from the upper to lower shore, and plate 18 is of the upper shore. These show the coast to be more dissected and steeper than on Oronsay, being composed of continuous rock instead of skerries. The steepness, combined with the high exposure, means that the tidal zones are extended upshore by splash (chapter 1).

There is less habitat diversity on this exposed shore. Plates 15 and 16 show there to be moderate to dense barnacle cover yet a light, patchy fucoid cover, concentrated largely below MTL. At the lower levels there is Fucus serratus and above this Ascophyllum nodosum. Pelvetia canaliculata occurs at higher levels.

Limpets are concentrated at lower levels with relatively few high tide specimens. At low levels there are much fewer large limpets than on Oronsay, due probably to the high degree of exposure and reduced food supply in comparison to Oronsay. A large proportion of the lower limpets are Patella aspera which favour exposed low level habitats (chapter 1). These have not been treated separately because of the uncertainty of identification outlined by Ebling et al (1962) and considered in chapter 1. It is likely that over 50% of the low level limpets are Patella aspera, so any differences in meat weight may be due to this high proportion of P. aspera (no P. aspera were noticed on the Oronsay sample area).

There are very few dogwhelks on the upper shore, and virtually no periwinkles on the lower shore, so only lower shore dogwhelks and upper shore periwinkles were collected. The dogwhelks were feeding on the densest patches of barnacles, though it is unclear why there were so few on the upper mid-shore barnacles. These were the typical exposed shore form as described by Crothers (1973, 1974, 1975a, 1975b, 1977a, 1979) with short body whorls and large apertures. They were generally smaller than on the low shore at Oronsay, and none of the occasional large specimens could be found.

Periwinkles do not have the tenacity of dogwhelks, so could not occur on the rocks directly exposed to wave action. Instead they clustered in sheltered cracks and under fucoids. These habitats were only present around mid to upper mid tide level. All periwinkles were small and there were none of the larger animals occurring individually as on Oronsay. There were far fewer dogwhelks and periwinkles than on Oronsay.

3. Processing of samples

Shellfish were bagged according to species and area of collection. For accurate and consistent weight values it was considered necessary that they remain alive until reaching the laboratory (at Sheffield), so they were kept in sea water which was changed daily while on the islands. Collection on the islands took between four to six days and processing began immediately on arrival at the laboratory. Periwinkles and dogwhelks live longer than limpets so these were collected first and processed last, whilst limpets were collected last and processed first. When processing, any dead animals were discarded. The following procedures were then adopted.

Limpets

They were laid on absorbent paper then shaken and wiped dry. Any barnacles, algae or other objects were removed from the shell. The purpose of shaking was to remove any water trapped by the animal within the shell. The animal was then weighed to .00 gram. Each animal was placed in an individually numbered bag and frozen. Freezing caused instant and uniform death. This did not alter the meat weight, as some animals were weighed before freezing and again afterwards, and there was no difference in meat weight.

To obtain dry meat weight, samples were removed from the freezer and placed in hot (not boiling) water for around five to ten seconds, whereupon they come cleanly out of their shells. Each limpet was treated individually so there was no possibility of confusing different limpets during the experiments (each bag was numbered instead of writing a number on each shell, as this proved to be quicker). The limpet flesh was placed in individually numbered aluminium containers and dried at 105°C for 24 hours. It was then weighed to .00 gram. Weights were taken within an hour of removal from the oven (about 150 limpets were dried in the oven at any one session). To check if the dry meat weight increased whilst waiting to be weighed, some samples were weighed immediately on removal from the oven, then after about one hour, and there was seen to be no difference. Shells were air dried for around 24 hours and then weighed to .00 gram. Tests on selected shells showed that they were dry after three hours, but for safety they were left for 24 hours.

Periwinkles and dogwhelks

As with limpets these were laid on absorbant paper then shaken and wiped dry, and shells were cleaned. The whole weight was taken to .00 gram and each individual placed in a numbered bag. The animals were then frozen. To remove their flesh periwinkles were placed in nearly boiling water for around one minute, after which time most animals could be removed from their shells with a pin. Those that could not be removed, or those in which some meat was left inside the shell, were broken with pliers. Care was taken to retain all the broken shell. Dogwhelks could not be removed from their shells so these were all broken and the fragments retained. (The majority of midden dogwhelks are broken - see chapter 6.) The opercula were not included in the dry meat weights, which were obtained in the same way as for limpets. Shells and shell fragments were air dried for 24 hours, then weighed to .00 gram.

Tests on data accuracy

As processing progressed it was considered necessary to make certain checks on methodological accuracy. To establish if the retaining of the shellfish in bags of sea water affects their whole weight, a selection was weighed immediately after collection and again on arrival in the laboratory. The results are shown in table 11. It may be seen that weights are not very different, though there are greater differences in limpets than in periwinkles and dogwhelks. There is no dominant trend towards being either heavier immediately after collection or in the laboratory, instead some are slightly lighter and some slightly heavier on reaching the laboratory. These variations are due to differing water content within the animals, and they emphasize the importance of using dry meat weight as a constant measurement of seasonal change in meat weights.

The importance of water within the limpet shell is demonstrated in table 12. When only the outside of the shell is dried with a paper towel the whole weight is heavier than when the animal is shaken hard ten times to remove some internal water. Thus, all shells were shaken before taking the whole weight. Even then some water remains in the animal, so all comparisons of meat weights were done using dry meat weight.

Limpets and periwinkles have been placed in hot water to allow clean removal from their shells. Tests were carried out to establish if this may cause a reduction in meat weight values. After removal from the shell the wet meat of the two species was weighed and found to be slightly lower than it was when calculated by the formula:

Whole Weight - Shell Weight = Wet Meat Weight

This discrepancy may be due to either water loss or to a reduction in the meat content when heated.

A number of tests were devised to establish the degree of meat loss after heating. Table 13 expresses the results of tests on limpets, and tables 14, 15 and 16 of tests on periwinkles. A beaker was weighed and then six limpets of varying sizes were thoroughly cleaned and heated for 30 seconds in deionized water (grade 1). They were then removed and weighed for wet meat weight. The water in the beaker was then boiled until all had evaporated, and thoroughly dried in the

TABLE 11 : WHOLE WEIGHT VALUES OF SOME LIMPETS, PERIWINKLES AND DOGWHELKS ON COLONSAY/ORONSAY AND IN THE LABORATORY

(-) = weighed less immediately after collection than in the laboratory

COLONSAY/ORONSAY	LABORATORY
Low Shore Limpets	
7.1 (-)	7.3
2.8	2.8
34.4 (-)	34.7
13.4	12.2
10.5 (-)	11.3
7.1 (-)	7.9
2.6	2.6
34.2	33.6
8.5 (-)	9.5
11.2	10.4
2.9 (-)	3.2
12.6	11.2
4.8	4.8
19.0	18.5
High Shore Limpets	
18.6 (-)	19.1
15.3 (-)	16.5
6.1	6.1
28.9 (-)	29.5
21.4	21.4
2.7 (-)	2.9
5.6 (-)	6.0
1.2	1.2
8.7	7.5
Periwinkles	
6.3	6.2
6.8 (-)	6.9
7.7	7.4
8.5	8.5
7.5	7.0
4.8	4.8
6.4	6.4
3.7 (-)	3.8
4.3	4.3
5.8	5.8
Dogwhelks	
4.2	4.2
2.3	2.3
3.4 (-)	3.5
5.5 (-)	5.6
4.0 (-)	4.3
3.9	3.9

TABLE 12 : WEIGHTS OF LOOSE INTERNAL WATER IN LIMPETS

Weight when just dry the outside of the shell	Weight when shook the shell to remove some internal water	Difference
10.64	10.36	0.28
24.98	24.75	0.23
5.88	5.72	0.16
6.62	6.49	0.13
17.00	16.67	0.33
29.16	28.99	0.17
16.96	16.53	0.43
2.19	2.15	0.04
4.66	4.56	0.10
8.82	8.79	0.03
15.85	15.75	0.10
7.27	7.14	0.13

TABLE 13 : CHANGES IN MEAT WEIGHT AFTER HEATING 6 LIMPETS FOR 30 SECONDS TO FACILITATE REMOVAL FROM THEIR SHELLS

Whole weight before extracted	Extracted meat (after heated)	Shell weight	Whole weight minus shell weight (calculated wet meat weight)	Difference between calculated and actual meat weight
6.55	2.64	3.76	2.79	0.15
11.16	5.35	5.59	5.57	0.22
12.29	5.53	6.47	5.82	0.29
4.84	1.19	3.11	1.73	0.54
29.46	9.05	19.77	9.69	0.64
6.66	2.81	3.73	2.93	0.12

Weight of 6 limpets before heating = 70.96 g
Weight of 6 limpets after heating = 69.00 g
Therefore weight loss = 1.96 g
Residue in beaker after boiled dry = 0.04 g

TABLE 14 : CHANGES IN MEAT WEIGHT AFTER HEATING 10 PERIWINKLES FOR 1 MINUTE TO FACILITATE REMOVAL FROM THEIR SHELLS

Weight of 10 periwinkles before heating = 64.53 g

Weight of 10 periwinkles after heating = 61.84 g

Therefore weight loss = 2.69 g

Residue in beaker after boiled dry = 0.17 g

TABLE 15 : CHANGES IN MEAT WEIGHT AFTER HEATING 10 PERIWINKLES FOR 30 SECONDS TO FACILITATE REMOVAL FROM THEIR SHELLS

Weight of 10 periwinkles before heating = 67.64 g

Weight of 10 periwinkles after heating = 67.03 g

Therefore weight loss = 0.61 g

Residue in beaker after boiled dry = 0.07 g

TABLE 16 : CHANGES IN MEAT WEIGHT AFTER BOILING 10 PERIWINKLES FOR 2 MINUTES TO FACILITATE REMOVAL FROM THEIR SHELLS

Weight of 10 periwinkles before boiling = 50.04 g

Weight of 10 periwinkles after boiling = 47.04 g

Therefore weight loss = 3.00 g

Residue in beaker after boiled dry = 0.36 g oven at 50°C for another two hours. The beaker was weighed again and found to have increased in weight by .04 g which must represent solid material originating from the limpets. This is not a significant increase for six limpets. Table 13 shows that prior to heating, the six limpets weighed 70.96 g and after heating 69.00 g. This difference of nearly 2 g must be largely due to water loss, as only .04 g may be explained by actual loss of solid material that would contribute towards meat weight.

Periwinkles also showed a higher calculated than actual meat weight, so the same experiment was applied. Ten periwinkles were cleaned and placed in deionized water (grade 1) in a beaker of known weight. They were heated for one minute then removed. The beaker was then boiled dry and dried in the oven at 50°C for two hours. The beaker was again weighed and was seen to have increased by 0.17 g (table 14). For ten periwinkles this is a negligible amount, though more than for the limpets, probably because they were heated for longer. The difference in total weight of the ten animals before and after heating was shown to be 2.69 g, the majority of which must be explained by water loss.

The experiment was repeated in exactly the same way for ten more periwinkles, but this time they were heated for 30 seconds. Now the increase in weight was only 0.07 g, virtually the same as the limpets, yet the difference in weight between the animals prior to and after heating was only 0.61 g (table 15).

A third experiment was conducted with periwinkles, where they were actually boiled (as opposed to just placed in hot water) for 2 minutes (table 16). This produced the greatest amount of residue in the beaker (0.36 g), though between ten periwinkles this is not a significant loss. There was also a greater decrease in total weight of the animals before and after boiling (3.0 g), though this is only slightly greater than the 2.69 g decrease after heating for one minute. It therefore seems that it does not really matter if the animals are placed in near boiling or boiling water, and that most weight loss occurs by around one minute.

Thus the reduction in meat weight caused by heating is insignificant. To overcome fluctuations in water content all meat weight values will be expressed as dry meat weight. When extracting the meat from the Oronsay samples limpets were only heated for up to 10 seconds and periwinkles for less than 1 minute. The residue remaining in the beakers probably represents some solid particles from inside the shell that could not be removed on initial cleaning.

The recording of data

It is considered unnecessary to include the raw data in this thesis. Once all the data had been gathered it was put into a filestore on the Sheffield University computer, where it could be accessed for the application of statistical tests. All data is now held by myself on computer tape.

Conclusions

Limpets, periwinkles and dogwhelks were collected from upper and lower shore areas on the sheltered eastern coast of Oronsay every second month throughout 1980, and comparative samples were taken from the more exposed western coast of Colonsay. Deliberate selection was made for a variety of sizes above the specified minimum. These were kept alive in sea water and returned to the laboratory at Sheffield, where information was obtained on whole weight, dry meat weights and shell weight for each individual shellfish.

B. PATTERNS OF SEASONAL CHANGES IN MEAT WEIGHT

1. Methods of data presentation

The above data has been used to test for seasonal changes in meat weight. The data are divided into species (limpets, periwinkles and dogwhelks) and tidal position (low shore and high shore). In future the word 'group' will be used to describe distinct species from distinct tidal positions, for instance Oronsay low tide limpets, Colonsay high tide limpets, Oronsay low tide dogwhelks; all are distinct groups. Seasonal changes in meat weights are established with relation to shell weight, which does not exhibit seasonal change.

Firstly scattergrams were produced for all groups using an SPSS computer programme (Statistical Package for the Social Sciences, formulated by Nie et al 1970) where the x axis = shell weight and the y axis = dry meat weight. Examples are given in figures 10, 11, 12 and 13. This allowed the distribution of points to be viewed to establish obvious trends and data patterns.

Secondly, for each group plots were made of the mean ratio of shell weight to dry meat weight (hereafter referred to as ratio S/M) against each collection month (figures 14, 15, 16, 17, 24, 25, 26, 32, 33, 34). SPSS was used to calculate ratios S/M and standard errors.

Groups were then divided into sizes by reference to shell weight, and the three species treated separately. Limpets were divided into small, medium and large (figures 18, 19, 20 and 21), and periwinkles and dogwhelks into small and large size groupings (figures 27, 28, 29, 35, 36, 37) by reference to the original scattergrams. From these it was seen that limpets with shell weights less than 3.5-4.0 g had the greatest relative amount of meat to shell. In animals between 3.5-4.0 g and 9.5-10.0 g the values moved slightly closer to the shell weight axis. Above this points generally occurred even closer to the shell weight axis, though the scatter was now greater. Figures 10 and 11 show Oronsay low shore limpets from November and Colonsay high shore limpets from September as examples. These 'cut-off-points' are not definite breaks of slope, but they represent the approximate position whereby the points generally change direction.

Two sets of plots were obtained, using both 3.5 g and 9.5 g, and 4.0 g and 10.0 g shell weight as cut-off-points dividing the small, medium and large limpets. These proved not to be significantly different, so it was decided to use 3.5 g and 9.5 g as these allowed for a more even distribution of limpets in each category. Even so, the largest size group usually only contains a few individuals.

The range of sizes was not so great for periwinkles and dogwhelks, and the sample sizes were smaller, so they were divided into two groups. For both these species, especially dogwhelks, the scatter of points on the scattergrams of dry meat weight and shell weight were wider than for limpets, and any trends far less obvious (as seen in figures 12 and 13). Nevertheless, at around 4 g shell weight OLD, OHD and CLD showed a general trend to a proportionally greater increase in meat weight with size (figure 12), this being the opposite to both limpets and periwinkles. OHP and CP showed a general trend towards an increase in relative shell/meat weight with size above around 4 g shell weight. OLP however, being larger, did not show this trend below 6 g shell weight (figure 13). All dogwhelk groups and OHP and CP were therefore split into smaller and larger animals at 4 g shell weight, whereas OLP were divided at 6 g shell weight.

2. Results

Limpets

Limpets show significant seasonal variations in meat weight, though the pattern and intensity of these variations alter with location and tidal position. This is demonstrated in figures 14, 15, 16 and 17 which represent OLL, OHL, CLL and CHL respectively. In these figures an increase in ratio S/M means a decrease in relative meat weight. The vertical bars refer to standard error, so where these overlap the differences between months is not significant, and where they do not overlap there is a significant difference.

To test the significance of variations between different sizes, and between different months, Student's T-tests were performed on selected values (table 17). From this it can be seen that where the standard errors overlap the difference is not significant to the 5% level, where the bars nearly touch then the difference is barely significant, yet the wider apart the standard error bars the more significant are the differences. For instance OHL (figure 19) in January show no significant difference between ratio S/M of small and medium limpets. In OLL (figure 18) for January the difference between small and medium limpets is just significant at the 5% level, and in CHL (figure 21) for July there is a very significant difference between the medium and large limpets.

As discussed in chapter 1, spawning usually occurs between September and November, and once the animals mature, rough weather is needed to trigger mass spawning. Seasonal trends in meat weight may be related at least in part to the reproductive cycle, though this cannot fully explain these distributions. There is general agreement about the size at which sexual maturity is reached. Choquet (1968:460), Das and Seshappa (1948:654), Orton (1928a:856) and Orton <u>et al</u> (1956:161) consider that the animals mature at around a shell length of 10 mm, Fretter and Graham (1976:27) say it occurs at between 10-15 mm, and Blackmore (1969a:205) at around 15 mm. All animals in the present survey are above 15 mm.

Figures 14, 15 and 17 show that meat weight values are lowest during the winter months. In the early part of the year there is an increase in meat weight to May-June, and after September there is a sharp decrease in meat weight to November. This decrease will represent spawning within the period September to November. By November the meat weight values have more or less decreased to their January levels. OHL (figure 15) are a classic representation of how meat weight gradually increases to the time of spawning, then sharply decreases. CLL (figure 16) do not show this decrease between September and November, probably indicating that they have not yet spawned. Spawning must occur after November for the meat weight to fall to the March level (there was no January sample). This evidence is contrary to that of Orton (1946), Orton <u>et al</u> (1956) and Thompson (1979) who,

TABLE 17 : T TESTS (1 tailed) TO EXAMINE THE SIGNIFICANCE OF DIFFERENT RATIO S/M VALUES

GROUP	T VALUE	DEGR.FR.	TABLE (.05)	COMMENTS
OLL1 S-M	1.93	99	1.66	Just significant at 5% level, not at 2.5% (1.98). On figure 18 standard errors nearly meet.
OLL1 M-L	3.99	58	1.67	Very significant, even to 0.0005. On figure 18 there is a good separation of standard errors.
OLL2 S-M	1.04	104	1.66	Not significant. On figure 18 there is an overlap of standard errors
OLL2 M-L	2.31	48	1.68	Significant difference
OHL1 S-M	0.40	64	1.67	Not significant
OHL2 S-M	0.97	72	1.67	Not significant
OHL3 S-M	3.01	78	1.67	Significiant difference
OHL3 M-L	1.81	64	1.67	Just significant at 5% level, not at 2.5%
OHL5 S-M	1.58	84	1.67	Not significant
CLL2 S-M	1.76	50	1.67	Just significant
CLL5 S-M	0.91	51	1.67	Not significant
CHL4 S-M	1.64	42	1.68	Not significant
CHL4 M-L	3.79	27	1.70	Very significant
OLP1	1.23	43	1.68	Not significant
OLP2	0.86	43	1.68	Not significant
OLP4	2.17	43	1.68	Significant difference
OHP1	0.66	43	1.68	Not significant
OHP3	0.15	36	1.68	Not significant
OHP6	0.21	43	1.68	Not significant
CP4	0.39	43	1.68	Not significant
CP5	1.48	43	1.68	Not significant
OHD2	1.35	43	1.68	Not significant
OHD3	0.85	43	1.68	Not significant
OHD4	0.42	43	1.68	Not significant
CLD3	0.49	43	1.68	Not significant
CLD4	1.23	43	1.68	Not significant
CLD6	1.18	43	1.68	Not significant

1 = January
2 = March
3 = May-June

4 = July
5 = September
6 = November

S = Small
M = Medium
L = Large

as reported in chapter 1, consider that P. aspera spawn very slightly earlier than P. vulgata. It is estimated that over 50% of CLL are P. aspera.

OLL, CLL and CHL all have meat values peaking at May-June, then decreasing to July. In CHL the differences between May-June and July are not significantly different, as there is a slight overlap in standard error, yet as the patterns are so evident in OLL and CLL perhaps this pattern is realistic. Spawning will not occur just before July so another explanation must be sought. Professor F.J. Ebling (pers. comm.) has suggested that this early peak could be due to intense spring feeding occurring on the new flush of algae after the reduced feeding of winter. Jones et al (1979) also note the importance of feeding early in the year in causing an increase in meat weight.

Blackmore (1969b) records high meat weight values for limpets from Robin Hood's Bay during the spring, declining sharply to July. He interprets this not as limpets consuming more algae at this time of year, but ingesting more heavy inorganic debris with the algae. At Robin Hood's Bay during the early part of the year algal cover was minimal, yet during the summer there was more available. For instance in February 1965 Blackmore recorded 8.6% organic matter in a limpet gut and 34.7% in August the same year. It could be therefore that as more algae becomes available less rock is incorporated into the gut.

As only total limpet dry weight was calculated for the Oronsay and Colonsay limpets it is not possible to say which of these two alternatives applies in this situation; both are possible. Thus it seems that both the reproductive cycle and feeding patterns may affect meat weights.

It was noted in chapter 1 that a number of studies have found an increase in growth rate during the spring (Blackmore 1969a; Choquet 1968; Orton 1928a, 1928b; Russell 1909). This may be attributed to the increase in feeding during this period. Certain of these studies also found there to be a slight reduction in growth rate during mid-summer (Choquet 1968; Orton 1928a, 1928b). It may be this that is reflected in the reductions in meat weight between May-June and July seen in figures 14, 16 and 17.

Figures 14 to 17 show there are slight differences in intensity of fluctuations between the four sites. This is to be expected due to biological and physical variations between high and low shore, and between the Oronsay and Colonsay coastlines (pers. comm. Professor F.J. Ebling). Indeed, given these variations, the patterns are remarkably similar. On Colonsay the upper shore limpets have overall higher meat values than those from the lower shore. This could be due to the high degree of exposure being more inhibiting to growth on the more wave-battered lower levels. Further up the shore some deep crevices provide slight protection from the main force of the waves. Perhaps the greater proportion of P. aspera at the lower levels is also significant.

Koloseike (1969) states that, as a general rule, in marine molluscs shell weight continues to increase more rapidly than flesh weight with increased age, particularly when the mollusc is mature. Larger older specimens therefore tend to have a relatively greater ratio of shell to meat than do smaller specimens. Jones et al (1979) found this to be the case for limpets aged up to 4 years (the total study period) on the east coast of Scotland. Shell weight was shown to increase relatively faster than length due to a simultaneous increase in breadth and height, and to shell thickening. Blackmore (1969b) also reports this phenomenon for limpets from Robin Hood's Bay. From a sample of 1,000 limpets collected from southern Arran, Russell (1909:250) noted how there was a considerable increase in shell thickness over a length of around 25 mm.

This increase in relative shell weight with size is shown by figures 18, 19, 20 and 21 representing OLL, OHL, CLL and CHL respectively. Here each group has been divided into small, medium and large as described above, with small limpets being below 3.5 g, medium between 3.51 and 9.5 g, and large above and including 9.51 g shell weight. In all cases, with the exception of OLL July, the small possess more meat with relation to shell than do the medium, and in every case the large have relatively more shell weight, though in OLL July and September there is an overlap of standard error bars, indicating that the difference is not significant.

When divided into three size classes (figures 18 to 21) the seasonal variations in ratio S/M generally maintain the same pattern. For instance CHL (figure 21) follow the same seasonal pattern for all sizes. Although the fairly large standard errors mean that statistically there is no significant difference between months for each size of limpet, the fact that this exact pattern is followed by all three sizes strongly suggests that the pattern is real. CLL (figure 20) also show generally the same seasonal variation between small and medium limpets (there were too few large limpets for meaningful consideration). As indicated in figure 16, it seems that spawning occurred after November. It is possible that some of the smaller limpets began spawning after September but, as can be seen by the standard errors, any differences are not significant.

The different sizes at Oronsay high tide level (figure 19) also show generally the same pattern. Although the smallest animals peak in meat weight in May-June, the medium in September and the large in both, the overall effect, as seen in figure 15, is a slight peaking in September. The decline after spawning is evident in all sizes, and as mentioned above, peaks in early summer probably represent increased feeding.

As with figure 14, figure 18 (OLL) shows by far the greatest range of meat weight values over the year. In July and September there is no great difference between the sizes, all have fairly high meat weights, especially the medium sized limpets, and all decline sharply after September. Both the large seasonal range of values and the similarity of sizes in summer probably reflect the shore environment. The richer biological habitat on the lower shore would mean increased feeding in summer, hence the unusually large difference between summer and winter. It would also mean that larger limpets (which by implication need more food) could increase in weight by a greater amount than would otherwise be possible.

The consistently greater meat weight of the upper shore compared to the lower shore limpets on Colonsay demonstrated in figures 16 and 17 is not so marked when viewing different sized limpets (figures 20 and 21). Only in March and May-June is there a significant difference between the small and medium low level limpets, yet those from the upper shore show a pronounced difference between the three sizes for each month. The small and medium upper shore limpets show the greatest relative meat weight values. For both Oronsay and Colonsay the differences in ratio S/M between small and medium sized limpets are generally less for lower than upper shore animals.

Discussion

A number of trends therefore emerge concerning changing seasonal meat weight values in limpets.

1. Lowest meat weight values occur in the winter months.

2. The reproductive cycle affects these values. In all but CLL there is a distinct drop in meat weight between September and November. CLL might spawn after November in 1980, which could possibly reflect the high proportion of P. aspera in this population. If so, this is in contrast to the accepted idea that they always spawn before P. vulgata.

3. These patterns cannot fully be explained by the reproductive cycle because of frequent peaks in May-June, which are probably due to increased feeding on the spring algal bloom.

4. Seasonal changes in growth rate outlined in chapter 1 are reflected in the changing meat weight data. There is a reduction in growth rate and meat weight during the winter and a corresponding increase in spring. Some researchers have also found a slackening of growth rate in mid-summer (Choquet 1968; Orton 1928a, 1928b) which correlates with the reduction in meat weight during this period observed in OLL, CLL and CHL.

5. Small, medium and large limpets show progressively less meat weight and more shell weight with increased size. This is generally more pronounced in high than low shore animals.

It would be a mistake to attempt to try and explain every small feature of these patterns. The significance of both the reproductive cycle and rates of feeding have been demonstrated, yet to go beyond this involves too much unfounded speculation (pers. comm. Professor F.J. Ebling, Dr. E. Williams). Given the great variations in exposure, biological habitat and tidal position of the four sites, these results are in fact remarkably consistent.

Other Studies

Similar results have been obtained by Blackmore (1969b) using ash-free dry flesh weight of a standard low water limpet from Robin Hood's Bay (figure 22). From January to April the meat weight is minimal, then increases rapidly from May to August. Blackmore considers this to be due to both increased feeding and gonad development, and that the drop after September is due to spawning.

Jones *et al* (1979) studied seasonal variations in meat weight over a four year period on the east coast of Scotland (figure 23). As with the Oronsay and Colonsay data, and that from Robin Hood's Bay, minimum meat weight values occur in the winter months around January. They reach a maximum just prior to spawning around September, after which time there is a rapid meat weight decrease. There are slight differences to the Oronsay and Colonsay data. For instance, in no season does the maximum meat weight occur in May-June, and only in 1976 is there a decrease in meat weight from May to July, which the authors make no attempt to explain.

It is evident from figure 23 that , although the seasonal patterns are similar over the years, there is a significant difference in magnitude of maximum and minimum meat weights, with 1975 and 1976 being particularly good years for flesh production. The decrease in meat weight due to spawning is seen to be proportional to the size of the summer maximum. Except for the late spawning CLL (figures 16 and 20) this is also seen to be the case for Oronsay and Colonsay. The importance of the reproductive cycle in explaining these patterns is indicated by the fact that in both 1974 and 1977 gonad development was negligible, as no animals were observed with gonad indices greater than Stage 2 (gonad indices developed by Orton et al, 1956, are discussed in chapter 1). Contrary to this, in September 1975 and 1976 many animals had gonads at Stage 5. Jones et al also note the significance of feeding intensity in altering meat weights, and they conclude that the rapid increase in condition which occurs in spring is due largely to increased feeding.

The authors consider there are two distinct periods in each year. Samples taken between May and September indicate reliably the general level of condition attained in that year, but values obtained between October and April are less useful as major changes in tissue production occur during this period. This study indicates that caution must be employed when interpreting the one year's results from Oronsay and Colonsay. We can only say that this is the pattern for 1980. Certainly the close comparisons with Blackmore's work at Robin Hood's Bay, and Jones et al in eastern Scotland, indicates that the patterns are representative, yet it must be remembered that variations on this theme are always likely.

Periwinkles

Periwinkles from all three sites (OLP, OHP and CP shown respectively in figures 24, 25 and 26) show a spawning related pattern. Spawning can occur from January to June, with maximum release in February to April (chapter 1), and the data from these sites may be related to this cycle. It was seen in chapter 1 that periwinkles over 18-20 mm (which was the minimum size used in these experiments) are sexually mature (Fish 1972; Moore 1937; Williams 1964).

OLP (figure 24) appear to spawn after March, as during this month there is a peak in meat weight, followed by a decline. Spawning on any one shore occurs over a longer period than for limpets, so it is probable that some spawning occurred into early summer. The steep increase in meat weight to March is probably an indication of the rapid maturation process referred to in chapter 1, and an increase in feeding in early spring. The majority of upper shore Oronsay periwinkles (figure 25) probably spawned in January or just before, as there is a decline in meat weight to May-June and July. After July there is an increase in meat weight to November, probably reflecting feeding and maturation.

Dr E. Williams (pers. comm.) considers differential spawning between low and high shore periwinkle populations to be a distinct possibility in this situation. At Craig-Yr-Wylfa he noticed that upper shore periwinkles mature faster than those from the lower shore (Williams 1964). There is every indication that it will be the same the following year. OLP reach the January level of ratio S/M by November, and have not yet begun maturation. Spawning therefore will probably not be much before March. OHP have high meat weight values by November, indicating that, as in 1980, 1981 spawning could occur in January or before.

Unfortunately no January sample was taken on Colonsay, yet as there is such a discontinuity between the March and November values we may assume that in January there was a lower shell/meat weight ratio than in March. In which case this population probably spawned before March, perhaps around January as did OHP. Certainly there is no decrease in meat weight after March if the sample is viewed as a whole.

If however the Colonsay periwinkles are divided into smaller and larger periwinkles a different pattern emerges (figure 29). The smaller animals show a decrease in meat weight between March and May-June, then increase until November, whereas the larger ones have a peak in flesh value at May-June, decrease to September then increase again to November. The large standard error in these samples does, however, mean that none of the values for July, September and November for either size of periwinkle are significantly different. The only significant difference is in May-June. It is possible that the smaller periwinkles had spawned before March and the larger ones not until May-June.

In both OLP and OHP the smaller and larger animals show basically the same seasonal patterns (figures 27 and 28). In general the larger animals have the higher shell/meat weight ratios, especially in OLP, though the differences are not as marked as in limpets. For OHP the only significant difference between the sizes is in March and September, and in OLP in May-June, July, September and November. The division between sizes of 6 g shell weight for OLP and 4 g shell weight for the others does not bring the ratio S/M values for the two sizes any closure in figure 27.

Figures 24, 25, 27 and 28 show that there is a difference in ratio S/M between periwinkles from the upper and lower shore, with the former having significantly more meat for a given shell weight. Even when OLP has a meat weight peak in May-June it does not reach the value of OHP when it is at its lowest meat weight (though there is an overlap of standard errors). The Colonsay periwinkles were collected from the mid to upper shore as there were very few at low tide level due to the high degree of exposure to wave action. Above mid shore the coast was more dissected and allowed for more sheltered microhabitats. The ratio S/M is closer to OHP than OLP.

The upper shore periwinkles and those from Colonsay are generally smaller (chapter 6) so the question arises, is it tidal position or size that governs the difference in ratio S/M? If size is the governing factor then one may expect an overlap in ratio S/M between the smaller low shore winkles and the larger high shore animals. This overlap does not occur so it seems that the different ratio S/M values are due to some factor or factors related specifically to position on the shore.

The complex and often poorly understood topic of periwinkle distribution over the shore has been discussed in chapter 1. Here it was concluded that, although a mobile species, general zonation patterns are established at the end of the first year (when the animals are around 8-12 mm long), and after this any movements tend to be over short distances, and are more horizontal than vertical in extent. Feeding excursions have been shown to involve an outward and a return journey. Periwinkles are able to adapt their behaviour to suit their level on the shore. In chapter 1 it was shown that those from the lower shore fed more slowly, and for a longer period, than those from the upper shore. The increased feeding rate of the upper shore animals compensated for reduced feeding time. Periwinkles displaced to a different tidal level were seen to adapt their behaviour, so it was concluded that this behaviour was acquired and not genetic.

We therefore have evidence indicating that the observed differences in ratio S/M between levels is due to the fact that the periwinkle inhabits a specific tidal level, and not simply because of its size. This is indicated by:-

1. The evidence for periwinkle zonation.

2. Their ability to alter behavioural patterns to suit their habitat. Even if there is some vertical movement the animal can adapt. This adaptive ability may be evident in other areas, such as metabolic rate, which could help explain the observed differences. Williams (1964) demonstrated that periwinkles mature quicker on the upper than lower shore. The reason for this is unknown, yet present data from Oronsay confirms that upper shore periwinkles breed before those on the lower shore.

Other studies

Williams (1970) and Grahame (1973) have investigated seasonal changes in periwinkle dry meat weights, the former from Robin Hood's Bay and the latter from Anglesey. More variations are evident between these three studies (including Oronsay and Colonsay) than was the case for limpets. This is probably due to the longer spawning season. Grahame found a general trend for higher meat weights in the late autumn and early winter, falling through the spring to low values in summer (figure 30). This trend is more pronounced in females than males though both followed the same pattern. Grahame interprets these changes as a fattening prior to winter spawning and a reduction in flesh weight as the animals become spent during spring. This correlates closely with the data for OHP (figure 28) where spawning occurred in winter, yet not with OLP which mainly spawned in spring (figure 27). The Robin Hood's Bay periwinkles also peak in the autumn and early winter and have low summer values (figure 31). Both males and females follow the same seasonal pattern.

Dogwhelks

The variations in relative meat weights in dogwhelks also exhibit seasonal trends, though these are not as precise as for periwinkles, due to the larger standard errors reflecting the greater variation in ratio S/M for any one month (figures 32 to 37). It was seen in chapter 1 that maturity is reached at around 2.5 to 3 years, and there is great variation in size attained at maturity, from around 20 to 30mm shell length. The larger size grouping is probably mature, as 4 g shell weight represents dogwhelks of around 24 to 28 mm on Colonsay (exposed) and 29 to 35 mm on Oronsay (sheltered). The smaller size group may or may not be mature.

Spawning generally occurs over a shorter period than for periwinkles, which usually centres around March-April (chapter 1). Figures 32, 33, 34, 35, 36 and 37 show large variations in ratio S/M between different sample months, and standard errors are large, especially after the division into small and large dogwhelks (figures 35, 36 and 37). When absolute values for dry meat weight are considered, the seasonal variations are much smaller and the standard errors less (figures 38, 39 and 40). The large fluctuations in ratio S/M probably reflects variations in shell thickness between individual dogwhelks.

Both methods show generally the same seasonal pattern. In both low and high shore Oronsay dogwhelks there appears to be a period of spawning between January and March. Unfortunately there is no January sample of Oronsay high shore dogwhelks, yet figures 33, 36 and 39 show that there are lower meat weights during this month than at any other time of the year, indicating that spawning has already occurred. Colonsay low shore dogwhelks also probably spawn prior to March, and then increase steadily in weight throughout the year (figures 34, 37 and 40). Spawning may also occur between May-June and July in the larger Oronsay dogwhelks, as there is a drop in meat weight between these months.

Figures 35, 36 and 37 show that the smaller dogwhelks have similar seasonal fluctuations to the larger animals, yet figures 38, 39 and 40 show them having much less variation in meat weight over the year, especially the dogwhelks from Oronsay low shore. It is possible that at least some of these smaller dogwhelks are immature. They all show a similar pattern of minimal meat weights in winter and maximum in spring and summer, which suggests the changes may be due to feeding intensity. The larger dogwhelks show increases in meat weight from July to November, probably indicating ripening prior to spawning, whereas the smaller ones show a decrease during this period.

Figure 41 shows the seasonal variation in tissue weight of a 25.5 mm shell length dogwhelk from near Plymouth as established by Moore (1938a). He attributes the rapid drop from October to the beginning of April to a combination of spawning and a lack of feeding whilst in winter aggregations. Instead of peaking in November-January this population peaks slightly earlier in October, probably indicating a lightly earlier spawning.

It is clear from figures 35 and 36 that, unlike limpets and periwinkles, Oronsay dogwhelks show an increase in relative meat weight with size. This is not, however, the case in Colonsay dogwhelks, where the two sizes are not significantly different (figure 37). A possible explanation for this relates to selection against crab predation (chapter 1). Crabs exist on the more sheltered shores, and consequently dogwhelks have adapted by developing smaller mouths and thicker shells. Hughes and Elner (1979:75) demonstrated that crabs can only successfully attack dogwhelks below 20-23 mm shell length. It is therefore reasonable to assume that any selective pressures against predation should affect the smaller shells, hence their greater relative amounts of shell to meat. This suggestion is borne out by the fact that the exposed shore Colonsay dogwhelks do not show this difference between size classes.

Hughes and Elner (1979) note how smaller dogwhelks produce thicker shells, and once the dogwhelks reach early adulthood there is an increase in relative tissue weight. They also demonstrate how sheltered shore animals have thicker shells and hence relatively less meat with relation to shell than those from a more exposed shore (chapter 1). When comparing CLD and OLD (figures 37 and 35 respectively) it may be seen that from May-June to November the more exposed Colonsay dogwhelks do have generally more relative meat than those from Oronsay. The difference is especially pronounced between the Colonsay dogwhelks and the smaller Oronsay animals.

As mentioned above, the smaller dogwhelks may not all be sexually mature. If this is so, the larger animals will be expected to show relatively more tissue weight. This is the case in OLD and to a lesser extent in OHD, but not in CD. On present evidence therefore it must be concluded that either selection against crab predation and/or the immaturity of the smaller dogwhelks accounts for the increase in shell weight with size.

Another feature of these distributions are the great differences between high and low shore dogwhelks, with both OLD and CLD having significantly less meat for a given shell weight than OHD. Much less work has been done on dogwhelks than periwinkles, so this difference cannot yet be adequately explained. Dogwhelks show no specific zonation patterns (chapter 1), moving around the shore to locate prey and for winter aggregations, which are usually on the lower shore. All individuals do not breed at the same time so 'there are always some at low levels, some at high levels and others either moving up or down' (Berry and Crothers 1968:9). This lack of specific zonation makes the difference in ratio S/M difficult to explain. Unlike periwinkles there does not appear to be any relationship between mean size and tidal level (chapter 6). On present evidence therefore this phenomenon cannot be explained.

Conclusions to periwinkle and dogwhelk relative meat weights

1. Both periwinkles and dogwhelks show spawning related changes in meat weight, though standard errors are smaller in periwinkles than dogwhelks.

2. Both species also show different seasonal meat weight peaks depending not only on whether they come from Oronsay or Colonsay, but also depending on whether they occupy the upper or lower shore.

3. Periwinkles show a general increase in relative shell weight with size, whereas Oronsay dogwhelks show an increase in relative meat weight with size. Colonsay dogwhelks show no significant difference in shell/meat weight ratio with size.

4. As a general rule dogwhelks show greater seasonal fluctuations in shell/meat weight ratio than do periwinkles (or limpets).

5. In both species, those from the upper shore have significantly more meat than those from the lower shore.

C. BIOCHEMICAL CHANGES

Detailed analysis of the biochemical composition of the three shellfish species is beyond the scope of this research for the reasons outlined by Koloseike:

> 'Unfortunately, the protein/meat ratios for molluscs may well exhibit complexities of variation comparable to the mollusc meat/shell ratios. If so, testing for protein would involve not only the same collecting and gross weight measurement program .... but also the task of detailed chemical analysis of each collected specimen. Such a testing program for variation in mollusc protein would indeed be a formidable task, certainly beyond the range of the archaeologist's technical talents and very likely beyond the limits of any man's patience.'
> (Koloseike 1969:153)

Fortunately earlier studies have provided a certain (if limited) amount of data concerning biochemical changes in seasonal composition of the bodies of the three species that is of relevance to the present study. These studies show a close correlation in nutritional peaks to the above mentioned peaks in total meat weight.

Limpets

Blackmore (1969b) has demonstrated significant seasonal variations in polysaccharide, lipid and protein nitrogen. (Blackmore [1969b:242] has found the polysaccharide to contain six sugars, the proportions of which vary with the reproductive state of the limpet. In the bodies of mature male and female limpets the approximate proportions are: glucose 55%, rhamnose 27%, fucose 8%, arabinose 5%, galactose 3% and ribose 2%.) Figure 42 compares the polysaccharide, lipid and protein nitrogen content of limpets in Robin Hood's Bay. When compared to the seasonal changes in meat weight (figure 22) the close association with the reproductive cycle is obvious. It will be seen that lipid and protein nitrogen peak in late summer, slightly after polysaccharide. After July the females contain slightly less polysaccharide than the males, but their peak lipid level is much higher. The females contain slightly less protein nitrogen throughout the year. In total there is a much greater weight of lipid than polysaccharide, and the peak in the protein nitrogen matches that of male limpets for lipid content, but is less than the females.

Seasonal changes in limpet carbohydrate levels were monitored by Barry and Munday (1959) by measuring blood glucose and tissue glycogen concentrations (figure 43). It will be seen that the peak in blood glucose occurs around November, then there is a steep fall to January, which the authors attribute to spawning. The blood glucose levels remain low until March when they begin to rise. This is the same as the meat weight increase noted for Oronsay and Colonsay and which is probably attributable to spring feeding. Analysis of tissue glycogen concentrations by Barry and Munday revealed essentially the same seasonal pattern.

The authors attribute the low winter levels partly to a period of non-feeding hibernation. Subsequent work has shown this not to be the case (Blackmore 1969a, 1969b) as limpets do feed and grow in winter, yet at a reduced rate. This finding does not, however, refute Barry and Munday's conclusions that the spring rise in glucose levels reflects an increase in spring feeding, though they were incorrect to assume that feeding stopped altogether.

No single study has been conducted on seasonal changes in protein content, but an extremely approximate idea may be obtained by combining information from three publications, Ansell et al (1964), Blackmore (1969b) and Townsend (1967). Blackmore provides information on values of protein and non protein nitrogen, and Ansell et al say that the weight of protein is approximately 6.25 times the value of total nitrogen. This is based on the assumed average figure for amino acid composition of protein, the identity of relative proportions of the amino acids present being unknown.

Table 18 shows the calculation of approximate total protein for three months using Blackmore's data for protein and non protein nitrogen for a standard animal of 36 mm shell length from the lower shore. Townsend examined the protein content of five limpets from Criccieth. She does not specify the tidal position of these samples, or even the season of collection. Nevertheless one of these limpets has a shell weight of 2.6 g, which will represent an animal of around 33-34 mm shell length. The protein content of this animal is 0.274 g, which correlates closely with the previously calculated off-peak values. Protein content is seen to peak just prior to spawning at a value nearly double that in early summer or after spawning.

TABLE 18 : CALCULATED PROTEIN CONTENT OF A 36 MM LIMPET
using data from Blackmore (1969a) and Ansell *et al* (1967)

Month	Protein nitrogen (g) (male + female)	Non-protein (g) nitrogen (male + female)	Total (g)	x 6.25 = approx. total weight of protein (g)
June	0.04	0.02	0.06	0.375
September	0.07	0.035	0.105	0.656
November	0.045	0.015	0.06	0.375

Periwinkles

Fluctuations in biochemical composition of periwinkles is mentioned by Williams (1970) and Grahame (1973). Williams' conclusions concerning fluctuations in lipid and carbohydrate are expressed in figure 44. These correlate closely with his results for changes in dry meat weight (figure 31). As with limpets, lipid levels are proportionately greater than carbohydrate.

Grahame expresses the seasonal biochemical fluctuations in terms of calorific value. Figure 45 shows calories per ash-free gram for males and females, which again correlate closely with his calculations for changes in dry body weight (figure 30). Calorific content is lowest in late spring, rising through summer and autumn to a maximum in December for males and January for females. The distinct seasonal trends are more marked in females than males, though the differences are not as great as may be expected, with the calorific cost of sperm production being 60-80% as great as that for egg production. The author again relates these changes to the reproductive cycle, with the rapid decline during late winter and spring representing spawning.

Peak values in both meat weight and calorific value occur slightly later in the year than at Robin Hood's Bay, probably reflecting slightly later spawning.

Dogwhelks

Seasonal variations in carbohydrate levels of dogwhelks has been investigated by Morgan (1971) with relation to varying diets (figure 46). He measured total carbohydrate in the digestive gland (glycogen being the only detectable polysaccharide and glucose the only detectable monosaccharide), so the results are not representative of changes due to reproduction. Nevertheless they do indicate that carbohydrate levels vary with diet. Maximum levels occur in September or October after the main period of summer feeding, and minimum levels around March after winter starvation (and spawning). Dogwhelks feeding on cockles have higher carbohydrate concentrations than the barnacle feeders, and Morgan associates this with a higher gross input of food. The levels in cockle feeders were, however, more variable due to more irregular feeding patterns.

Hughes (1972) found that in Nova Scotian dogwhelks calorific values of total dry tissue were lowest during May in males and June in females, and he considers this to correlate with the period of spawning. He also found that values increase to the summer months, and although he makes no interpretation of this, it is probably due to feeding.

Conclusions

Thus in the three species biochemical composition appears to be related to fluctuations in dry meat weight. it seems that biochemical changes are related specifically to the reproductive cycle, though Barry and Munday (1959) and Morgan (1971) indicate that feeding intensity can affect carbohydrate level. Feeding intensity also affects total meat weight, so it may be concluded that the periods of greatest meat weight are also the periods of highest biochemical composition.

CHAPTER 3 : POPULATION STRUCTURES OF LIMPETS, PERIWINKLES AND DOGWHELKS AT VARYING HABITATS ON THE ORONSAY COAST

Introduction

Before inferring anything from the midden shells it is necessary to establish what constitutes a 'natural population' of these shellfish. An examination is made of the size distribution of limpets, periwinkles and dogwhelks in differing intertidal habitats, and the relative proportions of the three species in their different habitats. Using this data as a basis, chapter 6 will examine the population structure of the middens to allow inferences to be made on the Mesolithic shellfish collection strategies.

Size and not age has been used as the criterion to examine population structure. There are a number of reasons for this. When interpreting the midden material it is shellfish size that is the important variable. Also it has been demonstrated in chapter 1 that there is not a constant relationship between limpet size and age due to variations in growth rate (table 6). It is also difficult to relate dogwhelk age to size because of varying shapes on shores of differing exposures, and genetic differences between populations (chapter 1). Periwinkle populations also show varying age/size structures in different localities (chapter 1).

Chapter 1 has demonstrated that in all three species fastest growth occurs before maturity. In limpets it is generally agreed that maturity is reached below a size of around 15 mm (Blackmore 1969a:205; Choquet 1968: 460; Das and Seshappa 1948:654; Fretter and Graham 1976:27; Orton 1928a: 856; Orton et al 1956:161). The sampled limpet population are all above 19 mm. Growth is still continuing at a seasonally variable rate in limpets above this size (chapter 1) but not at such a rate as in smaller limpets. Thus, although this population survey only covers one period of the year, shell growth is relatively slow in limpets above 19 mm, so there will not be as many seasonal fluctuations as in the smaller limpets. Nevertheless, it would have been ideal to do a number of similar surveys throughout the year, but this was beyond the means of the present research.

For periwinkles the minimum size sampled was 18 mm shell length, after which time growth is extremely slow (pers. comm. Dr. E. Williams). In dogwhelks most growth occurs before maturity is reached at around 2.5 to 3 years, when dogwhelks may be anywhere from 16 mm to 29 mm in length (chapter 1). It is not therefore known whether some of the smaller dogwhelks in the present survey, where the minimum size was 20 mm, are in fact still growing.

Both dogwhelks and periwinkles are mobile to varying degrees around the shore (chapter 1), so in considering natural populations most emphasis is placed upon limpets. Only major trends in dogwhelk and periwinkle distributions will be considered of significance, though it must be remembered that periwinkles do exhibit stricter zonation patterns than dogwhelks (chapter 1).

The size-shore position of periwinkles could answer one specific question. During the yearly sampling for meat weight changes (chapter 2) it had been noted that in the mid and lower mid shore zone periwinkles occur in large groups of small individuals, and at the lowest levels there are larger periwinkles living singly on the rocks. This phenomenon was also noticed by Gendron (1977), Moore 1940), Smith and Newell (1955) and Williams (1964). A sample was taken from an aggregation of periwinkles, yet most attention has been paid to those periwinkles existing singly or in small clusters (of less than 10 individuals) adhering to the rocks. An examination may therefore be made of the proportion of these to limpets, and a comparison made to the relative distribution of periwinkles in the middens. Chapter 6 will examine whether the midden levels indicate the collection of a large mass of periwinkles from a large cluster, and/or whether they were picked individually from the rocks along with limpets.

In the winter months dogwhelks will gather in aggregations at lower levels (chapter 1), yet in July they are scattered over the rocks individually or in small groups, feeding on barnacles. Attention will be paid to their relative proportions to the other species, and to their size in different habitats. It must be noted however that for dogwhelks this distribution will not be relevant to the winter months.

A. DATA COLLECTION

Limpets were measured using Vernier calipers accurate to 0.01 mm along length, width and height, periwinkles along length and dogwhelks along total length and aperture length (figure 47). Information on limpet size is obtained from their length measurement, and length/height has been used to distinguish between high and low shore forms. The more conical upper shore limpets will have a lower ratio length/height than the flatter animals from the lower shore. The only concern for periwinkles is with total size, to recognize any size variations in differing habitats.

Whereas the size of limpets and periwinkles may be assessed from measurements of total length alone, dogwhelk sizes must be assessed from both total length and aperture length. This is because the majority of midden dogwhelks are broken, allowing the measurement of the aperture but not total length. Thus, both total length and aperture length may be used to indicate the size distributions of contemporary dogwhelks, and in chapter 6 this data may be applied to the measurements of aperture length on Mesolithic shells.

No attempt was made to establish the total available shellfish population so it was not necessary to sample a set percentage of rock. As noted above, information was required on relative numbers of different species, and of individuals of varying sizes within the same species. Ideally this could have been done using a stratified sampling strategy to ensure the inclusion of the full range of available habitats. This would, however, have been a PhD topic in itself, so a modified smaller scale survey was undertaken which, nevertheless, would still provide the necessary data.

The sample sites were chosen with care to represent a variety of the common intertidal habitats. Attention was paid to tidal level, coastal morphology aspect and degree of exposure, and competition for space especially with barnacles and fucoids. More emphasis was placed on lower and mid tide sites because the majority of midden shells came from these zones (chapter 6) and there is greater uniformity in habitat types on the upper shore.

Seven areas of rock were selected for investigation, and some of these were sub-divided into different habitat types, making a total of eleven sample areas. These are marked on figure 48 and shown in plates 19 to 29. Skerries were measured into ELWS on July 18th and 19th 1981, which was the lowest spring tide of July, thus each habitat was given a relative tidal level.

For each sample area collections were made of all limpets 19 mm shell length and above. There were a number of reasons for choosing 19 mm as the lower cut-off point. There are very few midden limpets below this size (chapter 6). Also, it has been shown in chapter 1 that growth is rapid in smaller limpets, so as it was only possible to do one population survey the value of information on this seasonally changeable size range would be restricted. As will be seen below, the proportion of smaller limpets in differing tidal habitats is an important factor in any discussion of limpet population dynamics, so all limpets below 19 mm were counted. With practice it became easy to tell a limpet of 19 or 20 mm, but in any case of uncertainty a pair of calipers fixed at 19 mm were placed over the shell.

Measurements were taken of all periwinkles adhering singly to the rock, yet not of those in large clusters (as specified above). None of these periwinkles were below 18 mm shell length, all the small ones occurring in the large aggregations.

All dogwhelks were sampled as no very small individuals were found, the smallest being 20 mm shell length. These animals were scattered over the rocks adhering to the barnacles upon which they were feeding. The smaller animals were in sheltered crevices and could easily be ignored.

In some sample areas all the individuals were measured, but in others there were far too many to measure all so a sample was taken by thoroughly mixing them up, laying them out and picking every nth individual to constitute a representative sample for measurement. The others were counted and returned to the coast. After measurement all individuals were returned to the shore.

B. THE SIZE DISTRIBUTION OF LIMPETS, PERIWINKLES AND DOGWHELKS

Firstly an examination will be made of each sample unit, and then results will be compared. Plates 19 to 29 show the study areas, and figure 48 indicates their distribution around the island. Table 19 relates to limpets, table 20 to periwinkles and table 21 to dogwhelks.

Table 19 is a summary of mean lengths, the proportion of limpets under 19 mm (which were counted and not measured) and the actual percentage of the limpets above 19 mm that were measured. In all but Unit 1C all limpets above 19 mm were measured. In this unit there were far too many so a sample was taken. Units 1A, 1B and 1B-C contained a small number of limpets that could not be measured either because they were in inaccessible cracks in the rocks or they were broken when removed. Figures 49 to 60 show limpet length distributions over the shore.

Table 20 denotes periwinkles mean length, and in all but Unit 1A every periwinkle was measured. Figures 61 to 66 show periwinkle length distributions over the shore.

Table 21 expresses dogwhelk mean length, mean aperture length and mean ratio length/aperture length, and the sample size for each level. This table is ranked according to dogwhelk size, going from the largest animals at the top to the smallest at the bottom. There were no dogwhelks in Unit 1C-1 as it was too high (above MHWN) and there were no barnacles upon which the dogwhelks feed. Figures 67 to 74 show the dogwhelk length distributions over the shore, and figures 75 to 82 the aperture length distributions over the shore.

UNIT 1

This is 250 m to the north of Cnoc Coig, on the southern side of Port Dhũn à Gharaidh (figure 48). This bay is classed as exposed by Andrews (1981) using the non-biological exposure measurements of maximum fetch and frequency of wind from the direction of maximum fetch. Figure 48 shows the position of this skerry on the Oronsay coast and plates 19 to 24 show how it has been divided into habitat types.

TABLE 19 : LIMPET MEAN LENGTH AND SHAPE (MEASURED BY LENGTH/HEIGHT) AND THE PROPORTION OF SMALL LIMPETS PER SAMPLE AREA

									SHAPE	
UNIT	TOTAL > 19 MM	MEAN LENGTH	STAND. ERROR	NO. < 19 MM	< 19 MM AS % OF > 19 MM	NO. UNMEASURED	NO. MEASURED	% MEASURED	MEAN L/H	STAND. ERROR
1A	212	24.38	0.33	500	236%	22	190	90%	2.55	0.03
1B	200	29.63	0.43	707	354%	39	161	81%	2.62	0.03
1B-C	191	29.77	0.46	562	294%	27	164	86%	2.72	0.03
1C	2,843	38.05	0.39	1,769	62%	2,388	455	16%	2.89	0.02
1C-1	64	29.19	0.79	-	-	-	64	100%	2.47	0.07
2	187	42.40	0.73	117	63%	-	187	100%	2.71	0.03
3	152	43.76	0.63	96	63%	-	152	100%	3.12	0.05
4	118	39.03	0.69	49	42%	-	118	100%	3.31	0.04
5	137	38.19	0.63	76	55%	-	137	100%	3.55	0.07
6	163	38.65	0.58	118	72%	-	163	100%	3.31	0.04
7	157	38.37	0.66	31	20%	-	157	100%	2.95	0.03
Total Units	4,424	36.04	0.21	4,025					2.92	0.01

TABLE 20 : PERIWINKLE MEAN LENGTH

SAMPLE UNIT	TOTAL PERIWINKLES	MEAN LENGTH	STAND. ERROR	NUMBER UNMEASURED	NUMBER MEASURED	% MEASURED
1A	634	25.96	0.26	488	146	23
1C	149	26.40	0.32	-	149	100
2	300	26.64	0.16	-	300	100
3	83	29.55	0.27	-	83	100
4	30	31.67	0.44	-	30	100
6	4	31.03	0.67	-	4	100
7	56	30.40	0.33	-	56	100

TABLE 21 : DOGWHELK MEAN LENGTH, APERTURE LENGTH, AND RATIO LENGTH/APERTURE LENGTH

UNIT	TIDAL LEVEL	MEAN LENGTH	STAND. ERROR	MEAN APERTURE LENGTH	STAND. ERROR	MEAN RATLA	STAND. ERROR	TOTAL NUMBER	NUMBER MEASURED	NUMBER UNMEASURED	% MEASURED
4, 5, 6	MLWS-MTL	33.63	1.32	23.19	0.85	1.45	0.02	25	25	-	100
3	ELWS	33.21	0.30	22.57	0.22	1.48	0.01	174	174	-	100
7	MLWN-MTL	32.55	0.47	22.57	0.33	1.45	0.01	95	95	-	100
1B, 1B-C	ELWN-MHWN	32.11	0.16	22.08	0.11	1.46	0.01	598	320	278	53.5
1C	MLWS-MTL	31.42	0.14	22.01	0.10	1.43	0.01	703	431	272	61.3
2	MLWN	31.24	0.29	22.01	0.18	1.42	0.01	181	181	-	100
1A	MTL	30.28	0.29	21.44	0.19	1.41	0.01	123	123	-	100
TOTAL		31.81	0.10	22.11	0.07	1.44	0.00		1,349		

The whole skerry is 39 m long, varies between 17 and 12 m in width and stretches from MLWS to just below MHWS. It must be remembered that tidal height increases not only vertically up the shore, but also vertically up the individual rocks. For instance a skerry may have its base at MLWS and, being some metres tall, have its top at MHWS.

Unit 1A

This is a 17 m long vertical shoreward facing edge at around MTL which divides the skerry in two (plate 19). The base of this face is at MLWN, yet the top is at MTL. The north-south crevice, of which Unit 1A forms the eastern face, is sheltered from direct wave action, though the funnelling action of the tide along the gully upshore from this unit means that it is moderately exposed to the action of the sea. The face has a moderately heavy, though patchy, barnacle cover yet very few fucoids.

Figure 49 shows the distribution of different sized limpets in this habitat. The majority are between 19 to 21.9 mm (35.8%) and 22 to 24.9 mm (27.4%), tailing off to only 3.7% between 34 and 36.9 mm. There are very few over a shell length of 31 mm. The mean shell length is 24.38 mm. There are over twice as many limpets below 19 mm as there are above (table 19), indicating that this is a good settlement site. Indeed, it fulfills the requirements for optimum settlement outlined in chapter 1, being fairly sheltered, damp, and with patches of bare rock between barnacles. Most young limpets exist in the spaces between the groups of barnacles. The lack of larger limpets is probably due to the high population density in this habitat, causing competition for space. It is also likely that limpets migrate from this direct settlement site to Unit 1C (see below).

This face does not contain any individual periwinkles, instead at the base in with the fucoids there are a total of 634 animals, a 30% sample of which were measured (table 20). Figure 61 demonstrates the unimodal size distribution of this population, with few very large and few very small and a mean length of 25.96 mm (table 20).

Table 21 shows that this unit contains dogwhelks of a lower mean length and aperture length than any of the other units. Figure 68 shows there to be more dogwhelks of lengths 24 to 29.9 mm than in any of the other units, and figure 76 shows that Unit 1A has more dogwhelks of aperture length 17 to 20.9 mm.

Unit 1B

This near-vertical slope runs along the south side of the skerry (plate 20). Its lower eastern end is at ELWN and its lower western end at MLWN. As it is 2 m high the upper part is at MTL to MHWN. The splash zone does, however, extend higher than in the more sheltered Unit 1A. This is a moderately exposed face with heavy yet patchy barnacle cover, and more fucoids on the lower than higher areas. The face is very dissected, with cracks and overhangs providing areas of protection. It is in such areas, under and around the protection of fucoids, and between barnacle patches, that the young have settled in highest concentrations. There are also spat within the barnacle clusters, which will probably not live long. This unit has 3.5 times more limpets under 19 mm than above, the highest concentration of the whole survey (table 19).

The mean length of the measured limpets is longer than in Unit 1A, at 29.63 mm compared to 24.38 mm (table 19). Figure 50 shows how most limpets are between 25 and 30.9 mm shell length. The higher proportions of larger limpets probably indicates less competition for space in this more open habitat.

No periwinkles were measured from this habitat as there were none occurring individually. Two groups of approximately 50 animals each occurred on a ledge. These were not measured but appeared to cover essentially the same size range as those measured from Unit 1A. The dogwhelks from this unit are considered along with those from Unit 1B-C.

Unit 1B-C

Between Units B and C are two near-vertical slopes facing southeast (plates 20 and 21). These are more exposed than the southward facing Unit B, the barnacle cover is also greater. The lower half of these faces are at MLWN and the upper part at MTL. Due to their near-vertical aspect and higher exposure to wave action, the splash zone extends to the top of this unit. The proportion of limpets below 19 mm is slightly lower than in Unit B but it is still nearly three times the number above 19 mm (table 19). Many of these have, however, settled within the denser patches of barnacles so may either die or migrate.

For the limpets that do survive there is the potential to grow larger in Units 1B and 1B-C. This latter habitat has a mean size virtually the same as the former, yet figure 51 shows that this is deceptive. There are two peaks in shell length in Unit 1B-C: 26.2% are between 25 and 27.9 mm, there is then a drop to 13.4% for those between 28 and 30.9 mm, and a rise to 18.9% for the size group 31 to 33.9 mm. This could reflect mortality in the 28 to 30.9 mm size group in Unit 1B-C, or poor settlement here around 1978. Thus in 1B-C there are more 31 to 33.9 mm and less 28 to 30.9 mm than in Unit 1B. Over 34 mm the proportions in the two sites are very similar.

The differences between Units 1A, 1B and 1B-C are, however, minor and may be explained by slightly varying settlement patterns, growth rates, and mortality. Viewed together they indicate high settlement, relatively slow growth, migration into other habitats, and high mortality. This is in contrast to the fucoid dominated habitats discussed below.

There are no periwinkles (aggregations or individuals) in Unit 1B-C. The dogwhelks from Unit 1B and 1B-C were combined because the division between these two units only applies to the limpets. Both these units contain a similar pattern of dogwhelks feeding on the barnacles. Figures 69 and 77 show how most dogwhelks are between 30 to 35.9 mm long with apertures of between 21 to 24.9 mm.

Unit 1C

This consists of the top part of this skerry on the seaward side of Unit 1A, up to the top of the very distinct barnacle line (figure 48, plates 22, 23, 24). The barnacle line reaches to just below MHWN, so this unit extends from MLWS at the eastern end to MTL towards the top of the barnacle line. This large tidal range was chosen as one unit because of its biological uniformity. There is no evidence of major clusters of specific sized limpets over this area, nor are there major differences in the other organisms such as fucoids, barnacles or algae. It is morphologically similar, with a seaward slope of 6° at its eastern end and 12 to 18° further inland. Over the whole unit there are shallow cracks providing sheltered microenvironments. Barnacles exist in patches, though nowhere are they as dense as in Unit 1B-C. Fucoids are also patchy, some of the patches being fairly extensive. This evidence supports that of Lewis and Bowman (1975) who consider that the influence of biological habitat may often override any changes in tidal level that may occur within one specific community-habitat type. Most of this unit is exposed to the full force of the waves, thus they are exposed using the scale devised by Andrews (1981), nevertheless cracks provide more sheltered microhabitats. Table 19 shows that the small limpets less than 19 mm comprise 62% of the measured sample which is a much lower proportion than in the previous three habitats. These were seen to occur in the protected microhabitats, and very rarely on the exposed open rock.

Figure 52 shows a greatly different size distribution to Units 1A, 1B and 1B-C, with very few of the smaller size groups and many more limpets over 30 mm shell length. There are no distinct peaks, the highest being the 40 to 42.9 mm size range with 13% of the measured limpets. Instead there is a gradual increase in numbers up to a size of 40 to 42.9 mm shell length (except for a very small drop between 34 to 36.9 mm and 37 to 39.9 mm), then a gradual decrease to the largest size group, that is limpets above 49 mm shell length. The mean size is 38.05 mm (table 19).

This predominance of older limpets is an indication of the lack of suitable settlement sites. Also, those that do settle probably undergo high mortality due to the degree of exposure. This environment does, however, provide abundant small algae. It was observed in chapter 1 that such 'bare rock' habitats are ideal for growth. This unit therefore probably supports a relatively high growth rate, and also probably receives migratory limpets moving from direct settlement sites.

The periwinkles show a much more even size distribution than Unit 1A (figure 62), though their mean size is only slightly larger at 26.4 mm (table 20). Except for a reduction in the 24 to 25.9 mm group, proportions are fairly constant between 22 and 31.9 mm shell length. There are therefore some smaller individuals, of the same size that tend to cluster in aggregations around mid-shore, and some larger individuals more typical of the lower shore.

The dogwhelks are of a very similar size distribution to those in Units 1B and 1B-C (figures 70 and 78), though the mean size is slightly smaller (table 21).

Unit 1C-1

This is on the top of the skerry above the barnacle line (plates 23 and 24) and lies above MHWN, though the zone is extended by splash so in reality this area is wetted or covered at most tides. There are fewer fucoids, and those that exist are in shallow crevices.

Figure 53 shows there to be a predominance of smaller limpets, the average length being 29.19 mm. However, as this is a high tide habitat the limpets are relatively shorter yet taller. The lower the L/H (length/height) values the more conical the shell, and table 19 shows that Unit 1C-1 has the lowest L/H values. A comparison of L/H in Units 1C and 1C-1 shows that the latter are significantly more conical than the former. Variations in shape will be returned to in section C of this chapter.

Even taking account of the difference in shape, limpets are not as large above the barnacle line as below, sizes cluster between 22 and 39.9 mm shell length with very few individuals above this size. No limpets below 19 mm were discovered in this habitat, so the majority of limpets (if not all) have migrated here from direct settlement sites below the barnacle line. Despite their smaller lengths these animals are not necessarily younger than those of a greater shell length below the barnacle line. It was shown in chapter 1 that limpets in higher tide sites are slower growing than those from lower areas. There are no periwinkles or dogwhelks in this habitat.

UNIT 2

This small low rock skerry is situated at ELWN on the shore below CNG I and II (figure 48, plate 25). It is an isolated skerry amid a sandy beach, to the north there is a wide sandy bay and to the south there begins a more continuous gently sloping rocky coast. This skerry therefore provides an isolated unit. It contains a uniform biological habitat, being between 30 and 75 cm high, 9 m long and 4 m at its widest point. It has a heavy fucoid cover and a light to moderate patchy covering of barnacles. The surface is fairly uniform, with no deep crevices, though there are a series of small 'steps' on the surface. It has an average seaward slope of 5 to 8° and the low edges range from vertical to 20°. This is a sheltered habitat (Andrews 1981), being protected from the southeast by the small off-shore island of Eilean Ghaoideamal.

The limpet mean size is 42.4 mm (table 19) yet this disguises an unusual trend evident in figure 54. The size distribution is uniformly low for limpets below 48.9 mm shell length, then there is a peak to 33.7% of the population being over 49 mm. Settlement of small limpets is as low here as in Unit 1C (table 19), probably because of the dense cover of older fucoids and the barnacles. This skerry is of special interest because of its isolation, making the migration of limpets from direct settlement sites in different habitats impossible. This is probably the main reason for the high proportion of limpets above 49 mm and the uniformity in sizes below this. The only limpets that can grow are those that settle directly, and for a number of years there appears to have been uniform settlement. This low shore sheltered habitat is conducive to fairly fast growth, though in certain areas there may be competition for space with barnacles and fucoids. Nevertheless, once limpets are established they are known to graze on fucoid fronds (Fretter and Graham 1976). With increased age growth rate is reduced (chapter 1), so by the time they reach around 46 mm shell length, growth will be imperceptibly slow, thus there is a clustering of the larger sizes, and it is no longer possible to distinguish different year classes. Indeed, there is seen to be a slight increase in the size range upwards from the 40 to 42.9 mm size class.

Periwinkles appear to be of the same general size distribution as Unit 1A (figure 63) though the mean size is slightly larger, at 26.64 mm compared to 25.96 mm (table 20). There is not such an even distribution of sizes as in Unit 1C, with a peak between 24 and 27.9 mm shell length. The size distribution of periwinkles scattered over the skerry is therefore approximately the same as those existing in the large aggregations in Unit 1A which is at a slightly higher tidal level. Whether or not they exist in aggregations is largely reliant on coastal morphology and the availability of food. Unit 1 contains many crevices and uneven surfaces where they can congregate and feed on collected detritus. The more even surface of Unit 2 permits a more scattered distribution of essentially the same sized individuals.

Table 21 shows that the mean aperture length of these dogwhelks is the same as in Unit 1C, and the mean lengths are also very similar, and overlap when the standard errors are taken into consideration. Figures 70 and 71 do, however, show that Unit 2 has more extremely small and extremely large dogwhelks than Unit 1C. This trend is also revealed in figures 78 and 79.

UNIT 3

This larger yet still isolated skerry is at ELWS (figure 48, plate 25) and is 32 m east-north-east of Unit 2. Only the lower half of this skerry was sampled to provide an example of the lowest tidal habitat. It is slightly more exposed than Unit 2 though is still classed as sheltered by Andrews (1981). Morphologically these units are similar, though Unit 3 is higher, being up to 1.5 m at its highest point. There is extensive fucoid cover, with Laminaria around the edges and a moderate barnacle cover. Steps and crevices in the surface provide protected microhabitats.

Though larger than Unit 2, this skerry is also isolated from other rocks, and a similar size distribution pattern emerges from figure 55. The proportion of limpets below 19 mm, at 63%, is exactly the same as for Unit 2 (table 19), and the proportions of size groupings below 40 mm is virtually the same. The peak in limpets above 49 mm is not quite so marked, there being more animals in the 40 to 48.9 mm categories. This is reflected in the mean length which, at 43.76 mm, is 1.36 mm longer than in Unit 2. The explanation for this size distribution is probably the same as for Unit 2. The total number of limpets measured from Unit 3 was less than Unit 2, even though the area was larger. This is probably a reflection of the denser fucoid cover and greater exposure of the lower tide skerry.

This uniformity in limpet distribution is not shared by the periwinkles. The average periwinkle is nearly 3 mm longer from Unit 3 than Unit 2 (table 20) which, considering the slow growth rate of periwinkles of this size (chapter 1), is a significant difference. Figure 64 shows that there are many more periwinkles in the larger size groupings; instead of peaking between 24 to 27.9 mm, they peak between 28 to 31.9 mm, with a much higher percentage in the range 32 to 33.9 mm.

Table 21 shows that out of the sites on the east coast of Oronsay, dogwhelks from Unit 3 are of a slightly greater mean size, though if the standard errors are considered there is then an overlap with Unit 7. The mean aperture lengths are, however, exactly the same in Units 3 and 7, though a comparison of figures 80 and 82 will show that Unit 3 has more dogwhelks between 21 and 24.9 mm aperture length, whereas unit 7 has dogwhelks of a greater range of sizes. The same phenomenon is seen by comparing dogwhelk length in Units 3 and 7 (figures 72 and 74), with the former having more dogwhelks between 32 and 37.9 mm long and the latter having animals of a greater range of sizes.

UNITS 4, 5 and 6

These are on the west coast of Oronsay below Priory Midden on the northern edge of Port na Luinge. Although the coast here is generally exposed, this narrow bay is fairly sheltered expecially at its innermost end (figure 48). These three sample sites are close together in a moderately sheltered position half way along the bay on its northern side. None of the very exposed areas of this coast were accessible to sampling. In contrast to the east, apart from the two sandy bays adjacent to Priory Midden, it is composed of deeply dissected continuous rock which, as mentioned above, does not beckon even the most dedicated shellfish collector.

These units are shown in plates 26, 27 and 28. Unit 4 is at MLWS, Unit 5 is a near vertical face ranging from MLWS to MLWN, and Unit 6 is at MLWN ranging to low mid tide level at its top. Units 4 and 6 are morphologically similar, with ridges and crevices running along the length of the rocks. On Unit 4 the highest ridge is 90 cm, and 1.25 m on Unit 6. On this latter unit the top of the ridge is around low mid tide level. The rock face comprising Unit 5 has only been sampled up to 1.5 m above ELWS, bringing the top of this unit to MLWN. Fucoid cover is extremely dense and barnacle cover is light and patchy on the three rocks. Limpets occur in clusters between the large fucoids. Under the densest fucoids there is only the occasional large limpet and hardly any small ones.

Despite ranging from MLWS to MTL these units produce similar limpet populations, with mean lengths of 39.03, 38.19 and 38.65 respectively (table 19). They also have similarly low proportions of limpets below 19 mm, with Unit 4 having the lowest. This is probably because this has the highest large fucoid concentration. Figures 56, 57 and 58 also show this similarity in population structure. There is no major peak in limpet length in any of these habitats, instead a relatively greater proportion between 37 and 45.9 mm, especially from Unit 5. This predominance of larger limpets reflects the low direct settlement rate. Growth in these fairly sheltered habitats is probably quite rapid, though the dense fucoids provide competition for space. The relatively even size distribution up to 30.9 mm probably reflects a similar survival rate for spat over a number of years' settlement, with the evenness of the larger size groupings occurring as growth rate slows and different settlement years become indistinguishable. The lower proportion of very large individuals than Units 2 and 3 is probably a reflection of the slightly less favourable growth conditions in Units 4, 5 and 6 caused by the extreme density of large fucoids. Once again, the uniformity in limpet size distribution over the whole lower half of the tidal range indicates the overwhelming importance of biological habitat as suggested by Lewis and Bowman (1975).

There are no periwinkles from Unit 5, and only 4 from Unit 6, yet these and the 30 from Unit 4 have very similar mean shell lengths. At 31.67 (Unit 4) and 31.03 (Unit 6) these are the largest of all the periwinkles (table 20). Figure 65 shows how the majority of periwinkles in Unit 4 are between 30 to 33.9 mm, reflecting both the lower tidal position of this habitat, and possibly also the large amount of food amidst the fucoids.

Dogwhelks from Units 4, 5 and 6 have been combined because only a few were found from each site. Even after being combined there are only 25 dogwhelks. This is probably due to the lack of barnacles or any other prey such as mussels or cockles under the thick covering of fucoids. Table 21 shows that this very sheltered bay contains dogwhelks of the greatest total length and greatest aperture length, though the high standard error means that for both measurements these values overlap with Units 3 and 7.

Figure 73 shows that the dogwhelks peak at a total length of between 34 and 39.9 mm and figure 81 shows how aperture length peaks at between 23 and 26.9 mm. There should not, however, be too much emphasis placed on this distribution because of the small sample size.

UNIT 7

This skerry is situated in the very sheltered bay to the south of Cnoc Sligeach (figure 48, plate 29). The south of this bay, off the end of Eilean Treadhrach is continuous rock yet the remainder of the bay is composed of rock skerries. Unit 7 ranges from MLWN to MTL, yet is regarded as one unit due to its uniform morphology and biological community. The top is fairly level with some crevices. At the bases of the sloping sides there are no limpets due to the high amount of sandy silty sediment. The fucoid cover is very dense. This westward facing bay on the east coast provides great protection, making this the most sheltered of the sample areas.

The very low spat settlement (table 19) is probably a reflection of the high fucoid density. The limpet mean size is virtually the same as for units 4, 5 and 6 from below Priory Midden. Although these were of a lower tidal position they also had dense fucoid cover. Figure 59 does, however, indicate that the size distribution is much more evenly distributed over different size ranges in Unit 7, with very similar numbers between 28 mm to above 49 mm. This may indicate migration from the unsampled section of this skerry. As with the west coast samples this probably indicates fairly rapid growth to a size where age groupings become indistinguishable.

Periwinkles are again large, and with a mean length of 30.4 mm only very slightly smaller than those from the western coast (table 20). There is a uniform size distribution between the sizes of 28 to 33.9mm, and no individuals below 24 mm (figure 66). This again indicates the larger nature of these periwinkles existing individually on the rocks, a point to be returned to in the discussion below. The dogwhelk size distribution has been discussed above with relation to Unit 3.

Limpet size distribution in a combination of all units

Figure 60 is a combination of all units. It will be seen that above a shell length of 22 mm there is a very uniform distribution of limpets of all sizes. There are slightly less in the size range 19-21.9 mm. Table 19 shows that the mean limpet length for the whole shore is 36.04 mm. Thus, in exploiting the whole intertidal zone limpet collectors have approximately equal access to limpets of all sizes. However, figures 49 to 59 have demonstrated that different habitat types support different population structures.

DISCUSSION

A number of patterns emerge from this data.

Limpets

Sites below the mid-tide zone may be divided into 'limpet direct settlement' or 'limpet migratory', and this is dependent largely on the biological habitat. Direct settlement sites such as Units 1A, 1B and 1B-C do not have heavy concentrations of large fucoids. They may, however, possess varying concentrations of barnacles. It seems that these are not a direct barrier to settlement, but when the limpets grow only those between the barnacle patches, with enough space to graze, will develop. The others either die, migrate or stop growing. Thus, in such direct settlement habitats there is a high proportion of limpets below 19 mm, and the peak in measured limpets appears in the lower size range. The peak probably also reflects the slow growth rate in this habitat, with an early overlap in size between different year categories.

Sites with a dense fucoid cover inhibit settlement (Units 4, 5, 6 and 7) yet larger limpets are able to migrate to such areas and feed on the larger fucoids. This results in a predominance of larger limpets, though there is no major peak in any one size range. Units 2 and 3 are isolated from any direct settlement sites, and show a greater peak in the largest individuals, reflecting fairly rapid growth of the small numbers of directly settled limpets rather than migration.

Biological habitat rather than strict tidal level appears to be of overriding importance in determining population structure in sites below MTL. Tidal level determines distribution in a general sense, in that settlement does not occur on the exposed upper shore, and also tidal level governs broad species distribution, and hence limpet population structure. Nevertheless it is the biological habitat that asserts the direct influence. This is demonstrated by Unit 1C which ranges from MLWS to MTL yet because of its biological uniformity has a distinct limpet population structure. The similarities between Units 4, 5 and 6 are also probably due to biological uniformity.

Periwinkles

As a general rule there are more groups of periwinkles around mid and lower mid tide levels, and more existing individually at the lower levels. The periwinkles occurring in groups (1A) tend to be smaller, yet there appears to be no correlation between size and tidal level (table 22).

The degree of shelter is an important consideration when examining periwinkle size. Table 23 ranks sites from the most sheltered to the most exposed, and it may be seen that the larger periwinkles occur in the more sheltered sites. Both degree of shelter and tidal position must therefore be considered in conjunction. Unit 3, at ELWS, produces the largest periwinkles from the eastern shore, yet this is not as sheltered as sites 4, 6 and 7 where the periwinkles are even larger.

It was observed in chapter 1 that lower level periwinkles exhibit faster growth (Williams 1964), yet it seems that degree of shelter also affects growth. In such habitats there is ample detritus on which the periwinkles feed. The most favourable habitats may thus be ranked as: low shore sheltered, low to mid shore sheltered, low shore of moderate exposure, low to mid shore of moderate exposure, mid to upper shore in both sheltered and moderate exposure.

TABLE 22 : PERIWINKLE SIZE RANKED BY TIDAL LEVEL

TIDAL LEVEL	UNIT	MEAN PERIWINKLE LENGTH	STAND. ERROR
ELWS	3	29.55	0.27
MLWS	4	31.67	0.44
MLWN	2	26.64	0.16
MLWN-MTL	6	31.03	0.67
+	+	+	
MLWN-MTL	7	30.40	0.33
MTL	1A	25.96	0.26

Unit 1C not included because it spans a great tidal range.

TABLE 23 : PERIWINKLE SIZE RANKED BY EXPOSURE

	TIDAL LEVEL	UNIT	PERIWINKLE LENGTH
Sheltered	MLWN-MTL	7	30.40
	MLWN-MTL	6	31.03
	+	+	
	MLWS	4	31.67
	ELWS	3	29.55
	MLWN	2	26.64
	MTL	1A	25.96
Exposed	MLWS-MTL	1C	26.40

Dogwhelks

Dogwhelk size may be assessed from both total length and aperture length. Table 21 demonstrates that both these measurements give the same ranked order to mean size from different units, though the absolute differences between the values are less when measured by aperture length, and in two cases this measurement gives the same value whereas total length gives one value as larger than the other. When the standard error is taken into account, however, there is also overlap in the mean length values. Thus, in chapter 6 aperture length alone may be used to assess dogwhelk size.

The ratio mean length/aperture length shows that as a general rule the longer the dogwhelk the greater the difference between total length and aperture length. Because of the small sample size from Units 4, 5 and 6 too much emphasis should not be placed on the slightly smaller ratio length/aperture length value from these sites.

As dogwhelks are mobile around the shore, exhibiting no prolonged zonation pattern (chapter 1), too much emphasis should not be placed upon their tidal position on this one survey. There are, however, two factors which may be of significance. Firstly the largest dogwhelks occur in the sheltered bay below Priory Midden (Units 4, 5 and 6) and in the sheltered bay in front of Cnoc Sligeach (Unit 7). Secondly, large dogwhelks also occur at the ELWS site below CNG I and II (Unit 3), and the smallest at MTL in Unit 1A. Figure 68 shows clearly the lack of larger dogwhelks in Unit 1A.

The former observation is of more significance than the latter. As discussed in chapter 1, dogwhelks do not have a planktonic dispersal phase, so populations on an area of shore remain relatively isolated. Thus one survey is not adequate to chart the size distributions of dogwhelks over an area of shore as they may move around yet, regardless of tidal position, those in the more sheltered sites appear larger.

Further studies are required to examine the degrees of dogwhelk zonation around the shore at different seasons. For instance, as well as being at MTL, Unit 1A with the smallest dogwhelks is also a site of moderate exposure. Is it the case that dogwhelks here do not move to other areas? How are we to explain the large dogwhelks at Unit 3, which is not as sheltered as Units 4, 5 and 6 or 7 yet has dogwhelks of a similar size? Perhaps the correlations between exposure and dogwhelk size and shape referred to in chapter 1 are not the only factors involved, and such things as food availability and even tidal position may have a bearing on dogwhelk size and shape. These questions may only be answered by further fieldwork.

The present observations that dogwhelks appear larger on more sheltered shores are, however, in agreement with the general view that dogwhelks are larger on such shores. The general increase in ratio mean length/aperture length with size is indicative of this change in shape from sheltered to exposed shores discussed in chapter 1.

OTHER STUDIES

The distribution of limpets, periwinkles and dogwhelks over the shore has been examined in chapter 1, yet a number of factors require emphasis with relation to the present study.

Limpets

The population structures of limpets (*P. vulgata*) from various tidal habitats has been studied by Lewis and Bowman (1975) at Robin Hood's Bay. Figure 7 expresses their results. Most variation in size with shore position occurs in limpets below 20 mm shell length. Their main conclusions are as follows:

1. The largest limpets occur on bare rock and on bare rock near *Fucus* due to faster growth. The tri-modal pattern of one of the bare, low level alternatives probably depends upon very fast growth, low density, and short life-span. The other, more common alternative is due to an overlap of different age groups. No low tide bare rock was sampled on Oronsay (because none could

be found), yet Units 2 and 3 may be classed as low tide bare rock and Fucus, which Lewis and Bowman found to have a higher proportion of larger limpets, especially in the range 20 to 35 mm shell length. They consider that this latter peak reflects the lower settlement rate. Units 2 and 3 peak at a larger size than this, due possibly to the higher density of large fucoids and less bare rock than at the Robin Hood's Bay sample area. Larger limpets can graze on these fronds whereas smaller limpets do not (Fischer-Piette 1948; Fretter and Graham 1976; Jones 1948; Lewis and Bowman 1975).

2. On high level bare rock the presence of a distinct juvenile peak depends entirely on whether the area has suitable settlement sites. If so then there is an early peak, if not the area is colonized by migrants and the peak is later. Both examples are shown in figure 7. Unit 1C-1 (the high tide site above the barnacle line) reflects the latter case.

3. With increased barnacle cover Lewis and Bowman found a reduction in maximum size and a greater overlap in length range for each year class. On Oronsay a similar pattern was seen in Units 1A, 1B and 1B-C. With increased tidal height growth becomes even slower, and Lewis and Bowman found that at high tide no limpets in barnacle areas grow over 28 mm shell length, irrespective of age. Thus there is an early peaking of the population; the more unfavourable to growth are the conditions, the earlier this occurs. This feature is shown clearly on Oronsay where Units 1A, 1B and 1B-C have the most crowded conditions, and so peak in the smaller size range, whereas at the other extreme Unit 2 has fast growth with a peaking of the largest limpets. The authors make no mention of higher mortality and migration from these barnacle habitats yet, as noted above, this is seen to accentuate the trend towards an early peak.

4. At Robin Hood's Bay Lewis and Bowman demonstrated that where limpets are growing amongst mussels, recruitment at mid-upper levels is much higher than amongst barnacles alone, so there is always a recognizable early peak. Although growth is slightly

> faster and maximum shape slightly greater than amongst dry barnacles alone, both are still limited by the difficulty of grazing in confined surroundings. Growth is slower at higher tidal levels, hence the peak just below 20mm. At mid tide levels growth is slightly more rapid and the life-span slightly shorter. As most of the fluctuations are in animals below 20 mm, for those above this size the main difference between the barnacle and mussel sites is a greater concentration of limpets around or just over 20 mm in the latter, and nearly all limpets in the pre 19 mm phase in the former. Due to their biological instability low level mussel sites do not possess 'typical' population patterns. There are, however, no mussel colonies on Oronsay.

Thus there do seem to be relationships between shore position and limpet population structure. These relationships are not static, yet they provide a broad structure within which we may view limpet populations.

Periwinkles

Except for Fish (1972) no studies have related periwinkle size to biological habitat, reference has simply been made to tidal level (chapter 1). Biological habitat will not exert the same influence on periwinkles as on limpets, because they can move to the favoured zone. Fish (1972) has documented the population structure of periwinkles from the exposed coast at Craig-Yr-Wylfa and the sheltered Dyfi estuary. The results are expressed in figure 83. The small periwinkles below 15 mm are not shown on this diagram. On both coasts there is a tendency for the larger animals to concentrate at lower levels and, as at Oronsay, the more sheltered site provides a higher proportion of larger individuals. Fish notes how the exposed beach has relatively little algal cover, and the estuary has much detritus providing an ample food supply.

Dogwhelks

The study of dogwhelks has been very much concerned with variations in shell shape with exposure (chapter 1). To the author's knowledge there is no one study that examines the population structure of dogwhelks over a shore in such detail as has been done for limpets, though as outlined in chapter 1, a number of publications have a bearing on this problem.

It is generally assumed in the literature that dogwhelks do not show strong zonation patterns over the shore. For this reason there is little mention of concentrations of larger individuals at any specific tidal level. Limpets exhibit strong zonation and periwinkles, though exhibiting much less of a zonation pattern than limpets, do show certain size-shore related patterns. Dogwhelks, on the other hand, move around the shore for a variety of reasons. Whereas limpets and periwinkles are grazers, not having to move far for food, dogwhelks are carnivores and so will change their distribution with the distribution of their food supply. They also move into aggregations around the lower shore in the winter and lay egg capsules on the lower shore (chapter 1).

C. VARIATIONS IN LIMPET SHELL SHAPE

In the above discussions mention has been made of variations in the shape of limpets from different tidal levels. Such variations are of great significance to any interpretations of the midden limpets (chapter 6), so it is necessary to gather together the various strands of evidence relating to the distribution of varying shaped limpets around the shore.

A number of studies have recorded that limpets living on the upper shore are more conical than those on the lower shore (Ebling et al 1962; Fretter and Graham 1976; Jones et al 1979; Moore 1934; Orton 1928a, 1928b, 1933; Punt 1968; Russell 1909). This was discussed in chapter 1 where it was concluded that the combined effects of degrees of desiccation and exposure to wave action in varying habitats may affect shell shape. Drier, high tide habitats require limpets to hold tighter and/or for longer periods of time onto the substratum, thus they grow in a more upward direction. The conical shape also exposes a relatively smaller area of shell margin for potential desiccation. Branch and Marsh (1978) found that South African limpets had greater tenacity in positions of greater exposure, yet they found no relationship between tenacity or exposure and shell shape. No such study has been conducted on British limpets.

The present natural population survey provides support for this shore zonation of different shaped limpets. The results indicate that on the shore as a whole tidal level appears to govern both limpet mean size and shape.

Figure 84 shows the percentage of limpets from high and low tide sites over the shore in varying categories of length/height ratios. As described above, the more conical shells have a lower length/height ratio. Sites 1A and 1C-1 represent the high shore limpets, and sites 2, 3, 4, 5, 6 and 7 the lower shore. Figure 84 shows that the majority of upper shore limpets occur in the range 2.00-2.49, whereas most form the lower shore occur between 3.00-3.49. There are very few extremely conical shells on the lower shore and very few extremely flat shells on the upper shore. Those that do occur are probably either animals that have recently migrated up or down shore, and/or limpets that exist in habitats that cushion them from the typical extreme values of their tidal zone, such as upper shore limpets in a damp protected habitat which have no need to develop the conical form to avoid desiccation. The few conical limpets on the lower shore may have developed this form due to restrictions in their outward growth caused by competition for space by, for instance, barnacles.

In table 24 the sites are ranked in order of tidal height, from the lowest to the highest. Sites 1B, 1B-C and 1C are not included as they span too great a tidal range. It may be seen that mean length decreases and shells become more conical from low to high tide. Limpets at levels above MTL appear to be generally smaller and more conical in shape than limpets below this level. Limpets at and below MLWN have the potential to grow larger and are flatter. There is, however, no evidence that limpets below MLWN get progressively flatter down the shore. To the author's knowledge this phenomenon has not been previously noted and requires further investigation. In this survey the flattest limpets occur in Unit 5 (on the west coast of Oronsay below Priory Midden) which ranges from MLWS to MLWN. Limpets from Unit 3 (on the east coast below CNG) at ELWS are the largest, yet are not as flat as on other sites at MLWS. Contrary to this, the site at the highest tidal level (Unit 1C-1) has the most conical limpets.

These results suggest that resistance to desiccation is the most important factor governing shell shape. It is probable that no limpets on the lower shore are exposed to the air long enough to allow serious desiccation so there is no reason for there to be any difference in adaptive behaviour towards limiting desiccation between limpets at MLWN and ELWS. However, for limpets above MTL there is possibly increasing selective pressure to resist desiccation progressively up shore. If this desiccation-resisting mechanism has an effect on shell shape it follows that in the upper shore zone limpets will become progressively more conical towards the top of their range.

TABLE 24 : LIMPET SHAPE RANKED BY TIDAL LEVEL

TIDAL LEVEL	UNIT	MEAN LENGTH/HEIGHT	STANDARD ERROR
ELWS	3	3.12	0.05
MLWS	4	3.31	0.04
MLWS-MLWN	5	3.55	0.07
MLWN	2	2.71	0.03
MLWN-MTL	6	3.31	0.04
MLWN-MTL	7	2.95	0.03
MTL	1A	2.55	0.03
MHWN	1C-1	2.47	0.07

Note: 1B, 1B-C and 1C are not included as they span a great tidal range.

D. RELATIVE PROPORTIONS OF THE THREE SPECIES

The relative proportions of the three species in the different sample areas are recorded in tables 25 and 26. In the former, periwinkles and dogwhelks are expressed as a percentage of the limpets and in the latter each is expressed as a percentage of the total shellfish sample. Periwinkles in Unit 1A have not been included as these occur in a large cluster.

The proportion of periwinkles to limpets

From such a limited survey any conclusions on limpet-periwinkle relationships must be tentative. On all but Units 2 and 3 periwinkles form a small percentage of the limpet population, yet on Unit 2 periwinkles outnumber limpets, and on Unit 3 there are approximately half as many periwinkles as limpets. The high number in Unit 2 is probably due to the morphology of this low skerry. The periwinkles here are of virtually the same predominantly small size range as in Unit 1A. The rock morphology of Unit 1A allows this clustering, yet Unit 2 is more even, with an evenly distributed food source, so the periwinkles are more dispersed. There are no periwinkles in Units 1B, 1B-C and 5 because they are too steep and any food is at their base. Large groups of periwinkles congregate in places where there is a concentration of food. Unit 1C-1 is too high, yet there are a few in Unit 1C. When all units are considered together, periwinkles comprise 16.57% of the total number of shellfish.

Thus, the following trends present themselves:

1. Periwinkles do not exist individually on rocks that are too steep, where food (algae, detritus) is not available, or at high tide level.

2. If rock morphology allows, they usually occur in aggregations, mostly at mid to lower mid tide levels, yet an even protected habitat allows a more even distribution.

TABLE 25 : RELATIVE PROPORTIONS OF LIMPETS, PERIWINKLES AND DOGWHELKS (expressed as a percentage of limpets)

SAMPLE UNIT	NUMBER OF LIMPETS > 19 MM		NUMBER OF PERIWINKLES	NUMBER OF DOGWHELKS	PERIWINKLES AS % OF LIMPETS	DOGWHELKS AS % OF LIMPETS	TOTAL
1A	212		634	123	-	58.02	
1B	200		-		-		
		391		598		152.94	989
1B-C	191		-		-		
1C	2,843		149	703	5.24	24.73	3,695
1C-1	64		-	-	-	-	-
2	187		300	181	160.43	96.79	668
3	152		83	174	54.61	114.47	409
4	118						
5	137	418	34	25	8.13	5.98	477
6	163						
7	157		56	95	35.67	60.51	308
TOTAL	4,424		1,256	1,899	28.39	42.92	7,579

PERIWINKLES AND DOGWHELKS 3,155 71.32

TABLE 26 : RELATIVE PROPORTIONS OF LIMPETS, PERIWINKLES AND DOGWHELKS (expressed as a percentage of the total shellfish sample)

SAMPLE UNIT	% LIMPETS	% PERIWINKLES	% DOGWHELKS
1B, 1B-C	39.53	0	60.47
1C	76.94	4.03	19.03
1C-1	100	0	0
2	27.99	44.91	27.10
3	37.16	20.29	42.54
4, 5, 6	87.63	7.13	5.24
7	50.97	18.18	30.84
TOTAL	58.37	16.57	25.06

PERIWINKLES + DOGWHELKS 41.63

3. At low tide levels the larger individuals distributed over the rocks may comprise anything from around 2 to 50% of the limpet population, yet it is also likely that periwinkles may outnumber limpets on an area of shore.

4. Over the shore as a whole periwinkles comprise 28.39% of the limpets, and 16.57% of the three species.

Obviously there are numerous variables such as rate of limpet settlement, periwinkle movements, and mortality in both species, none of which can be examined here. These factors will vary over time, yet the importance of tidal level, rock morphology and food availability has been demonstrated.

The proportion of dogwhelks to limpets

It will be seen that dogwhelks comprise less than 50% of the limpets in Units 1C-1, 1C and in the bay below Priory Midden (here Units 4, 5 and 6 are combined due to small numbers of both periwinkles and dogwhelks). Unit 1C-1 contains no dogwhelks as it is above the barnacle line, and hence they have no food. Unit 1C has few because the barnacle patches are sparsely scattered in comparison to areas of rock a little lower down the skerry with a dense barnacle cover (Units 1B, 1B-C). In Units 4, 5 and 6 there are very few barnacles (or any other prey species) due to the dense fucoid cover. Where food is available, however, the dogwhelks form a substantial proportion of the total shellfish population, which amounts to 60.47% in Units 1B and 1B-C, and 42.54% in Unit 3. Over the shore as a whole the dogwhelks comprise 42.92% of the limpets, and 25.06% of all the shellfish.

On all sample units but Unit 2 and a combination of Units 4, 5 and 6, dogwhelks form a higher proportion of the limpet population than do periwinkles. This of course is not including the large groups of periwinkles but only those actually distributed over the rocks. Over the shore as a whole periwinkles comprise 28.39% of the limpets as opposed to 42.92% for dogwhelks.

The main distribution patterns are therefore as follows:

1. Dogwhelks exist in greatest concentrations in areas of plentiful food supply, which in this case is barnacles.

2. Where they have an available food supply dogwhelks generally form a higher proportion of the limpets than do periwinkles (which are existing on the rocks as opposed to in groups).

3. Over the shore as a whole dogwhelks comprise 42.92% of the limpet population compared to 28.39% for periwinkles, which is 25.06% compared to 16.57% of the total shellfish population for dogwhelks and periwinkles respectively.

Conclusions

Thus the distribution of the three species is dependent upon habitat availability. Chapter 1 has demonstrated that limpets exist over most of the intertidal range, yet their size and density is governed by a variety of local habitat conditions. Periwinkles are not as uniformly distributed over the shore as limpets, often occurring in large clusters in crevices and under fucoids (chapter 1). When they are distributed over the rocks, however, they usually comprise less than 50% of the limpet population, yet may occur in larger numbers than the limpets if food availability and rock morphology allow. In summer dogwhelks are dispersed around the shore in a pattern determined largely by the availability of the prey (chapter 1), yet this will usually be of a less patchy nature than the distribution of periwinkles, especially if they feed on barnacles. Dogwhelks usually comprise a higher proportion of the limpet population than do periwinkles (not in the clusters).

It must be emphasized that this survey only covers a limited range of habitats at one season of the year. Nevertheless, although the relative proportions of the three species in various habitats may alter over the year, especially as the dogwhelks move around the shore, the total numbers in a combination of all habitats should not substantially alter.

CHAPTER 4 : COMPARISONS BETWEEN THE MODERN AND MESOLITHIC COASTAL ENVIRONMENTS OF ORONSAY

In any application of contemporary data to archaeological material it is necessary to be clear as to the degree of accuracy with which such predictions may be made. The aim of this study is not to produce a one to one correlation between shellfish on the present shoreline and their Mesolithic forebears. Instead shellfish populations in a selection of contemporary habitats within clearly defined environmental parameters are compared to the population structures exhibited in the middens. Major differences and similarities may therefore be discussed. It is necessary to explain what is known of the coastal environment of Oronsay and how this may relate to that of the present. Firstly mention will be made of coastal morphology and exposure, and secondly of sea temperature regimes.

1. Coastal morphology and exposure

To what extent is the modern Oronsay coastline representative of that of the Mesolithic? There is the obvious point that it is the closest we are going to get, but more than this, it may be argued that the similarity is high. As mentioned in chapter 2, the east coast is composed of rock skerries interspersed with patches of sand, and gently sloping more continuous rocks. The higher sea level (figure 2) would not have exposed any great changes in slope for the Mesolithic shoreline. We may therefore assume that this Mesolithic shoreline also contained gently sloping rock skerries, probably interspersed with sand as at present. At extreme low spring tides it is evident that this same coastal morphology extends many metres down below present sea level.

The north coast is steeper in places, yet has no adjacent middens so is of no concern here. The west coast has only one midden (Priory Midden) and this is situated adjacent to the only area of this coast presently accessible for shellfish collection. The remainder of this coast is composed of deeply dissected rocks which slope very gently seawards thus providing a very wide tidal range and a large area of rock above MHWS. Thus there is a long (often impossible) scramble to reach the intertidal zone. Not ideal collecting country.

It is probable that during the Mesolithic the coast of Oronsay would have experienced a slightly lower degree of exposure than at present (Andrews et al 1983). It was noted in chapter 1 that dogwhelk shape varies with exposure: on more sheltered shores they are more elongated with small apertures, and on more exposed shores they are shorter with larger apertures. Thus the ratio of total length/aperture length is greater for dogwhelks on more sheltered shores. Andrews et al measured total length and aperture length on a total of 848 dogwhelks from the modern Oronsay shore and 242 from the middens. It was discovered that the mean ratio length/aperture length was 1.73 for modern dogwhelks and 1.80 for the midden dogwhelks (table 27). This table also shows that when middens were examined individually the dogwhelks were all found to represent shores of slightly lower exposure than exist at present.

TABLE 27 : RATIO TOTAL LENGTH/APERTURE LENGTH FOR DOGWHELKS ON THE PRESENT ORONSAY SHORELINE COMPARED TO MIDDEN SPECIMENS

	Mean Ratio Length/Aperture Length*
Modern shore	1.73
All middens (except Priory)	1.80
Priory Midden	1.92
Cnoc Coig	1.79
Premidden	1.83
CNG I	1.75
CNG II	1.97
Cnoc Sligeach	1.85

* aperture length measured in a different way to the present study so the figures are not directly comparable.

(This data supplied courtesy of M. Andrews, D. Gilbertson and M. Kent prior to publication.)

Thus it seems that the Mesolithic coastal morphology was much as it is at present, though the exposure to wave action was possibly slightly less.

2. Sea temperatures

a) Modern sea temperatures

Sea temperatures have a bearing on growth rates and shellfish feeding intensities and hence must be considered with relation to shellfish size distributions. It is important therefore to be aware of the modern temperature regime for Oronsay and then to compare this to the expected Mesolithic sea temperature.

Sea temperatures were therefore taken during the periods of fieldwork throughout 1980. It must be emphasized that these figures only represent one year's measurements. They were taken on as many days as possible during the survey periods, always at the same place off Scalasaig old pier, Colonsay. This slopes gently into deep water on eastern Colonsay, so temperatures taken at high tide were taken off the mid part of the pier, and those taken at low tide were obtained off the lower portion. At all times the minimum water depth was around 5 metres. This, plus the fact that the pier is directly adjacent to the open sea, means that the water will not have been warmed by contact with land. Although temperatures were always taken off the south side of the pier, tests showed that the water temperature was consistent all around the pier.

The results are expressed in table 28. It will be seen that minimum temperatures occur around January to March and maximum around July to September. The lowest single temperature recorded was 5.8°C in March, though the total mean temperature for March was 6.6°C. Due to practical difficulties very few temperatures were taken in January, but of those that were there was great consistency at 6.2, 6.0 and 6.2°C.

It will be seen that temperatures are usually lowest in the early morning. Most diurnal variation in temperature occurs in the summer on days such as July 26 when strong sunshine caused water temperatures

TABLE 28 : SEA TEMPERATURE REGIME FOR COLONSAY AND ORONSAY FOR 1980
(all temperatures are ^{o}C)

		PIER	DUN CHALLAIN		S. PORT MOR		N. PORT MOR		E. ORONSAY	
DATE	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP
JANUARY										
19	16.45	6.2								
20	10.10	6.0								
	16.45	6.2								
MARCH										
25	9.30	5.8								
	14.15	6.5								
	16.30	6.6								
	19.00	6.5								
Average		6.4								
26	8.00	6.1								
	14.15	7.0								
	17.30	7.1								
Average		6.7								
27	9.30	6.1	10.45	6.3						
	14.15	7.0	12.00	6.6						
	17.15	7.3								
	19.45	7.1								
Average		6.9								
28	8.50	6.4							11.00	6.2
	14.00	6.4								
Average		6.4								
29	10.00	6.2								
TOTAL AVERAGE MARCH		6.6								
MAY										
30	21.40	10.9								
31	9.30	10.0	11.45	11.3						
	13.30	10.6								
	17.00	10.3								
	20.15	10.6								
Average		10.4								
JUNE										
1	11.00	10.4							12.30	13.9
	16.45	10.7							14.30	13.2
	20.45	10.7								
Average		10.6								
2	10.15	10.3								
	14.30	10.5								
	20.45	11.3								
Average		10.7								
TOTAL AVERAGE MAY-JUNE		10.6								

Table 28 (cont.)

		PIER	DUN CHALLAIN		S.PORT MOR		N. PORT MOR		E. ORONSAY	
DATE	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP
JULY										
25	22.20	13.1								
26	9.45	12.9	11.15	13.4						
	13.45	14.4								
	18.30	15.3								
	21.00	14.4								
	Average	14.3								
27	10.40	13.2							13.30	14.7
	15.00	13.4								
	17.20	13.5								
	20.00	13.6								
	Average	13.4								
28	10.20	13.4			16.45	16.5	17.00	19.9		
	16.30	14.4								
	17.30	15.9								
	20.45	15.0								
	Average	14.7								
TOTAL AVERAGE JULY		14.0								
SEPTEMBER										
23	10.45	13.8			15.00	14.2	15.10	14.5		
	14.30	13.8								
	17.30	13.9								
	Average	13.8								
24	10.00	13.4							14.00	14.3
	15.00	13.6								
	17.30	13.7								
	Average	13.6								
25	10.00	13.2								
	16.20	13.6								
	20.00	13.6								
	Average	13.5								
26	10.15	13.4	14.00	13.6						
TOTAL AVERAGE SEPTEMBER		13.6								
NOVEMBER										
17	15.15	10.4								
	20.15	10.3								
	Average	10.4								
18	11.30	9.9								
	14.45	9.9								
	Average	9.9								

Table 28 (cont.)

		PIER	DUN CHALLAIN		S.PORT MOR		N. PORT MOR		E. ORONSAY	
DATE	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP	TIME	TEMP
NOVEMBER										
19	11.45	9.2								
	15.45	9.1								
	21.15	10.1								
Average		9.5								
20	11.30	10.2					12.15	9.8		
	16.45	10.1					16.30	10.1		
Average		10.2								
21	9.00	10.1								
	12.15	10.3								
	16.30	10.4								
	21.00	10.3								
Average		10.3								
22	10.30	10.4	12.15	10.6						
	13.00	10.6								
	16.30	10.6								
Average		10.5								
23	10.15	10.4							13.00	10.6
	14.30	10.6								
	17.45	10.4								
Average		10.5								
TOTAL AVERAGE NOVEMBER		10.2								

SEA TEMPERATURES FOR COLONSAY, MARCH 1982

MARCH		
15	16.30	6.2
	21.15	6.1
16	9.10	6.1
	18.15	6.3
17	10.30	6.2
	16.40	6.3
18	11.15	6.5
	18.00	6.6
TOTAL AVERAGE		6.3

to peak in late afternoon. Sea temperatures were also taken off Colonsay pier during a short visit in March 1982 (table 28). These were, on average, only slightly lower than March 1980 when temperatures ranged from 5.8°C to 7.3°C, with an overall average temperature of 6.6°C. In March 1982 (when fewer readings were taken) temperatures ranged from 6.1°C to 6.6°C with an overall average of 6.3°C. Temperatures at Colonsay pier were minimum because they were taken in deep open water. Table 28 also shows that temperatures were much higher in the shallower sheltered bay of Port Mor on Western Colonsay during the summer months, but in November it was much the same as the pier. This indicates that the shallow water is heated in the summer, but on dull winter days is not very different. Temperatures taken on the east coast of Oronsay in the shallow water adjacent to the sampling area in front of Cnoc Coig Midden (see below) show this same trend, being much the same as the pier in March and November, yet in June and September on clear days being warmer than at the pier. The Oronsay temperature on July 27 is only slightly above that at the pier, yet this was a dull day with full cloud cover and rain. Sea temperatures in the deep highly exposed water below the Colonsay sampling area of Dun Challain on the west coast (see below) are virtually the same as at the pier.

Thus, animals in shallow bays may expect greater variations in sea temperature than those in deeper water. These variations are more pronounced in the summer on clear days, so whereas animals in shallower water may experience higher summer temperatures than their counterparts in deeper water, it is unlikely that they will receive substantially lower winter temperatures. The present evidence indicates that in winter, temperatures are fairly uniform in deep and shallow water.

b) Mesolithic sea temperatures

The middens were occupied during the latter phases of the climatic optimum which is generally regarded as lasting from around 3,000-5,000 bc (Evans 1975:71-2; Goudie 1977:117; Lamb 1982:29; Mellars and Wilkinson 1980:32; West 1968:208). During this period average air temperatures around the region of Colonsay were probably around 1.5 to 2.0°C higher than at present (Evans 1978:71-2; Goudie 1977:117; Lamb

1977:290-3; Mellars and Wilkinson 1980:32; West 1968:208). The increase in sea temperature is likely to be less than that in air temperature, though sea temperatures are much harder to estimate. In a summary of the evidence Mellars and Wilkinson conclude that they were probably around 1.0 to 1.5°C above present. This must, however, be viewed as an average and, as with the modern shore, there would probably have been variations between deep and shallow water, with the latter experiencing greater summer temperatures.

Conclusions

Data gathered from shellfish living on the present shore will therefore provide information which may be applied to those animals found in the middens. In any interpretations, however, allowance must be made for the possibility that the Mesolithic coastline was slightly less exposed, and that the sea temperature was probably a little higher than at present.

SECTION B

CHAPTER 5 : BACKGROUND TO MIDDEN STUDIES

> 'Molluscan remains alone can .... yield a wealth of information about the Midden dwellers'
> (Voigt 1975:87)

No attempt will be made here to review all previous shell midden studies. Instead a brief examination will be made of certain analytical trends that may be applicable to an interpretation of the Oronsay middens.

Shell middens are usually fairly obvious features and hence have a long history of exploration. For instance the two prominent Oronsay middens of Caisteal nan Gillean I and Cnoc Sligeach (plates 2 and 4) were discovered and excavated during the late 19th century (Anderson 1898; Bishop 1914; Grieve 1885, 1922, Lacaille 1954; Mellars 1977, 1978, 1981, 1983).

More recently studies have concentrated in Australia and New Zealand (Anderson 1981; Bailey 1975, 1977; Shawcross 1967; Swadling 1976, 1977), the western USA (Botkin 1980; Cook 1946; Cook and Treganza 1950; Meighan 1959; Treganza and Cook 1948), Europe (Mellars 1978, 1983; Mellars and Payne 1971; Mellars and Wilkinson 1980; Peacock 1978; Straus _et al_ 1980) and South Africa (Voigt 1973, 1975). A survey of recent studies of shell middens in England and Wales is given by Jacobi (1980), and in Denmark by Bailey (1978). General reviews are provided by Bailey (1975), Meighan (1969) and Voigt (1975).

The actual importance of shellfish in the diet is a topic now suffering from overexposure and circular arguments, and of which only brief mention will be made here. Some consider shellfish to be of relatively minor importance (Bailey 1975, 1978; Coles 1971) while others emphasize the various ways in which shellfish could play a more predominant role in the annual subsistence round (Bigalke 1973; Botkin 1980; Cook and Treganza 1950; Evans 1969; Meehan 1977; Meighan 1969; Shawcross 1967, 1970; Voigt 1975).

Bailey (1975, 1978) considers that because of their good preservation, shellfish tend to be overrepresented in archaeological deposits at the expense of evidence for other sources of food. He also notes how they are of relatively low nutritional value, for instance around 31,360 limpets or 156,800 cockles or 52,267 oysters would be required to supply the calorific equivalent of one red deer (Bailey 1978:39). We should not therefore consider the gross value of shellfish over the whole year, but rather their seasonal importance within the total annual cycle.

Shell midden studies can generally be divided into three types: those that are 'purely archaeological', those that rely on 'ethnographic' comparisons, and those that consider themselves to be 'ecological' in format.

1. Purely archaeological

These often just produce species lists and offer very little interpretation (Wade 1967; Wallace *et al* 1956), yet some do use the archaeological data to offer some form of interpretation (Cook and Treganza 1947, 1950; Gould 1971; Straus *et al* 1980; Treganza and Cook 1948).

2. Ethnographic comparisons

The application of ethnographic examples to an interpretation of midden deposits has been used very successfully by Meehan (1977), Bowdler (1976), Voigt (1975) and Bigalke (1973). These studies show how observations on contemporary hunter-gatherers can indicate possible activities which may have been responsible for the original formation of the sites. The former two studies are concerned with contemporary Australian aborigines and Australian shell middens, and the latter two relate to South Africa. It is not possible to make direct comparisons to Oronsay, yet some of the trends evident from these and other ethnographic studies do have possible implications for the Obanian shellfish collectors.

The collecting of shellfish may be classed as a gathering rather than a hunting activity (Bigalke 1973; Bowdler 1976; 'In hunting societies world over it is women who gather and they gather the shellfish' (Bowdler 1976:249). Bowdler cites many references to qualify her statement. She notes that men may gather a few shellfish for immediate consumption, but it is not a male task to collect shellfish for delayed consumption. Voigt (1975) notes that in the Transkei shellfish are only eaten by women and very young boys. Bowdler concludes: 'It is worth remembering that a shell midden is itself a particular sort of artifact, deposited and structured by the unremitting efforts of woman the gatherer' (Bowdler 1976:256). Archaeologically this can never be proved, yet it remains very likely that the bulk of many middens do represent the gathering activities of women.

In her work with the Anbara aborigines Meehan (1977) emphasizes that shellfish should not be thought of purely for their calorific value. For the Anbara the calorific contribution of shellfish ranged from 6% in May to 17% in January. 'Thus at no time during the year was shellfish more than a supplementary food even in the flesh diet' (Meehan 1977:523). However, during January there was very little other available food, so at this period shellfish were relied upon to a much greater extent. 'The Anbara may well have suffered hardship during this month if shellfish had not been readily available' (Meehan 1977:523).

She continues: 'If the assessment of shellfish's importance was left at this point, it would remain vastly underrated' (Meehan 1977:523). The gathering of shellfish is easy and reliable and may involve a broad spectrum of the population that are unable to do more strenuous activities. Old women, pregnant women and children all become involved. Shellfish are a very dependable food source, being potentially available at all seasons. 'They were there for the taking, like food on a supermarket shelf....' (Meehan 1977:526). Thus, much time was devoted to shellfish collecting; Meehan noted it to occur on 58% of observed days which was as recurrent as fishing, and both took place more frequently than any other foraging pursuit. Because so many people were collecting, the total number of 'people days' involved was higher than for any other single food category.

Despite the relatively low flesh yield of the shellfish, the Anbara regarded them (especially Tapes hiantina) as one of the primary resources in their territory. Proximity to shell beds was a major consideration in the location of camps. They also characterized themselves as 'beach people'. They liked shellfish which they said added variety to their diet. After several days of eating fish they expressed a desire for shellfish flesh because it was 'wet' and not 'dry' like fish. They also valued its freshness as they often discarded meat that was more than a few hours old.

No apologies are made for quoting Meehan's (1977) last paragraph in its entirety:

> 'It is only within this wider cultural context that the real significance of shellfish in the Anbara economy can be fully appreciated. Perhaps the persistence of the activity of shellfish gathering over periods of thousands of years by coastal hunters in many parts of the world, as exemplified by the prominence of shell middens in the prehistoric record, indicates that the importance of molluscs in those economies also was not measured solely in terms of their gross energetic contribution to the diet. True, debris from shell gathering tends to withstand the ravages of time better than that from most other foraging activities and is thus perhaps over-represented in the archaeological record, but we should not let this factor blind us to the subtle role that shellfish may have played in ancient hunting economies'.
>
> (Meehan 1977:528)

Detailed ethnographic studies by Bigalke (1973) along the Transkei coast of South Africa support the view that shellfish are far more important to coastal communities than a simple assessment of their calorific value may indicate. His observations between 1969 and 1972 show some interesting attitudes to coastal exploitation.

Collecting was done almost only by women, young, old and pregnant. Bigalke only observed one man collecting shellfish. Boys contributed little to the collecting, but girls helped their mothers. The women worked both individually and in small groups. They were very aware of the state of the tides, and knew that spring tides were the best times for collection as it was possible to go to further rocks and obtain larger shellfish. As collectors were observed arriving at the shore later on successive days following the spring tide Bigalke considers that they were aware of time differences between daily tides. Although most collecting was done on spring tides, it seems that it could be done on any day that people felt a desire for shellfish. There was, however, little collecting in winter as the people said that the results did not justify the effort. Bigalke states that the condition of the shellfish was not good in winter, by which we may assume he means that spawning had just been completed, and/or the shellfish reduced their feeding during this season. People reported that the flavour was better in summer. It is reasonable to assume that any coastal group exploiting this resource may possess this detailed knowledge of the most advantageous times and seasons for exploitation.

The mode of collection was seen to be divided into two phases dictated by the falling of the tide. Initially the women picked what they could from the upper zones, then once the tide had fallen they collected as quickly as possible from the lowest tidal levels. Limpets were removed singly using a narrow flat iron or steel bar and placed with the other shellfish into a container either held in the hand or tied to a belt. When this was full it was taken to a nearby rock and emptied. Each collector made her own pile and children added to their mothers' piles. Before leaving the shore the piles were quickly sorted through to remove seaweed and some very small shells not worth taking home.

At all stages of procurement shellfish were treated as an important resource. This is demonstrated especially by the fact that women frequently travelled three miles to collect them. One group living about six miles away travelled to the coast one day then stayed overnight to catch the morning low tide. Bigalke notes that seven miles seemed to be the limit for people travelling to the coast. For anyone to embark on up to a fourteen mile round trip the resource must hold some value. The coastal people considered shellfish a substitute for meat, though it could never be a replacement as there were never enough shellfish. When asked, all agreed that shellfish were a 'good food'.

The bulk of the shellfish was taken home for preparation. A few uncooked limpets were eaten during collection, but most were cooked by boiling then frying in oil. Shellfish were always eaten alone, and never mixed with other foods. After the meal empty shells were disposed of in a number of ways. Sometimes they were thrown onto one heap a little removed from the main outdoor living area where they would not get underfoot. One village threw its empty shells into a stream. At other places the remains of each shellfish collecting expedition were thrown in separate small heaps in a midden area. Sometimes shells were scattered thinly over gardens to improve fertility.

Bigalke made the very important observation that there was some awareness amongst the shellfish collectors of the conservation of resources. People said that they did not take immature molluscs because they wished these to grow big for later use. Bigalke is, however, of the opinion that this state of affairs only refers to the optimum collecting conditions of low spring tides during calm weather. During unfavourable conditions he observed women taking many small limpets with the maximum length of 25 mm.

By implication, therefore, to conserve stocks the collectors must have been selective in their gathering strategy. Bigalke notes that they were selective in as far as they only collected what they intended to eat. The shellfish were nearly always eaten the same day as they were collected.

Voigt (1975) reports on her excavations of a modern Transkei midden which was the property of an elderly woman who had created the midden over fortysix years, during which time she had given birth to three daughters. Thus this valuable study concerns the development of a midden of known age by a group of known size. (For details of the excavation, consult the reference.) Voigt found a notable lack of similarity between the shellfish species on the shore and those found in the midden. She considers that this may be explained in two ways. Either the area which was chosen for the shore survey was not representative or had been cleaned out, or a midden cannot be regarded as being an accurate reflection of local molluscan populations. If the latter is true it supports the idea that a midden, although dependent on availability, reflects dietary habits rather than availability. Voigt found that most of the common species in the middens were at least present in the shore survey, but there was no similarity in numbers. She realizes that the issue can only be settled by a survey of a totally unexploited area of shore.

Another interesting observation was of the close similarity between the midden species and samples taken of species actually eaten on a number of days. Although this is to be expected, as meals give rise to the middens, it clarifies the point that, at least in this instance, the midden material does reflect the total shellfish diet and not just a certain portion of it.

3. The ecological approach

The third type of midden analysis draws upon ecological data. The pioneering work of Shawcross (1967) uses ecological data to suggest possible economic activities involved in the formation of a midden at Galatea Bay, New Zealand. Anderson (1981), Botkin (1980) and Swadling (1976, 1977) all use the size and species distribution of midden shells to interpret possible collection strategies. In contrast to these, a number of publications misuse the term 'ecological'. 'It has become a familiar sight to see anthropological papers bearing the titular afterthought "...an Ecological Approach" ' (Beaton 1971:37). For instance Meighan's (1959) excavation at Catalina Island, Southern California, though a valuable and interesting study, is not an ecological interpretation as the title suggests.

The work of Anderson (1981), Botkin (1980) and Swadling (1976, 1977) is related to the zoological economies of consumer choice expounded by MacArthur and Pianka (1966). They state:

> 'The basic procedure for determining optimal utilization of time or energy budgets is very simple: an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. When any further enlargement would entail a greater loss than gain no such enlargement should take place'.
>
> (MacArthur and Pianka 1966:603)

The model relates to a 'patchy environment', a good example of which is a rocky shore. In such an environment a collector would be expected to forage preferentially in the patch where the yield expectations are highest. During foraging the potential yield of that patch is lowered to a point which is sufficiently below that of another patch. Thus there is an incentive to move on.

> 'The result is that few patches will be cleaned out and most will be skimmed over with the better patches bearing the brunt of the exploitation until all patches are of approximately similar yield. ....sequential denudation of patches is not only an uneconomic procedure, it is likely to destroy the productivity of the resources altogether'.
>
> (Anderson 1981:112)

Anderson (1981) developed a model of shellfishing which may be used to explain the deposition of shell middens at Palliser Bay, New Zealand. To maximize yield a collector must consider three variables: differences in yield between patches or resources, differences in time taken to locate any resource (search time), and differences in the time taken by a consumer to capture and consume any resource (pursuit time) (MacArthur 1972). Anderson makes the profound observation '....once an individual shellfish has been located the decision whether or not to take it is unlikely to be affected by the comparative difficulty of stalking, slaughtering, butchering, cooking and consuming it' (Anderson 1981:113). He is only therefore concerned with the remaining two variables, search time and yield. Anderson considers that mean search time will decrease with the addition of each new resource to the diet, and no resistance to such additions is interposed by an increasing elusiveness of the prey, so shellfish collectors ought to gather most of the different shellfish species which they encounter.

Theoretically Anderson considers that if search time is invariable between resources, the highest yielding resource ought to be preferred, and if yield is invariable between resources the one encountered most frequently ought to be preferred. However, since search time and yield are, in practice, both variable, an optimal strategy will lie somewhere between these two extremes.

Working from this basis Anderson develops his model. He translates search time into 'abundance' and yield into 'mean size'. As a general rule there is a broad inverse correlation between these variables (Lewis and Bowman 1975), and this is seen to be the case at Palliser Bay (Anderson 1981). Thus he considers that the best strategy would be for the collectors to disregard all other factors except individual size, and forage in a patch where expectations of yield are highest, taking all the larger individuals encountered, regardless of species, until the mean size of returns drops below that which could be expected elsewhere.

Since some larger individuals of small species are larger than some smaller individuals of large species, a variety of species ought to be exploited at any one time. Also, since most large individuals of large species are likely to be larger than many of the large individuals of small species, the larger species ought to be selectively exploited. Thus, if shellfish are collected more frequently than the rate at which they can recover, there will be a selective depletion of the population of larger species and thus a progressive swing down through the size range of species as collectors were forced to gather increasingly more abundant but less desirable resources.

In the Palliser Bay middens Anderson discovered a trend from an earlier concentration on larger species towards a later concentration on smaller species. After a settlement hiatus the collection pattern at one site reverted almost to its original status.

Evidence that continuous exploitation of shellfish populations causes a reduction in average size over time is also found at the cockle beds of Llanrhidian, South Wales (Hancock and Urquhart 1965, 1966) and at various sites in New Zealand and New Guinea (Swadling 1976). Swadling demonstrates how changing shellfish populations may be related to differing economic activities over time. In every case, a predominance of smaller shellfish than would be found in a natural population may be associated with an intense exploitation of this resource.

Botkin (1980) also offers an ecological interpretation of shellfish exploitation. He stresses the importance of examining the interaction between human populations and shellfish populations. 'Human populations are active participants in their local ecology, altering their environments as needed and being directly affected by that alteration' (Botkin 1980:135). Using the theories of zoological economies of consumer choice outlined above, Botkin put forward an explanation for the observed distribution of shellfish species at Malibu, Southern California. In the early levels *Mytilus califorianus* greatly exceeds *Protothaca staminea* but in the latter stages their relative importance is reversed and *Protothaca* becomes the predominant shellfish.

Botkin explains this by reference to procurement times. Whereas *Mytilus* live in dense colonies on the rocks, *Protothaca* are free living bivalves buried in gravels. The collection of these requires different procurement techniques and thereby different procurement times, the *Mytilus* being easy and quick to collect in large quantities and the collection of the individual buried *Protothaca* much slower. Thus, *Mytilus* would initially have had a lower procurement time than *Protothaca*, yet as exploitation continued its availability would decrease and its procurement time, relative to other resources, would increase. Thus it became advantageous to collect more *Protothaca* once *Mytilus* had become scarce.

Conclusions

The above studies demonstrate 'an initial attempt to reach beyond the disintegrating shells to the living people who once collected them to eat long ago' (Voigt 1975:98). Of the three categories of midden investigation, those drawing upon ethnographic data and ecological theory allow the most valuable interpretations. Simple content lists provide minimal useful information if the analyses are taken no further. Ethnographic analogies are of immense importance, especially when they are used within the same geographical area, such as using contemporary Australian aborigines and Australian shell middens. Ethnographic analogies should, however, only be used to suggest trends and possibilities and open the way for further investigations. The rigorous use of ecological theory allows the application of testable contemporary data to archaeological material.

CHAPTER 6 : THE ANALYSIS OF THE MIDDEN DATA: SHELLFISH EXPLOITATION STRATEGIES

Introduction

Sample columns of midden shellfish have been analysed and compared to those in varying habitats on the modern shore (chapter 3), to examine the following questions. Was the extent of human predation sufficient to cause noticeable changes in shellfish size-frequency distribution upwards through the middens? When were the shellfish cropped, from which part of the tidal range, and at what intensity? Was the occupation of the middens continuous or is there evidence for gaps in occupation? How selective were the Mesolithic gatherers with respect to the size and species exploited? What was the relative importance of the three species in the middens?

This chapter is composed of four parts. Part 1 describes the collection of the midden shellfish data. Part 2 examines the midden limpets, their size and shape characteristics in different levels. Part 3 examines the distribution of periwinkles and dogwhelks, and part 4 the relative proportions of the three species.

PART 1 : DATA COLLECTION

These present studies derived from column samples taken from the middens by Dr P. Mellars during fieldwork on Oronsay between 1970 and 1979. The columns extend from the top to the base of the middens, and were divided into sample units corresponding as closely as possible to the natural stratigraphic divisions visible within the deposits, which were usually between 5 and 10 cm in thickness. Horizontally the sample units ranged from 70 to 150 cm in length. The levels in each column have been numbered consecutively, beginning at the top.

One sample column was taken from each of Cnoc Sligeach, Priory Midden and CNG I. More extensive sampling was undertaken in CNG II and Cnoc Coig with 4 separate sample columns taken from the former (Mellars 1983), and 23 from the latter (Mellars 1983; Peacock 1978). The present analysis has been confined to the deepest column from CNG II, and the two deepest columns from Cnoc Coig (pits 6 and 10). These two column samples were taken 6 metres apart, and although their exact stratigraphy is uncertain, pit 6 is probably of an earlier date than pit 10 (Mellars 1983).

The problems of interpreting midden stratigraphy are discussed in Mellars (1983) and of spatial distributions within middens by Nolan (1984). It must be emphasized that middens may be constructed in a number of complex ways. For instance deposition may occur in one area, then move to another area, and finally return to the original area, and there may be slumping of one deposit onto another, especially at the edges. Also, different activities are often undertaken on different areas of the midden (Nolan 1984). Bailey (1977:135) states:

> "...it is unlikely that shells would be discarded evenly over the whole surface of a midden, even if the same quantity of molluscs were brought back to the site each year. There is the further possibility that the deposits would be disturbed and a certain amount of material pushed to one side from time to time by the inhabitants in order to create a satisfactory living surface."

Thus, there are limits to any interpretations made from column samples which must be borne in mind throughout the discussion below.

Shells have been sorted into the following categories:

Limpet sample and remains

These are all the whole, measurable limpet shells. In some instances all these were measured and weighed, yet in cases where there were many shells a random sample was removed for measuring and weighing. This was done by thoroughly mixing the shells, laying them out on a table in rows, then removing every n^{th} shell until the desired sample was obtained. Thus, the sample represents the measured and weighed shells, and the remains are those whole limpet shells not included in the sample. The limpets were measured along length, width and height as described in chapter 3.

Limpet rejects

These are limpet shells which are virtually whole yet have pieces broken from them, making them useless for measuring or weighing.

Limpet apices

Many limpets have been fragmented into small pieces. The limpet apices were removed from these fragments to allow the calculation of the minimum number of individuals.

Periwinkle and dogwhelk complete shells

These were all measured as there was never enough for samples to be taken. Periwinkles were measured along total length, and the whole dogwhelks were also measured along total length and aperture length as described in chapter 3.

Dogwhelk measured apertures

Most dogwhelks were broken for the extraction of meat, yet this often left the aperture intact. Measurements could therefore be taken of the aperture length in exactly the same way as for the whole dogwhelk.

Dogwhelk siphonal canals and apices

Both these features were counted from all broken dogwhelks as both may indicate minimum number of individuals. The siphonal canals on the measured apertures were also included here. (Figure 47 shows the siphonal canal).

Thus, these data may be used to answer the questions given in table 29.

TABLE 29 : INFORMATION OBTAINED FROM THE COLUMN SAMPLES

Information required per column level	How obtained
Total number of limpets	Limpet sample + limpet remains + limpet rejects + limpet apices
Total number of periwinkles	Whole periwinkles + apices
Total number of dogwhelks	Whole dogwhelks + siphonal canals

It will be seen that siphonal canals and not apices have been used to calculate the minimum number of dogwhelks. After all samples had been examined, it was discovered that in 20 there were more siphonal canals than apices, and only 10 samples contained more apices than siphonal canals (table 30). Thus, it was considered that the siphonal canals provide a better indication of total dogwhelks. They are tougher and less subject to fragmentation than the apices.

Weights were taken of all the above categories for the calculation of meat weight (chapter 7). These data may also be used in further research whereby weights but not numbers of midden shells are available.

TABLE 30 : NUMBERS OF DOGWHELK SIPHONAL CANALS AND APICES PER MIDDEN LEVEL

MIDDEN	LEVEL	NUMBER OF SIPHONAL CANALS	NUMBER OF APICES
CNOC COIG PIT 10	9	29	17
	10	1	0
	11	14	8
	12	7	4
CNOC COIG PIT 6	17	28	38
	18	27	23
	20	27	23
	21	13	12
CNOC SLIGEACH	28	121	85
	29	157	125
	30	160	170
	31	77	66
	32	29	35
CNG I	1	60	66
	2	80	138
	3	69	82
CNG II	E	42	20
	F	25	13
	G	7	4
	H	2	1
PRIORY	1	30	33
	2	25	21
	3	5	10
	4	5	2
	5	5	0
	6	28	9
	7	21	13
	8	0	0
	9	0	1
	10	0	1

Total number with most siphonal canals = 20
Total number with most apices = 10

PART 2 : MIDDEN LIMPETS

An examination will be made of limpet size and shape distributions in each midden level, and these may then be compared to the size and shape distributions of the modern limpets discussed in chapter 3. As in chapter 3, size is measured by total length, and shape by length/height.

A. LIMPET SIZE

Methods

Figures 85 to 91 show the size distribution of limpets in 11 shell length groupings for each midden, and figures 92 to 122 the distribution of these same shell length groupings for each individual midden level. Figure 123 gives the distribution of the extremely small and extremely large limpets in each midden, and figure 124 their distribution in each individual midden level.

Figures 85 to 122 are of the same shell length groupings as figures 49 to 60 in chapter 3, to facilitate a comparison between the modern limpets from varying tidal habitats with those in the middens. Figures 123 and 124 were produced to emphasize the size distributions of the smallest and largest limpets. When interpreting limpet shell size it is often the extreme values that are indicative of changes in population structure which may have an important bearing upon human collection strategies (see below). Figures 123 and 124 represent the smallest and largest 10% of all the midden limpets, excluding those from the Premidden. These were not included because, as will be seen below, they are much smaller than any of the other midden levels. The 10% values were chosen as indicators of the largest and smallest animals because these isolate the two size extremes, yet provide enough individuals to provide a representative sample. There are a total of 3,673 midden limpets from all the sample columns except the Premidden, the lower 10% being animals up to and including 25.6 mm shell length, and the upper 10% being animals over and including 37.5 mm shell length. In the discussions that follow these animals will be referred to as the smallest and largest limpets.

In figures 85 to 122 size groups 0, 1 and 2 represent limpets below 25 mm, and groups 7 to 11 limpets over 37 mm, so for clarity of discussion these groups will be referred to as extreme small and extreme large, and groups 3, 4, 5 and 6 will be termed medium limpets. This avoids the confusion of continually repeating limpet length classes when discussing these figures.

Results

1. Mean size

The most striking feature of figures 85 to 91 is the similarity in size distribution of the limpets in each midden, all peaking in the medium size range. There are, however, certain differences which require examination. CNG I, Cnoc Sligeach and Priory Midden all peak in the size range 28 to 30.9 mm shell length, but Cnoc Coig peaks in the range 25 to 27.9 mm and CNG II in the range 31 to 33.9 mm.

Table 31 shows that CNG II and Priory Midden have limpets of the largest mean size, with lengths of 32.28 mm and 32.12 mm respectively. The smallest limpets are to be found in Cnoc Coig, where pits 10 and 6 have limpets of 30.11 mm and 28.65 mm mean shell length respectively. The Premidden has the smallest limpets with a mean length of 26.47 mm.

Figures 92 to 99 show the size distributions at different levels in Cnoc Coig (excluding the Premidden). Figures 92 to 95 represent pit 10, and figures 96 to 99 pit 6. In pit 10, levels 10, 11 and 12 have a fairly uniform limpet size distribution, with most limpets in the size range 28 to 30.9 mm. The uppermost level does, however, have a much higher proportion of limpets in the size range 25 to 27.9 mm. Table 32 shows that the mean size decreases slightly from the lower to the upper levels, though the difference between levels 9 and 12 is only 0.99 mm. The histograms show that in all levels most limpets are between 25 and 33.9 mm with very few above and below this range.

TABLE 31 : MEAN SIZE AND SHAPE OF LIMPETS FROM EACH MIDDEN

MIDDEN	MEAN LENGTH	STANDARD ERROR	MEAN RATIO LENGTH/HEIGHT	STANDARD ERROR
CNOC COIG PIT 10	30.11	0.20	3.08	0.02
CNOC COIG PIT 6	28.65	0.22	3.15	0.12
CNOC COIG Both Columns	29.44	0.15	3.11	0.04
PREMIDDEN	26.47	0.30	3.10	0.04
CNOC SLIGEACH	31.03	0.20	3.13	0.02
CNG I	30.52	0.26	3.02	0.02
CNG II	32.28	0.22	3.03	0.02
PRIORY MIDDEN	32.13	0.13	3.12	0.01

TABLES 32-37 : MEAN SIZE AND SHAPE OF LIMPETS FROM EACH MIDDEN LEVEL

TABLE 32 : CNOC COIG PIT 10

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
9	29.57	0.41	3.06	0.04
10	29.83	0.37	3.08	0.04
11	30.47	0.40	3.07	0.04
12	30.56	0.39	3.10	0.04

TABLE 33 : CNOC COIG PIT 6

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
17	27.43	0.75	3.16	0.07
18	28.46	0.45	3.13	0.05
20	29.34	0.39	3.12	0.04
21	28.61	0.35	3.19	0.04
Premidden	26.47	0.30	3.10	0.04

TABLE 34 : CNG I

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
1	31.02	0.45	3.02	0.04
2	30.10	0.44	3.01	0.04
3	30.38	0.43	3.04	0.03

TABLE 35 : CNG II

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
E	29.61	0.61	3.08	0.06
F	31.77	0.41	3.01	0.04
G	32.57	0.47	3.12	0.07
H	32.57	0.45	3.02	0.04
J	33.20	0.48	2.96	0.04

TABLE 36 : CNOC SLIGEACH

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
28	29.58	0.48	3.16	0.05
29	31.96	0.37	3.04	0.04
30	31.77	0.40	3.06	0.04
31	30.44	0.35	3.28	0.04

TABLE 37 : PRIORY MIDDEN

LEVEL	MEAN LENGTH	S.E.	MEAN RATIO LENGTH/HEIGHT	S.E.
1	30.74	0.46	3.16	0.04
2	31.03	0.44	3.19	0.04
3	31.75	0.52	3.04	0.04
4	32.02	0.38	3.15	0.04
5	30.73	0.40	3.15	0.05
6	32.02	0.39	3.22	0.04
7	32.73	0.42	3.00	0.03
8	33.99	0.35	3.16	0.04
9	33.10	0.38	3.00	0.03
10	32.12	0.36	3.17	0.03

Cnoc Coig pit 6 comprises levels 17, 18, 20 and 21 (level 19 is composed largely of sand). Level 17 has a different size distribution to the other levels, but the sample size is only 48, so little significance should be placed on these results. All the other levels from this core peak in the size range 25 to 27.9 mm, which is lower than in pit 10. Table 33 shows that the largest mean size occurs in level 20, though at 29.34 mm this is not as large as the smallest mean size in pit 10. Again the upper level has the smallest limpets, though in this case the second level up has the largest limpets and not the base as in pit 10.

The Premidden level which underlies the main midden levels at Cnoc Coig, separated by a layer of sand, has the highest percentage of small limpets of any level in any midden. The mean length is 26.47 mm (table 33), and figure 100 shows the large number of limpets in the size range 22 to 27.9 mm.

CNG I has a generally uniform size distribution in all levels (figures 101 to 103, table 34) with slightly more larger limpets in the upper level. All peak in the size range 28 to 30.9 mm, and show a clearly unimodal distribution.

CNG II (along with Priory Midden) contains the largest limpets (table 31). The middle three levels have limpets peaking in the size range 31 to 33.9 mm (figures 105, 106 and 107), while the top and bottom levels peak between 28 to 30.9 mm (figures 104 and 108). Despite this, however, the basal level does have a high proportion of larger limpets. Table 35 shows that there is a slight reduction in mean size from the lower to upper levels, though levels G and H have the same mean size. The difference in mean size between the top and bottom of the midden is 3.59 mm.

In Cnoc Sligeach, levels 28, 30 and 31 (figures 109, 111 and 112 respectively) peak at a size range of 28 to 30.9 mm, and level 29 (figure 110) has an equal number of limpets in the ranges 28 to 30.9 and 31 to 33.9 mm. Table 36 shows that limpets in the top level have a slightly smaller mean size, but the other three levels show no pattern of decreased mean size upwards through the midden; in fact the reverse is true. There are very few extremely small and extremely large limpets. Level 29 has no limpets below a size of 25 mm (figure 110).

The Priory Midden has limpets with a combined mean size nearly as great as CNG II (table 31). Table 37 shows that levels 1 and 5 have limpets of a slightly smaller mean size. Below level 1 there is a slight increase in mean size down to level 4, then there is a slight increase in mean size down to level 8. The basal levels, 9 and 10, are also of a relatively large size. Figures 113 to 122 show that all except level 8 have limpets peaking in the size range 28 to 30.9 mm, yet level 8 has relatively few limpets of this size, and peak in the size range 31 to 33.9 mm with a relatively high proportion in the size range 34 to 36.9 mm. This level has no limpets below 25 mm. Level 10 shows slight bimodality, peaking mainly in the range 28 to 30.9 mm and with a second lower peak in the range 34 to 36.9 mm (figure 122).

Excluding the Premidden, therefore, there is a general uniformity in size distribution between all the levels from each midden. The distributions are clearly unimodal, all peaking in the medium size range at either 28 to 30.9 mm or 31 to 33.9 mm, with the exception of limpets from Cnoc Coig pit 6, which peak in the range 25 to 27.9 mm. As a general rule, in all levels there are very few limpets below 25 mm, and above this size there is a steep increase in numbers. There is usually a steep decrease after either a size of 33.9 or 36.9 mm. The Premidden, however, is composed mainly of limpets between 22 and 30.9 mm shell length.

2. The distribution of the largest and smallest limpets

It is evident from figures 85 to 122 that, although most limpets occur in the medium size range, there are some smaller and larger individuals, and their numbers do fluctuate. These may be seen in figures 123 and 124. Figure 123 demonstrates a number of trends. The Premidden contains a high proportion of the smallest limpets, yet none of the largest. Except for a reversal in order of Cnoc Sligeach and CNG I, those middens grading progressively from having the highest to the lowest proportions of smallest limpets grade in reverse order with relation to their proportions of the largest limpets. Thus it is clear that Cnoc Coig contains the smallest limpets and Priory Midden and CNG II the largest. Within Cnoc Coig, pit 6 contains more smaller limpets and less larger limpets than pit 10.

Figure 124 reveals a number of size related distributional trends within the middens. In all of the column samples the uppermost levels contain more smaller limpets than the other levels, though they do not necessarily contain the lowest proportion of larger limpets. In Cnoc Coig pit 6, CNG II and Cnoc Sligeach the uppermost levels have noticeably higher proportions of smaller animals than the other levels, though in the case of pit 6 the uppermost level shown in figure 124, (level 18), is in fact below level 17, which is not shown here due to its small sample size of 48 individual limpets. Only CNG II shows a higher proportion of larger limpets in its basal level. In this midden there is a distinct predominance of larger limpets in the lower levels and smaller limpets in the upper levels. Priory Midden shows generally more larger limpets in levels 3, 4 and 6 to 10, and more smaller limpets in levels 1, 2 and 5. Cnoc Sligeach contains relatively more larger and fewer smaller animals in levels 29 and 30, yet in both columns from Cnoc Coig, and CNG I, the proportions of larger limpets in each level remains fairly consistent.

Thus, in CNG II and Priory Midden, the middens with relatively more larger limpets, there is a tendency for more larger, and fewer smaller limpets to exist at the base of the columns, and the reverse situation to occur in the upper levels. This trend is most noticeable in CNG II. Cnoc Sligeach has more smaller animals in its upper level, though there is no progressive trend for smaller animals up through the midden. In the other middens there are more smaller limpets in the upper levels, though there are not correspondingly less larger limpets.

It is necessary to re-emphasize the difficulties of interpreting midden stratigraphy outlined above. These levels do not necessarily represent consecutive occupations ranging from the initial to the final habitation horizons.

3. A comparison of midden and contemporary limpet size distributions

A comparison of figures 85 to 122 and tables 31 to 37 with figures 49 to 60 and table 19 makes the narrow size range of the midden limpets even more interesting. Chapter 3 demonstrated that on an uncropped shore there is a much higher potential for collecting a greater variety of sizes than is evident from the middens. Although the Mesolithic shoreline was obviously not exactly the same as that at present, we may assume that it was similar (chapter 4).

It has been demonstrated that on any shore a number of common factors govern limpet population structure (Choquet 1968; Fischer Piethe 1948; Hatton 1938; Lewis and Bowman 1975; Jones 1948; Jones et al 1977; Orton 1928b; Thompson 1979, 1980). These, along with the present study, have shown that all rocky shores will contain a variety of habitats which support varying limpet populations. Figures 49 to 60 show that in certain sites there is a predominance of smaller limpets, in others there is a fairly uniform distribution of limpets of a wide range of size classes, and others support mainly the larger limpets. Figure 60 represents a combination of all sample units on the modern shore, and shows that from 22 mm to 49.9 mm there is a virtually uniform distribution of different sized limpets. Thus, at least on initial occupation, Mesolithic shellfish collectors would have been faced with a coastline containing a much wider variety of different sized limpets than is evident in the middens.

It is unlikely that any one single habitat was being cleared of limpets at the expense of all others. Unit 1B (figure 50) has the closest distribution of any of the middens. This is the near vertical face of a large skerry occupying the low to mid tide level and containing a heavy yet patchy barnacle cover. It is difficult to imagine that such a habitat, or one with similar constraints on limpet growth, would be so predominant around the whole island. Thus, it is a logical assumption that the observed midden shellfish population structures are, at least in part, a reflection of the activities of the human populations.

4. Limpet fragmentation

One issue which is inevitably raised by the preceding discussions is the question of how far variation in the size distribution of limpets in different midden levels may be due to varying degrees of fragmentation of the shells in these levels.

If small limpets were more frequently broken than larger limpets the size-frequency distributions will underrepresent the numbers of small limpets in the middens. If there was preferential breakage of the smaller limpets then there should be more broken limpets in levels with less small limpets, and the levels with more smaller limpets should have less fragmented shells.

Figures 125 to 129 show that this is not the case. These represent Cnoc Coig pits 10 and 6, CNG I, CNG II, and Cnoc Sligeach respectively. Figures 128 and 129 show both the number of limpet apices as a percentage of the number of whole limpets, and the weight of fragments of limpet shell as a percentage of the weight of whole limpets. Figures 125, 126 and 127 show only the former category as data are not available on the weight of fragmented shells from these samples. Data are also not available from the Priory Midden.

From figures 128 and 129 it is evident that whether the degree of fragmentation is expressed in numbers or in weight, the patterns are very similar. In all cases the greatest fragmentation occurs in the upper levels, due probably to more trampling and weathering. A comparison of figures 125 to 129 with figure 124 demonstrates that there is no greater fragmentation in levels where there are fewer smaller limpets. In fact, as noted above, each midden contains more smaller limpets in its upper levels, where there is the highest degree of fragmentation.

It is most likely, therefore, that the fragmentation is due to more erosion on the top of the middens, irrespective of limpet size.

B. LIMPET SHAPE

Methods

Measurements were taken of total length and height on all the samples of whole limpets, and shell shape has been expressed as length/height, as in chapter 3. Tables 31 to 37 express these mean shell shape variations.

Results

Chapters 1 and 3 have demonstrated that limpet shape varies with tidal position. Two main factors are evident from the shape distributions of the midden limpets. Firstly, the majority of midden limpets are of a more uniform shape than those available on a modern uncropped shore (chapter 3), and secondly it seems that the vast majority of limpets were collected from the lower rather than the upper shore.

Table 31 shows that the flattest limpets occur in Cnoc Coig pit 6, Cnoc Sligeach and Priory Midden, with mean ratio length/height measurements of 3.15, 3.13 and 3.12 respectively, and the most conical in CNG I and CNG II with ratios of 3.02 and 3.03 respectively. When these figures are compared to those in table 19, it is evident that there is much less variation in shape than on an uncropped shore where the mean ratio length/height varies from 2.47 at sample unit 1C-1 (MHWN) to 3.55 at sample unit 5 (MLWS-MLWN). When the mean shapes of limpets of varying levels in the middens are considered it is evident that there are variations in shell shape ranging from 2.96 at the base of CNG II to 3.28 at the base of Cnoc Sligeach. Table 19, however, shows that from a variety of habitats on the uncropped shore values vary from 2.47 to 3.55.

It seems that limpets were collected mainly from the lower shore. No mean ratio length/height from any midden level falls as low as those at unit 1A (MTL) or unit 1C-1 (above MHWN) which are 2.55 and 2.47 respectively. Figure 130 and table 38 demonstrate that when all midden limpets are considered together the range of shape values corresponds almost exactly to the range of values on the present low

TABLE 38 : THE MEAN VALUES OF RATIO LENGTH/HEIGHT FOR LIMPETS FROM THE MODERN UPPER AND LOWER SHORE, AND A COMBINATION OF ALL THE MIDDEN LIMPETS

	Mean ratio length/height	Standard Error
Modern upper shore	2.53	0.03
Modern lower shore	3.11	0.02
Midden limpets	3.10	0.01

shore. Thus, all midden limpets could have been collected from the lower tidal range. The area of overlap in figure 130 between the virtually identical lines of the modern low shore limpets and midden limpets with the modern high shore limpets could represent midden limpets collected from the upper shore. This is, however, considered unlikely for a number of reasons. On the modern low shore there is an overlap in shell shape between lower and upper shore animals (figure 130). These fewer, more conical animals on the lower shore may have moved to this new tidal zone (as observed by Moore 1934). The few flatter animals on the upper shore may also have migrated to a new position or live in a damper microhabitat so have developed a less conical form. It is, however, possible that some of the midden limpets might have been collected from the upper shore.

Figure 130 shows that, although there is a very close similarity between the modern low shore and midden limpets, in group 3 (ie between shell length/height ratio 2.0 to 2.49) there are a small quantity of midden limpets that are more conical than exist on the modern low shore. Obviously it is not possible to say whether the Mesolithic low shore may or may not have supported these few individuals.

Thus, although some of the midden limpets may have come from the upper shore, the close association between the ratio length/height of the modern low shore animals and those from the middens strongly suggests that the vast majority of midden limpets were gathered from the lower tidal range.

Further work is required to establish the exact relationships between limpet shape and tidal position, yet from the present evidence it seems that most limpets came from around and below MLWN. If it proves to be the case, as is suggested in chapter 3, that there is no increase in flatness progressively down shore from this level, then it will not be possible to say if any specific area was exploited below this level. It does not, however, seem that many limpets were taken from the upper zone.

C. INTERPRETATION : Towards an idea of Mesolithic collection strategies

1. Trends in limpet size distributions

Although the midden limpets have a smaller mean size than those on the modern shore there is, nevertheless, a lower size limit. Figures 85 to 122 demonstrate that there are very few limpets below 19 mm shell length. The reasons for this are possibly twofold. The collection of animals below a certain size is not a cost-effective exercise, the amount of meat they contain not being sufficient reward for the effort of getting the animals. It is also possible that the Mesolithic gatherers realized that to collect the smallest limpets would mean that in the future they would have fewer larger animals. They probably, therefore, practised conservation of the resource which was to be of importance to them on a regular basis (below). For whatever reasons, therefore, there appears to be a lower threshold in limpet size below which the animals were not collected.

The large limpets observed in a variety of habitats on the modern shore do not exist in the middens. The lack of larger limpets could indicate a pressure on the limpet population caused by human predation. Assuming, for the moment, that the gatherers initially chose the largest limpets, once these had been exploited they would have to make do with slightly smaller animals. In this way, over a period of time, the collection of limpets over the threshold level of population recovery would mean a progressive decrease in mean size of modern limpets from earlier to later deposits.

There are, however, no major trends towards a decrease in the size of limpets upwards through the middens. Although in each midden the upper levels contain more smaller limpets, and in CNG II and to a lesser extent Priory Midden, the lower levels contain more larger limpets, these trends are not of the magnitude to suggest a major pressure on the resource. If this were the case, the order of magnitude of these size changes would be greater and the mean sizes would alter significantly more than they do here.

There does, however, appear to be slight pressure on the limpet populations in so far as it was necessary to collect more smaller limpets in the upper levels, and especially at CNG II there appears to be fewer of the larger animals than had been initially selected. In the other midden levels there is not such a change in the proportions of the largest limpets, indicating that there was a fairly small yet constant supply of these animals. This is not, however, the case during the occupation of the Premidden. Figures 100, 123 and table 31 show the predominance of smaller limpets at this occupation level, and a complete lack of larger limpets. Possible reasons for this are considered below.

It does, therefore, seem that there was some fairly light pressure on the limpet resource imposed by the human collectors. It is not possible to be more specific because of the problems of midden stratigraphy noted above. Also the timescale of occupation is uncertain. Although the radiocarbon dates (table 1) indicate that the middens were occupied over a period of around 600 years (pers. comm. Dr P. Mellars), the continuity of occupation of each midden within this period remains uncertain. In Cnoc Coig, however, the spatial distribution of midden components has been studied by Nolan (1984, forthcoming), who considers there to be no gaps in occupation for any significant period of time during the occupation of this midden.

2. Evidence for cropping rate of the limpet resource

Using data on the reproduction and growth rate of contemporary limpets it is possible to obtain the approximate age of the majority of midden limpets and hence get an idea of the cropping rate and intensity.

It was shown in chapter 1 that limpets usually spawn between September and late November, and then settle on the shore within about ten days. After a further six weeks they are just detectable at a size of around 1 mm. It was emphasized that the extent of settlement on any part of the shore varies with the local environment. By combining all information on rates of growth shown in table 6, it may be seen that by the end of their first year limpets may be anywhere from 10 to 35 mm mean shell length, and at the end of their second year anywhere from around 16 to 53 mm (excluding the Cornish example). At present the limpet growth rate on Oronsay is probably similar to that around Boulogne, due to the similarity in minimum winter temperatures, where both fall to around 6°C (Choquet 1968; chapter 4). This idea is supported by the fact that at Plymouth Orton (1928b) found a similar growth pattern and here the sea temperature falls to around 8°C in winter.

Sea temperatures during the period of midden occupation were probably an average of around 1 to 1.5°C above those of today (chapter 4). This is, however, an average figure; chapter 4 demonstrated that summer temperatures may be higher in shallow water where the effects of the warmer land temperatures and the direct rays of the sun serve to warm the water. It is clear from table 6 and chapters 1 and 2 that limpets grow faster in warmer waters.

Thus, taking into account the range of growth rates in varying environments, the probable present growth rates of Oronsay limpets, and the estimated Mesolithic sea temperature, we may arrive at an estimate of the growth rate of the midden limpets. It is probable that they attained a mean length of around 20 to 35 mm at the end of the first year, and around 40 to 55 mm by the end of the second year. Obviously these are average figures and they will vary over the shore.

Thus it may be postulated that the middens represent the collection of limpets which are predominantly around one year old, and only very few are allowed to reach the end of their second year.

The general uniformity in limpet size between the levels in different middens (with the exception of the Premidden), and the collection of limpets of predominantly one year old suggests that the periods of occupation of the middens were regular and continuous. Gaps in occupation would allow limpet stocks to recover so there would be levels containing significantly larger limpets. No such level exists in any of the sample cores. Obviously this does not preclude the possibility that such levels exist in other parts of the middens; however in his examinations of the stratigraphy of Cnoc Coig, Nolan (1984, forthcoming) has found no evidence for gaps in occupation.

Mellars and Wilkinson (1980) have demonstrated that the middens were occupied on a seasonal basis. Using data on the size distribution of saithe otoliths they have demonstrated that Cnoc Sligeach was occupied during the period from the end of June to late August, and Cnoc Coig from mid-summer until late November or early December, with the main period of occupation in the late summer and autumn. The Priory midden was probably occupied during the winter or early spring, and CNG II appears to have been occupied both from June to August and during the winter. (No otolith data are so far available from CNG I.) There is a strong possibility that limpets were exploited at the same time as the fish, though at present there is no information on the seasonality of limpet exploitation. Given the large amounts of limpets needed to make a meal (Bailey 1978), it is unlikely that shellfish were eaten alone, but were consumed with other resources.

There is other evidence of seasonality of occupation. For instance, Cnoc Coig contains many hazelnut shells which indicate autumn occupation, as does the heavy predominance of grey seal bones with some specimens of very young seals (Grigson 1981). Between mid September and late October seals come onto land to breed and are easy to capture. Support also comes for the interpretation of Priory midden as a winter site by the relative scarcity of fish remains from the lower levels of this midden (Mellars 1978; Mellars and Wilkinson 1980). At this time of year saithe migrate into deeper water. The upper layers contain more fish remains, and Mellars and Wilkinson suggest this may indicate a shift of occupation to the earlier part of the winter.

Thus, although there is a slight overlap of occupation, especially in the case of CNG II, it does appear that the middens were occupied on a seasonal basis.

There is therefore a potential parallel between the predominance of limpets around one year old and the occupation of each midden (with the exception of CNG II) once a year. An interesting model therefore presents itself. It is possible that during the occupation the largest available limpets were collected, and by the same time next year this same size range would be collected again, and so on throughout the occupation of the middens. On this model, the few larger limpets seen in figures 85 to 122 represent those few that were missed the previous year and so had more time to grow.

There are two problems with this model which require examination. Firstly the Premidden, being at the base of Cnoc Coig, would be expected to contain much larger limpets. The most probable explanation for this is that the limpets had been previously cropped and their remains not preserved or not discovered. It seems unlikely that the Mesolithic people should have selected this small size range on their initial occupation, only to select a larger size range later.

The time taken to collect limpets has a bearing on this question. Appendix 1 demonstrates the ease with which limpet stocks may be depleted. It shows that limpets may be collected at a minimum rate of around 83 to 100 and a maximum of around 300 to 600 limpets per hour, depending upon such variables as the skill of the collector and limpet distribution over the shore.

If the Mesolithic peoples began by collecting the larger limpets, it would not take long for these animals to be exploited. In fact, it is possible that the majority of large limpets could have been gathered in one or two collecting seasons. Perhaps, therefore, their absence from the middens is not as surprising as it first seems. Once these had been removed, the collectors were left with an annual crop of predominantly medium-sized limpets.

The second problem with this model is that as limpet settlement only occurs around the winter, Priory midden and possibly also CNG II (winter sites) should contain limpets at exactly one year old, whereas Cnoc Sligeach and Cnoc Coig should have access to limpets either of only a few months old or over one year old. This is not, however, such a problem as it may initially seem. It was emphasized above that the majority of midden limpets are around one year old; obviously it is not possible to tie them down to the exact month. The important thing is that, be they nine months or fifteen months old, the exploitation appears to be regular and to contain a high proportion of a specific size group (approximately one year old), along with some younger and some older animals. Also, if each midden was occupied for exactly the same amount of time and limpets were collected at exactly the same intensity at different middens, then the summer-autumn sites may be expected to contain larger limpets than the winter sites. It is likely, however, that length of occupation and intensity of limpet exploitation varies between sites.

Thus, the fact that limpet settlement occurs only at one season does not distract from the possibility that there was a regular, low intensity exploitation of limpets, the majority of which were approximately one year old.

3. Was there deliberate selection of a favoured size range?

In the above arguments it has been assumed that the Mesolithic gatherers were selecting the largest available limpets. We must, however, consider the argument that perhaps, instead of representing a uniform, continuous seasonal cropping, these limpet size distributions represent the deliberate selection of a favoured size range from within a much broader size range available on the shore. Whereas the above strategy requires a continuous light and uniform exploitation, this strategy may result from either this, or a heavier and more sporadic exploitation. Instead of taking the largest available limpets, they selected for the specific size range. A collection of a preferred size range would still cause a slight reduction in mean size upwards through the middens as the desired size became scarcer and they had to resort to smaller animals.

An obvious question is why this size range should be selected. Chapter 2 showed that larger limpets have relatively less meat with relation to shell than smaller animals. It is possible therefore that the very large limpets were considered to have too much shell weight for a given quantity of meat in comparison to the medium-sized individuals. Small limpets would be avoided as even more would have to be collected to obtain a given amount of meat. There is also the question of taste and cultural preference, variables that can never be proved. Some older people on Colonsay who remember collecting limpets (and some still eat them occasionally), say that they prefer the smaller animals and avoid the big ones, especially those from high tide levels. They consider the larger limpets are tougher and do not taste as good. Others, however, say that although they avoid the upper shore limpets, the larger lower shore animals are perfectly palatable.

This explanation does not satisfactorily explain the small sizes in the Premidden. It is hard to imagine why there should be an initial selection for smaller limpets. It is also not considered a likely collection strategy when account is taken of the distribution of limpets over the shore.

4. The distribution of limpet populations around the shore and their relationship to collection strategies

Of great importance in deciding the most likely collection strategy is a consideration of the practicalities of actually gathering the variously sized and shaped limpets from the shore. In chapter 3 it was shown that over the shore as a whole there is a fairly uniform distribution of varying sized limpets (figure 60), yet varying habitats contained varying degrees of different sized limpets (figures 49 to 59). Assuming, hypothetically, that a group of collectors were faced with a previously uncropped shore, in any one spot they would encounter limpets of varying sizes, though depending on their position there would be a higher proportion of limpets of one size than of another. For instance, if collecting from sample unit 1A (figure 49) the gatherers would be faced with a high proportion of limpets below around 30 mm shell length; if collecting from sample unit 1C (figure 52) they would have a fairly even choice of all sizes, yet in sample units 2 and 3 (figures 54 and 55) they would find a much higher availability of larger limpets. Faced with these varying proportional distributions, what would be the most cost-effective methods of collection?

If we accept for the moment the idea that the collectors were not selecting the restricted size seen in the middens but were obtaining the largest available, it is reasonable to assume that in this patchy environment they would forage preferentially in the patch where the yield expectations were highest. Thus, on initial exploitation they would go first to the area of shore where the largest limpets occurred in the highest density. This would be exploited until there was a reduction in these large limpets, when they would move to another area of shore containing a high density of large limpets. After a time they would discover that a greater yield could be obtained in a shorter time by collecting more limpets of a smaller size than by spending time searching for the few remaining large limpets. In this way they would move over the shore collecting gradually smaller limpets.

Under heavy exploitation, as discussed above, there would be a great reduction in size range from lower to upper levels of the midden. However, under a light, regular exploitation strategy such activity may well produce the limpet distributions observed in the middens. Once the large limpets had been collected, an annual exploitation would not allow the majority of limpets to regain this size; instead the small limpets which were not collected could grow to be of moderate size before being gathered. The fact that there are no levels with peaks of larger limpets suggests that during the formation of the middens the occupation was continuous.

The most efficient selection strategy does not involve the total depletion of all the largest limpets in any area, because they may be overlooked, or they may be so isolated that they are not worth collecting. This is why, at all levels, there are a few large limpets that have had more time to grow. There are also some small limpets. These would have been gathered because they were associated with the larger limpets. From much personal experience in the art of limpet collecting, it is clear that when a group of varying sized limpets are so close together it is just as easy to remove them all as to try and prise off only a few of the group.

If we adopt the idea that the collectors were deliberately choosing the medium sized limpets, a number of problems present themselves. Given the variability in size ranges from different shore environments expressed in figures 49 to 59, this would be a far from cost-effective exercise. More energy would be employed in search time than could ever be replenished by eating limpets of this size. It is hard to imagine why anyone should spend a long time searching for these limpets and ignoring most of the larger ones. It is not as if limpets of this size would have been the most common on the shore. Certainly some skerries would probably have had limpets whose size-frequency distribution was very similar to that found in the middens (eg Unit 1B, figure 50), yet it is highly unlikely that such a population structure would predominate over the whole shore.

5. Shell shape as an indicator of limpet collection strategies

The predominance of lower shore limpets in the middens indicates that the exploitation strategy was relatively light, and the people were not under any pressure to collect the less desirable upper shore limpets. A preference for the low tide limpets is easy to explain. Personal experience confirms that the high shore limpets are much tougher, and the people on Colonsay who remember collecting limpets specify that high shore limpets should be ignored because they are tougher and not as nice to eat.

D. CONCLUSIONS

What therefore do the limpets reveal about the Mesolithic gatherers of Oronsay? It has been shown that the population structure of the midden limpets differs to that of the uncropped modern shore, and an attempt has been made to explain these differences. The most obvious feature of the midden limpets is a much greater uniformity in size than is evident on an uncropped shore. By referring to aspects of contemporary limpet ecology, and estimates of sea temperature for Mesolithic Oronsay, it has been suggested that the majority of midden limpets are around one year old (plus or minus a few months). Any interpretation of Mesolithic limpet collection strategies must therefore be able to explain this feature, plus the variations in limpet size that do occur between different levels and between different middens. No one strand of evidence is enough to explain the midden limpet distributions, yet when a number of factors are combined some possible explanations present themselves.

1. Limpet collecting was relatively light and of low intensity

There are no major changes in limpet size upwards through the middens. The changes that do occur indicate a light pressure on the limpet resources. Any high intensity exploitation would result in greater reductions in size over time or, if all the desired limpets were removed, there would be either a change to another resource or a termination of occupation until such time as the stocks recovered, thereby causing a change from very small back to large limpets upwards through the column sample. The collection of contemporary limpets has shown that stocks may be depleted in a very short time. With a minimum collection rate of 83 to 100 and a maximum of 300 to 600 limpets per person per hour it would not take long for changes in mean size to appear in the middens.

It is probable that, prior to the occupation of the Premidden, there had been a period of activity when more of the larger limpets were removed, leaving only the smallest which the people were then forced by circumstances to collect.

Any sustained exploitation strategy is going to manifest itself in the size-frequency distribution of limpets, and in all the middens we see a slight increase in the proportion of smaller limpets in the upper levels of each midden, a trend most pronounced in CNG II.

It seems that limpets were collected mainly from the lower shore, and the majority of high shore limpets appear to have been ignored. If there were pressure on the shellfish resources, more high tide limpets should be found in the middens.

The implications are therefore that the middens were formed by a small group of people cropping limpets at a low intensity.

2. There was probably a regular, approximately annual cropping of the largest available limpets

As well as being of low intensity, cropping of limpets was probably for a few weeks, perhaps months, on an approximately annual basis. Instead of selecting the favoured size of limpets from a population containing large animals which were ignored, it is more likely that at every period of occupation the largest available limpets were cropped, and the small animals were left to grow until the next occupation.

This explanation may account for the smaller limpets in the Premidden at the base of Cnoc Coig. An earlier occupation could have removed most of the largest limpets, and these may either not have been preserved, or not yet found. Timed limpet collections have shown that this could be done in a short time. After this, the population settled down to collecting the largest limpets on a regular basis. The implication here is that there were no gaps in occupation of over approximately one year in duration, otherwise many more larger limpets would be evident in the middens.

It is not a cost-effective exercise to continually search out a particular size group, as the effort involved in search time is not being rewarded by a higher yield. The most productive strategy involving least effort and highest yield would be to initially exploit the largest limpets. Once, however, more effort has to be put into finding the few remaining large limpets, it becomes more economical to collect those that are slightly smaller yet more frequent. Some larger limpets probably occur in the middens because they were missed the previous year, and some small because when collecting it is often just as easy to remove a large batch of limpets rather than to pick out a few. Generally, however, the smaller animals would have been left to grow. If there were deliberate selection for the observed size range, it is hard to explain the few larger limpets that are seen in most levels.

Thus, the regular approximately annual cropping of the largest available limpets is a very likely explanation of the observed midden limpet distribution.

PART 3 : PERIWINKLES AND DOGWHELKS

Though eaten in smaller amounts than the limpets, data on the size distribution of periwinkles and dogwhelks also provide some information on the collection strategies of Mesolithic man.

A. PERIWINKLES

Methods

Table 39 gives the mean length of periwinkles from different middens and tables 40 to 44 show the variations between levels. Figures 131 to 136 show the total length distributions of periwinkles in each midden, and figures 137 to 150 the length distributions at each level. In some instances the sample size is small, so the results from these levels must be treated with caution. Statistics are not given where there are less than four individuals from each level, and histograms are not drawn in cases where there are less than eleven individuals. Table 39 shows that there are only 7 periwinkles in the Cnoc Sligeach sample, so these have not been divided into individual levels.

Results

1. The size distribution of midden periwinkles

Ignoring Cnoc Sligeach, table 39 shows that the largest periwinkles occur in Priory Midden and the smallest in CNG I. All the other middens contain animals of a very uniform mean length. Within the middens themselves there are slight fluctuations in the mean length of periwinkles between levels, yet many of them contain so few periwinkles that no great significance should be placed upon some of these variations. For instance, level 18 in Cnoc Coig pit 6 has winkles of a low mean size (22.62 mm), yet there are only six animals so the standard error is high. Both the upper levels in CNG II only contain six animals each, and level E has an especially high standard error.

TABLE 39 : MEAN PERIWINKLE LENGTHS FOR EACH MIDDEN

MIDDEN	MEAN LENGTH	S.E.	n.
CNOC COIG PIT 10	24.05	0.27	111
CNOC COIG PIT 6	24.74	0.33	73
CNOC COIG Both Columns	24.32	0.21	184
CNG I	22.19	0.29	87
CNG II	24.65	0.60	29
CNOC SLIGEACH	26.81	1.14	7
PRIORY	26.42	0.20	197
All periwinkles	24.83	0.14	504
All except Cnoc Sligeach	24.80	0.15	497

TABLES 40-44 : MEAN PERIWINKLE LENGTHS FOR EACH LEVEL

TABLE 40 : CNOC COIG PIT 10

LEVEL	MEAN LENGTH	S.E.	n.
9	24.21	0.40	37
10	23.66	0.47	47
11	24.56	0.59	23
12	24.18	0.86	4

TABLE 41 : CNOC COIG PIT 6

LEVEL	MEAN LENGTH	S.E.	n.
17	23.78	0.86	10
18	22.62	1.63	6
20	25.10	0.40	46
21	25.24	0.81	11

TABLE 42 : CNG I

LEVEL	MEAN LENGTH	S.E.	n.
1	-	-	-
2	22.30	0.33	68
3	21.54	0.65	16

TABLE 43 : CNG II

LEVEL	MEAN LENGTH	S.E.	n.
E	21.88	1.45	6
F	23.27	0.90	6
G	26.47	0.77	13
H	-	-	-

TABLE 44 : PRIORY MIDDEN

LEVEL	MEAN LENGTH	S.E.	n.
1	27.34	0.36	53
2	26.44	0.35	54
3	25.85	0.75	30
4	24.38	0.98	4
5	25.72	0.35	14
6	26.13	0.53	22
7	25.53	0.67	17

A comparison of figures 131 to 136 shows that both Cnoc Coig columns show the same range of periwinkle size distributions, peaking in the size range 22 to 25 mm shell length, whereas Priory Midden peaks between 24 to 27.9 mm and also has more animals above 28 mm in length than any other midden. CNG I, in contrast, has most animals peaking between 20 to 23.9 mm, and more animals below 20 mm than any other midden. CNG II has a wider range of sizes with a peak of 22 to 23.9 mm and at 26 to 27.9 mm. The sample size here is, however, relatively small.

Figures 137 to 150 show that there are fluctuations in the size distributions of periwinkles at different levels of the middens; some levels contain fewer extreme larger or extreme smaller animals. The overall trends are, however, as revealed by figures 131 to 136 for the whole middens. Both CNG I levels 2 and 3 contain significantly high proportions of smaller animals than the other middens, and all Priory levels (with an adequate sample size) show a high proportion of larger animals. There is no obvious pattern of size changes in periwinkles upwards through the middens.

2. A comparison of midden and contemporary periwinkle size distributions

The size distribution of periwinkles from different shore habitats has been discussed in chapter 3 where it was noted that these animals frequently occur in large clusters, often containing many hundreds of individuals, usually at mid and lower tide levels where rock morphology provides them with shelter and a supply of detritus upon which to feed. On the lower shore the periwinkles are often scattered over the rocks and on fucoids. These tend to be larger than those occurring in the groups. Periwinkles seem to be larger on more sheltered shores, where there are greater concentrations of detritus.

Table 20 shows that from the seven sample units on an uncropped modern shore periwinkle mean length varies from 25.96 mm in a sample of animals from a group at around MTL (Unit 1A) to 31.67 mm in a sheltered bay at MLWS (Unit 4). Figures 61 to 66 show the size distribution of periwinkles in the different sample areas.

These make an interesting comparison to the midden periwinkles. A comparison of table 20 with table 39 shows that mean lengths are generally greater in the modern than midden periwinkles, though the animals from Priory Midden are of a similar size to those from Units 1C and 2 and larger than those in the large cluster at Unit 1A. The seven periwinkles from Cnoc Sligeach are also of a similar large mean size.

A comparison of the size distributions of periwinkles from the modern shore and the middens reveals three significant points:

a) With the exception of Unit 1C, all the modern samples have a unimodal size-frequency distribution, and with the exception of CNG II, so have all the midden distributions (figures 131 to 136). The only significant difference is the peaking at lower sizes in the midden winkles. For instance, although containing slightly more larger periwinkles, Unit 1A (figure 61) is of a very similar size distribution to Cnoc Coig (figure 133), especially to pit 10 (figure 131). A comparison between Units 3 and 4 from the bay below Priory Midden (Port na Luinge) with winkles found in Priory Midden shows that the histograms are of a very similar shape, yet the midden shells are predominantly smaller.

b) The histograms show that there are fewer extremely large and more extremely small winkles in the middens. Whereas on the modern shore there are often quite substantial numbers of winkles above 30 mm, in the middens there are virtually none. In the modern population survey the minimum size collected was 18 mm, yet in all but Units 1A and 1C the smallest winkles found were 20 mm in length. Even in these two units there was a very low proportion of winkles in the range 18 to 19.9 mm. In some of the midden levels, however, there is a higher proportion of winkles in this size range, and even a few individuals below 18 mm.

c) On the modern shore, the largest winkles occur in greatest shelter, which is in Unit 7 below Cnoc Sligeach, and in Units 3, 4 and 5 below Priory Midden. The largest midden winkles also occur in Priory Midden and in Cnoc Sligeach, though here the sample size is very small.

3. Possible collection strategies for periwinkles

The above evidence may be brought to bear on two main questions. Firstly, is the relatively smaller size of the midden periwinkles a result of human exploitation, and secondly is there evidence to suggest that collection took place mainly from the groups of periwinkles, or simply from those scattered over the rocks?

a) Chapter 1 has shown that winkles appear to grow to different sizes at different locations. The reasons for this are uncertain, but it was noted that it may be at least partly due to variations in temperature. Moore (1937) and Williams (1964) have demonstrated that periwinkles show reduced growth in winter, and do not feed or grow below 8°C. Chapter 4 showed that modern sea temperatures around Oronsay fall to around 6°C in the winter, and table 28 indicates that the average sea temperature is probably below 8°C from around January to March. Chapter 4 discusses the probability that Mesolithic sea temperatures were probably approximately 1.0 to 1.5°C above present, which would mean a much shorter winter dormancy period for periwinkles. Thus, the Mesolithic periwinkles should in fact possess the potential to grow larger and faster than those on the present shore. Periwinkles also grow larger in areas of greater shelter (pers. comm. Dr E. Williams). From the dogwhelk evidence Andrews _et al_ (1983) have concluded that Mesolithic Oronsay was slightly more sheltered than at present. This is another reason to assume that the periwinkles would have the potential to grow larger. It has been noted above that on the modern shore the sheltered bays have the largest periwinkles, and Priory Midden and Cnoc Sligeach, both above sheltered bays, have the largest periwinkles. This indicates that the relative degrees of shelter between the middens was the same as at present.

There is a distinct possibility that the smaller size of most of the midden periwinkles is due to the pressure of human exploitation. If this is the case, it must be relatively consistent and light because there is no evidence of any changes in the mean size of periwinkles upwards through the midden. Given the high probability that the Mesolithic periwinkles were growing a little faster than at present, Dr E. Williams considers that the majority of these are approximately 2 years old, possibly a little less (pers. comm.). From his work at Craig-yr-Wylfa, Williams (1964) concluded that at the end of their first year winkles are 8 to 9 mm, at the second year 13 to 14 mm, at the third year 15.5 to 16.5 mm and at the fourth year above 17.5 mm. Smith and Newell (1955) however recorded a faster growth rate at Whitstable, and Moore (1937) even faster growth around Plymouth (table 7), both of which are likely to have slightly warmer sea temperatures than Craig-yr-Wylfa. As the majority of midden periwinkles are between 22 to 27.9 mm, and assuming the Mesolithic sea temperature was slightly warmer than at present, these animals may be approximately 2 years old. It must be emphasized that this is a very approximate estimate, and that this size range is likely to represent animals anywhere from 1 to 2.5-3 years old.

Thus, for this population structure to be maintained, cropping must not have been too heavy otherwise this age range would not be continually available for cropping. As with the limpets it would not take long to remove the relatively few larger winkles during the initial few years of occupation. After this a fairly light collection strategy would be necessary to avoid the depletion of stocks. Nevertheless, as will be seen below, the relative proportion of periwinkles in the middens indicates that the pressure on the resources was heavy enough to keep down the number of potentially available winkles (ie above the desired minimum size) to a level significantly below that of an uncropped shore. It also seems that there were no gaps in occupation long enough for the mean size of these animals to increase.

b) It is probable that all available periwinkles were gathered, providing they were of an adequate size. Figures 131 to 136 show that there are very few below 18 mm long. Although the smaller size of the midden periwinkles may indicate the collection only from clusters (such as Unit 1A), this is unlikely. While gathering limpets and dogwhelks from the rocks, it takes no extra effort to gather the periwinkles. There is no reason for ignoring the larger periwinkles as they are easier to remove from their shells (this is clear from the personal experience of myself and of Dr E. Williams) and they are not tougher and do not have a different taste (pers. comm. Dr E. Williams). There is also no reason why the groups should have been ignored. On an uncropped shore these often contain hundreds of animals, so the collection time from such clusters is minimal.

Conclusions

It does, therefore, seem probable that the consistently smaller winkles in the middens result from the light cropping by man of the larger individuals from wherever they were found on the shore. Because of this cropping the clusters of winkles would have contained fewer animals (see below). The rate of cropping was light enough during the period of occupation not to cause noticeable size decreases in winkles upwards through the middens. There must also not have been any gaps in occupation long enough to allow the mean size of the periwinkles to increase.

The small winkles were generally avoided by the gatherers. Those that do occur in the middens were probably included accidentally during collection, as the groups of winkles often contain some quite small individuals.

The areas of modern shore producing the largest periwinkles also seem to have produced the largest periwinkles in the Mesolithic, despite the higher sea level.

B : DOGWHELKS

Methods

The problems of measuring dogwhelk size have been discussed in part 1 of this chapter. In chapter 3 it was seen that both total length and aperture length may be used to assess the animals' size, although the absolute changes in the latter are not as great as in the former. Table 45 gives the mean aperture lengths from different middens and tables 46 to 51 show the variations between levels. Figures 151 to 157 show the total aperture length distributions of dogwhelks from each midden, and figures 158 to 175 the aperture length distributions at each level. As with periwinkles, statistics are not given where there are less than four animals, and histograms are not drawn where there are less than eleven.

Results

1. The size distribution of midden dogwhelks

Table 45 shows that the largest dogwhelks occur in CNG II and Priory Midden (mean aperture lengths 19.66 and 19.60 mm respectively) and the smallest in CNG I (18.91 mm), with the average aperture length from all the broken dogwhelks being 19.35 mm. The dogwhelks with the smallest apertures of all are the unbroken animals at 18.59 mm. There were not enough of these to be considered on a level by level or even a midden by midden basis, so they have all been combined.

These same patterns are revealed by figures 151 to 157, where it will be seen that all the broken dogwhelks peak in the size range 19 to 20.9 mm, but the apertures of the whole dogwhelks peak at 17 to 18.9 mm. All are distinctly unimodal with few extremely small and few extremely large values. As noted above, aperture lengths show much less variation than total length values. Of all the broken dogwhelks, CNG I is seen to contain the highest proportion of smaller animals, and Priory Midden, CNG II and Cnoc Sligeach the most extremely large animals. Cnoc Coig pit 6 also contains some large dogwhelks.

TABLE 45 : MEAN DOGWHELK APERTURE LENGTHS FOR EACH MIDDEN

MIDDEN	MEAN APERTURE LENGTH	S.E.	n.
CNOC COIG PIT 10	19.13	0.31	35
CNOC COIG PIT 6	19.46	0.61	130
CNOC COIG Both Columns	19.39	0.14	165
CNOC SLIGEACH	19.41	0.14	127
CNG I	18.91	0.15	91
CNG II	19.66	0.29	36
PRIORY	19.60	0.27	68
All broken dogwhelk apertures	19.35	0.08	487
All midden dogwhelks	19.27	0.08	547
All complete dogwhelk apertures	18.59	0.20	60

TABLES 46-51 : MEAN APERTURE LENGTHS OF DOGWHELKS FROM EACH LEVEL

TABLE 46 : CNOC COIG PIT 10

LEVEL	MEAN APERTURE	S.E.	n.
9	18.76	0.39	23
10	-	-	-
11	20.20	0.74	6
12	19.48	0.41	6

TABLE 47 : CNOC COIG PIT 6

LEVEL	MEAN APERTURE	S.E.	n.
17	18.94	0.43	14
18	19.08	0.42	23
20	19.86	0.20	70
21	18.90	0.43	23

TABLE 48 : CNOC SLIGEACH

LEVEL	MEAN APERTURE	S.E.	n.
28	19.50	0.28	44
29	19.59	0.23	44
31	19.07	0.29	26
32	19.18	0.31	13

TABLE 49 : CNG I

LEVEL	MEAN APERTURE	S.E.	n.
1	18.73	0.25	30
2	19.10	0.31	29
3	18.90	0.23	32

TABLE 50 : CNG II

LEVEL	MEAN APERTURE	S.E.	n.
E	19.32	0.35	22
F	20.20	0.58	12
G	-	-	-
H	-	-	-

TABLE 51 : PRIORY MIDDEN

LEVEL	MEAN APERTURE	S.E.	n.
1	19.68	0.52	15
2	18.93	0.37	18
3	-	-	-
4	-	-	-
5	-	-	-
6	18.95	0.52	11
7	19.99	0.48	15

Tables 46 to 51 show that the mean aperture length varies from 18.73 mm in the top of CNG I to 20.20 mm in CNG II level F and in Cnoc Coig pit 10 level 11, though in the latter instance the sample size is only 6. There is no noticeable pattern of size variation upwards through any of the middens.

Figures 158 to 175 show that there are variations in the population structure of dogwhelks from different levels, with animals in all levels peaking in either the range 17.0 to 18.9 mm or 19.0 to 20.9 mm. For instance, there are many more smaller dogwhelks at level 21 in Cnoc Coig pit 6, and more larger animals in level 20. CNG I has more dogwhelks in the size range 19 to 20.9 mm in level 3, and more in the range 17 to 18.9 mm in level 2, whereas there are more larger animals again in the top level. Priory Midden has equal proportions of whelks in both these size ranges in levels 1, 2 and 6, yet more larger animals at level 7. All the sample sizes from Priory Midden are, however, fairly small.

There are also fluctuations in the number of extremely large and extremely small dogwhelks. For instance some levels, such as Cnoc Sligeach 32 and 29, Priory 1 and 7 and CNG II F, contain no dogwhelks below an aperture length of 15 mm, and others such as the top two levels of Cnoc Coig pit 6, level 9 of Cnoc Coig pit 10, levels 31 and 32 of Cnoc Sligeach, levels 1 and 3 of CNG I and levels 2, 6 and 7 of Priory Midden contain no dogwhelks above 22.9 mm. There is no obvious pattern to these fluctuations, and nothing to suggest the exploitation of progressively smaller dogwhelks upwards through the middens.

2. A comparison of contemporary and midden dogwhelk size distributions

A comparison of tables 21 and 45 shows that the midden whelks have smaller apertures than those of the present. CNG II has the largest mean aperture size at 19.66 mm, yet the smallest mean aperture length on the modern shore is from Unit 1A at 21.44 mm. The highest mean aperture lengths (at 20.2 mm) are in CNG II level F and Cnoc Coig pit 6, level 11.

A comparison of figures 76 to 82 with figures 158 to 175 also clearly demonstrates these different size distributions, with the former peaking between 21 and 24.9 mm and often having a high proportion of dogwhelks in the size range 25 to 26.9 mm, and the latter peaking at between 17 to 20.9 mm and having relatively few animals above 22.9 mm. There are very few dogwhelks on the modern shore below 19 mm, yet the highest proportion of midden dogwhelks are often in the size range 17 to 18.9 mm.

The mean aperture length of all the unbroken dogwhelks is 18.59 mm (table 45), and their mean total length is 25.65 mm. This may be compared to a mean aperture length of 22.11 mm and a mean total length of 31.81 mm in the modern shore dogwhelks from all sample units (table 21). Thus the complete midden dogwhelks are smaller than those on the modern shore (as well as being shorter in aperture length than the broken animals in the middens).

Four trends therefore present themselves from these data:

a) There are no noticeable shifts in size distribution upwards through the middens.

b) The midden dogwhelks have significantly smaller apertures than the modern animals, and contain more extremely small and less extremely large dogwhelks.

c) The whole dogwhelks have smaller apertures than the broken animals, and they are of a shorter total length than dogwhelks on the modern shore.

d) The largest dogwhelks on the modern shore occur in the bay below the Priory Midden and along with those in CNG II, the Priory Midden contains the largest dogwhelks.

3. Possible collection strategies for dogwhelks

It is not possible to make as much interpretation of the dogwhelk as the periwinkle evidence. The great variations in shape of contemporary dogwhelks limits any interpretations. Nevertheless a number of points are raised by these data.

a) It is possible that the smaller mean size of the Mesolithic dogwhelks is a result of human exploitation. It is also, however, likely that this is a purely natural phenomenon. It is not possible to calculate the total length of these animals (see d below), yet table 21 demonstrated that in increasing shelter dogwhelks become longer, and there is an increasingly greater proportional increase in total length to aperture length. Andrews et al (1983) have concluded that midden dogwhelks are more elongated with smaller apertures than those on the modern shore, indicating a generally more sheltered coastline. Thus the smaller apertures in the midden dogwhelks may belong to animals of greater total length than those existing at present.

b) The relative size of dogwhelks between different sample units on the modern shore has a number of similarities to the relative size of dogwhelks between the middens. Larger dogwhelks appear to occur in greater shelter on the modern shore, and the sheltered bays below Priory Midden (Port na Luinge) and Cnoc Sligeach contain relatively larger animals. The whelks in the Priory Midden are of a relatively large size indicating that they were collected from a fairly sheltered bay. As discussed in chapter 4, the west coast of Oronsay is presently limiting to the prospective shellfish gatherer, with only the bays in the southwest of the island providing any suitable coastline. This was probably also the case with a higher sea level, when Port na Luinge would still have been a protected bay continuing to near the base of Priory Midden. The fact that there are relatively few dogwhelks in this bay at present, and also relatively few in the midden, also supports this view, as the increased shelter means more fucoids and less barnacles, hence a reduced food supply (see below).

CNG II also possesses some larger dogwhelks. Andrews (1981) has argued that Oronsay was at least two separate islands during the Mesolithic and that CNG II was on the southernmost island where shellfish collecting was done at least partly from the shallow inlet separating the islands. This would be a relatively sheltered habitat. The presence of some larger dogwhelks in CNG II therefore supports this argument.

c) The lack of any trends in size distribution upwards through the middens again possibly indicates a constant, yet not too heavy human exploitation. It is not possible to get any idea of the age or total size of these animals from their aperture length, yet at all levels dogwhelks are allowed to grow to a constant size which would not be the case if the collectors were forced to gather smaller and smaller animals. The middens contain very few dogwhelks below 17 mm aperture length. This is probably because the collecting of small dogwhelks is not a cost-effective exercise. As with limpets and periwinkles there is a size below which the returns do not repay the effort involved in collecting and removing the meat. This is especially true of dogwhelks, where the smaller animals contain less meat relative to shell than do the larger animals (chapter 2).

d) Within the middens the whole dogwhelks have generally smaller aperture lengths than the broken ones. They are also shorter in total length than animals from the modern shore. This implies that they were in fact smaller animals, and the reason they were not broken for meat extraction is that they were discarded as being too small during processing. It is for this reason that any attempt to use the whole dogwhelks to reconstruct total size from the aperture alone would be invalid, as it seems that these whole animals are not representative of those broken for the extraction of meat.

C. THE COMBINED EVIDENCE FROM PERIWINKLES, DOGWHELKS AND LIMPETS

There are no strands of conflicting evidence from these three species; in fact a number of factors point to the same conclusions.

1. All indicate the exploitation of shellfish at a rate causing no major changes in shellfish population structure over the period of midden occupation, yet the limpets do show changes indicating slight pressure on the resources through time. This is probably a reflection that limpets were the main shellfish resource (see below) and therefore were under more pressure from human predation than the other species.

2. The lack in limpets and periwinkles of any abrupt changes from concentrations of significantly smaller to significantly larger individuals suggests that there were no gaps in occupation during the period of midden formation.

3. The possibility that the limpets were cropped regularly, probably on an annual basis, is not hard to relate to the observation that most periwinkles seem to have been a little older, at nearer 2 years old. Two factors are of significance here. Firstly the pressure on the periwinkles does not seem to have been as great as on the limpets, so all periwinkles of the desired size were not necessarily removed at each occupation. Secondly, periwinkles of one year old would not have been large enough for collecting, so only when they reached this size would they have been gathered. Thus, on each approximately annual visit only those that had attained the desired size would have been collected. The important factor is that in both limpets and periwinkles a large proportion of the animals were gathered at a specific size/age which implies a regular cropping.

PART 4 : RELATIVE PROPORTIONS OF THE THREE SPECIES

Chapter 3 examined the relative proportions of the three species on an uncropped shore. Here an examination is made of these proportions in the middens, and suggestions made which may account for the observed patterns. Table 52 shows the percentage of each species per midden sample column, and table 53 gives the percentage of species in each level in the different middens. When compared to table 26, a number of trends present themselves.

1. In the middens the proportion of limpets is consistently high, usually comprising over 90% of the shellfish (tables 52 and 53), whereas over the modern shore limpets only comprise 58.37% (table 26).

2. In the middens there are far fewer dogwhelks and periwinkles than are available on the present shore. In a combination of all the middens, winkles and whelks together form 5.59% of the total shellfish population (table 52), whereas on the modern shore they were seen to comprise 41.63% (table 26). This observation becomes even more significant when it is remembered that in the survey of the modern shellfish, except for Unit 1A, the large groups of periwinkles were not considered.

3. The proportion of winkles and whelks in the middens is much more consistent than between different habitats on the modern shore (tables 52, 53, 25 and 26).

4. On the modern shore periwinkles comprise 16.57% of the total shellfish sample, and dogwhelks 25.06% (table 26), and in a combination of all the middens periwinkles comprise 2.29% and dogwhelks 3.3% (table 52). Thus, although these animals exist in the middens in much lower relative numbers, there are still more dogwhelks than periwinkles. If, however, the vast number of periwinkles occurring in the clusters is taken into consideration, the periwinkles would form a much greater percentage of the limpets on the modern shore, which would contrast to the relatively small number of periwinkles in the middens.

TABLE 52 : RELATIVE PROPORTIONS OF THE THREE SPECIES IN EACH MIDDEN

MIDDEN	% LIMPETS	% WINKLES	% WHELKS
CNOC COIG PIT 10	94.79	3.70	1.51
CNOC COIG PIT 6	94.81	2.05	3.15
CNOC COIG Both Columns	94.83	2.92	2.25
CNG I	91.59	3.02	5.39
CNG II	98.07	0.67	1.27
CNOC SLIGEACH	91.93	0.40	7.67
PRIORY	94.53	3.82	1.65
TOTALS	94.41	2.29	3.30

PERIWINKLES + DOGWHELKS 5.59

TABLE 53 : RELATIVE PROPORTIONS OF THE THREE SPECIES IN EACH LEVEL

CNOC COIG PIT 10

LEVEL	% LIMPETS	% WINKLES	% WHELKS
9	92.96	3.58	3.46
10	92.22	7.56	0.22
11	95.28	3.15	1.57
12	98.52	0.64	0.85

CNOC COIG PIT 6

LEVEL	% LIMPETS	% WINKLES	% WHELKS
17	94.59	2.00	3.41
18	96.15	0.83	3.02
20	92.77	3.79	3.44
21	95.96	1.52	2.53

CNOC SLIGEACH

LEVEL	% LIMPETS	% WINKLES	% WHELKS
28	94.18	0.31	5.51
29	92.17	0.27	7.56
30	89.36	0.70	9.94
31	90.65	0.33	9.02

CNG I

LEVEL	% LIMPETS	% WINKLES	% WHELKS
1	94.42	0.91	4.68
2	88.28	6.00	5.73
3	92.23	1.94	5.83

CNG II

LEVEL	% LIMPETS	% WINKLES	% WHELKS
E	94.04	0.93	5.02
F	97.98	0.64	1.39
G	98.80	0.83	0.36
H	99.53	0.33	0.13

PRIORY MIDDEN

LEVEL	% LIMPETS	% WINKLES	% WHELKS
1	87.81	8.13	4.06
2	89.32	7.90	2.78
3	90.28	8.18	1.53
4	96.28	2.33	1.40
5	90.16	7.25	2.59
6	95.37	3.07	1.56
7	96.42	2.25	1.34
8	99.75	0.25	0
9	99.55	0.45	0
10	99.79	0.21	0

5. Despite the predominance of dogwhelks from a combination of all the middens, table 52 shows that there are more periwinkles than dogwhelks in Cnoc Coig pit 10 and Priory Midden, and even though Cnoc Coig pit 6, CNG I and CNG II contain more dogwhelks overall, they all contain levels where periwinkles predominate (table 53). Cnoc Sligeach on the other hand contains very few periwinkles in any levels.

6. There appears to be no obvious pattern of changes in the relative proportions of the species through the middens.

Possible explanations for these trends

The fact that there are significantly less periwinkles and dogwhelks in the middens may result from a number of possible causes. Perhaps the Mesolithic shore supported relatively fewer of these species, regardless of the effects of the human populations. It is suggested in chapter 4, however, that the Mesolithic shoreline was probably very similar to today, and it has been shown above that the sizes of periwinkles and dogwhelks in Priory Midden, Cnoc Sligeach and CNG II may be explained by postulating relatively similar conditions between the middens as between the areas of modern shore adjacent to these middens.

It seems unlikely that the Mesolithic shellfish population was so different in structure to the modern population. There must have been rocks otherwise there would be no limpets; these are likely to have supported barnacles so dogwhelks are to be expected. There also seems no reason why there should have been so few periwinkles. There is also the fact that man was exploiting these species, so it is to be expected that his actions would have some effect on the shellfish population structure. There are two possible methods of cropping which would produce this pattern, and both have very different implications for the lifestyle of the midden-dwellers.

Firstly, it is possible, as suggested above, that there was an earlier undiscovered period of occupation, where a quite intense exploitation strategy had greatly reduced the stocks. The middens could than represent the latter part of a period of occupation, where the species population structure had become stabilized as a result of some fairly low scale, regular exploitation.

The main problems with this explanation are the obvious dangers of arguing from negative evidence, and the fact that there is no evidence for this occupation. As noted above, however, shellfish stocks, and especially limpets, may be depleted over a few seasons, so the deposits need not be large. Also, it is not altogether surprising if there are further middens as yet undiscovered over the island:

> "... the task of surveying the whole of this area for possible shell middens is seriously hampered by the thick deposits of wind-blown sand .... and by the heavy covering of heather and bracken, which makes the search for surface exposures particularly difficult. The possibility that further shell middens await discovery in this area should certainly not be ruled out".
>
> (Mellars 1981:518)

The second possible explanation is that the large clusters of periwinkles were gathered and taken away from Oronsay. Whereas limpets soon die after removal from the rock (chapter 1), periwinkles may be kept alive for a number of days, and even weeks. Presently periwinkles are exported from Colonsay and Oronsay to the mainland and to Europe in large sacks. Thus a group of people could easily land on Oronsay and very quickly gather a large number of periwinkles. (Present-day Oronsay periwinkles are famous as among the most tasty in Scotland; pers. comm. Mr P. MacAlister.)

If this is the case, then the middens could be task-specific sites for periwinkle collectors. They contain very few of these animals because they only ate some while living for some days or weeks on limpets, seal etc. They then took the periwinkles away with them. This would also explain the seasonality of settlement if they came to each site at a different time of year to collect the periwinkles.

Whatever the periwinkle collection strategy, there is no reason why the large clusters of these animals would have been ignored. It is possible that the levels containing slightly higher proportions of periwinkles represent the collection of one or more of the aggregations of these animals. During the excavations, a number of large clusters of periwinkles were discovered (pers. comm. Dr P. Mellars), yet none of any great number appear in the column samples. Thus, whereas the exploitation must have been light enough not to cause either a reduction in numbers or size of periwinkles upwards through the midden, it must have been heavy enough not to allow the animals to occur in the large numbers they do on an uncropped shore. This is, of course, unless we assume that the periwinkles were taken from the island, in which case the few animals in the middens are those which they chose to eat while actually on the island.

Another possibility is that the periwinkles and dogwhelks were not a particularly favoured food source, and so were only collected in small numbers. This explanation would not account for the smaller midden periwinkles. It may, however, be an explanation for the relatively small number of dogwhelks with comparison to the present, whose smaller mean aperture length may be due to a greater degree of shelter (above). When collecting limpets it would be easy to gather a few dogwhelks, yet processing would take longer than for limpets and periwinkles. The shells had to be broken and the meat extracted, and each dogwhelk only contains a relatively small amount of meat (chapter 2). A few may have been desirable, perhaps to add variety to the diet, yet they may not have been considered a major resource. Whereas limpets and winkles are fairly bland, dogwhelks, being carnivores, have a much stronger taste. Perhaps a few were desired to "spice-up" the diet.

The relative consistency of dogwhelks throughout the middens is easily explained if the above argument for their selective use is accepted. If, however, they were collected at the same intensity that is possible for limpets and winkles, then the fact that there is no reduction in their numbers upwards through the middens suggests that the collection rate was light and regular. This must also be the assumption from the periwinkle distributions which equally reveal no reduction in numbers upwards through the middens.

No level revealed by any of the columns indicates extreme pressure on the limpets, which are obviously the most important species, by showing a relative increase in any of the other species. If there were more dogwhelks available on the shore than were actually collected, a relative decrease in limpets and an increase in dogwhelks may be expected. No such change occurs.

Some of the fluctuations in numbers of periwinkles and dogwhelks between middens may be explained by their location. For instance on the modern shore there are very few dogwhelks in Port na Luinge due to the dense fucoid cover and lack of barnacles. There are also very few in the Priory Midden. This is yet another similarity between present day Port na Luinge and the shellfish in Priory Midden, indicating that relative conditions were similar between the present day and the Mesolithic. The middens where dogwhelks predominate probably had access to areas of shore where there were expanses of barnacle-covered rock, and the periwinkles were more likely to have been found where there were more fucoids.

Conclusions

1. The consistently high percentage of limpets relative to the other species indicates a definite preference for these animals.

2. It is possible, though unlikely, that the Mesolithic coastline supported less dogwhelks and periwinkles. It seems more probable, however, that the relatively low numbers of both these species in the middens is a result of human predation.

3. Two possible periwinkle collection strategies are suggested. Perhaps there was an earlier occupation which as well as removing the largest limpets also depleted most of the periwinkle stocks. Alternatively it is suggested that these animals were removed

from the island, as they are easily kept alive for a number of weeks. The implication here is that the middens represent task-specific periwinkle collection sites.

4. The rate of exploitation of the three species must have been heavy enough not to allow stocks to increase in number, and light enough not to cause a change in relative species composition during the period of occupation.

5. The small number of dogwhelks may be a result of continual human predation. It may also, however, result from the selective gathering of only a few dogwhelks to add flavour and variety to the meal.

6. Middens where periwinkles predominate would probably have had access to areas of shore containing fucoids, and where dogwhelks predominate there would have been more bare rock with barnacles and fewer fucoids. Cnoc Sligeach is an example of the latter category and Priory Midden of the former. Most middens probably had access to both habitat types. The observation that there are very few dogwhelks in the Priory Midden or in Port na Luinge is another indication of the relative similarity of conditions between the Mesolithic and modern coast around Priory Midden.

CHAPTER 7 : MEAT WEIGHT VALUES OF THE MIDDEN SHELLFISH

> '....testing for shellfish meat quantities is something the archaeologist can do for himself if he thinks the information important and wants to make unassailable mollusc meat reconstructions. To get this information, however, he will have to put aside his books and his shovel, screens and artifacts, take up a clamming fork and scales, and get his feet wet'.
>
> (Koloseike 1969:154)

Using the data on seasonal changes in meat weights of contemporary limpets, periwinkles and dogwhelks discussed in chapter 2, an attempt will be made to reconstruct the relative proportions of meat weight provided by these species in the middens at different seasons.

There have been a number of attempts to estimate the meat values of archaeological shell deposits, all with varying degrees of error. Some have obtained one 'average' meat weight for a species and transposed this value on different species (Ascher 1959; Meighan 1959), a procedure open to huge degrees of error. Cook and Treganza (1950) attempt a more thorough approach yet they also transpose meat weight values from one species of mussel to another, and also produce some meat/shell weight ratios with no explanations as to the origin of these values. Cook (1946) also transposes meat weight values across species lines even though he appears aware of the problems this may cause. Even when meat weights are established for the same species that exist in the middens, only one average value is often used, taking no account of variations in size or seasonal changes in weight of the animal (Cook 1946). Shawcross (1967) emphasizes the importance of obtaining comparative meat/shell weight ratios from shellfish of varying sizes, though he pays less attention to the possible seasonal variations in those values.

The present aim is to greatly reduce the possibility for errors and to take account of both variations in shellfish size, and variations which may result if they were collected at different seasons. Models are therefore presented of the relative proportions of the three species if they were exploited in January, March, May-June, July, September or November.

Data collection

Shells were analysed from the same column samples as described in chapter 6. The samples of all whole limpet shells and all the complete periwinkles were weighed to allow the calculation of shell/meat weight ratios as described below. As the majority of midden dogwhelk shells are broken, shell weights of the total animals could not be obtained, so the meat weight has been calculated by using the total number of dogwhelks only (below). Total numbers of the three species were obtained as described in chapter 6.

Meat weights

The meat weight values for each species will be calculated by reference to the data on contemporary shellfish given in chapter 2. Comparisons will be made to the Oronsay but not the Colonsay sample areas. Chapter 4 notes the probable similarities between the Oronsay collection area now and in the Mesolithic. These similarities are much greater than with Dun Challain on the exposed west of Colonsay, which was included in chapter 2 as a comparison to Oronsay.

The meat weight values for each species will be calculated for the column samples from each midden. These may then be compared to see the relative importance of the three species in different seasons, and at different levels in each midden.

Limpets

Chapter 6 demonstrated that most of the midden limpets appear to originate from the lower part of the tidal range. For this reason only the Oronsay low shore limpets (figure 18) will be used as a guide to estimating the meat weight of the midden limpets.

In chapter 2 limpets collected from the modern coastline were divided into three size groupings on the basis of shell weight (figures 18 and 19). This demonstrated that there were significant differences in ratio shell/meat weight between limpets of different sizes. Chapter 6 discussed the observation that the middens contain a higher proportion of smaller limpets than were discovered on the modern shore, and very few of the larger animals. It was therefore decided to further subdivide the modern limpet sample used in figures 18 and 19 to increase the accuracy of the midden meat weight estimates. In chapter 2 small limpets were below 3.5 g shell weight, medium from 3.5 g to 9.5 g, and large over 9.5 g. There are many midden limpets below 3.5 g so this group have been divided in two. The medium sized limpets are also split into two groups in such a way that allows each group to have a large enough sample size. Any further subdivisions would have meant that sample sizes would be too small.

Figure 177 expresses the mean dry meat weight values of five shell weight categories for each of the six sample months. A comparison with figure 18 reveals the same general patterns of meat weight alterations. There is an increase in meat weight from March to May-June, the smaller animals then show a slight decrease to July whereas the larger animals peak in July. The smaller animals have a slight secondary peak in September and the larger do not, yet both lose weight to November where they reach the same approximate level attained the previous January. It is worth remembering that figure 18 charts ratio shell/meat weight and figure 177 actual dry meat weight value. This explains the greater values and steeper peaks of the progressively larger limpets in figure 177.

The midden limpet samples were divided into the same five groupings by shell weight. Tables 54 to 59 show the percentage of limpets in each of these size groupings. This is based upon the selected samples of whole limpets (chapter 6). In chapter 6 it was noted that there appears no noticeable pattern of bias in the fragmentation of the midden limpets, so it may be assumed that these samples are representative of the size distribution of all the midden shells. Thus, in tables 54 to 59 the percentage of limpets in each size grouping has been taken as a percentage of the total number of limpets in each midden level, to give the estimated total number of limpets in each size grouping. For instance, in Cnoc Coig pit 10, level 9, 56% of the limpets from a sample of 125 complete animals are below 1.75 g shell weight. There are a total of 832 limpets in this level, so 56% of 832 makes a total of 465.9 limpets below 1.75 g. Thus, tables 54 to 59 show the calculated numbers of limpets in five shell weight groupings for each level in each midden.

These tables also show the calculation of meat weight values for these midden shells for each sample month, using the mean meat weight values given in figure 177. These have been obtained by multiplying the number of limpets in each size group by the average meat weight for limpets of that size. When these values are added together the total weight of limpet meat per level can be estimated, and from this the total meat weight in each column.

There will be errors in this technique:-

> '....by no stretch of the imagination can any calculations which may be derived from a midden be called exact. It is not that one should not try to reduce errors wherever possible, only that the inherent existence of error in archaeology ought to be more openly recognized'.
> (Shawcross 1970:282)

This method is, however, the most accurate without actually examining every whole shell, a task that no-one would undertake, and even then there are the vast number of broken shells. We must nevertheless be aware of the scope for error.

Being around 5,000 years old, the midden shells are likely to have undergone various degrees of leaching by rainwater, so actually be lighter than when they were collected from the shore. To attempt estimates of the degree of this weight loss is beyond the scope of this research. It is, however, probably quite small (see below). Because of the possibility of the midden shells being lighter, the divisions on shell weight may actually slightly over-emphasize the smaller limpets. This is not, however, considered a serious error because chapter 6 showed that, when considering size also, there are many more smaller limpets and far fewer larger ones than on the modern shore.

The use of average meat weight values is obviously open to certain degrees of error, yet this is minimized by the use of five size groupings, the maximum possible with the present sample size.

All attempts have therefore been made to get the most accurate possible meat weight estimates for the midden limpets. Account has been taken of both seasonal variations and different amounts of meat in animals of different sizes.

Periwinkles

Whereas we can say with a high degree of probability that the middens contain predominantly lower shore limpets, it is not possible to say which specific tidal level, if any, provided the majority of periwinkles. It was argued in chapter 6 that periwinkles were probably collected from over the whole shore, and that there seems no reason to ignore either the clusters of animals usually found around mid to lower mid tide level, or the individuals scattered over the rocks, more usually around the lower shore. Thus, it is considered most accurate to base the reconstructions of midden periwinkle meat weights upon a combination of both high and low tide specimens from the present Oronsay shore, even though figures 27 and 28 have shown that there are differences in relative meat weight values between animals from different tidal levels.

Another factor to consider when deciding how to reconstruct the meat contribution of the midden winkles is the observation (chapter 6) that the middens do not contain as many large periwinkles as were found on the present shore (chapter 3). Thus, it is more accurate to ignore the large low shore periwinkles (figure 27). Although these possess similar shell/meat weight ratios to the smaller lowshore animals in January and March, after this they diverge to a significant degree. Chapter 6 demonstrated that there are very few such animals in the middens.

It is not considered necessary to divide the midden periwinkles into smaller and larger individuals for comparison to the modern animals. There are no significant differences between the smaller and larger upper shore animals (figure 28) and the small low shore winkles are not different enough from the upper shore animals to warrant this separation.

Figure 178 shows the actual mean dry meat weights of the small low shore and upper shore winkles. These have been used in table 60 to calculate the meat weight values of the midden shells. The number of periwinkles in each level has been determined by combining the total number of whole winkles and apices (chapter 6), and this value multiplied by the mean meat weight for each month.

Dogwhelks

The calculation of the amount of meat represented by the midden dogwhelks presents a greater problem than the limpets and periwinkles because the majority of these animals are broken. Thus it is not possible to make direct comparisons between the relative weights of shell and meat of the modern and archaeological specimens. It is therefore necessary simply to calculate the average meat weight of one modern dogwhelk at each sample month, then multiply this by the total number of midden dogwhelks (table 61).

The best reconstruction of probable midden dogwhelk meat weights may be obtained by comparison to the modern low shore animals, although virtually the same seasonal pattern emerges when all low and high shore animals are combined (figures 179 and 180). Unfortunately no upper shore whelks were collected in January, yet in March and May-June the mean meat weights are the same when either all, or only low tide animals are considered. For the remaining sample months the values are 0.23 g, 0.28 g and 0.25 g by the former, 0.20 g, 0.26 g and 0.27 g by the latter calculations.

It seems that dogwhelks were not a major food resource in their own right, but were there to add a bit of 'spice' or 'variety' to the diet (chapter 6). They were therefore probably gathered when encountered whilst collecting limpets, which were taken mainly from the lower shore. Thus it is likely that most of the dogwhelks also stem from the lower shore.

Chapter 6 demonstrated that midden whelks are generally smaller than those on the present shore when measured by aperture length. Nevertheless it was also noted that as there is evidence for increased shelter during the period of midden accumulation, then the total length of these animals may be longer relative to their aperture length than present day dogwhelks. For this reason it is more accurate to include all modern low shore dogwhelks and not just the smaller ones. Another reason for this is the observation made in chapter 2 that these may contain some immature individuals (figure 38). Thus, all low shore dogwhelks have been used to obtain mean meat weight values for each sample month.

Table 61 shows the calculated meat weights for each midden level. The number of dogwhelks has been obtained by combining the total number of siphonal canals with the few complete animals (chapter 6). These have then been multiplied by mean meat weight values for each month, based upon the present day low shore dogwhelks.

The effects of sea temperatures on meat weight values

Sea temperatures have an important bearing on meat weight values, and must be taken into consideration when using contemporary values to reconstruct meat weights of the midden shellfish. Sea temperatures will affect meat weight values at two critical levels. Minimum winter temperatures govern the degree of winter feeding and growth, with certain levels at which both are either substantially reduced or cease. Secondly, maximum summer values may govern feeding and growth because increases in temperature may cause increases in feeding and growth rates.

Chapter 4 demonstrated the seasonal sea temperature regime for Colonsay. Unfortunately the present research could not extend to measuring growth rates of shellfish on Oronsay so it is necessary to refer to other studies where growth rates and temperatures are known. Of specific interest here are minimum winter temperatures, to establish if the Oronsay shellfish cease feeding in winter.

In chapter 1 it was noted that around Boulogne the winter temperature falls to around 6°C, and Choquet (1968) found continuous though reduced growth in limpets during the winter (figure 3). A similar pattern was found at Plymouth by Orton (1928b) where the winter temperature falls to around 8°C. As temperatures on Colonsay were also seen to fall to around 6°C we may assume that limpets continue to grow throughout the winter as at Boulogne.

Moore (1937) and Williams (1964) demonstrate that periwinkles show reduced growth in winter, and do not feed or grow at temperatures below 8°C. Chapter 4 showed that sea temperatures around Oronsay fall to around 6°C in the winter, and are probably below 8°C from around January to March. Thus we may assume a period of winter dormancy.

From the limited studies of dogwhelk growth it was shown in chapter 1 that this is reduced in winter. At Robin Hood's Bay Feare (1970b) noted that dogwhelks do not feed in their winter aggregations, though it is probable that this winter no feeding period is shorter on Oronsay due to higher winter temperatures, which reach around 6°C compared to 5°C and below for up to two months at Robin Hood's Bay (Feare 1970a).

Thus it may be concluded that on present day Oronsay, limpets will continue to feed over the winter, but at a lower rate than in summer. Periwinkles probably stop feeding in the coldest winter months, and dogwhelks probably stop feeding whilst in the winter aggregations, though the length of time spent in these aggregations is probably less on Oronsay than at Robin Hood's Bay.

Given the probability that sea temperatures on Oronsay during the Mesolithic were around 1-1.5°C warmer than present, it is likely that shellfish meat weight values may have been slightly higher than at present. Though this might be noticeable during the summer because of increased feeding, it would probably be more significant in the winter months. Limpets would have continued to feed and grow at a greater rate than at present and periwinkles and dogwhelks would probably have had a much shorter, or perhaps non-existent, dormancy period.

Thus, the relative values of the three species given below must be regarded as minimum values, especially during the winter months. It is not, however, considered desirable at this stage to increase these values to compensate for possible temperature changes, as current data is not adequate to establish the exact extent of such meat weight -temperature related changes.

Relative meat weight values of limpets, periwinkles and dogwhelks

Tables 62 to 67 show the relative percentages of meat weight contributed by each species at each midden level in the sample columns. This information has been obtained from tables 54 to 61. For instance in Cnoc Coig pit 10, level 9 in January (table 62) limpets contribute 88.79%, winkles 6.20% and whelks 5.01% to the total shellfish meat weight. Tables 54, 60 and 61 show that at this level in January limpet meat totals 164.88 g, winkles 11.52 g and whelks 9.3 g. This makes a total of 185.7 g shellfish meat weight. 164.88 is 88.79 percent of 185.7, 11.52 is 6.2 percent of 185.7 and 9.3 is 5.01 percent of 185.7.

Figures 181 to 186 show the total relative percentage of meat weight provided by each species per midden. From these, and tables 62 to 67 it is obvious that limpets are the most important of the three species, usually providing over 90% of the shellfish meat, whereas both winkles and whelks usually provide well below 10%. In Cnoc Coig pit 10 and Priory Midden, winkles provide a greater relative total of meat than dogwhelks; in Cnoc Coig pit 6, CNG I and CNG II both these species provide quite similar amounts of meat; and in Cnoc Sligeach the whelks provide significantly more meat than the winkles.

Although limpets provide less meat weight in the winter months and peak around May-June and July, their relative importance over the other two species is never in question. Both winkles and whelks provide relatively more meat during the winter months, and less in May-June and July. Chapter 2 indicated that the nutritional value of the three species increases and decreases with meat weight values.

The relative insignificance of winkles and whelks in comparison to limpets is emphasized by the fact that the seasonal change in meat weight of limpets is sometimes as great as, or greater than, the total relative meat weight value of winkles or whelks. For instance, the difference in meat weight between the total percentage of limpets in Cnoc Coig pit 10 in January and May-June is 3.65 (tables 62 and 64, figure 181),which is greater than the total percentage of dogwhelk meat weight in this column for January when it is at its seasonal best. Another example is Priory Midden level 1, where the difference in limpet percentage meat weight between January and May-June is 6.67, which is again larger than the January value for dogwhelks (tables 62 and 64 and figure 186).

A close examination of tables 62 to 67 reveals slightly more fluctuations between levels than may be seen from the relative total meat weights per column sample given in figures 181 to 186. For instance although Cnoc Coig pit 10 as a whole has more meat weight provided by winkles than whelks, level 12 has a greater amount of whelk meat weight in January and May-June,more winkle meat weight in March and approximately equal proportions in July, September and November. Although Cnoc Coig pit 6 has very similar proportions of winkles and whelks in all levels, CNG II, which has an overall similarity in relative importance of these two species, has a much higher proportion of whelks than winkles in level E. Limpets provide over 99% of the shellfish meat value in areas where the other species are scarce or non-existent (eg Priory Midden levels 8, 9 and 10). The lowest proportion of limpet meat weight is in Priory Midden level 1 and CNG I level 2 in January (with 82.59% and 82.60% respectively). The former has a relatively high proportion of winkles and the latter quite a high proportion of winkles and whelks. Also, in January limpets are at their lowest relative meat weight and winkles and whelks are at their highest.

It is quite possible that the Mesolithic dogwhelks contained slightly less meat than is indicated by a comparison to the modern animals. If the Mesolithic coast was less exposed than at present (as discussed by Andrews et al 1983), these dogwhelks may have had relatively thicker shells. Chapter 1 discussed the work of Currey and Hughes (1982) who found that dogwhelks have relatively more shell per gram of dry meat weight on shores of progressively lessening exposure. Thus, on a more sheltered coastline the dogwhelks might have provided a slightly lower proportion of the shellfish meat weight. It is not, however, likely that amounts would be greatly different, as the Mesolithic coast could only have been slightly less exposed than at present (Andrews _et al_ 1983).

Although there are differences in the meat weights of the three species in different months, because every level shows the high predominance of limpets with relatively low percentages of both winkles and whelks, these seasonal differences are not as significant as they would have been if limpets were relatively less important. Although limpets provide less meat, and are less nutritious (chapter 2) during the winter months, they are still significantly more important than the other species. Both winkles and whelks are of more value in the winter, yet because of their small numbers the overall impact of this advantage to the Mesolithic gatherers would have been minimal.

Thus it may be concluded that there are no major differences in the relative food value of the three species over the year. Throughout the year limpets would have provided the vast proportion of the shellfish food, with the other species contributing little. There are levels, however, where the other species are of more value, such as periwinkles in levels 1 and 2 of Priory Midden, and whelks in levels 30 and 31 of Cnoc Sligeach.

The lack of any major changes in dominance at difference seasons should not, however, be construed as an argument for ignoring seasonal changes. Far from it, seasonal changes in shell weights should always be considered. It is only via such analyses that we may conclude with any degree of certainty that in the Oronsay middens, at all seasons, limpets predominate and the other species generally provide a very small proportion of the total meat weight.

Conclusions

The size, seasonal meat weight values and tidal position of modern limpets, winkles and whelks have been used to reconstruct the relative meat weight contributions of the three species of midden shellfish. From these data the following conclusions have been drawn:

1. At all midden levels at all seasons limpets provide the most meat, this usually being over 90% of the total shellfish meat weight.

2. Periwinkles and dogwhelks usually provide below 10% of the shellfish meat weight, though in some levels they contribute a little more.

3. In Cnoc Coig pit 10 and Priory Midden, winkles are more important than whelks, in Cnoc Coig pit 6, CNG I and CNG II both provide very similar amounts of meat, and in Cnoc Sligeach whelks are more important than winkles. Even though a particular species may dominate the midden,the other species may predominate at certain levels.

4. Limpets provide relatively less meat in the winter months, when winkles and whelks provide relatively more.

5. On present evidence, fluctuations in meat weight may be assumed to correspond to fluctuations in nutritional value (chapter 2).

6. Because of the dominance of limpets in all levels the seasonal changes in meat weight values are of no major significance. Although limpets frequently differ by around 3 to 6 percent in relative importance to the other species between peak and minimum months, their position as the most important food source is never challenged by the other species. Thus, shellfish could have been

collected at any season of the year and there would be no major differences in relative proportions of meat weight provided by the three species. In all seasons limpets would have dominated. Only where the proportion of winkles and whelks are very similar would there have been a change in dominance of either of these two species.

.... AND WHAT NEXT?

There are a number of further lines of research which are beyond the scope of this thesis, yet which may build progressively upon the information presented here.

1. Nutritional values of limpets, periwinkles and dogwhelks

After examining the small amount published in this field, chapter 2 concluded that nutritional values seem to fluctuate with variations in meat weight. This general assumption does, however, require testing, yet to do so is a major piece of research requiring the skills and equipment of the biologist/zoologist. Samples would have to be collected at intervals throughout the year and examined for carbohydrates and proteins.

> '.... testing for protein would involve not only the same collecting and gross weight measurement program outlined above, but also the task of detailed chemical analysis of each collected specimen. Such a testing program for variation in mollusc protein would indeed be a formidable task, certainly beyond the range of the archaeologist's technical talents and very likely beyond the limits of any man's patience'.
>
> (Koloseike 1969:153)

2. The degree of midden limpet shell weight loss due to leaching

The extent of this weight loss is probably only small. The whole limpet shells look no 'weaker' than the modern ones. There are certainly no pores appearing in the shells. A selection of modern and midden shells of the same size have been compared, and there appeared to be no trend for the midden shells to be consistently lighter than the modern ones. Some were a little lighter, some a little heavier, and some the same weight. The problem to be faced here is that living limpets may vary in shell thickness, so it is not possible to say whether, at the time of collection, a midden shell was thicker than a modern shell of the same size.

3. Seasonality

Work is presently underway at the sub-department of Quaternary Research, Cambridge University (under the direction of Drs Shackleton, Bailey and Deith) examining the application of oxygen isotope analysis on limpet shells to establish the season of death, and hence the season of limpet collection. This technique is described in Killingley (1981) and Shackleton (1973). The 0-18 composition on the growth edge of the shell varies with temperature so it is possible to calculate the sea temperature at the time of the animal's death.

Before this information is applied to the midden shells, however, data is required on 0-18 composition of modern shells from a variety of habitats. During the six periods of fieldwork on Oronsay, samples of limpets were collected from specific shore environments for examination by oxygen isotope analysis. These results will then be used to interpret the 0-18 composition of the midden limpets. This analysis is not yet complete.

4. Information from the sample columns may be extended to the complete middens

This may be done with greatest accuracy on Cnoc Coig which has been excavated and analysed in most detail (Mellars 1983; Nolan 1984; Peacock 1978). The total volume of shell in this midden may be calculated with a high degree of accuracy, and the other middens with a slightly lesser degree of accuracy, to estimate the total shellfish weight contribution of each midden. This data may than be compared to the food value of the other main species: seal, fish and deer.

TABLES 54 to 59 : THE CALCULATION OF THE PROPORTION OF MIDDEN LIMPETS IN EACH SHELL WEIGTH GROUP, AND THEIR RESPECTIVE MEAT WEIGHTS FOR EACH MONTH.

All weights are given in grams.

See text for methods of calculation.

TABLE 54 : JANUARY.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.10			.26			.39			.72			1.08	
CNOC	9	832	56.0	465.9	46.59	32.8	272.9	70.95	7.2	59.9	23.36	4.0	33.3	23.98	0	0	0	164.88
COIG	10	842	48.8	410.9	41.09	39.2	330.1	85.83	10.4	87.6	34.16	1.6	13.5	9.72	0	0	0	170.80
PIT	11	908	46.4	421.3	42.13	40.0	363.2	94.43	8.8	79.9	31.16	4.8	43.6	31.39	0	0	0	199.11
10	12	930	40.8	379.4	37.94	45.6	424.1	110.27	10.4	96.7	37.71	1.6	14.9	10.73	1.6	14.9	16.09	196.65
																		731.44
CNOC	17	804	68.8	553.2	55.32	27.1	217.9	56.65	2.1	16.9	6.59	2.1	16.9	12.17	0	0	0	130.73
COIG	18	923	64.8	598.1	59.81	28.8	265.8	69.11	3.2	29.5	11.51	1.6	14.8	10.66	1.6	14.8	15.98	167.07
PIT	20	808	56.8	458.9	45.89	36.0	290.9	75.63	4.0	32.3	12.60	3.2	25.9	18.65	0	0	0	152.77
6	21	570	60.0	342.0	34.20	35.2	200.6	52.16	4.8	27.4	10.69	0	0	0	0	0	0	97.05
																		547.62
CNOC	28	2102	54.3	1141.4	114.14	38.0	798.8	207.69	5.4	113.5	44.27	2.2	46.2	33.26	0	0	0	399.36
SLIG.	29	2036	30.4	618.9	61.89	52.8	1075.0	279.50	14.4	293.2	114.35	2.4	48.9	35.21	0	0	0	490.95
	30	1528	33.6	513.4	51.34	52.0	794.6	206.60	12.0	183.4	71.53	2.4	36.7	26.42	0	0	0	355.89
	31	814	50.4	410.3	41.03	40.8	332.1	86.35	7.2	58.6	22.85	1.6	13.0	9.36	0	0	0	159.59
																		1405.79

TABLE 54 : JANUARY (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.10			.26			.39			.72			1.08	
CNG	E	805	41.3	332.5	33.25	52.2	420.2	109.25	4.3	34.6	13.49	2.2	17.7	12.74	0	0	0	168.73
II	F	1839	31.2	573.8	57.38	45.6	838.6	218.04	20.0	367.8	143.44	3.2	58.8	42.34	0	0	0	461.20
	G	1898	20.8	394.8	39.48	56.8	1078.1	280.31	15.2	288.5	112.52	6.4	121.5	87.48	0.8	15.2	16.42	536.21
	H	1492	23.2	346.1	34.61	52.0	775.8	201.71	18.4	274.5	107.06	4.0	59.7	42.98	2.4	35.8	38.66	425.02
																		1591.16
PRIORY	1	670	45.0	301.5	30.15	41.9	280.7	72.98	8.5	57.0	22.23	3.9	26.1	18.79	0.8	5.4	5.83	149.98
	2	803	39.3	315.6	31.56	50.0	401.5	104.39	8.9	71.5	27.89	1.8	14.5	10.44	0	0	0	174.28
	3	353	39.5	139.4	13.94	40.3	142.3	37.00	10.1	35.7	13.92	9.2	32.5	23.40	0.8	2.8	3.02	91.28
	4	414	36.0	149.0	14.90	47.0	194.6	50.60	11.0	45.5	17.75	6.1	25.3	18.22	0	0	0	101.47
	5	174	41.6	72.4	7.24	46.5	80.9	21.03	11.9	20.7	8.07	0	0	0	0	0	0	36.34
	6	1835	30.8	565.2	56.52	55.0	1009.3	262.42	10.8	198.2	77.30	3.3	60.6	43.63	0	0	0	439.87
	7	1587	25.8	409.4	40.94	46.5	738.0	191.88	22.0	349.1	136.15	3.8	60.3	43.42	1.9	30.2	32.62	445.01
	8	403	13.1	52.8	5.28	59.0	237.8	61.83	21.3	85.8	33.46	6.6	26.6	19.15	0	0	0	119.72
	9	441	23.2	102.3	10.23	51.6	227.6	59.18	17.4	76.7	29.91	6.3	27.8	20.02	1.6	7.1	7.67	127.01
	10	471	35.0	164.9	16.49	44.8	211.0	54.86	15.3	72.1	28.12	4.9	23.1	16.63	0	0	0	116.10
																		1801.06
CNG	1	1355	40.0	542.0	54.20	45.8	620.6	161.36	11.7	158.5	61.82	2.5	33.9	24.41	0	0	0	301.79
I	2	1295	50.9	659.2	65.92	38.0	492.1	127.95	7.4	95.8	37.36	2.8	36.3	26.14	0.9	11.7	12.64	270.01
	3	1140	45.5	518.7	51.87	42.7	486.8	126.57	8.2	93.5	36.47	3.6	41.0	29.52	0	0	0	244.43
																		816.23

TABLE 55 : MARCH.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.10			.27			.46			.61			1.04	
CNOC	9	832	56.0	465.9	46.59	32.8	272.9	73.68	7.2	59.9	27.55	4.0	33.3	20.31	0	0	0	168.13
COIG	10	842	48.8	410.9	41.09	39.2	330.1	89.13	10.4	87.6	40.30	1.6	13.5	8.24	0	0	0	178.76
PIT	11	908	46.4	421.3	42.13	40.0	363.2	98.06	8.8	79.9	36.75	4.8	43.6	26.60	0	0	0	203.54
10	12	930	40.8	379.4	37.94	45.6	424.1	114.51	10.4	96.7	44.48	1.6	14.9	9.09	1.6	14.9	15.50	221.52
																		771.95
CNOC	17	804	68.8	553.2	55.32	27.1	217.9	58.83	2.1	16.9	7.77	2.1	16.9	10.31	0	0	0	132.23
COIG	18	923	64.8	598.1	59.81	28.8	265.8	71.77	3.2	29.5	13.57	1.6	14.8	9.03	1.6	14.8	15.39	169.57
PIT	20	808	56.8	458.9	45.89	36.0	290.9	78.54	4.0	32.3	14.86	3.2	25.9	15.80	0	0	0	155.09
6	21	570	60.0	342.0	34.20	35.2	200.6	54.16	4.8	27.4	12.60	0	0	0	0	0	0	100.96
																		557.85
CNOC	28	2102	54.3	1141.4	114.14	38.0	798.8	215.68	5.4	113.5	52.21	2.2	46.2	28.18	0	0	0	410.21
SLIG.	29	2036	30.4	618.9	61.89	52.8	1075.0	290.25	14.4	293.2	134.87	2.4	48.9	29.83	0	0	0	516.84
	30	1528	33.6	513.4	51.34	52.0	794.6	214.54	12.0	183.4	84.36	2.4	36.7	22.39	0	0	0	372.63
	31	814	50.4	410.3	41.03	40.8	332.1	89.67	7.2	58.6	26.96	1.6	13.0	7.93	0	0	0	165.59
																		1465.27

TABLE 55 : MARCH. (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.10			.27			.46			.61			1.04	
CNG II	E	805	41.3	332.5	33.25	52.2	420.2	113.45	4.3	34.6	15.92	2.2	17.7	10.80	0	0	0	173.42
	F	1839	31.2	573.8	57.38	45.6	838.6	226.42	20.0	367.8	169.19	3.2	58.8	35.87	0	0	0	488.86
	G	1898	20.8	394.8	39.48	56.8	1078.1	291.09	15.2	288.5	132.71	6.4	121.5	74.12	0.8	15.2	15.81	553.21
	H	1492	23.2	346.1	34.61	52.0	775.8	209.47	18.4	274.5	126.27	4.0	59.7	36.42	2.4	35.8	37.23	444.00
																		1659.49
PRIORY	1	670	45.0	301.5	30.15	41.9	280.7	75.79	8.5	57.0	26.22	3.9	26.1	15.92	0.8	5.4	5.62	153.70
	2	803	39.3	315.6	31.56	50.0	401.5	108.41	8.9	71.5	32.89	1.8	14.5	8.85	0	0	0	181.71
	3	353	39.5	139.4	13.94	40.3	142.3	38.42	10.1	35.7	16.42	9.2	32.5	19.83	0.8	2.8	2.91	91.52
	4	414	36.0	149.0	14.90	47.0	194.6	52.54	11.0	45.5	20.93	6.1	25.3	15.43	0	0	0	103.80
	5	174	41.6	72.4	7.24	46.5	80.9	21.84	11.9	20.7	9.52	0	0	0	0	0	0	38.60
	6	1835	30.8	565.2	56.52	55.0	1009.3	272.51	10.8	198.2	91.17	3.3	60.6	36.97	0	0	0	457.17
	7	1587	25.8	409.4	40.94	46.5	738.0	119.26	22.0	349.1	160.59	3.8	60.3	36.78	1.9	30.2	31.41	388.98
	8	403	13.1	52.8	5.28	59.0	237.8	64.21	21.3	85.8	39.47	6.6	26.6	16.23	0	0	0	125.19
	9	441	23.2	102.3	10.23	51.6	227.6	61.45	17.4	76.7	35.28	6.3	27.8	16.96	1.6	7.1	7.38	131.30
	10	471	35.0	164.9	16.49	44.8	211.0	56.97	15.3	72.1	33.17	4.9	23.1	14.09	0	0	0	120.72
																		1792.69
CNG I	1	1355	40.0	542.0	5.42	45.8	620.6	167.56	11.7	158.5	72.91	2.5	33.9	20.68	0	0	0	266.57
	2	1295	50.9	659.2	65.92	38.0	492.1	132.87	7.4	95.8	44.07	2.8	36.3	22.14	0.9	11.7	12.17	277.17
	3	1140	45.5	518.7	51.87	42.7	486.8	131.44	8.2	93.5	43.01	3.6	41.0	25.01	0	0	0	251.33
																		795.07

TABLE 56 : MAY-JUNE.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.12			.37			.67			.87			1.44	
CNOC	9	832	56.0	465.9	55.91	32.8	272.9	100.97	7.2	59.9	40.13	4.0	33.3	28.97	0	0	0	255.98
COIG	10	842	48.8	410.9	49.31	39.2	330.1	122.14	10.4	87.6	58.69	1.6	13.5	11.75	0	0	0	241.89
PIT	11	908	46.4	421.3	50.56	40.0	363.2	134.38	8.8	79.9	53.53	4.8	43.6	37.93	0	0	0	276.40
10	12	930	40.8	379.4	45.53	45.6	424.1	156.92	10.4	96.7	64.79	1.6	14.9	12.96	1.6	14.9	21.46	301.66
																		1075.93
CNOC	17	804	68.8	553.2	66.38	27.1	217.9	80.62	2.1	16.9	11.32	2.1	16.9	14.70	0	0	0	173.02
COIG	18	923	64.8	598.1	71.77	28.8	265.8	98.35	3.2	29.5	19.77	1.6	14.8	12.88	1.6	14.8	21.31	224.08
PIT	20	808	56.8	458.9	55.07	36.0	290.9	107.63	4.0	32.3	21.64	3.2	25.9	22.53	0	0	0	206.87
6	21	570	60.0	342.0	41.04	35.2	200.6	74.22	4.8	27.4	18.36	0	0	0	0	0	0	133.62
																		737.59
CNOC	28	2102	54.3	1141.4	136.97	38.0	798.8	295.56	5.4	113.5	76.05	2.2	46.2	40.19	0	0	0	548.77
SLIG.	29	2036	30.4	618.9	74.27	52.8	1075.0	397.75	14.4	293.2	196.44	2.4	48.9	42.54	0	0	0	711.00
	30	1528	33.6	513.4	61.61	52.0	794.6	294.00	12.0	183.4	122.88	2.4	36.7	31.93	0	0	0	510.42
	31	814	50.4	410.3	49.24	40.8	332.1	122.88	7.2	58.6	39.26	1.6	13.0	11.31	0	0	0	222.69
																		1992.88

TABLE 56 : MAY- JUNE (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.12			.37			.67			.87			1.44	
CNG	E	805	41.3	332.5	39.90	52.2	420.2	155.47	4.3	34.6	23.18	2.2	17.7	15.40	0	0	0	233.95
II	F	1839	31.2	573.8	68.86	45.6	838.6	310.28	20.0	367.8	246.43	3.2	58.8	51.16	0	0	0	676.73
	G	1898	20.8	394.8	47.38	56.8	1078.1	398.90	15.2	288.5	193.30	6.4	121.5	105.71	0.8	15.2	21.89	767.18
	H	1492	23.2	346.1	41.53	52.0	775.8	287.05	18.4	274.5	183.92	4.0	59.7	51.94	2.4	35.8	51.55	615.99
																		2293.85
PRIORY	1	670	45.0	301.5	36.18	41.9	280.7	103.86	8.5	57.0	38.19	3.9	26.1	22.71	0.8	5.4	7.78	208.72
	2	803	39.3	315.6	37.87	50.0	401.5	148.56	8.9	71.5	47.91	1.8	14.5	12.62	0	0	0	246.96
	3	353	39.5	139.4	16.73	40.3	142.3	52.65	10.1	35.7	23.92	9.2	32.5	28.28	0.8	2.8	4.03	125.61
	4	414	36.0	149.0	17.88	47.0	194.6	72.00	11.0	45.5	30.49	6.1	25.3	22.01	0	0	0	142.38
	5	174	41.6	72.4	8.69	46.5	80.9	29.93	11.9	20.7	13.87	0	0	0	0	0	0	52.49
	6	1835	30.8	565.2	67.82	55.0	1009.3	373.44	10.8	198.2	132.79	3.3	60.6	52.72	0	0	0	626.77
	7	1587	25.8	409.4	49.13	46.5	738.0	273.06	22.0	349.1	233.90	3.8	60.3	52.46	1.9	30.2	43.49	652.04
	8	403	13.1	52.8	6.34	59.0	237.8	87.99	21.3	85.8	57.49	6.6	26.6	23.14	0	0	0	174.96
	9	441	23.2	102.3	12.28	51.6	227.6	84.21	17.4	76.7	51.39	6.3	27.8	24.19	1.6	7.1	10.22	182.29
	10	471	35.0	164.9	19.79	44.8	211.0	78.07	15.3	72.1	48.31	4.9	23.1	20.10	0	0	0	166.27
																		2578.49
CNG	1	1355	40.0	542.0	65.04	45.8	620.6	229.62	11.7	158.5	106.20	2.5	33.9	29.49	0	0	0	430.35
I	2	1295	50.9	659.2	79.10	38.0	492.1	182.08	7.4	95.8	64.19	2.8	36.3	31.58	0.9	11.7	16.85	373.80
	3	1140	45.5	518.7	62.24	42.7	486.8	180.12	8.2	93.5	62.65	3.6	41.0	35.67	0	0	0	340.68
																		1144.83

TABLE 57 : JULY.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.09			.32			.57			1.03			1.79	
CNOC	9	832	56.0	465.9	41.93	32.8	272.9	87.33	7.2	59.9	34.14	4.0	33.3	34.30	0	0	0	197.70
COIG	10	842	48.8	410.9	36.98	39.2	330.1	105.63	10.4	87.6	49.93	1.6	13.5	13.91	0	0	0	206.45
PIT	11	908	46.4	421.3	37.92	40.0	363.2	116.22	8.8	79.9	45.54	4.8	43.6	44.91	0	0	0	244.59
10	12	930	40.8	379.4	34.15	45.6	424.1	135.71	10.4	96.7	55.12	1.6	14.9	15.35	1.6	14.9	26.67	267.00
																		915.74
CNOC	17	804	68.8	553.2	49.79	27.1	217.9	69.73	2.1	16.9	9.63	2.1	16.9	17.41	0	0	0	146.56
COIG	18	923	64.8	598.1	53.83	28.8	265.8	85.06	3.2	29.5	16.82	1.6	14.8	15.24	1.6	14.8	26.49	197.44
PIT	20	808	56.8	458.9	41.30	36.0	290.9	93.09	4.0	32.3	18.41	3.2	25.9	26.68	0	0	0	179.48
6	21	570	60.0	342.0	30.78	35.2	200.6	64.19	4.8	27.4	15.62	0	0	0	0	0	0	110.59
																		634.07
CNOC	28	2102	54.3	1141.4	102.73	38.0	798.8	255.62	5.4	113.5	64.70	2.2	46.2	47.59	0	0	0	470.64
SLIG.	29	2036	30.4	618.9	55.70	52.8	1075.0	344.00	14.4	293.2	167.12	2.4	48.9	50.06	0	0	0	616.88
	30	1528	33.6	513.4	46.21	52.0	794.6	254.27	12.0	183.4	104.54	2.4	36.7	37.80	0	0	0	442.82
	31	814	50.4	410.3	36.93	40.8	332.1	106.27	7.2	58.6	33.40	1.6	13.0	13.39	0	0	0	189.99
																		1720.33

TABLE 57 : JULY (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.09			.32			.57			1.03			1.79	
CNG	E	805	41.3	332.5	29.93	52.2	420.2	134.46	4.3	34.6	19.72	2.2	17.7	18.23	0	0	0	202.34
II	F	1839	31.2	573.8	51.64	45.6	838.6	268.35	20.0	367.8	209.65	3.2	58.8	60.56	0	0	0	590.20
	G	1898	20.8	394.8	35.53	56.8	1078.1	344.99	15.2	288.5	164.45	6.4	121.5	125.15	0.8	15.2	27.21	697.33
	H	1492	23.2	346.1	31.15	52.0	775.8	248.26	18.4	274.5	156.47	4.0	59.7	61.49	2.4	35.8	64.08	561.45
																		2051.32
PRIORY	1	670	45.0	301.5	27.14	41.9	280.7	89.82	8.5	57.0	32.49	3.9	26.1	26.88	0.8	5.4	9.67	186.00
	2	803	39.3	315.6	28.40	50.0	401.5	128.48	8.9	71.5	40.76	1.8	14.5	14.94	0	0	0	212.58
	3	353	39.5	139.4	12.55	40.3	142.3	45.54	10.1	35.7	20.35	9.2	32.5	33.48	0.8	2.8	5.01	116.93
	4	414	36.0	149.0	13.41	47.0	194.6	62.27	11.0	45.5	25.94	6.1	25.3	26.06	0	0	0	127.68
	5	174	41.6	72.4	6.52	46.5	80.9	25.89	11.9	20.7	11.80	0	0	0	0	0	0	44.21
	6	1835	30.8	565.2	50.87	55.0	1009.3	322.98	10.8	198.2	112.97	3.3	60.6	62.42	0	0	0	549.24
	7	1587	25.8	409.4	36.85	46.5	738.0	236.16	22.0	349.1	198.99	3.8	60.3	62.11	1.9	30.2	54.06	588.17
	8	403	13.1	52.8	4.75	59.0	237.8	76.10	21.3	85.8	48.91	6.6	26.6	27.40	0	0	0	157.16
	9	441	23.2	102.3	9.21	51.6	227.6	72.83	17.4	76.7	43.72	6.3	27.8	28.63	1.6	7.1	12.71	167.10
	10	471	35.0	164.9	14.84	44.8	211.0	67.52	15.3	72.1	41.10	4.9	23.1	23.79	0	0	0	147.25
																		2296.32
CNG	1	1355	40.0	542.0	48.78	45.8	620.6	198.59	11.7	158.5	90.35	2.5	33.9	34.92	0	0	0	372.64
I	2	1295	50.9	659.2	59.33	38.0	492.1	157.47	7.4	95.8	54.61	2.8	36.3	37.40	0.9	11.7	20.94	329.75
	3	1140	45.5	518.7	46.68	42.7	486.8	155.78	8.2	93.5	53.30	3.6	41.0	42.23	0	0	0	297.99
																		1000.38

TABLE 58 : SEPTEMBER.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.10			.36			.59			.86			1.26	
CNOC	9	832	56.0	465.9	46.59	32.8	272.9	98.24	7.2	59.9	35.34	4.0	33.3	28.64	0	0	0	208.81
COIG	10	842	48.8	410.9	41.09	39.2	330.1	118.84	10.4	87.6	51.68	1.6	13.5	11.61	0	0	0	223.22
PIT	11	908	46.4	421.3	42.13	40.0	363.2	130.75	8.8	79.9	47.14	4.8	43.6	37.50	0	0	0	257.52
10	12	930	40.8	379.4	37.94	45.6	424.1	152.68	10.4	96.7	57.05	1.6	14.9	12.81	1.6	14.9	18.77	279.25
																		968.80
CNOC	17	804	68.8	553.2	55.32	27.1	217.9	78.44	2.1	16.9	9.97	2.1	16.9	14.53	0	0	0	158.26
COIG	18	923	64.8	598.1	59.81	28.8	265.8	95.69	3.2	29.5	17.41	1.6	14.8	12.73	1.6	14.8	18.65	204.29
PIT	20	808	56.8	458.9	45.89	36.0	290.9	104.72	4.0	32.3	19.06	3.2	25.9	22.27	0	0	0	191.94
6	21	570	60.0	342.0	34.20	35.2	200.6	72.22	4.8	27.4	16.17	0	0	0	0	0	0	122.59
																		677.08
CNOC	28	2102	54.3	1141.4	144.14	38.0	798.8	287.57	5.4	113.5	66.97	2.2	46.2	39.73	0	0	0	538.41
SLIG.	29	2036	30.4	618.9	61.89	52.8	1075.0	387.00	14.4	293.2	172.99	2.4	48.9	42.05	0	0	0	663.93
	30	1528	33.6	513.4	51.34	52.0	794.6	286.06	12.0	183.4	108.21	2.4	36.7	31.56	0	0	0	477.17
	31	814	50.4	410.3	41.03	40.8	332.1	119.56	7.2	58.6	34.57	1.6	13.0	11.18	0	0	0	206.34
																		1885.85

TABLE 58 : SEPTEMBER (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.10			.36			.59			.86			1.26	
CNG	E	805	41.3	332.5	33.25	52.2	420.2	151.27	4.3	34.6	20.41	2.2	17.7	15.22	0	0	0	220.15
II	F	1839	31.2	573.8	57.38	45.6	838.6	301.90	20.0	367.8	217.00	3.2	58.8	50.57	0	0	0	626.85
	G	1898	20.8	394.8	39.48	56.8	1078.1	388.12	15.2	288.5	170.22	6.4	121.5	104.49	0.8	15.2	19.15	721.46
	H	1492	23.2	346.1	34.61	52.0	775.8	279.29	18.4	274.5	161.96	4.0	59.7	51.34	2.4	35.8	45.11	572.31
																		2140.77
PRIORY	1	670	45.0	301.5	30.15	41.9	280.7	101.05	8.5	57.0	33.63	3.9	26.1	22.45	0.8	5.4	6.80	194.08
	2	803	39.3	315.6	31.56	50.0	401.5	144.54	8.9	71.5	42.19	1.8	14.5	12.47	0	0	0	230.76
	3	353	39.5	139.4	13.94	40.3	142.3	51.23	10.1	35.7	21.06	9.2	32.5	27.95	0.8	2.8	3.53	117.71
	4	414	36.0	149.0	14.90	47.0	194.6	70.06	11.0	45.5	26.85	6.1	25.3	21.76	0	0	0	133.57
	5	174	41.6	72.4	7.24	46.5	80.9	29.12	11.9	20.7	12.21	0	0	0	0	0	0	48.57
	6	1835	30.8	565.2	56.52	55.0	1009.3	363.35	10.8	198.2	116.94	3.3	60.6	52.12	0	0	0	588.93
	7	1587	25.8	409.4	40.94	46.5	738.0	265.68	22.0	349.1	205.97	3.8	60.3	51.86	1.9	30.2	38.05	602.50
	8	403	13.1	52.8	5.28	59.0	237.8	85.61	21.3	85.8	50.62	6.6	26.6	22.88	0	0	0	164.39
	9	441	23.2	102.3	10.23	51.6	227.6	81.94	17.4	76.7	45.25	6.3	27.8	23.91	1.6	7.1	8.95	170.28
	10	471	35.0	164.9	16.49	44.8	211.0	75.96	15.3	72.1	42.54	4.9	23.1	19.87	0	0	0	154.86
																		2405.65
CNG	1	1355	40.0	542.0	5.42	45.8	620.6	223.42	11.7	158.5	93.52	2.5	33.9	29.15	0	0	0	351.51
I	2	1295	50.9	659.2	65.92	38.0	492.1	117.16	7.4	95.8	56.52	2.8	36.3	31.22	0.9	11.7	14.74	285.56
	3	1140	45.5	518.7	51.87	42.7	486.8	175.25	8.2	93.5	55.17	3.6	41.0	35.26	0	0	0	317.55
																		954.62

TABLE 59 : NOVEMBER.

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
		total			meat			meat			meat			meat			meat	total
	level	no	%	no	wt	%	no	wt	%	no	wt	%	no	wt	%	no	wt	meat wt
					.09			.29			.46			.68			.95	
CNOC	9	832	56.0	465.9	41.93	32.8	272.9	79.14	7.2	59.9	27.55	4.0	33.3	22.64	0	0	0	171.26
COIG	10	842	48.8	410.9	36.98	39.2	330.1	95.73	10.4	87.6	40.30	1.6	13.5	9.18	0	0	0	182.19
PIT	11	908	46.4	421.3	37.92	40.0	363.2	105.33	8.8	79.9	36.75	4.8	43.6	29.65	0	0	0	209.65
10	12	930	40.8	379.4	34.15	45.6	424.1	122.99	10.4	96.7	44.48	1.6	14.9	10.13	1.6	14.9	14.16	225.91
																		789.01
CNOC	17	804	68.8	553.2	49.79	27.1	217.9	63.19	2.1	16.9	7.77	2.1	16.9	11.49	0	0	0	132.24
COIG	18	923	64.8	598.1	53.83	28.8	265.8	77.08	3.2	29.5	13.57	1.6	14.8	10.06	1.6	14.8	14.06	168.60
PIT	20	808	56.8	458.9	41.30	36.0	290.9	84.36	4.0	32.3	14.86	3.2	25.9	17.61	0	0	0	158.13
6	21	570	60.0	342.0	30.78	35.2	200.6	58.17	4.8	27.4	12.60	0	0	0	0	0	0	101.55
																		560.52
CNOC	28	2102	54.3	1141.4	102.73	38.0	798.8	231.65	5.4	113.5	52.21	2.2	46.2	31.42	0	0	0	418.01
SLIG.	29	2036	30.4	618.9	55.70	52.8	1075.0	311.75	14.4	293.2	134.87	2.4	48.9	33.25	0	0	0	535.57
	30	1528	33.6	513.4	46.21	52.0	794.6	230.43	12.0	183.4	84.36	2.4	36.7	24.96	0	0	0	385.96
	31	814	50.4	410.3	36.93	40.8	332.1	96.31	7.2	58.6	26.96	1.6	13.0	8.84	0	0	0	169.04
																		1508.58

TABLE 59 : NOVEMBER (continued).

Shell wt group			≤ 1.75			1.76-3.50			3.51-5.50			5.51-9.50			≥ 9.51			
	level	total no	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	%	no	meat wt	total meat wt
					.09			.29			.46			.68			.95	
CNG	E	805	41.3	332.5	29.93	52.2	420.2	121.86	4.3	34.6	15.92	2.2	17.7	12.04	0	0	0	179.75
II	F	1839	31.2	573.8	51.64	45.6	838.6	243.19	20.0	367.8	169.19	3.2	58.8	39.98	0	0	0	504.00
	G	1898	20.8	394.8	35.53	56.8	1078.1	312.65	15.2	288.5	132.71	6.4	121.5	82.62	0.8	15.2	14.44	577.95
	H	1492	23.2	346.1	31.15	52.0	775.8	224.98	18.4	274.5	126.27	4.0	59.7	40.60	2.4	35.8	34.01	457.01
																		1718.71
PRIORY	1	670	45.0	301.5	27.14	41.9	280.7	81.40	8.5	57.0	26.22	3.9	26.1	17.75	0.8	5.4	5.13	157.64
	2	803	39.3	315.6	28.40	50.0	401.5	116.44	8.9	71.5	32.89	1.8	14.5	9.86	0	0	0	187.59
	3	353	39.5	139.4	12.55	40.3	142.3	41.27	10.1	35.7	16.42	9.2	32.5	22.10	0.8	2.8	2.66	95.00
	4	414	36.0	149.0	13.41	47.0	194.6	56.43	11.0	45.5	20.93	6.1	25.3	17.20	0	0	0	107.97
	5	174	41.6	72.4	6.52	46.5	80.9	23.46	11.9	20.7	9.52	0	0	0	0	0	0	39.50
	6	1835	30.8	565.2	50.87	55.0	1009.3	292.70	10.8	198.2	91.17	3.3	60.6	41.21	0	0	0	475.95
	7	1587	25.8	409.4	36.85	46.5	738.0	214.02	22.0	349.1	160.59	3.8	60.3	41.00	1.9	30.2	28.69	481.15
	8	403	13.1	52.8	4.75	59.0	237.8	68.96	21.3	85.8	39.47	6.6	26.6	18.09	0	0	0	131.27
	9	441	23.2	102.3	9.21	51.6	227.6	66.00	17.4	76.7	35.28	6.3	27.8	18.90	1.6	7.1	6.75	136.14
	10	471	35.0	164.9	14.84	44.8	211.0	61.19	15.3	72.1	33.17	4.9	23.1	15.71	0	0	0	124.91
																		1937.12
CNG	1	1355	40.0	542.0	48.78	45.8	620.6	179.97	11.7	158.5	72.91	2.5	33.9	23.05	0	0	0	324.71
I	2	1295	50.9	659.2	59.33	38.0	492.1	142.71	7.4	95.8	44.07	2.8	36.3	24.68	0.9	11.7	11.12	281.91
	3	1140	45.5	518.7	46.68	42.7	486.8	141.17	8.2	93.5	43.01	3.6	41.0	27.88	0	0	0	258.74
																		865.36

TABLE 60 : THE CALCULATION OF MIDDEN PERIWINKLE MEAT WEIGHT VALUES FOR EACH SAMPLE MONTH

MIDDEN	LEVEL	TOTAL NO.	JAN.	MARCH	MAY-JUNE	JULY	SEPT.	NOV.	
			.36	.30	.28	.27	.34	.36	Modern meat weight
CNOC COIG	9	32	11.52	9.60	8.96	8.64	10.88	11.52	Calculated meat weight
PIT 10	11	30	10.80	9.00	8.40	8.10	10.20	10.80	
	12	6	2.16	1.80	1.68	1.62	2.04	2.16	
			24.48	20.40	19.04	18.36	23.12	24.48	Total
CNOC COIG	17	17	6.12	5.10	4.76	4.59	5.78	6.12	Calculated meat weight
PIT 6	18	8	2.88	2.40	2.24	2.16	2.72	2.88	
	20	33	11.88	9.90	9.24	8.91	11.22	11.88	
	21	9	3.24	2.70	2.52	2.43	3.06	3.24	
			24.12	20.10	18.76	18.09	22.78	24.12	Total
CNOC	28	7	2.52	2.10	1.96	1.89	2.38	2.52	Calculated meat weight
SLIGEACH	29	6	2.16	1.80	1.68	1.62	2.04	2.16	
	30	12	4.32	3.60	3.36	3.24	4.08	4.32	
	31	3	1.08	0.90	0.84	0.81	1.02	1.08	
			10.08	8.40	7.84	7.56	9.52	10.08	Total

(All weights are in grams)

TABLE 60 (continued)

MIDDEN	LEVEL	TOTAL NO.	JAN.	MARCH	MAY-JUNE	JULY	SEPT.	NOV.	
			.36	.30	.28	.27	.34	.36	Modern meat weight
CNG II	E	8	2.88	2.40	2.24	2.16	2.72	2.88	Calculated meat weight
	F	12	4.32	3.60	3.36	3.24	4.08	4.32	
	G	16	5.76	4.80	4.48	4.32	5.44	5.76	
	H	5	1.80	1.50	1.40	1.35	1.70	1.80	
			14.76	12.30	11.48	11.07	13.94	14.76	Total
PRIORY	1	62	22.32	18.60	17.36	16.74	21.08	22.32	Calculated meat weight
	2	71	25.56	21.30	19.88	19.17	24.14	25.56	
	3	32	11.52	9.60	8.96	8.64	10.88	11.52	
	4	10	3.60	3.00	2.80	2.70	3.40	3.60	
	5	14	5.04	4.20	3.92	3.78	4.76	5.04	
	6	59	21.24	17.70	16.52	15.93	20.06	21.24	
	7	37	13.32	11.10	10.36	9.99	12.58	13.32	
	8	1	0.36	0.30	0.28	0.27	0.34	0.36	
	9	2	0.72	0.60	0.56	0.54	0.68	0.72	
	10	1	0.36	0.30	0.28	0.27	0.34	0.36	
			104.04	86.70	80.92	78.03	98.26	104.04	Total
CNG I	1	13	4.68	3.90	3.64	3.51	4.42	4.68	Calculated meat weight
	2	88	31.68	26.40	24.64	23.76	29.92	31.68	
	3	24	8.64	7.20	6.72	6.48	8.16	8.64	
			45.00	37.50	35.00	33.75	42.50	45.00	Total

TABLE 61 : THE CALCULATION OF MIDDEN DOGWHELK MEAT WEIGHT VALUES FOR EACH SAMPLE MONTH

MIDDEN	LEVEL	TOTAL NO.	JAN.	MARCH	MAY-JUNE	JULY	SEPT.	NOV.	
			.30	.19	.25	.20	.26	.27	Modern meat weight
CNOC COIG	9	31	9.30	5.89	7.75	6.20	8.06	8.37	Calculated meat weight
PIT 10	10	2	0.60	0.38	0.50	0.40	0.52	0.54	
	11	15	4.50	2.85	3.75	3.00	3.90	4.05	
	12	8	2.40	1.52	2.00	1.60	2.08	2.16	
			16.80	10.64	14.00	11.20	14.56	15.12	Total
CNOC COIG	17	29	8.70	5.51	7.25	5.80	7.54	7.83	Calculated meat weight
PIT 6	18	29	8.70	5.51	7.25	5.80	7.54	7.83	
	20	30	9.00	5.70	7.50	6.00	7.80	8.10	
	21	15	4.50	2.85	3.75	3.00	3.90	4.05	
			30.90	19.57	25.75	20.60	26.78	27.81	Total
CNOC	28	123	36.90	23.37	30.75	24.60	31.98	33.21	Calculated meat weight
SLIGEACH	29	167	50.10	31.73	41.75	33.40	43.42	45.09	
	30	170	51.00	32.30	42.50	34.00	44.20	45.90	
	31	81	24.30	15.39	20.25	16.20	21.06	21.87	
			162.30	102.79	135.25	108.20	140.66	146.07	Total

(All weights are in grams)

TABLE 61 (continued)

MIDDEN	LEVEL	TOTAL NO.	JAN.	MARCH	MAY-JUNE	JULY	SEPT.	NOV.	
			.30	.19	.25	.20	.26	.27	Modern meat weight
CNG II	E	43	12.90	8.17	10.75	8.60	11.18	11.61	Calculated meat weight
	F	26	7.80	4.94	6.50	5.20	6.76	7.02	
	G	7	2.10	1.33	1.75	1.40	1.82	1.89	
	H	2	0.60	0.38	0.50	0.40	0.52	0.54	
			23.40	14.82	19.50	15.60	20.28	21.06	Total
PRIORY	1	31	9.30	5.89	7.75	6.20	8.06	8.37	Calculated meat weight
	2	25	7.50	4.75	6.25	5.00	6.50	6.75	
	3	6	1.80	1.14	1.50	1.20	1.56	1.62	
	4	6	1.80	1.14	1.50	1.20	1.56	1.62	
	5	5	1.50	0.95	1.25	1.00	1.30	1.35	
	6	30	9.00	5.70	7.50	6.00	7.80	8.10	
	7	22	6.60	4.18	5.50	4.40	5.72	5.94	
			37.50	23.75	31.25	25.00	32.50	33.75	Total
CNG I	1	67	20.10	12.73	16.75	13.40	17.42	18.09	Calculated meat weight
	2	84	25.20	15.96	21.00	16.80	21.84	22.68	
	3	72	21.60	13.68	18.00	14.40	18.72	19.44	
			66.90	42.37	55.75	44.60	57.98	60.21	Total

TABLES 62 to 67 : THE RELATIVE PROPORTIONS OF MEAT WEIGHT CONTRIBUTED BY EACH OF THE THREE SPECIES PER SAMPLE MONTH.

See text for method of calculation.

TABLE 62 : JANUARY.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC	9	88.79	6.20	5.01
COIG	10	87.04	12.66	0.31
PIT	11	92.86	5.04	2.10
10	12	97.73	1.07	1.19
	TOTALS	91.71	6.18	2.11
CNOC	17	89.82	4.20	5.98
COIG	18	93.52	1.61	4.87
PIT	20	87.98	6.84	5.18
6	21	92.61	3.09	4.29
	TOTALS	90.87	4.00	5.13
CNOC	28	91.02	0.57	8.41
SLIG.	29	90.38	0.40	9.22
	30	86.55	1.05	12.40
	31	86.28	0.58	13.14
	TOTALS	89.08	0.64	10.28

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	91.45	1.56	6.99
	F	97.44	0.91	1.65
	G	98.55	1.06	0.39
	H	99.44	0.42	0.14
	TOTALS	97.66	0.91	1.44
PROIRY	1	82.59	12.29	5.12
	2	84.06	12.33	3.62
	3	87.27	11.01	1.72
	4	94.95	3.37	1.68
	5	84.75	11.75	3.50
	6	93.57	4.52	1.91
	7	95.72	2.86	1.42
	8	99.70	0.30	0
	9	99.44	0.56	0
	10	99.69	0.31	0
	TOTALS	92.71	5.36	1.93
CNG I	1	92.41	1.43	6.15
	2	82.60	9.69	7.71
	3	88.99	3.15	7.86
	TOTALS	87.94	4.85	7.21

TABLE 63 : MARCH.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC	9	91.56	5.23	3.21
COIG	10	89.45	10.36	0.19
PIT	11	94.50	4.18	1.32
10	12	98.52	0.80	0.68
	TOTALS	93.72	4.99	1.29
CNOC	17	92.57	3.57	3.86
COIG	18	95.54	1.35	3.10
PIT	20	90.86	5.80	3.34
6	21	94.79	2.53	2.68
	TOTALS	93.36	3.36	3.28
CNOC	28	94.15	0.48	5.36
SLIG.	29	93.91	0.33	5.77
	30	91.21	0.88	7.91
	31	91.04	0.49	8.46
	TOTALS	92.95	0.53	6.52

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	94.26	1.30	4.44
	F	98.28	0.72	0.99
	G	98.90	0.86	0.24
	H	99.58	0.34	0.08
	TOTALS	98.39	0.73	0.88
PRIORY	1	86.26	10.44	3.31
	2	87.46	10.25	2.29
	3	89.50	9.39	1.11
	4	96.16	2.78	1.06
	5	88.23	9.60	2.17
	6	95.13	3.68	1.19
	7	96.22	2.75	1.03
	8	99.76	0.24	0
	9	99.55	0.45	0
	10	99.75	0.25	0
	TOTALS	94.20	4.56	1.25
CNG I	1	94.13	1.38	4.50
	2	86.74	8.26	4.99
	3	92.33	2.65	5.03
	TOTALS	90.87	4.29	4.84

TABLE 64 : MAY-JUNE.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC	9	93.87	3.29	2.84
COIG	10	92.43	7.38	0.19
PIT	11	95.79	2.91	1.30
10	12	98.79	0.55	0.66
	TOTALS	95.36	3.40	1.24
CNOC	17	93.51	2.57	3.92
COIG	18	95.94	0.96	3.10
PIT	20	92.51	4.13	3.35
6	21	95.52	1.80	2.68
	TOTALS	94.31	2.40	3.29
CNOC	28	94.37	0.34	5.29
SLIG.	29	94.24	0.22	5.53
	30	91.76	0.60	7.64
	31	91.35	0.34	8.31
	TOTALS	93.30	0.37	6.33

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	94.74	0.91	4.35
	F	98.56	0.49	0.95
	G	99.19	0.58	0.23
	H	99.69	0.23	0.08
	TOTALS	98.67	0.49	0.84
PRIORY	1	89.26	7.42	3.31
	2	90.43	7.28	2.29
	3	92.31	6.58	1.10
	4	97.07	1.91	1.02
	5	91.03	6.80	2.17
	6	96.31	2.54	1.15
	7	97.63	1.55	0.82
	8	99.84	0.16	0
	9	99.69	0.31	0
	10	99.83	0.17	0
	TOTALS	95.83	3.01	1.16
CNG I	1	95.48	0.81	3.72
	2	89.12	5.87	5.01
	3	93.23	1.84	4.93
	TOTALS	92.66	2.83	4.51

TABLE 65 : JULY.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC	9	93.02	4.07	2.92
COIG	10	91.56	8.26	0.18
PIT	11	95.66	3.17	1.17
10	12	98.81	0.60	0.59
	TOTALS	95.00	3.84	1.16
CNOC	17	93.38	2.92	3.70
COIG	18	96.12	1.05	2.82
PIT	20	92.33	4.58	3.09
6	21	95.32	2.09	2.59
	TOTALS	94.25	2.69	3.06
CNOC	28	94.67	0.38	4.95
SLIG.	29	94.63	0.25	5.13
	30	92.24	0.67	7.08
	31	91.78	0.39	7.83
	TOTALS	93.69	0.41	5.89

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	94.95	1.01	4.04
	F	98.59	0.54	0.87
	G	99.19	0.61	0.20
	H	99.69	0.24	0.07
	TOTALS	98.72	0.53	0.75
PRIORY	1	89.02	8.01	2.97
	2	89.79	8.10	2.11
	3	92.24	6.82	0.95
	4	97.04	2.05	0.91
	5	90.24	7.72	2.04
	6	96.16	2.79	1.05
	7	97.61	1.66	0.73
	8	99.83	0.17	0
	9	99.68	0.32	0
	10	99.82	0.18	0
	TOTALS	95.71	3.25	1.04
CNG I	1	95.66	0.90	3.44
	2	89.05	6.42	4.54
	3	93.45	2.03	4.52
	TOTALS	92.74	3.13	4.13

TABLE 66 : SEPTEMBER.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC COIG PIT 10	9	91.68	4.78	3.54
	10	90.30	9.49	0.21
	11	94.81	3.76	1.44
	12	98.55	0.72	0.73
	TOTALS	94.06	4.52	1.41
CNOC COIG PIT 6	17	92.24	3.37	4.39
	18	95.22	1.27	3.51
	20	90.98	5.32	3.70
	21	94.63	2.36	3.01
	TOTALS	93.18	3.14	3.69
CNOC SLIG.	28	94.00	0.42	5.58
	29	93.59	0.29	6.12
	30	90.81	0.78	8.41
	31	90.33	0.45	9.22
	TOTALS	92.62	0.47	6.91

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	94.06	1.16	4.78
	F	98.30	0.64	1.06
	G	99.00	0.75	0.25
	H	99.61	0.30	0.09
	TOTALS	98.43	0.64	0.93
PRIORY	1	86.95	9.44	3.61
	2	88.28	9.23	2.49
	3	90.44	8.36	1.20
	4	96.42	2.45	1.13
	5	88.91	8.71	2.38
	6	95.48	3.25	1.26
	7	97.05	2.03	0.92
	8	99.79	0.21	0
	9	99.60	0.40	0
	10	99.78	0.22	0
	TOTALS	94.84	3.87	1.28
CNG I	1	94.15	1.18	4.67
	2	84.66	8.87	6.47
	3	92.20	2.37	5.44
	TOTALS	90.48	4.03	5.50

TABLE 67 : NOVEMBER.

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNOC	9	89.59	6.03	4.38
COIG	10	87.77	11.97	0.26
PIT	11	93.39	4.81	1.80
10	12	98.12	0.94	0.94
	TOTALS	92.45	5.78	1.77
CNOC	17	90.46	4.19	5.36
COIG	18	94.03	1.61	4.37
PIT	20	88.78	6.67	4.55
6	21	93.30	2.98	3.72
	TOTALS	91.52	3.94	4.54
CNOC	28	92.13	0.56	7.32
SLIG.	29	91.89	0.37	7.74
	30	88.49	0.99	10.52
	31	88.05	0.56	11.39
	TOTALS	90.62	0.61	8.77

MIDDEN	LEVEL	% LIMPETS	% WINKLES	% WHELKS
CNG II	E	92.54	1.48	5.98
	F	97.80	0.84	1.36
	G	98.69	0.98	0.32
	H	99.49	0.39	0.12
	TOTALS	97.96	0.84	1.20
PRIORY	1	83.70	11.85	4.44
	2	85.31	11.62	3.07
	3	87.85	10.65	1.50
	4	95.39	3.18	1.43
	5	86.08	10.98	2.94
	6	94.19	4.20	1.60
	7	96.15	2.66	1.19
	8	99.73	0.27	0
	9	99.47	0.53	0
	10	99.71	0.29	0
	TOTALS	93.36	5.01	1.63
CNG I	1	93.45	1.35	5.21
	2	83.83	9.42	6.74
	3	90.21	3.01	6.78
	TOTALS	89.16	4.64	6.20

APPENDIX 1

THE TIME REQUIRED TO COLLECT LIMPETS

Over the course of fieldwork on the Oronsay coast a number of occasions have arisen when it has become obvious just how easy it would be to deplete the limpet stocks. When collecting limpets in front of Cnoc Coig every second month throughout 1980 (figure 9) to investigate seasonal meat weight changes, it was clear that by the end of the sixth visit limpet stocks were severely depleted. During each visit approximately 250 to 300 limpets were gathered, making a total of 1,500 to 1,800 limpets over the six collections. A total of 28 man-hours were spent collecting, though this includes the collection of winkles and whelks, so the actual time collecting limpets was less than this. If we assume a total of 18 man-hours collecting limpets, this represents a collection rate of between 83 to 100 limpets per person per hour. During the gathering there was deliberate selection for a variety of sizes, so collecting was not done at the fastest possible pace.

When collecting for the natural population survey in July 1981, seven skerries were totally cleared of limpets above 19 mm shell length. Table 19 shows that there were a total of 4,424 limpets. A total of approximately 54 man-hours were spent collecting, though again this also includes the collection of winkles and whelks, but this would only add slightly to the time as they were gathered at the same time as the limpets. This therefore represents a gathering rate of around 82 limpets per person per hour. Again the aim was not to collect as fast as possible.

A number of timed limpet collections were done on various occasions at locations away from both the Cnoc Coig collecting area and the skerries used in the natural population survey. Thus they were, to the author's knowledge, done on areas of previously unexploited shore. The results are expressed in table 68. This shows the three timed collections, A and B done in July 1981, and C in March 1982. It will be seen that the average number of limpets collected per person per hour is 490.9, a substantial increase on the previous two estimated rates of collection. This difference is because in these timed collections only limpets were collected. The area of shore had not been previously exploited and collecting was only done for 15 minutes. Over time stocks become depleted, and more time is taken looking for limpets than removing them from the rocks. Many variables affect the speed at which limpets may be collected. For instance as well as availability, experience seems to affect the numbers collected. In table 68 person 1 has had more collecting experience than person 2, and persons 3 and 4 have the same degree of collecting experience, which is less than persons 1 and 2. In session B, however, person 4 came across a large group of limpets, so he collected the largest number.

Thus, in these collections it was possible to collect between 312 and 628 limpets per hour, with a mean of nearly 500 per hour. This must, however, be regarded as around the maximum possible rate. Nevertheless, with a minimum collection rate of around 83 to 100 and a maximum of around 300 to 600 limpets per hour (depending on such factors as limpet distribution and skills of the collector), it would not take long for the stocks to dwindle.

(This research was carried out jointly by myself and Richard W. Nolan.)

TABLE 68 : RESULTS OF TIMED LIMPET COLLECTIONS CONDUCTED OVER PERIODS OF 15 MINUTES ON ORONSAY

Session	Person	Number of limpets per hour
A	1	612
	2	500
	3	324
	4	312
B	1	492
	2	472
	3	390
	4	504
C	1	652
	2	628
	3	524

Mean number of limpets per hour: 490.9

Personal rates based on total number of limpets and total time collecting:

1	585.3
2	533.3
3	409.3
4	408

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