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The distribution and dispersal of the dogwhelk Nucella lapillus in relation to habitat and community structure

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THE DISTRIBUTION AND DISPERSAL OF THE DOGWHELK *NUCELLA LAPILLUS* IN RELATION TO HABITAT AND COMMUNITY STRUCTURE.

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ABSTRACT.

The foraging pattern, microhabitat utilisation and community impact of *Nucella lapillus* was investigated by field observations and field interventions. Detailed recording sampling and experimental data were taken once every week (for two-three years), from each shore level (low, mid, upper), on each of six study shores varying in wave-exposure from very sheltered to very exposed. Results were compared in relation to those relevant environmental factors that affect dogwhelk activity, growth and survival.

It was apparent that *Nucella lapillus* feeding and refuging patterns are determined by a myriad of different factors including changes in the tidal cycle (and related environmental consequences), wave action, shore level, shore topography and exposure. On a local scale, prey size and availability, as well as microhabitat composition and availability, were important. In contrast to the North-Western Atlantic, populations of *Nucella lapillus* in North Wales do not seem to have keystone effects on the community structure of sessile assemblages, including their main prey item *Semibalanus balanoides*.

CHAPTER 1

GENERAL INTRODUCTION.

The intertidal gastropod *Nucella lapillus* (Neogastropoda: Muricacea: Thaidae), has a wide species range (Moore, 1936*),* is found on both sides of the temperate North Atlantic (Stephenson and Stephenson, 1972; Crothers, 1982b), and is present along most of the coast of Europe (Crothers, 1973). *Nucella lapillus* occurs from low shore to mid shore, and on all types of shores ranging from the most sheltered to the most exposed (Hughes and Burrows, 1993). This dogwhelk is found extensively in crevices, among barnacles and other sites providing refuge, particularly in the middle shore region, and preys almost exclusively on *Balanus* spp. (320/year/individual) and *Mytilus* spp. (15-40/year/individual), see Largen (1967). In the absence of these two prey organisms *Nucella lapillus* may feed upon limpets or other gastropods (Kirby et. al., 1994b). *Nucella lapillus* is found in numerous discrete populations, that each develop independently to some extent, in response to local selection pressures (Daguzan, 1967; Day, 1990; Cowell and Crothers, 1970), as it lacks an effective dispersal phase (Crothers, 1973).

Characteristics.

Sexes are separate in *Nucella lapillus*, fertilisation internal. The females lay eggs in capsules adhered to rocky surfaces in the lower shore (Feare, 1970a; Crothers, 1973). The average life-expectancy is about 3 years, although individuals can live up to 10 years (Colton, 1916). Growth rate is related to season, increasing in summer, decreasing in winter (Crothers, 1977a), and in exposed conditions (high wave-action), individuals grow more slowly and terminate growth earlier (Etter, 1989). Mature shells often develop a thickened lip, and row(s) of white "teeth"as indicators of cessation of growth (Cowell and Crothers, 1970; Crothers, 1985a). Adults usually breed at around 3 years (Feare, 1970b), when they usually stop growing (Crothers, 1977a). The resultant offspring hatch after four months, and juveniles (< 16mm) are found under low shore rocks where they feed on *Spirorbis borealis* (Moore, 1938b).

Foraging.

Finding food in a non-visual predator like *Nucella lapillus* seems to involve chemosensory detection (Charnov, 1976), and olfaction (Connell, 1961a; Morgan, 1972a; Palmer, 1980).

Tactile stimuli is also important (Fischer-Piette, 1935; Menge, 1974; 1978a; Bayne, 1981), as the whelks often crawl over their potential prey for prolonged periods before final selection (Hughes and Dunkin, 1984b; Palmer, 1984b). Ingestive conditioning plays a part in prey choice (Wood, 1968), is related to ranking and perception of risk (handling time), and has been demonstated in three *Nucella* spp. (Palmer, 1984b). *Nucella lapillus* particularly requires the ability to distinquish different prey types, as it inhabits a highly patchy environment, where prey availability is highly variable (Gosselin and Bourget, 1989). Individuals can develop a flexible search image (that is influenced by learning), that uses sensory cues (Murdoch, 1969), and promotes a directed searching pattern (Cornell, 1976).

Although slow moving (Miller, 1974), *Nucella lapillus* is still an efficient predator, being able to discriminate between prey species and between different individuals of the same species, choosing those with the higher expected food value (Palmer, 1984b). *Nucella lapillus* interacts with resident biota on the rocky shore on tidally, diurnally and annually rhythmic schedules (Edwards et. al., 1982), and exhibits seasonal variation in activity (Menge, 1976b; 1979; Lubchenco and Menge, 1978).

Environmental factors.

Many environmental features of the intertidal zone can determine distribution and dispersal of intertidal gastropods, particularly wave-shock and desiccation (Connell, 1961a, 1970; Lewis, 1964; Kensler, 1967; Glynn, 1968; Dayton, 1971; Harger, 1970; Harger and Landberger, 1971; Levin and Paine, 1974). The major mortality factors of juvenile *Nucella lapillus* are desiccation, heat stress and predation (Menge,1978a; Levings and Garrity, 1983; Crothers, 1985a; Hughes and Burrows, 1994;. The overall role of physical factors in the distribution patterns of intertidal organisms has been reviewed by Lewis (1964).

Desiccation and Thermal Stress.

Exposure to air and temperature cause significant environmental stress (Berry, 1983; Etter, 1988b; Burrows and Hughes, 1989), and are major factors influencing vertical zonation in intertidal gastropods (Chapman, 1941). Desiccation (fluid loss) tolerance varies with geographical distribution (Sandison, 1967), and increases with age. This is balanced to some extent by a general increase in desiccation at higher levels of the shore where more mature *Nucella lapillus* tend to be found. Thermal stress reduces prey availability and hence energy acquisition by influencing foraging behaviour, that is modified to the prevailing conditions (Burrows and Hughes, 1989).

Desiccation tends to decrease with an increase in wave-action, due to spray saturation of the microhabitat (Crothers, 1985a), and during neap tidal periods the lower and middle shore are often inundated or wetted with spray for prolonged periods (Hughes and Burrows, 1994). Mortality from desiccation is potentially higher at protected sites (Menge, 1978a), and intensified during spring tides (Hughes and Burrows, 1994), especially when out in the open (Levings and Garrity, 1983). Local variation in rock formations (Spight, 1982b; Garrity,1984), splash zone spray (Colman, 1933), waves and surf (Evans, 1957), algal cover (Chapman, 1941), and cloud cover (Menge, 1978a), can all modify the effects of desiccation. Also, heterogenous surfaces offer more cover and are "natural refuges"for *Nucella lapillus* (Coombs, 1973).

Juvenile snails have a relatively high surface area to volume ratio and are particularly vunerable to physical factors (Foster, 1971; Vermeij, 1972; Wolcott, 1973). They lose water faster than their older counterparts at higher tidal elevations (Coombs, 1973), and cannot survive moderate drying conditions at low tide, and therefore are restricted to certain microhabitats (Gosselin and Chia, 1995b). Correspondingly, juveniles and other lower size classes are usually found under small stones in the lower reaches of the shore (Dukes, 1994).

Wave action and water-borne debris impact.

Wave action is an important determining factor in species abundance and distribution (Colton, 1922; Lewis, 1953; 1954; 1955; Moyse and Nelson-Smith, 1963; Oliver et. al., 1979). The effect of wave-action on the distribution and dispersal of intertidal gastropods has been studied by Dayton (1971), Moran (1985a), and Shanks and Wright (1986). Wave-action is an important environmental stress factor (Moore, 1936; Lewis, 1968; Feare, 1970a; Menge, 1978a; Burrows and Hughes, 1989), and waves can dislodge intertidal organisms by imparting lift, acceleration reaction, and drag forces (Denny et. al., 1985). Mobile intertidal organisms like dogwhelks, can only resist dislodgement by having a shell morphology that reduces drag and adhering to the substratum, or by using sheltered microhabitats (Trussell et. al., 1993). Even so, on exposed sites, the large shearing stresses of large waves can remove *Nucella* from their site of anchorage (Paine and Levin, 1981). Wave strength depends on many factors, including angle of contact with the shore, wind and fetch distance, and residual currents (Ramster and Hill, 1969), and the relative wave forces are commonly estimated by subjective categorization of sites as either "exposed" or "protected" (see Bascom, 1964; Palumbi, 1984). The effects of wave-action increases with the degree of exposure (Crothers, 1985a), wave shock being frequent and an important factor in exposed areas, relatively unimportant in protected sites (Menge, 1978a). In response, *Nucella lapillus* forms aggregations to increase protection against wave-action (Feare, 1971b).

Substratum.

Heterogenous surface topography affects the distribution pattern as well as the abundance and diversity of *Nucella* spp. (Menge et. al., 1983; Bergeron and Bourget, 1986), by allowing the utilisation of refuges from temperature (Menge et. al., 1983), desiccation (Garrity, 1984), and wave-action (Menge,1978b). This habitat fragmentation benefits *Nucella lapillus,* directly increases its abundance (Kohn and Leviten, 1976) and performance (Gosselin and Bouget, 1989), and can alter the size-structure (Emson and Faller-Fritsch, 1976), persistence and distribution pattern of populations (Hogue and Miller, 1981). Community structure may also be influenced (Menge et. al., 1983). Basically, substratum heterogeneity reduces the impact of "environmental harshness" upon the snails, a process termed "substratum selection" by Gosselin and Bourget (1989). In Wales, the intertidal region is not susceptible to great climatic variations. Sea temperatures are fairly constant, even in winter, which has a mitigating effect on air temperatures, that rarely fall below freezing (Evans, 1957). Summer air temperatures rarely exceed 27 ^{0}C, with a daily mean temperature range between 8 ^{0}C and 14 ^{0}C.

Research background.

The main aim of this study was to determine the distribution and dispersal of *Nucella lapillus* in relation to habitat structure and community composition. This was done by investigating population structure and density along the intertidal physical gradient in relation to major topographical features (including the availability of refuges such as crevices, boulders, algae, and interstices of mussel beds), and how they influenced the foraging activity of dogwhelks. The range of spatial dispersal and timing of foraging activity throughout the tidal cycle, and on a seasonal basis were investigated, as well as temporal changes in diet and feeding habits.

Field studies.

Laboratory experiments have many limitations in ecological investigations. Every environmetal feature of the organism is held constant and biological interactions often excluded (Connell, 1983). In such an artificial situation, it is unlikely that organisms will behave normally. The chief value in field experimentation is that the results can be more directly applied to natural ecosystems, than investigations from laboratory experiments (Connell, 1983). The ideal field experiment is one where one particular factor is manipulated, whilst others vary naturally (Connell, 1983). Therefore all observational and experimental work for this study was undertaken in the field. Prelimininary field trials were carried at one location (Red Wharf Bay), to ascertain optimal methods for sampling and measuring of relevant variables. The patterns of correlation between abundances of *Nucella lapillus* and associated organisms and with environmental parameters was investigated.

General background.

Intertidal muricid gastropods feed on sessile prey. Their habitat requirements are relatively simple, and so manipulative experiments are feasible in the field (Connell, 1961b). The study to determine the movement and ecological impact of dogwhelks was carried out on five shores on Anglesey, North Wales and one nearby on the mainland. These were (with ordnance survey geographical coordinates): Menai Bridge, SH 556 715; Trwyn y Penrhyn, SH 629 795; Red Wharf Bay, SH 574 814; Llanfairfechan, SH 687 758; Porth Nobla, SH 574 814; Porth Defaid, SH 287 857. These study sites were chosen on the basis of accessibility, relative freedom from human interference, and a sufficient dogwhelk population density to enable experimental replication. These sites represent (in ordered pairs) sheltered, semi-exposed and exposed shores respectively. Research involved determining the distribution and dispersal of different life stages of *Nucella lapillus* (size classes) within and between geographical and temporal scales. This involved investigating the reasons for distribution and dispersal (the timing, amplitude and importance of different factors), within specified microhabitats within a shore, on different types of shores, and in relation to tidal and diurnal cycles and seasons. Field data were collected for two-three years to determine the foraging behaviour of *Nucella lapillus* in relation to ontogeny, microclimate, habitat topography, distribution of both prey types and refuges, and interactions with other intertidal organisms. Patterns of foraging, refuging, migration and passive dispersal were followed on daily, weekly and monthly temporal scales. The timing of samples in relation to breeding or non breeding times of the year (when whelks were dispersed), was noted in the same manner as Grant and Utter (1988), in their work on *Nucella lamellosa.*

Specific objectives.

a) To determine population size-frequency distribution, morphological variation and seasonal dispersal of different life-cycle stages of *Nucella lapillus.*

b) To look at the impact of physical environmental factors (desiccation, wave-action and topography) upon movement patterns of *Nucella lapillus* within shores.

c) To compare dispersal and foraging activity of *Nucella lapillus* within and between shores (exposed, semi-exposed and sheltered).

d) To ascertain characteristic microhabitat usage (prey patches and refuges).

e) To investigate the effect of dogwhelks upon the composition of sessile communities (primarily on boulder fields).

N.b. Photographs of field work are presented in Appendix 1 (page 279).

CHAPTER 2

NUCELLA LAPILLUS DISTRIBUTION.

2.1 INTRODUCTION.

Contrary to evidence that species with low dispersal (lecithotrophic development), tend to have a shorter geological record and lesser geographical range (Shuto, 1974) than those with high dispersal capabilities (planktotrophic development) (Hanson, 1978; 1980), *Nucella* spp. have a long fossil history and an extensive geographical distribution (Palmer, 1984a), determined to an extent by the configuration of the continents and oceans (Osman and Whitlatch, 1978). *Nucella lapillus* is found from Nova Scotia to the Southern USA, and along most of the Western Coast of Europe, including Britain and Ireland, wherever it can find lodgement (Cooke, 1915).

The presumed ancestor of *Nucella lapillus* moved into the Atlantic before the start of the last ice age to occupy an unexploited niche, obtaining a wide potential for dispersal and diversification (Crothers, 1983). Sequential advance and retreat of the ice sheets and the attendant rise and fall of the sea level lead to cycles of extinction and recolonization, or separation and subsequent reunion of populations in many areas (Cambridge and Kitching, 1982). Consequently the species is now a combination of several genetically distinct populations separated into a series of breeding enclaves (Crothers, 1992). Great morphological variation is exhibited along the distribution range, due to the restricted migration potential (Ward and Warwick, 1980).

The distribution of intertidal organisms is related in part to abiotic factors (Coleman, 1933; Evans, 1947*)*, that change in amplitude and importance during the tidal cycle (Gosselin and Chia, 1995b). In particular, imersion/emersion and shelter/exposure regimes govern their horizontal and vertical distribution (Lewis, 1976). Local distribution depends upon patterns in hydrography (currents, wave action and substrate formation), and how they affect the dispersal of the reproductive stages, as well as the survival of egg capsules and juvenile stages (Lewis, 1976; Lewis et. al., 1982). Superimposed upon this are the effects of desiccation (Menge, 1978b; Spight, 1982; Garrity, 1984; Yamada, 1977), heat stress (Gosselin and Chia, 1995), dislodgement by waves (Ricketts et al., 1968; Emson and Faller-Fritsch , 1976), and impacts by water-borne debris (Connell, 1961a; Dayton, 1971).

Important biotic factors also affect invertebrate distribution, including algal whiplash (Southward, 1956), bulldozing by grazers (Connell, 1961a; Fletcher, 1987), immobilisation by byssal threads (Petraitis, 1987), predation (Rawlings, 1990), as well as interspecific and intraspecific competition (Connell, 1972). Although the distribution and abundance of animals is often correlated with food, few field experiments have been done to test this association (Connell, 1983). Overall spatial distribution is influenced by feeding habits and patterns and related to relative densities of predator and prey. An individual dogwhelk may spend its entire life within the same small area of the shore (Crothers, 1981a), with the result that populations as a whole are contigously distributed, with a relatively low index of dispersion (Morgan, 1972b).

Horizontal Distribution (along-the-shore distribution).

Nucella lapillus presents as a series of discrete and diversified breeding populations (Crothers, 1981a), although migration levels of only a few individuals per year will be enough to maintain gene frequency over even an extensive geographical range (Lewontin, 1974). This species is capable of persisting under a wide range of physiological and ecological conditions (Palmer, 1984b), and within these broad physical limits, its distribution can be dependent upon the dispersal of its reproductive stages and the suitability of local conditions for the deposition of egg capsules and survival of the juvenile stages. Horizontal distribution is also limited by strong wave-action (Moran, 1985a).

Vertical Distribution

Often in intertidal marine snails there is a vertical size gradient with the mean size increasing upshore (Branch and Branch, 1981; Underwood and Chapman, 1985), such as *Gibbula umbilicalis* (Bakker, 1959) and *Oxystele variegata* (McQuaid, 1980). Specific age-groups occupy distinct tidal levels and this natural age progression is responsible for the natural zonation levels (Coombs, 1973). A similar occurrence is found in many limpet larvae, which also have a tendency to settle in the lower intertidal and move upward (Castenholz, 1961). This is contrary to the patterns of zonation proposed by Vermeij (1972), for low/mid intertidal species, as shown by Paine's (1969b) work on *Tegula funebralis,* which settles mainly at the top of the shore and undergoes age-dependent migration downshore. Differential vertical distribution can also be seen in the series: *Littorina littorea, Littorina littoralis* and *Littorina saxatilis* species complex which inhabit progressively higher intertidal zones, in relation to varying periods of submergence and exposure (Sandison, 1966). This vertical distribution can often obscure the actual patterns of spatial variability in the horizontal distribution of intertidal organisms (Underwood, 1981).

In *Nucella dubia* there was no size gradient between vertical zones, and individuals of all size classes occur in similar numbers up the shore (McQuaid, 1985), with the only distinction being an absence of the largest size classes above the upper balanoid zone. Extensive field studies have revealed distributional differences among the various stages in the life history of *Nucella lapillus* however, that clearly correspond to sequential upshore and downshore shifts in distribution during ontogeny. Different age groups do occupy distinct tidal levels (Moore, 1938; Berry and Crothers, 1968; Lawrence, 1972), worked out in detail by Coombs (1973). Dogwhelks emerging from egg capsules at low-tide-level migrate upshore as they grow, and as subadults return to the mid and low shore (Moore, 1938b). As a result, both the distribution and density of *Nucella lapillus* varies vertically. Early juveniles, subadults and adults are more abundant below mean tide level, smaller and larger juveniles more abundant (marginally) above according to Hughes et. al. (1992). The vertical distribution in different locations also changes: in the Severn Estuary it is almost sub-littoral (Crothers, 1974), in parts of North America, often centered high on the shore (Thomas, 1994). Long term vertical distribution patterns of *Nucella* spp. are associated with change in the season (Connell, 1961a; 1970; Feare, 1970a) and with reproduction (Moore, 1938b; Phillips, 1969; Feare, 1970b; Butler, 1979). The vertical distribution of *Nucella lapillus* is related to the environmental consequences of the tidal cycle. The vertical environment varies along the slope: the upper shore is a high stress environment, with low community diversity and high stability; middle and lower shores exhibit less stress, but have higher diversity and lower stability (Lewis, 1976), the environment changing more rapidly.

Passive Dispersal.

Movements by birds (Zach, 1978), as detached egg capsules (Sebens, 1977), or as hatchlings or juveniles afloat on drifting algae (Crothers, 1981a), are all examples of passive transportation that affect *Nucella lapillus*. Furthermore, drifting on mucous threads, as well as being carried on drift algae or other flotsam may be the way that some juvenile forms are transported from one site to another in *Nucella emarginata* (Gosselin and Chia, 1995b). These methods are probably unimportant in the overall distribution of *Nucella lapillus*, since along with strong wave action (that can move adults) they will deposit individuals in unsuitable areas (above high tide, or sublittorally), where they will not survive, see Palmer (1984a).

Shore classification.

On the west coast of Britain, and including the sudy areas in North Wales, the intertidal Eulittoral Zone (*sensu* Lewis, 1964) of sheltered shores is dominated by clearly defined bands of fucoid algae. On moderately exposed shores, *Fucus* cover becomes more patchy and alternates with areas of barnacles (primarily *Semibalanus balanoides,* some *Chthamalus* spp.), and bare rock interspersed with grazing *Patella* and predatory *Nucella* (Hartnoll and Hawkins, 1980; 1985). These habitats are zoned and dominated by barnacles, blue-green and green algae, with *L. saxatilis* in the upper zone, barnacles in the middle zones. There are fucoids and *Ascophyllum*, barnacles, *Littorina obtusata, L. littorea, Mastocarpus* (perennial red algae), *Chondrus*, and limpets in the lower zone. The balance is tilted in favour of plants, with increasing shelter and at higher latitudes in the mid-shore region. In very exposed conditions grazers and sessile animals dominate most of the Eulittoral Zone, limpets are even more numerous here, and mussels and barnacles dominate the rocks. Small patches of ephemeral algae and small clumps of the stunted bladderless form of *Fucus vesiculous* (*var. evesiculosus*) are common (Hawkins and Hartnoll, 1983a). This overall pattern is modified by small-scale topographic influences (shore aspect, shore profile, pits and crevices) that change over small distances.

On the intertidal rocky shores of Anglesey, patches of barnacles, mussels (and of both) are interspersed with small tufts of algae, bare rocks, stones, shingle and a complex of refuging space in the form of cracks, crevices and under boulder spaces. Size, distribution and abundance of algae, sessile organisms, herbivores and predators, all vary with vertical height about datum and in relation to the presence of other intertidal organisms. Primary space occupants include barnacles, mussels, other bivalves, sponges, ectoprocts, hydroids, holdfasts of erect algae, encrusting algae and lichens. Secondary space is occupied by thalli of *Chondrus*, and other erect shrubby plants. Free space (defined as primary space available for colonisation by barnacles and mussels), including that free from macroscopic organisms, and space occupied by encrusting organisms is constantly being renewed by physical and biological disturbances.

2.2 METHODS.

Hypotheses.

1. The vertical distribution of *Nucella lapillus* changes with season and in extent relative to the wave exposure of a particular shore.
2. The size-frequency distribution of dogwhelks varies with tidal height and shore type.

Data collection was on *Nucella lapillus* distribution and abundance, including population structure and density along the intertidal physical gradient. Six locations were examined: Menai Bridge, Trwyn y Penrhyn, Llanfairfechan, Red Wharf Bay, Porth Nobla, Porth Defaid (see Chapter 1 for geographical coordinates).

Shore classification.

The intertidal region of my study sites, like all other "beaches" in Western Britain are divisible into a number of strips (or zones), each with a distinctive composition of flora and fauna, that form a series from lower to upper shore. The number and extent of these zones varies from shore to shore depending upon a number of factors namely: aspect, slope, degree of exposure (Stephenson and Stephenson, 1972), zonation of littoral animals and plants being primarily caused by the tidal cycle (Southward, 1958). The amount of variation found is the number of subzones can be extensive, due to the extremely sensitive and rapid way zonation responds to the smallest changes in the degree (amplitude), amount, and strength of the wave-action to which a rocky shore is exposed (Stephenson and Stephenson, 1972).

Each study site (shore) was qualitatively described in terms of environmental variation (exposed shores directly faced the prevailing wave direction; sheltered shores were in bays or protected by headlands. The geographical position of each shore (and transects) was determined by use of GPS (Garmin eTrex personal navigator), and at each location an estimate of exposure was obtained from a measurement of the exposure angle (Lewis, 1964). The aspect of the shore was recorded using a field compass, frequency and direction of winds and fetch distance, wind velocity and duration, and the angle that waves hit the shore, were also all noted, as was the general topography of shore (including shore profile, slope, platforms, vertical ledges, and promontories). Slope was also measured along the whole vertical extent (full transect) on all six shores, being calculated in four metres sections, with separate determinations of dogwhelk distributions in the low, middle and upper shore levels. Percentage slope (vertical change) was calculated relative to the horizontal, so that a flat horizontal surfaces would be designated as 0%. In addition the Biological Exposure Scale (Ballantine, 1961) was used to give a qualitative value of wave-exposure (Burrows et. al., 1954). Other information was obtained from the meterological office at Valley, Anglesey, from fetch maps and synoptic weather charts of the North Atlantic (Darlyshire and Draper, 1963). Local wave heights were calculated from prediction tables (Demetropoulous, 1965), and the depth of water from maritime charts.

At each study shore, low tidal heights were calculated using a conversion factor C (calculated by measuring tidal range by observation), the height at Holyhead (nearest published records), and MSL at Holyhead by using the equation:

$$LT = MSL - C\,(MSL_H - LT_H)$$

Where: LT= Low tide height above chart datum at the study site; MSL=Mean shore level at the study site; MSL_H= Mean shore level at Holyhead (Admiralty tide tables); LT_H = Low tide height above chart datum at Holyhead. Low water level at each study shore was then used to determine the height above chart datum for each study area in conjunction with Menai Strait Tide Tables (Sherwin, 1996; 1997; 1998).

Submersion.

Relative percentage submersion times (the comparative time study sites are under water) were calculated for different levels on different shores using values for MSL, LW, MLWS, MLWN, MHWN and MHWS based on diurnal and lunar sinusoidal plots. The duration of submersion of points along the shore was calculated using published tide tables assuming the tide rose and fell between high and low levels following the sine-curve.

Insolation Index.

The Insolation Index (I), which was taken from a modification of Moran (1985a), by Rogers (1988), was calculated as:

$$I = \sin ((T-Dw)pie/2)\ 1/(Du-Dw/2)$$

where T = time of low tide; Dw = time of sunrise; Du = time of sunset.

Transects.

Temporal patterns in the utilisation of space by plants and sessile animals and in the densities of mobile animals was quantified by a transect-quadrat method (Fuji and Nomura, 1990). Periodic transects (Menge, 1972a; 1976), were used to determine the distribution of the different life-cycle stages of dogwhelks. Ten 0.25 m^2 quadrats were placed at randomly determined sites along a 30 m line parallel to the water's edge. The line was placed at approximately the same tidal level each time (Lubchenco and Menge, 1978). The abundance of sessile species was estimated by placing A4 transparencies bearing 100 randomly plotted dots over the substratum and counting the number of dots whose projection hit a particular species.

Determination of horizontal distribution.

The whole coastline of the Island of Anglesey was included in a study to investigate dogwhelk distribution along the shore. The information gathered was used in interpreting results of field observation and experimentation on shell shape (Chapter 3), dispersal and foraging (Chapter 4), association with various microhabitats (Chapter 5), and interactions with sessile fauna and flora (Chapter 6).

Determination of vertical distribution.

Two complete contiguous-quadrat, full-shore vertical transects (MLWS - MHWS) of the distribution of *Nucella lapillus* and other organisms (algae, limpets, snails, sea anemones etc.) were made at each of the six shores once every two months. *Nucella* abundance, and size frequency (shell length), were assessed along the transect line. Within each quadrat the broad distribution of flora and fauna, particularly barnacles, mussels and *Nucella lapillus,* in respect to algal cover, and refuges was recorded, in otherwords a microhabitat diagnosis (Kitching et. al., 1966). The activity of individual *Nucella lapillus* was recorded. Specifically foraging (presence on barnacle or signs of penetration if on a mussel), prey choice (species and approximate size), inactive (on bare rock, in crevice or under boulder), breeding (next to egg capsules), occupied habit (crevice, open rock, beneath algal canopy or on prey), and topography (rock, boulder, rock with algal canopy or sediment).

Size-frequency distribution.

Each quadrat was carefully searched and shell height of all dogwhelks was measured to 0.01mm. Dogwhelks were initially assigned to twenty size classes, from 2-3.9 mm to 40-41.9 mm. However, for stastistical purposes, whelks were put into four major groups: 2.0-11.9 mm (early and smaller juveniles), 12.0-21.9 mm (larger juveniles and subadults), 22.0-31.9 mm (adults), and 32.0-41.9mm (larger adults), and the distribution of these size-classes along the transect compared.

Survey for Nucella egg-capsules.

A survey of egg-capsule deposition sites (spawning sites) was undertaken at different shore levels once every two months. The numbers of capsules per aggregation, as well as position of clutch - whether on bare rock (horizontal/vertical surface), nestled against other organisms, or inside empty barnacle tests. The degree of canopy cover and the vertical and horizontal angle of exposure (to uv radiation) was also noted. As many of these sites that could be found in one low tide were mapped.

Sampling methods.

Ecological sampling may involve significant disturbance for dogwhelks and their prey on boulders (Connell, 1978). Therefore all counting and measuring in quadrats, was carried out with little or no handling (Chapman and Underwood, 1996), to reduce disturbance to negligible levels (Putnam, 1995). It is difficult to estimate the population densities of *Nucella* spp. on boulder fields, due to their tendency to retire into refuges, particularly during daytime exposure to air during low tides

(Garrity and Levings, 1981), or to copulate and lay egg capsules. Dogwhelks become aggregated in food patches and in response to environmental heterogeneity (Berry, 1983), which often makes accurate density estimation difficult (Frank 1965). Therefore representative samples were also taken from each microhabitat type within the boulder fields, and sampling carried out for a fixed time period (one hour per habitat; a total of four hours per shore level). That is: stratified random sampling, using a total of 200 m^2 quadrats, partitioned equally among habitats, and characterized according to exposure to wave action, shore level and aspect (Hughes et. al., 1992).

Statistical analysis.

Variables were examined for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). Where normality was borderline or in doubt, non-parametric (Kruskal-Wallis) analyses were carried out in addition to the usual GLM ANOVA test with post-hoc Bonferroni examination (or Tukey test if data sets large) of differences between means.

2.3. RESULTS.

2.31. Shore description and classification.

2.311. Observations.

Menai Bridge.

This was a very sheltered site, within steep walls that form a natural amphitheatre protecting the area from the brunt of any wind and waves. Intertidal benches were found in the upper zone, and at one side (at seaward) of the study area, with overhangs, depressions and landward faces sheltered from the full force of the waves, providing localised shade. The study area was only subject to strong and periodic currents from one direction, and consisted of mainly small-medium boulders with some small and one or two medium-sized boulders. *Ascophyllum nodosum*, is regarded as a biological indicator of sheltered conditions in western Britain (Crothers and Hayns, 1994), and was abundant in this location. In those areas devoid of *Ascophyllum*, barnacles were common. Shore crabs (*Carcinus maenas*) were extremely common (throughout the shore, especially in lower and middle levels) under boulders, and often took small dogwhelks (personal observation).

Trwyn y Penrhyn.

This shore was mostly sheltered, but occasionally subject to strong winds from the direction of the mainland. The study area was protected by small boulder areas on either side, and benches in the lower-upper shore, but still experienced periodic heavy waves. Large areas of sand, resulted in many individual boulders being isolated. On this shore there was a variety of boulders, with some large, many medium, and many small boulders forming the bulk of the available substrata. Barnacle densities were variable, rarely high, and *Semibalanus balanoides* was most common in the middle zones. Due to lack of large substrate formations, organisms were subject to insolation and confined beneath boulders, whilst periodic and mainly seasonal rough weather produced the same effect on dogwhelk distribution. Shore crabs were periodically abundant in the lower levels, but limited to a clumped distribution in mid shore levels.

Llanfairfechan.

Located on the edge of Menai Strait, this shore appears to be more exposed than Trwyn y Penrhyn. Open to wind, and to waves, there were no protective benches nor any sheltering promontories. However, heavy waves were uncommon due to the presence of both Anglesey and Puffin Islands, between this site and the usual directions waves reached this part of the North Wales shoreline. The lower part of this shore was sand, but the middle and upper regions contained some very large boulders, as well as many large, medium and small ones. All boulders were covered with barnacles (*Semibalanus balanoides*), with some of the highest densities seen in this study area, and the majority of boulders had an extensive top covering of mussels. Predatory shore crabs were present in low to moderate numbers, mainly confined to lower (and to a lesser extent mid-shore) levels.

Red Wharf Bay.

This location was open to the sea but protected to some extent by the jutting coastline to the North-West. Heavy waves were more common here than Llanfairfechan, especially during the winter months and overall more frequent. The rock substrata within the study area was comprised solely of boulder formations that were extremely variable and patchy in composition, even on a localised scale. This consisted of a few large boulders, as well as many medium and small ones. This mixture gave way to large boulders and small stones on a base of coarse gravel in the upper zones, where rocks were frequently smoothed and polished by the moving shingle. Mid-shore levels were dominated by grazing molluscs and sessile barnacles. *Carcinus maenas* were occasional to rare, and practically limited to the lower echelons of the shore.

Porth Nobla.

Porth Nobla was exposed to the open sea with an extensive fetch in many directions. The South-West coastline of Anglesey was fully exposed to the prevailing onshore winds (Lintas and Seed, 1994). The low shore was comprised mainly of rock bench, the mid shore boulders, and the upper shore again consisted mainly of rock benches. This provided a degree of protection in some areas, with a large difference in wave-exposure apparent betwen shore levels. Large waves were common, with extreme waves in Winter. The lower part of the shore consisted of bedrock, giving way to boulders just below mid-tide. At higher levels these gave way to fine stones and gravel from which the bedrock emerged again at the top of the shore. The rocks here are weathered into jagged reefs and ledges, that strike and dip, and vary considerably with the angle of slope ranging from the horizontal to the vertical. The irregularity of the rock configuration results in local variation in microhabitat type, with many pools, creeks, and gullies. Anemones and encrusting sponges were common in these refuges. Shore crabs were noticeably rare at this site, found only near low tide.

Porth Defaid.

This study location was very exposed to the open sea, and large waves were common even during the Spring and the Autumn. There was moderate wave-action in Summer, though still greater than on other shores. The rocky headland here is particularly exposed to prevailing winds, to which there was no protection in the study areas (all benches at all three shore levels). The degree of exposure was different at different shore levels but the disparities were less than at Porth Nobla. The varied structural topography of the rock platform: flat benches, rough pitted and eroded slopes, vertical faces, crevices and surge channels, created a maze of refuges within the benches and ledges, which was needed by the intertidal organisms to shelter from the extensive wave-action experianced by this site. Shore crabs were extremely rare and only seen one or two times during a three year period.

2.312. Shore characteristics (physical).

A number of environmental factors were determined for the six study shores, namely: compass orientation and direction of wave impact (Table 2.1), fetch distance (Table 2.2: the maximum distance waves from the open sea may travel from before impacting on the target shore from various directions), wave height (Table 2.3) and wave force (Table 2.4). Also, the relative percentage of submersion along the vertical of the shore (Figure 2.1), the relative Insolation Index (Table 2.6; Figure 2.2.A), air temperatures (Figure 2.2.B), and inshore water temperatures (Figure 2.2.C), were recorded on the six study shores from month to month. All these parameters were calculated from field determination and observations, charts, and the relevant tide tables.

Table 2.1. Compass direction of study shores and direction from which waves hit the shore.

Degrees	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
shore	250	150	340	356	266	302
waves	268	220	340	300	266	280
wave range	262-270	160-240	330-007	290-340	252-274	268-284

Data presented are shore direction, direction of origin of waves with range of directions (all degrees). 0=360=due North.

Table 2.2. Estimation of fetch distance for the six study shores.

Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Dg.	Dt.	Dg.	Dt.	Dg.	Dt.	Dg.	Dt.	Dg.	Dt.	Dg.	Dt.
140	2.3	130	15.3	040	65	030	90	200	25	220	5000
160	0.8	150	5.8	310	8	330	3	230	6000	330	60
180	1.2	170	8.9	330	45	350	100	330	90	350	2000
Mean	1.43	Mean	10.0	Mean	39.3	Mean	64.3	Mean	2038	Meane	2533

Data presented are degree angle of fetch (Dg), with distance of fetch in miles (Dt), and mean fetch distance (of the three).

Table 2.3. Wave height observations on the six study shores.

Metres	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
minimum	0.02	0.10	0.20	0.35	0.38	0.42
maximum	0.56	1.54	1.98	2.44	2.56	3.15
mean	0.24	0.36	0.51	0.58	0.66	0.79

Data presented are wave height observations (in metres) with an annual mean calculated from monthly figures of this parameter.

Table 2.4. Relative wave force readings from the six study shores.

Wave force	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
minimum	2	3	5	7	9	12
maximum	12	18	24	26	30	30
mean	6	9	12	14	18	22

Data presented are unmodified distance moved by indicator (cm) on a modified marine dynamometer indicating maximum force of the waves over a given time period (one week).

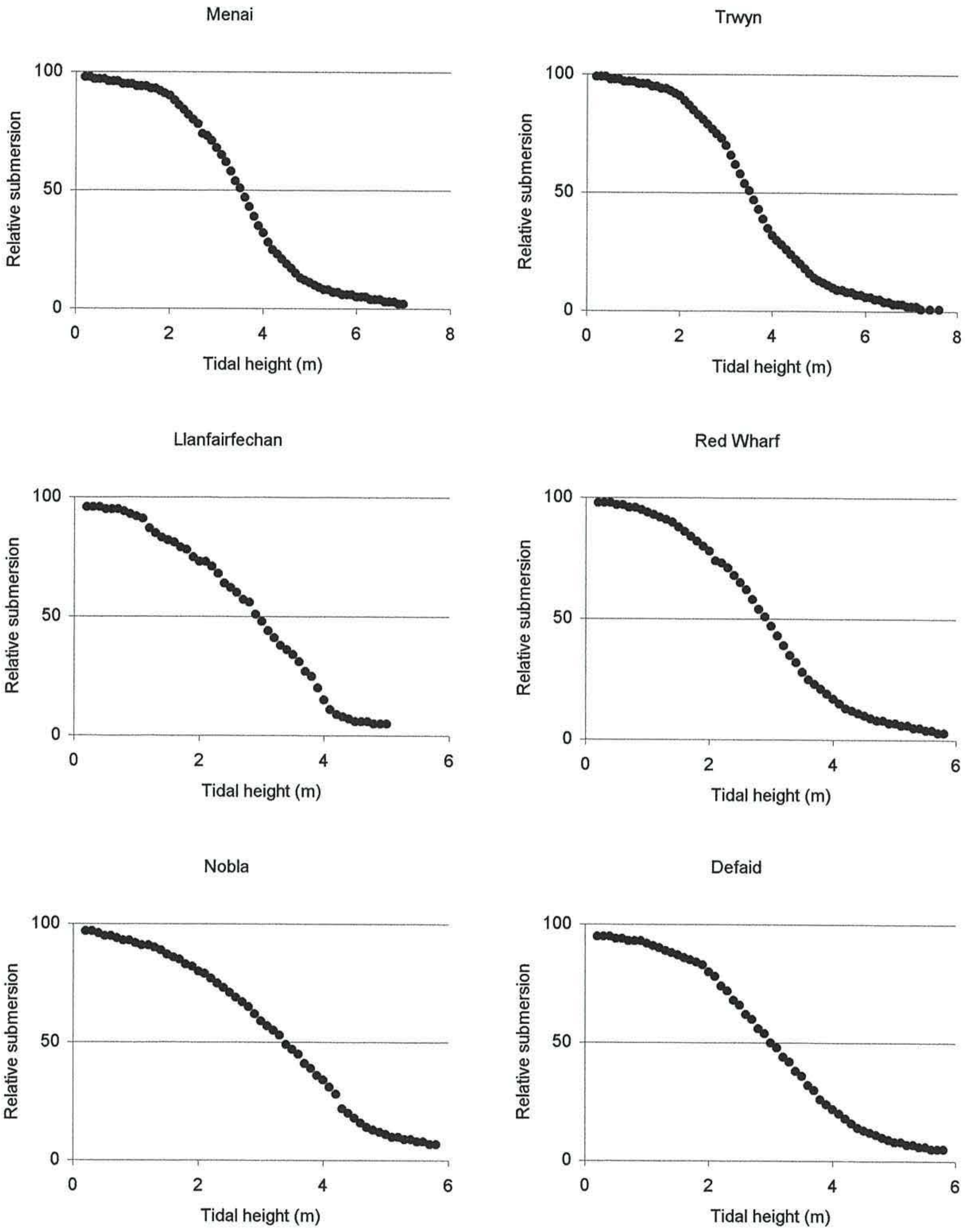


Figure 2.1. Relative percentage submersion (compared to low tide level) with tidal height, during one full tidal cycle.

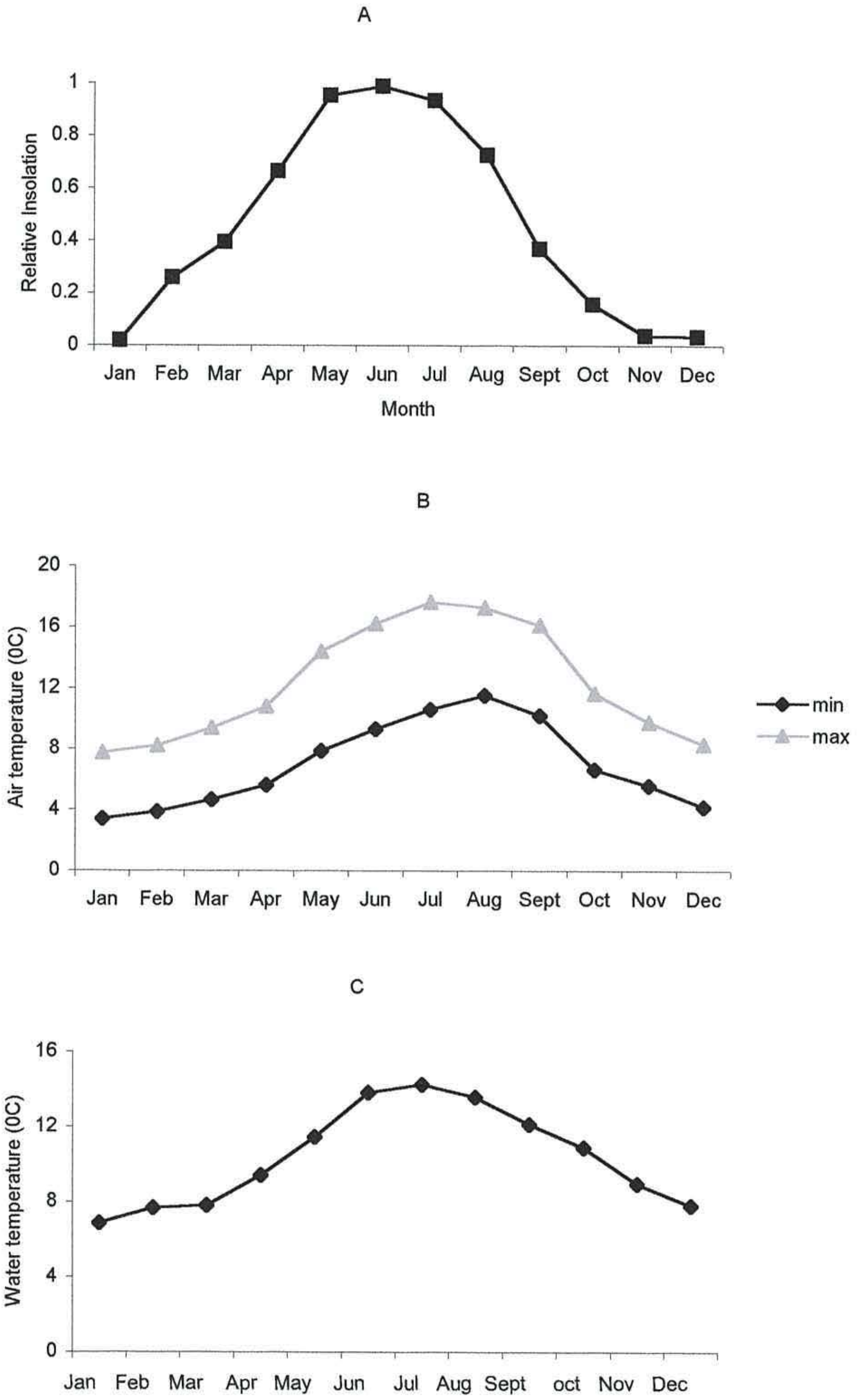


Figure 2.2. Monthly mean insolation values (A), air temperatures (B), and inshore water temperatures (C), for all the study areas (from April 96 to March 99).

Table 2.5 Measurements of percentage slope (vertical drop/horizontal distance), highlighting the slope at the three shore levels within the distribution of dogwhelks.

Slope (%)	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
Whole shore	9.98	5.68	2.03	3.92	3.62	6.92
Whelk areas	8.97	4.86	2.11	5.25	2.13	5.21
Low shore	11.89	5.60	0.35	6.33	2.53	9.33
Mid shore	7.49	5.03	2.35	6.04	2.06	4.50
Upper shore	9.50	5.10	5.70	5.08	2.52	3.22

Data presented represent the vertical change (m) over horizontal distance (m), expressed as a percentage; a flat horizontal surace having a zero slope.

Insolation Index.

The Insolation Index (I) was found to be significantly affected by month (GLM. F=5.820 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between some months (Table 2.6).

Table 2.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in Insolation Index between different months.

Months	*P*	Months	*P*	Months	*P*	Months	*P*
1-5	0.002	1-6	0.001	1-7	0.002	1-8	0.038
5-10	0.027	5-11	0.004	5-12	0.003	6-10	0.014
6-11	0.002	6-12	0.001	7-10	0.034	7-11	0.005
7-12	0.004						

Data presented are monthly pairs and probabilities (P) which are all significant values.
Key: months 1-12 are January through December respectfully.

2.313. Shore characteristics (biological).

The degree of wave exposure experienced by the different study shores was determined using selected components of the classic exposure scale developed by Ballantine (1961). See Tables 2.7, 2.8, and 2.9 overleaf.

Table 2.7. Results of Ballantine Exposure Scale Observations for Meni Bridge and Trwyn y Penrhyn.

	Menai Bridge	Trwyn y Penrhyn
General observation	permanent fauna beneath stones	fauna under most stones
Laminaria digitata	present, not common	common
Pelvetia and *F. spiralis*	rare	*Pelvetia* frequent, *spiralis* common
Ascophyllum nodosum	covers most of midlittoral	isolated short plants only
Semibalanus balanoides	frequent	common but fucoid incursion
P. vulgata	common, often very large	abundant in midlittoral
L. littorea; L.obtusata	abundant; abundant	both frequent on fucoids
Mytilus edulis	none	none
Gibbula sp.	common	rare to occasional
Nucella lapillus	common, shells are long and thin	common
Shore exposure	very sheltered to sheltered	sheltered to fairly sheltered

Table 2.8. Results of Ballantine Exposure Scale Observations for Llanfairfechan and Red Wharf.

	Llanfairfechan	Red Wharf Bay
General observation	semi-permanent flora and fauna on stones	large stones rarely moved
Laminaria digitata	none	common to abundant
Pelvetia and *F. spiralis*	none	*Pelvetia* occasional, *vesiculosus* rare *serratus* occasional
Ascophyllum nodosum	none	none
Semibalanus balnoides	abundant and dominant over all midlittoral	abundant and dominant over most of the midlittoral
P. vulgata	abundant	abundant and dominant
L. littorea; L.obtusata	abundant; none	localised; rare
Mytilus edulis	common	frequent
Gibbula sp.	none	rare
Nucella lapillus	abundant	common to abundant
Shore exposure	fairly sheltered to semi-exposed	semi-exposed

Table 2.9. Results of Ballantine Exposure Scale Observations for Porth Nobla and Port Defaid.

	Porth Nobla	Port Defaid
General observation	occasionally receive very heavy waves	few calm days
Laminaria digitata	abundant, dominant	abundant, dominant; *Alaria* present
Pelvetia and *F. spiralis*	*F. vesiculosus f. eviculosus*, *Pelvetia* and *F. serratus* rare	*F. vesiculosus f. eviculosus* rare, other fucoids efffectively absent
Ascophyllum nodosum	none	none
Semibalanus balnoides	abundant and dominant over lower midlittoral	common but fucoid incursion
P. vulgata	abundant and dominant over all midlittoral	common to abundant
L. littorea; L.obtusata	abundant in localised areas;very rare	none; none
Mytilus edulis	none	none
Gibbula sp.	few	rare and localised
Nucella lapillus	common	frequent
Shore exposure	exposed	very exposed

Preliminary survey of coverage on the boulder fields of the six study shores.

The sheltered shores (Menai Bridge and Trwyn y Penrhyn) showed the highest coverage of mature barnacles, and the most exposed shores (Porth Nobla and Porth Defaid) the lowest. Llanfairfechan and Porth Nobla had by far the most immature barnacles; whilst at the extremes of the wave exposure gradient, the most sheltered shore (Menai Bridge) and the most exposed (Porth Defaid) had only small numbers of mature barnacles. Mussels were only found on the moderately exposed shores such as Llanfairfechan with 6.5 % coverage, and Red Wharf Bay with only 1.5 % coverage. The approximate algal coverage was as follows: Menai Bridge 4%; Trwyn y Penrhyn 3.5%; Red Wharf Bay 5.3%; Porth Nobla 3%; Porth Defaid 0.3%, whilst no algae at all was found at Llanfairfechan during a three year period. Bare rock comprised between 6-12 % of substratum content at the three most sheltered shores (Menai Bridge, Trwyn y Penrhyn and Llanfairfechan) some 12-15 % at Red Wharf Bay and Porth Nobla, and over 80 % at the extremely exposed Porth Defaid.

2.32. *Nucella lapillus* survey.

2.321. Horizontal and transect (approxmates vertical) distribution.

The survey of *Nucella lapillus* distribution (Horizontal) around Anglesey revealed the wide range of this gastropod in relation to a variety of habitats it occupied. Given the essential pre-requisite of presence of prefered prey items, *Nucella* was found on most rock substrata between MTL and MHWN and occasionally even higher. The presence of sand, mud or shingle surrounding such substratum did not preclude viable enclaves of dogwhelks in these areas. Highest abundances were found at moderately exposed locations, particularly on boulder fields or large rock outcrops that had a profusion of refuge microhabitats. Exposed sites had moderately high densities of *Nucella*. Sheltered areas with high densities of fucoids and *Ascophyllum nodusum* are visibly devoid of dogwhelk populations to a greater extent, due to the whiplash effect of the algae, crab predation, profusion of sand, and most importantly the absence of suitable substratum. The sites sampled (including their map reference) during the survey of horizontal distribution of *Nucella lapillus*, along wth mean dogwhelk shell length, shape and relative density are shown in Appendix 2 (Table 2.1). Transect distribution of *Nucella lapillus* on the main six study shores is shown in Table 2.10.

Table 2.10.Transect Distribution of *Nucella lapillus*.

Mean (m) distribution	Menai Bridge	Trwyn y Penrhyn	Llanfairfechan	Red Wharf Bay	Porth Nobla	Porth Defaid
May	21-70	27-236	1-60	28-75	71-194	90-168
July	21-71	14-236	7-65	35-73	91-162	101-145
September	24-71	22-238	3-65	19-67	69-193	91-153
November	29-73	28-232	6-61	31-62	74-183	94-166
January	20-71	31-227	8-57	35-60	91-182	97-163
March	23-71	20-210	2-60	27-72	92-186	92-168

Data presented are mean transect ranges in metres measured along the substratum from the top of the shore.
Based on observed means. Two transects per shore per sampling month.

2.33. Variation in topography, microhabitat and *Nucella* activity within transects.

2.331. The effect of month on transect characteristics.

The value of particular shore transect characteristics, namely: topography, microhabitat and activity of *Nucella* were found to be significantly influenced by month on every shore when analysed by ANOVA (Table 2.11). Post Hoc Bonferonni paired multiple comparisons for Topography, Microhabitat and Activity showed significant differences between most months (see Appendix 2: Tables 2.2 , 2.3 , 2.4 , 2.5 , 2.6 , 2.7). A subsequent non-parametric (Kruskal-Wallis) test of these same data gave exactly the same result (see Appendix 2, Table 2.8),

Month and topography.

The topography of the transects sampled did not change much from month to month, except for the slightly higher proportion of boulders were included in the transects for January and May (Trwyn, Nobla and Defaid), July and September (Menai,Trwyn), and November to March (Llanfairfechan and Nobla). Porth Defaid still had 20 times less boulder surface than horizontal rock surfaces, at these time however. Topography types present on the shores included: boulder, rock (bench and other platforms), sand and rock pools, as well as boulders with algae and rock surfaces with algae.

Month and microhabitat.

At Menai Bridge and Trwyn y Penrhyn, dogwhelks were found in higher proportions under boulders or in crevices, compared to on top of the rock substrate (in both Summer and Winter), and in Winter at Llanfairfechan, Red Wharf Bay and Porth Defaid. Porth Nobla showed no significant differences between the months studied. Microhabitat types present included: on boulder, under boulder, in pit or crevice, and under algae.

Month and activity.

Most dogwhelk foraging was seen in September and May on all shores with also significant numbers of individuals active in July at Menai Bridge (under algae which was extensive), and Porth Defaid, which is very exposed and subject to wave splash throughout the year. On all shores a higher proportion of *Nucella* were refuging during the Winter period November to January, and at Llanfairfechan, Red Wharf Bay, (which are moderately exposed and exhibit low algal coverage), and Porth Nobla (exposed), substantial numbers of whelks were also refuging at the hottest time of the year in July. Activity types included: foraging, refuging, and spawning.

Table 2.11. Results of ANOVA (GLM) showing differences in Topography, Microhabitat and Activity between months.

	Topography		Microhabitat		Activity	
Shore	*F*	*P*	*F*	*P*	*F*	*P*
Menai Bridge	15.827	< 0.001	14.401	< 0.001	35.507	< 0.001
Trwyn y Penrhyn	12.966	< 0.001	24.466	< 0.001	6.859	< 0.001
Llanfairfechan	13.288	<0.001	3.334	0.005	16.398	< 0.001
Red Wharf Bay	4.101	0.001	4.836	< 0.001	19.965	< 0.001
Porth Nobla	322.841	< 0.001	22.608	< 0.001	45.093	< 0.001
Porth Defaid	33.101	< 0.001	15.842	< 0.001	21.014	< 0.001

Data presented are F-values (F), with probabilities (P) which are all significant values.

2.332. The effect of shore level on transect characteristics.

The values of particular shore transect characteristics, namely: topopgraphy, microhabitat and activity of *Nucella* were found to be significantly influenced by shore level in most cases and found not to be significantly influenced for Microhabitat at Llanfairfechan and not to be significantly associated with *Nucella* activity at Llanfairfechan and Porth Defaid. (Table 2.12). Post Hoc Bonferonni Paired Multiple Comparisons for Topography, Microhabitat and Activity showed significant differences between most months (Appendix 2, Tables 2.9, 2.10, 2.11, 2.12, 2.13, 2.14). Non-parametric (Kruskal-Wallis) test of these data gave exactly the same result (see Appendix 2, Table 2.15), except that Microhabitat at Llanfairfechan was seen to be influenced by shore level in this test.

Shore level and topography: Menai Bridge was the only shore to have the most extensive boulder fields at the very lowest shore levels, with Trwyn y Penrhyn, more boulders were present at the lower middle zone, whilst both had more bench substrate at upper levels. At Llanfairfechan all middle areas had many boulders; whilst the three most exposed shores: Red Wharf Bay, Porth Nobla and Porth Defaid, had more boulders in the upper and middle-upper intertidal regions. Nobla and Defaid transect were mainly comprised of rock benches.

Shore level and microhabitat: microhabitat availability tended not to vary significantly with transect station (height). The availability of refuges largely followed the presence of boulders along the different parts of the vertical transects, although Porth Nobla had large numbers of refuges in the lower shore. Variability in Microhabitat availability at Llanfairfechan was minimal.

Shore level and activity: Most foraging occured at the lowest levels on most shores, except for Trwyn y Penrhyn and Porth Nobla, where it was highest at the upper middle zone of *Nucella* distribution. Spawning was commonest at lower levels, absent in some cases at higher transect stations. Refuging increased with the level of the transect station, being much higher in the upper zone of *Nucella* distribution.

Table 2.12. Results of ANOVA (GLM) showing differences in Topography, Microhabitat and Activity between shore levels.

	Topography		Microhabitat		Activity	
Shore	*F*	*P*	*F*	*P*	*F*	*P*
Menai Bridge	9.729*	< 0.001	2.905*	0.013	5.431*	< 0.001
Trwyn y Penrhyn	9.716*	< 0.001	2.625*	< 0.001	0.714*	< 0.001
Llanfairfechan	20.736*	<0.001	2.876	0.130	1.696	0.132
Red Wharf Bay	11.774*	< 0.001	25.819*	< 0.001	5.899*	< 0.001
Porth Nobla	133.854*	< 0.001	31.663*	< 0.001	19.502*	< 0.001
Porth Defaid	28.650*	< 0.001	2.910*	0.013	0.404	0.846

Data presented are F-values (F),with probabilities (P). * which are significant values.

2.333. The effect of shore on transect characteristics.

GLM ANOVA analysis showed significant differences between shores for Topography (GLM 1006.388 P=<0.001), Microhabitat (GLM 1400.836 P=<0.001), and Activity (GLM 209.010 P= <0.001). Non-parametric (Kruskal-Wallis) test of this data showed corroborative significant differences between shores for all three of these parameters at all shore levels. However there were too many data cases to be analysed all at once by Kruskal-Wallis, so results had to be categorised into shore levels before analysis (Appendix 2, Table 2.16).

Topography: Menai Bridge had more rock benches, and substrata were covered with algae at all levels. Trwyn y Penrhyn, Llanfairfechan and Red Wharf Bay consisted almost entirely of boulderfields; the former with large regions of sand throughout the vertical distribution, the latter two with interspersed but sparse sand and rock pools. Porth Nobla is chiefly rock benches, but with an extensive boulder field in the mid shore. Porth Defaid is virtually all rock platforms, with very few boulders.

Microhabitat types: the availability of microhabitats varies necessarily in conjunction with the variation in topography above, with a distinctive higher proportion of crevices and pits on the two most exposed shores. The proportion of algal refuges increased with increasing shelter (no algae at Llanfairfechan).

Activity types: higher proportions of foraging dogwhelks were found at Llanfairfechan and Red Wharf Bay, followed by Porth Nobla and Trwyn y Penrhyn. Lower numbers were found at Menai Bridge and Porth Defaid. These trends in animals were similar for spawning, although the proportion of refuging animals was reversed in order, being higher at Porth Defaid..

2.34. Variation in size (shell length) with regard to topography, microhabitat, *Nucella* activity, transect and transect station. The overall trends in shell length in relation to these transect characteristics are depicted graphically in Figures 2.3, and 2.4.

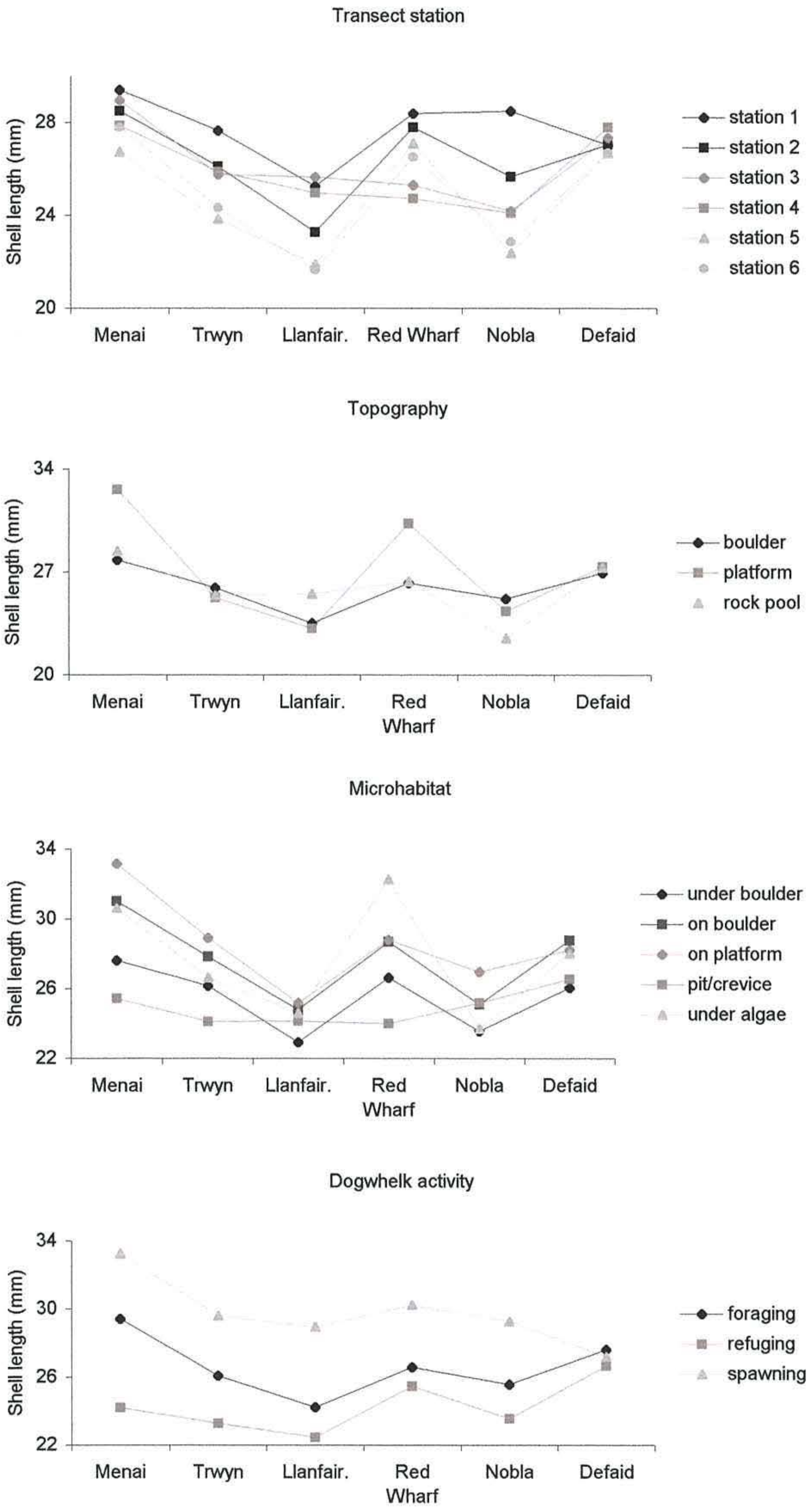


Figure 2.3. Variation in mean shell length with respect to transect station, topography, microhabitat and *Nucella lapillus* activity.

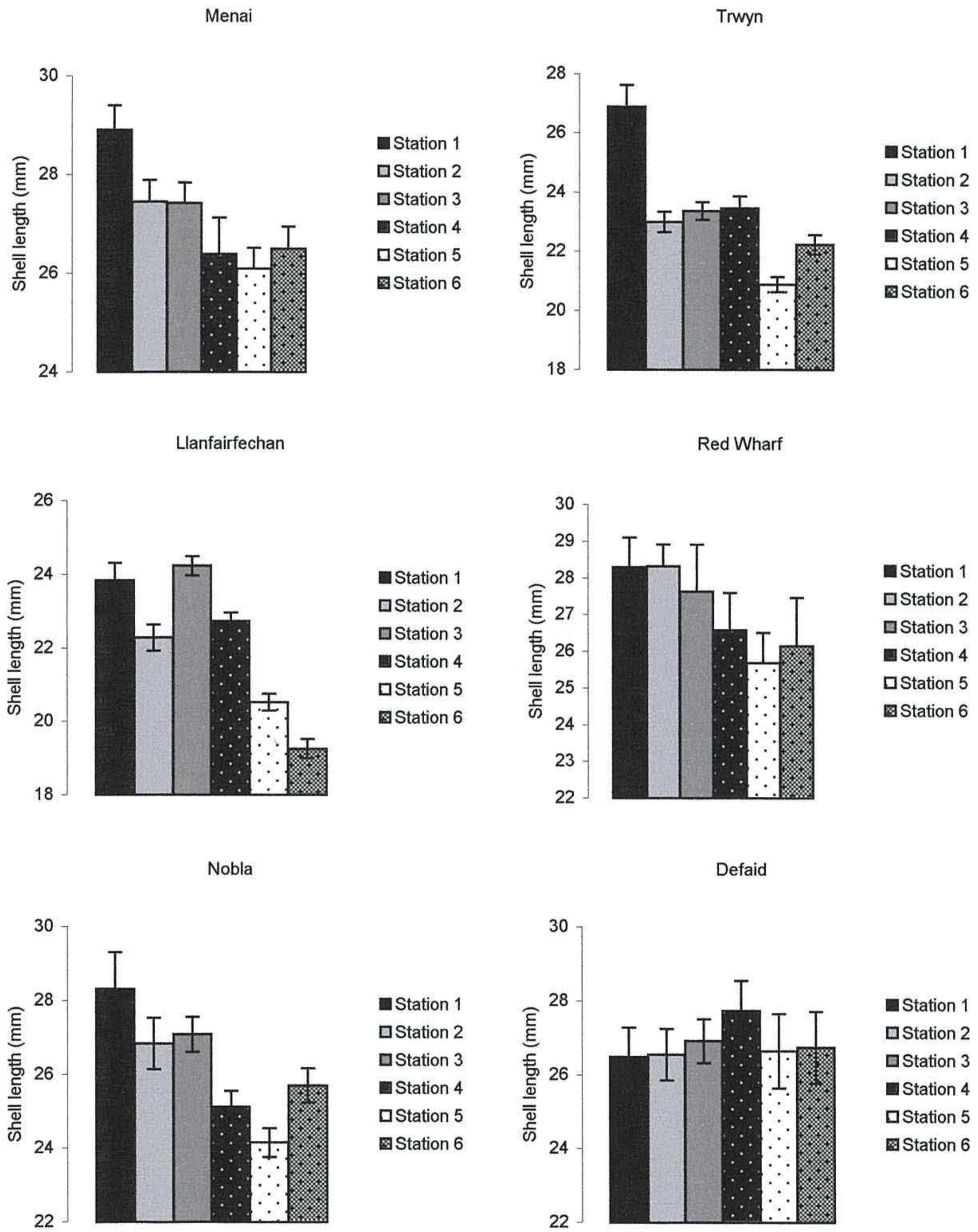


Figure 2.4. Mean shell length of *Nucella lapillus* at successive transect stations (1: low shore to 6: upper shore inclusive).

Key to Figures: Transect stations 1-6 - progressively low shore to upper shore. Topography: 1 - boulder; 2- rock platform; 3 - rock pools. Microhabitat types: 1- under boulder; 2- on boulder; 3 - on rock platform; 4 - in pit or crevice; 5 - under algae. Activity types: 1- foraging; 2 - refuging; 3 - spawning.

2.341. Shell size in relation to topography.

The size (shell length) of *Nucella* was found to be significantly influenced by topography at Menai Bridge (GLM. F=6.914 P=0.015), Trwyn y Penrhyn (GLM.F=8.762 P= 0.042), Llanfairfechan (GLM. F=5.391 P=0.005), Red Wharf Bay (GLM. F=5.620 P=0.004), and Porth Nobla (GLM. F=4.174 P=0.023), but not significantly influenced by topography at Porth Defaid (GLM.F=1.779 P=0.151). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between topography on the following shores (Appendix 2,Table 2.17): at Trwyn, those found on boulders were the largest, whilst at Menai, Red Wharf and Nobla, dogwhelks on the rock platforms. In addition, at Llanfairfechan the mean longest shells were of those individuals found within rock pools.

2.342. Shell size in relation to microhabitat.

The size (shell length) of *Nucella* was found to be significantly influenced by microhabitat at Menai Bridge (GLM. F=8.187 P=<0.001),Trwyn y Penrhyn (GLM. F=4.871 P=< 0.001), Red Wharf Bay (GLM. F=6.923 P= <0.001), and Porth Defaid (GLM.F=6.415 P=<0.001), but not significantly influenced by microhabitat at Llanfairfechan (GLM. F=2.291 P=0.057), and Porth Nobla (GLM.F=1.379 P=0.239). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length between microhabitats on the following locations (Appendix 2, Table 2.18). On all shores the same trends were apparent: larger dogwhelks were found in the open on rocks and boulders, then those under algae and under boulders and finally the smallest forms generally being in crevices.

2.343. Shell size in relation to activity.

The size (shell length) of *Nucella* was found to be significantly influenced by activity at Menai Bridge (GLM. 19.697 P=<0.001),Trwyn y Penrhyn (GLM. F=18.288 P=<0.001), and Llanfairfechan (GLM. F=15.256 P= <0.001), but not significantly influenced by activity at Red Wharf Bay (GLM. F=2.035 P=0.132), Porth Nobla (GLM. F=2.704 P=0.067), and Porth Defaid (GLM.F=0.098 P=0.907). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length for different activities at the following sites (Appendix 2, Table 2.19). On all shores but one, spawning *Nucella* were significantly larger than foraging whelks, which were larger than refuging animals. The exception was Defaid where foraging dogwhelks had the longest shells (refuging individuals were still the smallest).

2.344. Shell size in relation to transect.

The size (shell length) of *Nucella* was found to be significantly influenced by transect at Menai Bridge (GLM. F=11.518 P=<0.001), and Red Wharf Bay (GLM. F=38.019 P=<0.001), but not significantly influenced by transect at Trwyn y Penrhyn (GLM.F=0.465 P=0.495), Llanfairfechan (GLM.F=0.783 P=0.376), Porth Nobla (GLM.F= 0.538 P=0.464), and Porth Defaid (GLM.F=0.144 P=0.705). On Menai Bridge mean shell length of *Nucella* on transect 1 was 27.04 mm, on transect 2 it was 29.08 mm. At Red Wharf Bay the mean shell length of transect 1 was 25.02 mm, for transect 2, 28.35mm.

2.345. Shell size in relation to transect station.

The size (shell length) of *Nucella* was found to be significantly influenced by transect station at Trwyn y Penrhyn (GLM. F= 2.373 P=0.037), Llanfairfechan (GLM. F= 4.863 P=<0.001), and Red Wharf Bay (GLM. F=3.391 P=0.005), but found not to be significantly influenced by transect station at Menai Bridge (GLM.F=0.535 P=0.750), Porth Nobla (GLM. F=0.716 P=0.612), and Porth Defaid (GLM.F=1.460 P=0.202). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between the following levels (Appendix 2, Table 2.20). Five of the shores investigated followed the same pattern in size distribution: the largest snails were found at the lowest shore level, and the mean shell length got progressively shorter through the mid shore and into the upper shore location. At Defaid however the average size of *Nucella* in the mid shore areas was greatest, followed by the lower shore stations.

2.35. Size frequency investigation: proportion of *Nucella* in each size class.

The proportion (percentage) of some of the the different size classes (see key in the methods, page 15), were seen to be different on different shores (Table 2.13). Similar results were obtained by non-parametric testing (Kruskal-Wallis) of the same data (Appendix 2, Table 2.21). Overall size-frequency distributions at three shore levels (low, medium and upper shore regions of whelks vertical distributions), on all six main study shores are shown in Figures 2.5 (for sheltered shores), 2.6 (moderately-exposed shores), and 2.7 (exposed shores). Pictograms comparing size frequencies on all six shores, and variation in size-frequency (pooled data of all six shores) are represented in Figures 2.8 and 2.9 respectively.

Table 2.13 Results of ANOVA (GLM) showing differences in percentage of sizeclass, and Post Hoc Bonferonni multiple comparisons of the same variable showing significant differences between shores.

Sizeclass	F	Significance	Shores	Significance
1	0.021	1.000		
2	19.750*	<0.001	1-2	0.005
			2-3	<0.001
			2-4	<0.001
			2-5	<0.001
			2-6	<0.001
3	6.475*	0.004	2-4	0.009
			2-6	0.017
4	0.320	0.897		
5	4.145*	0.020	2-6	0.037
6	3.022	0.054		
7	3.656*	0.031		
8	7.201*	0.002	1-4	0.033

Data presented are F-values (F),with probabilities (P), * which are significant values.

Table 2.13 continued.

			2-4	0.023
			3-4	0.009
9	4.996*	0.011		
10	6.219*	0.005	3-4	0.021
			3-5	0.030
			3-6	0.044
11	1.581	0.239		
12	2.024	0.147		
13	5.396*	0.008	1-4	0.031
			1-6	0.009
14	4.938*	0.012	1-3	0.023
			1-4	0.035
			1-5	0.004
			1-6	0.001
15	4.037*	0.022	1-3	0.020
			1-4	0.016
			1-5	0.009
			1-6	0.002
16	8.195*	0.001	1-2	0.036
			1-3	0.002
			1-4	0.041
			1-5	0.006
			1-6	0.003
17	4.025*	0.022	1-3	0.026
18	2.290	0.111		
19	1.000	0.458		
20	1.064	0.427		

Data presented are F-values (F),with probabilities (P), * which are significant values.

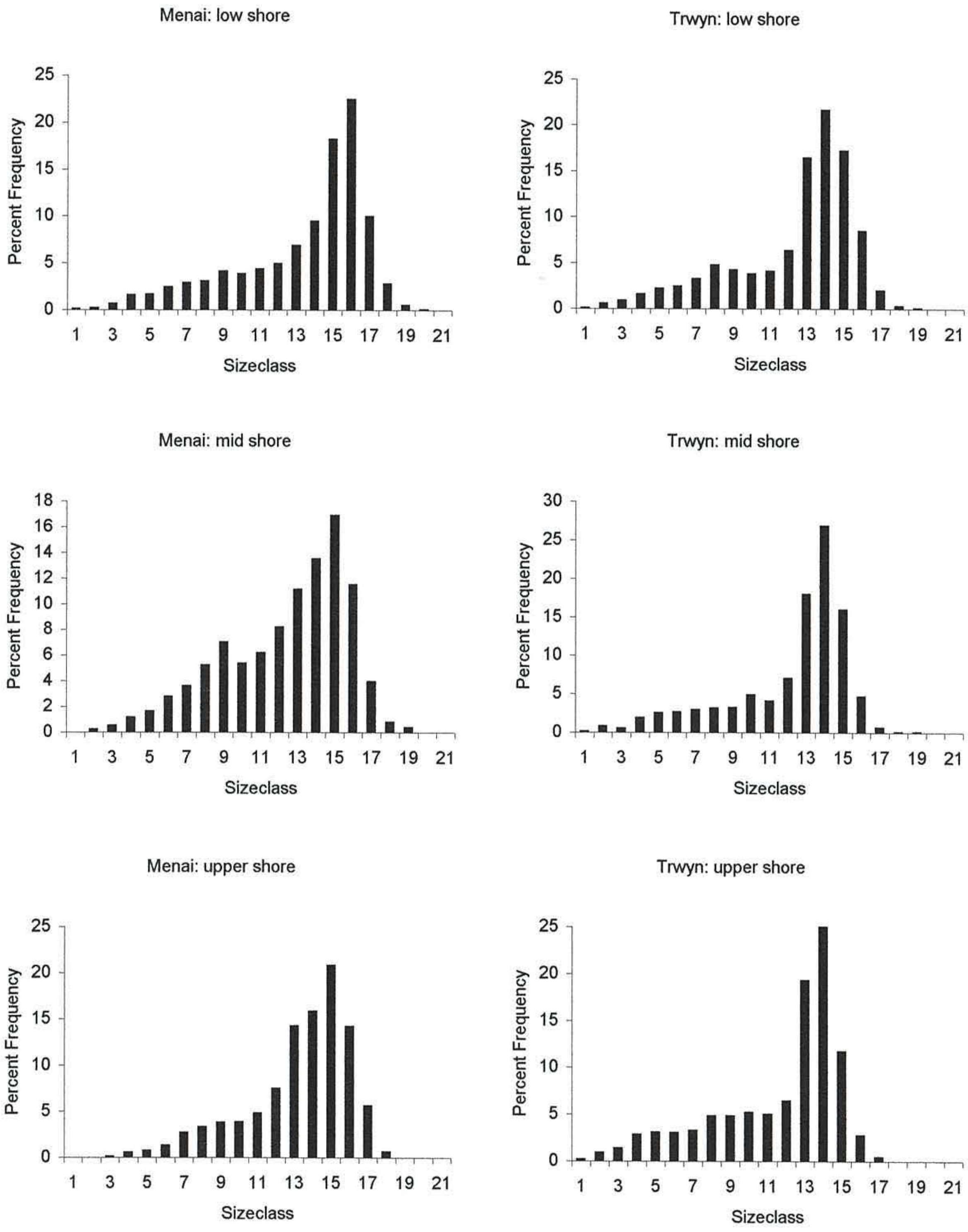
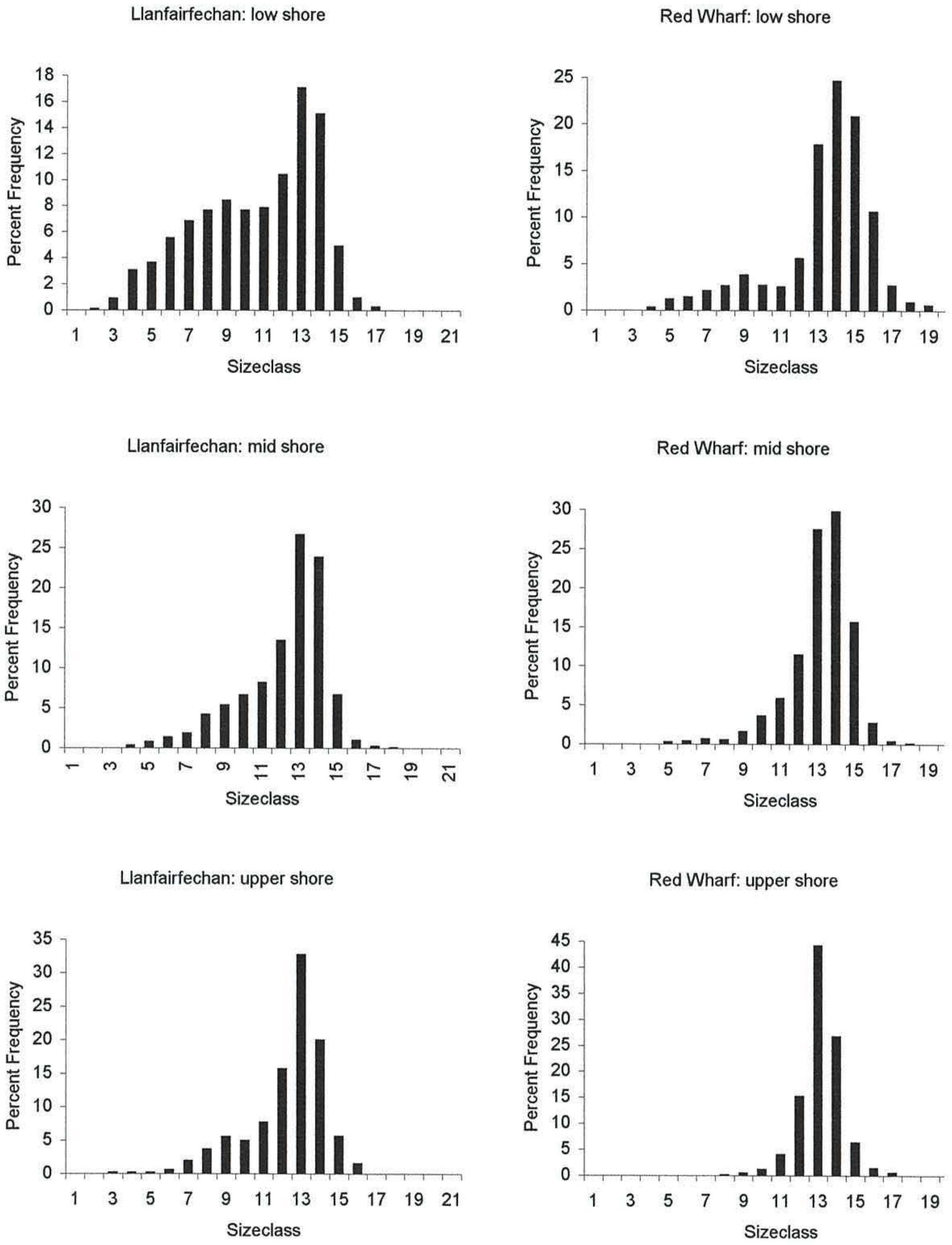


Figure 2.5. Size-frequency distribution at different shore levels on two sheltered shores.


Llanfairfechan: low shore

Red Wharf: low shore

Llanfairfechan: mid shore

Red Wharf: mid shore

Llanfairfechan: upper shore

Red Wharf: upper shore

Figure 2.6. Size-frequency distribution at different shore levels on two moderately-exposed shores.

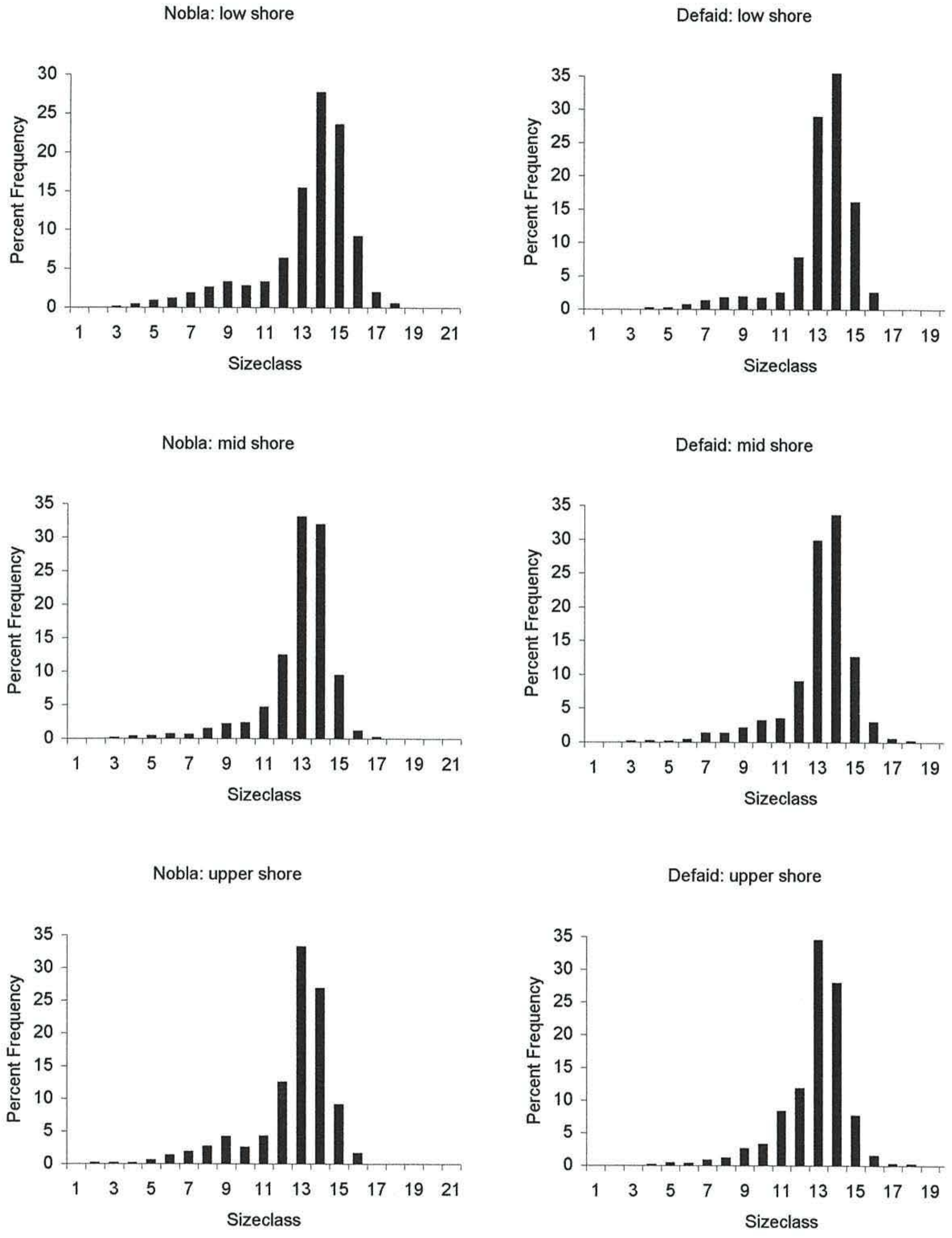


Figure 2.7. Size-frequency distribution at different shore levels on two exposed shores.

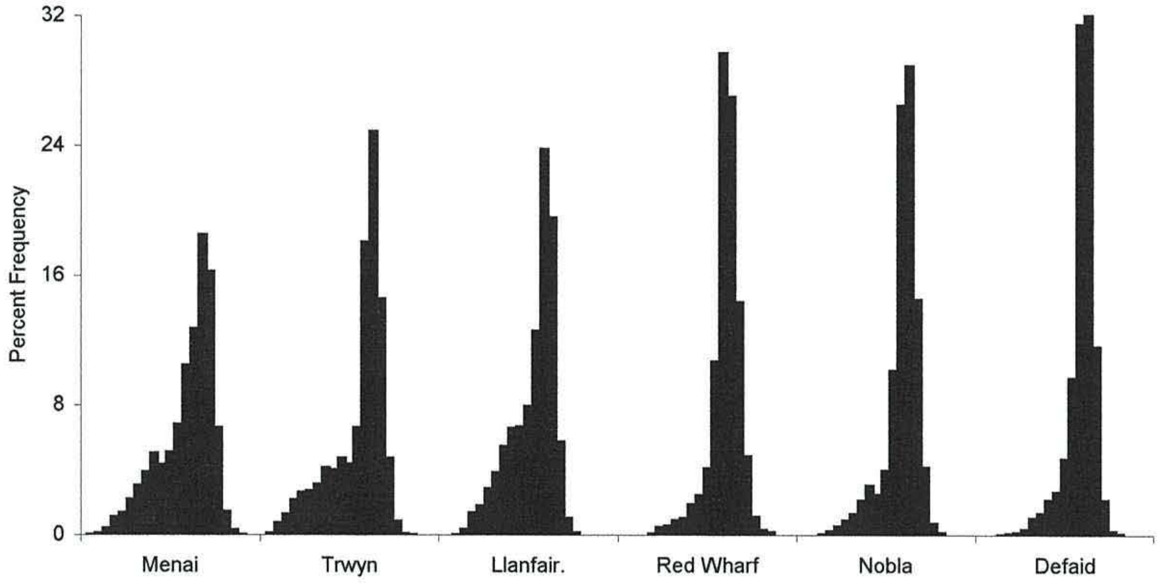


Figure 2.8. Pictogrammic representation of the comparison of size-frequency distribution on different shores. (2 years pooled data)

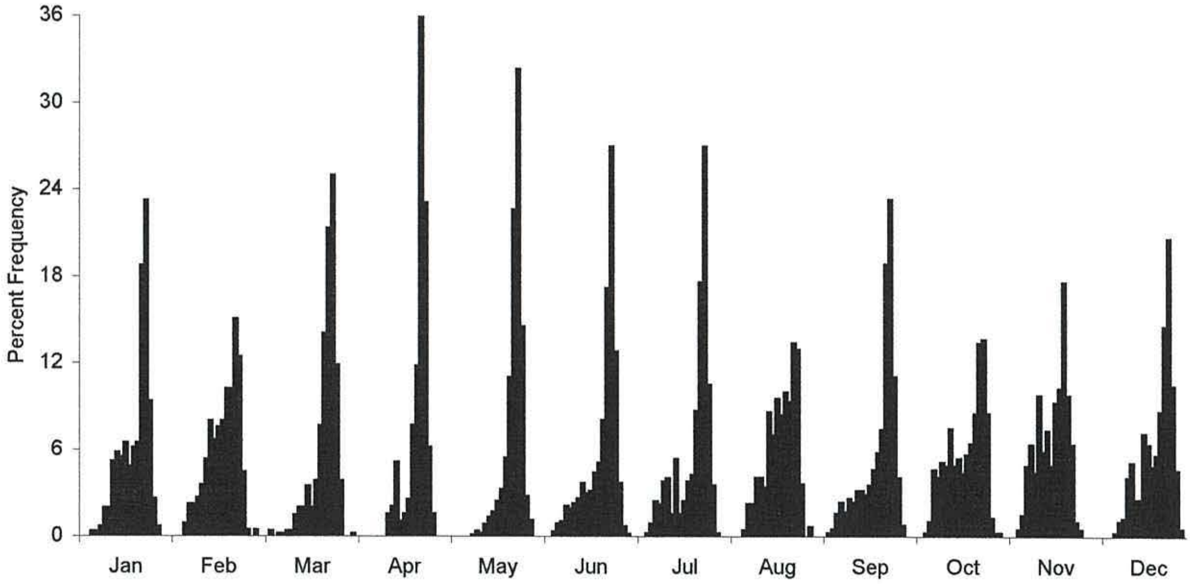


Figure 2.9. Pictogrammic representation of the monthly changes in size-frequency distribution (pooled data from all study shores and from 2 years data).

2.36. *Nucella* density estimation.

Density on the six main study shores between shore levels (low, medium and upper) was determined. It is apparent that from the density of dogwhelks at different shore levels (Figure 2.10), that *Nucella* is more common at the lower shore areas with the exception of Trwyn y Penrhyn, which has a lack of suitable boulder sites (there were few barnacles, but extensive obtrusive algae on the few boulders in this region). The density of *Nucella* was found to be significantly influenced by shore level at Menai Bridge (GLM. F=1904.946 P=<0.001), Trwyn y Penrhyn (GLM. F=2327.940 P=<0.001), Llanfairfechan (GLM. F=4579.924 P=<0.001), Red Wharf Bay (GLM. F=39.000 P=<0.001), Porth Nobla (GLM. F=316.817 P=<0.001), and Porth Defaid (GLM. F=570.445 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in density between most shore levels (Table 2.14).

Table 2.14. Post Hoc Bonferonni multiple comparisons of *Nucella* density showing significant differences between different shore levels within the same shore.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	8026*	<0.001	7087*	<0.001	777*	<0.001	313*	<0.001	159	0.308	62	0.178
1-3	9025*	<0.001	8218*	<0.001	8507*	<0.001	253*	<0.001	2122*	<0.001	951*	<0.001
2-3	999*	<0.001	1131*	<0.001	9284*	<0.001	61	0.360	1963*	<0.001	889*	<0.001

Data presented are mean differences (md), with probabilities (P), in which *are significant values.

The overall density shown in Figure 2.11, indicates higher overall numbers are found on the three more sheltered shores. The density of *Nucella* was significantly influenced by shore (GLM. F=39.686 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in density between most shores (Table 2.15).

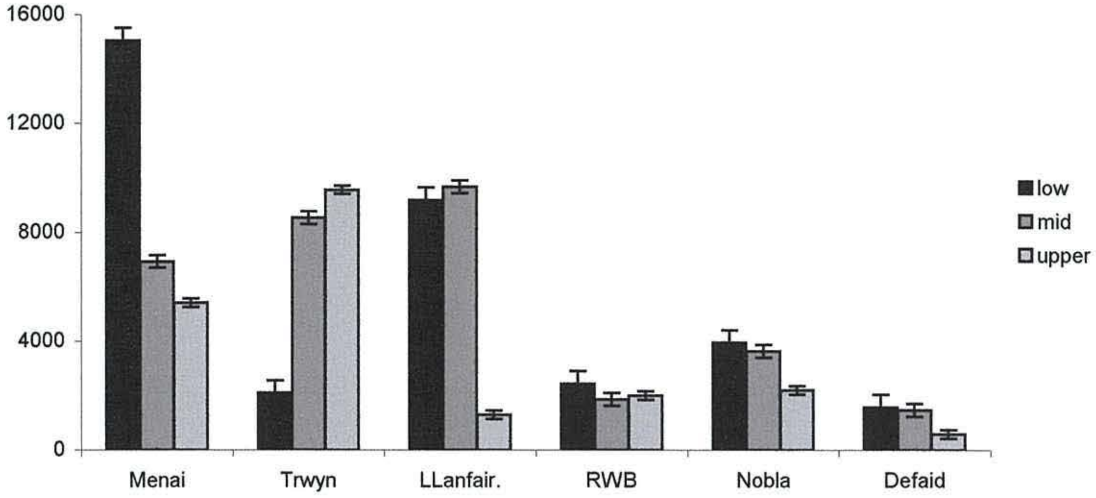


Figure 2.10. *Nucella lapillus* density on different shores. Bars represent the number of dogwhelks per 200 sq. metres.

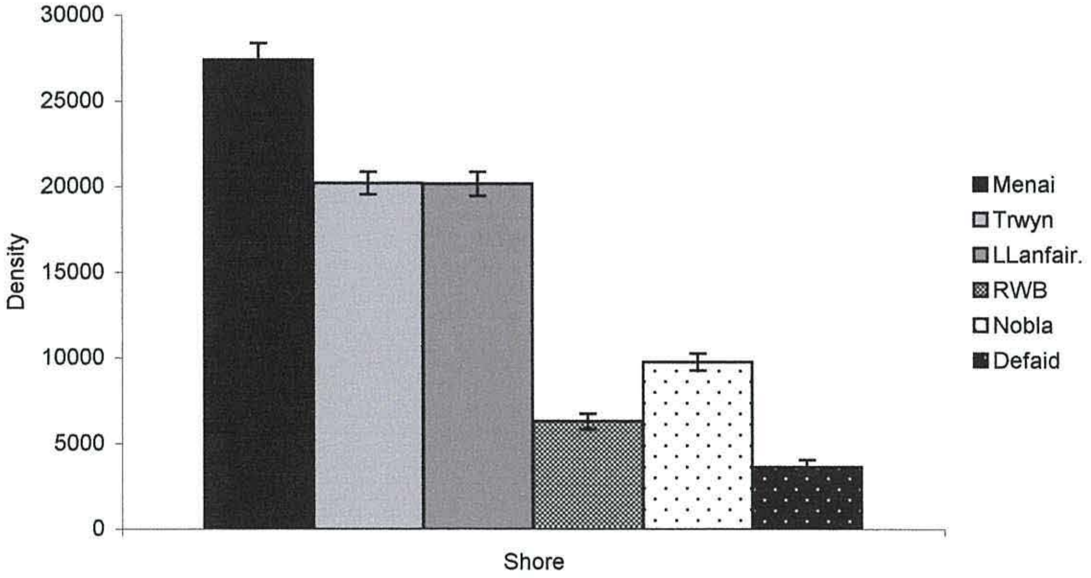


Figure 2.11. *Nucella lapillus* density on different shores. Bars represent the number of dogwhelks per 600 sq. metres.

Table 2.15. Post Hoc Bonferonni Multiple Comparisons of *Nucella* density showing significant differences between shores.

Shores	md	*P*	Shores	md	*P*	Shores	md	*P*
1-2	2336*	0.031	2-3	29	1.000	3-5	3901*	<0.001
1-3	2366*	0.028	2-4	5202*	<0.001	3-6	5832*	<0.001
1-4	7539*	<0.001	2-5	3931*	<0.001	4-5	1272	1.000
1-5	6267*	<0.001	2-6	5861*	<0.001	4-6	658	1.000
1-6	8197*	<0.001	3-4	5173*	<0.001	5-6	1931	0.160

Data presented are mean differences (md), with probabilities (P), in which* are significant values.

2.37. Survey of *Nucella* egg-capsules.

The percentage location-frequency for deposition of egg-capsules in different microhabitats showed different trends on the different types of study shore (figure 2.12). On sheltered shores (Menai Bridge and Trwyn y Penrhyn), and moderately exposed shores (Llanfairfechan and Red Wharf Bay), at least half of all capsule aggregations were found under boulders, with significant numbers of capsules found under algae (11-20%) on these shores (except for Llanfairfechan which has no algal growth), and within barnacle beds (10-13%). On exposed coastline (at Porth Nobla and Porth Defaid), 54-75% of all aggregations were located in other refuges (mainly crevices, some pits and trenches). The number of groups of capsules were greatest on moderately exposed shores: Llanfairfechan (2.65/m^2) and Red Wharf Bay (2.03/m^2), followed by the two most sheltered shores Trwyn y Penrhyn (1.95/m^2) and Menai Bridge (1.85/m^2). Lower numbers were found on the exposed shores Porth Nobla (1.23/m^2) and Porth Defaid (0.41/m^2).

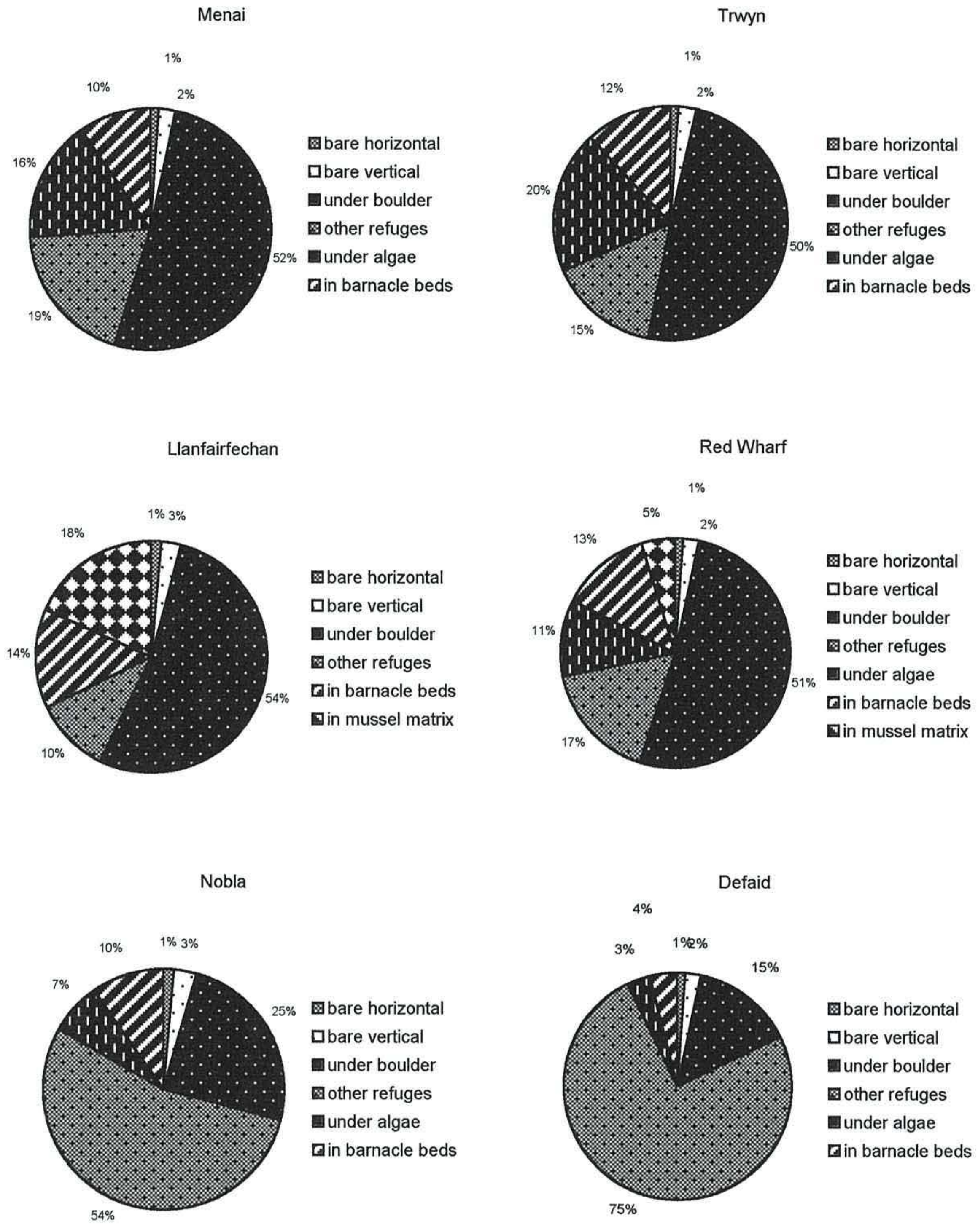


Figure 2.12. Percentage occupation of different spawning sites by *Nucella lapillus* egg-capsules on different shores. (2 years pooled data).

2.4. DISCUSSION.

Shore description and classification.

The walking survey of Anglesey showed that within a moderate stretch of coastline (around 40 miles), there is a great deal of variety in the physical and biological character of intertidal habitats of *Nucella lapillus*. The Ballantine classification revealed an ordered sequence in wave-exposure, from Menai Bridge (very sheltered to sheltered), to Trwyn y Penrhyn (sheltered to fairly sheltered), to Llanfairfechan (fairly-sheltered to semi-exposed), to Red Wharf Bay (semi-exposed), to Porth Nobla (exposed), to Porth Defaid (very exposed). All the inherent physical features of these shores namely: fetch distance, mean and maximum wave height, as well as mean and maximum waveforce confirmed this pattern, increasing with wave-action along this series. Similarities in biological composition and abundance did exist, within the following pairs of shores: Menai and Trwyn (sheltered); Llanfairfechan and Red Wharf (semi-exposed); Nobla and Defaid (exposed).

Horizontal distribution.

Around Anglesey, *Nucella lapillus* was found to be patchily distributed, but present in a wide range of intertidal habitats, absent only from areas of extreme wave exposure (e.g. cliff faces), and shelter (over 90% *Ascophyllum* coverage). Populations were not restricted to small areas of the shoreline as stated by Spight (1974, 1975), but were found wherever barnacles were present, excluding only locations in extreme upper shore. *Nucella* were not usually found on sandy or muddy stretches, although isolated individuals did exist on rock surfaces, some even hundreds of metres from their conspecifics at more favourable sites. The distribution of juveniles and subadults (shell lengths of <20 mm and 20-24.9mm respectively), reflected the fact that they are more susceptible to certain mortality factors (than larger whelks), until they reach protective microhabitats as are smaller *Nucella emarginata* (Gosselin and Chia, 1994). Juvenile snails are highly vunerable to predation, and wave-action (Faller-Fritch, 1977; Underwood, 1979; Werner and Gilliam, 1984), particularly when small (Branch, 1975). In addition they have a lower tolerance to desiccation than adults (Davies, 1969; Coombs, 1973; Branch, 1975). Study shores were noticeably different in topography and consequently in microhabitat availibility (although similarities were found in the boulder fields of Trwyn, Llanfairfechan, and Red Wharf). These factors influenced both the within shore distribution and activity of dogwhelks. Differences in spawning, foraging, and refuging were observed between sheltered (Menai and Trwyn), moderately-exposed (Llanfairfechan and Red Wharf Bay), and exposed (Nobla and Defaid) shores. The distribution and abundance of *Nucella lapillus* like all other organisms, represents an interplay between the physical limits imposed by its environment and the biological interactions it experiences (Hutchinson, 1957; Palumbi, 1984). For instance, the distribution of sessile prey organisms, which is related to the different wave conditions at these locations (Dayton, 1971), as well as spatial competition between sessile assemblages, affecting their availability (Lewis, 1976).

Vertical Distribution.

The vertical distribution of *Nucella* is also related to the features of the physical environment (Hatton,1938; Connell, 1972). Broekhuysen (1941), and Brown (1960), demonstrated a correlation between zonation of intertidal gastropods and their resistance to desiccation. The overall vertical distributions of dogwhelks in the study areas reflected the factors of slope, and ground distance (vertical extent of the shore), to a degree, but were chiefly determined by availabilty of suitable substrate and the availability of suitable prey (chiefly barnacles). Nevertheless, one important biological consequence of vertical position on the shore, is that it determines the proportion of time an animal is submerged (Menge, 1978b). Therefore, from the relative duration of submersion and percentage change in slope of the shore, a submersion factor was calculated. This is the relative submersion experienced by *Nucella* populations at the mid and upper levels of distribution, when compared to that found at the lower shore (Table 2.16). Marked differences were seen in the proportion of time dogwhelks are submersed (and therefore emmersed), particularly on four of the sites (Menai, Trwyn, Red Wharf, and Defaid).

Table 2.16.Submersion factor (relative submersion) experienced by *Nucella* at different shore levels.

Shore level	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
Low shore	1.00	1.00	1.00	1.00	1.00	1.00
Mid shore	0.34	0.33	0.67	0.35	0.65	0.33
Upper shore	0.11	0.13	0.34	0.11	0.30	0.15

Data presented are values of relative submersion compared to that at the low shore.

This can have a significant impact on both the amount of dessication, degree of wave action that dogwhelks are subjected to, dependant upon their relative vertical position on the shore and upon which shore they inhabit. Clearly at sheltered locations (Menai and Trwyn), desiccation can be severe at upper and sometimes mid shore levels, and therefore exposure to air will influence the upper limits of dogwhelk distribution (Audoin and Milne-Edwards, 1832). This factor limits the time available for foraging (Palmer 1983), and is pronounced in smaller animals with lower desiccation tolerances (Coombs, 1973), which were largely restricted to lower areas of the shore (Figures 2.5, 2.6, and 2.7). The cumulative force of wave-impact on stormy days (particularly at the exposed sites Nobla and Defaid), tended to dislodge whelks in the lower and upper shore. Tidal levels change more slowly in these parts of the shore, due to the sinusoidal nature of tidal variation, subjecting them to surface waves for prolonged periods (Denny,1988). More underwater waves also impact on those whelks found in the low shore, since they are submerged for far longer, rendering these animals particularly at risk.

There were clear seasonal changes in vertical distribution of *Nucella* along the shore (Underwood, 1973; Abe, 1989). In Winter there was a general migration downwards (paint marked individuals) with the onset of cold air temperatures. In Summer, a significant relocation of individuals at higher shore levels to positions lower down the gradient, with the onset of elevated air temperatures (Figure 2.2 B), particularly on those shores where seaweed is scarce or absent (Llanfairfechan, Red Wharf, Nobla and Defaid). In Spring, many individuals returned to higher shore areas. This pattern was also slightly modified by the availability of suitable crevices (as seen in other intertidal snails: Emson and Faller-Fritsch 1976; Raffaelli 1978; Raffaelli and Hughes 1978). On exposed shores, the normal upper limit of dogwhelks (between spring and neap high tides) was elevated by spray during heavy wave action, by making them less prone to desiccation (Lewis, 1964; Underwood, 1977; 1981). The vertical extent of shore occupied by *Nucella* increased with a reduction in the slope (less emersion time) and compressed with high wave-exposure (reduced vertical range of barnacles), similar to Vadas and Elner (1992). As a result of all the above interacting factors, there was a corresponding vertical shift in size distribution of dogwhelks on the shore during ontogeny (Hughes et. al., 1992).

Variation in size (shell length).

There were clear trends in the distribution of the intertidal gastropods and their size. Larger dogwhelks were found in the open on rock platforms and boulders, the next largest under algae and under boulders, and the smallest generally in crevices. Spawning *Nucella lapillus* were significantly larger than foraging individuals, which in turn were significantly larger than those refuging. Larger whelks (with a higher volume to surface area ratio), were able to cope better with the increased effects of desiccation, and with the threat of predation (size escape mechanism), both prevalent on the open substrate. The sizes of individuals located under boulders, and in crevices, was simply a reflection of the relationship between the size of the whelk and shape/volume of the refuge concerned. The size of *Nucella lapillus* was also related to the height that they were found on the shore, with both larger adults and smaller juveniles, generally more abundant lower on the shore (Hughes et. al. 1992). This trend is also apparent in the related species *Nucella lamellosa* and *Nucella emarginata* (Bertness, 1977). The only exceptions to these patterns occured at Porth Defaid, where foraging dogwhelks had the longest shells. At this site the absence of larger individuals on the low shore was due to the high probability of their being swept of the rocks in this high wave-energy environment. The general reduction in mean shell length in an upshore direction observed on all the study shores (Figure 2.4), tends to be characteristic of a species from the lower intertidal (Bertness, 1977).

Size-frequency gradients.

Lewis (1976), observed that factors such as recruitment, growth, maximum size, longevity (mortality) and age structure, may vary locally with vertical distribution, Etter (1989), that they also vary with exposure to wave action. The population structure (size-frequency distribution) of *Nucella lapillus* at each location varied with vertical height, and graphically resembled the size-frequency distribution of *Nucella lamellosa* from the North-Eastern Pacific (Spight, 1974). These intraspecific shore-level size gradients are a response to spatially and temporally variation in pre-reproductive mortality, effectively partitioning the different growth stages within different parts of the environment (Vermeij, 1972). They are a result of physical stresses, and the local availability (Fairweather, 1985), and distribution of prey (Ward and Quinn, 1988). Size class frequency distribution was also different between shores. The smaller size classes (<24 mm in shell length), were more common on the two sheltered locations (Menai and Trwyn), due to a higher algal coverage (including within the upper shore), and substantial availability of boulder refuge sites, both of which provide adequate cover against insolation, and against the moderate wave-action usually found in these low energy environments.

The sheltered areas also had a larger proportion of large dogwhelks (30-41.9 mm). So either survivorship is greater on these and/or relative growth rates are faster. Size-frequency distributions also varied with shore level. From November to March (Menai, Llanfairfechan and Red Wharf), and from June to September (these shores plus Porth Nobla), progressively more size classes (both smaller and larger individuals) were found from upper (through mid) to lower shore levels.

A concurrent increase in those whelks measuring 26-29.9 mm, at the expense of the smaller size-classes was seen towards the upper shore (all locations), which became more pronounced as wave intensity increased. This may reflect that the lower shore is a more suitable environment for *Nucella lapillus* as respective mortality rates do suggest (Figures 4.23-4.25). Related intraspecific size differences at different tidal levels have also been observed in several other intertidal gastropods (McCormack, 1982; Moran, 1985; Takada, 1996). The same percentage shift away from smaller size classes was seen when moving from sheltered to exposed shores (Figure 2.8; Table 2.13). These shore-related differences in size gradients appear to be related to size-specific growth rates, which are inversely correlated with wave action (Etter, 1989), and particularly on exposed shores, related to the availability of shelter (Lewis et, al., 1982).

Monthly changes in size-frequency distribution (similar on all study shores and represented as pooled data in Figure 2.9), showed a higher number of whelks in the smaller size classes from October to February, compared to a higher frequency of moderately-sized and large individuals that dominated populations from March to July. This increase in small juveniles follows periods when maximal numbers of dogwhelks are spawning (which is derived from the percentage spawning multiplied by overall density, in Figures 5.8 and 5.12 respectively).

Egg-capsules.

Dogwhelks mainly bred in winter, but continued this activity throughout the year in the more sheltered locations, where peaks were observed from February to May and from October to December. Some dogwhelks bred twice in one year, with newly deposited egg capsules were observed both in January and August.

Exposed shore forms deposited twice as many egg capsules per spawning site (with twice as many hatchlings, which were 25% smaller). Increased reproduction on exposed coasts tends to offset the higher mortality rates at these locations (Etter, 1989). The number of spawning sites however, were greatest on the two most sheltered shores Menai Bridge and Trwyn y Penrhyn, followed by the moderately-exposed shores Llanfairfechan and Red Wharf Bay, and least on the exposed shores Porth Nobla and Porth Defaid. This is solely a reflection of *Nucella lapillus* density, and the subsequent total numbers of whelks actively spawning (Table 2.17).

Table 2.17. Absolute numbers (tens) of *N.lapillus* spawning at different shore levels per 200m^2.

Shore level	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
Low	195	28	19	15	32	3.2
Mid	63	99	80	18	7.6	2.3
Upper	25	80	2.4	2.3	18.4	0
Mean	94	69	34	11.8	19.3	1.8

Very few egg-capsules were deposited on open bare surfaces (less than 5%), and at sheltered and semi-exposed locations, over half of all deposition sites were under boulders, protected from desiccation. On the two exposed shores most spawning sites were in crevices and deep pits (pocks) in the rock (Figure 2.12). This is partly a reflection of the relative availability of the different microhabitats on different shores (Figure 5.14), and partly due to these deep refuges providing better protection (than habitats under boulders), from the increased wave-action encountered on such exposed sites (Tables 2.3 and 2.4).

Nucella lapillus density.

The deeply indented coastline of Anglesey consists of many types of shores, each differing markedly in wave exposure. Contrary to the observations of Lubchenco and Menge (1978), the abundances of dogwhelks did vary between study shores in relation to wave shock, increasing with reduction in relative wave force (Table 2.4), as determined by Levinton (1995). The Anglesey survey (474 sites), revealed a scarcity of dogwhelks in extremely sheltered locations (Palmer, 1990a), such as parts of Menai Strait where *Ascophyllum nodosum* covered over 95% of all available space. Here (outside the study area), crabs were very abundant, and their intense predation on *Nucella* was an important reason for the dogwhelks relatively small numbers (Seed, 1978). Between the main study sites, *Nucella* density decreased along the wave exposure gradient from Menai (very sheltered to sheltered), to Trwyn (sheltered to fairly sheltered), to Llanfairfechan (fairly sheltered to semi-exposed), to Red Wharf Bay (semi-exposed), to Nobla (exposed), to Defaid (very exposed); to the extent that densities at the three more sheltered enclaves were 2-4 times greater than at the three most exposed.

Nucella lapillus densities were different at the three shore levels, being greatest in the lower shore, and least in the upper shore, throughout the year at Menai Bridge and Llanfairfechan, except for during the Summer, when more dogwhelks were found in the middle shore, under medium-large boulders. At the three most exposed locations (Red Wharf Bay, Porth Nobla, and Port Defaid), dogwhelk numbers were the same at all levels for most whole of the year, except that higher numbers were found on the lower shore in late Autumn/early Winter and Spring, and lower numbers in the upper zone towards the end of Summer, during May and October. Variation in densities that may have been caused by downward migrations in reponse to increased risk of desiccation. The Trwyn y Penrhyn site was unusual in that few suitable habitats for *Nucella lapillus* were present in the lower shore, and consequently this area was more sparse in these animals, except for Summer when numbers here were equivalent to the other two levels. Throughout the winter, and early Spring dogwhelk densities were greatest in the lower middle shore here (all year round from transect data results), being highest in the upper region during May and October.

CHAPTER 3.

NUCELLA LAPILLUS MORPHOLOGICAL VARIATION.

3.1. INTRODUCTION.

The pattern of shell shape in *Nucella lapillus* was first noted by Cooke (1895). There is a progressive environmental gradation in the form of the shell from short squat individuals on exposed headlands to more elongated ones with long spires in sheltered bays (Crothers,1977b; 1983). Much of this variation in shell shape is considered to have adaptive significance with respect to the different environments in which the snail is found (Seed, 1978). *Nucella lapillus* from different exposure regimes also differ in growth rates, size at maturity, population size structure, mortality rates, and reproductive effort (Crothers, 1982; Etter,1989). The final shell form appears to be the net affect of genotypic and phenotypic responses to the prevailing selection pressures (Etter, 1988a; Crothers, 1992) of the habitat encountered (Gosselin and Bourget, 1989), including wave-action, crab predation (Crothers, 1983) and desiccation (Osborne, 1977).

Shell size.

Body size determines the energetic requirements (Schmidt-Nielsen, 1984), resource exploitation and the outcome interactions of an organism with its environment (Werner and Gilliam, 1984), and with other species (Schoener, 1983; Wilson, 1975). Most organisms are characterised by size-structured populations (Werner and Gilliam, 1984). In *Nucella emarginata* young snails grow allometrically during the second year of life (Crothers, 1980), and so the ratio Length/Aperture Length (L/Lap) can be notably different in young and adults from the same population (Crothers, 1981a). Another factor that changes with ontogeny is the presence of apertural teeth, which are typical of mature snails in *Nucella lamellosa* (Marko and Palmer, 1991), and *Nucella lapillus* (Crothers, 1985a).

Wave action.

Wave action exerts a powerful and profound influence on the biology of intertidal marine organsims. The ecological effects of wave-generated forces can operate directly through the impact of waves and debris or through dislodgement (Shanks and Wright, 1986); also indirectly by altering food availability, biotic interactions, and foraging efficiency (Etter, 1989). Any organisms with distributions that span several exposure regimes, may experience differences in foraging time, growth rates, reproductive success, competition, predation intensity, and mortality rates between these spatially and temporally varying environments (Etter, 1988a).

Features of Nucella lapillus living in exposed and sheltered environments.

Considerable variation in shell shape is seen within and between populations of *Nucella lapillus* (Crothers, 1981a), there being a progressive gradation in shape from "exposed" to "sheltered" forms, with many intermediates (Crothers, 1982b). Dogwhelks from exposed habitats generally have a smaller size (Hughes and Burrows, 1994), and are thinner and less elongate than those from protected habitats (Moore, 1936; Osborne, 1977). They also have a greater pedal area with corresponding increased tenacity (Seed, 1978; Etter, 1988b). Sheltered forms (found in estuaries, narrow straits and sheltered open coasts as well as sheltered inlets (Crothers, 1981c), exhibit the opposite tendencies (Hughes and Elner, 1979; Curry and Hughes, 1982). Their shells are longer and narrower (Berry and Crothers, 1968), with an elongated narrow aperture, strong sculpturing and a thick, inflexible operculum (Vermeij, 1974). Intertidal organisms tend to be smaller on wave-swept shores (Lewis 1968, Harger 1970, Connell, 1972) especially snails (Emson and Faller-Fritsch, 1976). The shape of shells on these locations is related to cumulative wave action (Crothers, 1981b). Short and squat forms (Crothers, 1980), with a stunted short spire, and large broad shell aperture (Cooke, 1895; Crothers, 1982a), are better fitted to resist dislodgement (Berry and Crothers, 1968; Kitching et. al., 1966) from the exposed headlands (Kitching et. al., 1966; Crothers, 1981a), where they are found. This compact form reduces drag (Crothers, 1982b: 1985a), whilst the larger foot increases tenacity (Kitching and Ebling, 1967; Graham and Mill, 1986). These open coast forms also tend to have thinner shells (Crothers, 1985a), leading to a increased risk of predation (Crothers 1982b; 1985a), and desiccation (Osborne, 1977), primarily from a reduced ability to retract into their shells. On more exposed shores however, crab predation is minimal. Shells from sheltered shore habitats, where *Nucella lapillus* suffers more predation, are far stronger than those from exposed habitats (Curry and Hughes, 1982), although the thicker, more robust shells have a higher, metabolic cost (Etter,1988a). The shells here are more elongate (Kitching et. al., 1966; Crothers, 1985b), allowing full withdrawl into the shell to evade predators (Crothers, 1983), as well as increasing the ability to store water (Osborne, 1977).

The most commonly used morphological parameter used in comparing shell form is regression of shell shape (L/Lap) on shell length (L), see Crothers (1985a), where Lap is the length of the shell aperture. This ratio is different for *Nucella lapillus* and closely related species (Crothers, 1983). It has been used by many workers studying shape variation in dogwhelks that includes Moore (1936), Kitching et. al.(1966), Berry and Crothers (1968; 1974), Crothers (1973; 1974; 1975a; 1975b; 1977a; 1977b; 1978; 1979; 1980; 1981a; 1981b; 1981c; 1982a; 1982b; 1983; 1985a; 1985b; 1992), Crothers and Cowell (1979), Kitching (1977), Cambridge and Kitching (1982), and Seed (1978). Phillips et. al. (1973), expanded the number of parameters looked at to include overall length, length of spire, length of aperture, and width of aperture.

Shell colour.

Nucella lapillus populations frequently display great polymorphism in the shape and the colour of their shells (Crothers, 1977). Hoxmark (1970; 1971) and Bantock and Page (1976), have stated that the degree of colour variation varies randomly with respect to shore type. However, according to Berry (1983), Etter (1988b), and Harris and Jones (1995), low wave energy habitats (sheltered shores) are dominated by predominately white-shelled populations, whilst populations from high-wave-energy shores tend to be highly polymorphic (often dominated by pigmented morphs) and with an increased frequency of banding (Berry and Crothers, 1974), for instance around Anglesey (Berry, 1983). The selective advantage of colour and banding patterns are not fully understood, but may be related to insolation (incident light), and cryptic camouflage (Berry and Crothers, 1974), due to the activity of visual predators such as birds (Palmer, 1984a). Colour change appears to be related to experiencing traumatic physiological stress from adverse environmental factors, and can often be reversed. There is a genetic basis for colour, banding and sculpture in *Nucella lamellosa* (Campbell, 1978), and *Nucella emarginata* (Palmer, 1984a), and in juvenile *Nucella emarginata* and *Nucella lapillus* (Palmer, 1984a), shell colours are transient, changing during ontogeny, yet unrelated to diet (Osborne, 1977).

3.2. METHODS.

Hypotheses.

1. Shell shape, colour and banding of *Nucella lapillus* all change within small spatial scales.
2. Shell size frequency distributions of dogwhelks change seasonally within individual shores.
3. The frequency of shell teeth in mature *Nucella* increases with wave-exposure.

Morphological Variation.

I collected undamaged, mature *Nucella lapillus* without bias for colour, site elevation or type, but ignored damaged, empty, worn shells or those that could have been moved by passive transport, in order to attain a representative sample for each enclave (population) sampled. Comparative samples were taken from the same level on each shore to determine the distribution and abundance of different size classes and shell shapes (Edwards et. al., 1982). Since for studies of microgeographic variation it is better to take samples from breeding aggregations than from dispersed dogwhelks (to avoid the Wahlund effect in which genetically differentiated populations are included in a sample, see Grant and Utter, 1988). On each shore the particular habitat type and degree of wave exposure (rock platform, boulder field, sheltered etc.), were noted at the time of collection.

A number of adult shell parameters: length (L); width (W); aperture length (Lap); aperture width (Wap); spire length (Sp), see Appendix 3 (for shell diagram and collection areas); were measured (maximum attainable) to the nearest 0.1 mm, using Vernier callipers, and compared within and between several geographical (spatial) scales (see Levings and Garrity, 1983). From these parameters a number of shell variables were calculated: L/Lap; Wap x Lap (aperture area); Wap x Lap/ L^2 (designated as shape); L/W. These were used to examine particular attributes of morphology related to distribution, and to assess changes in shell shape with height on shore, habitat, shore type and season. During this study some 13,137 dogwhelks (an initial 65,685 shell measurements) were collected from 474 sites on Anglesey, as well as an additional five sites in North Wales and forty sites on mainland Scotland and a number of Scottish Islands (Lewis, Harris, North Uist, Benbecula, South Uist, Scarp, Eriskay, Barra, Skye, Lismore, Mull, Iona, Colonsay, Jura, Islay, Arran, and the

Orkney Islands). Repeated measurements (a series of different samples) were made of the original shell parameters at the six main study sites, namely: Menai Bridge, Trwyn y Penrhyn, Red Wharf Bay, Llanfairfechan, Porth Nobla, and Porth Defaid to determine seasonal variation in shell shape. The frequency distribution of shell teeth (see Crothers, 1985a; Carefoot and Donovan, 1995), as well as the frequency of colour and banding morphs were also examined at these same six sites.

Shore locations on Anglesey where dogwhelk populations were sampled were put in habitat categories, according to nature (topography) of substrate, orientation and, size of structure (Table 3.1).

Table 3.1 The different habitat categories from which dogwhelks were collected.

No.	Habitat	No.	Habitat	No.	Habitat	No.	Habitat
1	Boulder	5	Pitted Rock	9	Trench	13	Cave
2	Small Boulder	6	Mussel beds	10	Vertical Face	14	Boat Hull
3	Crevice	7	Stones/Pebbles	11	Large Boulder	15	Pier/Ramp
4	Bench/Outcrop	8	Slate Slabs	12	Sewage Pipe	16	Ledge

Data presented represent habitats types sampled on Anglesey.

In addition boulders, benches and crevices on shores of different wave exposure were examined to see if any differences in shell parameters were present within these groups between sheltered and exposed sites.

Statistical analysis.

GLM univariate and mutivariate analyses were supplemented by Post Hoc multiple comparisons (Bonferroni test) for significant mean differences. On occasion when normality of data was suspect, non-parametric analyses of the data were also undertaken (Mann-Whitney U test; Kruskal-Wallis test).

3.3 RESULTS.

The variation in shell shape parameters: shell length, aperture length, aperture width, spire length, and shell width between the different main six study shores is shown in Figure 3.1. The variation in shell shape ratios: length/aperture length, aperture area, shape (aperture area/length squared), and shell length/shell width between the different main six study shores is shown in Figure 3.2.
Key to figures: 1 - low shore; 2 - mid shore; 3 - upper shore.

3.31. The effect of habitat type on shell shape parameters.

3.311. Shell length.

The shell length of *Nucella* was found to be significantly influenced by habitat (GLM. F=3.200 P=0.041), being higher on piers, ramps, stones and small boulders; lower on vertical surfaces, in pits, crevices and trenches, in mussel beds, and on open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in shell length between most pairs of habitats (Table 3.2).

3.312. Aperture length.

The aperture length of *Nucella* was found not to be significantly influenced by habitat overall (GLM. F=2.263 P=0.104). However, Post Hoc multiple comparisons (Bonferroni test) showed significant mean differences in aperture length between some pairs of habitats (Table 3.3), very similar to those differences cited for shell length above.

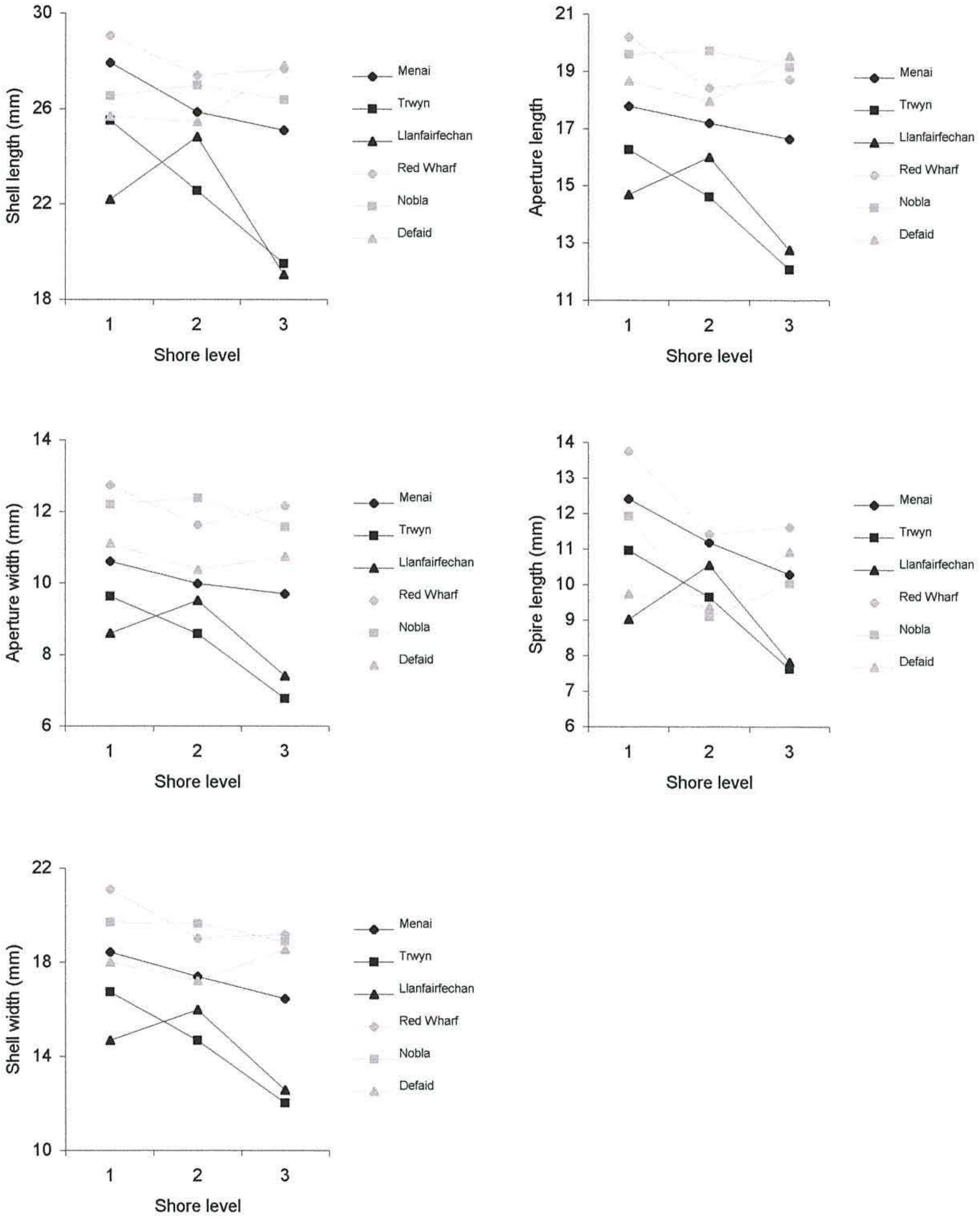


Figure 3.1. Variation in shell shape parameters at different shore levels.
Key to shore levels: 1: low shore; 2: mid shore; 3: upper shore.

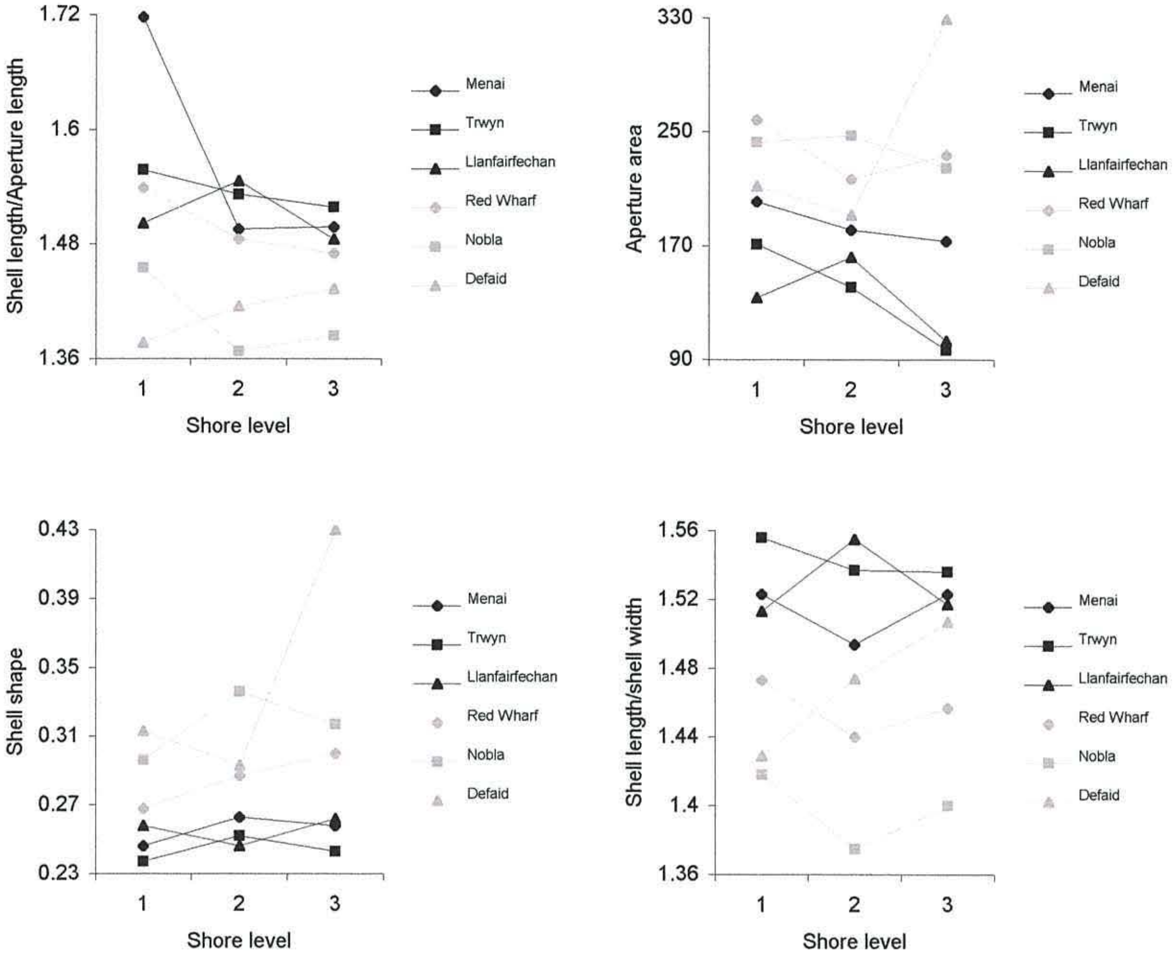


Figure 3.2. Variation in shell shape ratios at different shore levels.
Key to shore levels: 1: low shore; 2: mid shore; 3: upper shore.

Table 3.2. Post Hoc Bonferonni multiple comparisons of shell length between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-2	0.993	<0.001	3-6	1.349	0.004	7-10	4.057	<0.001
1-4	2.044	<0.001	3-7	1.760	<0.001	7-11	1.141	0.003
1-6	1.728	<0.001	3-10	2.297	<0.001	7-13	3.150	<0.001
1-7	1.381	<0.001	3-15	3.257	<0.001	7-15	1.497	0.001
1-9	1.612	<0.001	4-7	3.425	<0.001	8-15	3.502	0.011
1-10	2.676	<0.001	4-10	0.633	0.001	9-11	1.852	<0.001
1-15	2.878	<0.001	4-11	2.283	<0.001	9-15	4.490	<0.001
2-3	1.372	<0.001	4-15	4.922	<0.001	9-16	2.804	<0.001
2-4	3.037	<0.001	4-16	3.235	<0.001	10-11	2.916	<0.001
2-6	2.721	<0.001	5-15	4.149	0.001	10-14	3.593	0.006
2-9	2.605	<0.001	6-7	3.109	<0.001	10-15	5.554	<0.001
2-10	3.670	<0.001	6-10	0.948	0.046	10-16	3.868	<0.001
2-11	0.754	0.017	6-11	1.967	<0.001	11-13	2.009	0.014
2-13	2.763	<0.001	6-15	4.606	<0.001	11-15	2.639	<0.001
2-15	1.885	<0.001	6-16	2.919	<0.001	13-15	4.648	<0.001
3-4	1.665	<0.001	7-9	2.993	<0.001	13-16	2.961	0.006

Data presented are mean differences, with probabilities (P), which are all significant values.

Table 3.3. Post Hoc Bonferonni multiple comparisons of aperture length between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-4	0.837	<0.001	3-10	1.183	<0.001	6-10	0.749	0.040
1-10	1.233	<0.001	3-15	1.249	<0.001	6-15	1.713	<0.001
1-15	1.199	<0.001	4-7	1.149	<0.001	6-16	1.788	0.005
2-4	0.874	<0.001	4-10	0.397	0.015	7-9	1.041	0.016
2-10	1.270	<0.001	4-11	0.934	<0.001	7-10	1.546	<0.001
2-15	1.162	<0.001	4-15	2.036	<0.001	8-15	2.551	0.018
3-4	0.786	0.001	4-16	2.111	<0.001			

Data presented are mean differences, with probabilities (P), which are all significant values.

3.313. Aperture width.

The aperture width of *Nucella* was found to be significantly influenced by habitat (GLM. F=5.360 P=0.005), being higher on piers, ramps, ledges,stones,small boulders, crevices and pits; lower on vertical surfaces, in trenches, in mussel beds, and on open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in aperture width between many pairs of habitats (Table 3.4).

Table 3.4. Post Hoc Bonferonni multiple comparisons of aperture width between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-2	0.718	<0.001	3-9	0.847	0.011	6-11	0.647	0.013
1-4	0.806	<0.001	3-10	1.663	<0.001	6-15	1.256	<0.001
1-10	1.213	<0.001	4-6	0.530	0.027	7-9	0.865	0.008
1-11	0.370	0.050	4-7	1.244	<0.001	7-10	1.651	<0.001
1-15	0.980	<0.001	4-10	0.407	<0.001	9-10	0.785	0.004
2-4	1.523	<0.001	4-11	1.176	<0.001	9-11	0.798	0.005
2-6	0.994	<0.001	4-13	1.559	<0.001	9-15	1.408	<0.001
2-9	1.145	<0.001	4-15	1.786	<0.001	10-11	1.583	<0.001
2-10	1.931	<0.001	4-16	1.596	<0.001	10-13	1.996	<0.001
3-4	1.226	<0.001	6-7	0.714	0.026	10-15	2.193	<0.001
3-6	0.696	0.037	6-10	0.937	<0.001	10-16	2.003	<0.001

Data presented are mean differences, with probabilities (P), which are all significant values.

3.314. Spire length.

The spire length of *Nucella* was found not to be significantly influenced by habitat (GLM. F=2.603 P=0.074). Post Hoc multiple comparisons (Bonferroni test) showed significant mean differences in spire length between some pairs of habitats (Table 3.4). Spire lengths tended to be longer on piers, stones, small boulders; shorter on vertical surfaces and benches, in mussel beds and trenches (Table 3.5).

Table 3.5. Post Hoc Bonferonni multiple comparisons of spire length between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-2	1.896	<0.001	3-9	1.284	<0.001	7-9	2.496	<0.001
1-4	1.693	<0.001	3-10	2.565	<0.001	7-10	3.776	<0.001
1-6	1.989	<0.001	3-15	1.686	<0.001	7-11	1.224	<0.001
1-7	1.605	<0.001	4-7	3.298	<0.001	7-13	2.149	<0.001
1-9	0.891	0.001	4-8	2.267	0.009	7-14	3.045	<0.001
1-10	2.171	<0.001	4-9	0.802	0.004	8-10	2.745	<0.001
1-15	2.079	<0.001	4-10	0.478	<0.001	9-10	1.280	<0.001
2-4	3.589	<0.001	4-11	2.074	<0.001	9-11	1.272	<0.001
2-6	3.885	<0.001	4-15	3.772	<0.001	9-15	2.970	<0.001
2-9	2.786	<0.001	4-16	2.194	<0.001	10-11	2.552	<0.001
2-10	4.067	<0.001	5-6	2.244	0.034	10-13	1.357	0.009
2-11	1.515	<0.001	5-10	2.426	0.007	10-15	4.250	<0.001
2-13	2.710	<0.001	6-7	3.594	<0.001	10-16	2.672	<0.001
2-14	3.336	<0.001	6-8	2.563	0.002	11-15	1.698	<0.001
2-16	1.395	0.015	6-9	1.098	0.001	13-15	2.894	<0.001
3-4	2.087	<0.001	6-11	2.370	<0.001	14-15	3.519	<0.001
3-6	2.383	<0.001	6-15	4.069	<0.001	15-16	1.578	0.007
3-7	1.211	<0.001	6-16	2.490	<0.001			

Data presented are mean differences, with probabilities (P), which are all significant values.

3.315. Shell width.

The shell width of *Nucella* was found to be significantly influenced by habitat (GLM. F=3.194 P=0.041), being higher on piers, ramps, ledges, stones, all boulders; lower on vertical surfaces, in trenches, crevices and pits in mussel beds, and on open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in shell width between many pairs of habitats (Table 3.6).

Table 3.6. Post Hoc Bonferonni multiple comparisons of shell width between habitat types.

Habitats	md.	P	Habitats	md.	P	Habitats	md.	P
1-4	0.788	<0.001	4-10	0.397	0.006	7-15	1.371	<0.001
1-10	1.185	<0.001	4-11	1.071	<0.001	8-15	2.655	0.004
1-15	1.726	<0.001	4-15	2.514	<0.001	9-11	0.934	0.006
2-4	0.735	<0.001	4-16	2.090	<0.001	9-15	2.377	<0.001
2-10	1.132	<0.001	5-15	3.141	<0.001	9-16	1.954	0.001
2-15	1.780	<0.001	5-16	2.717	0.030	10-11	1.468	<0.001
3-4	0.676	0.004	6-9	1.115	0.003	10-15	2.911	<0.001
3-10	1.074	<0.001	6-10	1.649	<0.001	10-16	2.488	<0.001
3-15	1.838	<0.001	6-15	1.262	<0.001	11-15	1.443	<0.001
4-6	1.251	<0.001	7-9	1.006	0.011	13-15	1.834	0.001
4-7	1.142	<0.001	7-10	1.540	<0.001			

Data presented are mean differences, with probabilities (P), which are all significant values.

3.32. The effect of habitat type on shell shape ratios.

3.321. The shell length/aperture length ratio.

The shell length/aperture length ratio of *Nucella* was found to be significantly influenced by habitat (GLM. F=20.736 P=<0.001), being especially higher on all boulders, piers, ramps, and stones, lower on vertical surfaces, in refuges and mussel beds, and on ledges and open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in the shell length/aperture length ratio between habitats in these different groups (Table 3.7).

3.322. The aperture area.

The aperture area of *Nucella* was found to be significantly influenced by habitat (GLM. F=52.670 P=<0.001), being considerably higher on piers, ramps, ledges, and on stones; moderately so on all sizes of boulders, crevices and pits; lower on vertical surfaces, in trenches, in mussel beds, and on open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in aperture area between many pairs of habitats (Table 3.8).

Table 3.7. Post Hoc Bonferonni multiple comparisons of shell length/aperture length ratio between habitat types.

Habitats	md.	P.	Habitats	md.	P	Habitats	md.	P
1-2	0.055	<0.001	2-10	0.114	<0.001	6-11	0.061	0.042
1-4	0.054	<0.001	2-11	0.062	<0.001	6-15	0.119	<0.001
1-6	0.069	0.001	2-13	0.167	<0.001	7-9	0.081	0.032
1-10	0.059	<0.001	3-7	0.068	0.046	7-10	0.101	<0.001
1-13	0.112	0.040	3-15	0.077	0.025	7-13	0.154	0.001
2-3	0.081	<0.001	4-7	0.098	<0.001	9-15	0.089	0.017
2-4	0.108	<0.001	4-11	0.046	<0.001	10-11	0.052	0.002
2-6	0.117	<0.001	4-15	0.104	<0.001	10-15	0.109	<0.001
2-9	0.094	<0.001	6-7	0.110	<0.001	13-15	0.162	<0.001

Data presented are mean differences, with probabilities (P), which are all significant values.

Table 3.8. Post Hoc Bonferonni multiple comparisons of aperture area between habitat types.

Habitats	md.	P	Habitats	md.	P	Habitats	md.	P
1-2	10.276	0.001	3-10	37.499	<0.001	6-16	37.046	0.010
1-4	20.475	<0.001	3-15	18.997	0.012	7-9	29.949	<0.001
1-10	30.067	<0.001	4-7	32.099	<0.001	7-10	41.691	<0.001
1-15	26.428	<0.001	4-10	9.592	<0.001	8-15	49.352	0.017
2-4	30.751	<0.001	4-11	26.299	<0.001	9-11	20.148	0.002
2-6	21.885	<0.001	4-13	30.010	0.004	9-15	40.752	<0.001
2-9	24.600	<0.001	4-15	46.903	<0.001	9-16	35.762	0.005
2-10	40.343	<0.001	4-16	41.903	<0.001	10-11	35.891	<0.001
2-15	16.152	0.011	6-7	23.233	<0.001	10-13	39.602	<0.001
3-4	27.907	<0.001	6-10	18.458	<0.001	10-15	56.495	<0.001
3-6	19.041	0.005	6-11	17.432	0.002	10-16	51.504	<0.001
3-9	21.756	0.004	6-15	38.037	<0.001	11-15	20.605	<0.001

Data presented are mean differences, with probabilities (P), which are all significant values.

3.323. Aperture area/ shell length squared.

The shape (aperture area/shell length^2) of *Nucella* was found to be significantly influenced by habitat (GLM. F=11.140 P=<0.001), being lower on vertical surfaces, stones and piers. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in the shape between a number of habitats (Table 3.9).

Table 3.9. Post Hoc Bonferonni multiple comparisons of shape (aperture area/shell length^2) between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-3	0.015	<0.001	3-13	0.039	<0.001	7-11	0.016	0.001
1-6	0.017	<0.001	3-15	0.021	0.001	7-13	0.063	<0.001
1-13	0.054	<0.001	4-6	0.015	<0.001	8-13	0.071	<0.001
2-3	0.012	0.039	4-7	0.011	0.034	9-13	0.049	<0.001
2-6	0.014	0.013	4-13	0.052	<0.001	10-11	0.011	0.008
2-7	0.122	0.040	5-7	0.044	0.040	10-13	0.058	<0.001
2-13	0.051	<0.001	6-7	0.026	<0.001	11-13	0.047	<0.001
3-4	0.014	0.001	6-10	0.021	<0.001	13-14	0.059	0.001
3-7	0.025	<0.001	6-13	0.037	<0.001	13-15	0.059	<0.001
3-10	0.020	<0.001	6-15	0.022	<0.001	13-16	0.038	0.012

Data presented are mean differences, with probabilities (P), which are all significant values.

3.324. The shell length/shell width ratio.

The ratio shell length/shell width of *Nucella* was found to be significantly influenced by habitat (GLM. F=160.591 P=<0.001), being higher on stones, small boulders, then pits and all other boulders; lower on vertical surfaces, in trenches, crevices, in mussel beds, and on open benches. Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences in the shell length/shell width ratio between the vast majority of habitat pairs (Table 3.10).

Table 3.10. Post Hoc Bonferonni multiple comparisons of shape (shell length/shell width) between habitat types.

Habitats	md.	*P*	Habitats	md.	*P*	Habitats	md.	*P*
1-2	0.054	<0.001	3-10	0.044	<0.001	6-16	0.090	<0.001
1-4	0.052	<0.001	3-13	0.072	<0.001	7-9	0.082	<0.001
1-6	0.121	<0.001	3-16	0.035	<0.001	7-10	0.099	<0.001
1-7	0.043	<0.001	4-5	0.088	0.001	7-11	0.053	<0.001
1-9	0.039	<0.001	4-6	0.069	<0.001	7-13	0.128	<0.001
1-10	0.057	<0.001	4-7	0.095	<0.001	7-16	0.074	<0.001
1-13	0.086	<0.001	4-8	0.088	0.001	8-9	0.075	0.022
2-3	0.068	<0.001	4-11	0.042	<0.001	8-10	0.094	<0.001
2-4	0.106	<0.001	4-15	0.073	<0.001	8-13	0.121	<0.001
2-6	0.175	<0.001	5-9	0.076	0.035	9-11	0.029	0.007
2-9	0.094	<0.001	5-10	0.094	<0.001	9-13	0.046	0.032
2-10	0.112	<0.001	5-13	0.122	<0.001	9-15	0.060	<0.001
2-11	0.065	<0.001	6-7	0.164	<0.001	10-11	0.047	<0.001
2-13	0.140	<0.001	6-8	0.157	<0.001	10-15	0.078	<0.001
2-15	0.036	<0.001	6-9	0.082	<0.001	11-13	0.075	<0.001
2-16	0.086	<0.001	6-10	0.064	<0.001	11-15	0.031	<0.001
3-4	0.038	<0.001	6-11	0.111	<0.001	13-15	0.106	<0.001
3-6	0.107	<0.001	6-14	0.115	<0.001	15-16	0.052	0.008
3-7	0.056	<0.001	6-15	0.142	<0.001			

Data presented are mean differences, with probabilities (P), which are all significant values.

3.33. The effect of exposure to wave-action on shell shape parameters.

The shell parameters length, length of aperture, width of aperture, spire length and shell width, were all found to be significantly influenced by wave exposure (GLM. F=22.329; F=23.458; F=18.214; F=12.637; F=25.314 respectfully: P=<0.001 in all cases). Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences between sheltered and exposed sites within some habitat types (Table 3.11).

Table 3.11. Post Hoc Bonferonni multiple comparisons of shell shape parameters (shell length, aperture length, aperture width, spire, shell width), between sheltered and exposed locations.

	Shell length		Aperture length		Aperture width		Spire		Shell width	
Habitat	md.	*P*	md.	*P*	md.	*P*	md.	*P*	md.	*P*
boulders	2.496*	<0.001	1.577*	<0.001	0.473	0.075	0.473	0.278	1.968*	<0.001
small boulders	0.071	1.000	0.043	1.000	0.213	1.000	0.337	1.000	0.018	1.000
large boulders	3.502*	<0.001	1.649*	<0.001	1.065*	<0.001	2.487*	<0.001	1.858*	<0.001
benches etc.	1.987*	0.006	2.354*	<0.001	2.623*	<0.001	2.022*	<0.001	1.206	0.069
crevices	0.414	0.077	0.565*	<0.001	0.142	1.000	0.067	1.000	0.149	1.000

Data presented are mean differences, with probabilities (P), * which are significant values.

3.34. The effect of exposure to wave-action on shell shape ratios.

The shell parameter ratios, shell length/aperture length, aperture area, aperture area/length ^{2}, shell length/shell width) were all found to be significantly influenced by wave exposure (GLM. F=17.466; F= 48.161; F=14.375; F=120.642, respectfully: P=<0.001 in all cases). Post Hoc multiple comparisons (Bonferroni test) showed significant overall mean differences between sheltered and exposed sites within some habitat types (Table 3.12).

Table 3.12. Post Hoc Bonferonni multiple comparisons of shell shape ratios (shell length/ aperture length, aperture area, aperture area/length^2, shell length/shell width) within habitat types, but between sheltered and exposed locations.

	Length/ Aperture length		Aperture area		Aperture area/ Length squared		Shell length/ Shell width	
Habitat	md.	*P*	md.	*P*	md.	*P*	md.	*P*
boulders	1.081	1.000	20.657*	<0.001	0.064	1.000	0.012	1.000
small boulders	0.053	0.656	3.021	1.000	0.024	1.000	0.046	1.000
large boulders	0.054*	<0.001	30.260*	<0.001	0.008*	0.002	4.745*	<0.001
benches etc.	0.088	0.542	67.160*	<0.001	0.065*	<0.001	0.016	1.000
crevices	0.031*	0.003	6.206*	0.041	0.046	0.511	0.011*	0.002

Data presented are mean differences, with probabilities (P), * which are significant values.

3.35. The effect of shore level on shell shape parameters (Figure 3.1.)

Menai Bridge: only spire length was significantly influenced by shore level (GLM. F=3.397 P=0.036). The shell parameters Length (GLM. F=1.893 P=0.154), length of aperture, (GLM. F=0.855 P=0.427), width of aperture (GLM. F=1.386 P=0.253), and shell width (GLM. F=1.971 P=0.143), were not significantly influenced by shore level. Post Hoc multiple comparisons (Bonferroni test) showed some significant overall mean differences in shell shape parameters between shore levels (Appendix 3, Table 3.1).

Trwyn y Penrhyn: the shell parameters length (GLM. F=10.247 P=<0.001), length of aperture, (GLM. F=10.486 P=<0.001), width of aperture (GLM. F=11.317 P=<0.001), spire length (GLM. F=8.667 P=<0.001), and shell width (GLM. F=10.630 P=<0.001), were all significantly influenced by shore level.

Llanfairfechan: shell length (GLM. F=9.390 P=<0.001), length of aperture, (GLM. F=7.797 P=0.001), width of aperture (GLM. F=7.354 P=0.001), spire length (GLM. F=9.949 P=<0.001), and shell width (GLM. F=6.877 P=0.001), were all significantly influenced by shore level.

Red Wharf Bay: shell length (GLM. F=14.253 P=<0.001), length of aperture, (GLM. F=8.418 P=<0.001), width of aperture (GLM. F=5.601 P=0.005), spire length (GLM. F=12.706 P=<0.001), and shell width (GLM. F=11.249 P=<0.001), were all significantly influenced by shore level.

Porth Nobla: only spire length was significantly influenced by shore level (GLM. F=10.259 P=<0.001). The shell parameters length (GLM. F=3.919 P=0.022), length of aperture, (GLM. F=0.799 P=0.379), width of aperture (GLM. F=2.633 P=0.076), and shell width (GLM. F=1.203 P=0.304), were not significantly influenced by shore level.

Porth Defaid: only spire length was significantly influenced by shore level (GLM. F=3.965 P=0.023). The shell parameters length (GLM. F=2.934 P=0.059), length of aperture, (GLM. F=2.217 P=0.116), width of aperture (GLM. F=2.315 P=0.105), and shell width (GLM. F=1.755 P=0.180), were not significantly influenced by shore level.

3.36. The effect of shore level on shell shape ratios. (Figure 3.2)

Menai Bridge: all of the shell shape ratios, shell length/aperture length (GLM. F=1.026 P=0.361), aperture area (GLM. F=1.434 P=0.242), aperture area/length^2 (GLM. F=0.871 P=0.420), and shell length/shell width (GLM. F=0.915 P=0.403), were not significantly influenced by shore level. Post Hoc multiple comparisons (Bonferroni test) are shown in Appendix 3 (Table 3.2).

Trwyn y Penrhyn: only aperture area (GLM. F=12.540 P=<0.001), was significantly influenced by shore level. The other shell shape ratios, namely: shell length/aperture length (GLM. F=1.818 P=0.166), aperture area/length^2 (GLM. F=2.394 P=0.094), and shell length/shell width (GLM. F=1.349 P=0.262), were not significantly influenced by shore level.

Llanfairfechan: shell length/aperture length (GLM. F=8.063 P=<0.001), aperture area (GLM. F=9.093 P=<0.001), aperture area/length^2 (GLM. F=5.049 P=0.007), and shell length/shell width (GLM. F=10.717 P=<0.001), were all significantly influenced by shore level.

Red Wharf Bay: shell length/aperture length (GLM. F=8.035 P=0.001), aperture area (GLM. F=7.751 P=0.001), aperture area/length^2 (GLM. F=11.060 P=<0.001), were significantly influenced by shore level. Shell length/shell width (GLM. F=2.072 P=0.131), was not significantly influenced by shore level.

Porth Nobla: shell length/aperture length (GLM. F=18.610 P=<0.001), and aperture area/length^2 (GLM. F=18.331 P=<0.001), were significantly influenced by shore level. Aperture area (GLM. F=1.959 P=0.145), and shell length/shell width (GLM. F=1.333 P=0.268), were not significantly influenced by shore level.

Porth Defaid: shell length/aperture length (GLM. F=3.614 P=0.031), and shell length/shell width (GLM. F=4.695 P=0.012), were significantly influenced by shore level. Aperture area (GLM. F=2.589 P=0.081), and aperture area/length^2 (GLM. F=1.477 P=0.235), were found not to be significantly influenced by shore level.

3.37. The variation of shell shape parameters between shores.

The changes in these parameters within shore levels on different shores in shown in Figure 3.3, with a summary of variation between shores in Figure 3.4. Shell length (GLM. F=24.204 P=<0.001), length of aperture, (GLM. F=50.586 P=<0.001), width of aperture (GLM. F=23.581 P=<0.001), spire length (GLM. F=15.480 P=<0.001), and shell width (GLM. F=42.276 P=<0.001), were all found to be significantly influenced by shore. Post Hoc multiple comparisons (Bonferroni test) showed some significant overall mean differences in shell shape parameters between shores (Appendix 3, Table 3.3).

3.38. The variation of shell shape ratios between shores.

The changes in these ratios within shore levels on different shores in shown in Figure 3.5; with a summary of ratio variation between shores in Figure 3.6. Shell length/aperture length (GLM. F=42.633 P=<0.001), and aperture area (GLM. F=34.458 P=<0.001), were found to be significantly influenced by shore. Aperture area/length^2 (GLM. F=0.802 P=0.549), and shell length/shell width (GLM. F=0.927 P=0.462), were found not to be significantly influenced by shore. Post Hoc multiple comparisons (Bonferroni test) showed some significant overall mean differences in shell shape ratios between shores (Appendix 3, Table 3.4).

3.39. Shell teeth and shell colour.

3.391. Shell teeth.

The presence of shell teeth between different levels within shores at six locations.

The frequency of shell teeth were all found to be significantly influenced by shore level at Llanfairfechan (GLM. F=4.350 P=0.014), and Porth Defaid (GLM. F=17.238 P=<0.001), but not

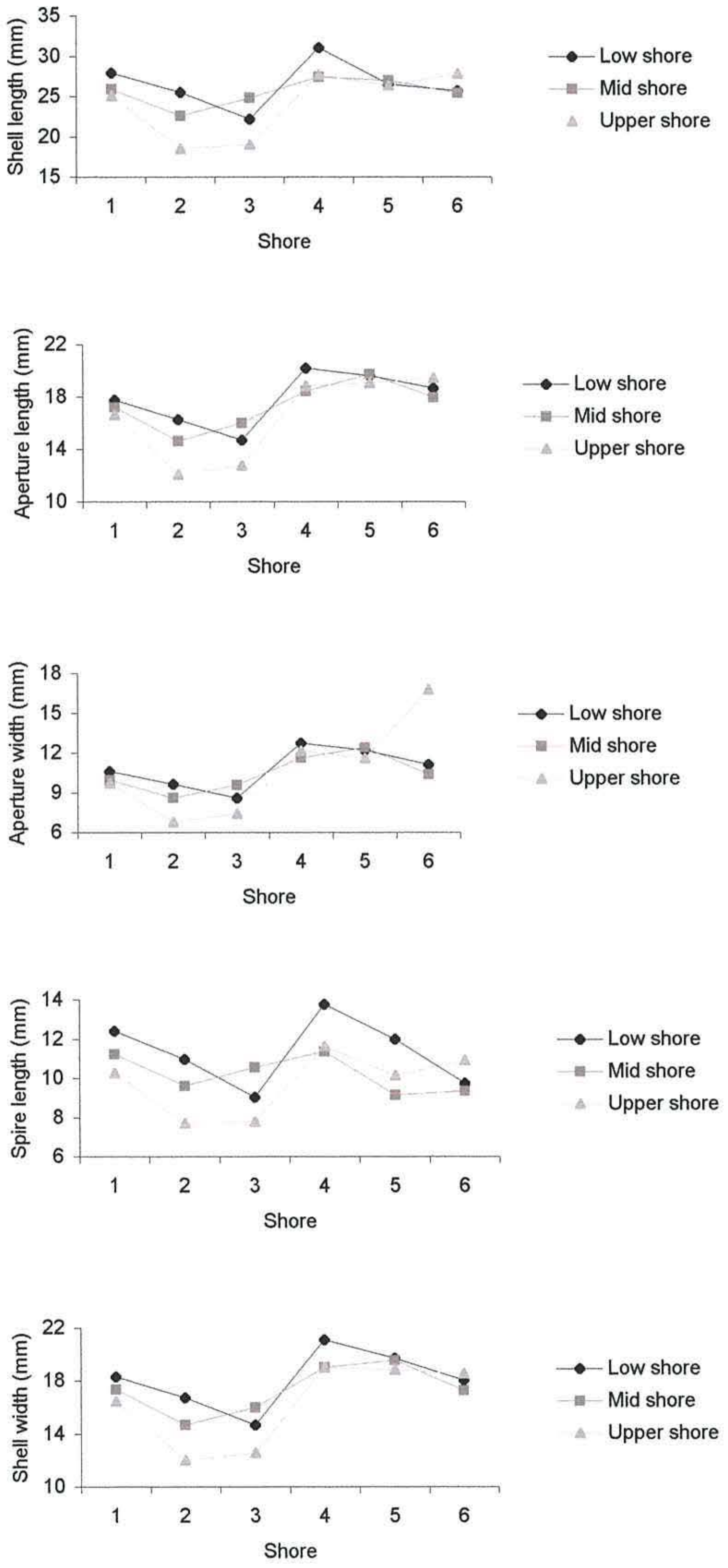


Figure 3.3. Variation in shell shape parameters within shore levels on different shores. Key to shores is on page 75.

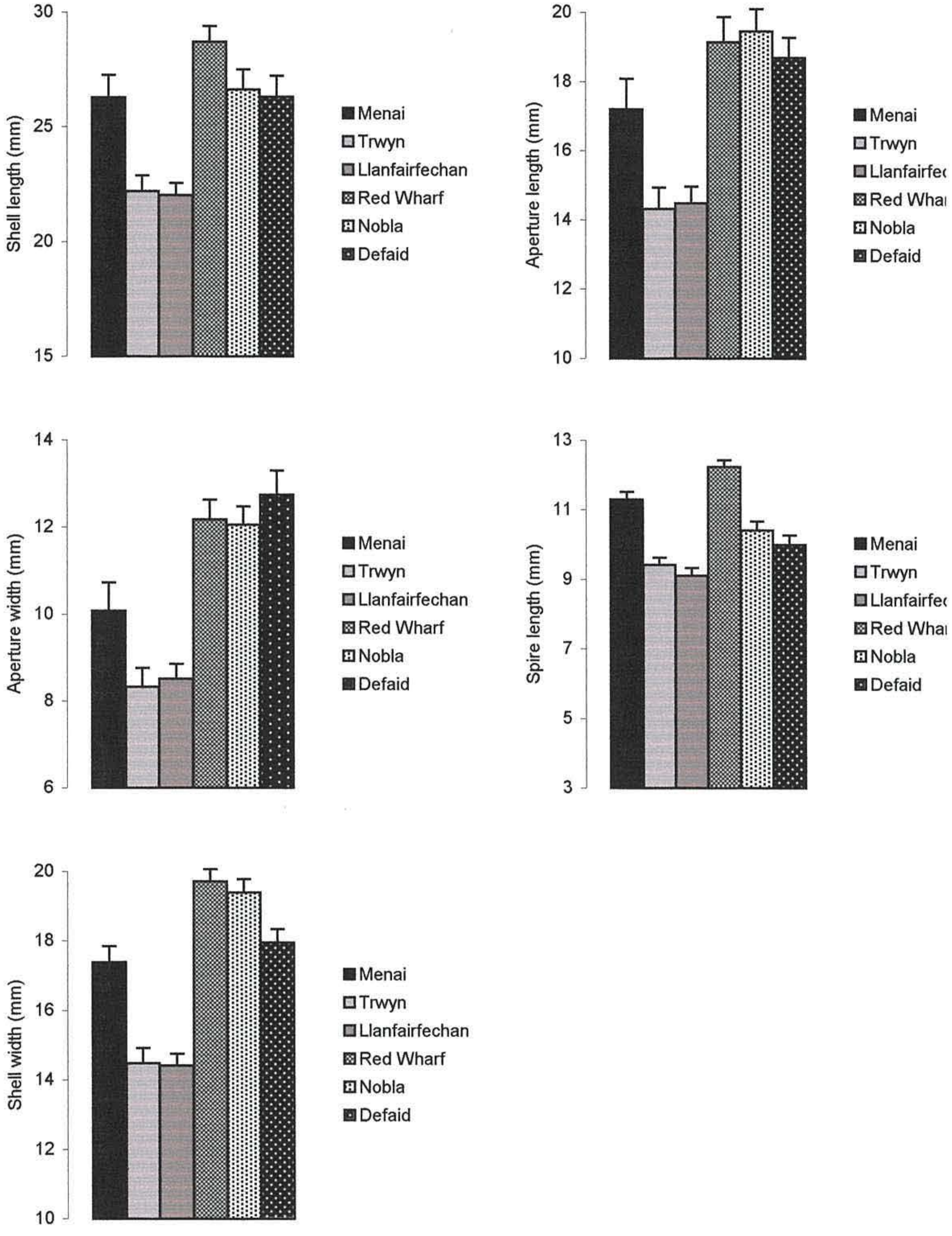


Figure 3.4. Summary of the variation in shell shape parameters on different shores.

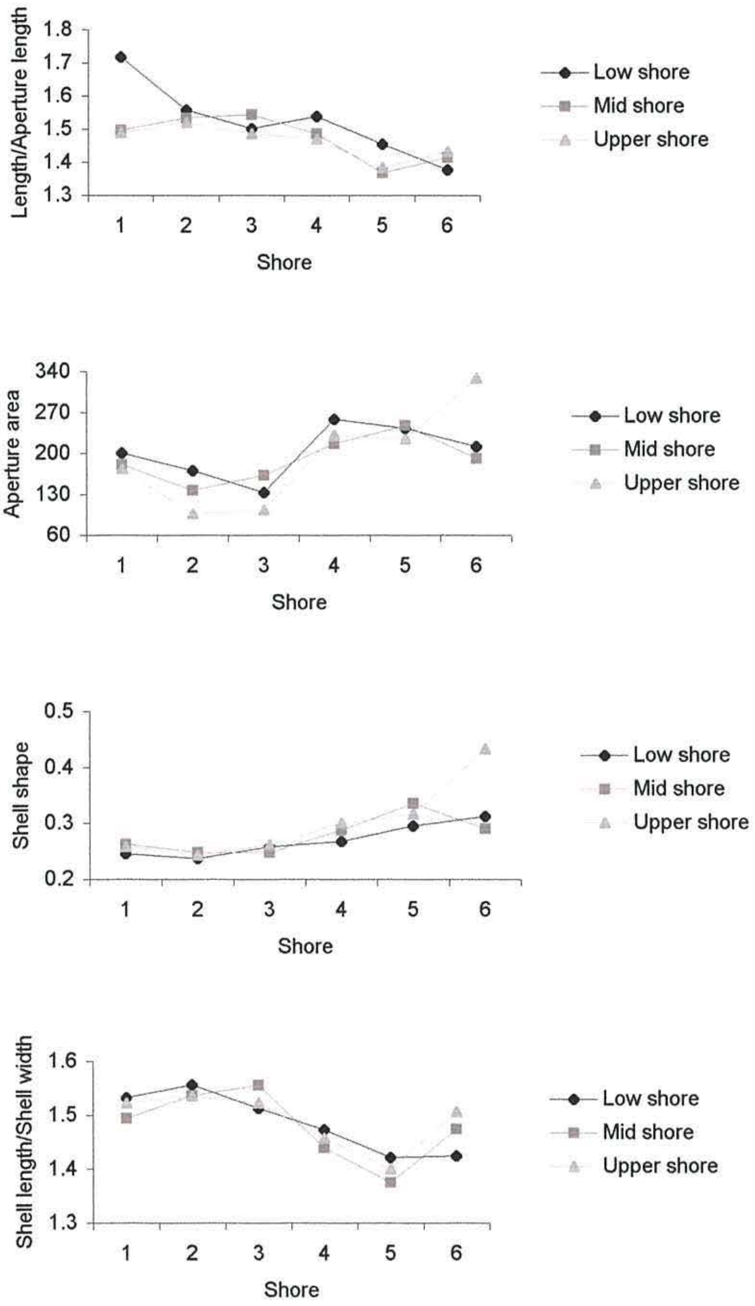


Figure 3.5. Variation in shell shape ratios within shore levels on different shores. Key to shores is on page 75.

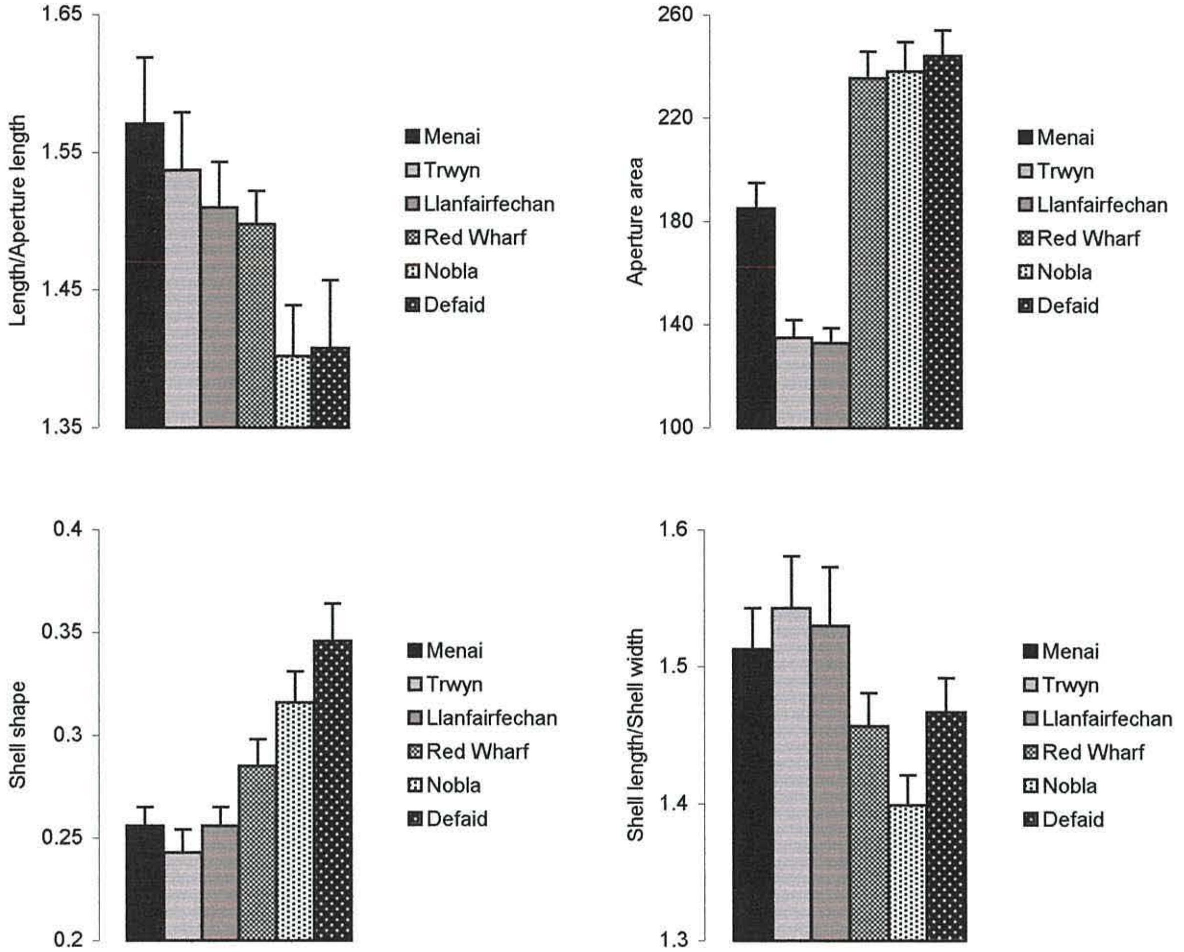


Figure 3.6. Summary of the variation in shell shape ratios on different shores.

significantly influenced by shore level at Menai Bridge (GLM. F=0.646 P=0.526), Trwyn y Penrhyn (GLM. F=1.678 P=0.190), Red Wharf Bay (GLM. F=0.026 P=0.974), and Porth Nobla (GLM. F=2.430 P=0.092). Post Hoc Bonferonni multiple comparisons of shell teeth frequency showed differences between low and mid levels (P=0.012) at Llanfairfechan and between low and mid (P=<0.001), and between mid and upper (P=<0.001) shore levels at Porth Defaid, as well as differences between most shores (Table 3.13). Data measured were the mean number of shell teeth per individual per shore level per shore.

Table 3.13 Post Hoc Bonferonni multiple comparisons of shell teeth frequency on different shores showing significant differences.

Shores	md.	*P*	Shores	md.	*P*	Shores	md.	*P*
1-3	0.134	0.031	2-3	0.247	<0.001	3-4	0.705	<0.001
1-4	0.571	<0.001	2-4	0.459	<0.001	3-5	0.624	<0.001
1-5	0.490	<0.001	2-5	0.377	<0.001	3-6	0.500	<0.001
1-6	0.367	<0.001	2-6	0.254	<0.001	4-6	0.205	0.014

Data presented are mean differences, with probabilities (P), which are all significant values.

Key to shores 1: Menai Bridge; 2: Trwyn y Penrhyn; 3: Llanfairfechan; 4: Red Wharf Bay; 5: Porth Nobla; 6: Porth Defaid.

The differences in shell shape parameters and shell shape ratios between those *Nucella* with and without shell teeth is represented in Figures 3.7. and 3.8 respectively.

3.392. Shell colour.

The presence of light and dark morphs between different levels within shores at six locations. The frequency of light and dark morphs were all found to be significantly influenced by shore level at Menai Bridge (GLM. F=4.670 P=0.011), Llanfairfechan (GLM. 26.570 P=<0.000), Red Wharf Bay (GLM. F=5.511 P=0.005), and Porth Nobla (GLM. F=6.511 P=0.002), but not found to be significantly influenced by shore level at Trwyn y Penrhyn (GLM. F=0.456 P=0.635), and Porth Defaid (GLM. F=0.184 P=0.832). Post Hoc Bonferonni multiple comparisons of the frequency of light and dark morphs showed many differences between levels at four of the shores investigated (Table 3.14), and between shores (Table 3.15).

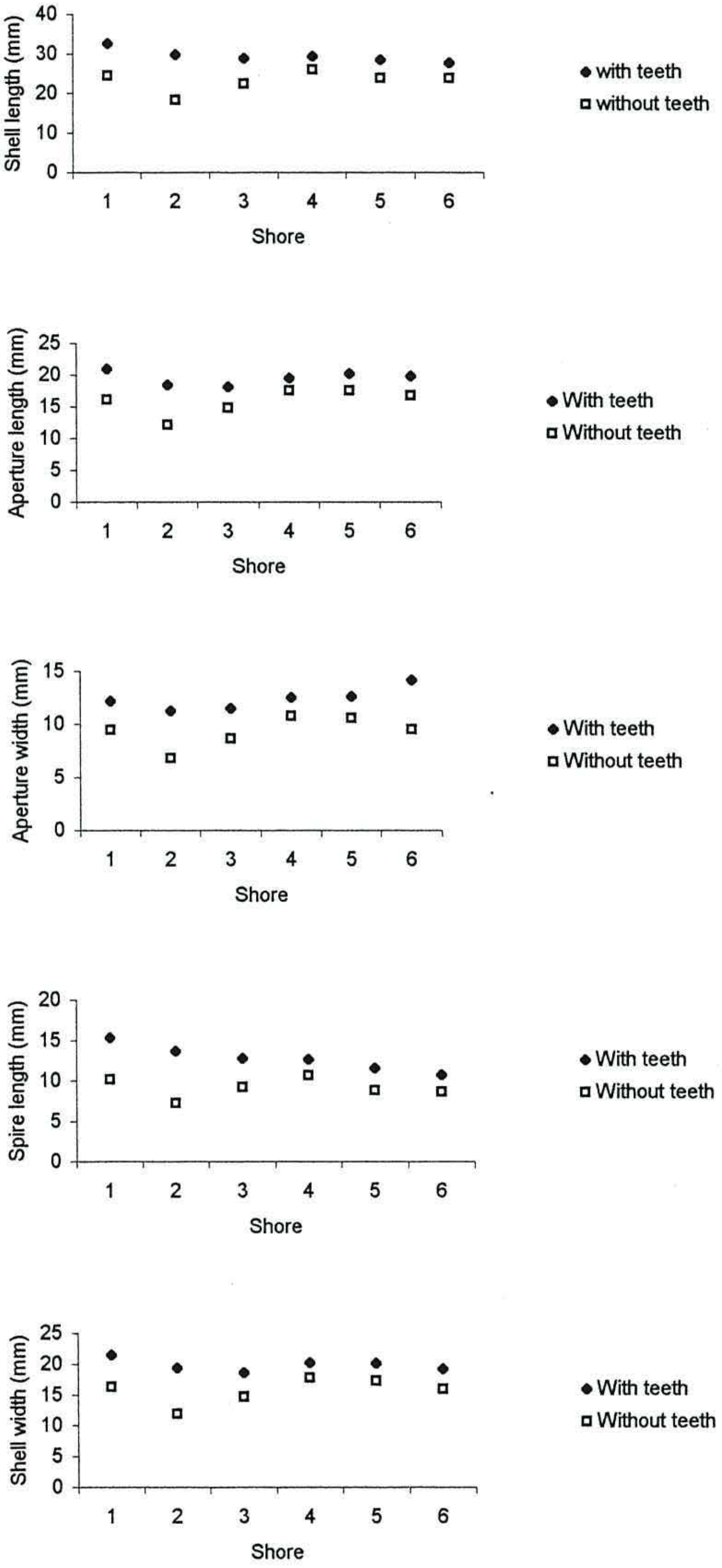


Figure 3.7. Differences in shell shape parameters with presence/ absence of shell teeth. (key to shores on page 75).

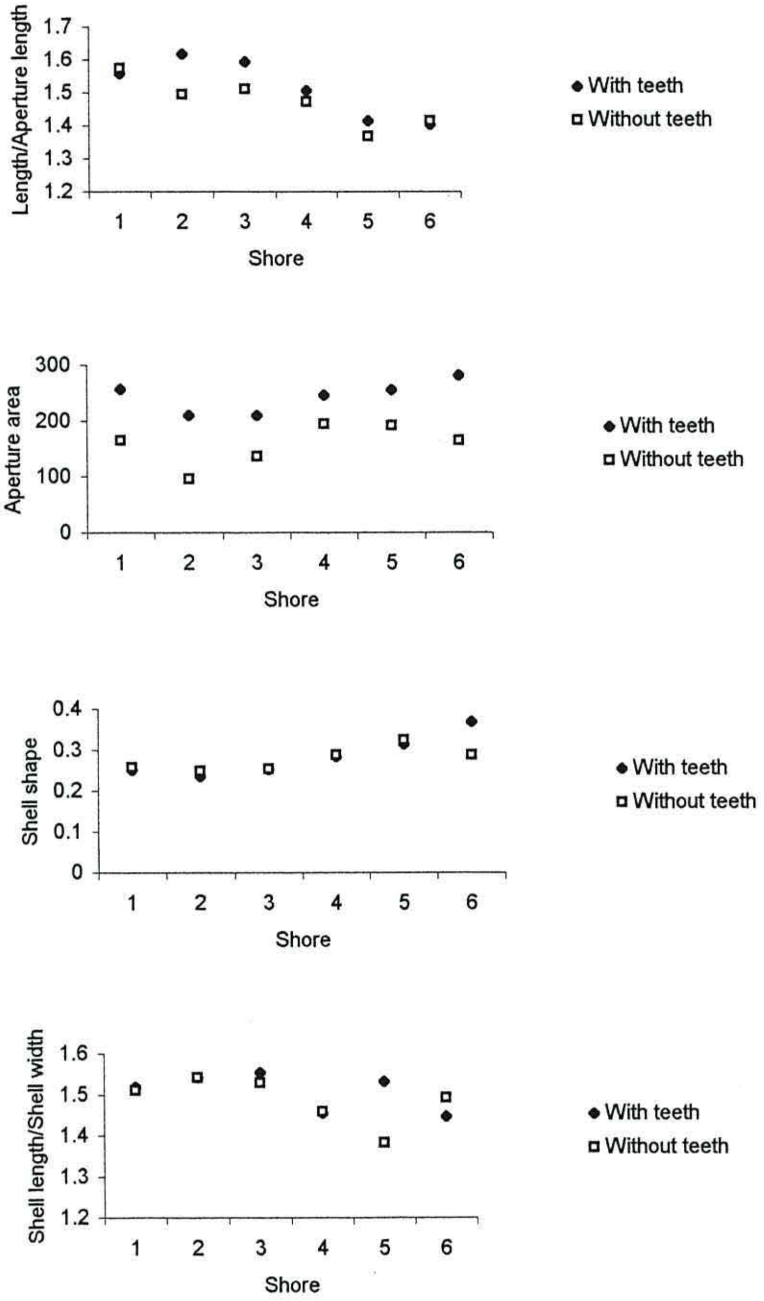


Figure 3.8. Differences in shell shape ratios with presence/ absence of shell teeth. (key to shores on page 75).

Table 3.14. Post Hoc Bonferonni multiple comparisons of the percentage frequency of light and dark morphs from different shore levels showing significant differences.

Shore	Levels	md.	*P*	Levels	md.	*P*
Menai Bridge	1-2	0.361	0.048	1-3	0.448	0.016
Llanfairfechan	1-2	0.638	<0.001	2-3	0.644	<0.001
Red Wharf Bay	1-2	0.560	0.031	1-3	0.688	0.008
Porth Nobla	1-2	0.693	0.002	2-3	0.469	0.039

Data presented are mean differences, with probabilities (P), which are all significant values.

The presence of light and dark morphs between shores at six locations.

The frequency of light and dark morphs were found to be significantly influenced by shore (GLM. F=35.679 P=0.001). Post Hoc Bonferonni multiple comparisons of the frequency of light and dark morphs showed many differences between shores (Table 3.15).

Table 3.15. Post Hoc Bonferonni multiple comparisons of the percentage frequency of light and dark morphs between shores showing significant differences.

Shores	md.	*P*	Shores	md.	*P*	Shores	md.	*P*
1-3	0.944	< 0.001	2-3	0.905	<0.001	2-6	0.310	0.049
3-4	0.737	<0.001	3-5	0.722	<0.001	3-6	1.215	<0.001
4-6	0.479	0.001	5-6	0.493	<0.001			

Data presented are mean differences, with probabilities (P), which are all significant values.

Comparisons of shell shape parameters and shell shape ratios between light and dark coloured morphs of *Nucel*la are depicted in Figures 3.9 and 3.10 respectively.

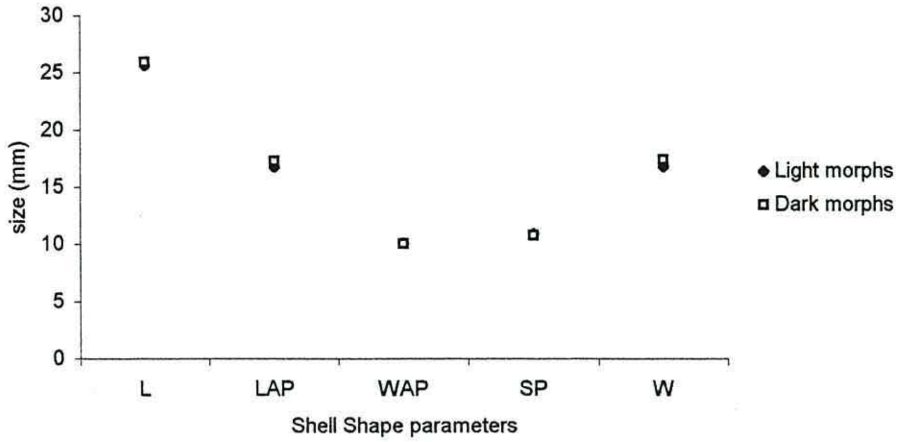


Figure 3.9. Comparison of Shell Shape parameters between light and dark colour morphs (pooled data from all study shores).

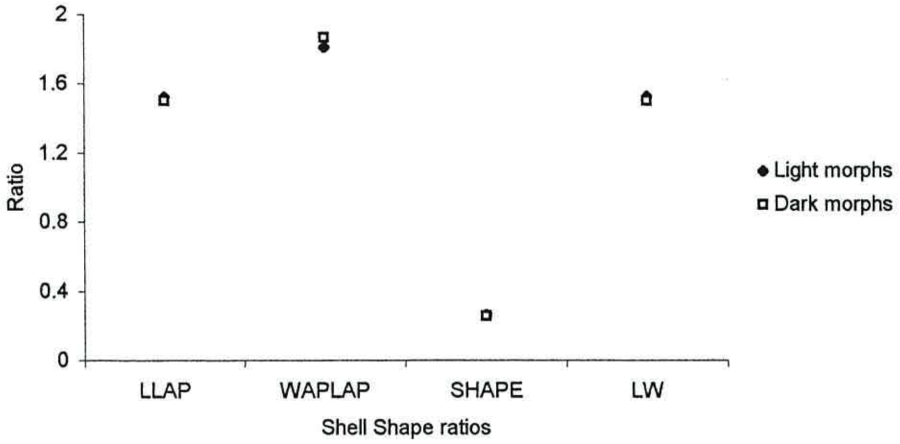


Figure 3.10. Comparison of shell shape ratios between light and dark colour morphs (pooled data from all study shores).

3.4. DISCUSSION.

All observations were made on adult dogwhelks (22.0-41.9 mm in shell length) to eliminate changes in shape that occur with ontogenic development in the mid-to-late juvenile stages (12.0-16.9 mm) of *Nucella lapillus* , except (where stated) juveniles were examined seperately.

Variation in shell shape between habitats (SeeAppendix 3, Figure 3.1).
Samples from four hundred and seventy-four different sites on Anglesey, showed clear trends in the relationship between *Nucella lapillus* shell dimensions and habitat type. The largest (longest, widest, most extensive spire) dogwhelks were most often found on open surfaces: on piers, ramps and ledges, or on small stones and pebbles. Most of these whelks also had a very large aperture area, a good indication of a relatively large foot (Etter, 1989), which is neccessary to maintain a position in the open, particularly when subject to heavy wave action. The next largest on average, were boulder and crevice populations. They were slightly shorter in length, and with a marginally reduced aperture area compared to the first group. Next in mean size, were individuals from rock benches, outcrops, caves and large trenches (fairly exposed), and those found in small pits (pocks), and in mussel beds. These whelks need to be fairly small to negotiate the resticted environment within which they are found. By far the smallest grouping of whelks, in all respects (length, width, spire and aperture area), were those usually found on vertical surfaces. In this habitat, the animal's hold is often tenuous, and larger shells can be subject to increased drag forces from water flow. Short, compact shell forms are less prone to dislodgement, which is disadvantageous and can even be lethal for *Nucella lapillus.* The extremely large number of individuals measured from so many sites ensured that these x-sectional surveys, produced statistically significant comparisons of dogwhelk distribution in relation to the different topographical features. The observed habitat-specific differences in shape and body form of *Nucella* are probably due to environmental selection on the phenotype (Phillips et.al., 1973), and show that whelk populations can be molded by ecological conditions (Seed, 1978).

Variation in shell shape ratios between habitats.

The three measurements of shape: maximum length/maximum aperture length (Crothers, 1973), length/width (Seed, 1978) and aperture area/ length^2 (Hughes personal communication), also showed significant mean differences between the habitat categories:

Length/aperture length (L/Lap).

The largest ratio (an indication of long, elongate forms), was seen in those *Nucella* on ramps, piers, stones and pebbles, and all sizes of boulders; dogwhelks of all other habitat types fell into a second group with a smaller ratio. Most *Nucella lapillus* shell forms in Europe conform to the characteristic form of correlation between shell shape and shell length (Crothers, 1985b) exhibited by Pembrokeshire samples:

$y = 1.214 + 0.036x$ where the L/Lap ratio is 1.22-1.50 (Crothers 1973).

Deviation from the "Normal form" to "elongate" with L/Lap ratios of 1.59-1.86 (Crothers, 1982), is found in some specific locations in Britain including the West Coast of Scotland (Crothers, 1982a), Somerset (Crothers, 1977), North Wales (Crothers, 1985b), and the Severn Estuary (Crothers, 1974). In my work on Anglesey (L/Lap maximum of 1.86), very elongate forms were predominant in sheltered locations (see Appendix 2, Table 2.1.).

The length/width ratio.

Relatively long elongated shells were observed on stones, pebbles and small boulders, and in pits. Rounder, more squat shells were found consistantly in refuges and on vertical open benches, as well as in trenches, mussel beds, and caves. Long elongated shells on open vertical faces and in trenches, will be exposed to the full force of waves and currents at all times. Snails that are in these locations will find it difficult to maintain tenacity, even in sheltered areas that only experiance periodic harsh weather conditions. Round flat forms are more suited to these environments due to their lower drag coefficients.

Aperture area/length^2.

The mean ratio of aperture area/length^2 was highest in dogwhelks found in refuges, in exposed stretches of the coastline, than in those on boulders, benches and trenches. Individuals on piers, stones and pebbles and particulaly vertical surfaces had the smallest value of this ratio. It was suprising to find that whelks on vertical rock structures had proportionately smaller aperture areas (and hence smaller feet), than many individuals from other microhabitats, although this was probablty related to their intrinsically smaller overall size.

Variation in shell shape within populations.

The above comparisons in form, though statistically significant do not reveal the extensive variation in shell shape that occurs within shores, within niche types upon the shore, and even within separate breeding populations of *Nucella lapillus*. Within breeding enclaves, individual shape can be size-dependent and influenced by local food availability (Vermeij, 1982). Even the small and isolated Hebridean islands tended to support an extended range of sizes shapes. Unfortunately very little is known about the relative importance of intrinsic (genetic) and extrinsic (environmental) influences on the development of shell shape in this species (Crothers, 1982).

The variation of shell shape in relation to boulder size.

Whelks from small boulders had longer spires, larger aperture areas, and were more elongate (L/W ratio) (all $P < 0.001$), but in all other aspects were similar to those found both on medium and large boulders. The refuges associated with small boulders, including under boulder spaces, are reduced in size compared to those on larger substrate formations, and only thin, and elongate forms of *Nucella lapillus* were able to manoeuvre into and through these spaces with ease. Large boulders exhibited a greater variety in size and shape distribution of dogwhelks consistent with their greater microhabitat diversity.

Variation in shell shape between shore levels.

There was little variation in any of the shell measurements or measurement ratios in relation to tidal height investigated, with only one exception. This was in the length/width ratio and specific to

Porth Defaid. In the wave-swept reaches of this site (that is particularly in the lower shore), shorter squater forms predominated. Characteristically longer and thinner forms were found in the mid shore. Whelks in the upper zone, also had a much larger aperture area (especially so, when compared to shell length). This could be related to the extreme wave conditions (both surface waves and underwater fronts), that are more frequently experianced by animals at lower shore levels on this very exposed shoreline. Less elongated forms will find it easier to remain attached to the substrate in these adverse conditions. Dogwhelks in the upper shore also experiance a prolonged buffering from surface waves around the turn of the tide for much of the year, for which a substantial foot anchorage would prove beneficial.

Despite the lack of statistical verification, we can still see obvious trends in dogwhelk shape in relation to shore level at the five other study sites (Figures 3.1). Those *Nucella lapillus* from the lower shore tend to be longer, wider (greater mean overall size), with a longer spire, when compared to populations from the upper shore, although the relative proportions of these shell paramters rarely change with tidal height (Figure 3.2). These trends are more pronounced on the three most sheltered shores (Menai, Trwyn and Llanfairfechan). It is dificult to explain the observed trends between shore levels. To a certain extent, animals at all three levels are subject to broadly similar physical and biological factors. However, there is variation up the shore in the degree of slope, presence of brake-water structures, available cover etc., which all contribute to the amount of desiccation and wave-action, that individuals experience in their different positions on the shore. The particular physical factors encounted in the high intertidal, cause higher mortality rates in small individuals that tend to be more susceptible to these factors, although a pattern of increasing body sizes with tidal height that could result from this (Vermeij, 1972), was not apparent. In fact mean body size clearly decreased with tidal height on the three most sheltered shores, which had appreciable populations of the *Nucella* predator *Carcinus maenas* (shore crab), particularly in the lower shore (see section 2.311). Larger whelks in the lower shore region, which have escaped predation by their size, could then predominate in conditions where other mortality factors (dessication, cold temperatures), are reduced compared to higher tidal elevations.

Variation in shell shape between shores (see Appendix 3, Figure 3.2).

Dogwhelks from exposed areas tended to have short squat shells in comparison to those from sheltered sites, which had longer spires (Crothers, 1977;1983), as first described by Cooke (1895). The considerable variation in shell shape between different populations in the survey, is primarily a reflection of adaptation to wave action, desiccation and predation (Crothers, 1992), and secondarily a response to water temperature, diet, and substratum (Phillips et. al., 1973). These intrinsic shell shape patterns can even be used as a valid assesment of wave exposure (Crothers, 1985). Both shell size and shape parameters, differed between sheltered and exposed boulders, benches and crevices: Medium to large boulders in sheltered locations had more elongate individuals with longer spires. Similarly, sheltered benches contained longer shelled (with longer shell spires) forms, but with relatively smaller aperture areas, than animals in exposed conditions. Clearly, the severity of wave impact in exposed locations favoured shorter rounded forms, better able to cope with the conditions. Large snails also have fewer crevices that they can exploite as refuges from this wave action (Etter, 1989). There was no selective advantage associated with tall narrow shells in exposed conditions (Crothers, 1973), as they were readily dislodged (Seed, 1978).

There were few differences in the dogwhelks found in crevices on sheltered shores and those found in crevices at exposed locations, except that whelks at the former had larger L/Lap and L/W ratios, and smaller aperture areas, which means they were longer and thinner. Juveniles differed significantly between sites for all these indices of shell shape (one-way ANOVA, both $P < 0.01$). Adults differed significantly among sites for all four indices (shell length/aperture length, aperture area, aperture area/length^2, shell length/shell width) of shell shape (all $P < 0.001$), with *Nucella lapillus* from exposed crevice habitats having shorter, squatter (=wider) shells with larger apertures, than those from sheltered locatons. Shell shape is influenced by food availibility and is size-dependent (Vermeij, 1982), and since the dogwhelks from sheltered sites were consistently larger than from wave-swept ones (Seed, 1978), these differences in proportion might have been considered to be due to size effects, except for the fact that regression correlations of all these shell variables upon shell length were not significant.

Foot area and shell aperture.

The pedal surface area (PSA) of several intertidal prosobranchs, varied among shores differentially exposed to wave action, increasing with wave-shock (Etter, 1989), and other hydromechanical forces (Etter,1988a). Foot size is larger in high-wave-energy environments for *Nucella lapillus* (Kitching et al.,1966), and *Nucella emarginata* (Miller, 1974), and is positively correlated with the speed of movement in snails, and with their ability (tenacity) to cling to the rock at sites with strong wave action (Kitching et. al.1967; Fairweather, 1988c*)*. This ability to resist dislodgement derives entirely from differences in pedal surface area (Etter, 1988a), which develop in later juveniles as values in this parameter between hatchlings from differently exposed shores are statistically indistinguishable (Etter,1988b)

A larger shell aperture was found on exposed shores in Ireland (Kitching et al., 1966), allowing for a large pedal area, and therefore permitting greater adhesion to rock surfaces and enhancing the ability to withstand the high shear forces produced by vigorous wave-action (Seed, 1978). Measurement of shell aperture is therefore a good estimate of actual foot area. Therefore the former parameter can be utilised as an estimation of the former, and as an indication of the relative tenacity of whelks from different habitats and different shore locations. Dogwhelks on the three most wave-swept shores had much larger aperture areas than the three relatively sheltered ones, as we might expect from the physical attributes of the respective locations (see section 2.3). The fact that aperture areas on the most sheltered shore (Menai) were significantly greater than on either Trwyn or Llanfairfechan is partly a reflection of the general larger sizes found at Menai Bridge. The narrower shell apertures found on sheltered shores (Figure 3.4) are beneficial to those *Nucella lapillus* inhabiting these sites. This, along with the presence of thicker more robust shells (Kawai personal communication; Vermeij, 1982), increases their protection against crab predation (Etter, 1988a), a trend that has been observed in many earlier studies on whelks (Ebling et. al., 1964; Hoxmark, 1971; Curry and Hughes, 1982; Crothers, 1983; Etter, 1989). It is known that variation in wave action modifies both the biotic and abiotic conditions that dogwhelks are subject to (Etter,1988a), affecting their morphological, physiological and behavioural characteristics (Crothers 1985; Etter, 1989). In particular, high amplitude and frequency of wave impact induces a relative increase in size of the aperture, by eliminating less tenacious individuals, indicating interaction between the genotype and the environment (Osborne, 1977).

Drag and dislodgement.

As drag and lift increase in proportion to an organism's size (Rees, 1972; Chamberlain and Graus, 1975), larger snails on exposed sections of Anglesey tended to experience greater drag forces, increasing the probability of dislodgement, particularly when actively moving (Taylor, 1976). To avoid this they often relocated to sheltered microhabitats, reducing drag (low coefficient). Exposure to wave action was inversely related to *Nucella* distribution on these shores (Chapter 2). Whelks at these locations increased adhesion with a large foot (Galley, 1991; Trussell et. al., 1993), and were shorter, squatter and smaller, offering less resistance to water movement (reduced maximum projected surface area: MPSA).

Shell size.

There were differences in relative shell size on different shores associated with wave-exposure (Trussell, 1997). Whelks from exposed shores grew more slowly and terminated growth at a smaller size than those from protected areas in investigations by Etter (1989). Environmental forces depress growth on wave-swept shores (Brown and Quinn,1988; Etter, 1996), although small (shell length) adult size appears to be favoured on exposed shores, as large snails (>30mm in length) are more vulnerable to dislodgement by wave action (Denny et. al., 1985). On the other hand, a larger asymptotic size is favoured on less exposed shores, where *N. lapillus* suffers more intense predation, since larger individuals are less vulnerable to predation (Crothers, 1985a). Populations on exposed and intermediate study shores were dominated by small adults and had fewer juveniles, whilst protected-shore populations were dominated by large adults with considerately more juveniles (Chapter 2). The exposed study shores had few (Red Wharf), or virtually no (Nobla and Defaid), crab predators, and much of the predation that did take place in these locations was centered on juvenile dogwhelks (Personal observation). Variation in the size/shape response of *Nucella lapillus* to geographical differences in wave action may reflect the advantage of a variable (plastic) response to these environmental factors (Etter, 1988a).

Shell teeth.

A relatively thick-lipped whelk shell with pronounced "teeth"immediately inside the shell aperture, indicates a periodic episode of interrupted growth due to environmental stress (Crothers, 1971; Seed, 1978). There were consistent trends in the proportion of individuals with this trait with respect to shore level on the main study sites. At five of these locations, a greater percentage of individuals (adults) in the mid and upper reaches of the shore had teeth. At these tidal heights, the fluctuations in the environmental factors of desiccation and temperature are frequently more extreme and therefore stressful. The one exception was Porth Defaid (very exposed), where increased teeth frequencies were found in the lower shore where dogwhelks are subject to both more frequent surface and submarine waves of high amplitude. Predominances of double (and more) rows of teeth (evidence of repeated stress), closely followed these patterns on all six shores. Greater proportions of dogwhelks had shell teeth on the three more exposed shores (Defaid, Nobla and Red Wharf), fewer at sheltered locations (Menai andTrwyn), and least at Llanfairfechan. This is a reflection on the amount of environmental stress experienced by dogwhelks in places with differing degrees of wave exposure (Etter, 1989). The results from both shore levels and shores combined suggests that both repeated wave action and prolonged exposure to air and low temperatures, can results in the growth of shell teeth.

Shell colour morphs.

The pattern of distribution of light and dark colour morphs at the three different levels (lower, mid and upper) were the same on all of the study shores except one. Relatively more light coloured morphs were present in mid and upper levels, darker morphs were predominant in the lower. The proportion of dark coloured morphs was far greater at Llanfairfechan than all the other shores. These individuals are more inconspicuous on the extensive mussel beds atop boulders, that are only found at this one shore of the six investigated (although some mussels are found at Red Wharf Bay). Light shell morphs (white, offwhite, cream), were more common at the most sheltered locations (Menai and Trwyn), but also at Porth Defaid which is very exposed to waves. Interpopulation variation in shell colour of *N.lapillus* is in part a response to a selective gradient in physiological stress (Etter,1988b), and generally lighter forms predominated in areas subject to more insolation.

CHAPTER 4

NUCELLA LAPILLUS DISPERSAL AND FORAGING PATTERNS.

4.1 INTRODUCTION.

The movement and orientation of motile intertidal animals are important factors in determining their distribution and abundance. Many complex and interacting factors affect the movements of intertidal snails (Underwood and Chapman, 1985). Environmental influences include: polarised light (Burdon-Jones and Charles, 1959; Charles, 1961), geomagnetic fields (Brown, 1960), gravity (Fraenkel, 1927); strong wave action (McQuaid, 1981), and water currents (Gendron, 1977). Active migration is often constained by competition (Thain, 1971; Branch, 1975b), escape from predators (McQuaid, 1982), and the need to maximize reproductive output (Paine, 1969a). Snail movement has been closely investigated on a number of occasions (Miller, 1974; Dunkin and Hughes, 1984; Fairweather, 1988c; Rogers, 1988; Hughes and Burrows, 1994), although the orientation of intertidal gastropods has only rarely been studied (Chelazzi et. al., 1986).

Movement Patterns.

Dogwhelks exhibit an intrinsic activity cycle (Chelazzi et. al., 1983), which can be modified by the environment and interactions with other intertidal organisms. Most rocky shore gastropods adopt what is known as an energy saving "isospatial strategy", which means that they tend to remain within a narrow belt of the intertidal, along the sea-land axis (Chelazzi et. al., 1986). This is due to their low speed and the high energetic cost of their particular type of locomotion. There are different types of movement: occasional (e.g.during storms and at the sudden appearence of predators), continuous (e.g. progressive migration along the sea-land axis), and rhythmic (e.g. movements related to seasonal, synodic, tidal and diel fluctuations), which often appear as zonal migrations up and down the shore (Chelazzi et. al., 1986). Periodically, some intertidal gastropods may move randomly, such as generalist herbivores when grazing (Petraitis 1982; Chapman 1986). *Nucella lapillus* seems only capable of moving short distances in one day (Hughes and Burrows,1994; Hughes and Drewett, 1985), although *Nucella emarginata* has been seen to forage horizontally as far as 15 metres in a two week period (Dayton, 1971). Major fluctuations in density occur due to immigration and emigration of whelks to and from particular areas on the shore (Fairweather, 1988b). All these migration patterns are probably an interaction of endogenous and exogenous factors (Vannini and Chelazzi, 1978). There have been many studies on the movement of intertidal gastropods using net displacement and direction (eg. Underwood, 1977; Petraitis, 1982; Hawkins and Hartnoll, 1983b; Chapman, 1986; Chapman and Underwood, 1992 a; 1992b).

Foraging Patterns.

Most dogwhelk movement is related to the availability of food, which in turn is dependent upon prey density, predator density, and the time available for foraging (Crowe, 1996). Mobile predators usually have behavioural patterns that serve to increase detection of prey beyond their immediate perceptual range (Osborn and Scotti, 1996), and complex behavioural responses to the presence of food is frequently seen in *Nucella* (Connell, 1961b, 1970, 1972; Harvey, 1962). Food has a particular influence on the dispersal of intertidal gastropods (Morgan, 1972a), and in simple terms areas with "sufficient prey" attract them (Carriker, 1955; Connell, 1961b; Morgan, 1972b; West, 1986; Fairweather, 1988c). Movement is not always constant during feeding excursion (McFarlane, 1980), and several different modes of feeding excursions (e.g. ranging pattern, zonal shuttling, and central place foraging) are seen (Chelazzi et. al., 1986). In addition, three patterns of prey selection have also been identified in *Nucella* spp.: non-selective, frequency dependent, and energy maximization (Palmer, 1984b). *Nucella lapillus* is very efficient at locating new food sources (Connell, 1970), and when hungry moves in straighter paths, showing area-restricted searching only when already partially satiated (Hughes and Dunkin, 1984b). Whelks also have a marked tendency to move away from those areas without (or with few) prey (Fairweather, 1988a). This has a significant effect on the dispersal of dogwhelks, who move more during times when prey is scarce (Moran,1985a), often migrating upshore (Underwood, 1977). This migration to and from areas varying in prey availability is a major cause of temporal variation in the density of whelks at different positions on the shore (Fairweather, 1988b). Prey provide a "stopping" cue for the snails, and since they feed on an usually abundant sedentary prey (several years supply may be found within one m ^{2}), they usually have no need to forage widely across the shore (Feare, 1971b). The foraging behaviour of *Nucella lapillus* individuals, can vary widely in space (Hughes and Burrows, 1991), in whelks of similar age and size (Hughes and Burrows, 1993), and with time (Hughes and Burrows, 1994).

Different components of the physical environment can alter the movement and hence foraging patterns of dogwhelks (Menge, 1978a). These include wave action, insolation and desiccation (Menge, 1978; Etter, 1989). The effects they cause in feeding behaviour are varied and unpredictable, since the combination of physical factors act in a non-linear and complex way (Menge, 1978b). These include desiccation with increasing height on the shore (increasing desiccation), presence of algal canopy (moderated desiccation), month of the year (different temperatures and insolation at low tide), and exposure to wave action (Underwood, 1985). Physical parameters, can be constraints on foraging, determining where and for how long an animal can forage (Garrity and Levings, 1981; Menge and Lubchenco, 1981), and so reduce the potential of whelks for feeding selectively (Burrows and Hughes, 1989; Hughes and Burrows, 1990). In sheltered locations dogwhelks can eaily forage over the whole of their expected range, but in wave-exposed areas many *Nucella* must remain for a greater part of the time in crevices to avoid being washed away (Menge, 1978a). Many refuges become devoid of suitable prey, requiring foraging excursions into the open (Menge and Sutherland, 1987).

The different age groups of dogwhelks show different foraging patterns. According to Rogers, (1988), juveniles forage throughout the year and remain widely dispersed (compared to adults who shelter) for longer at the onset of winter, in order to attain the best possible degree of growth. Conversely adult snails tend to move for longer distances on average than their juveniles, as seen in work on *Nucella calviger* (Abe, 1989), and on *Nucella emarginata* (Goselin and Chia, 1995b).

Foraging Cycle and Feeding Bout Length.

Foraging dogwhelks display a distinct foraging cycle which though it can be moderated by environmental factors, still follows a set pattern. Many of them have a well documented characteristic diel activity pattern of foraging and refuging (Connell, 1961b), also seen in other intertidal snails (Cook et. al., 1969; Mackay and Underwood, 1977; Zann, 1973a). *Nucella* spp. such as *Nucella dubia* (McQuaid, 1985), and *Nucella lapillus* (Hughes and Dunkin, 1984a), mostly search for prey only when covered by the tide and are more active in darkness. They are very seldom seen searching for prey at low tide in daylight, a behaviour which protects them to some degree from desiccation and avian predation (Connell, 1961b).

Feeding dogwhelks however, often remain in the open on top of their their prey (Boyle et.al., 1979). *Nucella* foraging can be for extended periods, even up to several days (West, 1986), the actual time depending upon whether the prey are barnacles or mussels (Hughes and Drewett, 1985), and upon the previous feeding history and general morphology of the snail (Moore, 1936b; Kitching et. al., 1966).

Movement and Refuges.

When not feeding many species of intertidal gastropod are found in crevices (Fairweather, 1988a), and major fluctuations in density estimations are due to immigration and emigration to and from these and other refuges (Fairweather, 1988b). The presence (or absence) and distribution of refuges is known to influence movement patterns in some intertidal gastropods. *Acanthina punctulata* tends to restrict its movement while exposed and when not drilling, searching for, or consuming prey, will seek the protection of a refuge (Menge J.L., 1974). In wave-exposed areas the lack of suitable crevices, can lead to an increase in emigration rates in *Morula marginalba* (Moran, 1985a). In addition most *Nucella lapillus* retreat to the protection of crevices during unfavourable environmental conditions (Burrows and Hughes, 1989).

Topography and movement.

The complexity of the local microhabitat topography can limit intertidal gastropod movement and the timing of activity (Chelazzi et. al., 1986), and so interupt continued linear dispersal in the field (Gosselin and Chia, 1996b). For example, migration rates of the periwinkle *Littorina unifasciata,* are greater in simple areas (where they move with more direction), than in places with more complex surfaces (Erlandsson et. al.,1996). The natural barriers, obstacles and surface irregularities created by rough rocks and barnacles leads to limpets (*Cellana grata*) making tortuous foraging paths (Erlandsson et. al., 1996). This often leads to "trapping effects" that result in higher abundances of the snail being concentrated within the rough areas of microhabitat. Similarly, *Nodilittorina pyramadilis* has a higher dispersal rate in, and actively avoids simple areas, returning to habitats with more complex topography (Erlandsson et. al., 1996). In fact, the presence of 'unsuitable' habitat, actually causes adult intertidal snails to move greater distances than from plots surrounded by'suitable'microhabitat (Crowe, 1996). These types of microhabitat movement restriction can also mediate interactions between species of the assemblage, and ultimately affect community composition (Thompson et. al., 1996). Very little is known about the ability of gastropods to detect and respond to differences in surface morphology (Cook and Cook, 1975), though it is certain that spatial heterogeneity does affect the movement of *Nucella lapillus* (Gosselin and Bourget, 1989).

Substratum types.

The ability of intertidal snails to move across surface substratum also varies with the type of substratum encountered. For instance they move far more easily on hard substrata than on soft substrata (Crowe, 1996), and *Nucella lapillus* normally avoids crawling across sand or mud (Crothers, 1983), and so is not often found below the tide marks for this reason (Crothers, 1981a).

Dispersion.

A standard measurement of dispersion is useful to compare variation in snail dispersion in space and time. There are three aspects of spatial pattern: the spatial pattern of dispersion of each species, the amount of spatial segregation between two species, and the presence or absence of symmetry between the species. Pielou (1959), and Mountford (1961), derived an index of spatial dispersion based on the distances between random points on the substrate and the nearest neighbours of the same species. This association index can also be used to assess changes in spatial associations among species, including consideration of the specific dispersion pattern of nearest neighbour relationship (Levin and Paine, 1974). Many interspecific associations will decrease, increase or remain unchanged in relation to abundances of interspecific individuals. Only a few investigations using nearest-neighbour analyses of dispersion of more motile intertidal gastropods have been attempted (Underwood, 1976a; 1976b). *Nucella lapillus* exhibits at least three different types of aggregation: summer on open rock surface; feeding, protected from water movement; and non-feeding winter aggregations in pools or clefts; which become a breeding aggregation for mature whelks (Feare, 1971b). A similar pattern is observed in *Nucella emarginata* in New England (Menge, 1978a), where most adult dogwhelks breed with other nearby adults (Spight, 1974), and *Nucella clavigera* in Japan (Abe, 1983).

4.2. METHODS.

The movement of *Nucella lapillus* was initially investigated on diurnal, tidal and seasonal scales. The range of spatial dispersal and timing of foraging pattern (activity pattern) of individuals were observed by mark and recapture at different shore levels on six different shores namely: Menai Bridge, Trwyn y Penrhyn, Llanfairfechan, Red Wharf Bay, Porth Nobla, and Porth Defaid.

Measurement.

Nucella maximum shell length was recorded, measured from the shell apex to the tip of siphonal canal (see Chapter 3), using vernier calipers (to ±0.1mm). Individuals were classified into four major size groups and their dispersal compared. These size classes were: 2.0-11.9 mm (early and smaller juveniles), 12.0-21.9 mm (larger juveniles and subadults), 22.0-31.9 mm (adults), and 32.0-41.9mm (larger adults),

Marking.

Two different methods were used to mark individual shells. The shell was swabbed with alcohol to remove dirt and water and the surface was allowed to dry and tippex fluid used to put a round spot on the shell. A number was written on the spot using a permanent marker pen, and after drying it was waterproofed by covering the number with super glue. Alternatively, whelks were individually tagged with numbered tape glued to the shell using quick-setting epoxy formulation.

Dogwhelk location and dispersal measurement.

Preliminary mapping of the daily dispersal of seven populations of dogwhelks (five at Red Wharf Bay; two at Menai Bridge) from April 1996 to January 1997, was carried out to discern the characteristic diel activity pattern of foraging and refuging on these shores (see Leviten and Kohn, 1980). I looked at the range of spatial dispersal, and timing of foraging pattern (activity pattern) of *Nucella lapillus,* by observing undisturbed individuals at different times of day and therefore during different stages of the tidal cycle. The frequency and rate of dispersal was compared to patterns of environmental variation, to delineate when and to what extent the latter affected the former. Later, dispersal (net distance moved on weekly/monthly/yearly basis) as well as cumulative distance moved, direction of dispersal, and size of dogwhelk was estimated for each of three enclaves (individually tagged groups of 200 individuals) at three different shore levels, low, mid, and upper. Lower and upper levels were located at the extremes of the vertical distribution of *Nucella lapillus*. A total of 600 dogwhelks were initially marked per shore, on each of the study shores: Menai Bridge, Trwyn y Penrhyn, Llanfairfechan, Red Wharf Bay, Porth Nobla and Porth Defaid. Animals were marked in position and not translocated so disturbance was minimal and starting points were actual locations of individuals on the shore.

The dispersal of a maximum of 100 whelks was determined per shore level per visit. Further marking of whelks was carried out at three monthly intervals as necessary to keep up numbers in the face of known mortality (marked dead found), or loss (individual not observed for three months). In locating individual marked animals for calculation of distance moved (in metres), a time standardized search pattern was used (90 minutes). One enclave was selected at the lower edge of *Nucella* distribution; one in the middle, and one at the upper levels of dogwhelks, on each shore, provided they occured in sufficient numbers (eighteen enclaves and 3,600 marked individuals in total). The dispersal of dogwhelks was measured in straight line (net) distance moved by mark and recapture from September 1996 to September 1998. This involved geometrical description of patterns of foraging, the tracking of marked individuals monitored by trigonometric methods (Hughes and Drewitt, 1985). By noting co-ordinates from fixed markers on the rock it is possible to follow the net movement of tagged *Nucella lapillus* for short or even prolonged periods (Burrows and Hughes, 1990). Position co-ordinates (defining the data collected as directional i.e. to have a significant non-random mean orientation) and body axis direction (orientation) of individual dogwhelks, along with activity (feeding, moving, refuging or spawning, as per Levings and Garrity, 1983) were also recorded. All displaced distances were log transformed prior to analysis (as recommended by Underwood, 1977), to create homogeneity of variances. In total some 129, 974 measurements of each of the following: movement distances, angle of movement, and size of whelks were taken (389,922 data cases).

Densities of Nucella monitored on fixed boulder units.

During this series of experiments the mean densities of foraging *Nucella* were monitored at three shore levels (on 100 boulders per shore level), in order to assess the predator impact of dogwhelks by combining this data with information on changing barnacle densities, with and without dogwhelks. The number of dogwhelks foraging in designated food patches (barnacles) was determined within four similar (equivalent barnacle size frequency and barnacle density) prey assemblages on each of the six study shores in relation to the tidal cycle. Monitoring within prey patches began at the same point within the tidal cycle each month (January to December), so that phase comparisons in feeding activity could be made between months and between shores.

Prey Selection.

Density, growth and life-history of the predator may vary in accordance with the availability of different sizes of prey (Moran et al., 1984). Changes in diet and feeding habits were recorded, by estimation of prey consumption by identifying and measuring the diameter of exoskeletal remains of barnacles (Frank, 1965; Chapman, 1986), that were attacked by individually marked dogwhelks. I measured *Nucella* densities at the three different heights of different shores and calculated daily (estimated) mean distances moved, to determine how intraspecific (*Nucella* - *Nucella*) interactions (density-dependent) affect movement in relation to competiton (Menge, 1974; 1978b). I also looked for evidence for competiton: two *Nucella* on top of one prey item, or displaced predators (out in the open, not in the process of feeding), and compared their incidence to the number of conspecifics\unit area.

Mortality Risk.

An estimation of potential mortality risk (wave-action; desiccation-insolation index; proximity to unsuitable habitat; active predators) was derived (a "vunerability factor") for different sites (different levels) and shores and compared to estimated mortality figures from mark and recapture data. Site-specific mortality rates were determined by recording the loss of marked individuals from monthly samples in each population.

Movement in Relation to Environmental Factors.

I recorded activity of *Nucella* on different days in order to determine times of maximal activity and inactivity and relate these to physical variables and determine environmental constraints on activity (e.g the degree of exposure to air and water movement that inhibit locomotion).

Environmental data were also collected from Valley air force meterological station, Anglesey.

Dispersion.

The mean level and dispersion of the scattered snails, as well as the number of snails clustered together were determined (Vannini and Chelazzi, 1978). Specific dogwhelk spatial dispersal patterns can be based on measurement from random points and nearest neighbours of the same species (Pielou, 1969). This index of spatial dispersion called alpha (Morgan, 1972b), has been calculated for the intertidal gastropod *Nerita* (Underwood, 1976b). I used this technique for my work on dispersion of *Nucella lapillus*. On each shore the shells of six populations of whelks from succesive levels (height) were marked with different coloured dots of oil paint and their distance from their nearest conspecific measured every month for two years. The index of dispersion was tabulated along with *Nucella* density, substrate configuration, shore type and month. A total of 212,319 observations of distance to nearest neighbour were measured in total.

Statistical analysis.

Both dispersal and dispersion data were log transformed to guarantee their normal distribution prior to univariate and multivariate GLM ANOVA analysis. All variables were then examined for normality by Kolmogorov-Smirnov tests and Q-Q plots; and for homogeneity of variance by Levene's test.

4.3 RESULTS.

4.31. Comparisons of weekly movement distances between different months within shore levels. The monthly dispersal of *Nucella lapillus* at three different shore levels on the six study shores is shown in Figure 4.1, with overall monthly dispersal in Figure 4.2 (Both two years pooled data).

Menai Bridge.

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=14.596 P=<0.001), mid shore (GLM. F=8.132 P=<0.001), and upper shore (GLM. F=12.910 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.1).

Trwyn y Penrhyn.

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=8.184 P=<0.001), mid shore (GLM. F=12.615 P=<0.001), and upper shore (GLM. F=8.540 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.2).

Llanfairfechan.

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=8.966 P=<0.001), mid shore (GLM. F=4.798 P=<0.001), and upper shore (GLM. F=5.791 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.3).

Red Wharf Bay

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=7.134 P=<0.001), mid shore (GLM. F=9.979 P=<0.001), and upper shore (GLM. F=5.182 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.4).

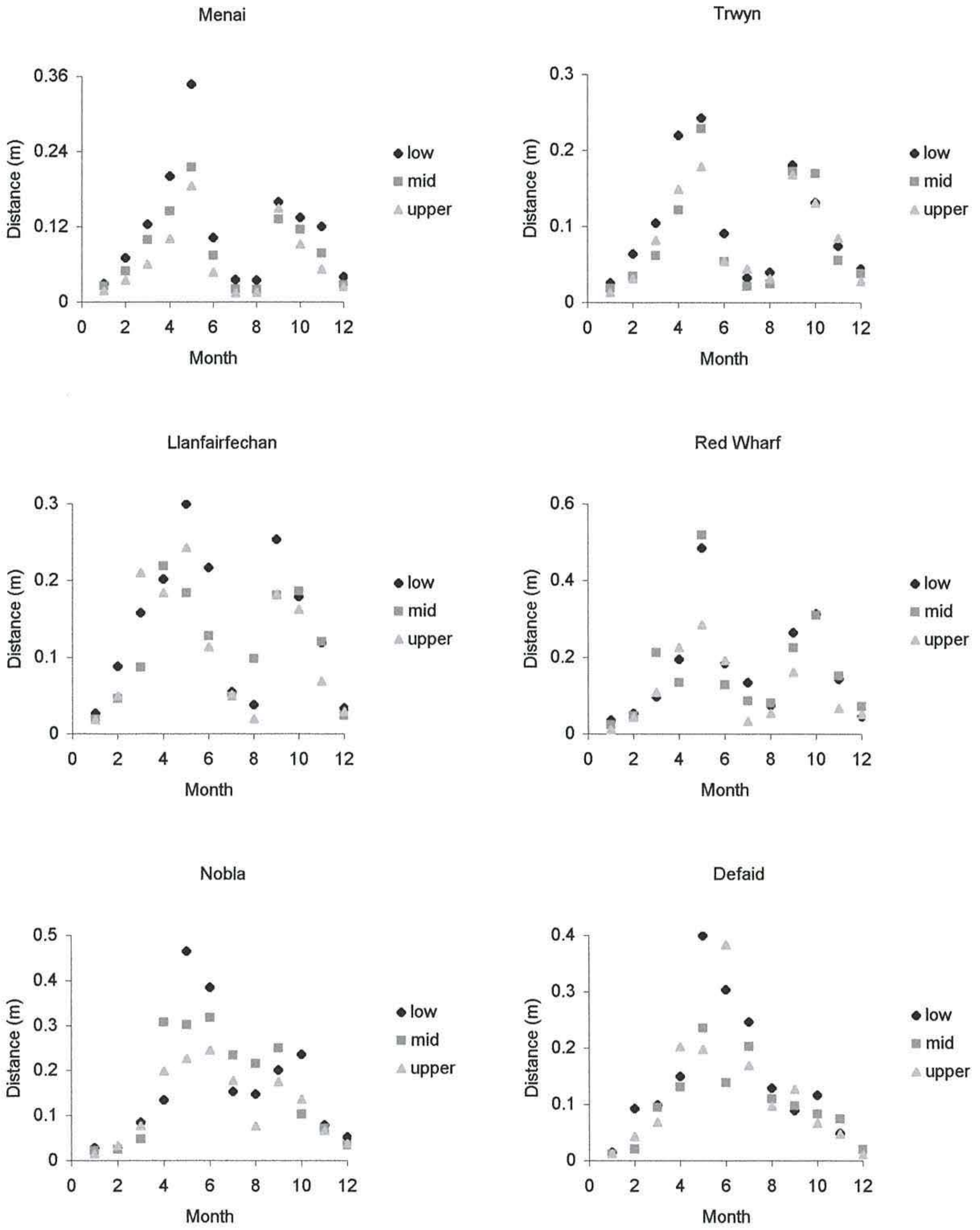


Figure 4.1. Monthly figures for weekly dispersal of *Nucella lapillus* at different shore levels. Months 1-12 represent January to December inclusive (2 years pooled data).

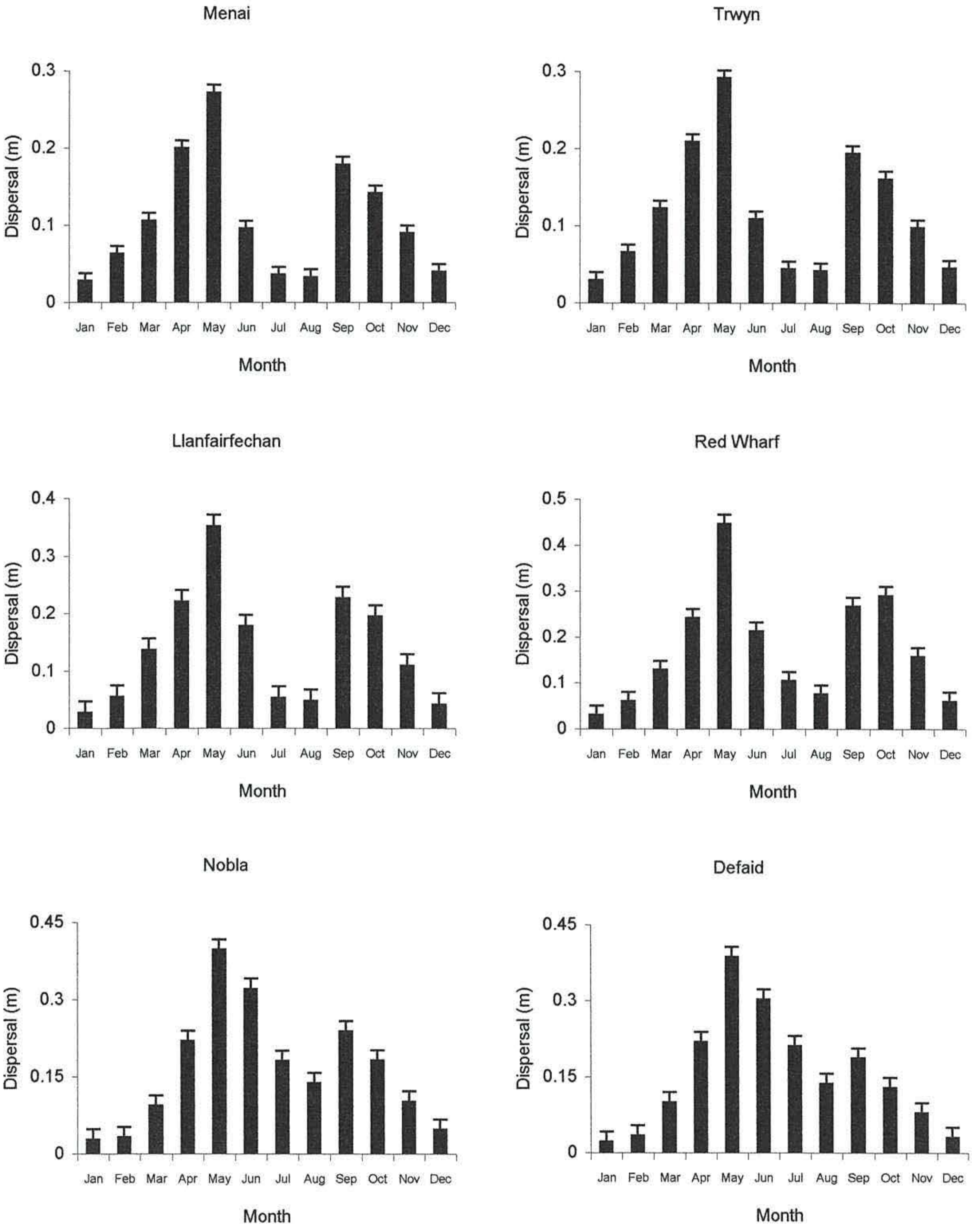


Figure 4.2. Monthly figures for weekly dispersal of *Nucella lapillus* on different shores. (2 years pooled data).

Porth Nobla.

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=10.863 P=<0.001), mid shore (GLM. F=5.259 P=<0.001), and upper shore (GLM. F=5.596 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.5).

Porth Defaid.

The movement of *Nucella* was significantly influenced by month at low shore (GLM. F=7.401 P=<0.001), mid shore (GLM. F=2.352 P=0.007), and upper shore (GLM. F=3.710 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.6).

4.32. Comparisons of weekly movement distances between shore levels within shores.

The distance moved by *Nucella* was significantly influenced by shore level on all six shores namely: Menai Bridge (GLM. F=68.941 P=<0.001), Trwyn y Penrhyn (GLM.F=68.248 P=<0.001), Llanfairfechan (GLM. F=32.887 P=<0.001), Red Wharf Bay (GLM. F=46.811 P=<0.001), Porth Nobla (GLM. F=26.077 P=<0.001), and Porth Defaid (GLM. F=29.241 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant differences in distances moved by dogwhelks between all three shore levels (low, mid and upper) on all shores (Table 4.1).

Table 4.1. Results of Post Hoc multiple comparison (Bonferroni test) showing mean differences in *Nucella lapillus* movements between shore levels.

shore levels	1-2		1-3		2-3	
shore	mean difference	*P*	mean difference	*P*	mean difference	*P*
Menai Bridge	0.028	<0.001	0.048	<0.001	0.020	<0.001
Trwyn y Penrhyn	0.035	<0.001	0.049	<0.001	0.015	0.014
LLanfairfechan	0.015	0.010	0.038	<0.001	0.024	<0.001
Red Wharf Bay	0.022	0.001	0.059	<0.001	0.037	<0.001
Porth Nobla	0.020	0.002	0.044	<0.001	0.024	<0.001
Porth Defaid	0.020	0.001	0.042	<0.001	0.022	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.33. Comparisons of weekly movement distances between shores.

The distance moved by *Nucella* was found to be significantly influenced by shore (GLM. F=168.407 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant differences in distances moved by dogwhelks between all of the shores (Table 4.2., Figure 4.3).

Table 4.2. Results of Post Hoc multiple comparison (Bonferroni test) showing mean differences in *Nucella lapillus* movements between shores.

shores	mean difference	significance
Menai and Trwyn	0.012	<0.001
Menai and LLanfairfechan	0.032	<0.001
Menai and Red Wharf	0.067	<0.001
Menai and Porth Nobla	0.057	<0.001
Menai and Porth Defaid	0.045	<0.001
Trwyn and LLanfairfechan	0.020	<0.001
Trwyn and Red Wharf	0.055	<0.001
Trwyn and Porth Nobla	0.045	<0.001
Trwyn and Porth Defaid	0.033	<0.001
Llanfairfechan and Red Wharf	0.034	<0.001
Llanfairfechan and Porth Nobla	0.025	<0.001
Llanfairfechan and Porth Defaid	0.013	<0.001
Red Wharf and Porth Nobla	0.096	0.018
Red Wharf and Porth Defaid	0.021	<0.001
Porth Nobla and Porth Defaid	0.012	0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.34. Summary of the mean weekly dispersal of *Nucella* lapillus for shore level, season and year on the six study shores.

The weekly movement of *Nucella* was found to be significantly influenced by shore level (GLM. F=12.721 P=<0.001), and significantly influenced by season (GLM. F=117.643 P=<0.001), but not significantly influenced by year (GLM. F=0.986 P=0.323). Mean weekly dispersal figures for shore level, season and year for all six study shores are shown in Table 4.3.

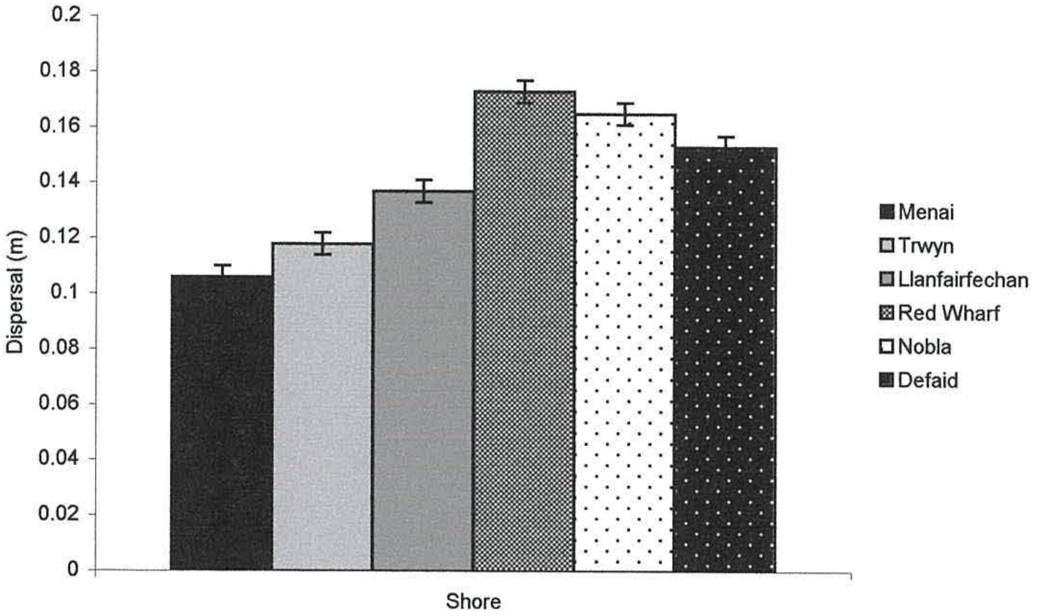


Figure 4.3. Weekly dispersal of *Nucella lapillus* on different shores. (2 years pooled data).

Table 4.3. Summary of mean weekly dispersal of *Nucella lapillus* at different shore levels, different seasons, and between years.

	Shore Level			Season				Year	
Shore	Low	Mid	Upper	Spring	Summer	Autumn	Winter	First	Second
Menai Bridge	0.148	0.114	0.110	0.207	0.065	0.162	0.048	0.124	0.117
Trwyn y Penrhyn	0.129	0.105	0.084	0.190	0.053	0.140	0.040	0.113	0.098
Llanfairfechan	0.205	0.178	0.143	0.275	0.132	0.245	0.048	0.181	0.169
Red Wharf	0.160	0.143	0.118	0.237	0.093	0.188	0.042	0.144	0.136
Porth Nobla	0.191	0.167	0.146	0.258	0.195	0.185	0.035	0.170	0.167
Porth Defaid	0.171	0.156	0.134	0.235	0.212	0.138	0.030	0.153	0.154

Distances indicated are mean weekly displacements measured in metres.

4.35. Different size clases of *Nucella* and foraging activities.

4.351. Comparisons of weekly movement distances between different size classes within shore levels. The dispersal of different size classes with respect to shore level is shown in Figure 4.4.

Results of analysis of movement distances with respect to size class for the different study shores:
Menai Bridge.

The movement of *Nucella* was significantly influenced by size class at low shore (GLM. F=8.045 P=<0.001), mid shore (GLM. F=15.372 P=<0.001), and upper shore (GLM. F=15.695 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement betwen most size classes (Appendix 4, Table 4.7).

Trwyn y Penrhyn.

The movement of *Nucella* was significantly influenced by size class at low shore (GLM. F=56.039 P=<0.001), mid shore (GLM. F=70.923 P=<0.001), and upper shore (GLM. F=41.585 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most size classes (Appendix 4, Table 4.8).

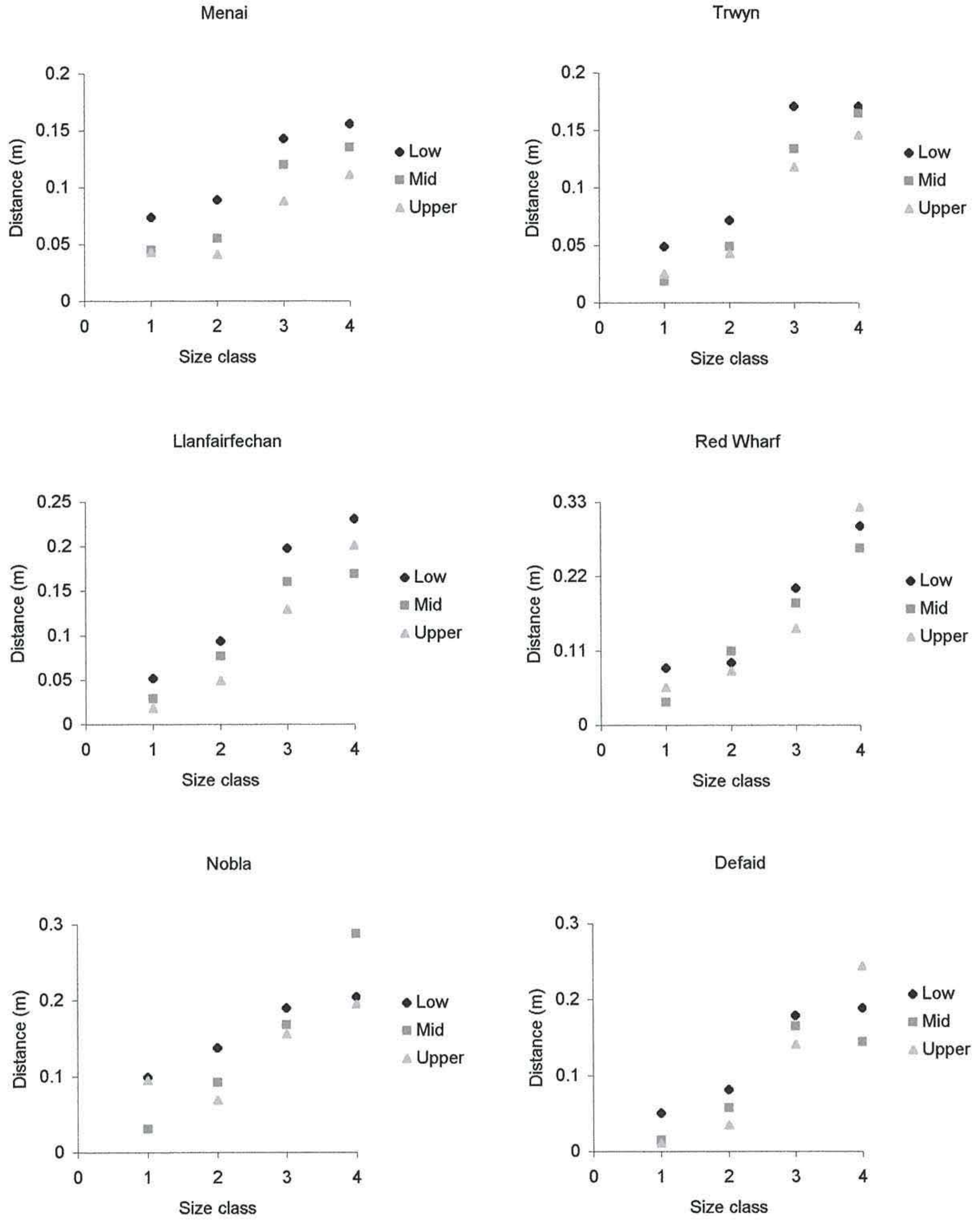


Figure 4.4. Dispersal of different size classes at different shore levels.
key to size class: 1: 2-11.9mm; 2: 12-21.9mm; 3: 22-31.9mm; 4: 32-41.9mm.

Llanfairfechan.

The movement of *Nucella* was significantly influenced by size class at low shore (GLM. F=90.442 P=<0.001), mid shore (GLM. F=27.421 P=<0.001), and upper shore (GLM. F=13.629 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most size classes (Appendix 4, Table 4.9).

Red Wharf Bay

The movement of *Nucella* was found to be significantly influenced by size class at low shore (GLM. F=31.388 P=<0.001), mid shore (GLM. F=5.515 P=0.001), and upper shore (GLM. F=6.005 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most size classes (Appendix 4, Table 4.10).

Porth Nobla.

The movement of *Nucella* was significantly influenced by size class at low shore (GLM. F=16.363 P=<0.001), mid shore (GLM. F=16.137 P=<0.001), and upper shore (GLM. F=34.037 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most size classes (Appendix 4, Table 4.11).

Porth Defaid.

The movement of *Nucella* was significantly influenced by size class at low shore (GLM. F=20.590 P=<0.001), mid shore (GLM. F=27.526 P=<0.001), and upper shore (GLM. F=31.170 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most size classes (Appendix 4, Table 4.12).

4.352. Comparisons of the proportion of different size classes feeding between shore levels.

The proportion (maximum =1) of different size classes of dogwhelks foraging at three different shores levels is shown in Figure 4.5, whilst the overall proportion foraging (pooled data from all three shore levels) is in Figure 4.8.

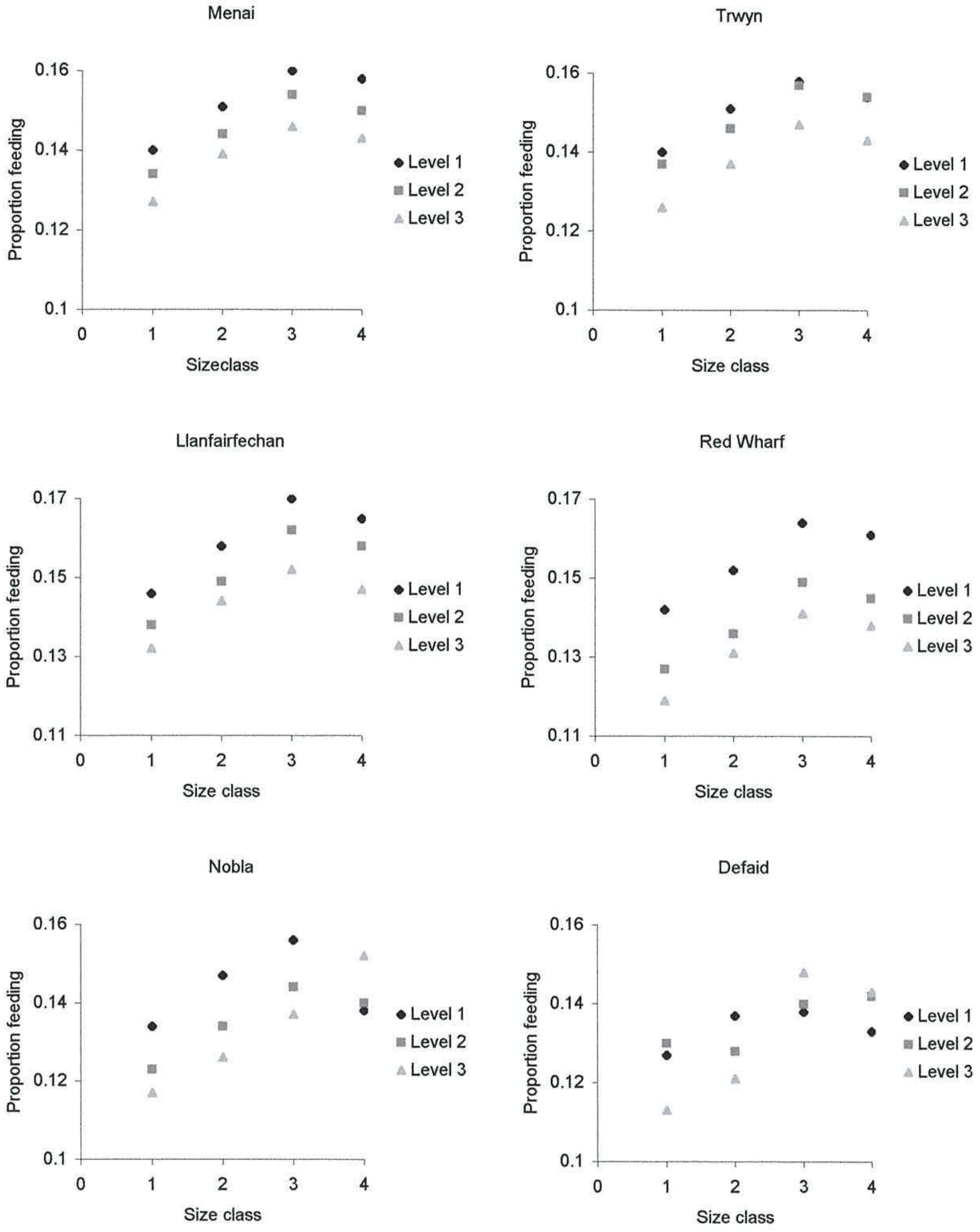


Figure 4.5. Proportion of different size classes feeding at different shore levels. Key to Level: 1: low shore; 2: mid shore; 3: upper shore.

Size classes: the proportion feeding was significantly influenced by size class at Menai Bridge (GLM. F=18.268 P=<0.001), Trwyn y Penrhyn (GLM. F=31.109 P=<0.001), Llanfairfechan (GLM. F=18.226 P=<0.001), Red Wharf Bay (GLM. F=23.359 P=<0.001), Porth Nobla (GLM. F=20.177 P=<0.001), and Porth Defaid (GLM. F=10.796 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in proportion feeding between most size classes (Table 4.4).

Table 4.4. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in proportion of *Nucella* feeding between size classes.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Size classes	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.011	0.003	0.011	<0.001	0.009	0.005	0.010	0.005	0.011	0.003		
1-3	0.020	<0.001	0.019	<0.001	0.022	<0.001	0.022	<0.001	0.021	<0.001	0.019	<0.001
1-4	0.017	<0.001	0.016	<0.001	0.018	<0.001	0.009	<0.001	0.019	<0.001	0.016	0.001
2-3	0.009	0.019	0.009	0.001	0.011	0.007	0.012	0.001	0.010	0.009	0.013	0.006
2-4							0.008	0.028			0.011	0.044

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Shore levels: the proportion feeding was found to be significantly influenced by level at Menai Bridge (GLM. F=15.177 P=<0.001), Trwyn y Penrhyn (GLM. F=22.452 P=<0.001), Llanfairfechan (GLM. F=16.817 P=<0.001), Red Wharf Bay (GLM. F=44.073 P=<0.001), and Porth Nobla (GLM. F=9.470 P=<0.001), but not significantly influenced by shore level at Porth Defaid (GLM. F=0.687 P=0.508). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in proportion feeding between most shore levels on those five shores (Table 4.5)

Table 4.5. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in proportion of *Nucella* feeding between shore levels at the study shores.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.007	0.026			0.008	0.013	0.002	<0.001	0.008	0.008
1-3	0.014	<0.001	0.012	<0.001	0.016	<0.001	0.023	<0.001	0.011	<0.001
2-3	0.007	0.024	0.009	<0.001	0.008	0.024	0.007	0.019		

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.353. Comparisons of feeding bout period of different size classes between shore levels.

The length of the feeding bout of different size classes of dogwhelks foraging at three different shores levels is shown in Figure 4.6., overall length of feeding bout (pooled data from all three levels) is shown in Figure 4.9.

Size classes.

The feeding bout period was found to be significantly influenced by size class at Menai Bridge (GLM. F=443.472 P=<0.001), Trwyn y Penrhyn (GLM. F=325.873 P=<0.001), Llanfairfechan (GLM. F=367.028 P=<0.001), Red Wharf Bay (GLM. F=432.322 P=<0.001), Porth Nobla (GLM. F=215.085 P=<0.001), and Porth Defaid (GLM. F=165.493 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in the duration of the feeding bout between most size classes (Table 4.6).

Table 4.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in duration of the feeding bout between size classes.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Size classes	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.303	<0.001	0.300	<0.001	0.301	<0.001	0.288	<0.001	0.316	<0.001	0.312	<0.001
1-3	0.703	<0.001	0.689	<0.001	0.665	<0.001	0.700	<0.001	0.716	<0.001	0.731	<0.001
1-4	0.563	<0.001	0.573	<0.001	0.504	<0.001	0.562	<0.001	0.534	<0.001	0.559	<0.001
2-3	0.403	<0.001	0.401	<0.001	0.394	<0.001	0.406	<0.001	0.388	<0.001	0.419	<0.001
2-4	0.263	<0.001	0.266	<0.001	0.251	<0.001	0.260	<0.001	0.249	<0.001	0.247	<0.001
3-4	0.140	<0.001	0.137	<0.001	0.128	<0.001	0.141	<0.001	0.133	<0.001	0.173	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Shore levels.

The feeding bout period was found to be significantly influenced by level at Red Wharf Bay (GLM. F=6.059 P=0.005), but not significantly influenced by shore level at Menai Bridge (GLM. F=1.240 P=0.299), Trwyn y Penrhyn (GLM. F=0.894 P=0.416), Llanfairfechan (GLM. F=0.944 P=0.396), Porth Defaid (GLM. F=3.089 P=0.055), and Porth Nobla (GLM. F=0.988 P=0.380). Post Hoc

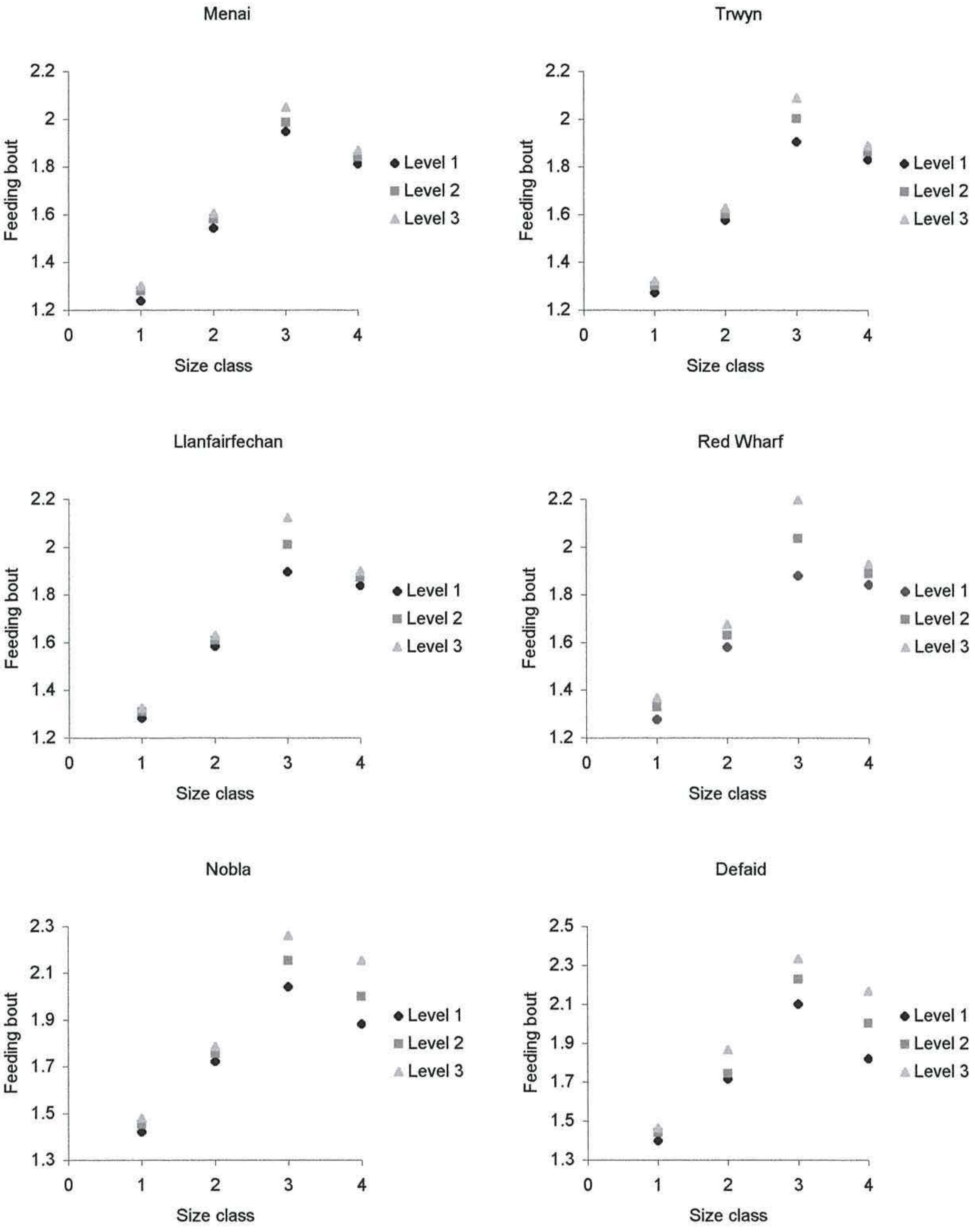


Figure 4.6. Mean length of feeding bout (in days) of different size classes feeding at different shore levels.

multiple comparison (Bonferroni test) showed significant overall mean differences in duration of feeding bout between shore levels 1 (low shore) and 3 (upper shore) at Red Wharf Bay (mean difference=0.063 P=0.004).

4.354. Comparisons of mean prey size (barnacles) for different size classes between shore levels.

The length of the feeding bout of different size classes of dogwhelks foraging at three different shores levels is shown in Figure 4.7, overall mean prey size (pooled data from all three levels) is in Figure 4.10.

Size classes.

The mean prey size was found to be significantly influenced by size class at Menai Bridge (GLM. F=183.425 P=<0.001), Trwyn y Penrhyn (GLM. F=198.163 P=<0.001), Llanfairfechan (GLM. F=166.244 P=<0.001), Red Wharf Bay (GLM. F=146.396 P=<0.001), Porth Nobla (GLM. F=135.353 P=<0.001), and Porth Defaid (GLM. F=130.321 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in mean prey size between most size classes (Table 4.7).

Table 4.7. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in mean prey between size classes.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Size classes	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.027	<0.001	0.028	<0.001	0.024	<0.001	0.029	<0.001	0.033	<0.001	0.032	<0.001
1-3	0.059	<0.001	0.063	<0.001	0.057	<0.001	0.064	<0.001	0.061	<0.001	0.066	<0.001
1-4	0.049	<0.001	0.054	<0.001	0.045	<0.001	0.054	<0.001	0.051	<0.001	0.053	<0.001
2-3	0.032	<0.001	0.035	<0.001	0.029	<0.001	0.037	<0.001	0.034	<0.001	0.031	<0.001
2-4	0.022	<0.001	0.025	<0.001	0.022	<0.001	0.028	<0.001	0.019	<0.001	0.021	<0.001
3-4	0.095	0.007	0.077	0.051	0.011	0.002	0.007	0.026	0.015	<0.001	0.013	0.005

Data presented are mean differences (md), with probabilities (P), which are all significant values.

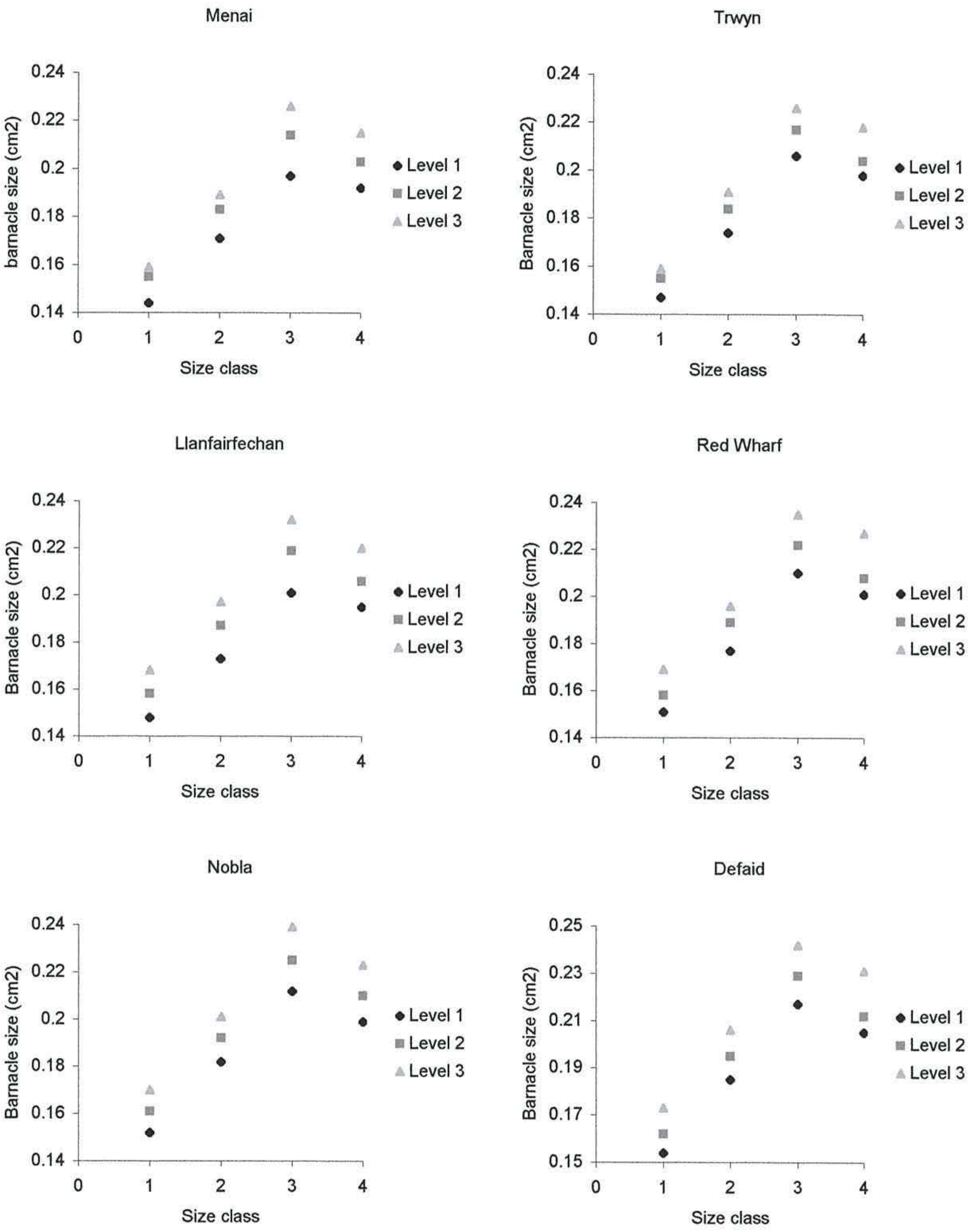


Figure 4.7. Mean prey size (barnacle) consumed by different size classes feeding at different shore levels.

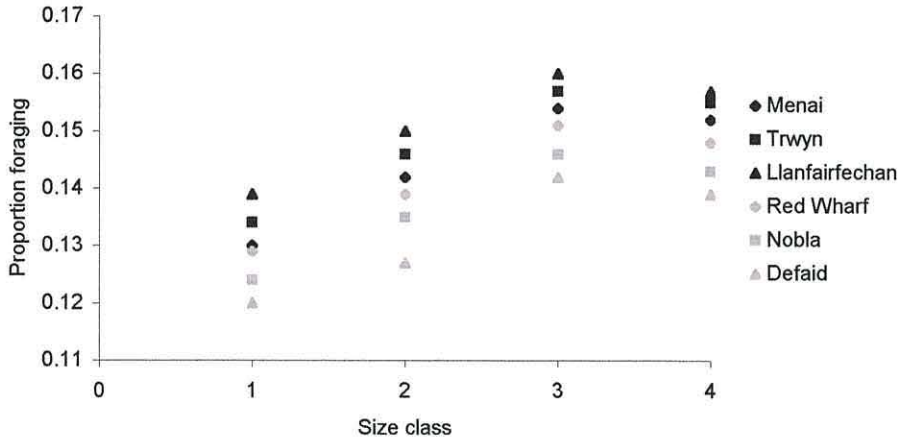


Figure 4.8. Comparison of the proportion of *Nucella lapillus* foraging on different shores

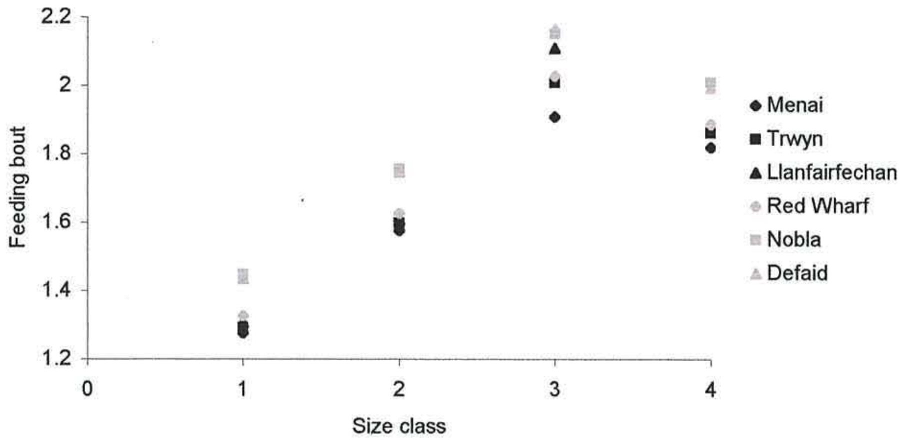


Figure 4.9. Comparison of the feeding bout (in days) of *Nucella lapillus* on different shores.

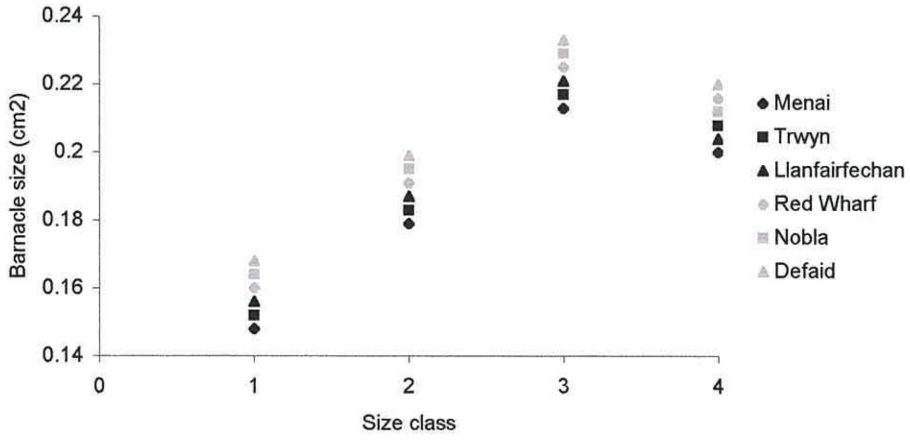


Figure 4.10. Comparison of the mean prey size (barnacle) consumed by *Nucella lapillus* on different shores.

Shore levels.

The mean prey size was found to be significantly influenced by level at Menai Bridge (GLM. F=15.142 P=<0.001), Trwyn y Penrhyn (GLM. F=6.112 P=0.004), Llanfairfechan (GLM. F=13.353 P=<0.001), Red Wharf Bay (GLM. F=4.894 P=0.012), Porth Nobla (GLM. F=10.782 P=<0.001), and Porth Defaid (GLM. F=8.686 P=0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in mean prey size between most shore levels (Table 4.8.).

Table 4.8. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in mean prey size between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.008	0.005			0.007	0.012						
1-3	0.013	<0.001	0.008	0.003	0.012	<0.001	0.009	0.010	0.014	<0.001	0.013	<0.001
2-3									0.005	0.043	0.009	0.034

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.36. *Nucella lapillus* foraging in relation to the state of the tidal cycle and population migration patterns.

4.361. The tidal cycle.

The mean number of dogwhelks foraging per prey patch (barnacles) in relation to the tidal cycles is shown in Figures 4.11 (for January to June), and 4.12 (for July to December).

4.362. Population migration patterns.

The direction of *Nucella lapillus* movement in degrees was summarised in four equal quarters up, down, right, and left (each of 90^0), which represent the general direction of whelks in relation to the vertical transect of the shore (MHWST to MHWST). The monthly changes in direction of movement of dogwhelks on the study shores are shown in Appendix 4 (Figures 4.1 to 4.12 inclusive).

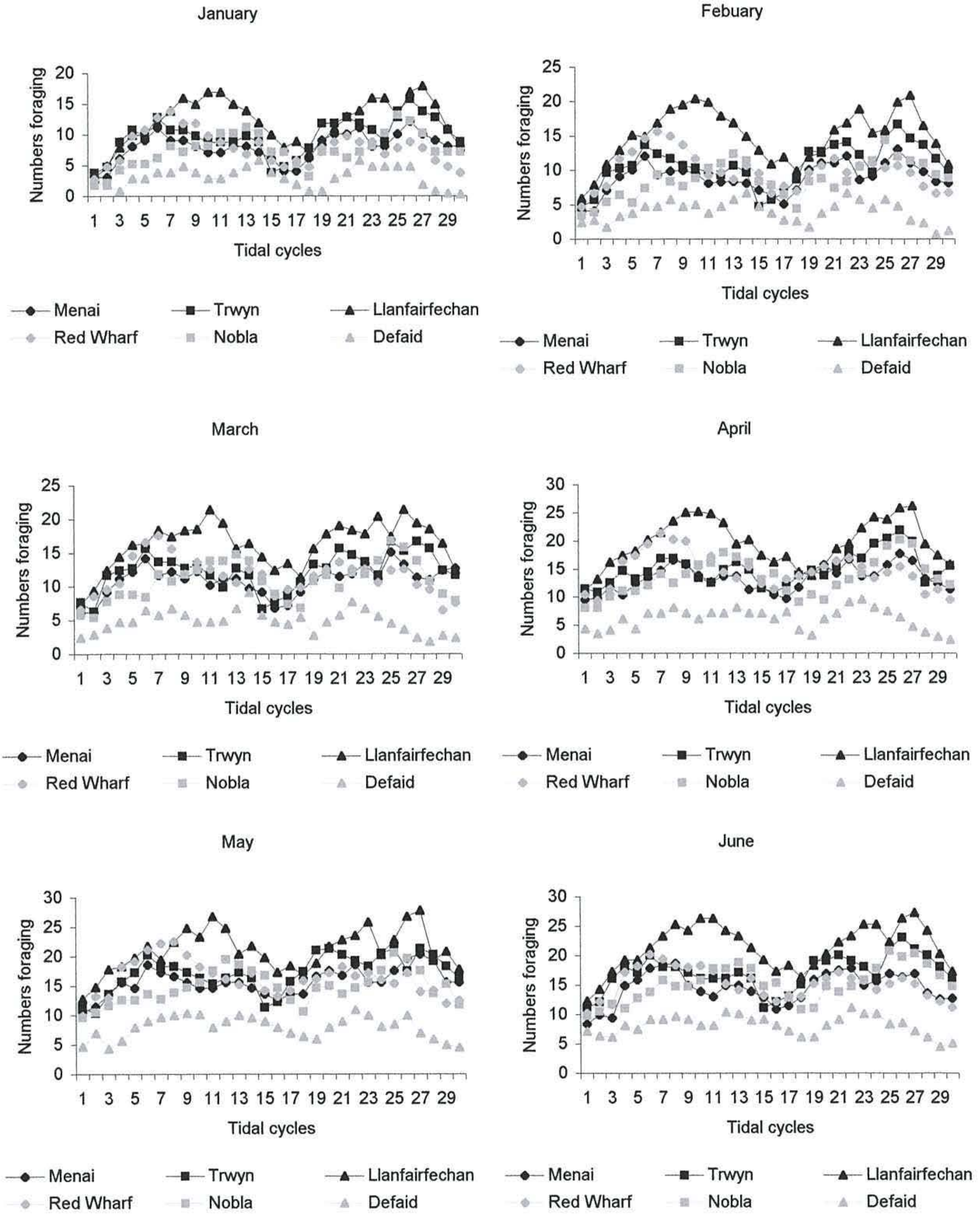


Figure 4.11. Mean number of *Nucella lapillus* foraging per prey patch (barnacles) in relation to the tidal cycle (from January to June).

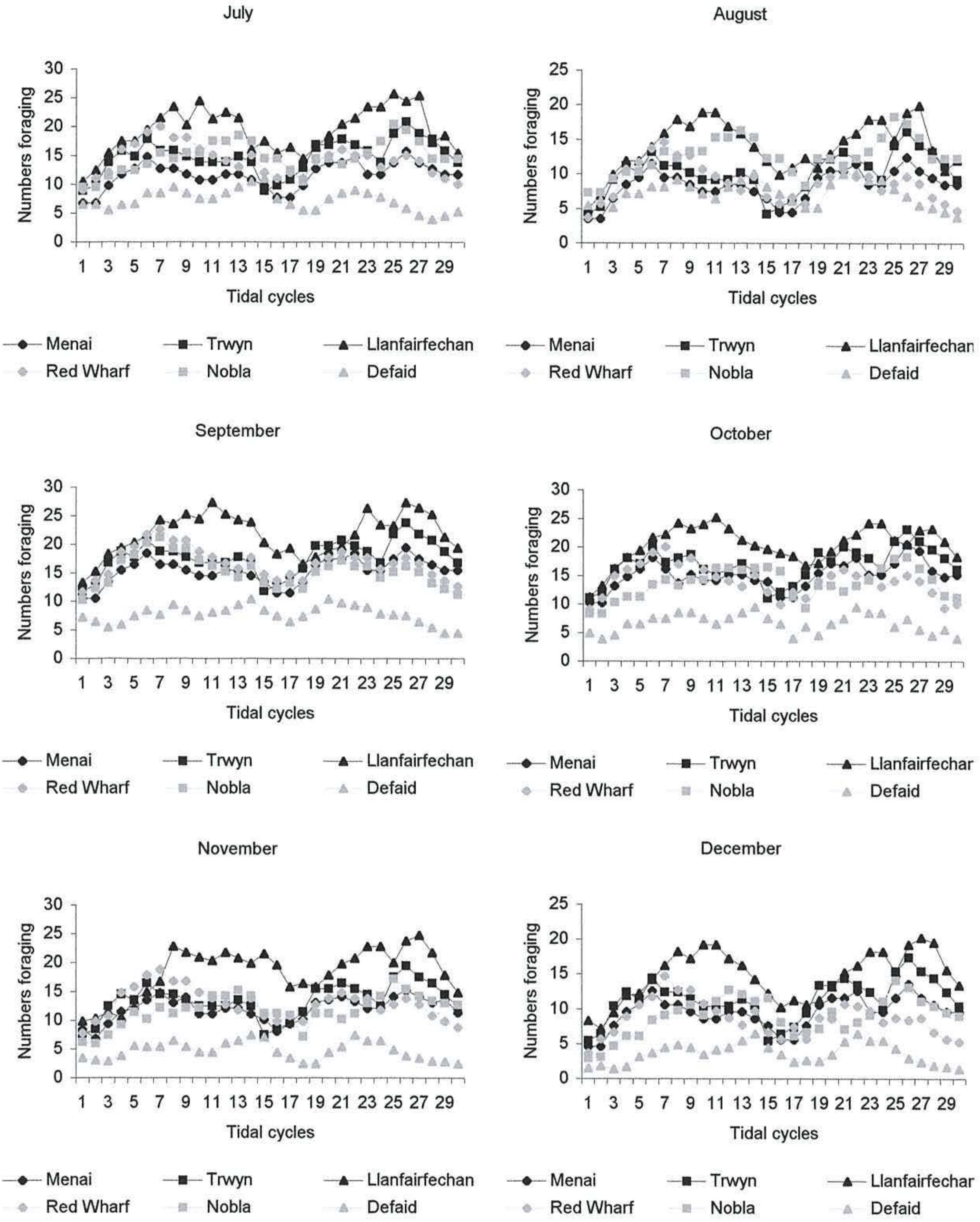


Figure 4.12. Mean number of *Nucella lapillus* foraging per prey patch (barnacles) in relation to the tidal cycle (from July to December).

GLM ANOVA revealed differences in the number of dogwhelks migrating in different directions at all shore levels on all shores (Table 4.9), and differences in the direction of migration between shore levels (Table 4.10; Figure 4.13), and between shores (Table 4.11; Figure 4.14). Post Hoc multiple comparisons showing significant mean differences in *Nucella lapillus* migration direction within shore levels are presented in Appendix 4 (Table 4.13), between shore levels (Appendix 4, Table 4.14), and between shores (Appendix 4, Table 4.15).

Table 4.9. GLM ANOVA of the number of dogwhelks and their direction of migration within shore levels.

Shore level	Low Shore		Mid Shore		Upper shore	
Shore	F	*P*	F	*P*	F	*P*
Menai Bridge	411.495	<0.001	291.500	<0.001	848.924	<0.001
Trwyn y Penrhyn	1153.776	<0.001	473.084	<0.001	1797.945	<0.001
Llanfairfechan	180.796	<0.001	168.442	<0.001	1042.552	<0.001
Red Wharf Bay	304.732	<0.001	58.091	0.001	458.516	<0.001
Porth Nobla	113.956	<0.001	936.512	<0.001	406.404	<0.001
Porth Defaid	44.379	0.002	103.469	<0.001	361.059	<0.001

Data presented are F test values (F), with probabilities (P), which are all significant values.

Table 4.10. GLM ANOVA of differences in dogwhelk migration direction between shore levels.

Direction	Down		Right		Up		Left	
Shore	F	*P*	F	*P*	F	*P*	F	*P*
Menai Bridge	89.518	<0.001	52.045	0.005	78.130	0.003	86.349	0.002
Trwyn y Penrhyn	239.120	<0.001	49.224	0.005	1223.908	<0.001	124.373	0.001
Llanfairfechan	297.283	<0.001	109.074	0.002	10.048	0.047	48.396	0.005
Red Wharf Bay	1364.412	<0.001	11.543	0.039	59.871	0.004	44.307	0.006
Porth Nobla	286.909	<0.001	77.483	0.003	66.205	0.003	98.575	0.002
Porth Defaid	248.881	<0.001	56.755	0.004	17.900	0.021	44.122	0.006

Data presented are F test values (F), with probabilities (P), which are all significant values.

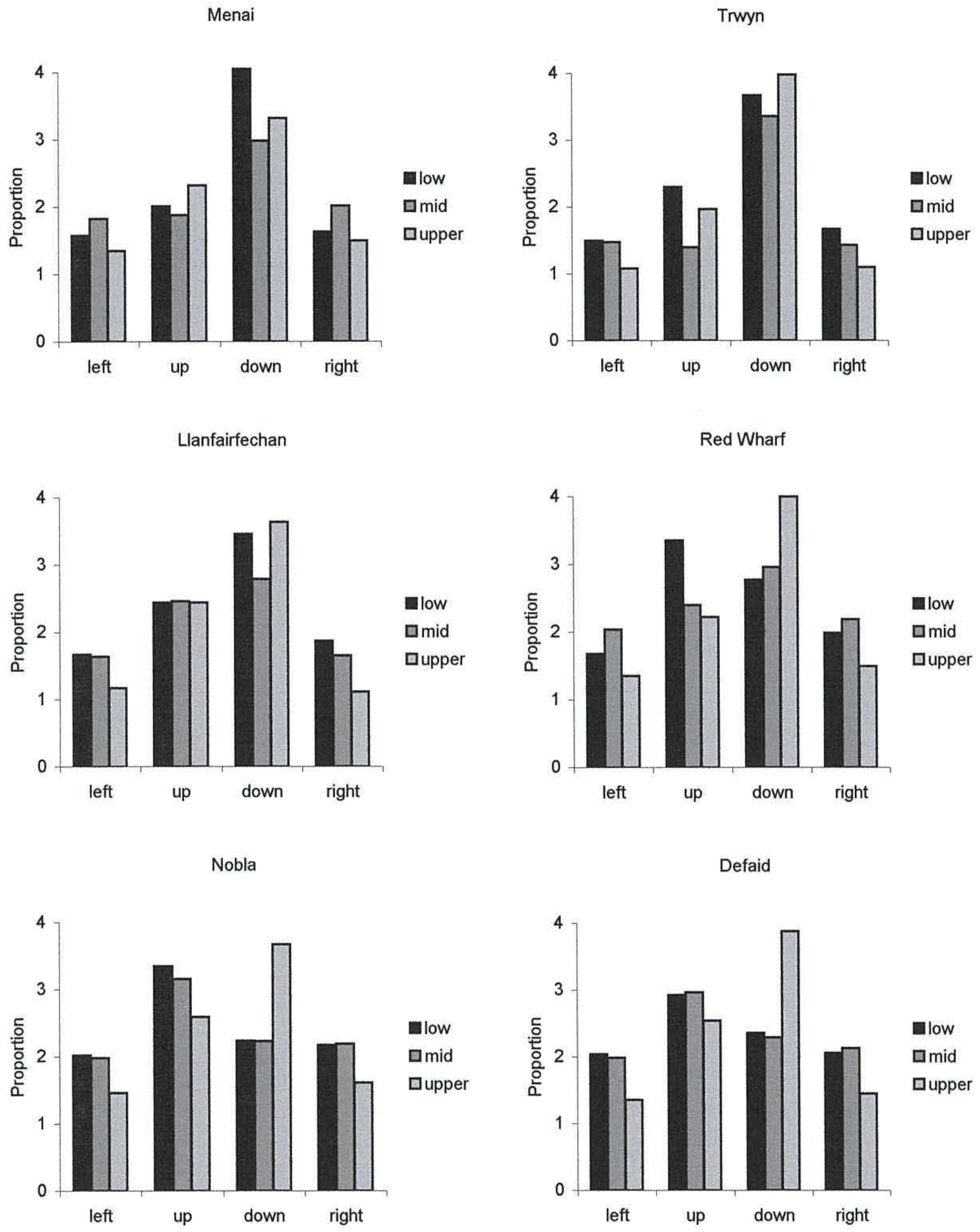


Figure 4.13.*Nucella lapillus* migration patterns at different shore levels on the study shores. Bars represent the relative proportions of whelks moving in specified directions. (2 years pooled data)

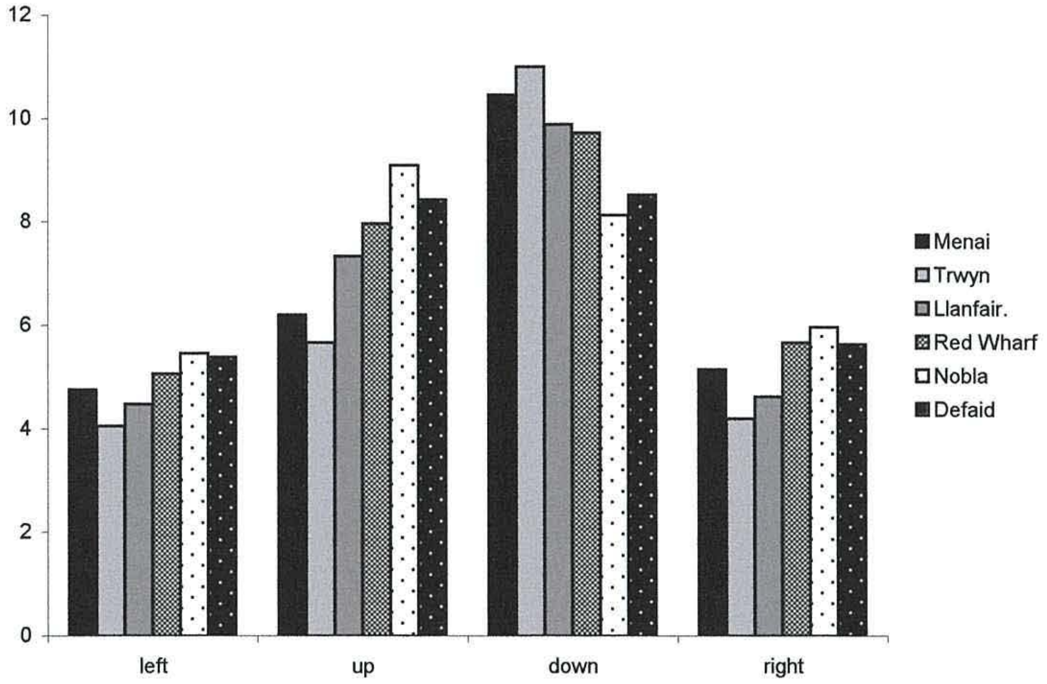


Figure 4.14. *Nucella lapillus* migration patterns on different shores (2 years pooled data). Bars represent the relative proportion of whelks moving in specified directions.

Table 4.11. GLM ANOVA of differences in dogwhelk migration direction between shores.

Shore level	Low Shore		Mid Shore		Upper shore	
Direction	F	*P*	F	*P*	F	*P*
Down	321.627	<0.001	241.366	<0.001	127.085	<0.001
Right	11.404	0.005	41.662	<0.001	22.260	0.001
Up	71.093	<0.001	217.921	<0.001	24.649	0.001
Left	13.859	0.003	77.443	<0.001	13.212	0.003

Data presented are F test values (F), with probabilities (P), which are all significant values.

4.37. *Nucella* dispersion (degree of aggregation).

4.371. Dispersion between different months, within shores.

Mid shore results are only shown here. In the low shore and upper shore dispersion within shores showed similar monthly trends. Monthly dispersion for all three shore levels are represented in Figure 4.15.

Menai Bridge.

The dispersion of *Nucella lapillus* was found to be significantly influenced by month (GLM. F=176.645 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.16).

Trwyn y Penrhyn.

The dispersion of *Nucella* was found to be significantly influenced by month (GLM. F=170.288 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.17).

Llanfairfechan.

The dispersion of *Nucella* was found to be significantly influenced by month (GLM. F=137.326 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.18).

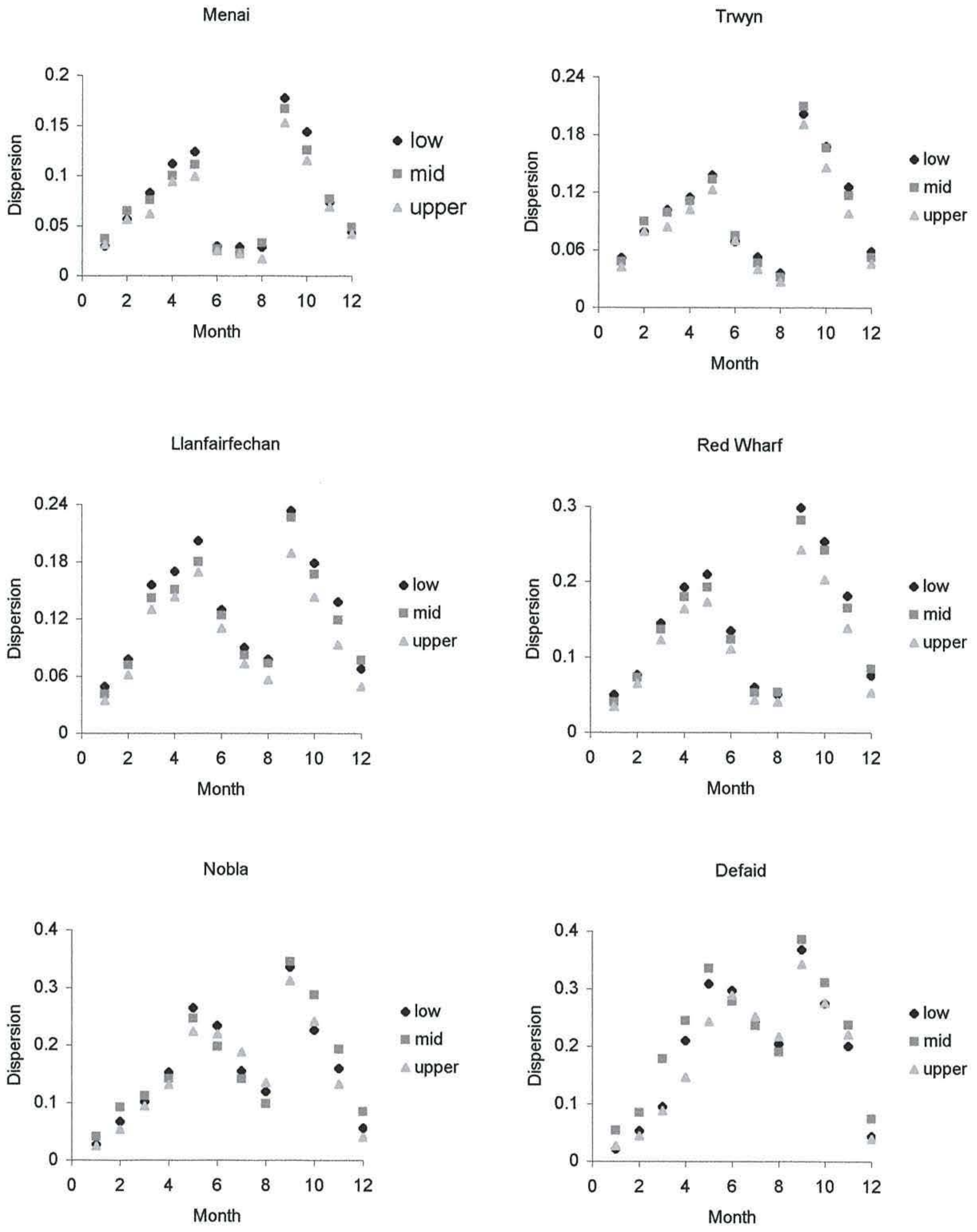


Figure 4.15. Monthly dispersion (degree of aggregation) of *Nucella lapillus* at different shore levels. Months 1-12 represent January to December inclusive.

Red Wharf bay.

The dispersion of *Nucella* was found to be significantly influenced by month (GLM. F=182.619 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.19).

Porth Nobla.

The dispersion of *Nucella* was found to be significantly influenced by month (GLM. F=207.956 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.20).

Porth Defaid.

The dispersion of *Nucella* was found to be significantly influenced by month (GLM. F=112.654 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in movement between most months (Appendix 4, Table 4.21).

4.372. Comparison of degree of dispersion between shore levels.

The dispersion of *Nucella* was found to be significantly influenced by shore level at Menai Bridge (GLM. F=32.338 P=<0.001), Trwyn y Penrhyn (GLM. F=34.456 P=<0.001), Llanfairfechan (GLM. F=26.541 P=<0.001), Red Wharf Bay (GLM. F=23.414 P=<0.001), Porth Nobla (GLM. F=6.749 P=0.002), and Porth Defaid (GLM. F=7.935 P=0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in *Nucella* dispersion between all shore levels on all study shores (Table 4.12.).

Table 4.12. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* between different shore levels.

shore	shore levels	md	*P*	shore levels	md	*P*	shore levels	md	*P*
Menai	1-2	0.014	0.001	1-3	0.040	<0.001	2-3	0.026	<0.001
Trwyn	1-2	0.014	0.002	1-3	0.035	<0.001	2-3	0.021	<0.001
Llanfairfechan	1-2	0.011	0.005	1-3	0.032	<0.001	2-3	0.021	<0.001
Red Wharf	1-2	0.019	<0.001	1-3	0.031	<0.001	2-3	0.012	0.023
Porth Nobla	1-2	0.009	0.034	1-3	0.023	<0.001	2-3	0.014	0.016
Porth Defaid	1-2	0.014	0.011	1-3	0.039	<0.001	2-3	0.025	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.373. Comparisons of degree of dispersion between shores.

The overall dispersion of *Nucella* was found to be significant between shores (GLM. F=755.931 P=<0.001). Post Hoc multiple comparisons (Bonferroni test) showed significant mean differences in degree of aggregation between all shores (Table 4.13).

Table 4.13. Results of Post Hoc multiple comparison (Bonferroni test) showing the significant mean differences in degree of aggregation between shores.

shores	mean difference	significance
Menai and Trwyn	0.025	<0.001
Menai and Llanfairfechan	0.066	<0.001
Menai and Red Wharf	0.045	<0.001
Menai and Porth Nobla	0.079	<0.001
Menai and Porth Defaid	0.148	<0.001
Trwyn and Llanfairfechan	0.041	<0.001
Trwyn and Red Wharf	0.021	<0.001
Trwyn and Porth Nobla	0.054	<0.001
Trwyn and Porth Defaid	0.123	<0.001
Llanfairfechan and Red Wharf	0.021	<0.001
Llanfairfechan and Porth Nobla	0.133	<0.001
Llanfairfechan and Porth Defaid	0.082	<0.001
Red Wharf and Porth Nobla	0.033	<0.001
Red Wharf and Porth Defaid	0.102	<0.001
Porth Nobla and Porth Defaid	0.069	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

4.38. Dispersal and Dispersion.

The plotting of mean dispersal and dispersion (aggregation) values on the same axes, shows that they both decrease with increasing shore level (Figure 4.16). The same data are plotted to show how both dispersal and dispersion at the three shore levels varies from shore to shore in Figure 4.17.

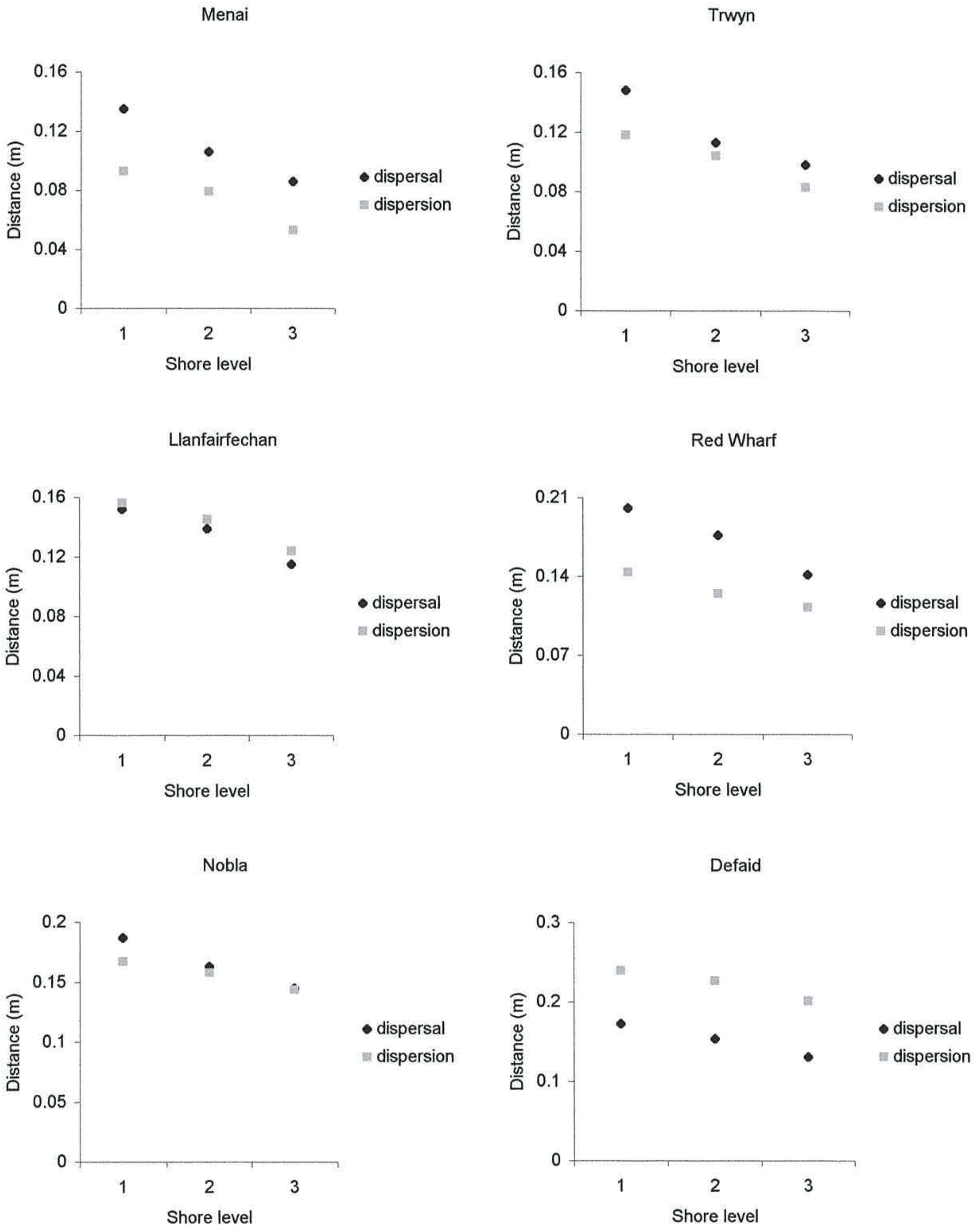
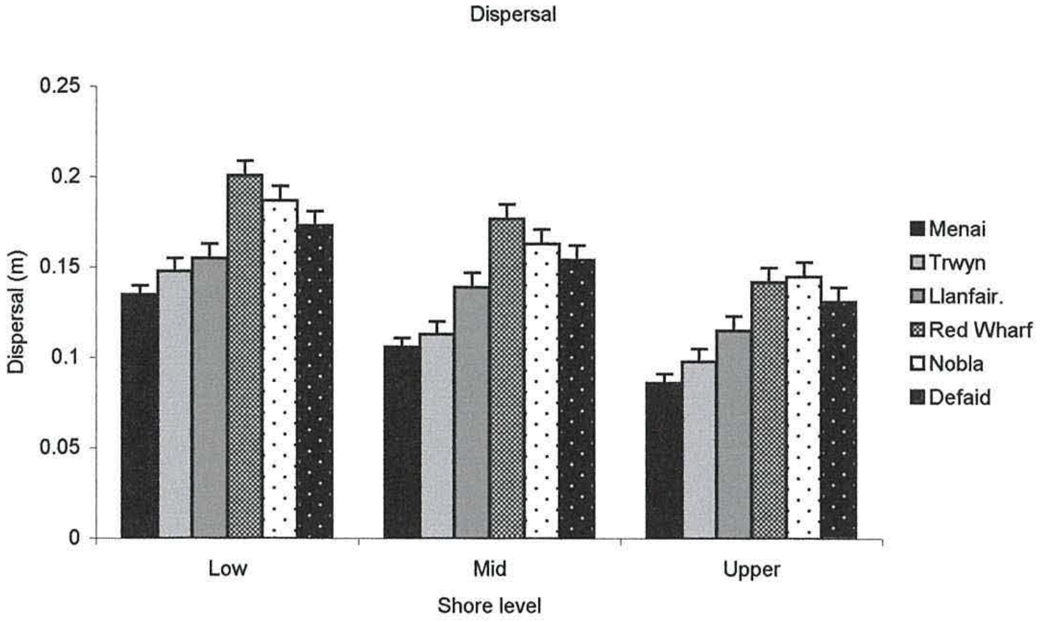


Figure 4.16. Comparison of mean weekly dispersal (distance moved), and weekly dispersion (degree of aggregation) at different shore levels.Y axis represents both distance moved (metres) and distance apart (metres).



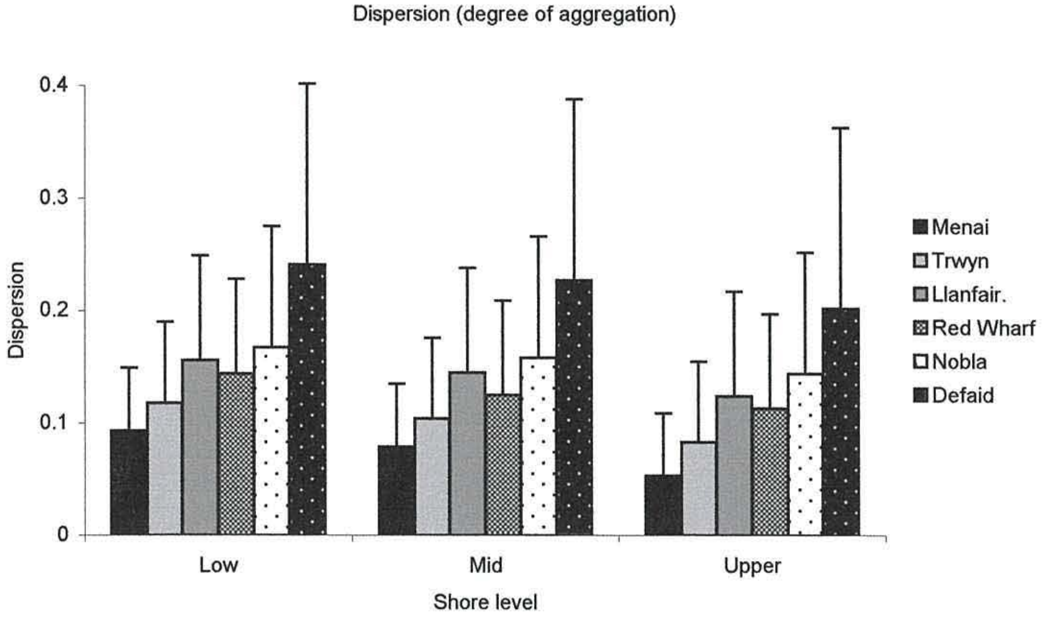


Figure 4.17. Summary of weekly dispersal (distance moved), and weekly dispersion (degree of aggregation) patterns at different shore levels (2 years pooled data).

4.39. *Nucella lapillus* density and mortality.

4.391. *Nucella* density.

The numbers of dogwhelks were monitored on fixed boulder units at three shore levels. The results of mean foraging densities of foraging *Nucella* at three shore levels (low, mid and upper), are graphed in Figure 4.18; overall density comparison between study shores in Figure 4.19 (Both two years pooled data).

The density of *Nucella* was found to be significantly influenced by shore level at Menai Bridge (GLM. F=160.762 P=<0.001), Trwyn y Penrhyn (GLM. F=1611.776 P=<0.001), Llanfairfechan (GLM. F=1166.989 P=<0.001), Porth Nobla (GLM. F=140.066 P=<0.001), and Porth Defaid (GLM. F=65.989 P=0.016), but not significantly influenced by shore level at Red Wharf Bay (GLM. F=0.353 P=0.710). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in *Nucella* density between most shore levels on five of the study shores (Appendix 4, Table 4.22).

The density of *Nucella* was found to be significantly influenced by shore (GLM. F=41.723 P=<0.001), with significant differences between the densities of Menai Bridge, Trwyn y Penrhyn, and Llanfairfechan, and each of Red Wharf Bay, Porth Nobla and Porth Defaid (all with significance of <0.001).

4.392. *Nucella* mortality.

The mortality of *Nucella* was found to be significantly influenced by size class at Menai Bridge (GLM. F=13.393 P=<0.001), Trwyn y Penrhyn (GLM. F=12.388 P=<0.001), Llanfairfechan (GLM. F=23.866 P=<0.001), Red Wharf Bay (GLM. F=19.659 P=<0.001), Porth Nobla (GLM. F=23.754 P=<0.001), and Porth Defaid (GLM. F=24.072 P=<0.001). This results are shown in Figures 4.20 (individual shores), and 4.21 (pooled data from all six shores). Comparisons of overall percent mortality is graphed in Figure 4.22 (depicting three shore levels), and Figure 4.23 (comparison between shores). Monthly variation at three shore levels on the six shores is compared in Figure 4.24.

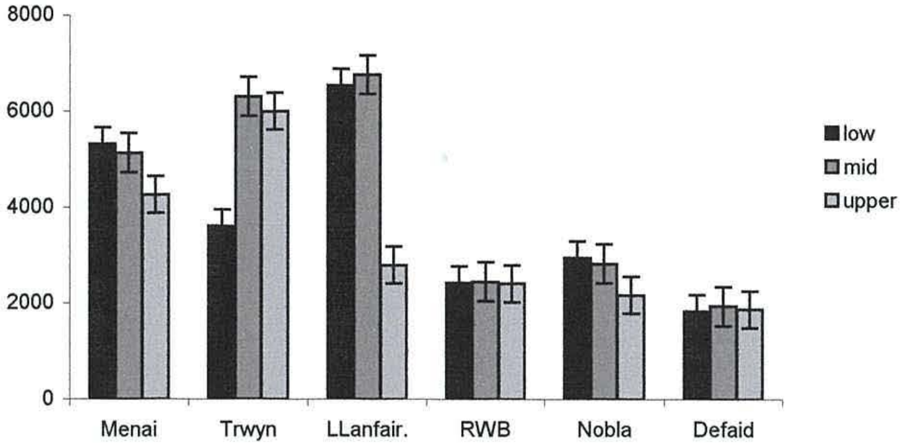


Figure 4.18.Mean densities of *Nucella lapillus* on different shores, monitored on fixed boulder units. Numbers represent dogwhelks per 100 ~~sq. metres.~~

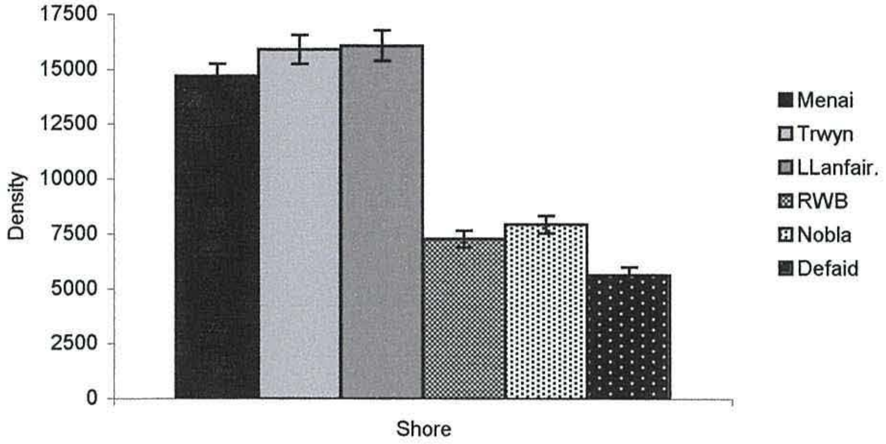
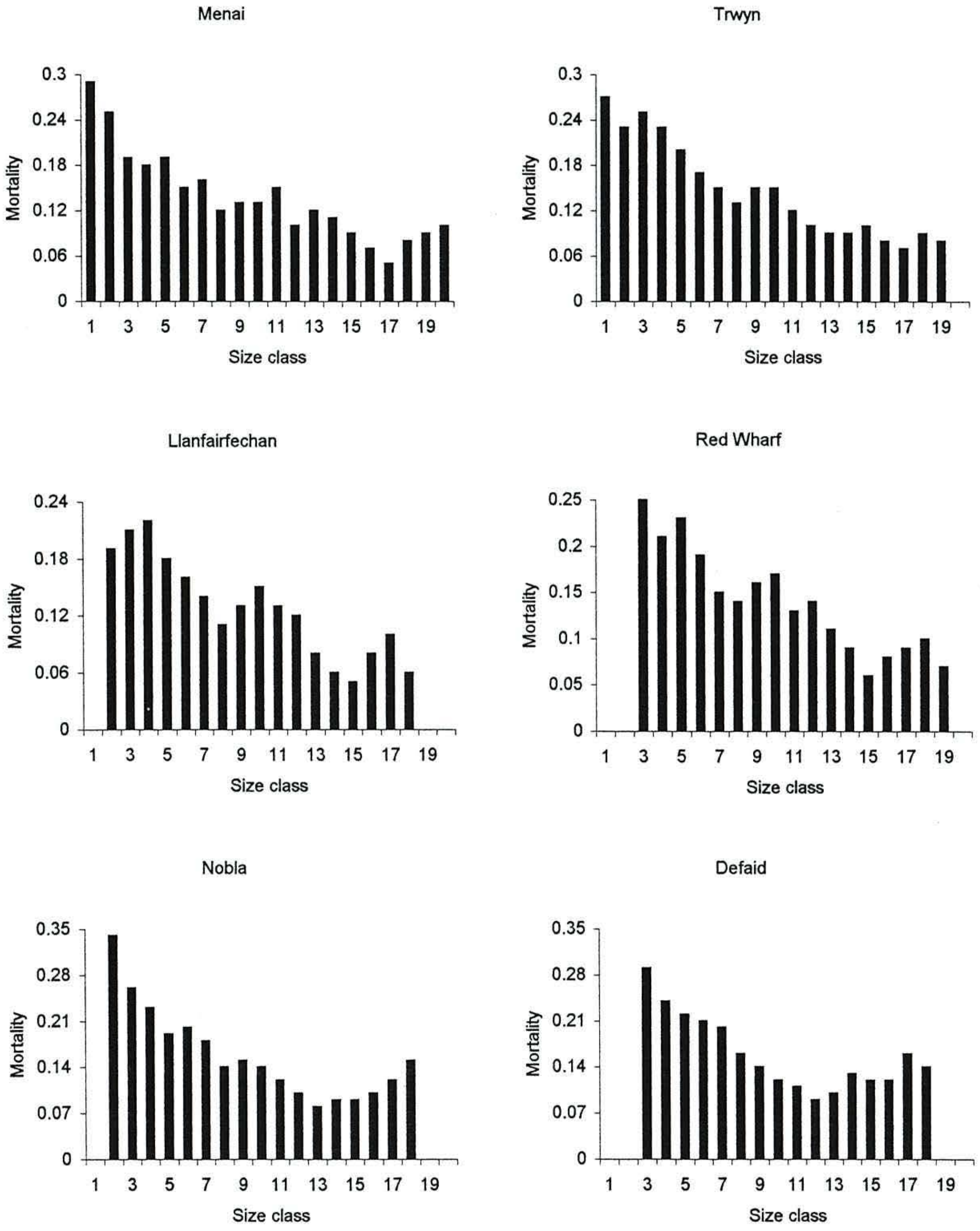


Figure 4.19.Mean densities of *Nucella lapillus* on different shores, monitored on fixed boulder units. Numbers represent dogwhelks per 300 ~~sq. metres.~~



Menai

Trwyn

Llanfairfechan

Red Wharf

Nobla

Defaid

Figure 4.20. Mortality of *Nucella lapillus* in relation to size class on different shores. (2 years pooled data).
Size classes are from 2-3.9mm (class 1) to 40-41.9mm (class 20) inclusive.

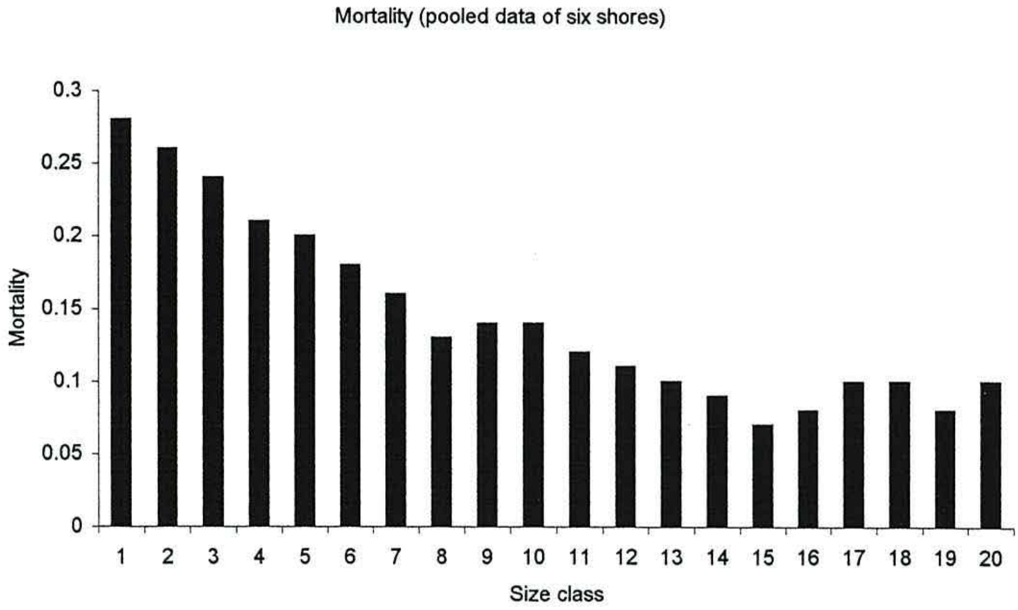


Figure 4.21.Mortality of Nucella lapillus in relation to size class(pooled data from all study shores and 2 years pooled data).
Size classes are from 2-3.9mm (class 1) to 40-41.9mm (class 20) inclusive.

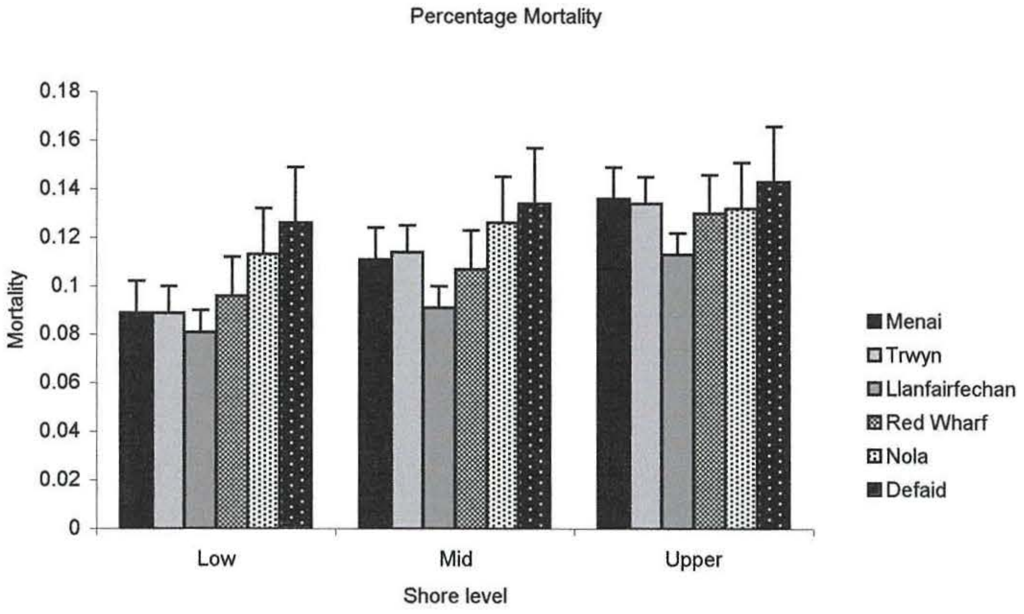


Figure 4.22.Comparison of the mortality of *Nucella lapillus* at different shore levels. (2 years pooled data).

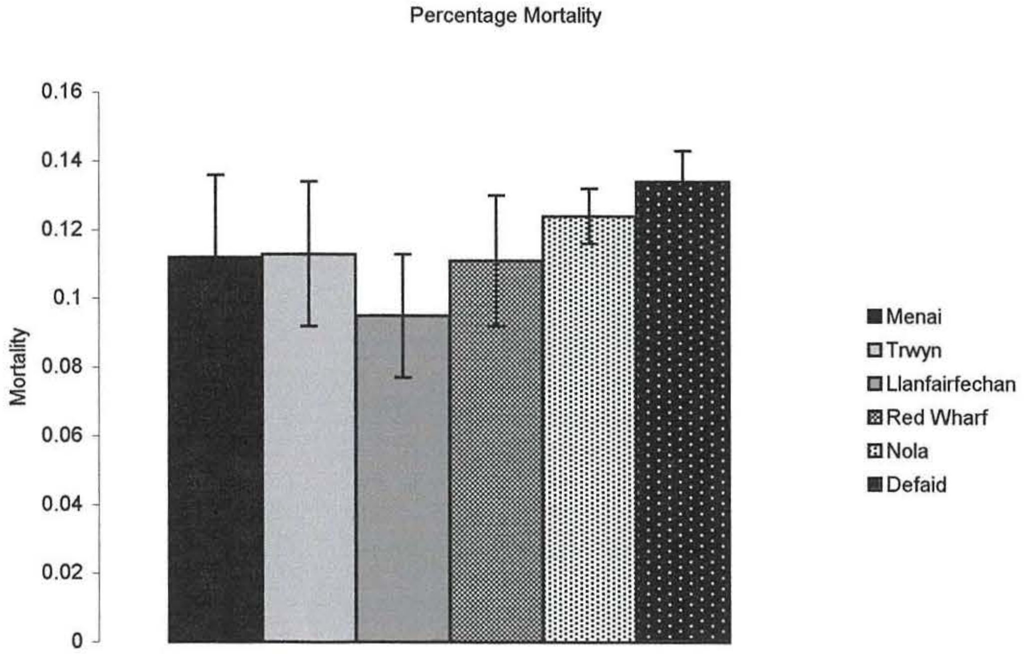


Figure 4.23. Comparison of the mortality of *Nucella lapillus* on different shores. (2 years pooled data).

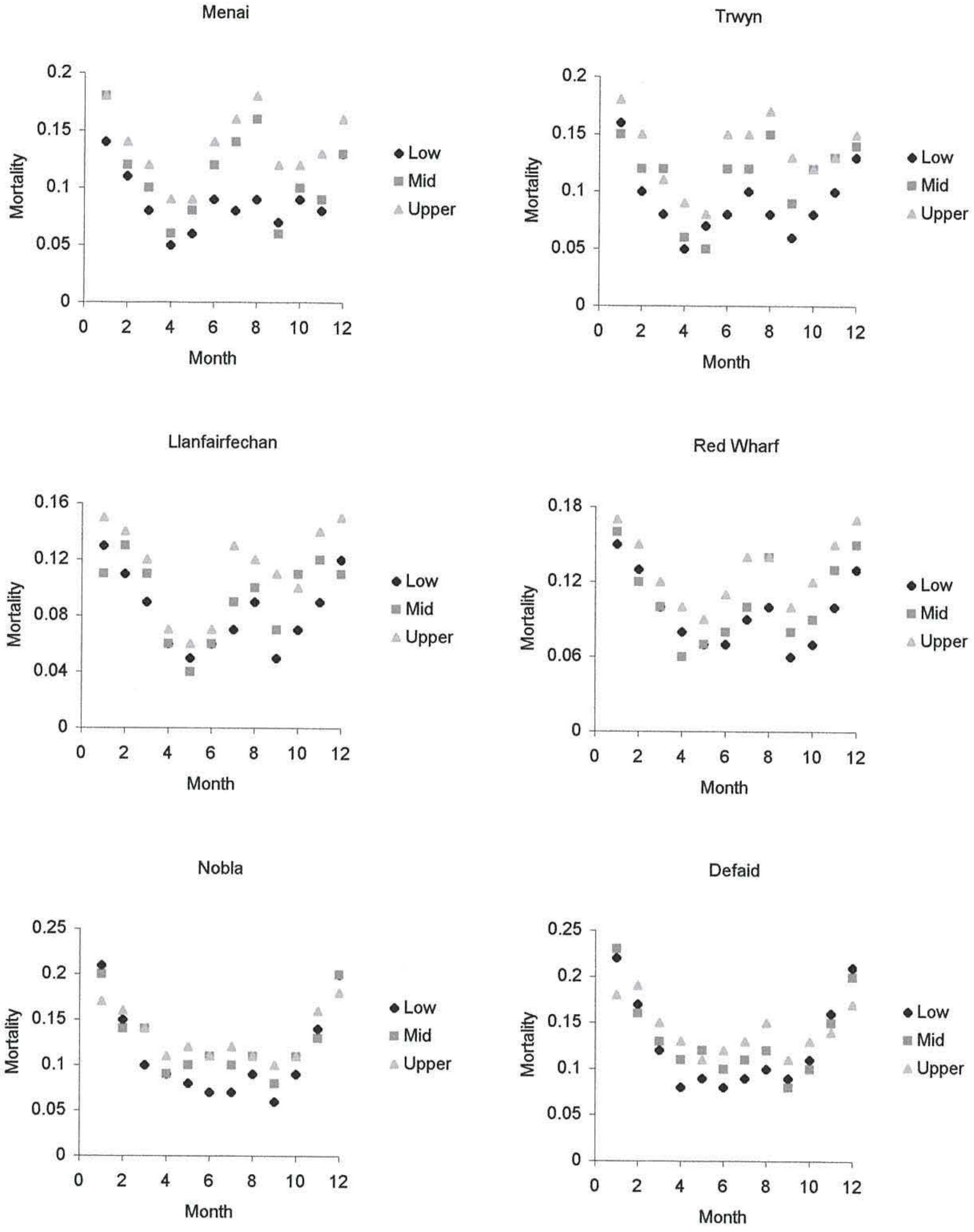


Figure 4.24. Monthly overall mortality of Nucella lapillus at different shore levels. (2 years pooled data).

The mortality of different size classes at different shore levels on sheltered, semi-exposed and exposed shores is shown in Figures 4.25, 4.26, and 4.27. The mortality of *Nucella* was found to be significantly influenced by shore level on sheltered (Menai and Trwyn), and semi-exposed (Llanfairfechan and Red Wharf) shores, but not at exposed locations (Nobla and Defaid), as shown in Table 4.14. Post Hoc Bonferroni multiple comparisons of mortality between different shore levels are presented in Appendix 4 (Table 4.23). Mortality was (only marginally) significantly influenced by shore (GLM. F=2.257 P=0.047), although Post Hoc Bonferoni multiple comparisons had no significant differences between any of the paired shores tested.

Table 4.14. GLM ANOVA analysis of the differences in mortality between shore levels.

Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
9.239*	<0.001	3.560*	0.032	3.996*	0.021	3.854*	0.024	0.427	0.653	1.173	0.313

Data presented are F test values (F), with probabilities (P), of which* are significant values.

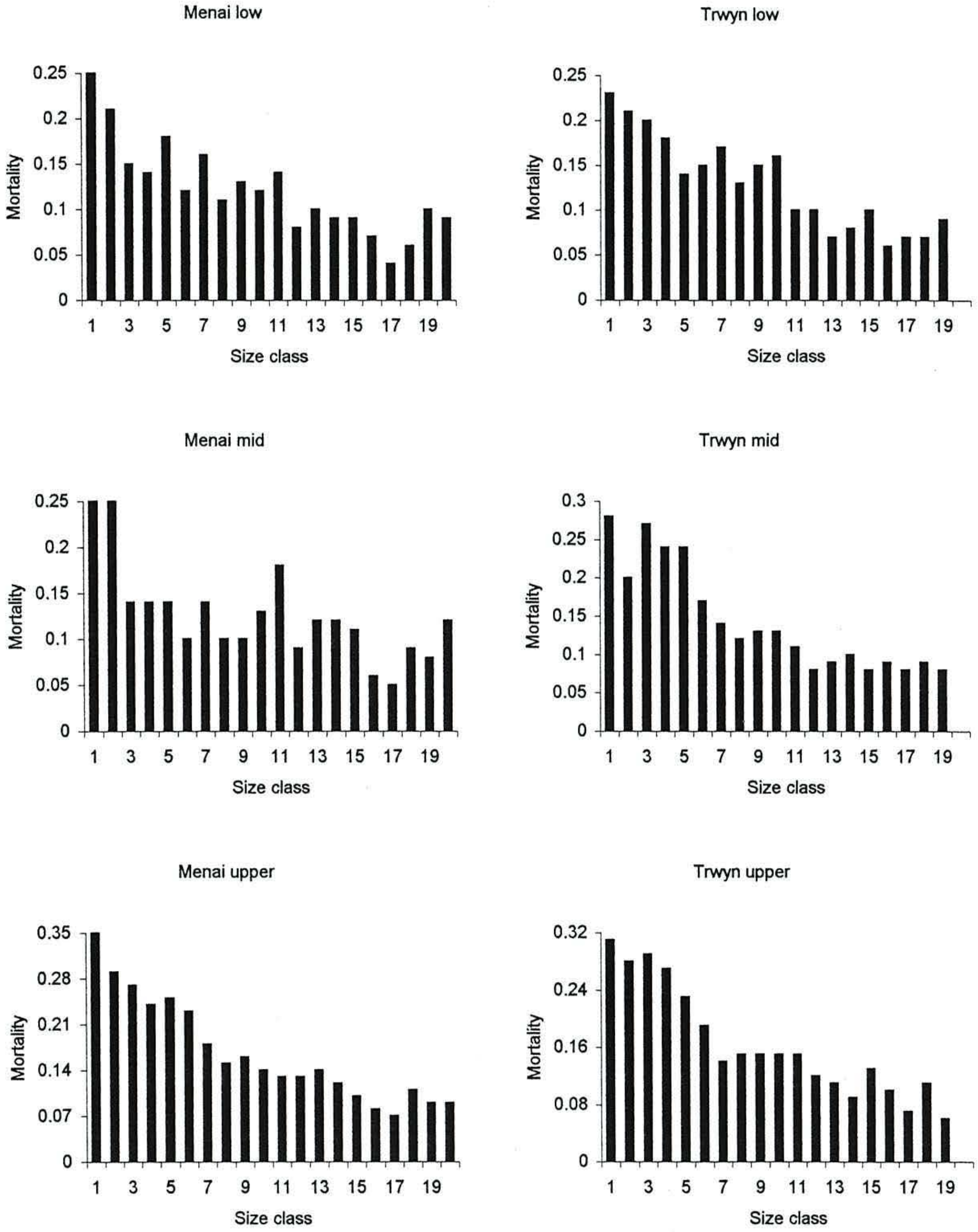


Figure 4.25. Mortality of *Nucella lapillus* at different shore levels on two sheltered shores. Size classes are from 2-3.9mm (class 1) to 40-41.9mm (class 20) inclusive.

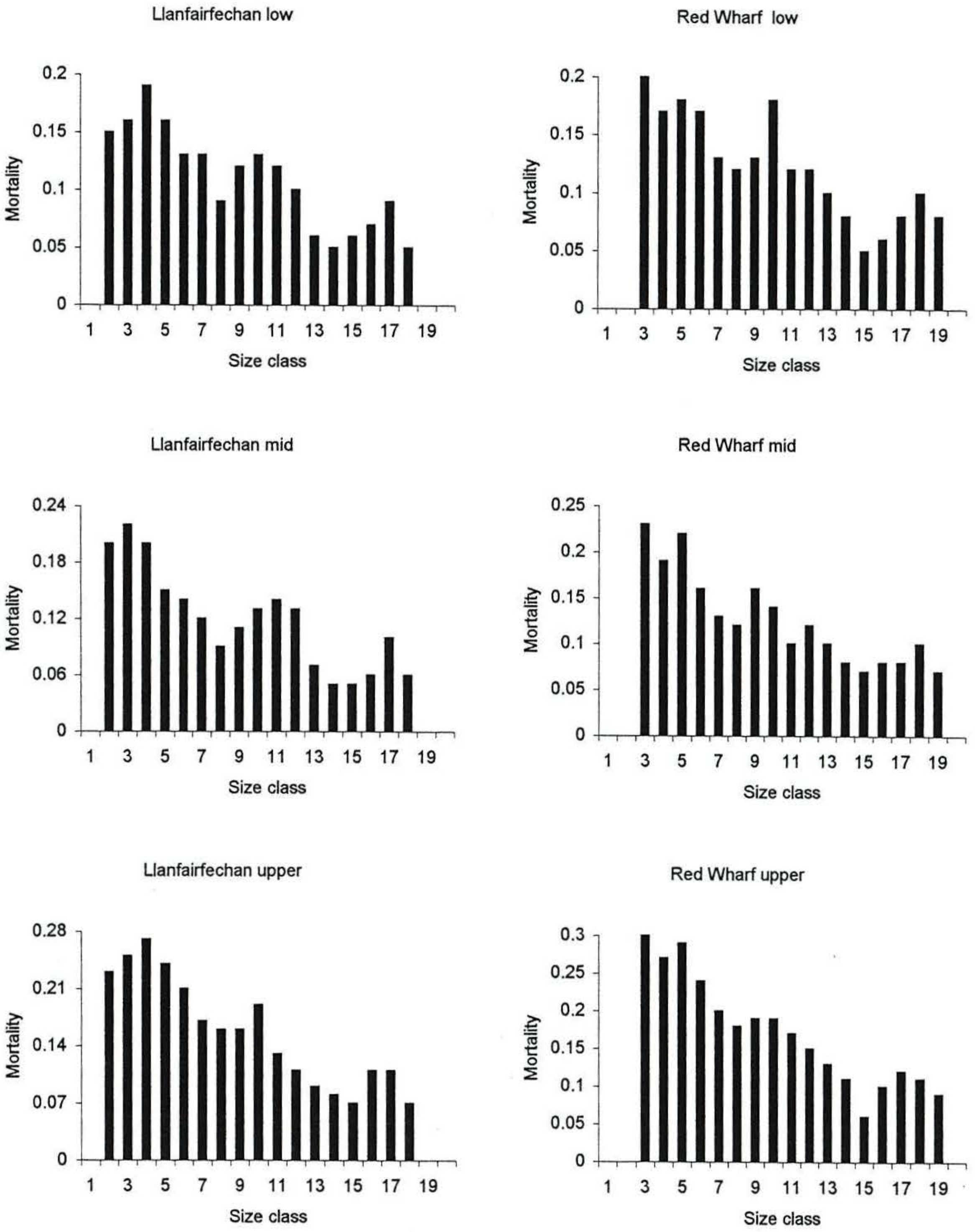


Figure 4.26. Mortality of *Nucella lapillus* at different shore levels on two semi-exposed shores.
Size classes are from 2-3.9mm (class 1) to 40-41.9mm (class 20) inclusive.

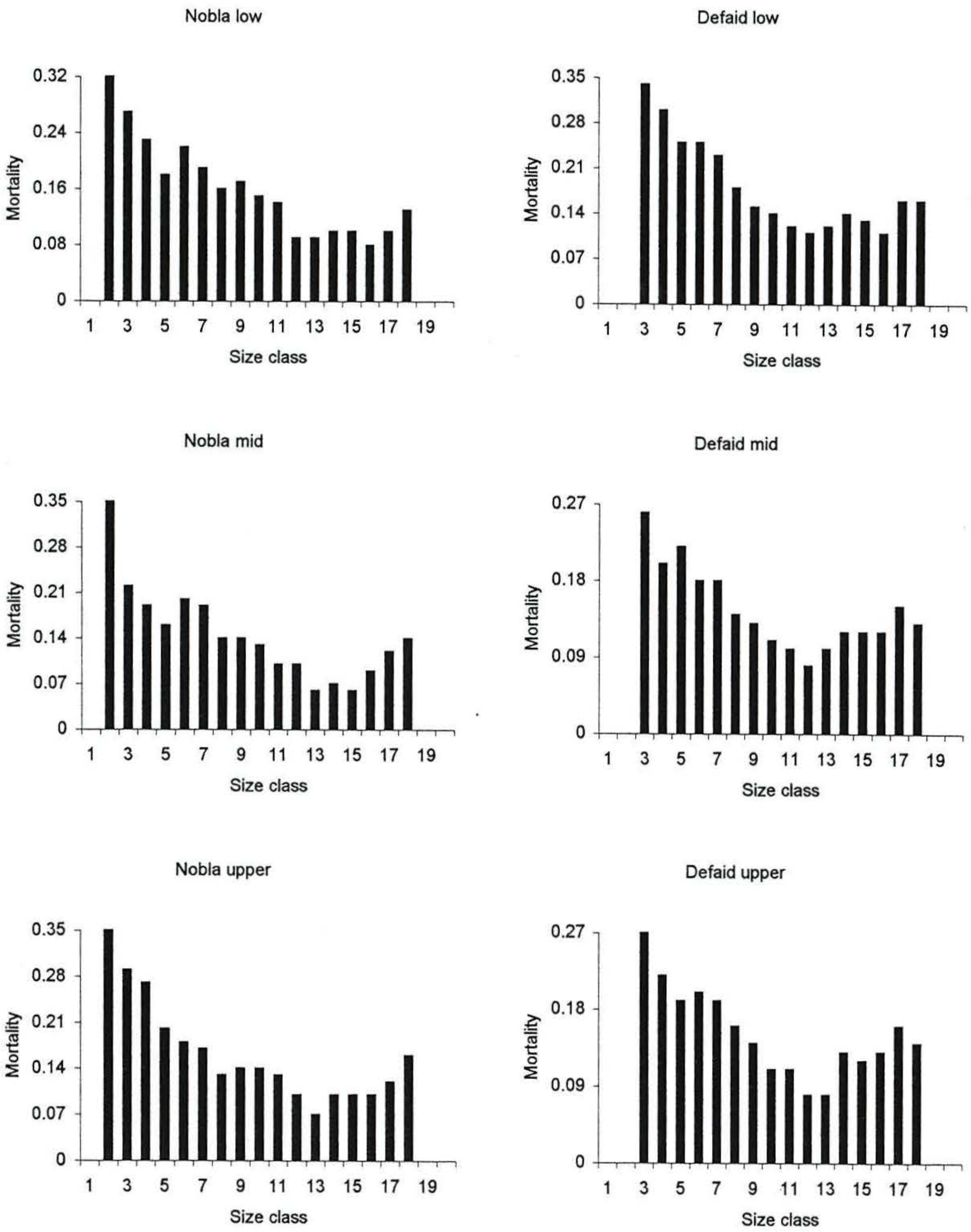


Figure 4.27. Mortality of *Nucella lapillus* at different shore levels on two exposed shores. Size classes are from 2-3.9mm (class 1) to 40-41.9mm (class 20) inclusive.

4.4. DISCUSSION.

Monthly dispersal patterns.

Nucella lapillus exhibited marked seasonal differences in activity (Kawai and Nakao, 1993), and although snails were observed moving throughout the year, more than 75% of all dogwhelk dispersal episodes took place between April and October. These differences mirror the changes seen in numbers and percentages actively foraging throughout the year (Chapter 5). There was a pronounced seasonal periodicity in all populations, corresponding to the invasion of foraging areas in the Spring and migration to low-shore aggregation sites in the Autumn. Seasonal reductions of activity occured from December to February and June to August (Menge, 1976b; 1979; Lubchenco and Menge, 1978). During the cold periods of the year foraging was relatively low and fairly constant, but was more variable during the warmer months (Menge, 1978a). These observations on *Nucella lapillus* are similar to those on related species *Nucella emarginata, Nucella canaliculata* (inactive during the winter months), and *Nucella lamellosa* (ceases feeding and forms breeding aggregations in winter) (Dayton, 1971). In the United States, all these predators are most active in Summer and Autumn, *Nucella lapillus* being especially abundant in the low intertidal (Lubchenco and Menge, 1978). Dispersal and feeding rates were greater in the cooler parts of Spring\Summer (than the warmest times) in both North Wales and North America (Menge, 1978b).

These monthly patterns are a response to environmental conditions, particularly desiccation and wave impact, which vary seasonally (Burrows and Hughes, 1989). Foraging is limited by exposure to air (Gosselin and Chia, 1996b), desiccation (Bingham, 1972), and heat stress (Bock and Johnson, 1967), during daytime low tides (Hughes and Burrows, 1994). As a result, the whelks are often restricted to shaded or wetted microhabitats during these periods, such as under the algal canopy (Garrity and Levings, 1981), where the effects of desiccation are reduced (Menge (1978a). Temperatures, or effectively desiccation, influenced the periodicity of activity on all six study shores. Temperatures increased in April and May, becoming optimal and foraging behaviour also increased at this time, as whelks were able to actively move around and even forage in horizontal areas of the substrate in appreciable numbers. These are areas which received more incident sunlight but significantly, are also where larger prey organisms (barnacles) were found. In July and August, temperatures became higher and the the physical impact from heat stress significant, increasing the probability of desiccation (Abe, 1989). During this period dogwhelks mainly foraged in more protected (from the sunlight) areas on vertical surfaces, and in refuges (Kawai and Nakao, 1993). This includes foraging under discrete patches of algae, within which they were able to feed on barnacles without being vulnerable to predation themselves (Crowe, 1996), and at cooler times in the open (Menge, 1978b). Consequently, net dispersal distances were reduced. By September and October, mean daily temperatures fell enough again to allow the whelks to move around more, and another seasonal peak in dispersal occured. Environmental conditions that restrict *Nucella* movement were most stressful in the winter, including considerable reductions in water (and air) temperatures (Stickle and Bayne, 1987) to which they were very sensitive (Largen, 1967), leading to inactivity and the formation of aggregations.

Temporal differences in wave-action were also seen to affect dogwhelk dispersal. Qualitative observations showed that foraging activity was negatively associated with rough weather, and positively associated with calmer seas (Menge, 1978a), particularly on the more exposed shores (Porth Defaid, Porth Nobla and Red Wharf Bay), where monthly variation in dispersal was greatest. During the winter period (November to February), *Nucella lapillus* moved only small distances and less often than at other times of the year in relation to observed higher wave amplitudes. These dogwhelk activity patterns tend to minimize mortality risk (Menge, 1978a).

The Tidal and Diurnal Cycles.

A secondary periodicity in dogwhelk dispersal and associated foraging activity was evident in populations on all six study shores that corresponded to feeding/resting and digestion cycles (Burrows and Hughes, 1991b). This was apparent in the observed changes in numbers of *Nucella lapillus* actively foraging (two years data) in similarly-sized patches of barnacles, that were graphically standardized to minimum values to allow comparison between months of the year (Figures 4.11 and 4.12). Population fluctations in foraging activity showed similar periodicity in relation to the tidal cycle (if not in amplitude), throughout the year. These cyclical changes in numbers foraging (qualitative increase and decrease), took place irrespective of wave-action and temperature, although quantitative differences were related to season, and presumably the predominating environmental conditions. Even extreme periodic events such as heat waves and violent storms did not affect the length of the cycle.

The state of the tidal cycle is of particular importance to the movement patterns of intertidal snails (Dexter, 1943; Alexander, 1960; Underwood, 1972a; 1972b), as the organisation of short-term activity is determined by tidal and diel variations in physical and biological factors (Edwards et. al., 1982; Chelazzi et. al., 1986), resulting in complex diel-tidal rhythms (Zann, 1973b). The timing of low water and tidal amplitude (Moran, 1985c), are critical factors as *Nucella* spp. only search for prey when submerged (Fairweather and Underwood, 1983; Palmer, 1984; West, 1986), being motionless during low tide (Underwood, 1976). As a result, foraging patterns are constrained by the tidal state (Lucas and Schmid-Hempel, 1988), and change at different times of day, with different stages of the tidal cycle (Garrity and Levings, 1981).

Dogwhelks move around to feed during both daylight and the dark (Connell, 1961b; Cook et. al., 1969; Zann, 1973a; Mackay and Underwood, 1977), in the dark following more tortuous paths, as measured by the meander ratio (total distance moved/straight-line distance moved) (Hughes and Dunkin, 1984). They move further (and a higher proportion are active) during nocturnal ebb tides when the rock substrate remains wet for longer (Levings and Garrity, 1983, and in relation to the period of submergence (Ward and Quinn, 1988). During daytime spring low tides, however the substrate was subject to high insolation and feeding rates were reduced (Underwood, 1985).

Spatial differences in foraging activity.

The spatial distribution of prey items varied within shores and between sites. Partly as a result of this *Nucella lapillus* predation varied significantly not only in time, but also in space, even within very small spatial scales. Dogwhelk distribution in space was particularly variable in the vertical direction. As a result different parts of the intertidal habitat were subjected to different predation regimes: some areas had whelks present most of the time, others were rarely visited at all . In general dispersal and feeding rates of *Nucella lapillus* were inversely proportional to tidal level, highest in the lower intertidal, where the predators were covered longer, which is similar to observations on other intertidal snail predators (Menge, 1978b; McQuaid 1982; Underwood, 1985), elevated under algal canopy compared to bare surfaces (see work by

McQuaid, 1985 on *Nucella dubia*), and greater in the cooler parts of Spring\Summer (than the warmest times) (Menge, 1978b). Foraging of intertidal snails is dependent on the time availible to search and consume prey, and consequently, foraging cycles are generally out of phase at the different tidal levels (McQuaid, 1985), to ensure the maximization of potential encounters with, and utilisation rates of prey (Spight, 1974; Townsend and Hughes, 1981; Fairweather, 1988a; Navarrete, 1996). In the study areas, *Nucella lapillus* in the upper shore foraged proportionately more often when the duration of submersion was extended (spring tides), and tended to shelter more frequently during periods of long emersion (neap tides), compared to those at lower levels. At heights below mid-tidal level, there is a longer period of submersion during neap tides (Underwood, 1985), and foraging activity tended to increase in these periods at this level. These differences in foraging at different levels on the shore, may even account for the differences in population structure and therefore size-frequency distribution observed (Connell, 1972).

There were significant differences in dispersal and foraging rates of *Nucella lapillus* between those on exposed (higher dispersal) and those on protected shores (Menge, 1978b). Mean weekly migrated distances were clearly longer for those dogwhelks in exposed conditions, particularly during the Spring and Autumn, which was in response to variation in wave-action. High wave energies on more exposed shores tended to reduce foraging time efficiency of *Nucella* spp. (Menge 1974; 1978a; 1978b; Richardson and Brown, 1990), by increasing handling time (Etter, 1996), and this frequently restricted *Nucella lapillus* to refuges at the exposed (less so at protected) areas. So *Nucella* consumed fewer prey items at these sites (Menge 1978b; Burrows and Hughes, 1989; so reducing predation intensity (density x activity) on barnacles. A reduction in predation upon barnacles on more expose coastlines has been observed in many intertidal systems (Connell, 1961a; Dayton, 1971; Paine, 1966; Menge, 1978a; 1978b; Menge and Sutherland, 1976; Roughgarden, 1986), especially when compared to extremely sheltered shores (Menge, 1978b). In North Wales, higher densities of whelks were found at sheltered sites (the opposite of the findings of Kitching and Lockwood, 1974), increasing predation intensity in these locations). High wave action can reduce relative growth rates for intertidal snails on exposed shores (Richardson and Brown, 1990; Etter, 1996), although growth was not monitored in these experiments.

These effects on dogwhelk activity occur because in extreme wave-exposed habitats, breaking waves generate greater water velocities (Jones and Demetropoulos, 1968; Denny, 1985; 1988; Denny et. al., 1985; Bell and Denny, 1994; Gaylord, 1997). The larger waves here impact on the shore subjecting organisms there to significant abrasion, pressure, and drag forces (Demetropoulous, 1965), which may dislodge moving gastropods from their intertidal habitats (Taylor, 1976; Leviten and Kohn, 1980), including dogwhelks (Moran, 1985c), which once detached do not easily re-attach in moving water (Lawrence, 1972). This interferes with feeding and refuging (Brown and Quinn, 1988), and may be lethal for individuals removed from their typical environment (Etter, 1988a). In sheltered conditions whelks are more subject to increased desiccation than wave action, with foraging often restricted to cool, wet days (Hughes and Taylor, 1997; Burrows and Hughes, 1989). These factors seem to explain the distinct foraging patterns seen on the study shores.

Differences in whelk foraging behaviour between different types of shores has been extensively investigated on the North-eastern Pacific coast of the United States. Intensity of predation is variable among shores there, between seasons of the year, (Menge, 1978a), and higher at sheltered sites (Menge, 1976). Dogwhelk foraging activity at different sites is variable, and a combination of various factors (particularly wave-action), act at this spatial scale to modify their feeding pattern (Menge, 1978a; 1978b; 1983). Exposed whelks have intrinsically higher feeding rates (greater rate of prey consumption), in nearly all circumstances (Menge, 1978a), but particularly in calmer conditions (Menge, 1978b). On more sheltered sites, dogwhelks exhibit more selectivity in their choice of prey, being released from environmental foraging constraints, resulting in more rapid growth (as for *Nucella canaliculata*, see Garton, 1986).

Dogwhelks moved (dispersed) further per unit time on exposed shores. Prey items (barnacles) are further apart on these shores (lower density, clumped distribution), as shown by a lower substrate coverage (Chapter 6). Therefore *Nucella* need to track greater distances to assimilate the same amount of protein, so do move further when they can, spending more time in refuges (in winter). Following elimination of prey in the refuges (a variable and sometime unreliable resource), whelks then have to travel far to find more barnacles. This is especially true for foragers at Porth Defaid, where barnacle density is particularly low, especially when compared to *Nucella* foraging densities on this shore (Chapter 6). Also at wave-swept locations, whelks had a greater tendancy to be accidently displaced (passive dispersal), than at sheltered sites. This spatial variability in predation can have important consequences for prey populations and even whole sessile community assemblages (Duggins, 1983, Fairweather, 1988b; Menge et. al., 1994), depending on pelagic settlement patterns, and the ability of prey poulations to recover (Navarrete, 1996).

Dogwhelk size and dispersal.

Mean weekly dispersal distances were positively related to the size of *Nucella lapillus,* at all shore levels upon all six study shores. Adult snails dispersed at greater rates and moved greater overall distances, than juveniles in these experiments, identical results to many other studies on intertidal gastropods (Desai, 1966; Lambert and Farley, 1968; Micallef, 1970; Underwood, 1973; McQuaid, 1980; 1982; Levings and Garrity, 1983; Crowe, 1996; Takada, 1996*)*. This is partly due to the fact that small dogwhelks cannot move as fast (Menge, 1978a), but is also related to the effect of detrimental environmental factors acting disproportionately on the smaller forms. Early juvenile snails (size class 1) are particularly vulnerable to predation, desiccation and wave-action (Faller-Fritch, 1977; Underwood, 1979; Werner and Gilliam, 1984), because of their small size (Branch, 1975). Water loss and therefore desiccation, can be a serious problem for them due to their higher surface area to volume ratio (Gosselin, 1997). This explained the greater proportional reduction in foraging in these size of whelks, particulaly in summer periods on sheltered shores. They cannot survive even moderate drying conditions at low tide and so are restricted to certain microhabitats (Gosselin and Chia, 1995b). Hatchling *Nucella emarginata* are observed to cease movement when emersed (Gosselin and Chia, 1996b). They, and and the other lower size class (size class 2), of *Nucella lapillus* were usually found under small stones in the lower reaches of the shore (Dukes, 1994). Contrary to the findings of Menge (1978a), and Hughes et. al. (1992), I did not find that juveniles of *Nucella lapillus* spend more time on exposed surfaces, nor did they remain foraging later into the winter when adults retire in refuges. Rather the contrary was true.

Dogwhelk size and proportion feeding.

Both the height of low water (Table 4.15) and the insolation index (Table 4.16) produced significant correlations with the proportion (postive in the former, negative in the latter) of dogwhelks feeding on most shores.

Table 4.15. Absolute values of Pearson correlation coefficient and ANOVA test of significance of the regression slope of the proportion of whelks feeding in relation to the height of low water.

	Menai	Trwyn	Llanfairechan	Red Wharf	Nobla	Defaid
R	0.606	0.714	0.584	0.552	0.449	0.413
F	29.131	41.265	19.456	22.347	14.193	11.227
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Data presented are correlation coefficient (R), F-values (F), and probabiliies (P), which are all significant values.

Table 4.16. Absolute values of Pearson correlation coefficient and ANOVA test of significance of the regression slope of the proportion of whelks feeding in relation to insolation.

	Menai	Trwyn	Llanfairechan	Red Wharf	Nobla	Defaid
R	0.779	0.689	0.614	0.626	0.487	0.234
F	48.134	37.267	22.104	16.555	3.227	6.214
P	<0.001	<0.001	<0.001	0.001	0.028	0.048

Data presented are correlation coefficient (R), F-values (F), and probabiliies (P), which are all significant values.

Both factors are related to the tidal spring-neap cycle. The peaks of foraging (proportion foraging) occured at different times between the different size classes in relation to the this cycle. At all shore levels, on all shores, there was a greater proportion of the larger two size classes (adults and larger adults 22.0-41.9 mm) feeding, than larger juveniles and subadults (12.0-21.9 mm), than early and smaller juveniles (2.0-11.9 mm), although overall differences were negligible (Figure 4.5). The different sized whelks had preferred positions on the beach with respect to chart datum (Chapter 2; Feare, 1970a).

Overall the environmental data did not point to any one or two particular factors controlling foraging in the different size classes. It seems likely that foraging behaviour is affected by these factors in combination, with one or another temporally becoming more important (eg. wave action during severe storms). Most of the environmental factors can be reduced in some way to their affect upon desiccation stress and dislodgement risk. It is not suprising to find a close correlation to the tidal cycle, as this is often the only regular environmental cue available.

The effects of exposure to air (and the resultant insolation) seems to have limited foraging activity by the smallest size classes with increasing desiccation stress. Small whelks have a higher surface area to volume ratio and dehydrate more quickly than the larger whelks, when caught in the open during periods of sunshine. Larger animals avoid this to an extent by their greater size.

Dogwhelk size and feeding bout.

Snails were found to forage in distinct periods (Hughes and Drewett, 1979), usually for several days at a time, followed by a period of rest or shelter (in a refuge), either scattered, or clustered (protected from wave-action), until the next feeding bout (Connell, 1961b; Menge, 1978a), in order to minimize metabolic costs and reduce mortality risk (Hughes and Burrows, 1994). The elapsed time between successive foraging bouts depends on the prey consumed (Hughes, 1988). The smaller whelks exhibited a larger number of short bouts, whilst larger whelks had a reduced number of longer bouts up to class 3 (the feeding bout in class 3 was equivalent to that in class 4). The gradual change in bout length may be attributed to the changing diet selection and anatomy of the growing whelks. Since the smallest whelks consumed only the smallest barnacles (see below) during a short bout, the digestive system needs only to cope with a small quantity of flesh at once. Foraging continues until a certain consumption threshold has been ingested, therefore bout length is related to the size (volume) of the dogwhelk. As the gut capacity increases (in larger dogwhelks), more flesh must be consumed to terminate the foraging bout (Hughes et. al., 1992). These ontogenetic changes in the foraging behaviour of dogwhelks can be explained in terms of greater energy demand accompanying a larger body size, and explains the respective foraging patterns of different size classes of *Nucella* on the shores of North Wales.

The feeding bout length is constrained by external factors (Lucas and Schmid-Hempel, 1988), including physiological stress from desiccation (Menge, 1978a; 1978b; Moran, 1980; Spight, 1981; 1982), wave shock (J.Menge, 1974; Menge and Sutherland, 1987), the presence of active predators (Hughes and Burrows, 1991), and prey availability (Hughes, 1979). The overall mean length of feeding bout increased with the degree of wave exposure experienced by different shores (Figure 4.6). Moreover, feeding bout changed differently on different shores with respect to the prevailing environmental conditions. On sheltered shores, exposure to air is longest at neap tides in upper zones; whilst on exposed shores emersion is effectively reduced during periods of rough weather. In calm weather at exposed sites, emersion is determined solely by the tidal cycle as on sheltered shores (Moran, 1985c).

Dogwhelk size and prey size.

In over 302,093 recorded feeding episodes by *Nucella lapillus* on six shores in a three year period, only 1 was on the mussel *Mytlus edulis*. All the rest were upon barnacles (predominantly *Semibalanus balanoides*). This is no surprise, for at four of the study locations, mussels were absent. However, on those shores which had extensive mussel beds (Llanfairfechan, and to a lesser degree Red Wharf Bay), and even in the mussel bed themselves, whelks fed upon barnacles in the spaces (interstices), between mussels, and significantly upon barnacles attached to mussel shells. Mussels in these locations were usually too large for *Nucella lapillus* predation.

Throughout its range (different shores, different shore levels), *N. lapillus* has a choice of prey species upon which to feed. The observed patterns of prey selection were related to prey size, distribution, and abundance (Crothers, 1985a). Palmer (1984b), discovered whelk species *Nucella emarginata, N. canaliculata* and *N. lamellossa* did not simply eat potential prey in proportion to their relative abundance, but positively selected different prey types (species and size). The different size classes of whelks in my observations, consistently selected prey of different sizes, prey size being generally correlated to predator size (Figures 4.7 and 4.10), as seen in previous work in this field (Connell,1961a, 1970; Fenchel, 1976; Werner and Gilliam, 1984; McQuaid, 1985; Burrows and Hughes, 1991; Hughes et. al., 1992). A succesful attack by a large whelk on a larger prey yields far more flesh (Bayne and Scullard, 1978), reducing handling time per unit flesh gained (Hughes and Dunkin, 1984). On the other hand, small whelks probably attacked small barnacles as handling time (it is difficult for them to drill larger barnacles), and the quantity of flesh ingested at one time is limited by predator size. Within the same size class, *Nucella lapillus* selected prey of successive larger sizes with increasing tidal height, on each study shore. This possibly reflected the declining availability of time for foraging at the higher level due to relative submersion factors, and the need for dogwhelks to maximise energy gain in limiting conditions (Wootton, 1993).

Large individuals of both *Nucella lapillus* and *Nucella emarginata* preferred large barnacles over small ones as prey in field observations by Connell (1961a, 1970). The only times when larger whelks chose smaller prey (which have a shorter handling time) in my investigations, was during heavy wave-action. This is because they need to reduce the time exposed to waves in order to avoid dislodgement and possible mortality (Menge,1974; 1978b; Hughes and Dunkin, 1984; Denny et al, 1985; Brown and Quinn, 1988; Richardson and Brown, 1990).

Dogwhelk prey selection is necessarily related to prey availability, and prey consumed reflected availability on the shore. It is logical to assume that prey densities are primarily determined by barnacle settlement patterns. Major settlement on the study shores occured in May and June, although precise timing varied from year to year (Kendall et. al., 1985). Settlement of barnacle cyprids is greatest at lower shore levels (Rangely and Thomas, 1988), and usually at more wave-exposed site (Bertness et al 1992), although barnacles grow fastest in sheltered locations, (increased food content of the water) (Bertness et al 1991). Obviously the mean barnacle size in the lower intertidal immediately after major settlement episodes, is small due to a large number of new recruits. On my study shores the overall (year round) availability of barnacles was greater in the sheltered locations.

Monthly migration patterns.

There were certain times of the year when appreciable numbers of dogwhelks in the same location on the shore, showed similar and repeated movements in the same general direction for one or several months. These relatively uniform movement patterns can be considered as limited population migrations to an extent, particularly as a majority of individuals (though not necessarily the same ones) repeated the same phased movements again in the second year. In the short term the periodicity of migrated distance was related, to both shore type and tidal level. Seasonal mass movements of intertidal gastropods have been identified, including Spring upshore migrations (Lambert and Farley, 1968); Summer downward displacements (Micallef, 1966), and Autumn downshore migrations (Lambert and Farley, 1968). In North Wales, *Nucella lapillus* moved vertically throughout the year, but this varied substantially with season (Abe, 1989). Identical long-term (a minimum of one month) vertical movements of whelks (Fairweather, 1988c), modifying their vertical distribution (Takada, 1996), and regulating their vertical densities (Berlow and Navarrete, 1997), took place at the same times of year over the two year period. Population migration patterns on the six shores were clear and consistent, but changed from sheltered to exposed along the wave-exposure gradient (Table 4.17).

Table 4.17.General population migration patterns at different shore levels in relation to season.

Season	Sheltered shores	Exposed shores
October to January	all 3 levels down	low shore up; mid up Dec-Jan; upper down
February	all directions equal including left and right	all directions equal including left and right
March to April	low and mid down; upper up	low and mid down; upper up
May	mid and upper continue to move upshore	mid and upper continue to move upshore
June to August	all 3 levels downward	down mainly in upper shore.
September	no major movements	limited upward movement

Data presented show subjective assessment of majority movements (pooled from two years data).

A number of general observations were made on these migratory patterns. Distances moved by individuals as well their direction of movement were often correlated from one day to the next: animals persisted in moving in the same direction on consecutive days. Localised fluctuations in density also occurred during certain times of prolonged significant migration. Moore (1938a), observed migratory patterns in *Nucella lapillus,* that following hatching (and growing to 5mm), the whelks migrated up the inter-tidal region to the high shore, and in their second year they returned to mid and low inter-tidal areas (see also Feare, 1969).

Migration patterns in inertidal snails are probably an interaction of endogenous and exogenous factors (Vannini and Chelazzi, 1978). For instance, water movements play (in combination with light and gravity), a part in controlling zonal orientation (Newell, 1979; Underwood, 1979), and in regulating both short-term (diurnal and/or tidal) or long-term (seasonal) zonal migrations up and down the shore (Chelazzi and Focardi, 1982). An example of this are the vertical migrations of *Nerita textilis,* which responds to changes in tidal level (Taylor, 1971).

Intertidal snails often tend to move back to their original area of origin or to a preferred height, or preferred habitat (McQuaid, 1981; Doering and Phillips, 1983). According to Underwood (1977), animals displaced downshore from their usual zones undergo negatively geotactic movement up the shore until they reach areas with sufficient prey densities, while animals transported up the shore, only return if the normal geotactic response is reversed by starvation (McQuaid, 1982). Movement up and down the shore can be in search of prey (Connell, 1970), or related to reproduction (Feare, 1970b).

Monthly dispersion patterns.

In every month sampled, there were significant departures from random dispersion. In many cases (December to Febuary, and June to August), the departure from randomness was in the direction of clumped or aggregated, dispersion. This corresponded to the formation of dogwhelk aggregations in the winter and hottest parts of the Summer, when the mean distance from one *Nucella lapillus* to its nearest neighbour was noticably shorter (Figure 4.15). Both the size and degree of aggregation changed markedly with season.

Air temperatures at low tide alter appreciably throughout the year (Underwood, 1976). High air temperatures and therefore the liklehood of dessication (Feare, 1971b) can be a predominant factor in causing dogwhelks to form aggregations. This has been clarified in other whelk species. For instance, in Summer, *Nucella freycinetti* tends to aggregate in crevices or on rocks at the low intertidal level (Kawai and Nakao, 1993); similarly aggregations of *Morula marginalba* shelter in crevices and pools from the effects of emersion (Moran, 1985a). Cold temperatures (both water and air), also affect the dispersion of *Nucella lapillus,* which is easily washed off the substratum at temperatures <5℃, being unable to retain a foothold; so in these conditions they form aggregations (Largen, 1967), as solitary exposed *Nucella lapillus* are at more risk from dislodgement than those refuging in such groups (Bell and Gosline, 1997). This aggregation has been shown to reduce the stress from wave-action in many intertidal gastropods (Underwood, 1979; Branch, 1981), and is particularly important in exposed areas (Focardi and Deneubourg, 1985). Very strong wave action (e.g.storms) rapidly causes snails to move into dense local aggregations (Connell, 1961b; Lewis, 1964; Frank, 1965).

For almost all the year, the degree of aggregation was appreciably greater in the upper levels of the shore, (and the degree of dispersal largest in the lower levels) on all but the most exposed shores (Nobla and Defaid). At those two locations, Winter aggregation was even more pronounced in the lower shore (subject to intense wave action) and to a certain degree in the upper shore (where whelks are exposed for longer and prone to cold air temperatures), although much less noticeable in the mid shore.

Overall dispersion is significantly different between all of the six shores. Throughout the year the mean shortest distance between *Nucella lapillus* conspecifics in descending order was: Porth Defaid, Porth Nobla, Red Wharf equivalent to Llanfairfechan, Trwyn y Penrhyn, and Menai Bridge. This follows the biologically-defined exposure scale results obtained from these shores (Ballantine, 1961), very closely (Chapter 2). It is only during the extreme conditions of Winter (December to Febuary), that this order become reversed to a degree. This shows that dispersion is a function of wave exposure, although the particular regulating factors on those shores may vary with shore level and with season.

Density and alpha (index of dispersion), can be interdependent. For instance when aggregations of whelks form at a restricted number of favourable sites, resulting in a localised increase in density (Underwood, 1976; 1985). There was no correlation between index of dispersion and density on any of the shores in these investigations (Table 4.18), so the observed dispersion of dogwhelks is unlikely to be due to density-dependent biological interactions alone.

Table 4.18. Absolute values of Pearson correlation coefficient and ANOVA test of significance of the regression slope of the index of dispersion and density.

	Menai	Trwyn	Llanfairechan	Red Wharf	Nobla	Defaid
R	0.449	0.438	0.386	0.356	0.235	0.193
F	17.257	19.456	11.313	12.965	10.193	8.334
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Data presented are correlation coefficient (R), F-values (F), and probabiliies (P), which are all significant values.

Others factors also determine dispersion of *Nucella* spp., and more work needs to be done on the effects of the following in modifying the above patterns in dispersion:

the tidal cycle: dispersion of *Nerita textilis* is greatest during spring tides and aggregation is highest during neap tides (Vannini and Chelazzi, 1978).

size: juvenile *Nucella lapillus* can remain widely dispersed longer than adults and sometimes delay retreating to shelter according to Menge (1978a), and being small they can utilise even the smallest of crevices.

reproduction: many species form pre-breeding aggregations (Feare, 1970b; Abe, 1983, Chari, 1950; Knudsen, 1950; D'Asaro, 1966; Feare, 1971; Spight, 1974).

prey: the dispersion of *Nucella spp.* is clearly affected by the abundance of suitable prey on different shore levels (Connell, 1970). *Nucella lapillus* aggregates when feeding (Connell, 1961a). Spatial distribution is influenced by feeding habits and patterns, and is related to relative densities of predator and prey (Morgan, 1972a), (see Figures 6.18 and 6.19).

substrate and community heterogeneity: the degree of aggregation varies with spatial scale (Hurlbert, 1990)

Dogwhelk density.

Changes in dogwhelk numbers can and did occur within only a few metres of the shoreline due to local movements, and with variation in substratum topography (Spight, 1974). Densities also varied seasonally (Richardson and Brown, 1990), from year to year (Carroll, 1996), and from shore to shore in exposed and protected areas (Menge, 1978a). Due to this, density estimations were taken over large areas of the shore to minimise sampling bias due to these confounding factors.

In summary, *Nucella lapillus* density varies significantly from shore level to shore level, particularly in response to changes in environmental and biological interactions at the different tidal heights, as preferred microhabitats on the substratum are usually plentiful at naturally occurring densities (Underwood, 1976). Density of some intertidal gastropods also vary along the wave exposure gradient, decreasing with wave force (Etter, 1989).

Dogwhelk mortality.

Overall mortality rates in *Nucella lapillus* showed specific trends, with clear seasonal variation in mortality. Increased mortality took place at the upper ends of their vertical distribution

(Figure 4.24), particularly during hot, dry weather when low tides occur in daylight, on moderately-exposed, but particularly on sheltered shores. This has been observed in other intertidal species (Lewis, 1954; Hodgkin, 1959; Frank, 1965; Sutherland, 1970; Branch, 1975c), and it is clear that desiccation is an important cause of dogwhelk mortality (Menge, 1978a), along with predation, dislodgement by waves (Denny,1985; Levinton et. al., 1995), as well as immobilization by mussels (Crothers, 1985a). All shores are made up of directional "environmental gradients" that act differentially upon individual snails of different body size, shape and mobility (Menge and Sutherland, 1987), explaining the observed differences in mortalities at different tidal levels on the shore (Werner and Gilliam, 1984). *Nucella lapillus* on the exposed study shores experienced the highest mortality rates, those on protected shores the least, identical results to those obtained by Etter (1989), whilst working on other intertidal molluscs.

Shore populations showed increasing mean body sizes in the smaller size classes with elevated tidal height (Chapter 2), presumably as smaller individuals were more susceptible to physical factors at these higher levels, with resultant increased mortality rates (Vermeij, 1972). This was true for all six shores. Exposed shores generally suffer less overall predation and the predation that takes place is more intense on juveniles according to Feare (1969). Sheltered shores in the study area had a greater level of crab predation of *Nucella lapillus* (personal observation), meaning juveniles here had a greater mortality risk, since as whelks increase in size, vunerability to predation is reduced (Hughes and Elner, 1979).

CHAPTER 5.

NUCELLA AND MICROHABITAT USAGE.

5.1. INTRODUCTION.

On intertidal rocky shores there is enormous variability in substrate composition (Sebens, 1991), within even only a few metres (Underwood, 1981). The result is a vast mosaic of patchly distributed and seperated resources (Kareiva 1990), forming unique microhabitats (Keough and Butler, 1983), This occurs over a wide range of spatial scales (Whittaker and Levin, 1977), to the extent that even closely adjacent populations of *Nucella* may have disparate biological characteristics (Spight, 1974). Today, benthic communities are considered as a mosaic of patches (Underwood and Chapman, 1985), and the patch as the fundamental unit of community structure (Levin and Paine, 1974), particularly in relation to local patterns of heterogeneity and stability (Smith, 1972).

Microhabitat diversity.

Increased heterogeneity of the environment increases species diversity (Lubchenco et. al., 1984; Menge et. al., 1985). More structurally complex habitats tend to contain a wider variety of different microhabitats with different microclimates (Menge and Sutherland, 1976; Huston 1979; Sebens 1991), and hence contain more niches, allowing more species to coexist within the area (Connor and McCoy, 1979; McGuinness, 1984a). These include extra refuges from predation, which can maintain otherwise unstable predator-prey interactions (Kohn and Leviten, 1976; Menge and Lubchenco,1981). These structures include crevices (Levings and Garrity, 1983; Fairweather et al., 1984), pits (Raffaelli and Hughes, 1978; Underwood and Chapman, 1992; Chapman, 1994), biogenic structures such as tests of barnacles (Reimer, 1976), or branches of algae (Underwood and McFadyen, 1983). All increase the fractal dimension of the substratum (Mandelbrot 1983), and provides small species in particular with protection from physical stress (Emson and Faller-Fritsch, 1976; Kohn and Leviten,1976; Menge, 1976b; Palmer, 1992). The total abundance of animals however, is more dependent on the available surface area than upon the substratum type (McGuinness and Underwood, 1986).

Species dispersal and microhabitat preference.

The resources of many ecosystems are unevenly distributed (Underwood, 1992). Consequently, gastropod dispersal patterns in the intertidal are related to microhabitat composition and distribution (Fotheringham, 1974; Underwood, 1976b). These movement patterns may not be proportional to the observed frequencies of microhabitat occupation however (Buckland and Elston, 1993). Microhabitat heterogenity and distribution can also restrict movement in dogwhelks, which are usually found more in shaded than in open habitats (Hughes et. al., 1992*)*. As a result of this, neighbouring populations of whelks found in areas of complex topography can be quite distinct (Chapman and Underwood, 1994). Similarly, *Nodilittorina pyramidalis* (another intertidal snail) is restricted by areas of complex topography and only rarely moves across intervening patches of smooth rock (Erlandsson et. al., 1996).

Species that move in the intertidal, experience various types of microhabitats during their life history (Takada, 1996). This is especially true for dogwhelks, which migrate to varying degrees depending upon their age and the season (Moore, 1936; 1938b; Feare, 1970a), with habitat selection playing a major role in maintaining vertical distribution patterns (Underwood, 1979; Byers and Mitton, 1981; Janson, 1983; Byers, 1989). The previous feeding history, availability of food resources and general morphology (especially size) of a dogwhelk (Moore, 1936b; Kitching et. al., 1966; Fotheringham, 1974; Berry, 1983; Gosselin, 1997), can also be important in determining microhabitat distribution. In addition, adult *Nucella lapillus* tend to converge on microhabitats that enhance the survival of their offspring (Grant and Utter, 1988). It is apparent that intertidal snails are capable of distinguishing between horizontal or sloping surfaces (open faces), and refuge environments (Garrity, 1984), as during low tides, most prefer crevices or vertical surfaces (Newell, 1976).

Prey Patch Size and Composition.

It is very difficult to estimate accurately the amount of food available for an animal population (McKillup and Butler, 1983). In the intertidal zone, the major nutritional variables for the dogwhelk are the size and composition of prey in the patch it is exploiting (Svane and Setyobudiandi, 1996).

There is a strong relationship between patch size and the numbers of consumers utilising the patch (Kareiva, 1990). The degree of spatial heterogeneity varies considerably within, but not between large areas of the intertidal (Garrity and Levings, 1981). On the other hand, variation in composition between patches of sessile organisms tends to exceed that within. Once formed, each patch becomes unique in terms of its structure and succession, dependent on the initial constituents (Levin and Paine, 1974), the time of the season it is formed, its size, and tidal height (Paine and Levin, 1981). Composition of the patch (turnover) constantly changes with time (Keough and Butler, 1983). This is due to the fact that neighbouring patches experience differences in the intensity, periodicity and history of disturbances to which each is subjected (Berlow, 1995), and patches of various sizes are successively formed, and broken down as a result of changing weather conditions, varying predation and competition (Svane and Ompi, 1993; Navarrete, 1996). Some of the variability can also be explained by spatial and temporal stochasticity in settlement and recruitment (Berlow, 1995).

Refuges.

The physical structure of the rocky shore habitat can often reduce the susceptibility of intertidal animals (including carnivorous gastropods) to potential mortality factors such as wave exposure Menge, 1978a), desiccation (Garrity and Levings, 1981; Garrity, 1984; Williams and Morritt, 1995), and predation (Lubchenco et. al., 1984; Menge et. al., 1986), chiefly by providing refuge niches (McGuiness and Underwood, 1986; Sebens, 1991). Crevices and other refuges have also been shown to permit rocky intertidal organisms to expand their upper limits to higher than the usual levels (Kensler, 1967; Dayton, 1971; Connell, 1972).

Nucella spp. have a marked tendency to retire into crevices, under algae, under anemones or into the mussel matrix during low tide (Dayton, 1971). This is especially so when the low tide is near mid-day, and the potential stress of desiccation is far greater (Underwood, 1985), even more so during Spring tides. *Nucella emarginata* and *Nucella canaliculata* have been obseved to retreat into crevices during the Summer months to copulate and to lay eggs (Dayton, 1971), *Nucella lapillus* does so as Winter approaches (Feare, 1970b). During Winter most gastropods will actively avoid open rock surfaces in order to seek refuge in cracks, crevices or rock pools (Menge et. al., 1983; 1985; Williams, 1993), with some even sheltering beneath larger organisms (Connell, 1972). *Nucella lamellosa, N. emarginata, N. canaliculata* (Dayton, 1971; Connell, 1970), and *N.orbita* (Phillips, 1969; Black, 1978; Butler, 1979), may be restricted to these refuges for prolonged periods at this time, due to reduced food availability and extreme wave forces (Menge, 1978a). This is particularly true during gales (McQuaid, 1985), and periods of particularly cold weather (Connell, 1961a).

Space Utilisation on different Shores.

Space utilisation by *Nucella* spp. is often different at exposed and sheltered sites (Menge and Lubchenco, 1981). At the former there is little space available, low cover of algae, and dense barnacle and mussel coverage (Lubchenco and Menge, 1978). On moderately exposed shores fluctuating mosaics of fucoids and barnacles are present (Hawkins et al, 1992), with different types of patches being found within a matter of metres. Protected areas are clearly divided into more obvious zones, with higher algal coverage at certain times of the year, and where mussels are rare, often providing more suitable space for *Nucella lapillus* (Menge, 1978b). This leads to very different patterns of space utilisation by dogwhelks in these differing habitats.

Rationale.

Leviten and Kohn (1980), examined the influence of microhabitat timed resources and environmental timed resources, and environmental change on populations of different species of *Conus* (Indo-Pacific Region), in order to see what governs species distribution characteristics in this intertidal habitat. Garrity (1984), also used designated habitat types to investigate *Nucella melones* distribution in different rock microhabitats varying in slope and availability of refuges, whilst Berlow and Navarrete (1997), measured the type of microhabitat available in six designated types, and looked at presence of the predator *Nucella emarginata* in these different "zones". To date no similar studies have been carried out in any detail on the Western coast of Britain where intertidal communities are different in composition and structure from those in the United States and the tropics.

5.2. METHODS.

Hypotheses.

1. Microhabitat diversity is significantly different at different tidal levels on the same shore and at sites on different shores which are exposed to differing degrees of wave-action.
2. This diversity in microhabitat composition affects dogwhelk distribution and hence habitat utilisation.
3. The pattern of refuge utilisation by *Nucella* is dependent on the type, size, and position of the refuge on the shore.

Experimental Design.

On each of six shores, Menai Bridge, Trwyn Y Penrhyn, Llanfairfechan, Red Wharf Bay, Porth Nobla, and Porth Defaid (see Chapter 2 for coordinates) two replicate 4 m^2 experimental grids were located (marked on the substrate) at each of three shore levels (lower, middle and upper). Each grid (a total of six on each shore), was subdivided into 16 subunits and once a month for two years the position (in subunit 1-16), activity (spawning, foraging in the open, foraging in a refuge, or refuging), and size (length of shell) of every dogwhelk in each grid was determined on all six shores.

Microhabitat utilisation .

The research also included a survey of microhabitat abundance at the different study sites. On each shore different aspects of habitat structure were quantified by determining microhabitat diversity (Karieva, 1990), and concurrent utilization by *Nucella lapillus* (Garrity and Levings, 1981). The differences in microhabitat preferences and requirements for different size groups of *Nucella lapillus*, their mean level of dispersion, and the relationship between the proportion in substratum type and the area of substratum within each grid (in otherwords in relation to habitat composition), were also investigated. The degree of substrate heterogeneity (in the form of canopy cover, presence of cracks, trenches etc.) was calculated. In particular the number and size distribution of boulders, the percentage of flat substrate, horizontal and vertical surfaces, the number and size (length and depth) of crevices\pits, as well as the presence of sand\shingle and algae (see Vannini and Chelazzi, 1978). *Nucella* foraging activities (position, degree of patch and refuge utilisation, and movement patterns, were compared to the changes in distribution and composition of microhabitats in a similar manner to Karieva (1990), and Garrity and Levings (1981). In total, 87,921 individual data observations of the microhabitat utilisation of *Nucella lapillus* were made on the six study shores.

Prey patch size and composition.

In order to study individual prey patch size and composition, two barnacle patches were chosen at each of six sites per shore (four patches at each of the three shore levels: upper, middle and lower). Patches were demarcated using fixed spatial coordinates painted in oil paint upon the rock to delineate (establish the borders) patches. Patch borders and hence relative size of the barnacle assemblage were determined every two months for the duration of the study by approximating areas from the spatial coordinates. Patch composition was investigated from two monthly determinations using overhead transparencies marked with a random 100 dots (Lubchenco et. al., 1984). I monitored changes in circumference, diameter, species present, and percentage (%) composition. The distance between patches was determined by measuring the shortest navigable (by *Nucella lapillus)* distance from each patch to its nearest neighbour, as well as the within-patch pattern, by noting the approximate individual size- frequency distribution of patch residents (using a limited number of size classes). Any gaps, clumps or other noticeable features were also recorded.

Prey recruitment.

The recruitment of barnacles affects the intensity of predation by whelks upon them (Fairweather, 1988d). Barnacle recruitment patterns (level and time) were determined by monitoring the abundance (percentage coverage) of new barnacle spat present in each experimental grid, again at two monthly intervals. This was done using the method of Dethier et. al. (1993).

Dogwhelk movement in relation to patch pattern and distance between patches.

One species of whelk, *Nucella orbita,* shows intermittent but rapid movement between prey patches, slower movement within; and movement from areas with damaged or depleted prey (Fairweather, 1988c). The movement of *Nucella lapillus* in relation to the structure and distribution of prey assemblages was investigated. The distribution of prey patches was mapped within each experimental grid by photography and measurement to ascertain distance between separate patches as well as the patterns of both mature and new barnacle spat within patches. Net distances moved between designated foraging patches (as per Hughes and Drewett, 1985), as well as movement within patches was determined by trigonometrically examining the change in spatial coordinates (see Chapter 4) of individually numbered dogwhelks.

Patch exploitation.

Patch exploitation is quantified as the time allocated to a given resource patch (patch residence time). This was extremely hard to approximate since as each shore was only visited once in every week. With this in mind the design of this part of the experiment was simplified to determine the the number of dogwhelks in each patch, and where possible their identity (and hence size) on each occasion.

Refuge utilisation.

The availability and importance of refuges such as crevices, boulders, algae, and interstices of mussel beds upon the foraging activity of *Nucella* was studied. Refuges were measured and mapped within and between different heights of the shore as well as on all six shores. This was done to examine if the degree of availability of refuges varies significantly on these scales, since spatial subdivision can alter the stability of species interactions. The type and size of refuges occupied *by Nucella lapillus* were measured to see if there were any size-specific differences in this dogwhelk for refuge preference.

Statistical analysis.

GLM multivariate and univariate analysis of data with Bonferroni Post Hoc multiple comparison testing of differences between means was carried out following evaluation of normality (Q-Q normal probability plots) and homogeneity of variances. This revealed the appropriateness of these parametric tests in these investigations. In addition a 2-tailed t-test procedure was used to determine the relationship between relative availability of microhabitats, and the proportion of dogwhelks occupying them. GLM univariate analysis was carried out on the data cases, and Post Hoc multiple comparisons on the effect of activity, level and shore (Bonferroni test) and of microhabitat type (Tukey HSD test), on *Nucella* shell length.

Data were regularly collected at three levels (1: lower shore; 2: middle shore; 3: upper shore), on the six different shores (1: Menai Bridge; 2: Trwyn y Penrhyn; 3: Llanfairfechan; 4: Red Wharf Bay; 5: Nobla; 6: Defaid) from May 97 to May 99. Dogwhelk activity at low tide was recorded in five major different categories (1: spawning; 2: foraging in the open; 3: foraging in a refuge; 4: refuging; 5: moving over substrate, although too few examples of this last category were recorded for any meaningful analysis). Broad activity patterns were subdivided to take account of microhabitat, into 40 habitat/activity classifications (Table 5.1).

Table 5.1 Microhabitat classification.

No.	Activity/habitat	Description	No.	Activity/habitat	Description
1	SPUB	Spawning under boulder	21	FPEBB	Foraging on pebbles
2	SPPIT	Spawning in pit	22	RUB	Refuging under boulder
3	SPC	Spawning in crevice	23	RPIT	Refuging in pit
4	SPT	Spawning in trench	24	RC	Refuging in crevice
5	SPA	Spawning under algae	25	RT	Refuging in trench
6	SPPOOL	Spawning in rock pool	26	RA	Refuging under algae
7	SPSA	Spawning under sea anemone	27	RPOOL	Refuging in rock pool
8	SPIM	Spawning in mussel matrix	28	RSA	Refuging under sea anemone
9	HF	Foraging/ horizontal surface	29	RUB	Refuging under boulder
10	VF	Foraging/ vertical surface	30	RBB	Refuging between barnacles
11	FUB	Foraging under boulder	31	RIM	Refuging in mussel matrix
12	FPIT	Foraging in pit	32	RPEBB	Refuging on pebbles
13	FC	Foraging in crevice	33	RROCK	Refuging on rock
14	FT	Foraging in trench	34	RSTAR	Refuging under starfish
15	FA	Foraging under algae	35	RSHELL	Refuging in mussel shell
16	FPOOL	Foraging in rock pool	36	RSAND	Refuging on sand
17	FSA	Foraging under sea anemone	37	MROCK	Moving on rock
18	FIB	Foraging in mussel matrix	38	MPEBB	Moving on pebbles
19	FBB	Foraging between barnacles	39	MSAND	Moving on sand
20	FIM	Foraging in mussel matrix	40	MMM	Moving on mussel matrix

5.3. RESULTS.

5.31. Comparisons of shell length between activities (activity 1: spawning, activity 2: foraging in the open, activity 3: foraging within a refuge, and activity 4: refuging) within shore levels (low, mid and upper). Variation in mean shell length with shore level, for whelks involved in the four activities are illustrated in Figure 5.1, while the same data are re-arranged in Figure 5.2 to show how the mean shell length of *Nucella* in different activities follows a similar pattern at all shore levels, on all six study shores. The overall difference (Pooled data from all six study shores) in mean shell length between those animals occupied in different activities is summed up in Figure 5.3.

Menai Bridge: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=338.880 P=<0.001), mid shore (GLM. F=230.647 P=<0.001), and upper shore (GLM. F=66.303 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between all activities (Appendix 5, Table5.1).

Trwyn y Penrhyn: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=28.625 P=<0.001), mid shore (GLM. F=208.485 P=<0.001), and upper shore (GLM. F=342.948 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between most activities (Appendix 5,Table 5.2).

Llanfairfechan: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=392.893 P=<0.001), mid shore (GLM. F=474.154 P=<0.001), and upper shore (GLM. F=26.716 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between most activities (Appendix 5, Table 5.3)

Red Wharf Bay: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=65.446 P=<0.001), mid shore (GLM. F=94.813 P=<0.001), and upper shore (GLM. F=28.383 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between most activities (Appendix 5, Table 5.4).

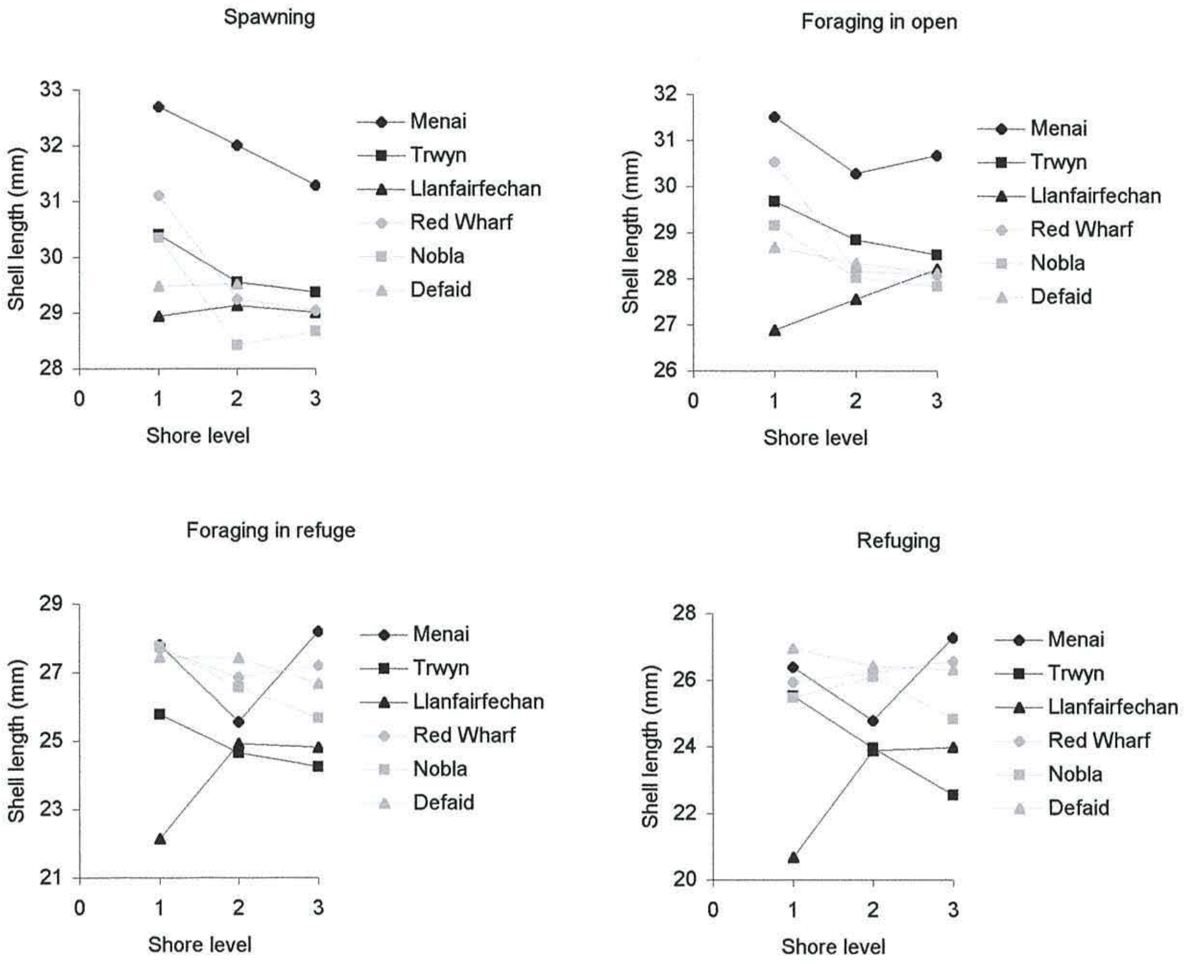


Figure 5.1. Shell length of *Nucella lapillus* in different activities at different shore levels. Key to shore level: 1: low shore; 2: mid shore; 3; upper shore.

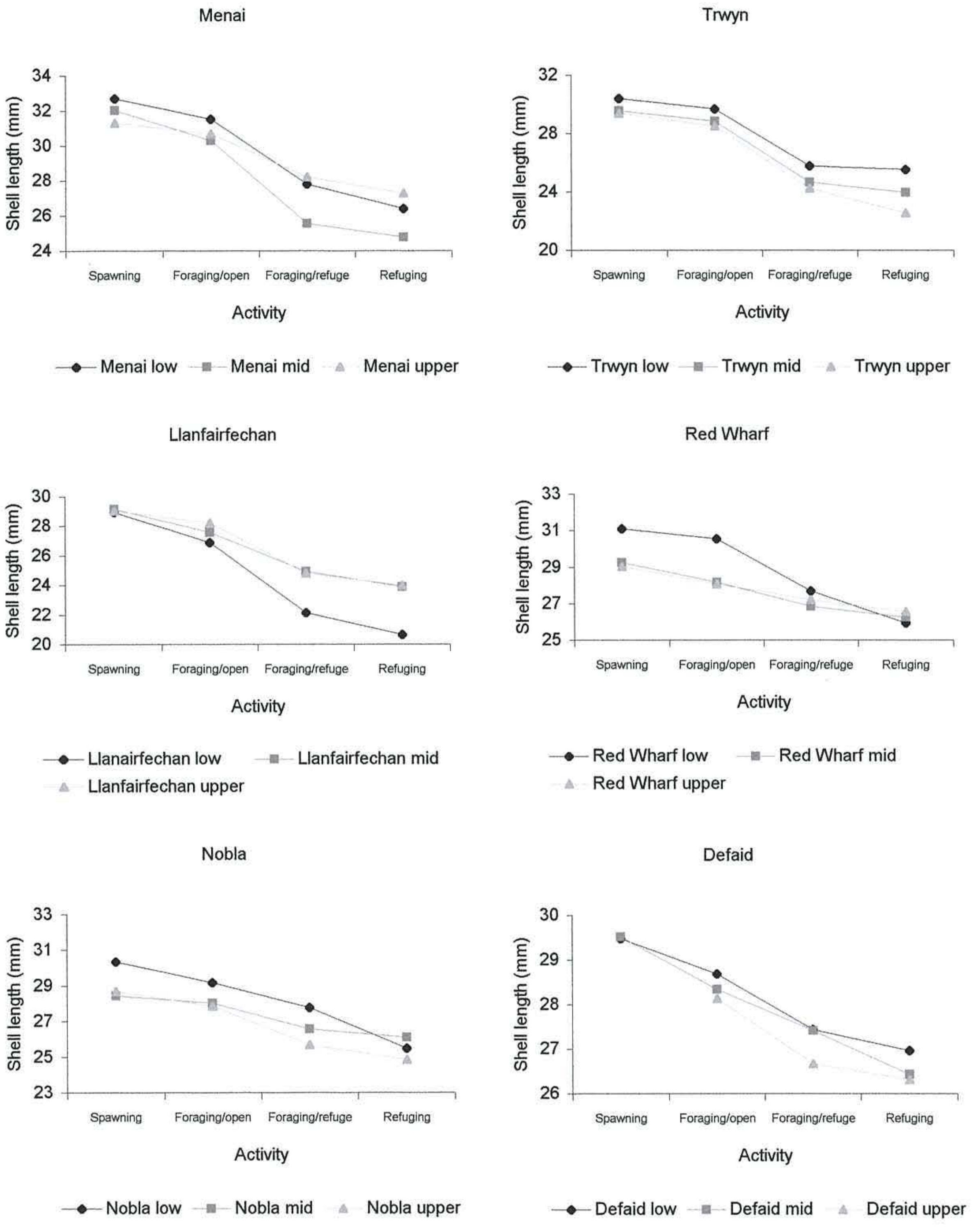
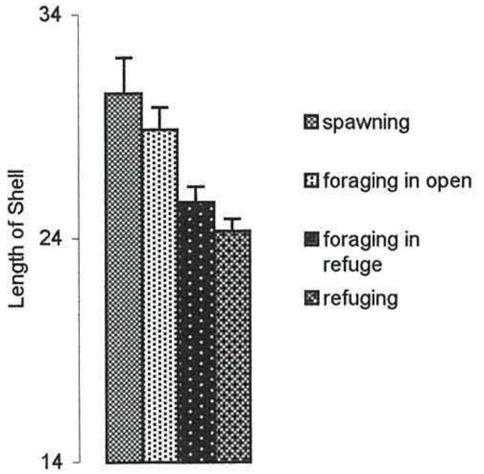


Figure 5.2. The mean shell length of *Nucella lapillus* at different shore levels in different activites.



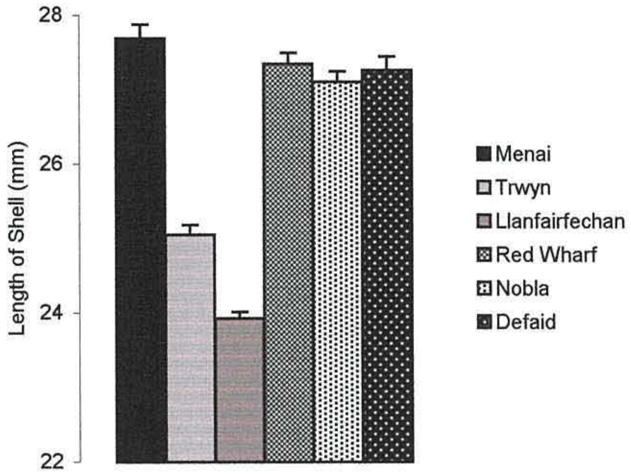


Figure 5.3. Mean shell length of *Nucella* in different activities (2 years data pooled).

Figure 5.5. Mean shell length of *Nucella* on different shores (2 years data pooled).

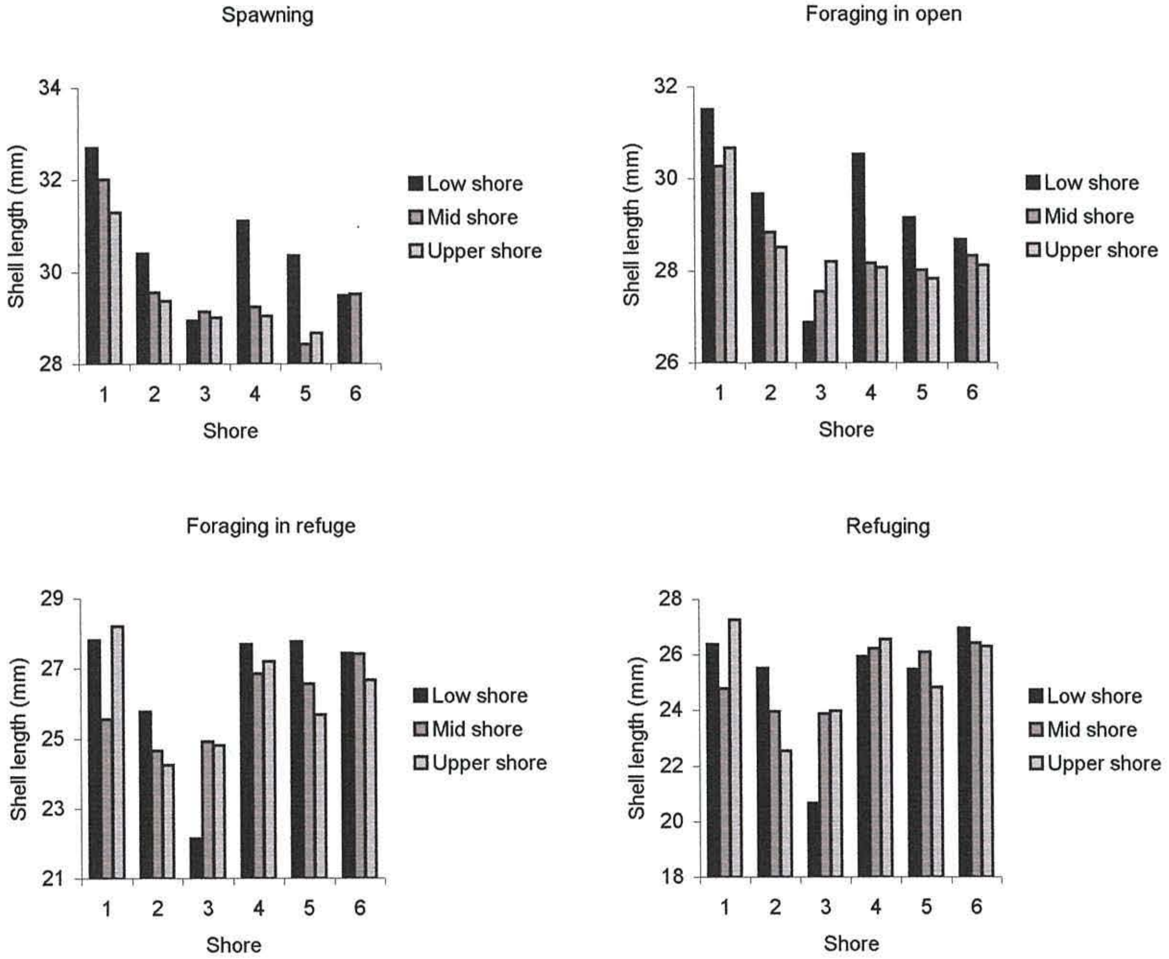


Figure 5.4. Mean shell length of *Nucella lapillus* in different activities at different shore levels.(2 years data pooled).
Key to shores: 1- Menai Bridge; 2- Trwyn y Penrhyn; 3- Llanfairfechan; 4- Red Wharf bay; 5- Porth Nobla; 6- Porth Defaid.

Porth Nobla: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=140.626 P=0.000), mid shore (GLM. F=61.275 P=<0.001), and upper shore (GLM. F=70.369 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between most activities (Appendix 5, Table 5.5).

Porth Defaid: the overall shell length of *Nucella* was significantly different for different activity at low shore (GLM. F=26.363 P=<0.001), mid shore (GLM. F=4.804 P=0.001); but found to not be significant for the upper shore (GLM F=2.406 P=0.066). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in shell length between most activities (Appendix 5, Table 5.6).

5.32. Comparisons of shell length between microhabitat within shore levels.

Significant differences in the shell length of dogwhelks in different microhabitats (1-40), see Table 5.1) were found at all three levels on all shores (Table 5.2).

Table 5.2. GLM Univariate analysis of variance of the different microhabitat type and shell length.

	low shore		mid shore		upper shore	
Shore	F	P	F	P	F	P
Menai Bridge	134.724	<0.001	122.666	<0.001	33.518	<0.001
Trwyn y Penrhyn	14.472	<0.001	100.126	<0.001	163.555	<0.001
Llanfairfechan	142.139	<0.001	145.692	<0.001	21.518	<0.001
Red Wharf Bay	27.449	<0.001	20.499	<0.001	14.474	<0.001
Porth Nobla	44.978	<0.001	41.192	<0.001	46.979	<0.001
Porth Defaid	22.363	<0.001	12.095	<0.001	2.042	<0.001

All mean differences are significant at the .05 level.

N.B. The results of non-parametric Tukey HSD Post Hoc multiple comparisons of shell length and microhabitat gave substantially the same results as those presented (GLM ANOVA) above.

5.33. Comparison of shell length within activity (spawning, foraging in the open, foraging within a refuge, and refuging), between shore levels within shores (see Figure 5.4).

Menai Bridge. The overall shell length of *Nucella* was found to be significantly different for different shore level (GLM. F=221.437 P=0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks spawning (GLM. F=22.324 P=<0.001), foraging in refuges (GLM. F=34.895 P=0.001), and refuging (GLM. F=117.632 P=0.001); but not for those foraging in the open (GLM. F=2.893 P=0.056), (Table 5.3).

Table 5.3. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Menai Bridge.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	2.311*	<0.001	0.690*	<0.001	0.619	0.069	1.683*	<0.001	1.454*	<0.001
1-3	0.027	1.000	1.251*	<0.001	0.352	0.779	0.833*	0.018	1.812*	<0.001
2-3	2.284*	<0.001	0.561	0.077	0.267	1.000	2.516*	<0.001	3.266*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Trwyn y Penrhyn. The overall shell length of *Nucella* was found to be significantly different for different shore levels (GLM. F=133.442 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks spawning (GLM. F=6.365 P=0.002), foraging in the open (GLM. 13.672 P=<0.001), foraging in refuges (GLM. F=30.102 P=<0.001) and refuging (GLM. F=48.092 P=<0.001), (Table 5.4).

Table 5.4. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Trwyn y Penrhyn.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	1.591*	<0.001	0.582*	0.004	1.115*	<0.001	1.793*	<0.001	1.840*	<0.001
1-3	2.623*	<0.001	0.621*	0.002	1.282*	<0.001	2.194*	<0.001	3.020*	<0.001
2-3	1.033*	<0.001	0.039	1.000	0.167	1.000	0.401	0.178	1.181*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Llanfairfechan. The overall shell length of *Nucella* was found to be significantly different for different shore level (GLM. F=535.982 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks foraging in refuges (GLM. F=99.392 P=<0.001) and refuging (GLM. F=388.323 P=<0.001); but found not to be significant for those spawning, (GLM. F=2.170 P=0.115), and foraging in the open (GLM. F=2.823 P=0.060), (Table 5.5).

Table 5.5. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Llanfairfechan.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	2.983*	<0.001	0.205	0.195	0.788	0.057	2.692*	<0.001	3.462*	<0.001
1-3	2.929*	<0.001	0.134	1.000	0.983	0.121	2.854*	<0.001	4.088*	<0.001
2-3	0.057	1.000	0.339	0.725	0.195	1.000	0.163*	1.000	0.626*	0.036

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Red Wharf Bay. The overall shell length of *Nucella* was found to be significantly different for different shore levels (GLM. F=19.193 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks spawning, (GLM. F=23.224 P=<0.001), foraging in the open (GLM. F=47.154 P=0.060), foraging in refuges (GLM. F=9.046 P=<0.001), and refuging (GLM. F=13.869 P=<0.001), (Table 5.6).

Table 5.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Red Wharf Bay.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.655*	<0.001	1.583*	<0.001	1.970*	0.069	0.934*	<0.001	1.198*	<0.001
1-3	0.720*	<0.001	2.102*	<0.001	2.245*	<0.001	0.479	0.062	1.325*	<0.001
2-3	0.066	1.000	0.519	0.706	0.275	1.000	0.456	0.160	0.127	1.000

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Porth Nobla. The overall shell length of *Nucella* was found to be significantly different for different shore levels(GLM. F=80.746 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks spawning, (GLM. F=40.645 P=<0.001), foraging in the open (GLM. F=38.868 P=<0.001), foraging in refuges (GLM. F=18.773 P=<0.001) and refuging (GLM. F=10.910 P=<0.001), (Table 5.7).

Table 5.7. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Porth Nobla.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.805*	<0.001	1.534*	<0.001	0.951*	<0.001	0.820*	0.001	0.298	0.881
1-3	1.540*	<0.001	1.753*	<0.001	1.594*	<0.001	1.725*	<0.001	0.952*	0.002
2-3	0.736*	<0.001	0.220	<0.001	0.643*	0.006	0.950*	0.001	1.250*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Porth Defaid. The overall shell length of *Nucella* was found to be significantly different for different shore levels (GLM. F=22.821 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant mean differences in shell length for those dogwhelks foraging in refuges (GLM. F=3.708 P=0.025) and refuging (GLM. F=11.849 P=<0.001); but found not to be significant for those spawning, (GLM. F=1.345 P=0.252), and foraging in the open (GLM. F=1.782 P=0.169), (Table 5.8).

Table 5.8. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella* shell length between shore levels at Porth Defaid.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.419*	0.011	0.448	0.252	0.130	1.000	0.124	1.000	0.256	0.125
1-3	1.104*	<0.001			0.447	0.359	0.880*	0.030	1.384*	<0.001
2-3	0.684*	<0.001			0.577	0.223	0.756	0.069	0.862*	0.005

Based on estimated marginal means. *Mean difference is significant at the .05 level. N.b. no spawning individuals observed at level 3 (upper shore).

5.34. Comparison of shell length within activity between shores.

The overall shell length of *Nucella* was found to be significantly different between shores (GLM. F=1061.098 P=<0.001), see Figure 5.5, as was the shell length of spawning *Nucella* (GLM. F=374.520 P=<0.001), of *Nucella* foraging in the open (GLM. F=201.797 P=<0.001), of *Nucella* foraging whilst within a refuge (GLM. F=212.180 P=<0.001), and of refuging *Nucella* (GLM. F=392.093 P=<0.001). Post Hoc multiple comparisons (Bonferroni test) showed significant mean differences in shell length between most shores (Table 5.9), for all of these categories.

Table 5.9. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella* shell length between shores.

Activity	All		Spawning		Foraging/open		Foraging/refuge		Refuging	
Shores	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	2.696*	<0.001	2.731*	<0.001	2.323*	<0.001	2.364*	<0.001	2.734*	<0.001
1-3	4.179*	<0.001	2.989*	<0.001	4.093*	<0.001	3.550*	<0.001	3.689*	<0.001
1-4	0.332*	0.003	2.144*	<0.001	1.703*	<0.001	0.141	1.000	0.372	0.390
1-5	0.643*	<0.001	2.852*	<0.001	2.758*	<0.001	0.397	0.126	0.024	1.000
1-6	0.496*	<0.001	2.711*	<0.001	2.984*	<0.001	0.027	1.000	0.863*	<0.001
2-3	1.483*	<0.001	0.258	0.219	1.770*	<0.001	1.136*	<0.001	0.955*	<0.001
2-4	2.364*	<0.001	0.587*	0.002	0.619*	0.002	2.505*	<0.001	3.106*	<0.001
2-5	2.053*	<0.001	0.120	1.000	0.436*	0.042	1.967*	<0.001	2.710*	<0.001
2-6	2.201*	<0.001	0.020	1.000	0.661*	0.010	2.337*	<0.001	3.597*	<0.001
3-4	3.847*	<0.001	0.845*	<0.001	2.390*	<0.001	3.641*	<0.001	4.061*	<0.001
3-5	3.536*	<0.001	0.138	1.000	1.335*	<0.001	3.103*	<0.001	3.665*	<0.001
3-6	3.683*	<0.001	0.278	1.000	1.109*	<0.001	3.473*	<0.001	4.553*	<0.001
4-5	0.311*	0.032	0.707*	<0.001	1.055*	<0.001	0.538*	0.041	0.396	0.667
4-6	0.164	1.000	0.567	1.000	1.280*	<0.001	0.167	1.000	0.492	0.415
5-6	0.147	1.000	0.141	1.000	0.225	1.000	0.370	1.000	0.887*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level. Key to shores: 1: Menai Bridge; 2: Trwyn y Penrhyn; 3: Llanfairfechan; 4: Red Wharf Bay; 5: Porth Nobla; 6: Porth Defaid

5.35. The proportion of *Nucella* in different activities.

5.351. Comparison between shore levels within shores.

The overall proportion of *Nucella* in different activities was found not to be significant between shore levels within all six shores using GLM repeated measures analysis (GLM. F=317.001 P=<0.001). However some differences in Post Hoc multiple comparisons (Bonferroni test) of the proportion of *Nucella* in different activities between shore levels were observed for all of the categories (Table 5.10; Figure 5.6).

Table 5.10. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in proportion of *Nucella* in designated activities between shore levels.

	Activity	Spawning		Foraging/open		Foraging/refuge		Refuging	
Shore	Levels	md	*P*	md	*P*	md	*P*	md	*P*
Menai	1-2	3.495*	0.024	7.643	0.051	3.957	0.758	15.062	0.123
	1-3	7.841*	0.002	5.983	0.091	0.030	1.000	13.805	0.152
	2-3	4.346*	0.013	1.660	1.000	3.988	0.749	1.258	1.000
Trwyn y Penrhyn	1-2	3.435*	0.006	2.236	1.000	2.458	1.000	5.623	0.063
	1-3	5.345*	0.002	7.131	0.124	0.760	1.000	13.210*	0.006
	2-3	1.909*	0.032	4.895	0.299	0.785	1.000	7.588*	0.028
Llanfairfechan	1-2	5.734*	0.006	2.207	0.655	3.044	0.344	1.649	1.000
	1-3	0.041	1.000	0.426	1.000	7.378*	0.038	6.611	0.621
	2-3	5.775*	0.005	1.780	0.898	4.334	0.155	8.260	0.416
Red Wharf Bay	1-2	3.609*	0.038	0.986	1.000	4.320*	0.024	1.736	0.833
	1-3	4.036*	0.028	7.583*	0.014	7.120*	0.006	4.498	0.125
	2-3	7.645*	0.004	6.597*	0.020	11.440*	0.001	2.762	0.378
Porth Nobla	1-2	5.425*	0.006	0.614	1.000	6.207	0.053	1.315	1.000
	1-3	1.170	0.352	6.090*	0.039	8.227*	0.024	13.145 *	0.004
	2-3	6.595*	0.003	6.703*	0.030	14.434*	0.005	14.459*	0.003
Porth Defaid	1-2	0.380*	0.035	2.139	0.451	4.332*	0.022	1.817	0.695
	1-3	1.380*	0.001	1.748	0.642	6.604*	0.006	3.523	0.187
	2-3	1.000*	0.002	0.391	1.000	2.273	0.125	1.709	0.761

Based on observed means. *Mean difference is significant at the .05 level

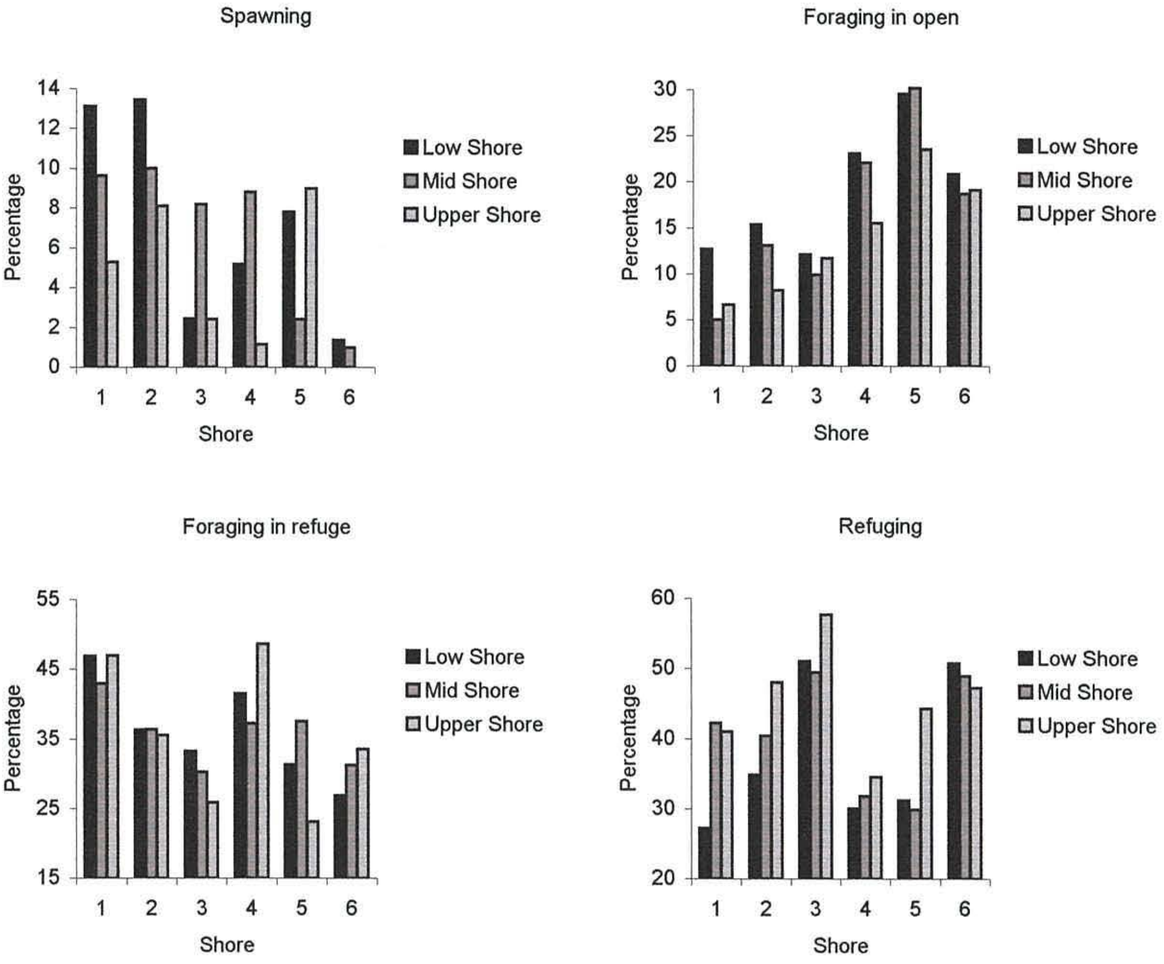


Figure 5.6. Percentage of *Nucella lapillus* in different activities at different shore levels. (2 years data pooled).

Key to shores: 1- Menai Bridge; 2- Trwyn y Penrhyn; 3- Llanfairfechan; 4- Red Wharf bay; 5- Porth Nobla; 6- Porth Defaid.

5.352 Comparisons between shores.

The overall proportion of *Nucella* in different activities (Figure 5.7), was found to be significant between most shores using GLM repeated measures analysis (GLM. F=406.273 P=<0.001). Differences in Post Hoc multiple comparisons (Bonferroni test) of proportion of *Nucella* in different activities between shores were observed for all of the categories (Table 5.11).

Table 5.11. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in proportion of *Nucella* in designated activities between shores.

	Spawning		Foraging/open		Foraging/refuge		Refuging	
Shores	md	*P*	md	*P*	md	*P*	md	*P*
1-2	1.180*	0.009	4.096*	0.001	9.536*	<0.001	4.276*	0.180
1-3	5.018*	<0.001	3.018*	0.021	15.837*	<0.001	15.935*	<0.001
1-4	4.314*	<0.001	12.109*	<0.001	3.120*	0.026	4.694*	0.100
1-6	2.953*	<0.001	19.655*	<0.001	14.972*	<0.001	1.692	1.000
1-7	8.572*	<0.001	11.459*	<0.001	15.072*	<0.001	12.176*	<0.001
2-3	6.198*	<0.001	0.988	1.000	6.301*	<0.001	11.660*	<0.001
2-4	5.494*	<0.001	8.012*	<0.001	6.415*	<0.001	8.970*	<0.001
2-6	4.133*	<0.001	15.559*	<0.001	5.436*	<0.001	5.968*	0.016
2-7	9.751*	<0.001	7.363*	<0.001	5.536*	<0.001	7.900*	0.001
3-4	0.704	0.352	9.000*	<0.001	12.717*	<0.001	20.629*	<0.001
3-6	2.065*	<0.001	16.547*	<0.001	0.866	1.000	17.627*	<0.001
3-7	3.553*	<0.001	8.351*	<0.001	0.765	1.000	3.759	0.367
4-6	1.361*	0.002	7.546*	<0.001	11.851*	<0.001	3.002	0.983
4-7	4.258*	<0.001	0.649	1.000	11.952*	<0.001	16.870*	<0.001
6-7	5.618*	<0.001	8.196*	<0.001	0.101	1.000	13.868*	<0.001

Based on estimated means. *Mean difference is significant at the .05 level.

5.36. Monthly changes in *Nucella* activity.

5.361. Spawning (Figure 5.8).

The monthly percentage of *Nucella* spawning was significantly influenced by shore level on all six study shores namely: Menai Bridge (GLM. F=102.326 P=0.002), Trwyn y Penrhyn (GLM.

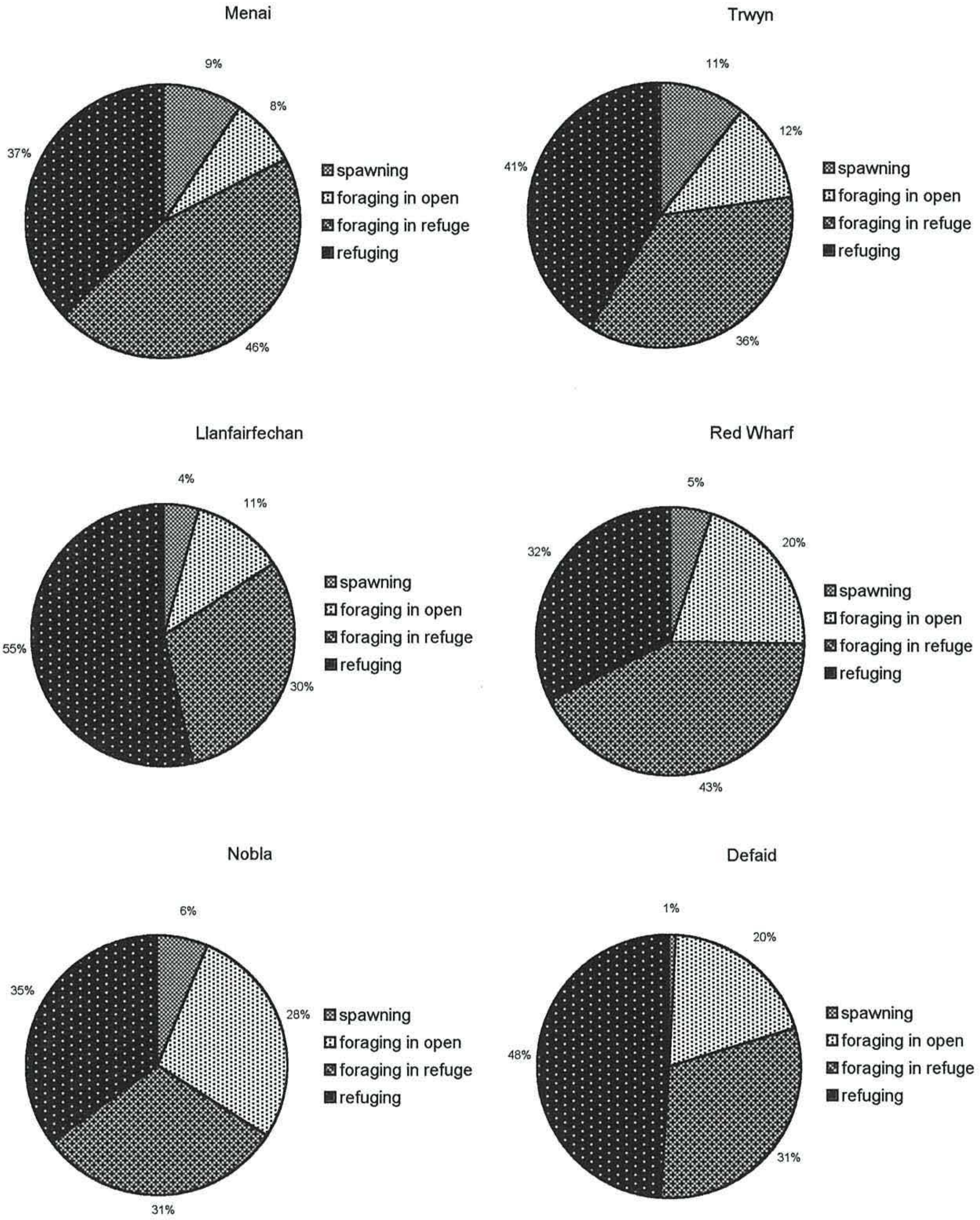


Figure 5.7. Percent of *Nucella lapillus* in different activities on different shores. (2 years data pooled).

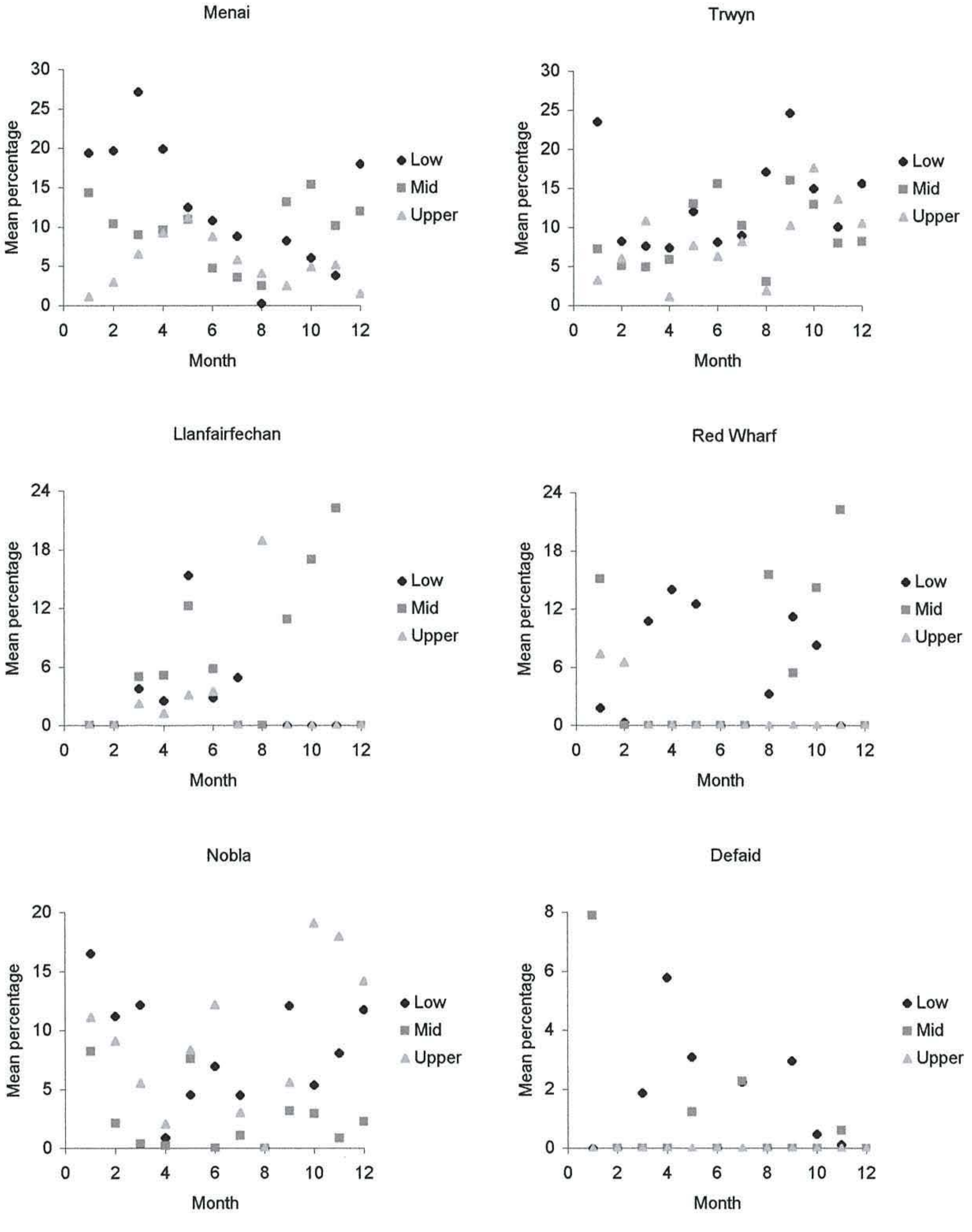


Figure 5.8. Monthly changes in percentage of *Nucella lapillus* spawning at different shore levels. Months 1-12 are January - December inclusive. (2 years pooled data).

F=132.385 P=0.001), Llanfairfechan (GLM. F=73.620 P=0.003), Red Wharf Bay (GLM. F=64.911 P=0.003), Porth Nobla (GLM. F=85.952 P=0.002), and Porth Defaid (GLM. F=213.586 P=0.001). Post Hoc multiple comparison (Bonferroni test) showed significant differences in the monthly percentage of *Nucella* spawning between most shore levels (low, mid and upper) on the study shores (Appendix 5, Table 5.7).

The percentage of *Nucella* spawning was significantly influenced by month on all six study shores namely: Menai Bridge (GLM. F=17.684 P=<0.001), Trwyn y Penrhyn (GLM. F=14.176 P=<0.001), Llanfairfechan (GLM. F=18.013 P=<0.001), Red Wharf Bay (GLM. F=20.882 P=<0.001), Porth Nobla (GLM. F=15.081 P=<0.001), and Porth Defaid (GLM. F=3.574 P=0.002).

5.362. Foraging in the open (Figure 5.9).

The monthly percentage of *Nucella* foraging in the open was found to be significantly influenced by shore level at Menai Bridge (GLM. F=13.511 P=0.031), Red Wharf Bay (GLM. F=34.891 P=0.008), and Porth Nobla (GLM. F=20.993 P=0.017), but found not to be significantly influenced by shore level at Trwyn y Penrhyn (GLM. F=6.177 P=0.086), Llanfairfechan (GLM. F=1.356 P=0.381), and Porth Defaid (GLM. F=2.096 P=0.269). Post Hoc multiple comparison (Bonferroni test) showed significant differences in the monthly percentage of *Nucella* foraging in the open between some shore levels (low, mid and upper) on the study shores (Appendix 5, Table 5.8).

The percentage of *Nucella* foraging in the open was found to be significantly influenced by month on all six study shores namely: Menai Bridge (GLM. F=39.913 P=<0.001), Trwyn y Penrhyn (GLM. F=36.708 P=<0.001), Llanfairfechan (GLM. F=50.603 P=<0.001), Red Wharf Bay (GLM. F=60.827 P=<0.001), Porth Nobla (GLM. F=142.342 P=<0.001), and Porth Defaid (GLM. F=35.462 P=<0.001).

5.363. Foraging within refuges (Figure 5.10).

The monthly percentage of *Nucella* foraging within refuges was significantly influenced by shore level at Llanfairfechan (GLM. F=14.416 P=0.029), Red Wharf Bay (GLM. F=144.395 P=0.001), Porth Nobla (GLM. F=61.276 P=0.004), and Porth Defaid (GLM. F=51.283 P=0.005), but found

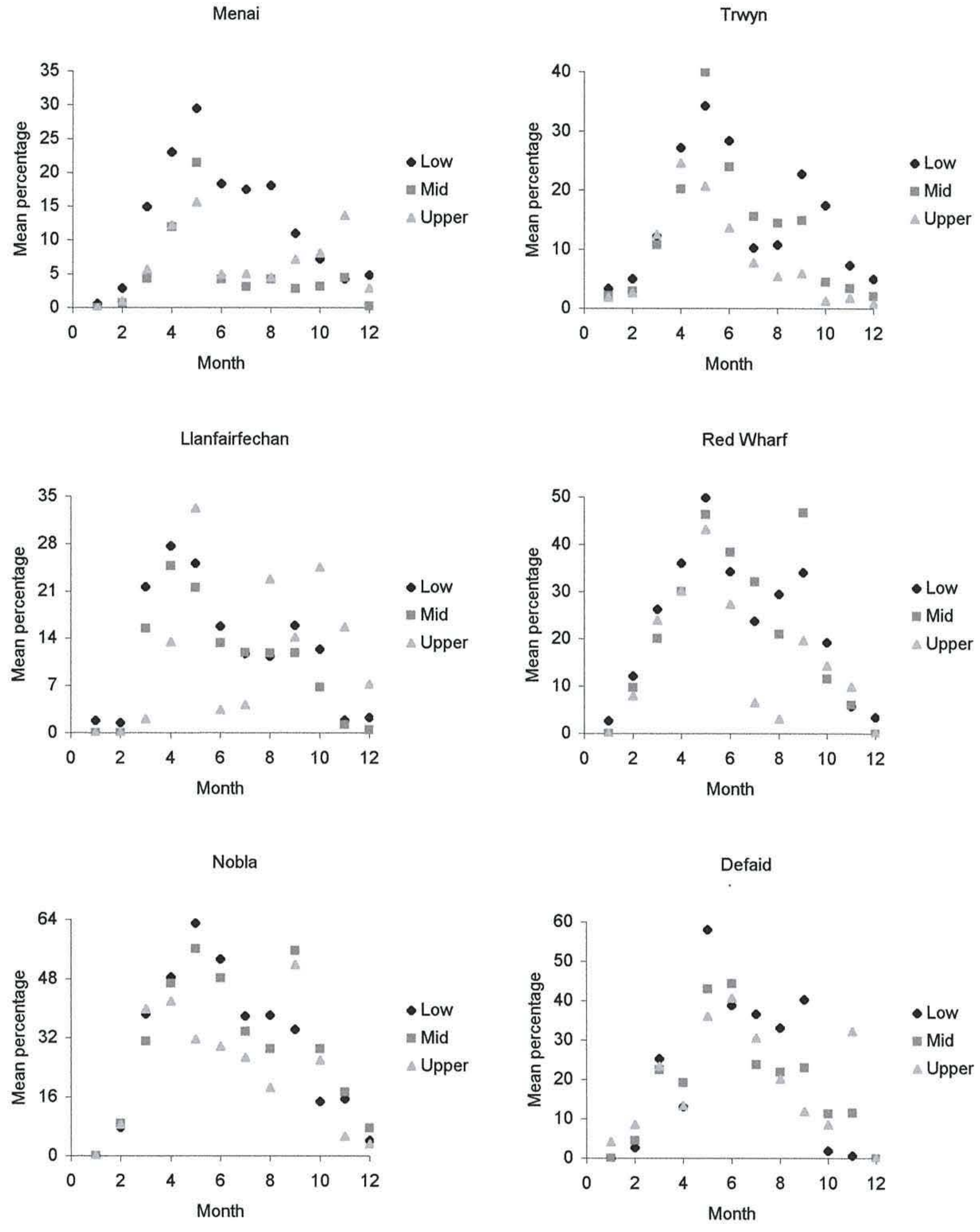


Figure 5.9. Monthly changes in percentage of *Nucella lapillus* foraging in the open at different shore levels. Months 1-12 are January to December inclusive. (2 years pooled data).

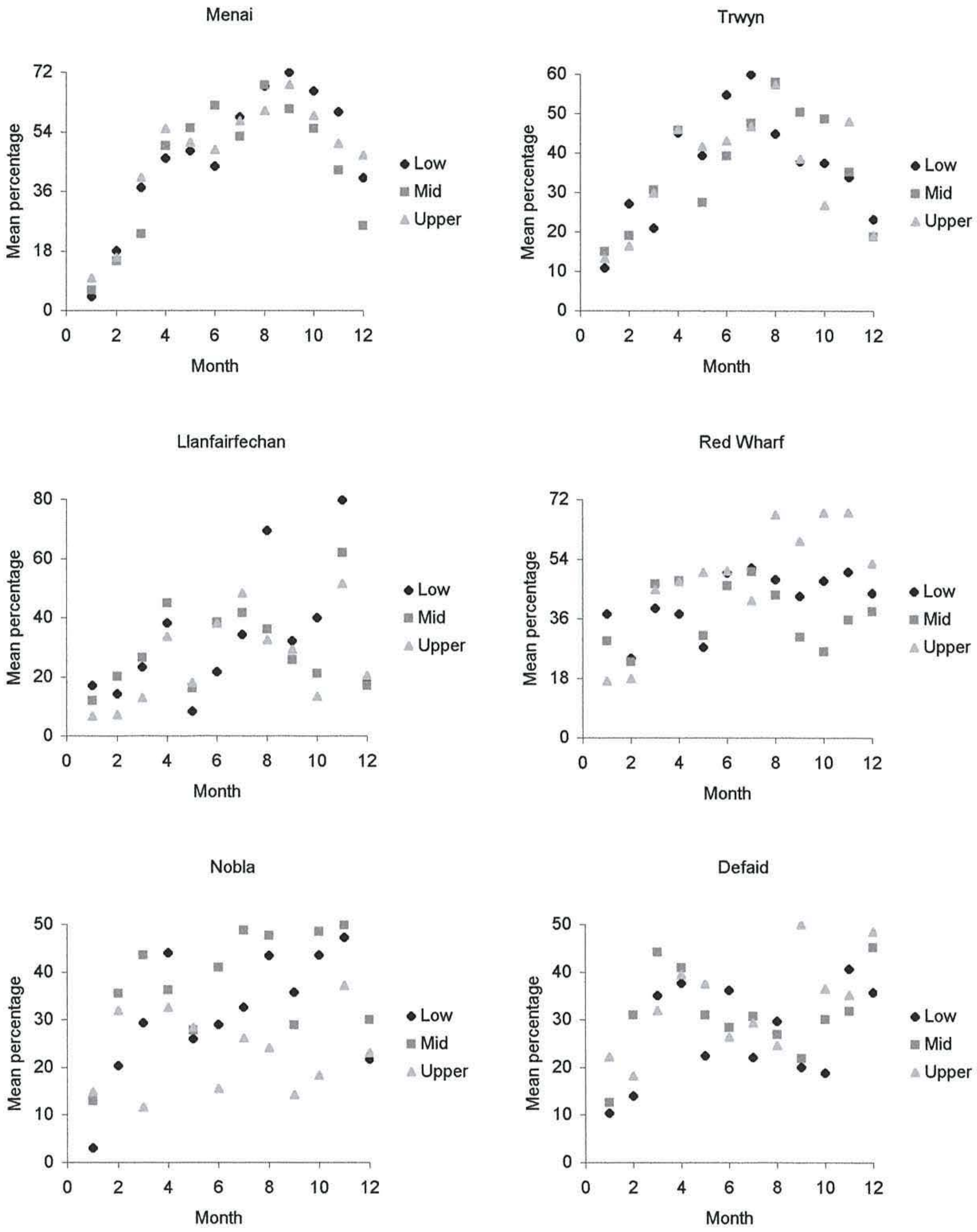


Figure 5.10. Monthly changes in percentage of *Nucella lapillus* foraging within a refuge at different shore levels. Months 1-12 are January to December inclusive. (2 years pooled data).

not to be significantly influenced by shore level at Menai Bridge (GLM. F=1.341 P=0.384), and Trwyn y Penrhyn (GLM. F=0.708 P=0.560). Post Hoc multiple comparison (Bonferroni test) showed significant differences in the monthly percentage of *Nucella* foraging within refuges between shore levels (low, mid and upper) on some of the study shores (Appendix 5, Table 5.9). The percentage of *Nucella* foraging within refuges was found to be significantly influenced by month on all six study shores namely: Menai Bridge (GLM. F=54.217 P=<0.001), Trwyn y Penrhyn (GLM. F=77.766 P=<0.001), Llanfairfechan (GLM. F=50.352 P=<0.001), Red Wharf Bay (GLM. F=63.187 P=<0.001), Porth Nobla (GLM. F=35.383 P=<0.001), and Porth Defaid (GLM.F=16.598 P=<0.001).

5.364. Refuging (Figure 5.11).

The monthly percentage of *Nucella* refuging was found to be significantly influenced by shore level at Trwyn y Penrhyn (GLM. F=55.053 P=0.004), and Porth Nobla (GLM. F=94.042 P=0.002), but found not to be significantly influenced by shore level at Menai Bridge (GLM. F=7.326 P=0.070), Llanfairfechan (GLM. F=2.252 P=0.253), Red Wharf Bay (GLM. F=5.971 P=0.090), and Porth Defaid (GLM. F=4.217 P=0.134). Post Hoc multiple comparison (Bonferroni test) showed significant differences in the monthly percentage of *Nucella* refuging between shore levels (low, mid and upper) on only two of the study shores (Appendix 5, Table 5.10). The percentage of *Nucella* refuging was found to be significantly influenced by month on all six study shores namely: Menai Bridge (GLM. F=36.561 P=<0.001), Trwyn y Penrhyn (GLM. F=201.924 P=<0.001), Llanfairfechan (GLM. F=8.060 P=<0.001), Red Wharf Bay (GLM. F=70.162 P=<0.001), Porth Nobla (GLM. F=190.606 P=<0.001), and Porth Defaid (GLM. F=61.464 P=<0.001).

5.37. Monthly changes in density of *Nucella* (Figure 5.12).

The monthly density of *Nucella* was found to be significantly influenced by shore level at Menai Bridge (GLM. F=15.317 P=0.027), Trwyn y Penrhyn (GLM. F=29.330 P=0.011), Llanfairfechan (GLM. F=94.086 P=0.002), and Porth Defaid (GLM. F=11.783 P=0.038), but found not to be significantly influenced by shore level at Red Wharf Bay (GLM. F=6.914 P=0.075), and Porth Nobla (GLM. F=6.550 P=0.080). Post Hoc multiple comparison (Bonferroni test) showed significant

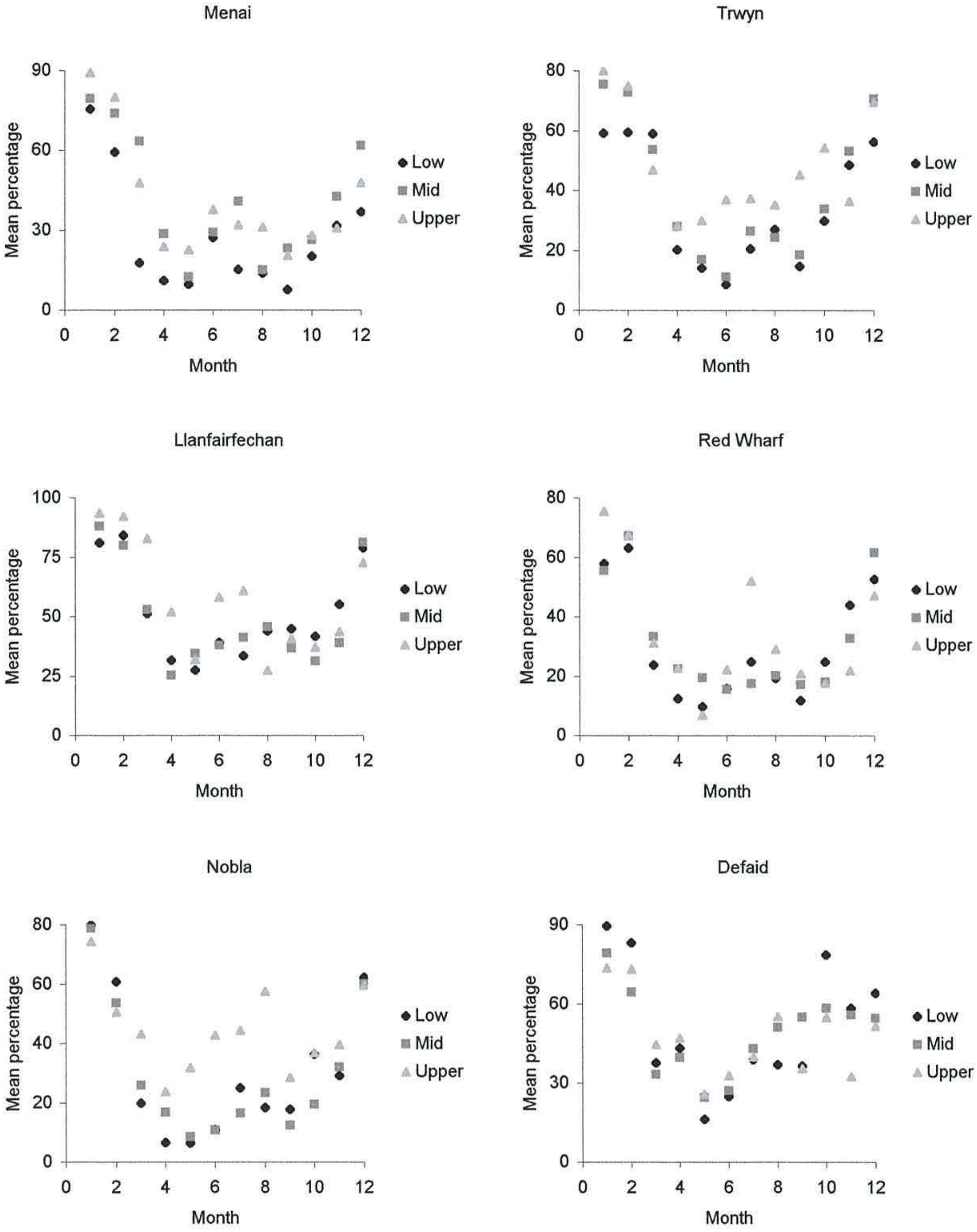


Figure 5.11. Monthly changes in percentage of *Nucella lapillus* refuging at different shore levels. Months 1-12 are January to December inclusive. (2 years data pooled).

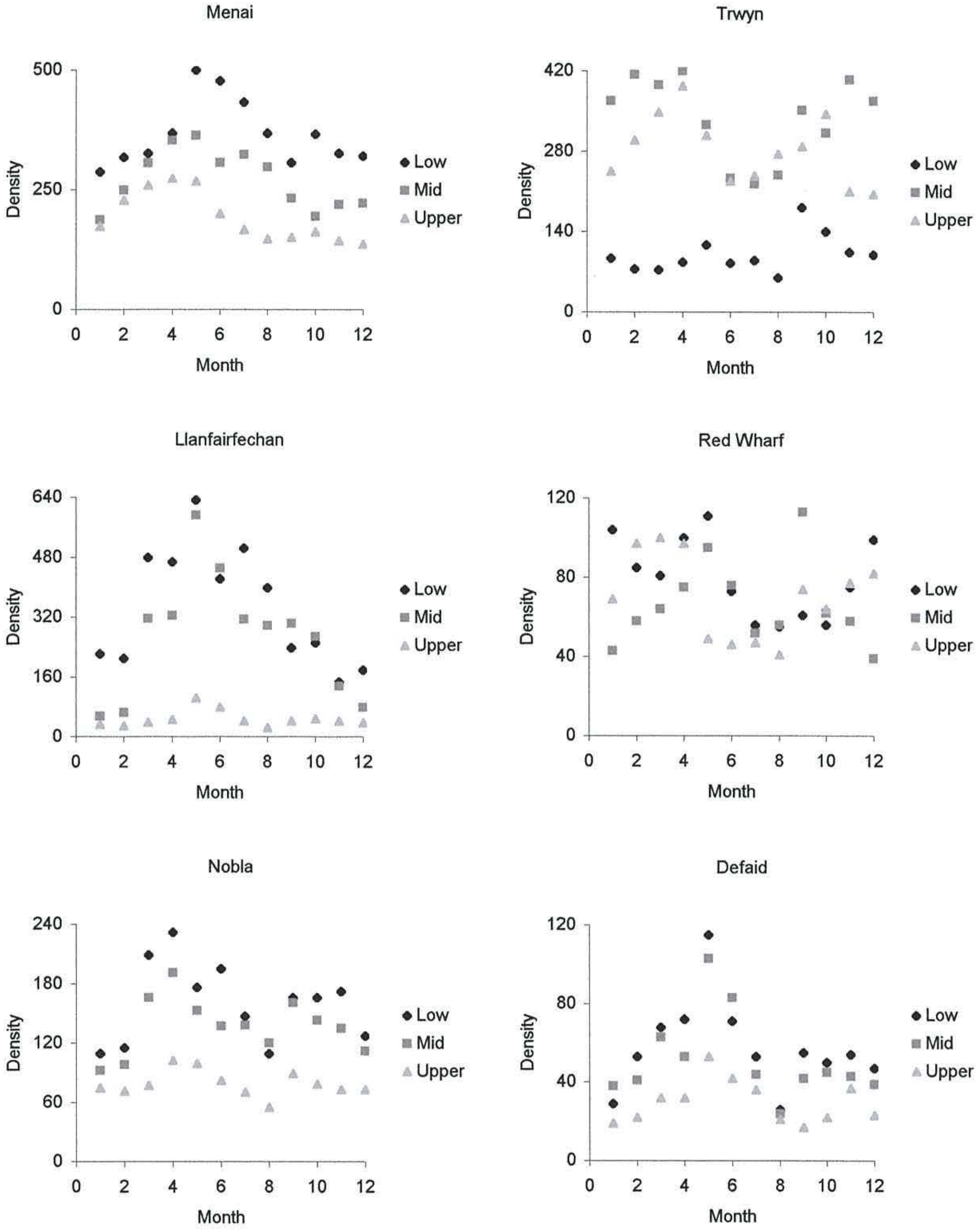


Figure 5.12. Monthly changes in density of *Nucella lapillus* at different shore levels. Months 1-12 are January to December inclusive. (2 years pooled data).

differences in The monthly density of *Nucella* between shore levels (low, mid and upper) on some shores (Appendix 5, Table 5.11). The density of *Nucella* was found to be significantly influenced by month at Menai Bridge (GLM. F=4.176 P=0.001), Llanfairfechan (GLM. F=19.876 P=<0.001), Red Wharf Bay (GLM. F=4.830 P=<0.001), Porth Nobla (GLM. F=6.081 P=<0.001), and Porth Defaid (GLM. F=6.963 P=<0.001), but found not to be significantly influenced by month at Trwyn y Penrhyn (GLM. F=1.247 P=0.297).

5.38. The proportion of *Nucella* in different microhabitats.

The observed proportion (Figure 5.13), and expected proportion (the relative proportion of each microhabitat in effect, see Figure 5.14) of *Nucella* in selected microhabitats, were significantly different for most microhabitat types (were present) on the six study shores (Table 5.12).

A more detailed depiction of dogwhelk activity combined with the concurrent occupation of specific microhabitats is shown in figures 5.15 (on different shores), and 5.16 (at different shore levels).

Table 5.12. Results of one sample T test procedure (2-tailed) showing significant mean differences in proportion of expected and observed *Nucella* occupying specified microhabitas on six shores.

Shore	Menai Bridge		Trwyn y Penrhyn		Llanfairfechan	
Microhabitat	t	Sig.	t	Sig.	t	Sig.
Open horizontal	-102.703*	< 0.001	-139.750*	< 0.001	-152.554 *	< 0.001
Open vertical	3.972*	0.001	3.042*	0.006	4.364*	< 0.001
Under boulder	38.204*	< 0.001	54.313*	< 0.001	27.683*	< 0.001
In pit	6.421*	< 0.001	5.844*	< 0.001	2.822*	0.009
In crevice	9.193*	< 0.001	12.205*	< 0.001	7.085*	< 0.001
In trench	-2.270	< 0.033				
Under algae	5.510*	< 0.001	2.327*	0.029		
In rock pool	-14.311*	< 0.001	-0.312	0.758	3.480*	0.002
In mussel matrix					1.368	0.184
In barnacle bed	-9.608*	< 0.001	-4.674*	< 0.001	4.786*	< 0.001

N.b. Table 5.12 is continued on page 183.

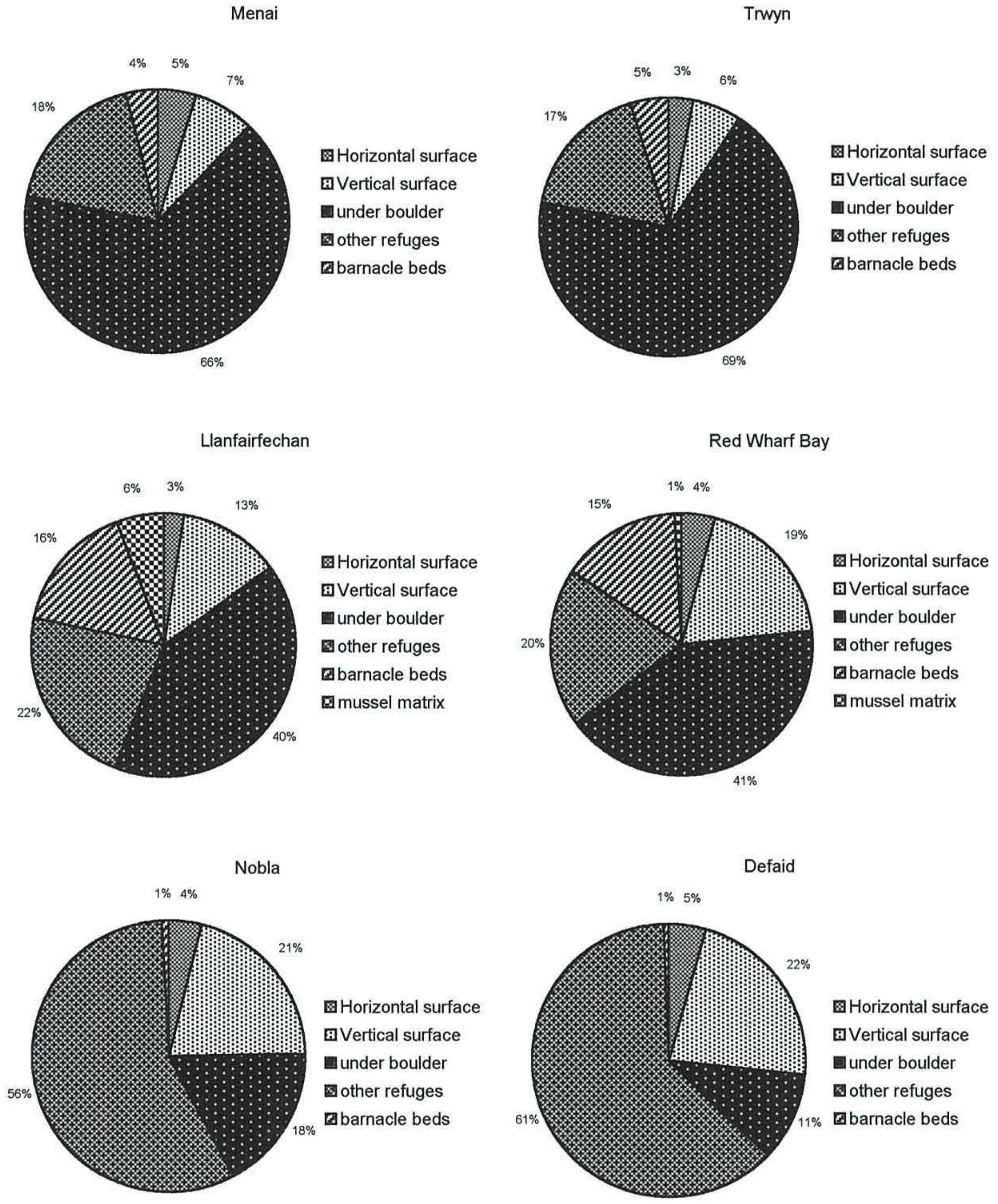


Figure 5.13. Percentage occupancy of microhabitats by *Nucella lapillus*.
(2 years pooled data)

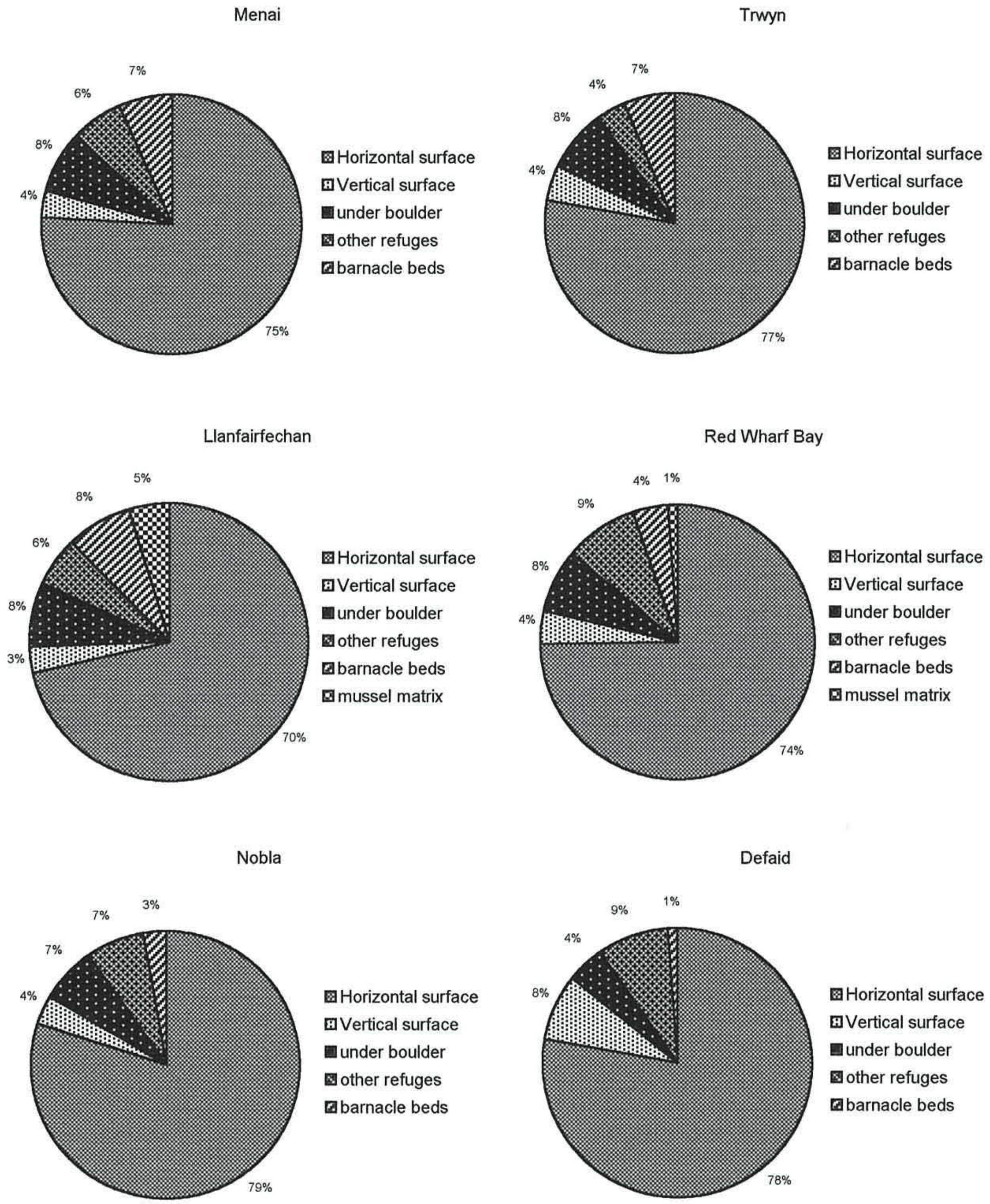


Figure 5.14. Availability of microhabitat types.
(2 years pooled data).

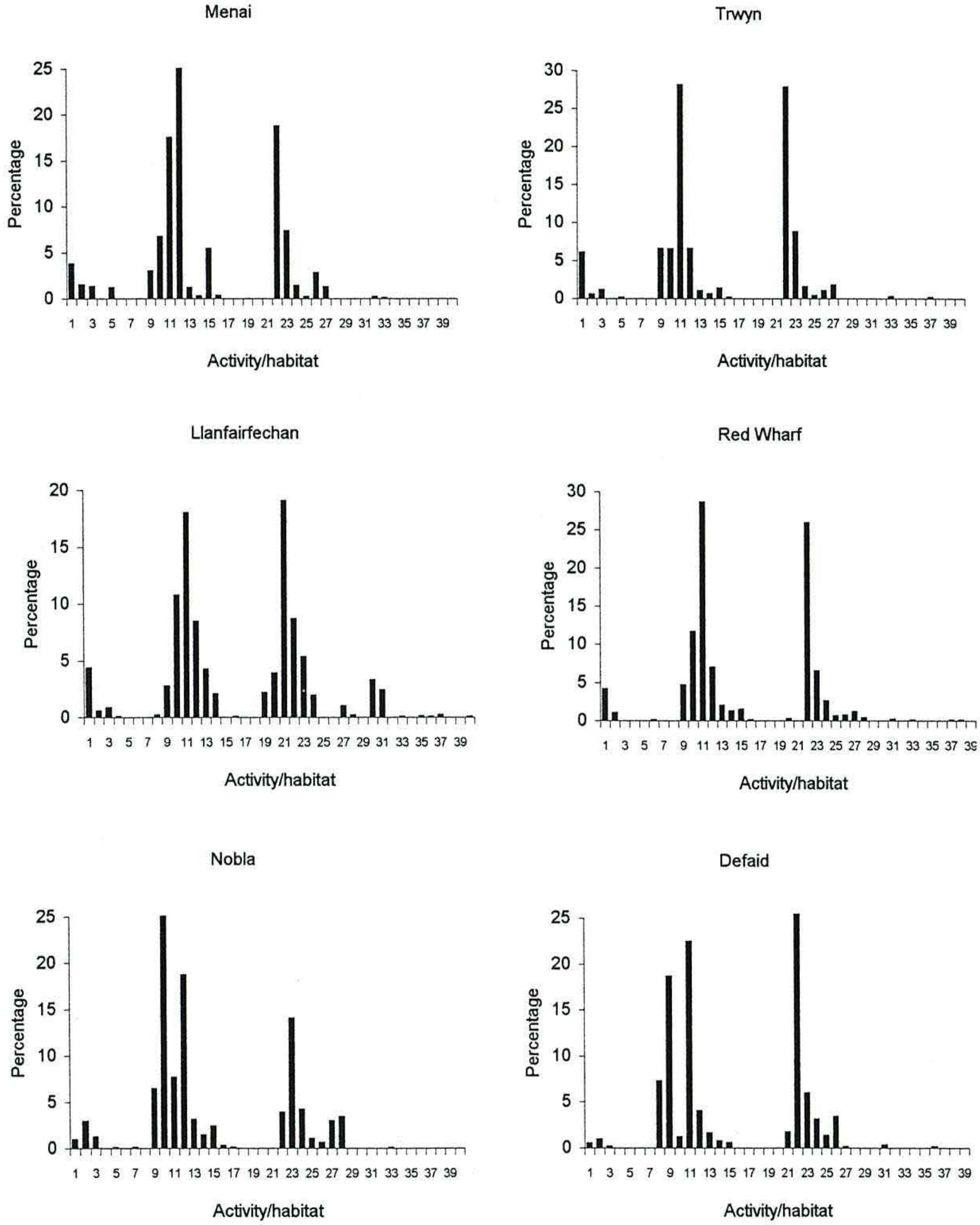


Figure 5.15. Percentage activity/occupation of habitat by *Nucella lapillus* on different shores. See Table 5.1. (Chapter 5) for explanation of activity/habitat.

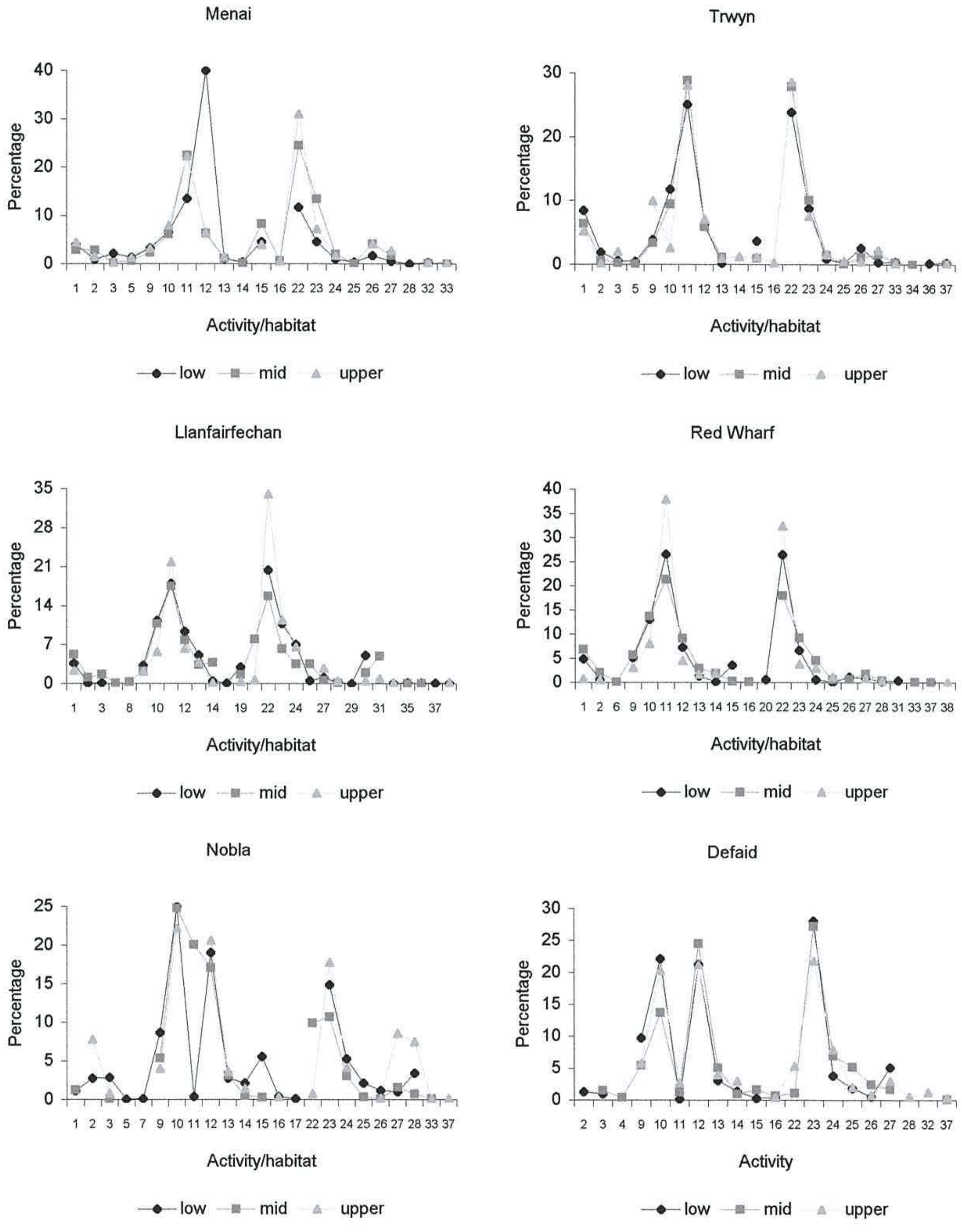


Figure 5.16. Percentage activity/occupation of habitat by *Nucella lapillus* at different shore levels. See Table 5.1. (Chapter 5) for explanation of activity/habitat.

Table 5.12 continued.

Shore	Red Wharf bay		Porth Nobla		Porth Defaid	
Microhabitat	t	Sig.	t	Sig.	t	Sig.
Open horizontal	-114.319*	< 0.001	-124.578*	< 0.001	-109.353*	< 0.001
Open vertical	8.208*	< 0.001	7.982*	< 0.001	4.920*	< 0.001
Under boulder	18.509*	< 0.001	6.270*	< 0.001	5.773*	< 0.001
In pit	3.699*	< 0.001	10.736*	< 0.001	9.730*	< 0.001
In crevice	8.314*	< 0.001	13.140*	< 0.001	11.747*	< 0.001
In trench	15.550*	< 0.001	-9.291*	< 0.001	1.236	0.229
Under algae	0.218	0.829	1.046	0.306	5.306*	< 0.001
In rock pool	3.717*	0.001	-2.568*	0.017	4.504*	< 0.001
In mussel matrix	4.263*	< 0.001				
In barnacle bed	10.123*	< 0.001	-67.440*	< 0.001	-7.219*	< 0.001

Data presented are t-values (t), with probabilities (P) which are all significant values. *Mean difference is significant at the .05 level

5.39. Prey patch size and composition and exploitation by *Nucella lapillus*. Different sized prey patches of barnacles were utilised by whelks to different degrees (Table 5.13).

Table 5.13. Patch composition and exploitation by *Nucella lapillus*.

Shore	Patch size (cm^2)	Mean barnacle size (cm^2)	Mean dogwhelk size (mm)	Mean residence time in patch (weeks)
Menai Bridge	80-160	0.17	22.8	2.1
	200-400	0.21	28.3	3.3
Trwyn y Penrhyn	80-160	0.17	23.1	1.7
	200-400	0.22	26.4	3.2
Llanfairfechan	80-160	0.19	23.3	1.4
	200-400	0.22	25.8	2.9
Red Wharf Bay	80-160	0.19	24.8	1.5
	200-400	0.23	27.9	2.8
Porth Nobla	80-160	0.19	25.5	1.3
	200-400	0.23	27.5	2.6
Porth Defaid	80-160	0.18	25.2	1.1
	200-400	0.22	26.7	2.4

5.4. DISCUSSION.

Size and activity: comparisons within shore levels.

There were clear distinctions in size distribution between those *Nucella lapillus* engaged in different activities within particular shore levels. Dogwhelks spawning and foraging in the open were significantly larger than those foraging in refuges, which in turn were larger than those refuging. This applied to all shore levels, and to all shores. Clearly only dogwhelks of a certain size (mature adults) are able to breed and spawn. The general and significant decrease in size from whelks foraging in the open to those refuging, appears to be related to the comparative risk, associated with these different activities, for whelks of different sizes.

Size and activity: comparisons between shore levels.

There were also clear differences in the size of dogwhelks (mean shell length) involved in the four main activities, between different shore levels on each of the shores investigated. Animals at low shore were larger or equal in size to those at mid shore, which in turn, were larger or equal to those at the upper shore, in all activities (spawning, foraging in the open, foraging in refuge, refuging). Exceptions (larger whelks found in refuges, both feeding and resting, progressively towards the upper shore) were found at Menai Bridge and Llanfairfechan. At Porth Defaid there were no noticeable size differences between any of the shore levels for whelks engaged in all activities. These trends are simply a reflection of the basic size distribution in relation to vertical shore height (Chapter 2), with some modification. The relative increase in mean size of snails found within refuges in upper shore levels at sheltered locations, is an indication of the increase in severity of certain environmental stresses at higher tidal levels (e.g. desiccation), that restricts even larger individuals to shelter. Mean shell length decreased with tidal height (Figure 2.4), even though proportions of whelks in the smallest size classes decreased in the same direction (Figures 2.5-2.7).

Size and activity: comparison between shores.

Comparing the overall size distribution of dogwhelks recorded in all activities, between shores, there is not a great deal of variation in mean shell length between locations (Table 5.14).

Table 5.14. Mean shell length of dogwhelks on the study shores.

Shore	Shell length (mm)	Shore	Shell length (mm)
Menai Bridge	27.65	Red Wharf Bay	27.32
Trwyn y Penrhyn	24.96	Porth Nobla	27.01
Llanfairfechan.	23.48	Porth Defaid	27.16

Data presented are overal mean shell lengths (mm) of dogwhelks over the two year period.

The mean size of *Nucella lapillus* at the three most exposed shores Red Wharf Bay, Porth Nobla, and Porth Defaid were not significantly different. Exposed shore whelks were larger than those at Trwyn y Penrhyn (sheltered) and Llanfairfechan (fairly sheltered), and smaller than those at Menai Bridge (very sheltered). Basically the same pattern was observed when sizes of whelks in all four different activities were analysed, except that at Trwyn whelks foraging in the open were larger than those at either Nobla or Defaid. The differences in overall mean size between shores are related to different growth rates in shores fundamentally exposed to different amounts of wave action, as well as being a reflection of the varying size-dependent mortality rates experienced in these locations due to desiccation, dislodgement and predation.

Despite the fact that requirements of whelks for prey and crevices were strong and consistent, space utilisation by *Nucella lapillus* was clearly different at shores with differing intensities of wave action, with obvious biological differences between similar habitats subject to different exposure (Dayton, 1971), with a significant heterogeneity in substrate composition (Hawkins and Hartnoll, 1983a). The two sheltered shores exhibited a clearly defined zonation with a greater degree of algal abundance (Lubchenco and Menge, 1978), and a moderate number of refuges (19-21% of total substratum). At the moderately-exposed shores (Red Wharf and Llanfairfechan), there was little space availible, a low cover of algae (none at Llanfairfechan), fairly dense barnacle assemblages (Menge and Lubchenco, 1981) and limited areas of mussel (high mussel coverage at Llanfairfechan), with a high availability of potential refuges (22-27%). The exposed sites (especially Defaid), were characterised by an abundance of free space, but had a deficiency in availability of refuges (only 13-14% of total substratum).

Seasonal changes in activity.

Seasonal (even monthly) fluctuations in the proportion of dogwhelks involved in the four main activities were similar on every shore. The timing of spawning patterns was clearly different at different shore levels on each shore. At the two most sheltered locations, Menai and Trwyn, spawning continued throughout the year at all shore levels, was highest during the coolest periods and much reduced in Summer. This may be related to the amount of insolation that resultant egg-capsules are subjected to at these different times, as the potential for lethal dessication is highest in the warmest months. On all other shores spawning was discontinuous, particularly in the upper shore, usually more frequent at lower levels. Spawning was also low at Llanfairfechan and Nobla, virtually absent at Red Wharf and Defaid, during the Summer. It reached quite significant levels in the Winter at Nobla (exposed shore), but was always minimal at Defaid (very exposed), where the wave action was often extreme. This suggests that within certain environmental parameters, the degree of spawning may be synchronised to the absence of specific mortality factors for the egg-capsules, and that capsules from exposed shores may be more susceptible to higher temperatures, and more adapted to colder temperatures and wave-action, than those in sheltered locations. The size of animals spawning in each specific location did not change significantly within shore levels, nor between months. Foraging on the open substrate was observed all year round at the two sheltered shores, and only ceased (at mid and upper shore levels) on other shores during the Winter. There were similar seasonal patterns in visible foragers *(Nucella* actively foraging as opposed to those foraging inside refuges) on all shores with maxima in April and September and reduced numbers from December-Febuary. There was little change in the size distribution of foraging whelks from month to month, particularly when temperatures were favourable. The proportion of individuals on open, exposed surfaces increased significantly among snails above 24 mm, with large whelks often remaining on open surfaces, even where there were considerable microhabitats suitable for shelter. Foraging in the open, whelks are often subject to the full force of environmental conditions. A greater percentage of whelks (relative to intrinsic level densities) were found to forage in the open in the low shore (when compared to other levels), where exposure to desiccation and variation in air temperatures is least. Foraging in the open was lowest at all shore levels on all shores during the winter, when the force of wave impact is greater than at other times of the year, particularly at lower shore levels. During the Summer, open surface foraging was reduced throughout the shore at the three most sheltered locations (and in the upper shore at Red Wharf Bay).

Seasonal changes in *Nucella lapillus* size were seen in those foraging from within a refuge, and particularly so in sheltered locations, where larger forms predominated from May to July (all shore levels), September to December (Menai low and upper shores), and December to March (Trwyn upper). Smaller sized *Nucella* were seen from November to January at Trwyn y Penrhyn. At Llanfairfechan (upper shore) and Red Wharf Bay (lower shore), the only significant size differences were relatively smaller individuals from November to April. At Defaid, animals were smaller in December (low shore); December, Febuary and March (upper shore), larger in April in the mid shore (upper shore at Nobla). Higher proportions of foraging in refuges occured from August to September on all shores (August to November at Red Wharf Bay and Porth Defaid), a lower proportion during January to March (on all shores). The proportion of dogwhelks foraging within refuges was inversely related to wave action and positively related to high temperature increases in the Summer months, particularly on sheltered shores (and negatively related to the concurrent proportion foraging in the open). During winter, many of the adults remained together with their prey in refuges (most actually refuging), which reduces search time as well as many foraging related risk factors (Menge, 1978b), although the proportion of dogwhelks foraging in refuges remained fairly high throughout the year (Appendix 5, Table 5.12). On moderately-exposed and exposed shores the situation was not as clearly defined, with no obvious trends between shore levels, except for a gradual increase from January to December. The highest proportion of whelks refuging (on all six shores) occured during winter (December to March), with a lower (but still substantial) peak in Summer in most locations. Refuging was higher in the upper shore levels (than mid and lower) throughout the year, except for in the lower reaches in winter at the exposed shores when whelks were forced into refuges to avoid being swept away. In winter *Nucella lapillus* and other marine snails suffer a loss of adhesion to substrate surfaces and lose contact (particularly with vertical and other exposed rock surfaces) (Largen, 1967a; Gowanloch and Hayes, 1986), due to heavy wave action.

On sheltered shores, overall smaller adults were seen from September to January (all levels), larger from May to June (mid and upper levels). At Llanfairfechan smaller individuals were present January to May (low and mid shore), during September to May (upper shore). At Red Wharf the mean size of whelks was smaller in December and January (upper shore), larger from June to August (low shore), Porth Nobla larger during November and December (upper level), and at Porth Defaid, larger whelks from May to July (upper shore). The reasons for these seasonal changes in the mean size of dogwhelks are not apparent, as there are no trends related to shore level or shore type.

Proportions of dogwhelks in activity.

Comparisons between shore levels. At the two most sheltered (Menai and Trwyn) and the most exposed (Defaid) shores, a higher proportion of dogwhelks were found spawning on the lower shore than the mid shore, which in turn had a greater proportion spawning than the upper shore (none at Port Defaid in a two year period. The two moderately exposed shores Llanfairfechan and Red Wharf Bay had their highest proportions spawning at mid shore, and lowest proportions at the upper shore particularly from September to November. The exposed shore Nobla had more spawning at the upper shore, and less at the mid shore throughout the whole year. In summary, the proportion of *Nucella lapillus* spawning increases progressively up the shore as wave action increases, except for Porth Defaid which is at the extreme end of the wave action spectrum, and which has intrinsically low levels of spawning (none in the upper region).

Foraging in the open: the proportion of *Nucella* foraging in unsheltered conditions was basically unaffected by the shore level at all shore locations (slightly reduced at the upper levels of Red Wharf Bay and Nobla). A higher percentage of whelks foraged in the open from March to September (very high from April till May), lowest values from October to Febuary, on all six shores. Like Menge (1978b), I found that dogwhelk feeding rates were greatest in the coolest periods of the warmer season, when there was a reduced risk of desiccation. The proportion of *Nucella* foraging in the open was greater at exposed shores during the Summer, due to ameliorating effects of wave splash. On each shore there was an increase in activity from high to low tidal levels.

Foraging in refuges: at the majority of shores, higher proportions of dogwhelks foraged within shelter at lower levels, followed by the mid shore. At Red Wharf and Porth Defaid, more snails were involved in this activity at the upper shore however, fewer in the mid shore (Red Wharf Bay), or low shore (Defaid). Overall foraging activity (foraging in the open + foraging in refuges) was greater at lower heigths on the shore, markedly in sheltered and semi-exposed locations.

Refuging: in most cases, shore level had no effect on the proportion of whelks refuging at any one time, except for Trwyn and Nobla, that had more refuging whelks in the upper shore. The density of whelks decreased with tidal height, and with distance from crevices and other refuges (Fairweather et. al, 1984). A comparative lack of utilisation of refuges low on the shore may be due to fact that physical stress was less important here. Connell (1972), identified a need for crevices in *Nucella emarginata* and *Nucella canaliculata* individuals, which were often only present on smooth surfaces, where large barnacles (*Balanus cariosus*) provided some shelter.

Different types of refuges (Table 5.1, p157) were used by different sizes of whelks (Dayton, 1973; Van Blaricom, 1978), including occupation of crevices, according to their (the refuge's) maximal width (Table 5.15). According to Menge and Lubchenco (1981), dogwhelks often show variable cycles of refuge utilisation, in response to consumer pressure, desiccation and strong wave action.

Table 5.15 Size of whelks and refuge utilisation.

Shore	Crevice size	small juveniles	large juveniles/ subadults	adults	large adults
Menai Bridge	small	0.88	0.64	0.11	0.00
	medium	0.10	0.27	0.86	0.33
	large	0.02	0.09	0.03	0.67
Trwyn y Penrhyn	small	0.70	0.54	0.05	0.00
	medium	0.18	0.28	0.86	0.19
	large	0.12	0.18	0.09	0.81
Llanfairfechan	small	0.62	0.43	0.02	0.00
	medium	0.24	0.38	0.72	0.16
	large	0.14	0.19	0.26	0.84

Table 5.15. Continued.

Red Wharf Bay	small	0.57	0.51	0.04	0.00
	medium	0.35	0.25	0.81	0.23
	large	0.08	0.24	0.15	0.77
Porth Nobla	small	0.75	0.67	0.11	0.00
	medium	0.22	0.26	0.79	0.44
	large	0.03	0.09	0.10	0.56
Porth Defaid	small	0.85	0.75	0.24	0.00
	medium	0.15	0.20	0.73	0.39
	large	0.00	0.05	0.03	0.61

Data presented represent proportion of whelks in particular crevice size out of all those refuging at that location in that size group.

Key for size groupings (shell length): small juveniles: 2.0-11.9mm; large juveniles/subadults: 12.0-21.9mm; adults: 22.0-31.9mm; large adults: 32.0-41.9 mm.
Key for maximum crevice width: small 5-24.9mm; medium: 25-44.9mm; large: 45-64.9mm.

There were some very interesting trends (and differences), in refuge (crevice) occupation by similarly sized whelks on the different shores. Dogwhelks occupied relatively smaller crevices (width) in locations where there was predation by crabs (small whelks on sheltered shores), desiccation (all whelks on very sheltered shores), and dislodgement from heavy wave action (all individuals on very exposed, and to a lesser extent on exposed shores), within certain size limitations (e.g. large adults were too large for the smallest crevices). The quality of refuges in an area (availability of usable crevices) can effect gastropod population density, particularly steep-sided depressions or those containing rubble favoured by whelks (Kohn and Leviten, 1976). Gastropods activiely seek protected sites and experiance, higher mortality in the open, leading to increased densities in crevices (Fairweather, 1988b). Individuals on the study sites were selective in their choice of crevice and did not simply occupy any convienient refuge following foraging as also observed by Leviten and Kohn (1980). Indeed most of the smallest-sized dogwhelks (2-8 mm) remained within complex microhabitats for the duration of the study

Comparisons between shores.

The proportion spawning was highest at the two sheltered shores (Menai and Trwyn), followed by Nobla, then Red Wharf Bay; low at Llanfairfechan, very low at Porth Defaid. Foraging in the open was highest at the three most exposed shores, lower at more sheltered locations. Foraging in refuges was highest at both the sheltered shores and Red Wharf Bay, relatively lower at Llanfairfechan and the exposed shores. The proportion of *Nucella lapillus* refuging was equally greatest at Llanfairfechan and Defaid, moderate at the sheltered shores (Menai and Trwyn), and least and Nobla and Red Wharf Bay (inverse of foraging in the open). These results show general trends with foraging in the open being more extensive at exposed sites, foraging in shelter and spawning more frequent on the sheltered shores.

Size and microhabitat utilisation.

Dogwhelks were divided into (significantly different) size groups from the largest to smallest. Within each group those in different microhabitats were not significantly different in size distribution (from Tukey HSD). There were constant similarities in the relationship between dogwhelk size and microhabitat utilisation patterns, not only within shore levels, but also between shore levels, and between different shores. This shows that the relationship between size and microhabitat requirement generally remains constant, (notwithstanding inter-shore differences in substratum topography).

The size distribution at the lower shore of Menai Bridge (Table 5.16), shows that the main trends in microhabitat occupation, with the largest individuals in Group1, and dogwhelks become progressively smaller until Group 4. These trends are modified at other levels and on other shores.

Table 5.16. Different size-groups and microhabitat occupation at Menai Bridge lower shore.

Group 1	Group 2	Group 3	Group 4
all spawning, horizontal foraging, foraging under algae, foraging and refuging in trenches	vertical foraging, foraging and refuging in pits, refuging under algae, in rockpools and on the rock substrate	foraging and refuging under boulders	foraging and refuging in crevices, refuging under sea anemones

Menai mid and upper shores, all Trwyn shore levels, Llanfairfechan low shore, and all Red Wharf shore levels, had basically the same pattern as Menai low, except for no differences between groups 1 and 2. At Llanfairfechan and Red Wharf, certain microhabitats were utilised significantly in the low shore, namely foraging and refuging between live barnacle shells and refuging in dead barnacle shells. In the mid and upper shores at Llanfairfechan, no dogwhelks were found refuging in dead barnacle shells, but many refuged within the mussel matrix. Red Wharf Bay mid and upper shore size distributions were identical to the lower shore, except those refuging under boulder and in pits were smaller. The situation on exposed shores is shown by results from Porth Nobla (which had benches and no boulders) from the lower shore (Table 5.17). The largest individuals in Group 1, had a composition at mid and upper shore levels at Nobla the same as for the lower shore, except for the addition of those foraging under boulders, due to the availabilty of this substratum type, absent in the low shore. Group 2 consisted of refuging under boulders, and Group 3, foraging and refuging in crevices (for the mid shore). Group 2 contained those animals foraging in pits and trenchs, refuging in pools and under algae, Group3 whelks refuging in pits and under sea anemones, and a smaller Group 4 foraging foraging and refuging in crevices and refuging under boulders (for the upper shore).

Table 5.17. Different size-groups and microhabitat occupation at Porth Nobla lower shore.

Group 1	Group 2	Group 3	Group 4
all spawning, horizontal foraging, vertical foraging, foraging and refuging under algae, foraging and refuging in trenches	foraging in pit, refuging in pool	refuging in pit, refuging under sea anemones	foraging and refuging in crevices

At the very exposed shore Porth Defaid, all three levels had the same size distribtion/habitat occupancy, with only two major size groups. Group 1 (larger animals) contained those individuals spawning, foraging in the open, foraging and refuging in trenches, refuging under algae, foraging and refuging in pools, and foraging and refuging in pits. Group 2 had whelks foraging and refuging in crevices, and refuging under sea anemones.

In summary, there were clear size differences between dogwhelks found in different microhabitats This has been determined for *Nucella* spp. in other parts of the world. The distribution of whelks clearly changes in relation to body size (Gosselin and Chia, 1995b; Gosselin, 1997), reflecting some degree of size resource partitioning in the utilisation of microhabitats (Underwood, 1977; Gosselin, 1997). Whelks exhibit a non-random distribution (Gosselin and Chia, 1995a). Hatchlings (*Nucella emarginata*) are cryptically located in tufts of filamentous algae, mussel clusters, and densely packed barnacles, whereas the adults are mostly located on open surfaces. Differential intraspecific utilisation of microhabitat resources is likely in regions of high diversity in *Nucella lapillus* morphology (shape and size), such as North Wales. Furthermore, differences in microhabitat substratum preferences and requirements for different groups of intertidal snails during periods of low tide, have already been identified in studies on *Nerita textilis* (Vannini and Chelazzi, 1978). Underwood (1976b) analysed patterns of dispersion of fanother four species of intertidal gastropods, to determine their preferences for major substrata, with different results for adult and juveniles according to the substratum in which they are found (Underwood, 1976a), indicating as my studies did, that investigations on the effect of habitat complexity upon predator-prey interactions need to include the interacting effects of body size (Pennings, 1990). *Nucella lapillus* was found in a great variety of habitats including on bare rocks, within the indentations of the substratum, under algal masses or in association other invertebrates, including in the empty spaces between clumps of barnacles (Guisado and Castilla, 1983). The relatively large study replicates (4 m^2), tended to have a large number of varied microhabitats (Connor and MacCoy, 1979; MacGuiness, 1984b), which had a positive effect on the number of species present in the community, and upon the number of dogwhelks availible for study. This microhabitat diversity (with a high abundance and variety of micro-habitats) within each of the study sites (Connor and McCoy, 1979; McGuinness, 1984a), included a large number of refuge microhabitats, that reduce the efficiency of predators of *Nucella* (Menge and Lubchenco, 1981), as well as reduce physical stress (Emson and Faller-Fritsch, 1976; Kohn and Leviten, 1976; Menge, 1976). As long ago as Fischer-Piette (1935), *Nucella lapilllus* has been observed feeding mainly in the cracks in the rocks opposed to on the flat parts of the substrate, as does *Nucella melones* (Bertness et. al., 1981), and during these experiments *Nucella lapillus* individuals were repeatedly recorded feeding on barnacles from within refuges such as crevices, trenches, and pits. This shows the common tendency for *Nucella lapillus* in North Wales to forage within refuges, thus largely avoiding the risks from these physical factors (Burrows and Hughes, 1989), and predation (Garrity and Levings, 1981). It is remarquable that many papers on the foraging of dogwhelks in the 1970's and 1980's hardly refer to this important component of dogwhelk behaviour in *Nucella lapillus* that even comprise the major activity at certain shore levels, at certain times of the year. Certainly only one or two inactive snails were recorded on homogenous vertical, sloping or horizontal surfaces, which were detached and located in situ as if by accident (as with *Nerita* Spp: Levings and Garrity, 1983). It also appears that many dogwhelks preferentially converge on microhabitats that enhance the survival of their resultant offspring (Grant and Utter, 1988), but the relative importance of this factor compared to the survival of the adults themselves, still needs to be determined. Crevices and other refuges, provide shelter for whelks as well as for their egg capsules, from wave impact and dessication, so it is not suprising that these microhabitats have much higher concentrations of *Nucella* than do exposed parts of the substratum (Gosselin and Chia, 1996a).

Topography.

This term is used here to denote how the structural holistic effects of the structure of the local substratum determines microhabitat diversity, availibility (and suitability), and consequently microhabitat utilisation, and how that relates to dogwhelk activity. Surface heterogeneity can be beneficial to both dogwhelks and barnacles, and it is possible for their upper distribution limits to be elevated on more heterogenous shores Menge (1976). Increased rock surface complexity has a moderating action on the effects of wave action (Menge,1978a; Crothers, 1992) and desiccation (Garrity 1984), increasing the range of usable microhabitats (Sebens 1991). This often alters the size-density scaling of intertidal communities (Gee and Warwick, 1994a; 1994b), by creating a disproportionate share of available spaces for the smaller animals there (Morse et al. 1985), and so allowing for more species to coexist per microsite (Palmer,1992). There tended to be more microhabitas, certainly more refuges on the three more sheltered study sites, particularly at Llanfairfechan, where both mussel beds and barnacle shells where used extensively as refuges in contrast to other shores. This was important for dogwhelks as there was no macroalgal growth whatsoever at Llanfairfechan. However, algal fronds on other shores were used by much larger whelks to forage and refuge beneath, than those that generally refuged in the mussel matrix on Llanfairfechan, and by substantially larger individuals than those that were found between or in barnacle shells at that same shore. Gosselin and Bourget (1989), found that dogwhelks preferentially selected areas of heterogenous substrate, and differences in substrata do appear to regulate the dispersion patterns (degree of aggregation) of *Austrocochlea* (Underwood, 1976b). The amount of cover provided by canopy forming algae influenced dispersion in *Nucella lapillus*, dogwhelks often used algal fronds to prolong foraging in Summer (particularly on sheltered shores) in North Wales (personal observation). The ability of *Nucella lapillus* to move varies with the type of substrate encountered. They move far more easily on hard substrata than on soft substrata (Crowe,1996), and normally avoid crawling across sand or mud (Crothers, 1983). The spatial heterogeneity of the shore also affects the movement patterns of *Nucella lapillus* (Gosselin and Bourget, 1989), the population distribution pattern (Hogue and Miller, 1981; Menge et. al., 1983), as well as abundance and diversity of this snail (Bergeron and Bourget, 1986), and its effects on community structure (Menge et. al., 1986).

Microhabitat utilisation in relation to microhabitat availability.

There were general trends in the way that *Nucella lapillus* positively (or negatively) descriminated in its choice from the microhabitats available. Dogwhelks on all shores avoided open horizontal surfaces as far as possible, despite the fact that this comprised over 70% of substrate composition in all locations. *Nucella lapillus* preferentially selected vertical surfaces, to a greater extent (relative larger proportion of whelks) progressively up the wave-exposure gradient (the relative proportion of vertical surfaces was virtually the same on all shores). By far the most important (highly utilised) habitats were the refuges: pits, crevices, and particularly the underside of boulders. Occupation of pits and crevices increased sequentially from sheltered to exposed locations and was significant despite the comparative rarity of these structures. The utilisation of the underneath of boulders changed substantially from shore to shore (even though their availability does not), and was inversely related to wave-action. Dogwhelks under the algal canopy were found there in expected proportions except for the two most extreme environments Menai Bridge (very sheltered) and

Porth Defaid (very exposed), where this habitat appears to have a major importance for *Nucella lapillus*. Dogwhelks only occupied trenches and rock pools, and the mussel matrix (only present at Llanfairfechan and Red Wharf Bay), in numbers close to unity (expected values from the percentage habitat availability data). *Nucella lapillus'* utilisation of the clumped barnacle patches, was different from expected on all shores. In sheltered and exposed locations, there were fewer whelks than expected, but at the moderately exposed sites (Llanfairfechan and Red Wharf Bay), there were far more than expected. This shows a clear preference for certain microhabitats that is summarized in tabular form in Table 5.18. Presence in habitats showed either a positive (+ve) selection, or negative (-ve) preference for microhabitats (obtained by subtracting % percentage availability from percentage occupation), giving an investigation of the strength of the association between *Nucella lapillus,* and the named microhabitat type on that particular shore, a measure of its relative importance for dogwhelks in that location. This method enabled the comparison of unlike shores to be undertaken, as it examines the direct relationship between exploitation and availability. Similar investigations of microhabitat abundance on different shores and their utilization by intertidal gastropods in were carried out by Garrity and Levings (1981).

Table 5.18. Comparisons of proportion of *Nucella lapillus* in selected microhabitats with the proportion of microhabitat available.

Microhabitat	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
horizontal	- 70	- 74	- 67	- 70	- 75	- 73
open vertical	+ 3	+ 3	+ 10	+ 15	+ 17	+ 14
under boulder	+ 58	+ 61	+ 32	+ 33	+ 11	+ 7
in pit	+ 3	+ 4	+ 5	+ 6	+ 33	+ 37
in crevice	+ 1	+ 1	+ 7	+ 11	+ 13	+ 16
in trench	=	=	=	+ 1	- 1	=
under algae	+ 4	=	N/A	=	=	+ 3
in rock pool	- 1	- 1	- 1	- 1	- 1	+ 2
mussel matrix	N/A	N/A	+ 1	+ 1	N/A	N/A
barnacle test	- 3	- 3	+ 8	+ 10	- 2	- 1

Data of the result of subtracting percentage habitat availability from percentage occupation by *Nucella* for each microhabitat.
N/A: habitat unavailable in this location.

In a theoretical homogeneous population (all animals would behave in the same way to the presence of a substratum), we would have seen a random dispersion with respect to the substratum (Underwood, 1976), but like Leviten and Kohn (1980), I found many within species differences in the use of microhabitat resources by *Nucella lapillus,* which were determined to some degree by shore type (amount of wave exposure). Individuals exhibited variation in the use of different types of refuges at different times of the year, presumably in response to changes in the prevailing environmental conditions. This is similar to the results obtained for *Nucella emarginata,* which also showed a discriminatory preference for certain microhabitats (Berlow and Navarrete, 1997). More work needs to be done on both the temporal heterogeneity and the spatial heterogeneity in microhabitat composition, such as quantifying the diversity and abundance of microhabitats between and within different heights of the shore, as their spatial subdivision can alter the stability of species interactions (Karieva, 1990). We might also expect that snails do not discriminate between availible microhabitats to the same degree, during prolonged periods of movement (Levings and Garrity, 1983), as at times of obvious vertical migration (see Chapter 4).

Prey patch size, composition, and exploitation by Nucella lapillus.

Larger dogwhelks tended to occupy larger prey patches (where the mean individual barnacle size was also higher), and remained within a single patch for a longer time. This was particularly true on more sheltered shores where selective feeding (prey choice) is more likely to occur than on exposed shores (where forgaing time is frequently suppressed because of higher wave energies). Mean residence time was greater in the larger patches, for when food is not limited, dogwhelks can remain in the same area for prolonged periods of time (Crothers, 1981a). In addition, the intrinsically larger dogwhelks needed to forage longer to support a larger mass, and so they exhibit more prolonged feeding bouts (Chapter 4). Thay are also less susceptible than smaller whelks to unfavourable environmental factors, and can remain in the open, and away from refuges for longer. It is also probable that the increased mass of barnacles (individual barnacles were also larger) in the larger patches, offered more protection against wave dislodgement, than the smaller sessile assemblages, as was found within the mussel matrix in a different study (Lintas and Seed, 1994), though this effect is likely to be minimal in exposed conditions.

CHAPTER 6.

COMMUNITY STRUCTURE AND THE IMPACT OF *NUCELLA LAPILLUS* ON SESSILE FAUNAL COMMUNITIES.

6.1. INTRODUCTION.

Although the basic mechanistic processes of competition and predation in rocky intertidal communities were outlined almost fifty years ago (Hatton, 1938), and refined later in temperate habitats (Connell, 1961a), the detailed organization of the rocky intertidal community of Western Britain is still poorly understood. Early work on the important component species can be seen in the papers of several workers (Barnes and Powell, 1950; 1954; Barnes, 1956; Bayne, 1964). The rocky shore intertidal comunities of the Northeast Atlantic including North Wales (where this study was carried out), exhibit a dynamic and changing balance between barnacles, limpets and fucoid algae. The balance between these organisms operates geographically as well as on various smaller spatial scales. The first part of this work was to examine intertidal community structure.

Community structure.

The community structure of any particular location needs to be understood in relation to the governing processes that are responsible for community dynamics (Werner and Gilliam, 1984). Community distribution patterns and community stability are strongly affected by both physical disturbances and biological processes (Lewis, 1976). Wave-action, temperature and desiccation, competition and predation all play a part in structuring intertidal communities (Conell, 1961b; 1972; 1975; Paine, 1974; 1977; 1980; Menge, 1976b; Menge and Sutherland, 1976;1987; Peterson, 1979). Interspecific spatial competition has a major role in producing this pattern of distribution. (Dayton, 1971; Lewis, 1978; Connor and Simberloff, 1979; Strong et. al., 1979), particularly competition for space between species (Neill, 1977). High local diversity can occur and is often regulated by predation and disturbance (Dayton, 1971; Osman, 1977), or by competition for space in others (Paine, 1974).

Primary space.

Biological interactions and physical conditions can create a complex pattern of patches of sessile animals and algae, interspersed with discrete visible spaces (Lewis, 1976). Free primary space is defined as that bare, unoccupied rock substratum that is available for colonization by algae and invertebrates (Lubchenco and Menge, 1978), and macroscopic species depend directly on it for attachment sites or foraging areas (Paine, 1974). There is always an excess of this unused substratum on the shore (Dayton, 1973), which suggests that space formation is a constant process (Berlow and Navarrete, 1997). Bare patches are constantly created by waves (Paine and Levin, 1981), or the combination of winter freezes and waves dislodging mussels (Brosnan, 1994). This patchiness in variety and abundance of sessile organisms is observed in many rocky intertidal communities (Dayton, 1971; Underwood et. al., 1983), which as a result exhibit substantial spatial and temporal heterogenity in structure and composition (Barry and Dayton, 1991; Connell, 1972). There is great variation in the amount of bare space available from year to year, and even between seasons (Dayton, 1971). Most of the interspecific interactions between sessile organisms in the intertidal boulder zone involve competion for this primary space, which is therefore a potentially limiting resource for this component of this community (Paine, 1977), as well an important factor in preventing dominance of space by one or two species (Osman, 1977; Sousa, 1979a; 1979b).

While both physical and biological disturbances can moderate competitive interactions within the community (Cowen et. al., 1982), the intensity and direction of these interactions are largely governed by underlying physical factors (Hawkins et. al., 1992). Competition for primary space results in clear dominance hierarchies between barnacles and algae, that are variable and dynamic. Small changes in patterns of barnacle/fucoid patches occur naturally (Burrows and Lodge, 1950; Southward, 1953; Lewis, 1970; Hawkins and Hartnoll, 1983a), and are due to both environmental factors and community interactions (Hartnoll and Hawkins, 1985). The intrinsic spatial variation in substratum complexity can have a profound influence on how organisms respond to both environmetal factors and biological interactions (Paine and Levin, 1981).

Habitat complexity and spatial heterogeneity.

The boulder-strewn shores of Anglesey where the research was carried out, bear a mosaic of densely settled barnacles and mussels, interspersed with areas of small stones and shingle, or sometimes sand. The habitat complexity (ie. the material and the number of micro-habitats it contains) and spatial heterogeneity found here, are both important in structuring rocky shore communities (Underwood and Denley 1984; Menge et al. 1985). Their contribution to regulation of diversity and abundance of intertidal animal communities is well documented (see Hawkins et al, 1992).

Intertidal boulder fields can be considered to be mosaics of patches (each boulder) at different stages of succession due to their individual history of disturbance (Osman, 1977; Connell and Keough, 1985). Their habitat structure (microhabitat diversity and frequency) affects the number, type, and abundance of species in the natural asssemblage (Menge and Sutherland, 1976; MacGuinness and Underwood, 1986). The presence of more micro-habitats has a positive effect on the number of species in a community, in other words larger areas tend to have both a greater number and more varied microhabitats (Connor and McCoy, 1979; MacGuinness, 1984a). Refuge microhabitats in particular (pits, cracks and other depressions are often common on larger rocks), can reduce the efficiency of predators (Menge and Lubchenco, 1981), as well as lower physical stress (Emson and Faller-Fritsch, 1976; Kohn and Leviten, 1976; Menge, 1976a), which can lead to greater species diversity (Sousa, 1979a; MacGuiness, 1984b). Remarkably, even different sides of the same boulder can exhibit substantial variation in community structure (Figures 6.1 and 6.2). The particular regime of wave-action (amplitude and frequency, see Underwood, 1980), as well as the vertical dimension of boulders (rocks of different heights have different times of emersion), also effects community structure, as increased exposure to air retards growth of algae (Underwood and Jernakoff, 1984).

Wave exposure and community structure.

There is a great deal of detailed information on how changes in community composition are correlated with different exposure regimes (Dayton, 1971; Menge, 1976a; Lubchenco and Menge, 1978; McQuaid and Branch 1985). Wave action affects primary productivity (Leigh et. al., 1987), predation intensity (Menge 1978a; 1978b; 1983), and the effective competitive abilities of different community members (Menge, 1974).

The effect of Nucella on the community.

Intertidal predators (including *Nucella lapillus*) can have a significant effect on the abundance of a number of sessile prey (Navarrete, 1996). Predation by carnivorous gastropods such as *Nucella lapillus* (found in densities of up to 75/sq.m. in North Wales intertidal boulder fields) can have dramatic effects on the distribution of intertidal organisms (Connell, 1961b; 1970; Dayton, 1971), causing high barnacle mortality. Being selective upon prey and acting patchily in space or time, they can locally disrupt the pattern of ecological succession (Spight, 1967; Addicott, 1974; Caswell, 1978). The importance of a predator (its impact on the community), is dependent upon its intrinsic characteristics, those of the prey (e.g. escape in growth-refuge in size) and the state of the environment (e.g. the ability to drill and consume a barnacle related to submergence time) (Menge, 1978b). Most major patterns of distribution, abundance, and local species richness can be explained by mortality from predation or competition (Menge, 1978a). Community structure, shading, wave-action and other physical differences can also affect the predation rate, often confounding the measurement of the direct impact of a predator upon the intertidal community (Garry and Levings, 1981). In addition, environmental stress may operate indirectly on prey organisms via the predator, as it can be more localised than its prey (Lewis, 1976). A predator that preferentially consumes a prey species that itself is a competitive dominant in sessile interactions (Paine, 1969a), controls the basic pattern and structure of the community (Paine, 1969b). By removing mussels, organisms that readily outcompete fucoid algae, *Nucella lapillus* on the North-Eastern Pacific may be considered as a keystone organism in certain conditions (Menge, 1976b).

Research rationale.

Competition and predation in intertidal communities has been examined by many workers for the North-eastern United States (Menge, 1976b; Lubchenco and Menge, 1978), the North-western United States (Paine, 1966; Dayton, 1971), Japan (Hoshiai, 1964), and New Zealand (Luckens, 1970; Paine, 1971). Although few studies have attempted to quantify both the direct and indirect interactions that occur between pairs of species, and how they influence the whole community. Experimental field work on species interactions and patterns of community structure has been limited in Britain and the Europe (Hawkins et. al., 1992), especially that related to the importance of dogwhelks in relation to sessile species assemblages.

Experimental manipulation (selective removal and exclusion of different species and species combinations) is a powerful tool for identifying the factors responsible for community pattern (Nowell and Jumars, 1984; Castilla and Paine, 1987). A large majority of intertidal organisms that have been studied experimentally have been sessile (algae, barnacles), or relatively sedentary (limpets, gastropods), (see Luckins, 1970; Dayton, 1971; Harger, 1971; Woodin, 1974), and as a result experimental manipulations can be done in a relatively small area and be replicated easily in space and time (Underwood and Chapman, 1992). The distribution and abundance of species within an intertidal community change markedly in relation to spatial and temporal variation effects, requiring accurate *in situ* data on comunity interactions from controlled experimental manipulation (see Conell, 1974). One major experimental procedure used to elucidate the role of predators is the simple manual removal of all predators from an area at regular intervals, with the aim of keeping their density at or near zero (Paine, 1966; 1971; 1974; Dayton, 1971; Garrity and Levings, 1981).

6.2. METHODS.

Few studies have been repeated at sufficiently varied spatial or temporal scales (Foster, 1990), for any conclusion to be reached about the general effects of predation and competition in the intertidal community (Underwood, 1992). Most comparisons between different intertidal sites (and even between different habitats within a shore) have only been made qualitatively, with no attempt to quantify the differences (Patterson et al., 1986). With this is mind I set up multiple replicates of the exclusion experiments at different tidal levels within each of six shores that themselves were varied in degree of wave exposure. This experiment was also repeated at different times on one of the shores (Red Wharf Bay) to look into the temporal variation in community effects of predation by *Nucella lapillus*. This study was designed to investigate the effects of the dogwhelk *Nucella lapillus* and the limpet *Patella vulgata* upon the composition and abundance of sessile organisms within intertidal boulder communities, specifically, to determine if these species actually influence sessile community structure and population dynamics in the study region (North Wales).

Hypotheses.

1. The structure of the rocky intertidal community in North Wales varies along the wave-exposure gradient.
2. Predators (*Nucella lapillus*) and herbivores (*Patella vulgata*) have important influences on the patterns of space occupancy and relative abundances of species in the sessile assemblages of the intertidal zone.
3. The effects of these consumers vary in relation to shore level within each shore, and also vary between different shores.

Experimental procedure.

Experimental manipulation was undertaken to investigate the role of dogwhelks and limpets upon population dynamics, and in the organisation of intertidal boulder communities, in particular to measure the effect of *Nucella lapillus* predation in the presence and absence of limpets, the influence of both species upon barnacle recruitment and survival, algal cover, and mussel dominance. Four sites, each containing 4x4 rows of boulders were used for setting up the experiment on community effects of herbivore and predator exclusion (a total of 64 boulders) at Red Wharf Bay in April 96. Sites A and D; sites B and C were contiguous and paired units served as replicates. Sample units were placed in a randomized-stratified block design containing four treatments located at four sequential tidal heights. Within each row, one of four treatments: 1-remove *Nucella lapillus*; 2-remove *Patella vulgata*; 3 - remove both; and 4 - control, were assigned to boulders at each of four tidal heights. The appropriate organisms were removed every 7 days from all experimental units.

As well as the usual manipulation of the presence of the predators (see Connell, 1972), limpets were also removed from some plots to give four factors: presence or absence of 'Predators' and presence or absence of 'Limpets'. This allowed a test of spatial variation as the factor 'Blocks' which was nested in the interaction of 'Predators' and 'Limpets'. By comparison with undisturbed control areas, the effects of removal of the predator and the herbivore may, in theory, be measured. The total number of whelks and limpets removed and found in controls were also counted, as well as the apparent diet of whelks at these times (Fairweather, 1985). Coverage of sessile organisms was concurrently monitored. Namely: barnacles (mainly *Semibalanus balanoides*), mussels (*Mytilus edulis*) and green, brown and red algae (*Enteromorpha*, fucoids and *Chondrus*). Densities of *Gibbula cineraria*, *Littorina littorea*, *Littorina saxatilis* species complex, *Littorina obtusata*, as well as the anemone *Actinia equina,* were also followed for the duration of the experiment.

In September 96, manipulations of the same experimental design as series A were started: a further two boulder sites (each of 16 units) at each of six shores (sites) varying from the very sheltered to the very exposed (with regard to wave-action) were initiated, namely: Menai Bridge, Trwyn y Penrhyn, Llanfairfechan, Red Wharf Bay, Porth Nobla, and Porth Defaid respectively. In addition to the boulder experiments I carried out similar exclusions at the same time on large non-isolated vertical rock faces at Porth Nobla and Porth Defaid (again two replicate blocks of 16 units each). All experiments were continued until September 1998. Series B comprised a total of 256 experimental units.

Removal and monitoring of dogwhelk and limpet populations.

Due to the subsequent movements of dogwhelks and limpets, frequent monitoring and removal from all treatments was required. In addition 'buffer' zones were created around the boulders in all experimental areas (see Fairweather et. al., 1984), and any *Nucella lapillus* or *Patella vulgata* found within the zone, were removed at the same time intervals as boulder exclusions were carried out.

Sessile organisms.

The abundance of sessile organisms namely: barnacles, mussels, and algae, were determined by taking colour photographic prints of the treatment units. These were then viewed under a binocular microscope to determine cover expressed as percentage area cover of primary space using the random dot technique reported by Connell (1970) and Dayton (1971). Alternatively the camera was used to take 35-mm slides of each boulder, later projected onto a screen and using randomly placed dots superimposed on the slide (McGuiness and Underwood, 1986). When bad weather prevented photography, percent cover was estimated directly in the field using a random dot (100 permanent dots) overlay drawn on an overhead transparancy sheet, that was placed on the substratum and percentage coverage was estimated by counting the number of dots whose projection hits a particular species (Lubchenco and Menge, 1978).

To evaluate the direct effect of *Nucella lapillus* upon barnacle population dynamics, 100 points were randomly selected on each side of each boulder, and the number of dead and alive barnacles were recorded, again at the interval of two months, in randomly selected subplots (see Richardson and Brown, 1990), permanently marked on the rock, to allow accurate determination of survival. A second method of estimation of sessile organisms used, was the point quadrat method (Goodall, 1952; Greig-Smith, 1964; Lubchenco et. al., 1984; Underwood, 1980). Coverage was obtained by the use of subdivided (0.25 m^2) quadrats (Jones et. al., 1980), divided into 25 equal squares by string strung across the frame, forming a grid (Dethier et. al., 1993). The coverage of individual species was determined by placing perspex sheets over these 10cm x 10cm squares, tracing the outline of the individual or groups of individuals and determining area coverage later in the laboratory, by placing the transparency sheets over graph paper. Five full quadrats (equal to1.25 m^2 per boulder) were examined at random with equal weighting given to each side of the boulder (seaward, landward, right side, left side and top). N.b all boulders used in this study had a total of five accessible sides (and one surface underneath). This type of percent cover data is bimodally distributed and violates the assumption of a normally distributed "population" (Lubchenco and Menge, 1978). Therefore for statistical analysis, these results were transformed using the arcsine square root transformation (an angular transformation) to normalise the distribution of percentage (Sokal and Rohlf, 1981).

To make certain that the study units were representative of shore areas in which they were placed concurrrent background checks were carried out. Ten randomly positioned, 0.25 m^2 quadrats were placed over non-experimental boulders at each level. From the data obtained in this manner, I estimated the coverage of each prey species and algae in the area surrounding the study units but at the same tidal level.

Barnacle impact upon dogwhelk predation.

Interactions between prey (barnacles) and predator (whelks) can be investigated by manipulating the recruitment of barnacles, which then affects the intensity of predation by whelks upon them (Fairweather, 1988d). This experimentation involved removing visible recruits (barnacles) to see the impact upon the community structure and dogwhelks in particular, and was carried out on all six shores. Four treatments were manipulated to give the following approximate barnacle densities. Treatment 1: normal barnacle density; treatment 2: 80% of normal; treatment 3: 60% of normal; treatment 4: 40% of normal.

Statistical analysis.

The target variables asinbarn, asindeadbarn, asinalga, asinmuss and asinbare (the transformed variables of coverage) were examined for normality within the factors of treatment and shore using a normal probability plot (Q-Q plot), and the Kolmogorov-Smirnov and Shapiro-Wilk's tests for normality. Levene's test was used to determine homogeneity of variances of these dependent variables across factor groups. All data sets were normally distributed and exhibited homogeneity of variances except for samples from both boulder fields and vertical surfaces at Porth Defaid, which were not normally distributed. As a result, data from these locations were analysed by the non-parametric Kruskal-Wallis H test in addition to GLM univariate, multivariate and repeated measures analyses, that were used on all shores to examine significant differences in the dependent variables. The determination of the Pearson correlation coefficient with associated F-test, were carried out upon the regression of *Nucella* foraging numbers upon barnacle densities.

Data were obtained from the six shores mentioned in the methods: shore S: S1 - Menai Bridge; S2 - Trwyn y Penrhyn; S3 - Llanfairfechan; S4 - Red Wharf Bay A (experiment started in April 96); S5 - Red Wharf Bay B (experiment started in September 96); S6 - Porth Nobla; S7 - Porth Defaid.

Data on the target variables asinbarn, asindeadbarn, asinalga, asinmuss and asinbare (the transformed variables of coverage), were examined with respect to treatment T: T1 - removal of *Nucella*; T2 - removal of *Patella*; T3 - removal of both *Nucella and Patella*; T4 - control. In Repeated measures GLM the variation in these dependent variables was investigated over the duration of the experiment from September 1996 to September 1998. Month M: M1- September 1996; M2 - November 96; M3 - January 1997; M4 - March 97; M5 - May 97; M6 - July 97; M7 - September 97; M8 - November - 97; M9 - January 1998; M10 - March 98; M11 - May 98; M12 - July 98; M13 - September 98.

Repeated measures GLM.

This method provided analysis of variance for the repeated measurement of relevant dependent variables being made several times on each boulder, testing differences on between subject factors such as treatment and on within subject factors such as month. If differences were observed among the means then pairwise multiple comparisons were made to determine which means differed by use of the Bonferroni test, where the observed significance level is adjusted for the fact that multiple comparisons are being made. Assumptions (hypotheses) were tested at significance level of 0.05 (ie. confidence intervals are 95%).

6.3. RESULTS.

6.31. Boulder fields.

6.311. Preliminary investigation on the influence of boulder aspect (different sides of the boulder) upon the percent coverage of sessile organisms on boulder fields on the six study shores as shown in Figure 6.1 (a comparison of the six shores), and Figure 6.2 (a comparison of starting times for the exclusion). Key for Aspect. aspect 1: seaward side; aspect 2: right side, clockwise from aspect 1; aspect 3: landward side; aspect 4: clockwise from aspect 3; aspect 5: top of boulder.

Aspect and barnacle coverage.
The percentage coverage of barnacles was significantly influenced by aspect at Llanfairfechan (GLM. F=12.553 P=<0.001), Porth Nobla (GLM. F=2.733 P=0.031), and Porth Defaid (GLM. F=5.706 P=<0.001), but not significantly influenced by aspect at Menai Bridge (GLM. F=0.301 P=0.877), Trwyn y Penrhyn (GLM. F=0.335 P=0.840), Red Wharf Bay A (GLM. F=0.330 P=0.857), and Red Wharf Bay B (GLM. F=0.155 P=0.960).

Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between the tops of boulders (aspect 5) and other aspects at Llanfairfechan: aspects 1-5 (P=<0.001), aspects 2-5 (P=<0.001), aspects 3-5 (P=<0.001), and aspects 4-5 (P=<0.001); at Porth Nobla: for aspects 1-5 (P=0.035); Porth Defaid for aspects 1-5 (P=0.007), aspects 2-5 (P=0.002, aspects 3-5 (P=0.009), and aspects 4-5 (P=0.001).

Aspect and algal coverage.
The percentage coverage of algae was found to be significantly influenced by aspect at Porth Nobla (GLM. F=5.351 P=<0.001), and Porth Defaid (GLM. F=7.158 P=<0.001), but not significantly influenced by aspect at Menai Bridge (GLM. F=1.833 P=0.126), Trwyn y Penrhyn (GLM. F=0.234 P=0.919), Red Wharf Bay A (GLM. F=0.877 P=0.479), and Red Wharf Bay B (GLM. F=0.323 P=0.862).

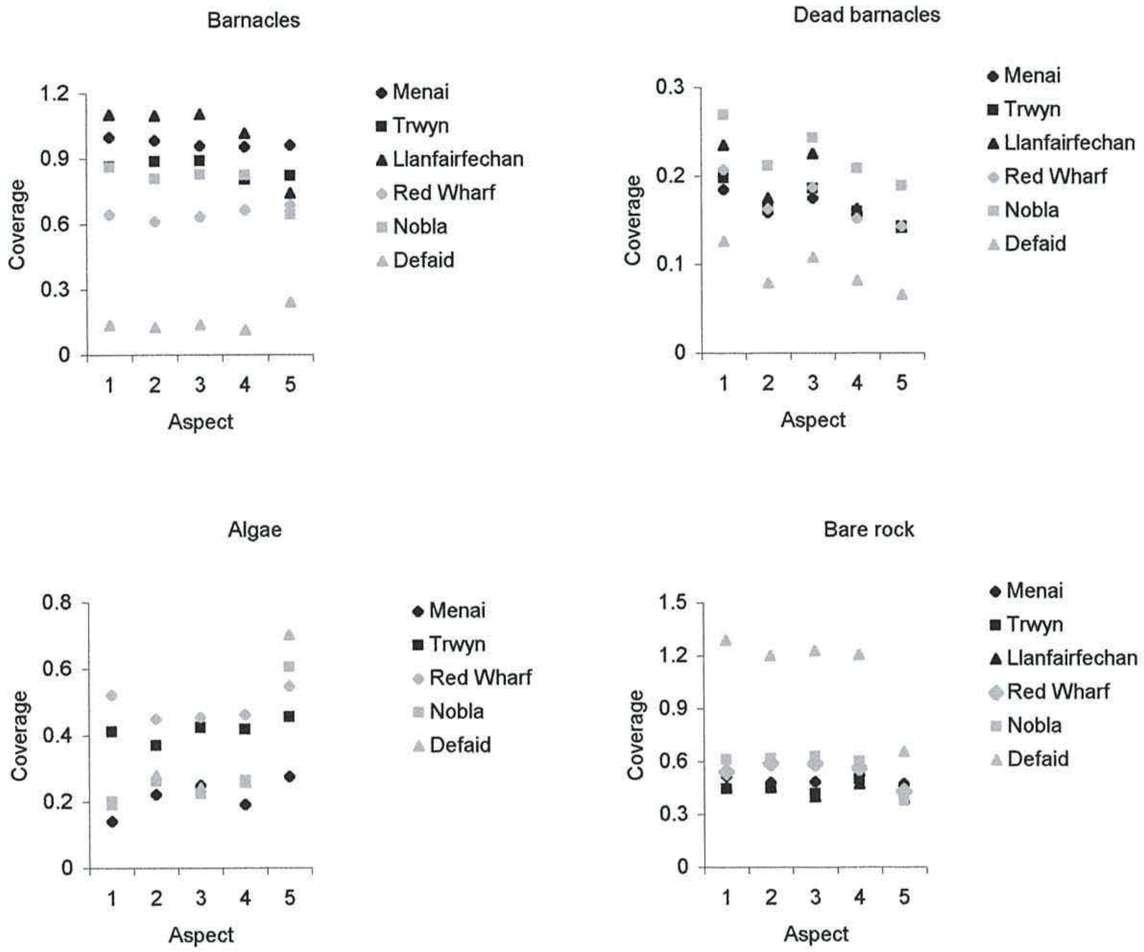


Figure 6.1. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock between different aspects (sides) of boulder. 1 - seaward side. 2 - right side. 3 - landward side. 4 - left side. 5 - top of boulder.

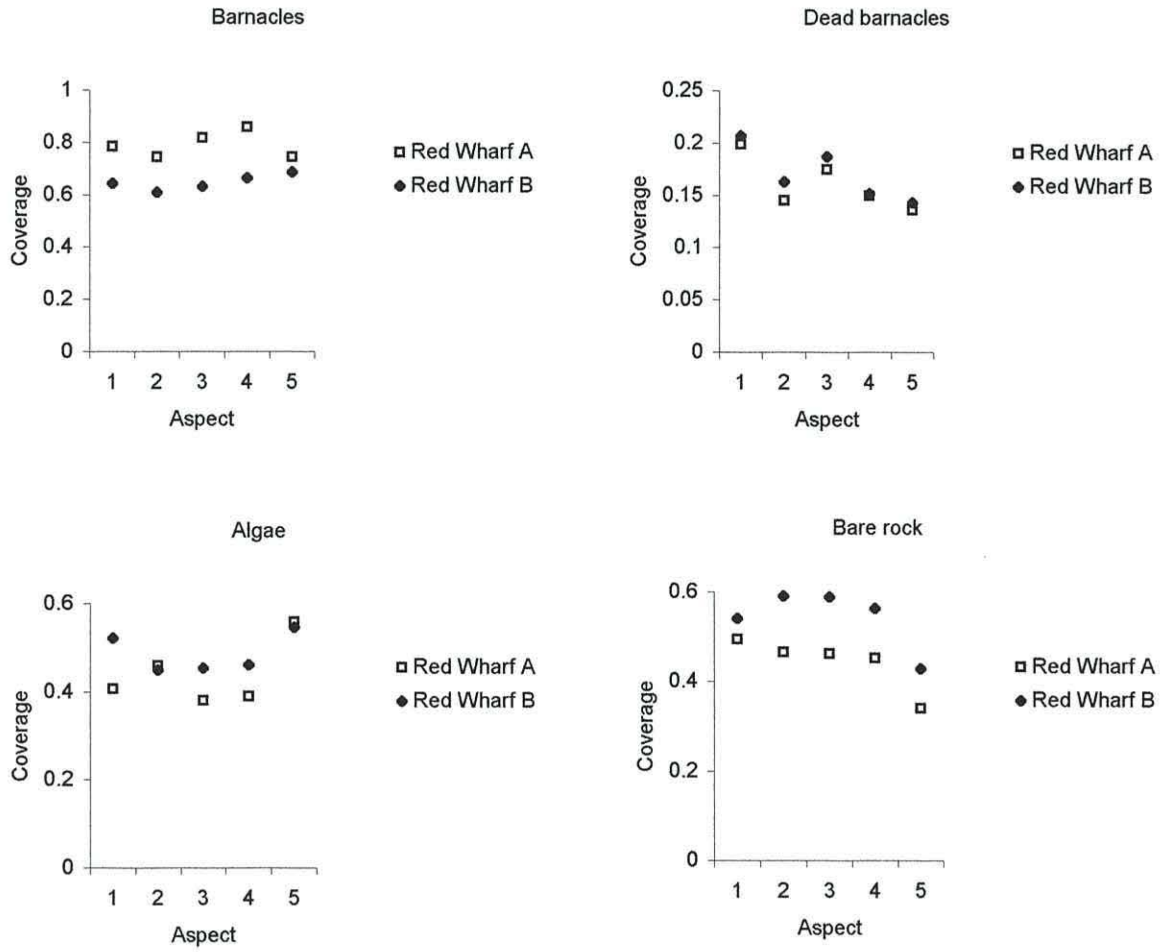


Figure 6.2. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock. A comparison of Red Wharf Bay A (started in April) and Red Wharf B (started in September on different aspects (sides) of the boulder.

Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between the tops of boulders (aspect 5) and other aspects at Porth Nobla: aspects 1-5 (P=0.001), aspects 2-5 (P=0.009), aspects 3-5 (P=0.003), and aspects 4-5 (P=0.011);and at Porth Defaid: for aspects 1-5 (P=<0.001), aspects 2-5 (P=0.002), aspects 3-5 (P=0.001), and aspects 4-5 (P=0.001).

At Llanfairfechan where no algal growth was present, even after exclusion, the coverage of mussels was found to be significantly influenced by aspect (GLM. F=7.416 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in mussel coverage between aspects 1-5 (P=<0.001), aspects 2-5 (P=<0.001), aspects 3-5 (P=<0.001), and aspects 4-5 (P=<0.001).

Aspect and percentage of free space.

The percentage of bare rock substratum was found to be significantly influenced by aspect at Red Wharf Bay A (GLM. F=2.936 P=0.023), Red Wharf Bay B (GLM. F=3.249 P=0.014), Porth Nobla (GLM. F=14.80 P=<0.001) and Porth Defaid (GLM. F=17.669 P=<0.001), but not significantly influenced by aspect at Menai Bridge (GLM. F=0.497 P=0.738), Trwyn y Penrhyn (GLM. F=0.847 P=0.498), and Llanfairfechan (GLM. F=0.918 P=0.458).

Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in free rock space at Red Wharf Bay A: aspects 2-5 (P=0.037), and aspects 3-5 (P=0.042); at Red Wharf Bay B, for aspects 2-5 (P=0.023), and aspects 3-5 (P=0.028); at Porth Nobla: for aspects 1-5 (P=<0.001), aspects 2-5 (P=<0.001), aspects 3-5 (P=<0.001), and aspects 4-5 (P=<0.001), and for Porth Defaid, for aspects 1-5 (P=<0.001), aspects 2-5 (P=<0.001), aspects 3-5 (P=<0.001), and aspects 4-5 (P=<0.001).

Since the only significant differences in aspect were observed between tops of boulders in relation to other surfaces, the tops of boulders were alone excluded from all calculations and analyses for all remaining experimentation in this Chapter.

6.312. Removal experiments. The following sections 6.313 to 6.318 inclusive, all apply to removals carried out on boulder fields (see Figures 6.3, 6.4, 6.5, 6.6 for monthly changes in coverage, and Figure 6.7 for comparison of shores); sections 6.321 to 6.325 concern removal experiments performed on single but relatively large, vertical surfaces; sections 6.331 to 6.335 are comparisons of coverage between the boulder fields and the vertical rock formations. The trends in differences between treatments are depicted in Figure 6.8; a summary of boulder coverage for the two year period in Figure 6.9. Key for treatment: Treatment 1: *Nucella* removal, Treatment 2: *Patella* removal, Treatment 3: *Nucella* and *Patella* removal, Treatment 4: control. Month 1- month 13, represent September 1996 to September 1998 inclusive at two monthly intervals.

General observations on the impact of the exclusion of *Nucella lapillus* and *Patella vulgata*. Barnacles: there was no difference between the four treatments on total barnacle coverage, on any of the six shores within the first six months. The only significant result was in the coverage of cyprid and metamorphosed larvae (not graphed) on Trwyn y Penrhyn which was higher in the two treatments where *Patella,* and both *Patella* and *Nucella* respectively were removed. A similar effect had been seen on other shores at an earlier stage of the experimental removals. However from May 1997, to the end of the removals (September 1998), periodic differences in barnacle coverage were seen between treatments on most shores.

Dead barnacles: the removal of *Nucella lapillus* on a regular basis resulted in significant reductions in barnacle mortality (as measured by numbers of empty shells) within six months of the initiation of expermental manipulations on all six shores.

Algae: within 5-6 months on moderately exposed and exposed shores, significantly denser algal coverage was observed within both treatments that involved *Patella* removal. This expanded canopy persisted for over two years despite large seasonal fluctuations. Following the removal of *Patella* from specified boulder units (and to a lesser extent vertical surfaces), algal types colonised the rock surface in a set orderr of succession: firstly green, then brown, and then red, irrespective of height on the shore, wave-exposure, and timing of initial exclusion. This series of events did

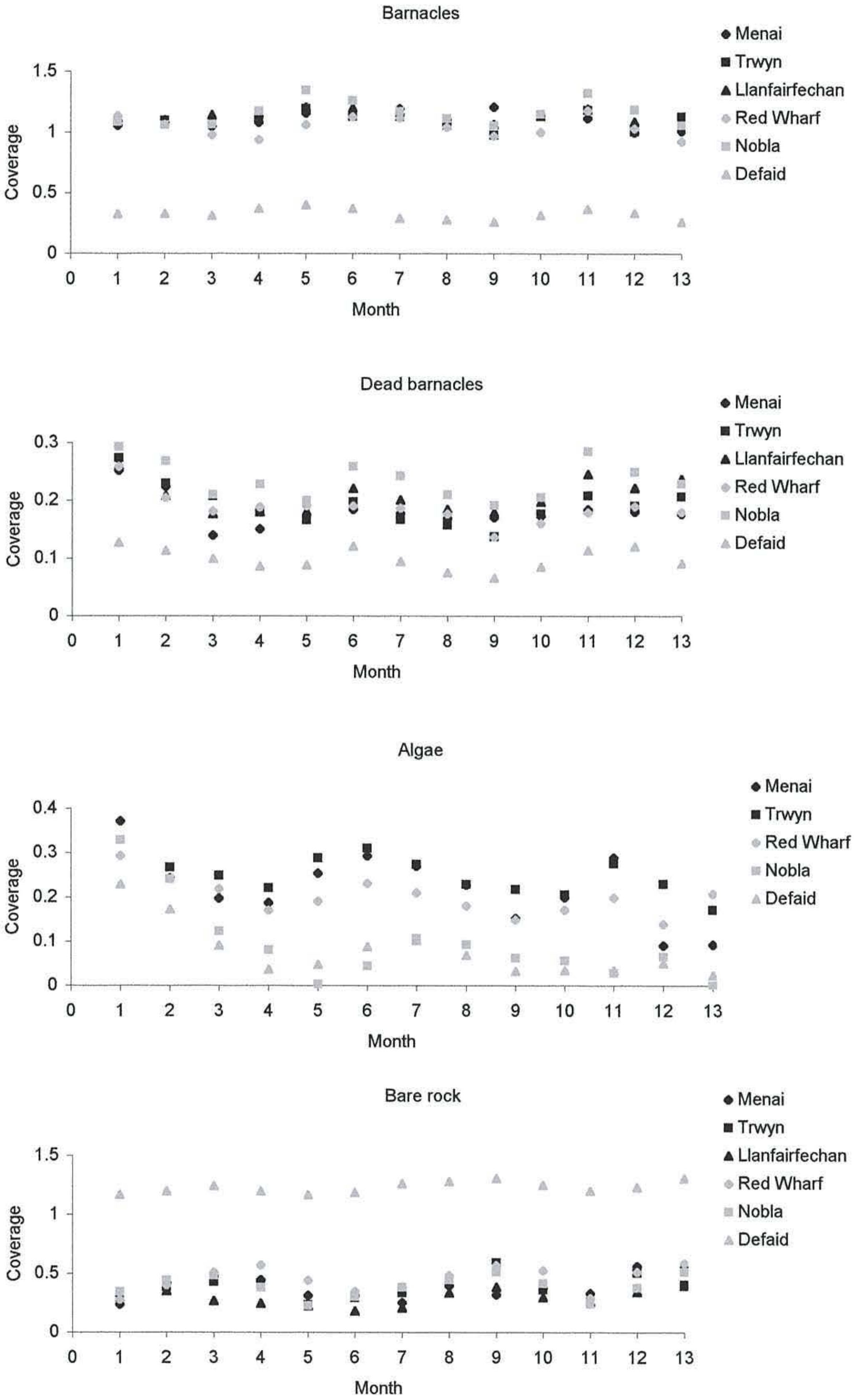


Figure 6.3. Bi-monthly changes in percent coverage(arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 1(*Nucella* removal) on different shores.

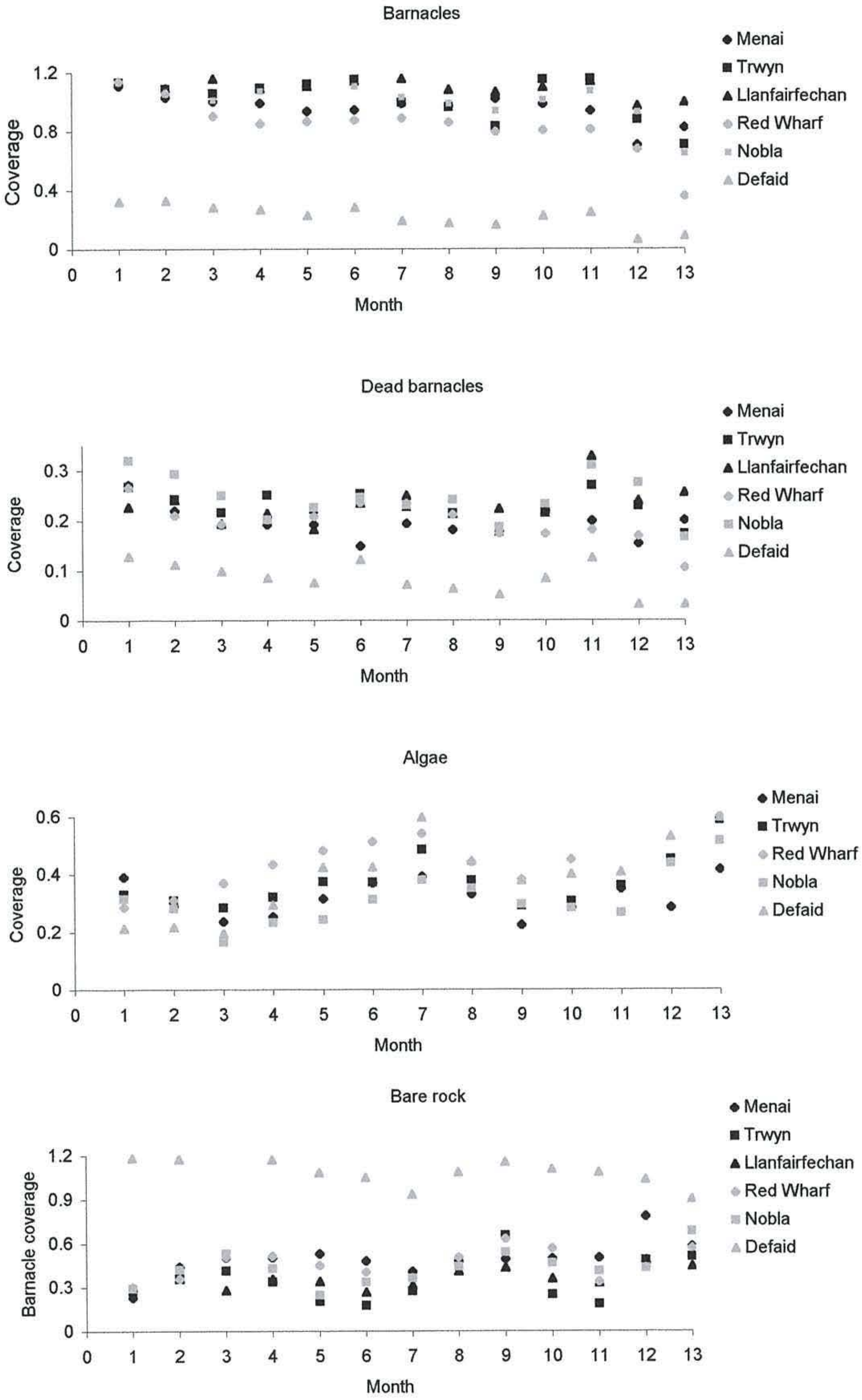


Figure 6.4. Bi-monthly changes in percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 2 (*Patella* removal) on different shores.

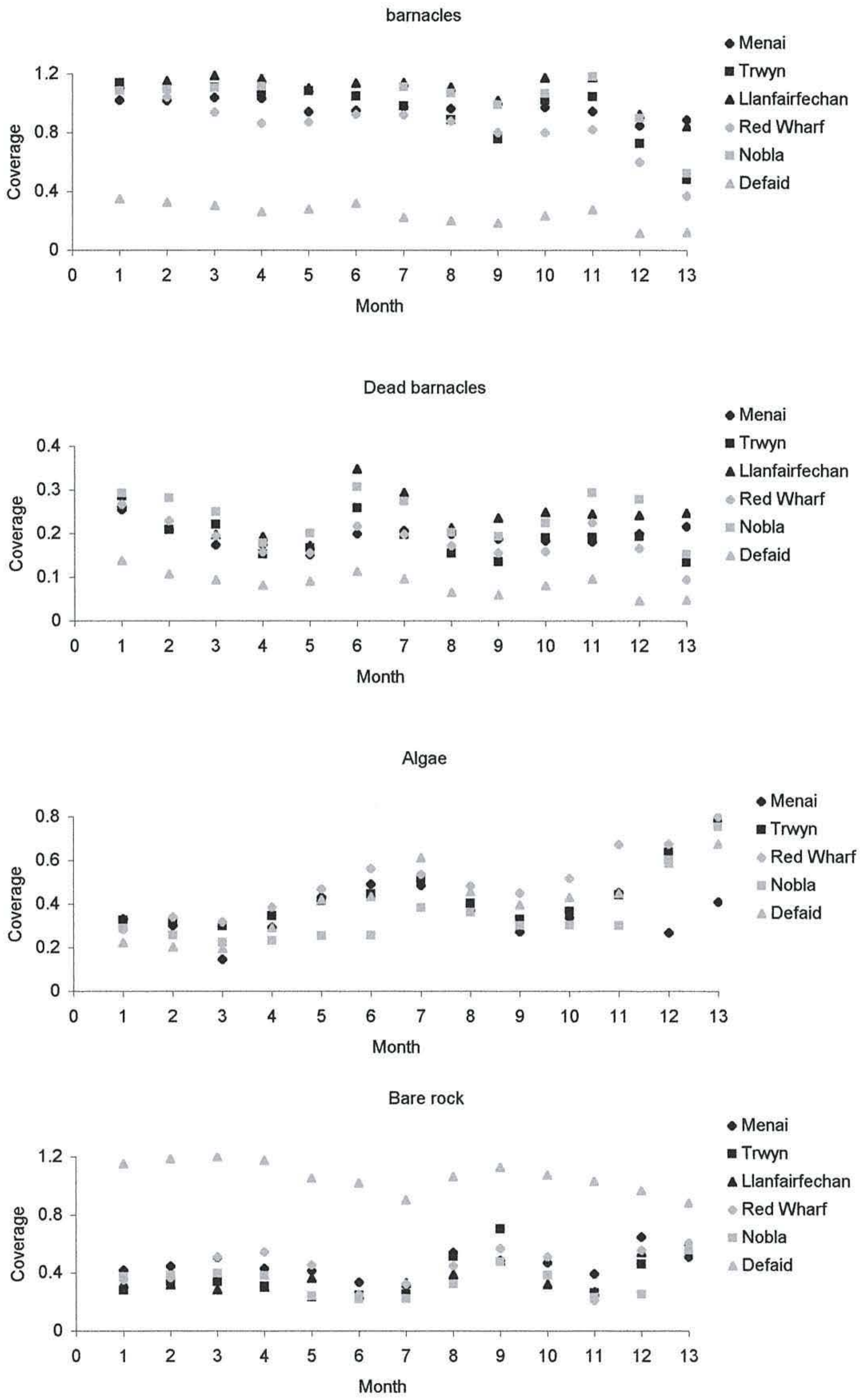


Figure 6.5. Bi-monthly changes in percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 3 (*Nucella* and *Patella* removal) on different shores.

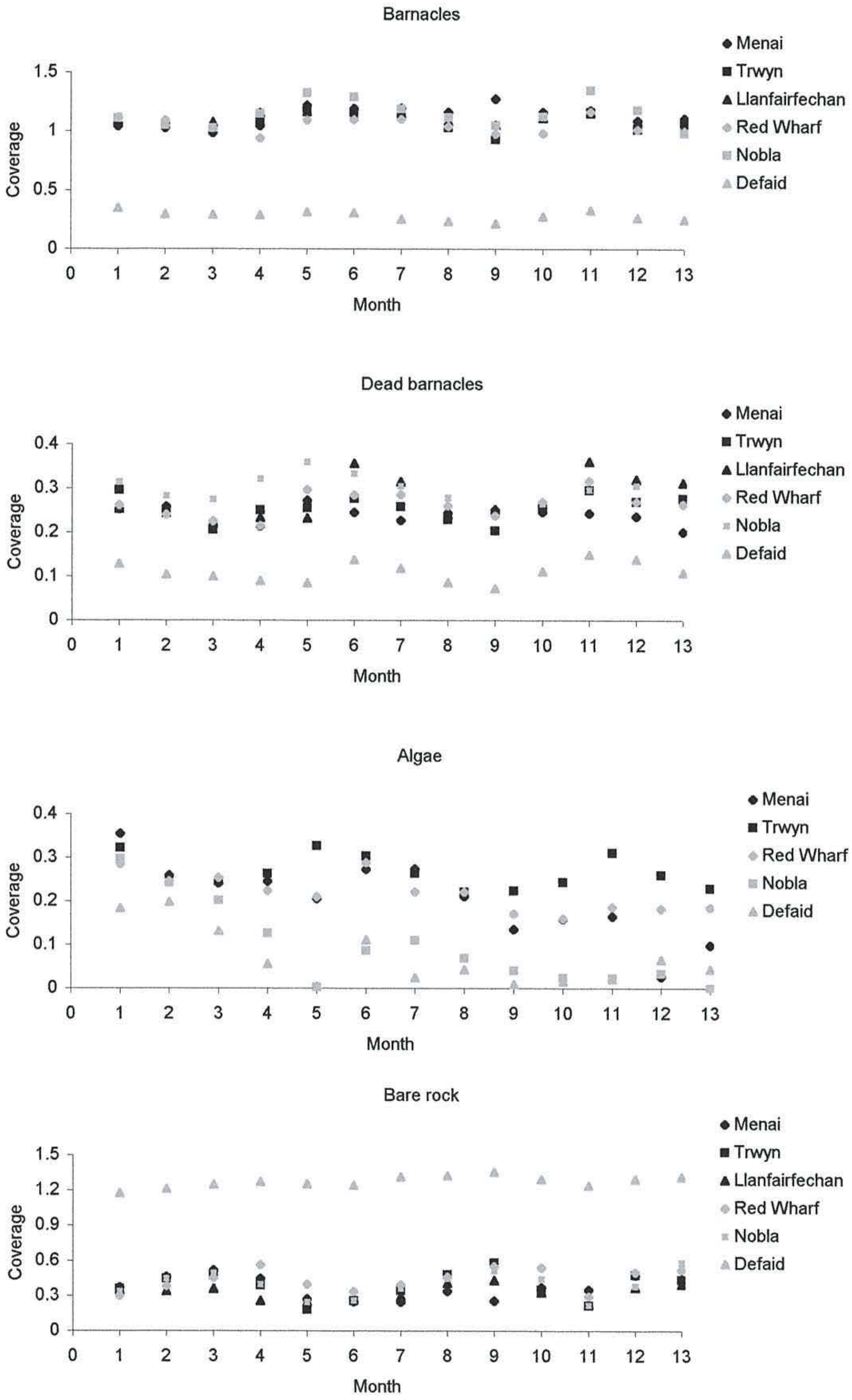


Figure 6.6. Bi-monthly changes in percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 4 (control) on different shores.

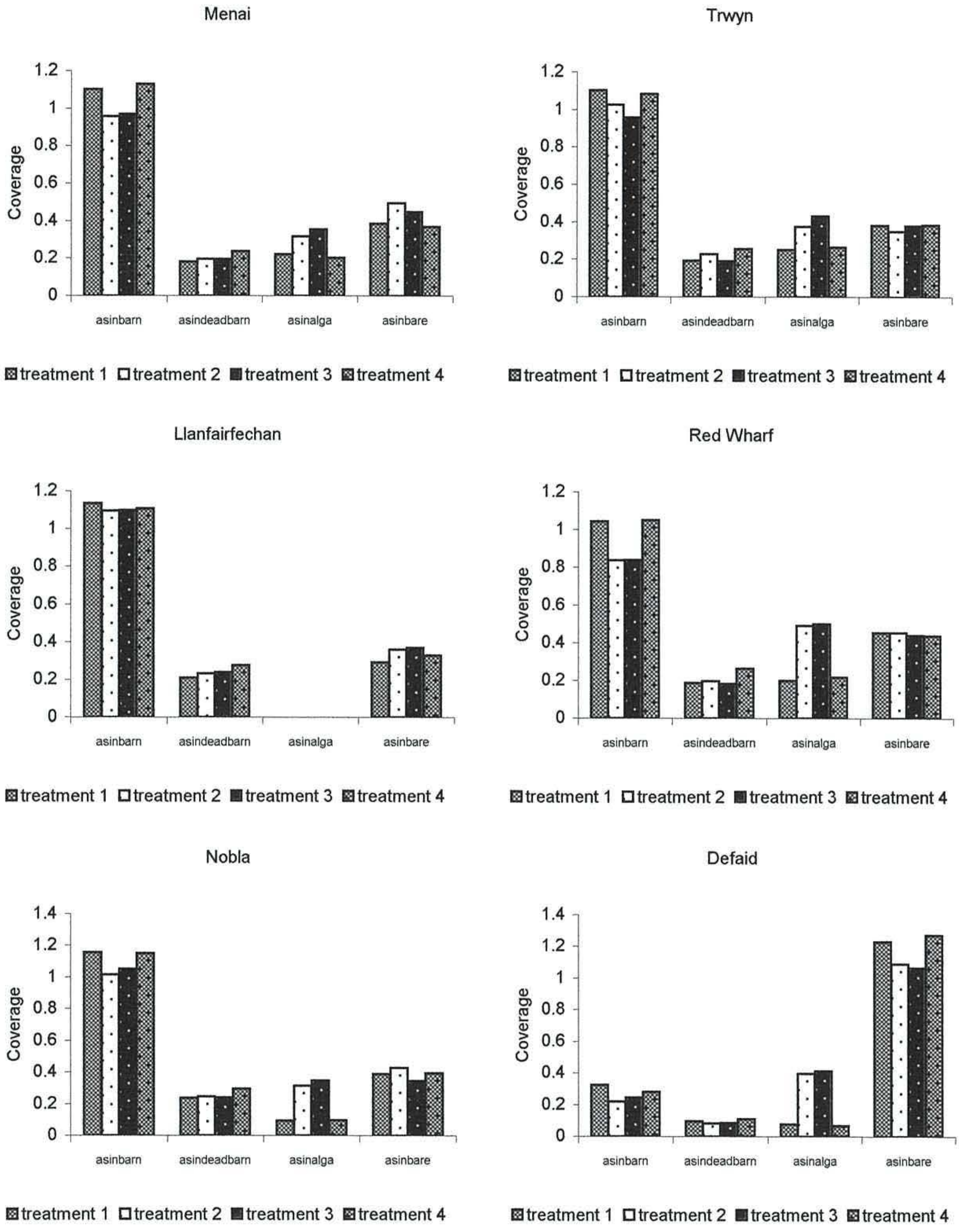


Figure 6.7. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock. A comparison of the effect of treatment on different shores.

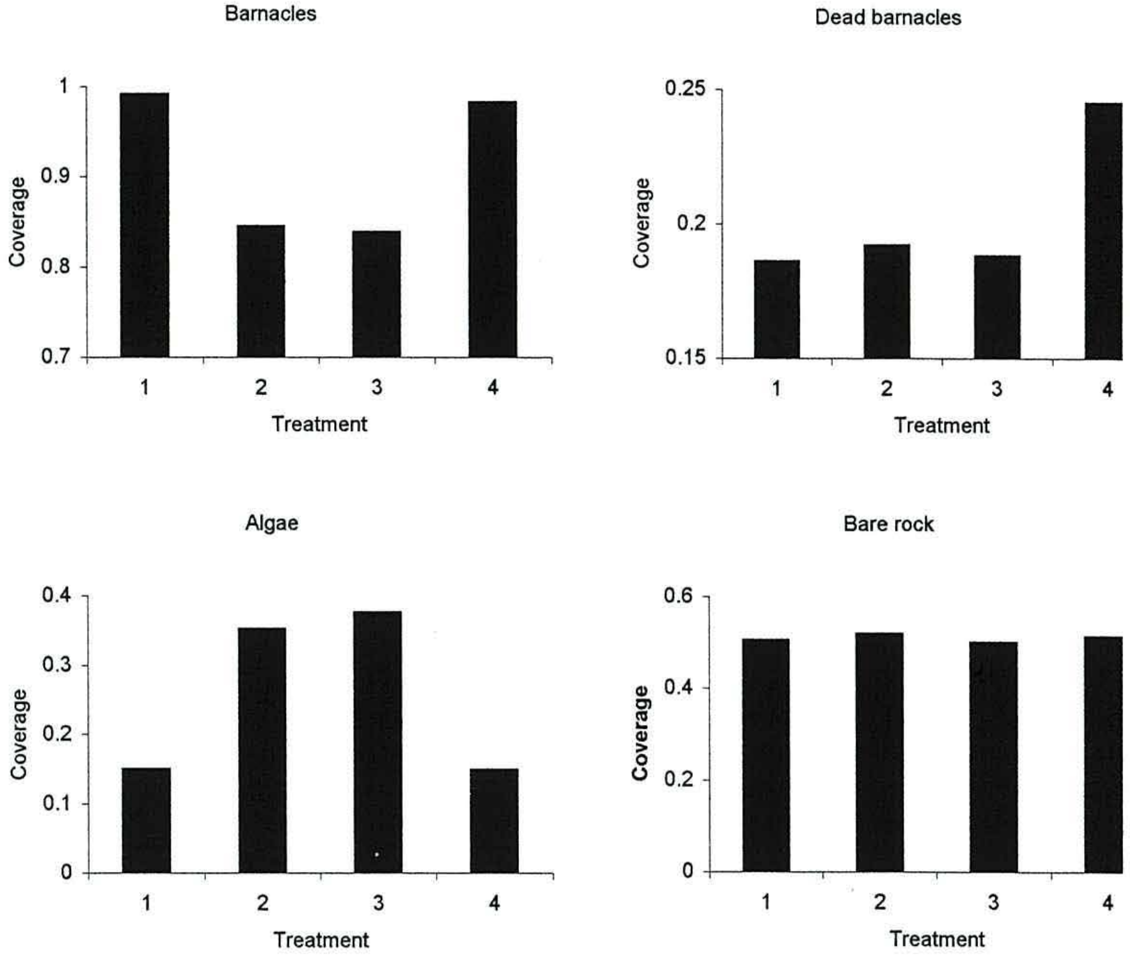


Figure 6.8. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock between different treatments (pooled data from all six study shores).

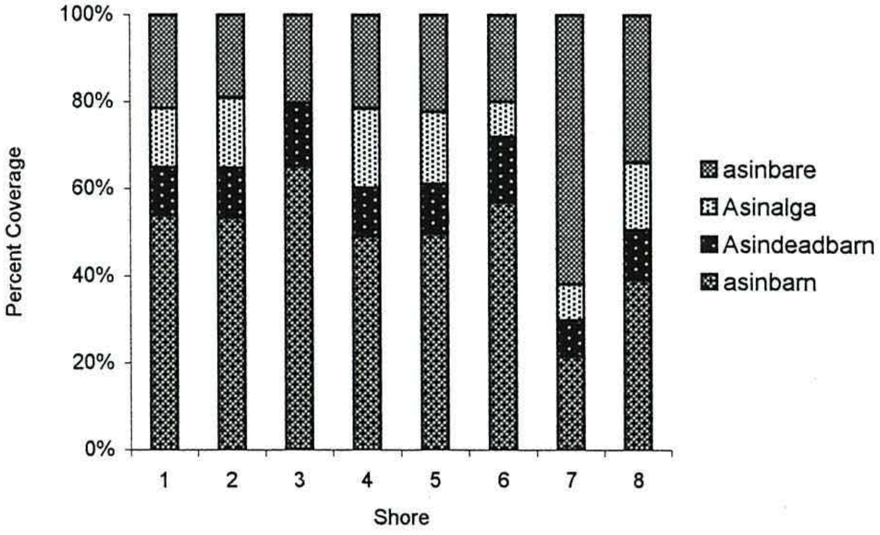


Figure 6.9. Summary of boulder coverage (mean of two years data) for the following: 1 - Menai Bridge. 2 - Trwyn y Penrhyn. 3 - Llanfairfechan. 4 - Red Wharf A. 5 - Red Wharf B. 6 - Porth Nobla. 7 - Porth Defaid. 8 - Red Wharf small boulders.

take place at different rates in different locations (different shore levels and different shores), and may be partly reversible.

Mussels: only found on Red Wharf Bay and Llanfairfechan. Only the control treatment at Llanfairfechan location showed any significant higher mussel bed coverage. Earlier on at Red Wharf Bay, experiments had higher mussel coverage under control conditions, but the differences between this and the other treatments became insignificant later on in the experiment.

Bare substratum surface: there was no significant difference in the amount of available rock substrate between treatments on any of the shores studied apart from Porth Defaid where the amount of bare rock became depleted in treatments 2 and 3 (related to *Patella* exclusions).

In addition to the measurement of substratum coverage by sessile organisms, repeated counts of a number of herbivorous gastopods (mainly littorinids) within treatments on the same boulder fields were taken. *Littorina littorea* - There were differences in the abundances of this species, particularly on sheltered shores where *Patella* removal and removal of both *Patella* and *Nucella* treatments resulted in population numbers of *Littorina littorea* of 100-450 % (Menai Bridge) and 63-89 % (Trwyn Y Penrhyn) higher than controls, depending on season. At Red Wharf Bay *Nucella* removal and removal of both herbivore and predator resulted in *L.littorea* populations that were 2.8 - 339 % above controls respectively. Conversely on the other three experimental shores number of *L.littorea* were higher in control areas, namely: 23-28% higher (Llanfairfechan); 42-63 % higher (Porth Nobla); and 28-97 % greater (Porth Defaid). *Littorina saxatilis* species complex: at Llanfairfechan all treatments showed 21-782 % increases above control. More exposed shores showed controls higher populations in controls - 27-82 % higher (Red Wharf Bay), 20-78 % higher (Porth Nobla), and 45-110 %greater (Porth Defaid). *Littorina obtusata* : density of this species was related directly to algal coverage, and independent of treatment, there being no significant differences between treatments and controls. *Gibbula cineraria:* topshells were found at the most sheltered (Menai Bridge) and most exposed shores (Porth Nobla and Porth Defaid). There were no discernible difference in numbers of topshells between treatments at these locations.

6.313. Barnacle coverage.

Menai Bridge.

The coverage of barnacles was found to be significantly influenced by treatment (GLM. F=35.395 P=0.002), being consistently higher in treatments 1 and 4 from from May 97 (that is some six months after iniation of *Nucella* and *Patella* removals). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=0.015), treatments 1-3 (P=0.020), treatments 2-4 (P=0.007) and treatments 3-4 (P=0.010). However significant differences in coverage of barnacles between treatments were only apparent at certain times of the year (Table 6.1).

Table 6.1. Results of ANOVA (GLM repeated measures) showing significant differences in barnacle coverage between specified treatments at Menai Bridge.

	May 97	July 97	January 98	March 98	May 98	July 98	Sept. 98
Treatments	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*
1-2	0.221 0.047	0.189 0.030		0.153 0.049	0.179 0.017	0.292 0.005	0.186<0.001
1-3		0.181 0.035		0.165 0.037	0.174 0.019		0.124 0.001
2-4	0.285 0.019	0.247 0.011	0.256 0.050	0.176 0.030	0.239 0.006	0.387 0.002	0.284<0.001
3-4	0.278 0.020	0.239 0.012	0.278 0.037	0.189 0.023	0.233 0.006	0.244 0.011	0.222<0.001

Data presented are F-values (F), with probabilities (P) which are all significant values.

No significant differences between treatments 1 and 4, or between treatments 2 and 3 were seen at any time during the manipulation.

Trwyn y Penrhyn.

The coverage of barnacles was significantly influenced by treatment (GLM. F=15.444 P=0.012), tending to be higher in treatments 1 and 4 from from May 1997 (that is some six months after initiation of *Nucella* and *Patella* removals), to the end of the manipulation experiment. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage only between treatments 1-3 (P=0.021), and treatments 3-4 (P=0.035). Significant differences in coverage of barnacles between particular treatments were only clearly apparent by the end of the experiment in September 1998: between treatments 1-2 (GLM. F=0.421 P=<0.001), between treatments 1-3 (GLM. F=0.647 P=<0.001), between treatments 2-3 (GLM. F=0.226 P=0.002), between treatments 2-4 (GLM. F=0.312 P=<0.001), and treatments 3-4 (GLM. F=0.588 P=<0.001).

Llanfairfechan.

The coverage of barnacles was found not to be significantly influenced by treatment (GLM. F=0.477 P=0.716). The only significant differences in coverage of barnacles between treatments were observed in September 1998 at the end of the experiment: between treatments 1-3 (GLM. F=0.239 P=0.008), between treatments 2-3 (GLM. F=0.156 P=0.041), and treatments 3-4 (GLM. F=0.193 P=0.019).

Red Wharf Bay (A).

Removals were started five months earlier than all other experimental blocks.

The coverage of barnacles was found to be significantly influenced by treatment (GLM. F=141.570 P=<0.001), being consistently higher in treatments 1 and 4 from September 96 (that is some five months after initiation of *Nucella* and *Patella* removals). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=<0.001), treatments 1-3 (P=<0.001), treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001). Significant differences in coverage of barnacles between treatments were apparent from this time and throughout the duration of the experiment (Table 6.2).

Table 6.2. Results of ANOVA (GLM repeated measures) showing significant differences in barnacle coverage between specified treatments at Red Wharf Bay (A).

	Sept. 96		Nov. 96		January 97		March 97		May 97		July 97		Sept. 97	
Treatments	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
1-2			0.106	0.048	0.104	0.048	0.152	0.006	0.146	0.028	0.361	0.025	0.364	0.030
1-3	0.171	0.049	0.181	0.007	0.207	0.024	0.209	0.002	0.148	0.027	0.395	0.018	0.405	0.021
2-4			0.123	0.029			0.117	0.016	0.182	0.013	0.406	0.016	0.384	0.025
3-4			0.198	0.005	0.211	0.023	0.174	0.004	0.184	0.012	0.440	0.012	0.425	0.017

Table 6.2. continued.

	Nov. 97	January 98	March 98	May 98	July 98	Sept. 98
Treatments	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*
1-2	0.331 0.004	0.337 0.017	0.404 0.047	0.368 0.018	0.490 0.012	0.822<0.001
1-3	0.388 0.002	0.466 0.038	0.483 0.030	0.361 0.019	0.537 0.009	0.786<0.001
2-4	0.347 0.003		0.406 0.046	0.348 0.022	0.428 0.020	0.785<0.001
3-4	0.404 0.002	0.455 0.042	0.495 0.027	0.341 0.024	0.474 0.014	0.784<0.001

Data presented are F-values (F), with probabilities (P), which are all significant values.

No significant differences between treatments 1 and 4, or between treatments 2 and 3 were seen at any time during the manipulation.

Red Wharf Bay (B).

The coverage of barnacles was found to be significantly influenced by treatment (GLM. F=109.221 P=<0.001), being consistently higher in treatments 1 and 4 from May 97 (that is some six months after initiation of *Nucella* and *Patella* removals). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=<0.001), treatments 1-3 (P=<0.001), treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001). Significant differences in coverage of barnacles between treatments were only apparent at certain from May to September (Table 6.3).

Table 6.3. Results of ANOVA (GLM repeated measures) showing significant differences in barnacle coverage between specified treatments at Red Wharf Bay (B).

	May 97	July 97	Sept. 97	March 98	May 98	July 98	Sept. 98
Treatments	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*	*F* *P*
1-2	0.224 0.029	0.157 0.049	0.229 0.025	0.139 0.040	0.366 0.031		0.571 0.021
1-3			0.198 0.043		0.359 0.033	0.432 0.046	0.559 0.023
2-4	0.228 0.033	0.186 0.027	0.214 0.032		0.355 0.035		0.571 0.021
3-4	0.221 0.037		0.183 0.056		0.348 0.037		0.634 0.014

Data presented are F-values (F), with probabilities (P), which are all significant values.

No significant differences between treatments 1 and 4, or between treatments 2 and 3 were seen at any time during the manipulation.

Porth Nobla.

The coverage of barnacles was found to be significantly influenced by treatment (GLM. F=13.421 P=0.015), being consistently higher in treatments 1 and 4 from May 97 (that is some six months after iniation of *Nucella* and *Patella*). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=0.040), and treatments 2-4 (P=0.048), significant differences in coverage of barnacles between treatments were only apparent at certain times of the year (Table 6.4).

Table 6.4. Results of ANOVA (GLM repeated measures) showing significant differences in barnacle coverage between specified treatments at Porth Nobla.

	July 97		March 98		September 98	
Treatments	*F*	*P*	*F*	*P*	*F*	*P*
1-2	0.157	0.049	0.139	0.040	0.411	< 0.001
1-3					0.534	< 0.001
2-4	0.186	0.027			0.341	< 0.001
3-4					0.464	< 0.001

Data presented are F-values (F), with probabilities (P), which are all significant values.

No significant differences between treatments 1 and 4, or between treatments 2 and 3 were seen at any time during the manipulation.

Porth Defaid.

The coverage of barnacles was found to be significantly influenced by treatment (GLM. F=22.720 P=0.006), being consistently higher in treatments 1 and 4 from May 97. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=0.009), and treatments 1-3 (P=0.025). Significant differences were found in coverage of barnacles between treatments (Table 6.5).

Table 6.5. Results of ANOVA (GLM repeated measures) showing significant differences in barnacle coverage between specified treatments at Porth Defaid.

	March 98		May 98		July 98		September 98	
Treatments	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
1-2	0.093	0.032	0.121	0.037	0.271	0.008	0.174	0.002
1-3	0.085	0.043	0.112	0.044	0.221	0.017	0.140	0.005
2-4					0.201	0.024	0.162	0.003
3-4					0.170	0.047	0.128	0.007

Data presented are F-values (F), with probabilities (P), which are all significant values.

No significant differences between treatments 1 and 4, or between treatments 2 and 3 were seen at any time during the manipulation.

6.314. Dead barnacle coverage.

Menai Bridge.

The number of dead barnacles was significantly influenced by treatment (GLM. F=14.383 P=0.013), being consistently higher in treatment 4 from May 97 to May 98. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in coverage of dead barnacles between treatments 1-4 (P=0.021), treatments 2-4 (P=0.046) and treatments 3-4 (P=0.048).

Trwyn y Penrhyn.

The number of dead barnacles was found to be significantly influenced by treatment (GLM. F=17.857 P=0.009), usually being lower in treatments 1 and 3, particularly from May 1997 to May 1998. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in coverage of dead barnacles only between treatments 1-4 (P=0.021), and treatments 3-4 (P=0.021).

Llanfairfechan.

The number of dead barnacles was found to be significantly influenced by treatment (GLM. F=8.410 P=0.033), although any noticeable trends in time were hard to discern. Post Hoc multiple comparison (Bonferroni test) showed only slight significant overall mean differences in coverage of dead barnacles between treatments 1-4 (P=0.046).

Red Wharf Bay (A).

The coverage of dead barnacles was found to be significantly influenced by treatment (GLM. F=248.385 P=<0.001), being consistently higher in treatment 4 (control) from May 97 till the end of the experiment. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-2 (P=0.006), between treatments 1-3 (P=0.048), between treatments 1-4 (P=<0.001), treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001).

Red Wharf Bay (B).

The number of dead barnacles was found to be significantly influenced by treatment (GLM. F=53.155 P=0.001), being consistently higher in treatment 4 (control) from May 97 till the end of the experiment. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-4 (P=0.003), treatments 2-4 (P=0.005), and treatments 3-4 (P=0.002).

Porth Nobla.

The number of dead barnacles was found to be significantly influenced by treatment (GLM. F=44.975 P=0.002), being higher in treatment 4 (control) from March 1997 till January 1998. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage between treatments 1-4 (P=0.003), treatments 2-4 (P=0.006) and treatments 3-4 (P=0.004).

Porth Defaid.

The number of dead barnacles was found to be significantly influenced by treatment (GLM. F=7.512 P=0.040), although significant differences between treatments were only discernible towards the end of the experimental period in July 1998, and September 1998 (Table 6.6).

Table 6.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in dead barnacle coverage between treatments at Porth Defaid.

	July 98		September 98	
Treatments	Mean difference	*P*	Mean difference	*P*
1-2	0.088	0.012	0.059	0.001
1-3	0.075	0.022	0.043	0.003
2-4	0.106	0.006	0.076	<0.001
3-4	0.092	0.010	0.059	0.001

Data presented are mean differences, with probabilities (P), which are all significant values.

6.315. Algal coverage.

Menai Bridge.

The coverage of algae was found to be significantly influenced by treatment (GLM. F=72.025 P=0.001), being consistently higher in treatments 2 and 3 from May 1997 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-2 (P=0.008), between treatments 1-3 (P=0.002), between treatments 2-4 (P=0.004) and treatments 3-4 (P=0.002).

Trwyn y Penrhyn.

The coverage of algae was found to be significantly influenced by treatment (GLM. F=22.138 P=0.006), being consistently higher in treatments 2 and 3 from around May 97 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-3 (P=0.014), and treatments 3-4 (P=0.019), but not between treatments 1-2 (P=0.054), nor between treatments 2-4 (P=0.083).

Llanfairfechan.

No macroalgae appeared on this shore, neither in preliminary surveys (Summer 1996), nor for the duration of field manipulations (September 96 to September 98).

Red Wharf Bay (A).

The coverage of algae was found to be significantly influenced by treatment (GLM. F=378.759 P=<0.001), being consistently higher in treatments 2 and 3 from November 96 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-2 (P=<0.001), between treatments 1-3 (P=<0.001), between treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001).

Red Wharf Bay (B).

The coverage of algae was found to be significantly influenced by treatment (GLM. F=3185.132 P=<0.001), being consistently higher in treatments 2 and 3 from May 97 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-2 (P=<0.001), between treatments 1-3 (P=<0.001), between treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001).

Porth Nobla.

The coverage of algae was found to be significantly influenced by treatment (GLM. F=750.601 P=<0.001), being consistently higher in treatments 2 and 3 from March 97 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-2 (P=<0.001), between treatments 1-3 (P=<0.001), between treatments 2-3 (P=0.046), between treatments 2-4 (P=<0.001) and treatments 3-4 (P=<0.001).

Porth Defaid.

The coverage of algae was found to be significantly influenced by treatment (GLM. F=136.746 P=<0.001), being consistently higher in treatments 2 and 3 from May 97 till the end of the manipulation. Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in algal coverage between treatments 1-2 (P=0.001), between treatments 1-3 (P=0.001), between treatments 2-4 (P=0.001) and treatments 3-4 (P=0.001).

6.316 Availability of bare rock substratum.

The only shores where availability of bare space was found to be significantly influenced by treatment were Menai Bridge (GLM. F=8.536 P=0.033), and Porth Defaid (GLM. F=42.879 P=0.002. In fact Post Hoc multiple comparison (Bonferroni test) showed no significant overall mean differences in the amount of bare space between treatments on any of these shores including Menai Bridge, but excepting Porth Defaid (see Table 6.7). On the former shore the degree of bare space in all four treatments closely followed one another in time. In the latter the available bare space began to get progressively more limited in treatments 2 and 3 (especially when compared to treatments 1 and 4) from May 97.

Table 6.7. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in availability of bare space between treatments at Porth Defaid.

Treatments	Mean difference	*P*
1-2	0.140	0.019
1-3	0.166	0.010
2-4	0.182	0.007
3-4	0.208	0.004

Data presented are mean differences in percent bare space, with probabilities (P), which are all significant values.

6.317. Comparison of coverage of sessile organisms between large and small boulders at Red Wharf Bay (see Figure 6.10).

Barnacles.

The coverage of barnacles was found not to be significantly influenced by size of boulder for treatment 1 (GLM. F=8.491 P=0.100), treatment 2 (GLM. F=0.905 P=0.442), treatment 3 (GLM. F=0.066 P=0.822), and treatment 4 (GLM. F=2.326 P=0.267).

Dead barnacles.

The coverage of dead barnacles was found not to be significantly influenced by size of boulder for treatment 1 (GLM. F=0.515 P=0.547), treatment 2 (GLM. F=2.036 P=0.290), treatment 3 (GLM. F=1.298 P=0.373), and treatment 4 (GLM. F=57.582 P=0.083).

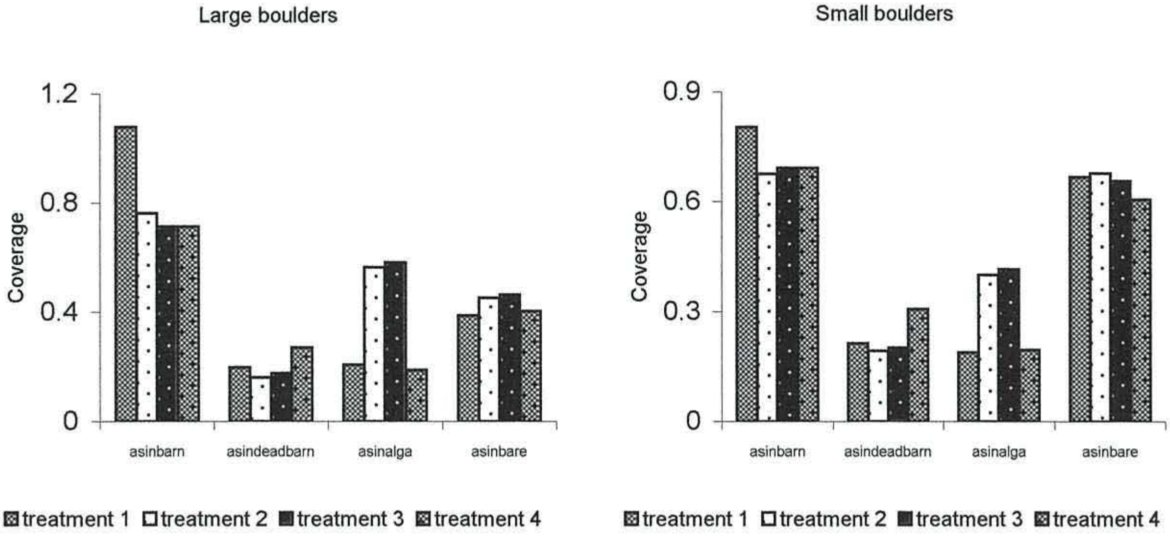


Figure 6.10. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock. A comparison of large and small boulders at Red Wharf Bay.

Algal coverage.

The coverage of algae was found not to be significantly influenced by size of boulder for treatment 1 (GLM. F=0.833 P=0.458), treatment 2 (GLM. F=3.429 P=0.205), treatment 3 (GLM. F=4.283 P=0.174), and treatment 4 (GLM. F=0.031 P=0.877).

Bare Space.

The availability of bare space was found to be significantly influenced by size of boulder for treatment 1 (GLM. F=278.626 P=0.004), treatment 2 (GLM. F=41.8126 P=0.023), treatment 3 (GLM. F=116.019 P=0.009), and treatment 4 (GLM. F=1476.107 P=0.017). Post Hoc multiple comparisons (Bonferroni test) gave exactly the same significance values for all the treatments within the above variable.

6.318. Comparison of coverage of sessile organisms between different shore levels.

The coverage of boulders at level 1 (low shore), level 2 (lower middle), level 3 (upper middle), and level 4 (upper shore) showed some trends on all six shores (Figure 6.11), and when comparing different starting times at Red Wharf Bay (Figure 6.12).

Barnacle coverage.

The percentage coverage of barnacles was found to be significantly influenced by shore level at Menai Bridge (GLM. F=6.378 P=0.003), Trwyn y Penrhyn (GLM. F=11.556 P=<0.001), Red Wharf Bay A (GLM. F=68.215 P=<0.001), Red Wharf Bay B (GLM. F=28.733 P=<0.001), and Porth Defaid (GLM. F=6.088 P=0.004), but not significantly influenced by shore level at Llanfairfechan (GLM. F=1.024 P=0.403), and Porth Nobla (GLM. F=1.995 P=0.147).

Dead barnacle coverage.

The percentage coverage of dead barnacles was found to be significantly influenced by shore level at Menai Bridge (GLM. F=6.129 P=0.004), and Porth Defaid (GLM. F=8.281 P=0.001), but not significantly influenced by shore level at Trwyn y Penrhyn (GLM. F=1.716 P=0.196), Llanfairfechan (GLM. F=2.801 P=0.066), Red Wharf Bay A (GLM. F=1.936 P=0.156), Red Wharf

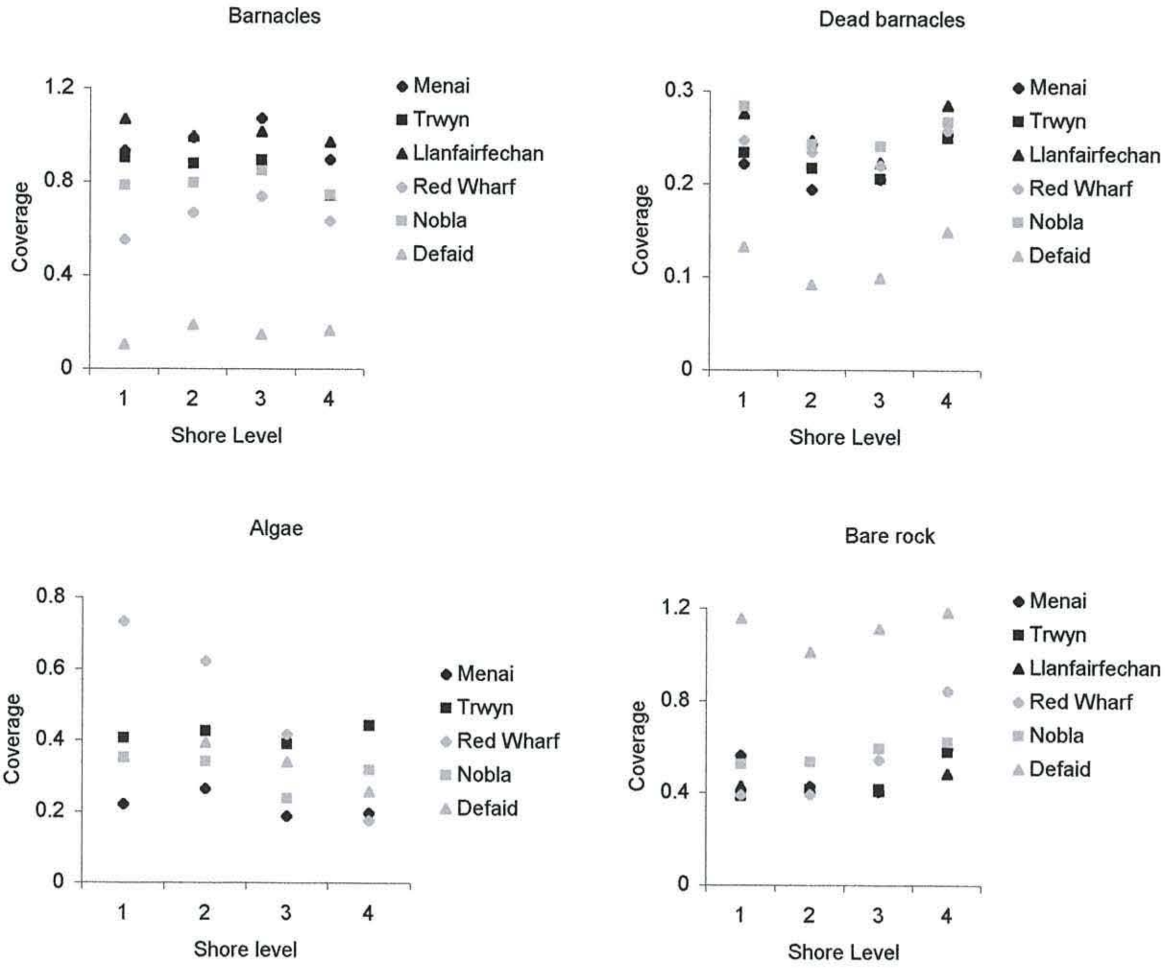


Figure 6.11. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock at different shore levels: 1- low shore. 2- lower middle. 3-upper middle. 4- upper shore.

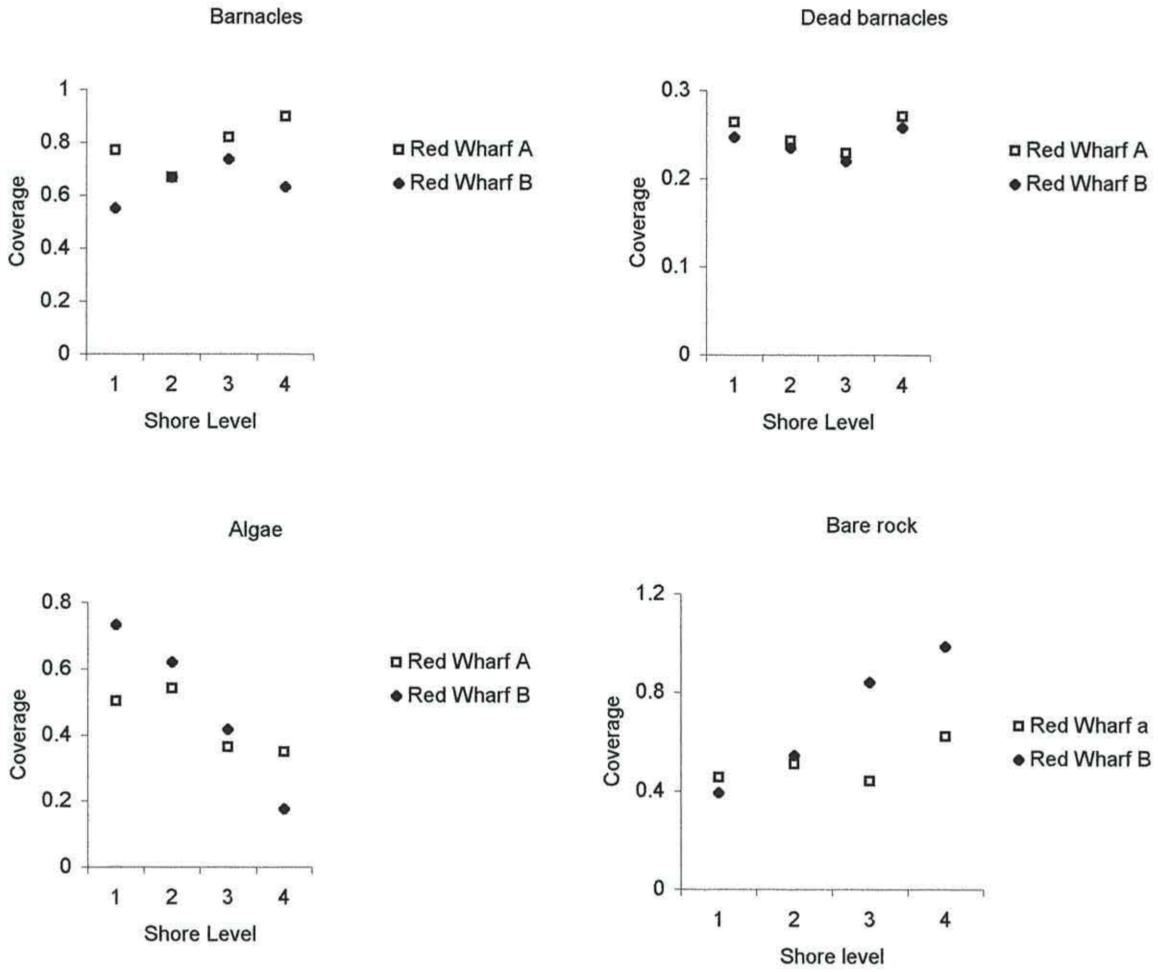


Figure 6.12. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock. Comparison of Red Wharf A (started in April) and Red Wharf B (started in September) at different shore levels.

Bay B (GLM. F=1.802 P=0.179), and Porth Nobla (GLM. F=1.354 P=0.285).

Algal coverage.

The percentage coverage of algae was found to be significantly influenced by shore level at Red Wharf Bay A (GLM. F=159.744 P=<0.001), Red Wharf Bay B (GLM. F=130.948 P=<0.001), Porth Nobla (GLM. F=32.205 P=<0.001), and Porth Defaid (GLM. F=19.424 P=<0.001), but not significantly influenced by shore level at Menai Bridge (GLM. F=2.206 P=0.119), and Trwyn y Penrhyn (GLM. F=0.260 P=0.853).

Bare Space.

The availability of bare space was found to be significantly influenced by shore level at Menai Bridge (GLM. F=48.375 P=<0.001), Trwyn y Penrhyn (GLM. F=63.897 P=<0.001), Llanfairfechan (GLM. F=9.001 P=<0.001), Red Wharf Bay A (GLM. F=99.234 P=<0.001), Red Wharf Bay B (GLM. F=48.988 P=<0.001), and Porth Defaid (GLM. F=30.231 P=<0.001), but not significantly influenced by shore level at Porth Nobla (GLM. F=0.808 P=0.504).

6.319. Comparison of coverage of sessile organisms between different shores.

Barnacle coverage.

The coverage of barnacles was found to be significantly influenced by shore for treatment 1 (GLM. F=646.635 P=<0.001), treatment 2 (GLM. F=170.349 P=<0.001), treatment 3 (GLM. F=216.806 P=<0.001), and treatment 4 (GLM. F=608.748 P=<0.001). See Appendix 6,Table 6.1 for Post Hoc multiple comparisons of means.

Dead barnacle coverage.

The coverage of dead barnacles was found to be significantly influenced by shore for treatment 1 (GLM. F=113.092 P=<0.001), treatment 2 (GLM. F=39.135 P=<0.001), treatment 3 (GLM. F=220.933 P=<0.001), and treatment 4 (GLM. F=83.660 P=<0.001). See Appendix 6, Table 6.2 for Post Hoc comparisons of means.

Algal coverage.

The coverage of algae was found to be significantly influenced by shore for treatment 1 (GLM. F=160.056 P=<0.001), treatment 2 (GLM. F=596.478 P=<0.001), treatment 3 (GLM. F=196.770 P=<0.001), and treatment 4 (GLM. F=43.146 P=<0.001). There was no algae at all on shore 3, that is Llanfairfechan. See Appendix 6 (Table 6.3), for Post Hoc comparisons of means.

Bare Space.

The availability of bare space was found to be significantly influenced by shore for treatment 1 (GLM. F=1063.128 P=<0.001), treatment 2 (GLM. F=94.527 P=<0.001), treatment 3 (GLM. F=96.646 P=<0.001), and treatment 4 (GLM. F=408.164 P=<0.001). See Appendix 6 (Table 6.4), for post Hoc comparison of means.

A comparison of sessile organism coverage between experiments started in April (Red Wharf A) and started the following September (Red Wharf B), showed that the coverage of barnacles was found to be significantly influenced by the starting time (GLM. F=31.253 P=<0.001), as was the availability of bare space (GLM. F=6.345 P=0.015). The coverage of dead barnacles was found not to be significantly influenced by starting time (GLM. F=0.072 P=0.789), nor was the coverage of algae (GLM. F=0.338 P=0.564). See monthly changes in barnacles, dead barnacles, algae and bare rock substrate in Appendix 6 (Figures 6.1, 6.2, 6.3, and 6.4 for removal treatments 1,2,3, and 4 respectively).

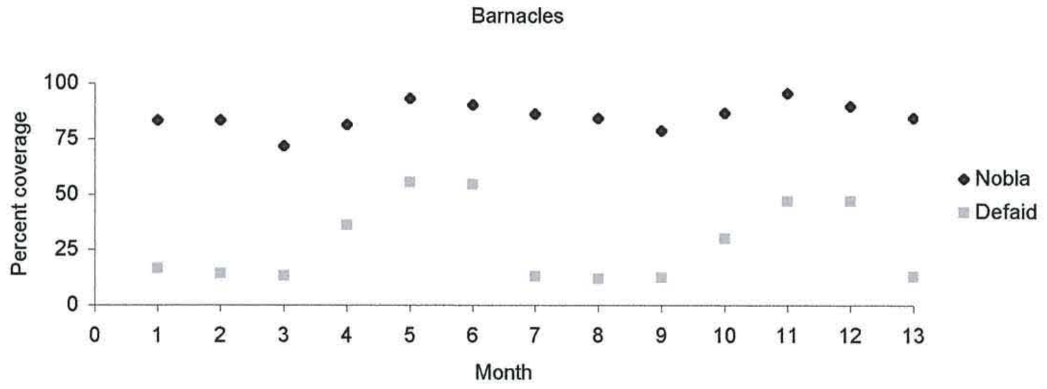
6.32. Vertical rock surfaces.

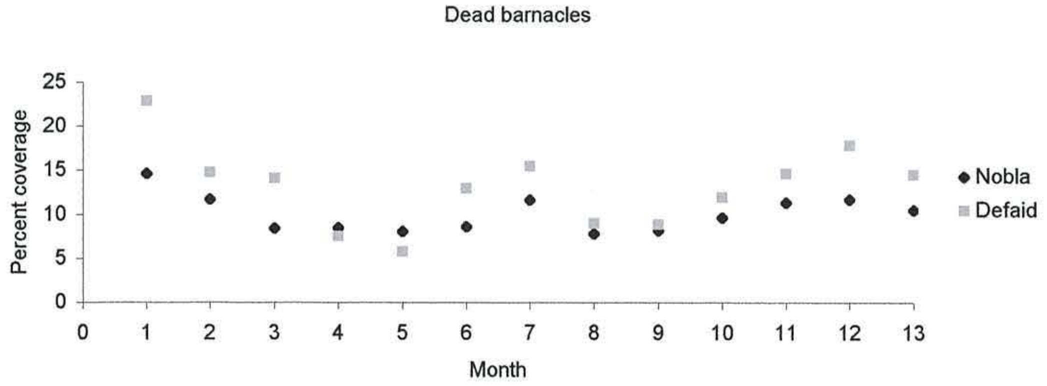
The monthly changes in percent coverage of barnacles, dead barnacles, algae and available rock substrate on the vertical surfaces at Porth Nobla and Porth Defaid are graphed in Figures 6.13, 6.14, 6.15, and 6.16 for treatments 1, 2, 3, and 4 respectively.

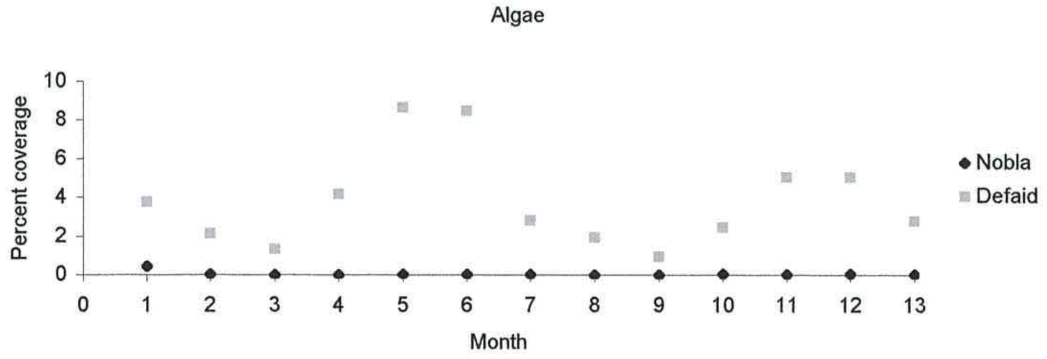
6.321. Removal experiments.

6.322. Barnacle coverage.

The coverage of barnacles was found not to be significantly influenced by treatment at Porth Nobla







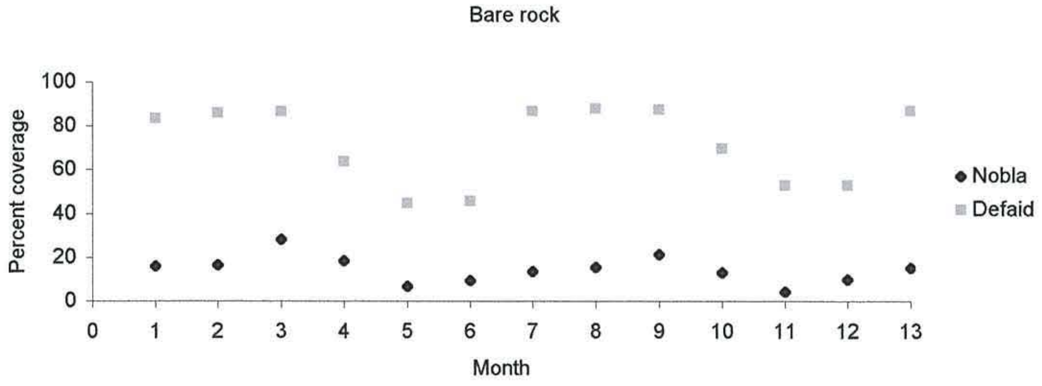


Figure 6.13. Percent coverage of barnacles, dead barnacles, algae and bare rock following treatment 1 (*Nucella* removal) for vertical surfaces at Nobla and Defaid.

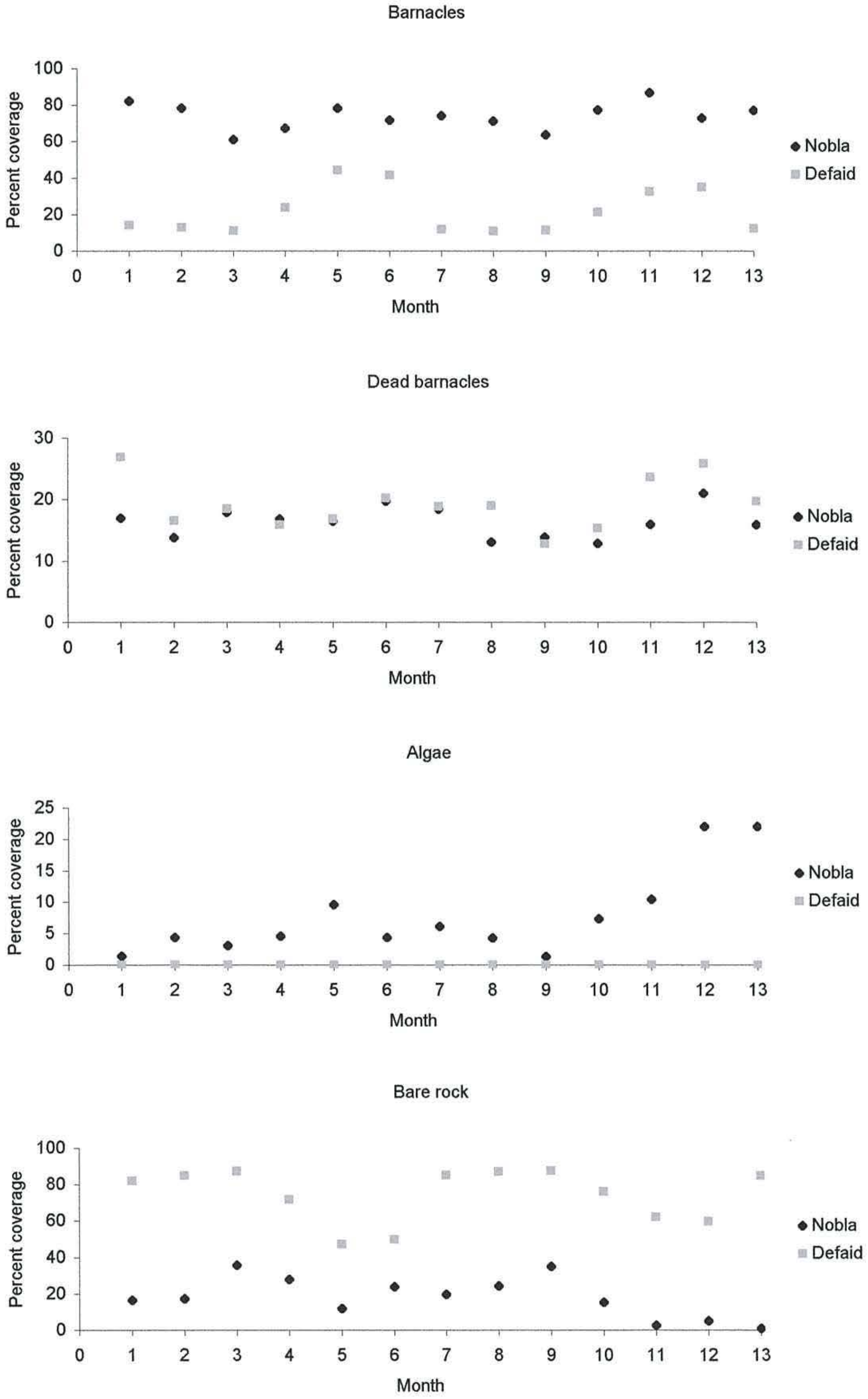


Figure 6.14. Percent coverage of barnacles, dead barnacles, algae and bare rock following treatment 2 (*Patella* removal) for vertical surfaces at Nobla and Defaid.

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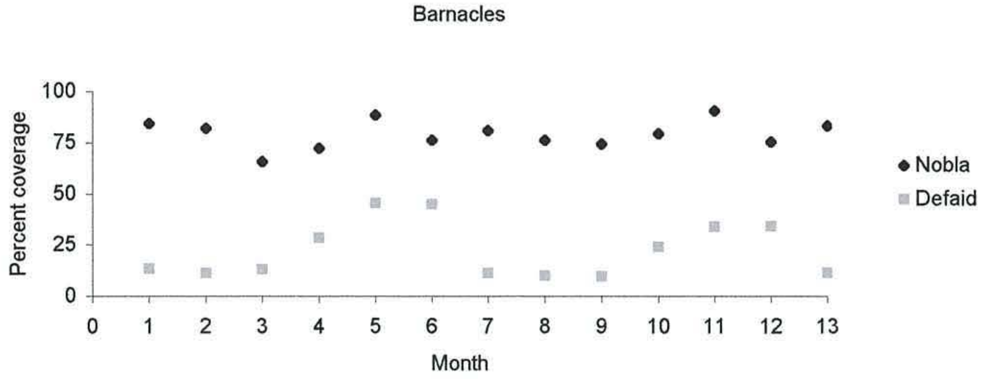

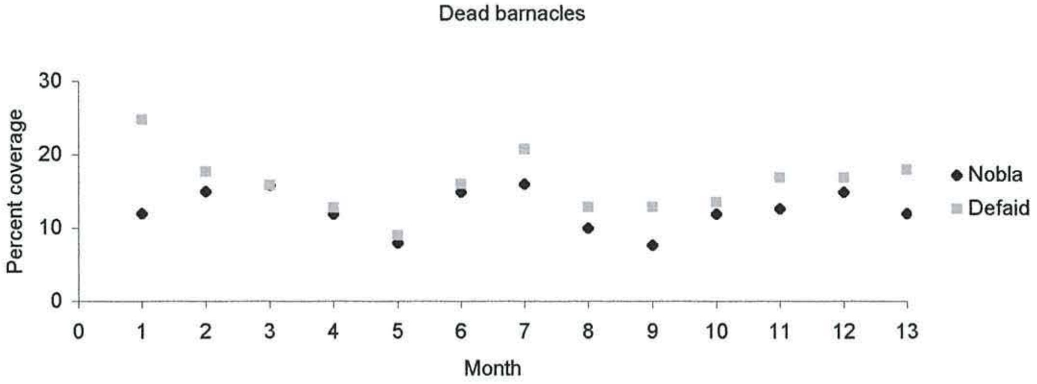

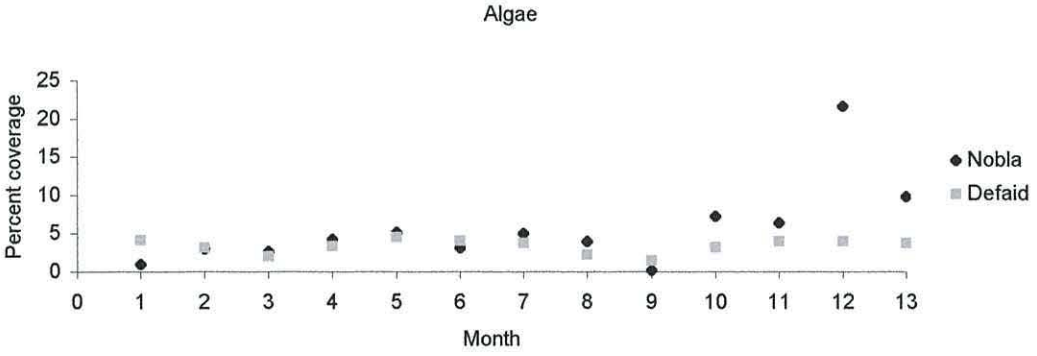

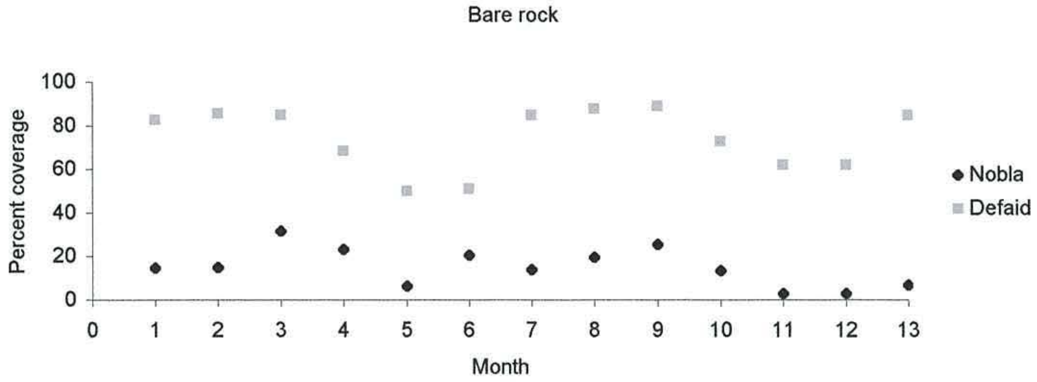

Figure 6.15. Percent coverage of barnacles, dead barnacles, algae and bare rock following treatment 3 (*Nucella* and *Patella* removal) for vertical surfaces.

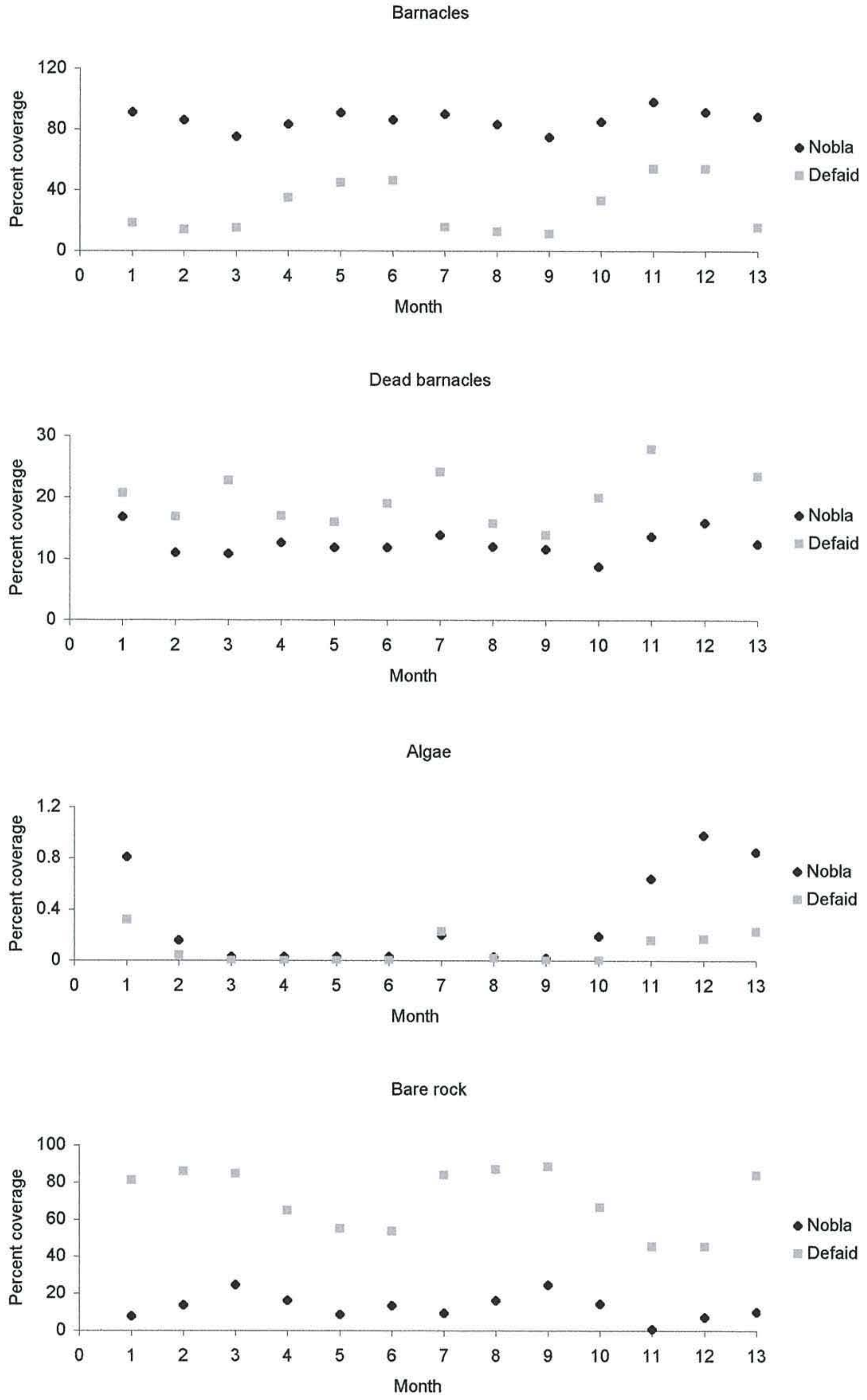

Figure 6.16. Percent coverage of barnacles, dead barnacles, algae and bare rock following treatment 4 (control) for vertical surfaces at Nobla and Defaid.

(GLM. F=5.008 P=0.077), or at Porth Defaid (GLM. F=2.510 P=0.198). In addition Post Hoc multiple comparison (Bonferroni test) showed no significant overall mean differences in barnacle coverage between any of the treatment pairs. Barnacle coverage did exhibit concurrent peaks in May within all four treatments and on both shores.

6.323. Dead barnacle coverage.

The percent coverage of dead barnacles was found to be significantly influenced by treatment at both Porth Nobla (GLM. F=25.501 P=0.005), and Porth Defaid (GLM. F=26.016 P=0.004). In addition Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage for treatments 1-4 (P=0.008), treatments 2-4 (P=0.021) and treatments 3-4 (P=0.014) at Porth Nobla, and for treatment pairs 1-4 (P=0.007), 2-4 (P=0.020), and 3-4 (P=0.013) at Porth Defaid. Barnacle mortality did increase during May-July in both years and within all four treatments on both shores.

6.324 Algal coverage.

The percent coverage of algae was found to be significantly influenced by treatment at both Porth Nobla (GLM. F=180.447 P=<0.001), and Porth Defaid (GLM. F=499.896 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle coverage for most treatment pairs (Table 6.8).

Table 6.8. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in algal coverage between treatments on vertical surfaces at Porth Nobla and Porth Defaid.

	Porth Nobla		Porth Defaid	
Treatments	Mean difference	*P*	Mean difference	*P*
1-2	0.210	<0.001	0.179	<0.001
1-3	0.186	<0.001	0.175	<0.001
2-4	0.214	<0.001	0.170	<0.001
3-4	0.190	0.001	0.166	<0.001

Data presented are mean differences of percent coverage, with probabilities (P), which are all significant values.

6.325. Availability of bare rock substratum.

The availability of bare space was found not to be significantly influenced by treatment at both Porth Nobla (GLM. F=0.119 P=0.944), and Porth Defaid (GLM. F=0.133 P=0.936). Post Hoc multiple comparison (Bonferroni test) showed no significant overall mean differences in the amount of bare space.

6.326. Comparison of coverage of sessile organisms between shores (vertical surfaces).

The coverage of three variables, namely: barnacles, dead barnacles, and availability of bare space (all arcsine transformed) were all found to be significantly influenced by shore between Porth Nobla and Porth Defaid for all four treatments (Table 6.9). The coverage of algae (Asinalga), was only found to be significantly different in treatment 3.

Table 6.9. Results of ANOVA (GLM repeated measures) showing the differences in coverage variables on vertical surfaces between Porth Nobla and Porth Defaid.

	Asinbarn		Asindeadbarn		Asinalgae		Asinbare	
Shores 6-7	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment 1	760.719	0.001*	1298.347	0.001*	11.370	0.078	837.818	0.001*
Treatment 2	285.425	0.003*	224.482	0.004*	13.892	0.065	925.312	0.001*
Treatment 3	898.963	0.001*	159.818	0.006*	161.414	0.006*	881.209	0.001*
Treatment 4	401.96	0.002*	194.417	0.005*	4.832	0.159	360.630	0.003*

Data presented are mean differences, with probabilities (P), * which are significant values.

6.33 Comparison of horizontal to vertical rock surfaces at Porth Nobla and Porth Defaid.

The coverage of barnacles, dead barnacles, algae and bare rock on horizontal and vertical surfaces are all visibly compared in Figure 6.17 for treatments 1, 2, 3, and 4.

6.331. Exclusion experiments.

6.332. Barnacle coverage.

Porth Nobla. The coverage of barnacles was found not to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=0.083 P=0.800), treatment 2 (GLM. F=1.944 P=0.298),

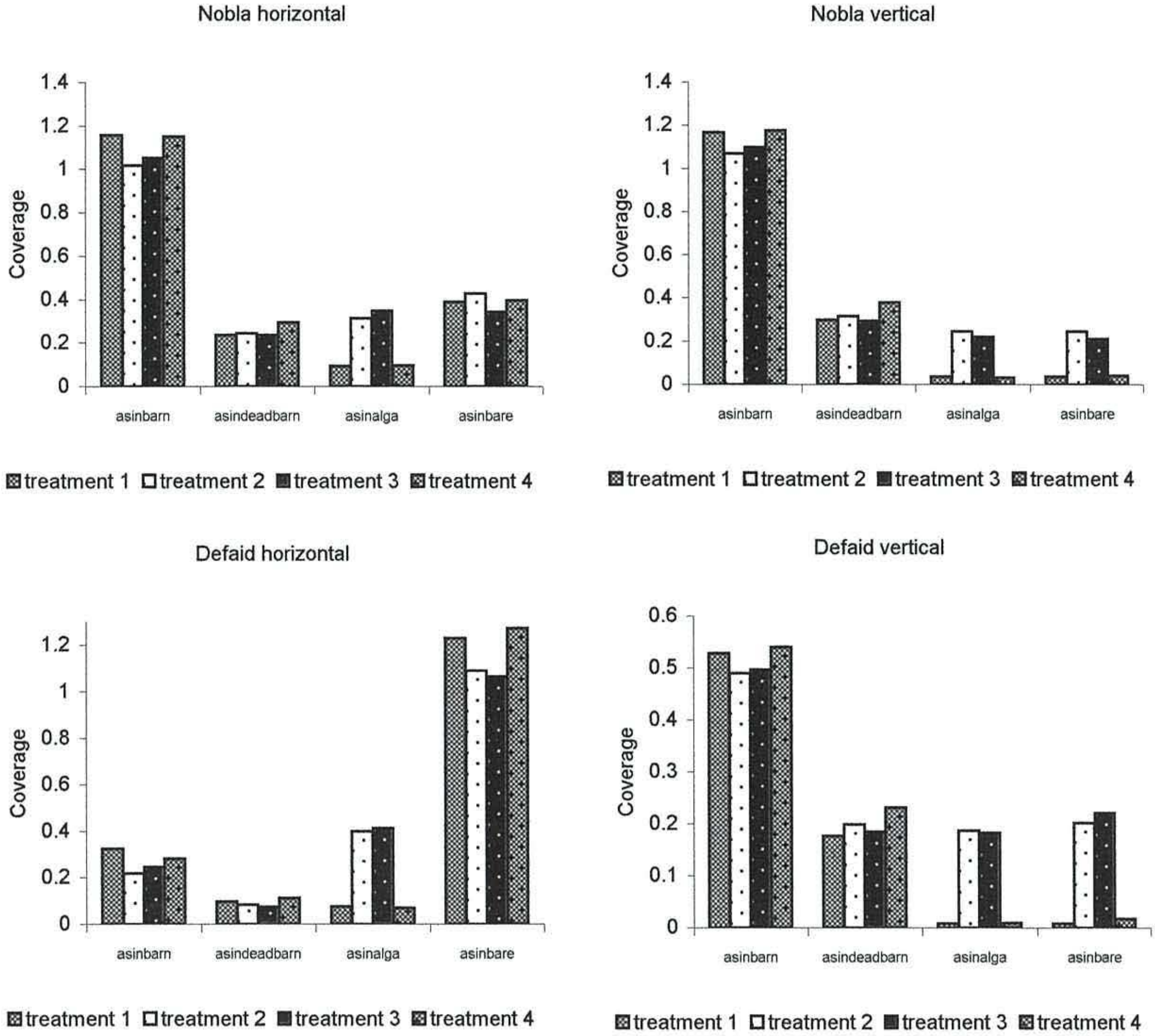

Figure 6.17. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock. A comparison of horizontal and vertical surfaces at two exposed shores.

for treatment 3 (GLM. F=77.341 P=0.822), and treatment 4 (GLM. F=0.546 P=0.537).
Porth Defaid. The coverage of barnacles was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=167.898 P=0.006), treatment 2 (GLM. F=151.656 P=0.007), treatment 3 (GLM. F=152.586 P=0.006), and treatment 4 (GLM. F=426.702 P=0.002).

6.333. Dead barnacle coverage.

Porth Nobla. The coverage of dead barnacles was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=297.022 P=0.003), treatment 2 (GLM. F=60.556 P=0.016), treatment 3 (GLM. F=52.355 P=0.019), and treatment 4 (GLM. F=93.197 P=0.011).
Porth Defaid. The coverage of dead barnacles was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=266.005 P=0.004), treatment 2 (GLM. F=446.962 P=0.002), treatment 3 (GLM. F=256.669 P=0.004), and treatment 4 (GLM. F=193.417 P=0.005).

6.334. Algal Coverage.

Porth Nobla. The coverage of algae was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=27.402 P=0.035), treatment 2 (GLM. F=18.802 P=0.048), treatment 3 (GLM. F=1281.761 P=0.001), and treatment 4 (GLM. F=112.175 P=0.009).
Porth Defaid. The coverage of algae was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=71.810 P=0.014), treatment 2 (GLM. F=1357.896 P=0.001), treatment 3 (GLM. F=54.346 P=0.018), and treatment 4 (GLM. F=31.652 P=0.030).

6.335. Availability of bare rock substratum.

Porth Nobla. The availibility of bare space was found not to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=0.169 P=0.721), treatment 2 (GLM. F=0.661 P=0.501), treatment 3 (GLM. F=19.477 P=0.051), and treatment 4 (GLM. F=0.030 P=0.879).
Porth Defaid. The availability of bare space was found to be significantly influenced by type of substrate surface for treatment 1 (GLM. F=155.445 P=0.006), and treatment 4 (GLM. F=426.214 P=0.002, but not found to be significantly influenced by type of substrate surface for treatment 2 (GLM. F=7.951 P=0.106), and treatment 3 (GLM. F=0.933 P=0.436). Post Hoc multiple

comparisons (Bonferroni test) gave the same significance values for all treatments within all the above variables for both shores.

6.34 The effect of barnacle density upon *Nucella* foraging numbers.

Barnacle densities of plots on six shores were manipulated to give the following barnacle 'concentrations' as far as was possible - treatment 1: normal barnacle density; treatment 2: 80% of normal; treatment 3: 60% of normal; treatment 4: 40% of normal. The relationship between barnacle density and the numbers of *Nucella* foraging upon them is depicted in Figures 6.18 (showing effect of treatment) and 6.19 (overall trend in changing densities).

6.341. Barnacle density in respect to experimental treatments.

The density of barnacles was found to be significantly influenced by treatment at Menai Bridge (GLM. F=92.371 P=<0.001), Trwyn y Penrhyn (GLM. F=77.192 P=<0.001), Llanfairfechan (GLM. F=320.030 P=<0.001), Red Wharf Bay (GLM. F=180.970 P=<0.001), Porth Nobla (GLM. F=214.632 P=<0.001), and Porth Defaid (GLM. F=8.353 P=0.001). In addition Post Hoc multiple comparison (Bonferroni test) showed significant overall mean differences in barnacle density between all treatments on all six shores (Table 6.10).

Table 6.10. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in barnacle density between experimental treatments.

	Menai		Trwyn		Llanfairechan		Red Wharf		Nobla		Defaid	
Treatments	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	2.78	<0.001	2.36	<0.001	2.22	<0.001	2.21	<0.001	2.49	<0.001	3.15	0.016
1-3	5.09	<0.001	4.49	<0.001	4.18	<0.001	4.06	<0.001	4.79	<0.001	4.37	0.019
1-4	7.22	<0.001	6.77	<0.001	6.31	<0.001	5.81	<0.001	6.84	<0.001	6.49	<0.001
2-3	2.31	<0.001	2.13	0.001	1.96	<0.001	1.84	<0.001	2.29	<0.001	1.21	0.010
2-4	4.44	<0.001	4.39	<0.001	4.09	<0.001	3.59	<0.001	4.34	<0.001	3.34	0.011
3-4	2.13	0.001	2.27	<0.001	2.13	<0.001	1.76	<0.001	2.05	<0.001	2.13	0.037

Data presented are mean differences (md) and probabilities (P), which are all significant values.

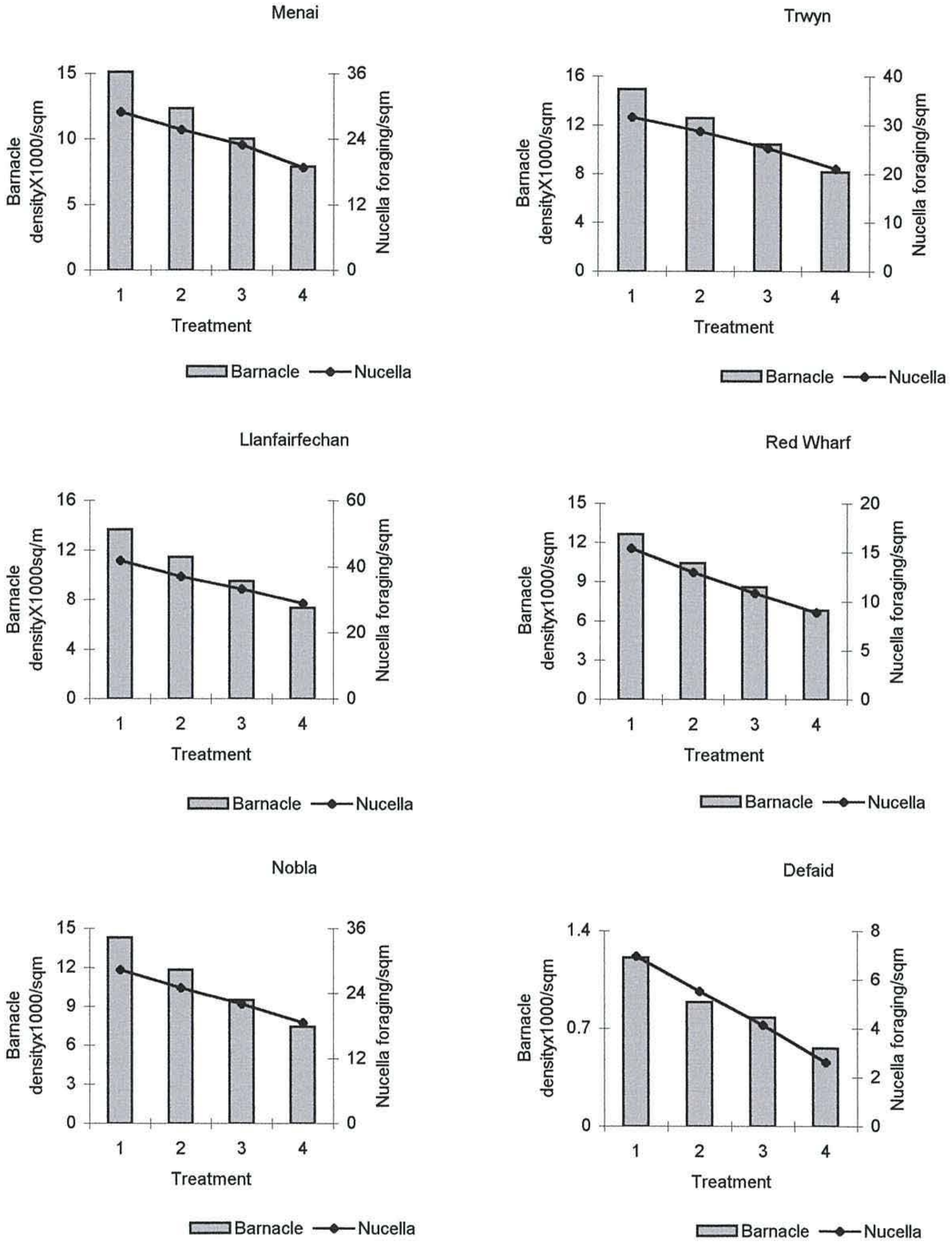

Figure 6.18. Comparison of barnacle density and *Nucella lapillus* foraging numbers on different shores.

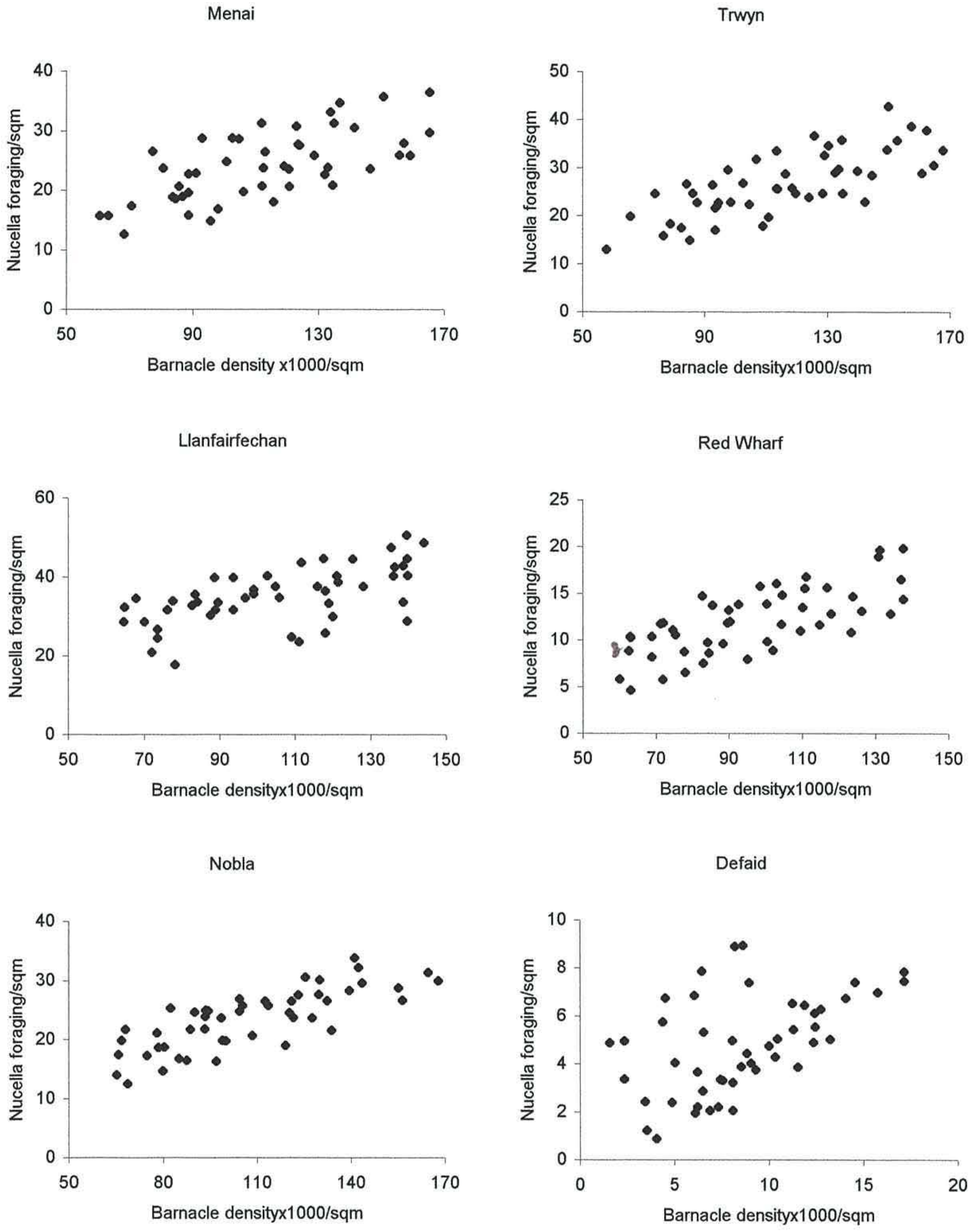

Figure 6.19. The relationship between barnacle density and *Nucella lapillus* foraging on different shores.

6.342. *Nucella* density with repect to experimental treatments.

The numbers of foraging *Nucella* was found to be significantly influenced by treatment at Menai Bridge (GLM. F=27.937 P=<0.001), Trwyn y Penrhyn (GLM. F=42.121 P=<0.001), Llanfairfechan (GLM. F=117.029 P=<0.001), Red Wharf Bay (GLM. F=47.359 P=<0.001), Porth Nobla (GLM. F=45.943 P=<0.001), and Porth Defaid (GLM.F=112.101 P=<0.001). Post Hoc multiple comparison (Bonferroni test) showed significant differences in the numbers of *Nucella* foraging between all treatments on all six shores, except for some combinations at menai Bridge (Table 6.11).

Table 6.11. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in *Nucella lapillus* foraging numbers between experimental treatments.

	Menai		Trwyn		Llanfairechan		Red Wharf		Nobla		Defaid	
Treatments	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	3.22	0.061	2.90*	0.044	4.92*	<0.001	2.46*	0.002	3.39*	0.004	1.45*	<0.001
1-3	6.04*	<0.001	6.37*	<0.001	8.69*	<0.001	4.58*	<0.001	6.34*	<0.001	2.83*	<0.001
1-4	10.17*	<0.001	10.56*	<0.001	13.03*	<0.001	6.54*	<0.001	9.82*	<0.001	4.35*	<0.001
2-3	2.83	0.133	3.47*	0.011	3.76*	<0.001	2.12*	0.007	2.94*	0.015	1.38*	<0.001
2-4	6.95*	<0.001	7.64*	<0.001	8.11*	<0.001	4.08*	<0.001	6.43*	<0.001	2.89*	<0.001
3-4	4.12*	0.009	4.17*	0.002	4.34*	<0.001	1.96*	0.014	3.48*	0.003	1.52*	<0.001

Data presented are mean differences (md) and probabilities (P) , * which are significant values.

6.343. Linear regression of *Nucella* foraging numbers upon barnacle densities.

GLM. Linear Regression of *Nucella* foraging numbers upon barnacle density, showed reasonable positive correlation (values of Pearson coefficient R), as well as strong significance (*P*) results for the ANOVA test of the regression slope (Table 6.12).

Table 6.12. Absolute values of Pearson correlation coefficient and ANOVA test of significance of the regression slope of *Nucella lapillus* foraging numbers in relation to barnacle density.

	Menai	Trwyn	Llanfairechan	Red Wharf	Nobla	Defaid
R	0.629	0.745	0.603	0.714	0.786	0.511
F	30.069	57.359	26.298	47.722	74.227	16.214
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Datapresented are correlation coefficient (R), F-values (F), and probabilities (P), which are all significant values.

6.4 DISCUSSION.

The effect of aspect (side) of boulder.

Generally, there were more barnacles, a higher percentage of dead barnacles, and less than fifty percent of the coverage of algae, on the sides, compared to the tops of boulders on all six experimental shores. Primary (bare rock) space was more or less uniform on all sides of control boulders (including the top) at five of the locations (more bare space on top at Porth Defaid).

These trends are to be expected, since barnacle recruitment is inversely related to the height of settlement upon the substratum (Crisp, 1960; Roughgarden, 1986). Dogwhelks were rarely active on the top surface of boulders, but frequently fed upon concentrations of barnacles on the sides, which explained the increased percentge mortality in barnacles in those area of the substratum. The reduced activity of *Patella vulgata* on top surfaces clearly enabled algae to become established more readily. The one exception was Porth Defaid which had more barnacles on top aspects, for this is the only location where bare substrata dominated the boulder field and the available number of barnacles approached a limiting factor for dogwhelk foraging. These main trends also appeared uniform in time, and (in controls) they occurred irrespective of the date of data collection, and despite different initiation times for experimental removals on the boulder fields of Red Wharf A and Red Wharf B.

The top surfaces of intertidal boulders differ in their composition and abundance of both plants and animals compared to the underneath surface (MacGuiness and Underwood, 1986). The tops, tend to support more species of grazing gastropods (Menge, 1976; 1983; Fairweather et al., 1984), while an increased number of sessile species occurs on undersurfaces of rocks, which protects them from physical disturbance (Boyle, 1972; MacGuinness, 1984a; MacGuinness, 1984b).

Seasonal trends in coverage of sessile organisms.

There were clear seasonal differences in coverage before any removal of selected consumers took effect (and for the duration of the experiment in the controls), at all locations. Specifically, the coverage of adult barnacles tended to change repeatedly and cyclically over the two year period, peaking in May on all shores and within all treatments (two months earlier in treatment 3). The coverage of dead barnacles changed inversely to live barnacle densities, with fewer empty shells observed from March-May in year 1, and from January to March in year 2, in all treatments, on all shores. Algal coverage showed symmetrical sinusoidal increases and decreases, peaking every April-September, falling off in Winter (January-March), and the amount of bare rock was inversely related to algal coverage to a degree. The same trends were observed on the vertical surfaces of Nobla and Defaid with one or two modifications. These included very low percentages of dead barnacles from November-Febuary, with complex changes in algal coverage, which peaked from May to July (September in controls).

These findings are contrary to those of MacGuinness (1984b), who stated that seasonal patterns in the recruitment and the abundances of species assemblages in intertidal boulder fields are not pronounced. Clearly distribution and abundance patterns within the North Wales intertidal community were strongly affect by temporal and spatial heterogeneity, with particularly marked seasonal changes in both for algal coverage, which is related to variations in both temperature and wave-action. Even the timing and speed of community regeneration, usually depends on seasonal abiotic environmental factors according to Niell (1977), who worked on algal communities in Spain.

Barnacle coverage.

In the boulder fields of all the shores investigated, the exclusion of *Nucella lapillus* had no stastistically significant effect on barnacle coverage, although barnacle coverage was consistently higher in treatments 1 (*Nucella* removal) and 4 (control), than treatments 2 (*Patella* removal) and 3 (removal of both), from May 97 on Menai Bridge and Red Wharf bay A (from January 98 at Red Wharf Bay B). A similar effect was observed on all other shores but took longer to materialise: March 98 (Porth Nobla and Porth Defaid), September 98 (Trwyn y Penrhyn and Llanfairfechan). The exclusion of limpets had a significantly (and pronounced) negative effect on the *Semibalanus* populations on all shores. The overall effect of removal of both *Nucella* and *Patella* was a decrease in barnacle coverage comparable to *Patella* removal alone, emphasising the greater impact of

Patella vulgata on overall barnacle coverage compared to that of *Nucella lapillus.*

Although *Patella* inadvertently consumes and dislodges settling barnacle cyprids or newly metamorphosed larvae) (Hatton, 1938; Lewis, 1954; Southward, 1956; Menge, 1976; Hawkins 1983; Miller and Carefoot, 1989; Underwood, 1992; Safriel et. al., 1994), these effects are usually very limited in comparison to the overall barnacle density, especially during times of barnacle recruitment (Gateno et. al., 1996). Where there are sufficient limpets present to keep an area free from algae, barnacles can settle in large numbers (Lewis, 1976; Underwood and Fairweather, 1985; Hawkins et. al., 1992). In those treatments where limpets were excluded, the decrease in barnacle coverage was an indirect consequence of limpet removal, due to an increase in algal cover, and there was an inverse correlation between barnacle cover and fucoid cover (Hartnoll and Hawkins, 1985). A major reason for a lack of barnacles at low levels on the shore, is the lack of space for settlement, due to the dense cover of algae on sheltered shores (Denly and Underwood, 1979). The fucoid canopy can also form dense beds at mid-shore levels (Lewis, 1964), also inhibiting barnacle recruitment there (Lewis and Bowman,1975; Hawkins, 1983), by effectively creating a barrier for cyprid attachment (Southward, 1956), whilst whiplash effects of algal fronds dislodge young settled larvae (Hatton, 1938; Southward, 1956; Lewis, 1964). Limpets tend to disperse from areas where they have high densities (Aitken, 1962; MacKay and Underwood, 1977), which can lead to these effects on barnacles becoming spatially localised. On the Western Atlantic coast, an overall elevated barnacle coverage occurred following limpet exclusions (Dayton, 1971), when algal growth was also kept in check.

Fucoids provide shelter, enabling dogwhelks to utilize fronds as refuges, and can migrate higher up the shore, remaining protected from predation and desiccation (Vadas and Elner, 1992), leading to localised increased feeding rates (Menge, 1978b). The algal canopy also enhances post-settlement survival of the dogwhelks' barnacle prey (Dayton 1971). Barnacles tend to occupy space left vacent by other forms (Lewis, 1976), and adult *Semibalanus* (at times forming especially dense clusters), actually can have a positive effect on algae (Berlow and Navarrete, 1997; Jernakoff, 1985b), in some areas, by providing surface irregularities that reduce herbivore grazing

(Burrows and Lodge, 1950; Jernakoff, 1985a; Fairweather, 1994). In the absence of whelks, barnacles provide a refuge for fucoid algae (Lubchenco 1983), and the two jointly pre-empt space (Vadas and Elner, 1992). At most locations on both sides of the Atlantic it appears that the sessile community structure is primarily related to the population dynamics of *Semibalanus balanoides*. This species dominated much of the available substratum on most shores following exclusion of dogwhelks and limpets.

Variation in the distribution and population structure of sessile organisms including barnacles, is affected by both predation and physical disturbance (Paine, 1974, Menge, 1976; Osman, 1977). Interactions between carnivorous whelks and their sessile barnacle prey in rocky shore habitats have been examined in detail (Menge, 1978a; Katz, 1985; Fairweather et. al., 1984), showing that *Nucella lapillus* can have dramatic effects on the distribution of intertidal organisms (Connell, 1961b; 1970; Dayton, 1971). When these predators are very abundant they can cause high barnacle mortality (Hawkins et. al., 1992), and even affect the structure of the community (Menge 1972b, Menge and Menge, 1974). The relative abundance of prey greatly affect predation on them (Fairweather, 1985, 1987), and on the population dynamics of the predator (Underwood et. al., 1983), affecting its impact on community structure (Fairweather et al., 1984). On all the study shores examined, the numbers of whelks feeding, increased with increasing barnacle density within prepared experimental field plots (Figure 6.18). In time however, we can expect that increased levels of predation in areas of prey concentration will ultimately depress barnacle numbers and change the localised community structure for a while. Predators like *Nucella lapillus* tend to be much more localised than their prey, and barnacles are able to survive to reproduce, especially in high level "refuge" populations above the normal vertical distribution of the whelks (Fairweather, 1988d). On the Atlantic coast of the United States *Nucella* spp. are considered to be disturbing predators (Connell, 1970; Dayton, 1971; Spight, 1981), as whelk predation had marked effects on the spatial distribution and population dynamics of both barnacles and mussels (Dayton, 1971). On the shores of Western Britain, barnacle densities attained high levels in spite of *Nucella lapillus* predation, with local patches often escaping elimination. On the six study shores dogwhelks were often present in large numbers on the study shores (over 85/m^2), yet still failed to have a controlling influence on their prey. In North Wales, the variation in coverage of barnacles (and percentage of dead barnacles) can be explained by patterns of barnacle recruitment as much as patterns of predation (Underwood and Denley, 1984). Barnacle cover decreased from September to January, but noticeably, increased in May following new settlement on most of the study shores.

The specific pattern of temporal variation in predation (both the timing of predation, as well as the time interval between predation events or frequency), can have a distinctive impact not only on prey populations, but also upon the sessile communities as a whole (Navarrete, 1996). Predator impact is not usually related in a linear fashion to predator density (Abrams, 1993; Andrew and Underwood, 1993), and the final abundances of whelks and barnacles in the main exclusion areas bore little relationship to their initial levels two years earlier. This poor correlation between whelks and barnacles was also found by Hartnoll and Hawkins (1985), who therefore linked fluctuations of barnacles to another factor (algal overgrowth). Therefore, extreme caution is needed in interpreting the causes of static patterns of abundance in the field (Fairweather, 1988a), as differences between predator removals and controls may be produced equally by direct or indirect effects of predators. This problem is highlighted by the fact that results of whelk removals by Navarrete (1996), contrasted sharply with those obtained by Wootton (1994). Comparisons between sites and different research personnel are made difficult by differences in experimental protocols and a lack of information on the within-site variability (Underwood and Petraitis, 1993), for instance differences in initial composition of prey patches (Navarrete, 1996).

Predator exclusion areas in the North-Western Atlantic developed a strong bloom of algae, followed by a dense settlement of barnacles (Dayton, 1973), and in Australia there was little variation in barnacle densities at sites without whelks (Fairweather, 1988c). In North Wales however, *Nucella lapillus* had no effect on algal coverage, but like in Australia, rapidly fluctating densities of dogwhelks on a seasonal (monthly, even weekly basis), did lead to wider variations in prey densities, than in areas where whelk populations were kept at, or near zero (removal zones).

Similar trends in barnacle coverage were observed on the vertical surfaces at Porth Nobla and Porth Defaid: specifically, coverage in treatments 1 (*Nucella* removal) and 4 (control) was consistently higher than in both treatment 2 (*Patella* removal) and treatment 3 (*Patella* and *Nucella* removal), although these differences were less distinct (and slower to occur) in part because of the non-isolated nature of these vertical rock faces.

Percentage variation in dead barnacles.

Barnacle mortality rates in controls were higher than all boulder removals. The mortality of barnacles in areas without whelks were considerably lower than plots with whelks at all locations, and can reliably be interpreted as being due to the removal of whelks, because significant results were obtained despite heterogeneity between the sites. *Nucella lapillus* killed barnacles in significant numbers but without affecting the overall coverage of live barnacles in the long term. The results for vertical surfaces (Porth Nobla and Porth Defaid) matched those for boulder fields. Spatial patterns of barnacle mortality are a result of numerous different regulating processes. One of them is the presence of an extensive fucoid canopy, that can modify whelk behaviour, even reducing the *Nucella* foraging period and effectiveness, and enhancing barnacle survival under the canopy compared to cleared areas (Dayton, 1971). On the study shores barnacle coverage decreased in areas with more canopy, whilst the percentage of dead barnacles either fell or stayed the same.

Algal coverage.

The removal of *Nucella lapillus* had no effect on algal coverage at any of the study locations. Removal of limpets on the other hand, resulted in a heavy growth of algae (Jones, 1948; Lodge, 1948; Southward 1956), primarily ephemeral green algae (within the first 4-6 months), followed by extensive cover of *Fucus* spp. two months later (similar results to Hawkins, 1981a; 1981b; Hartnoll and Hawkins, 1985), and finally carpets of the red alga *Chondrus crispus*. This succession occured in the same order, irrespective of the timing of initiation of exclusions at Red Wharf Bay (whether in April or later in September). The composition, but not the sequence of this colonizing algae (succession) following limpet removal, varied with season unlike in studies by Hawkins (1981a), and Jernakoff (1983), in which both factors changed with the time of year. Seasonal changes in distribution patterns of algae peaked during May and September, and decreased in the Summer, and was variable from year to year. Exactly the same results (as in *Patella* removal) followed removal of both *Nucella* and *Patella* as we might expect due to the lack of effect of *Nucella* removal on algal coverage.

The growth of intertidal algae on a local scale is determined by the interaction of *Patella* grazing, and seasonally changing physical features of the environment, such as temperature, light intensity, and desiccation stress (Underwood, 1980; Underwood and Jernakoff, 1984), that vary both with wave exposure and tidal height (Lodge 1948; Hawkins et. al., 1992). Complete occupancy of primary substratum by algae is rare and restricted by season (although *Fucus serratus* can occupy over 75% of base substratum: Williams and Seed, 1992), particularly on sheltered shores, and is dependent upon the ability of algae to escape limpet-grazing (Schonbeck and Norton, 1978, 1980; Hawkins and Hartnoll, 1983b).

This shows that these herbivores (*Patella*) can control the distribution and species composition of the attached macroalgae (Sutherland, 1970; Vadas et. al., 1977; Vadas and Elner, 1992), even in the most wave-exposed conditions (Hawkins et. al., 1992). In fact, limpets even graze on settling algal spores and sporelings (Moore, 1938; Southward, 1953; 1956), and have a pronounced negative impact on algal recruitment and survival (Dayton, 1971; Underwood, 1980; Hartnoll and Hawkins, 1985; Underwood and Jernakoff, 1984). By reducing the cover of foliose or crustose algae, limpets prevent them from pre-empting the hard substratum and thus provide algae-free space. Foraging by grazers such as *Patella vulgata* may also indirectly influence larval settlement of sessile organisms and hence the survival of intertidal animals (Bertness et. al., 1983; Underwood et. al., 1983; Underwood, 1985; Dungan, 1986; Menge et. al., 1986; Van Tamelen, 1987). Algal growth was not nearly as abundant on the vertical substrata of Porth Nobla and Porth Defaid, probably because vertical surfaces receive less insolation, and drain more quickly, making them less damper than horizontal faces, probably reducing algal growth (Haven, 1971). The results of removals here were fundamentally the same as for boulder fields, only differing in the degree of change of coverage, not in their direction.

Availability of free (primary) space.

On all the shores except for Porth Defaid (which had consistently lower amounts of primary space where *Patella* was removed), the overall availability of bare space was unaffected by any removals. Primary space availability did change with season on those other shores however, tending to be higher from January to March, and lower from May to July on all shores (a reciprocal trend to algal coverage). Space occupancy within intertidal assemblages is determined by many conflicting and often simultaneous proceses (Berlow and Navarrete, 1997). These include the presence/absence of different sessile species, settlement of their juvenile forms, their comparative rate of growth, their competition with other sessile organisms, and their mortality from density independent factors such as wave shock and desiccation (Menge, 1976). These physical factors free substrate for recolonisation. (Lewis, 1976), realigning the local community structure (Underwood, 1992). This illustrates how free space is a spatially and temporally unpredictable resource, (Lewis, 1976; Horn and MaCarthur, 1972), particularly on sheltered shores where dense populations of littorinids and dogwhelks recycle this limiting resource by removing algae and barnacles respectively (Vadas and Elner, 1992). On vertical surfaces, the availability of bare space also showed no differences between treatments on either shore (Nobla and Defaid).

Comparison between large and small boulders.

Overall barnacle coverage and algal coverage were higher on larger boulders, whilst dead barnacle coverage, and bare space were higher on small boulders, but only the values for the availability of bare space significantly so. This suggests that prey populations on smaller boulders are more vulnerable to biological disturbance (predation), and are more variable in nature. Large boulders are infrequently disturbed, so remain stable for long periods, leading to domination by one or two single species, (Menge and Sutherland, 1987), even though they have a greater number of microhabitats, such as pits, cracks and other depressions (Sousa, 1979a). Assemblages of species on small boulders are usually different (reduced microhabitat diversity), from those on larger boulders (MacGuiness, 1984a; MacGuiness and Underwood, 1986; Underwood, 1986). The tops of these larger boulders are often emersed (exposed to air), considerably longer during low tide than those of small boulders, which limits floral diversity (Underwood, 1980; Underwood and Jernakoff, 1984), particularly during the Summer months. Only in Spring, when the defoliation of the algal canopy the previous Winter has provided sufficient space for colonization, did diversity increase in these habitats (personal observation). The impact of any physical disturbance can be modified by the size or shape of the boulder (Osman, 1977). Small, round boulders are more likely to be overturned by waves than larger ones (Chapman and Underwood, 1996), particularly on wave-swept shores (MacGuinness, 1984b), and therefore they tend to be dominated by early-successional algae due to the regular interruption of the succession process they experience by this overturning (Cusson and Bourget, 1997). They contain fewer species than intermediate sized boulders, which tend to remain stable long enough to support a more diverse community (Osman, 1977).

Comparison of shore levels.

Within each study shore, the prey distribution (of *Semibalanus balnoides)*, as well as the predator impact (as determined by percentage of dead barnacles) were not constant. The coverage of barnacles tended to be highest at the low shore and gradually decreased with tidal height, although at the two most exposed shores coverage was fairly uniform along the vertical drop of the shore. The largest number of dead barnacles were found in the middle shore levels, for all the experimental shores, indicating that *Nucella lapillus* had a greater impact upon their prey in these areas. Predator densities were usually higher in the lower and middle parts of the shore, especially at sheltered and semi-exposed locations. The pattern of algal distribution did not change significantly with respect to vertical height, apart from on Red Wharf Bay, where coverage markedly decreased upwards. Finally, the amount of bare space generally increased with tidal height at all the study sites. These patterns are largely a reflection of barnacle settlement regimes, natural extrinsic environmental factors such as desiccation, as well as community interactions, such as competition and predation (Connell, 1961a; Hartnoll and Hawkins, 1985).

On the moderately-exposed shores of the North-Western Atlantic, the nature of the sessile communities of intertidal boulder fields also changes with shore level. The lower shore has higher levels of growth and recruitment and very high densities of barnacles and mussels, with concurrent larger numbers of predators, including *Nucella lapillus* (Paine, 1977). The upper shore there, has stable formations of barnacles, mussels and limpets. This is similar to the situation found at Llanfairfechan and Red Wharf Bay to a degree, but with differences in algal coverage, and the lack of any significant asteroid predation in North Wales. At Llanfairfechan the scarcity of fucoids (and other macroalgae) seems to be a result of competition with mussels, which dominated the available substratum, at all levels due to the gentle slope on this shore. This vertical variation in species composition and cover of epiphytic animals and algae has been documented under many different environmental conditions (Boaden et. al., 1975), at different tidal heights (Wood and Seed, 1980), and during different seasons of the year (Seed et. al., 1980; Oswald and Seed, 1986).

Comparison of shores. (see Appendix 6, Table 6.5)
Generally speaking, exposure to wave-action increases along the series Menai Bridge, Trwyn y Penryn, Llanfairfechan, Red Wharf Bay, Porth Nobla and Port Defaid. The specific results from controls were very different from removals. In the former, overall barnacle coverage and dead barnacle coverage were not significantly different between any of the shores except for Porth Defaid, which is extremely exposed, and had intrinsically lower numbers of barnacles than all other shores. In the controls too, algal coverage was consistent between shores, only being significantly reduced on the two exposed shores, Porth Nobla and Porth Defaid (absent on Llanfairfechan). Bare space was fairly uniform between shores, but was much higher on Port Defaid.

Following removals, considerable differences in coverage of sessile organims developed between shores. Barnacle coverage and dead barnacle coverage at Porth Defaid was still considerably less than all other locations. Of the rest, the three more sheltered shores had higher barnacle coverage (and a bigger percentage increase following *Patella* removal) than their more exposed counterparts, Red Wharf Bay and Porth Nobla. The percentage of dead barnacles was lower on the two sheltered shores (with a larger decrease in dead barnacles following *Nucella* removal), than the rest. Patterns of differences in algal coverage also generally followed wave exposure, with higher coverage on the sheltered shores (including a bigger percentage in increase in coverage) than the moderately-exposed Red Wharf Bay, which in turn exhibited greater algal densities than exposed shores. Availability of bare space remained fundamentally the same on all shores, and there were no overall differences in proportion of free primary space between most of the study shores (14.1-17.5%). Porth Defaid still had considerably higher amounts of free space than the rest (90.6%), and it tended to be less at Menai Bridge (most sheltered), and Llanfairfechan (with consistently lower bare substratum <9%). No differences were observed in exclusions between Red Wharf Bay A and Red Wharf Bay B except for the appearance of more algae on the former, where the experimental removals had run for more time. There were seasonal differences (more bare spaces in Winter, less in Spring and Summer) on all of the experimental shores. Seasonal storms can temporally free up to 90% of primary space on very exposed shores, where wave forces are of a bigger amplitude (such as Defaid), and boulders are frequently overturned by waves, and many sessile organisms are directly or indirectly killed, providing free primary space for recolonization (Sousa, 1979a*)*.

These events show that when the dominant consumers are removed, colonisation by sessile organisms and possibly subsequent interaction events, depend on the physical harshness of the environment (differences in wave exposure), reflecting the different importance of these species to the stability of sessile community assemblages in different locations (Connell, 1975). Before removal, coverage of barnacles, percentage of dead barnacles, algal coverage and bare space were fundamentally the same. Following removals of *Patella vulgata* barnacle coverage and algal coverage increased on all shores, but substantially more on sheltered shores than moderately-exposed ones, where increases were much greater than on the two exposed shores. The decreases in percentage barnacle mortality (dead barnacles) following *Nucella lapillus* removal, mirrored this same series, changing more markedly at sheltered locations. Therefore the importance of these two consumers was seen to be progressively greater with reduction in wave exposure following their artificial removal to zero or near zero levels, which is rarely seen in natural conditions on the shores of Western Britain (except perhaps for severe and prolonged storms and gales). It is important to note that the predation intensity (numbers of predators x time actively foraging) on barnacles increased on both horizontal and vertical substrata with decreasing wave exposure in unmodified conditions, whilst both the amount of interspecific and intraspecific competition decreased (lower coverage of sessile organisms, increased bare space), with exposure, similar to reaults obtained by Lubchenco and Menge (1978).

The fact that the intertidal community on rocky shores changes as a result of differences in the degree of interactions between sessile organisms and consumers along the wave exposure gradient, was stated by Connell (1972). This variation explains the divergent views in the literature on the relative importance of competition and predation on these shores, which are due to the basic intrinsic differences in composition, seen between exposed (many sessile filter feeders) and sheltered (many algae and mobile consumers) locations (McQuaid and Branch, 1985).

Sheltered areas exhibit a patchiness of sessile animals along the shore (Underwood, 1981), and are characterised by high densities of small algae and fucoids (Menge, 1976), that largely prevent barnacle and mussel settlement to any degree (Lewis, 1976). In conditions of extreme shelter (such as Menai Bridge), mats of dense *Ascophyllum nodosum* dominate most available surfaces. Very exposed shores are characterized by continuous physical and biological disturbances, and like Porth Defaid, have an abundance of free space (Dayton, 1971). They are very distinct from sheltered shores in their trophic structure, there being a gradual change from a fucoid community to one being dominated by barnacles, limpets and mussels (McQuaid and Branch, 1985), as wave action progressively increases (Menge and Lubchenco, 1981). Both the prevailing physical conditions (Lewis, 1976) and high numbers of limpets (Jones, 1946; Lodge, 1948), hold most fucoids in check, particularly when winter storms free space for barnacles by removing macroalgae. Predation intensity is related to wave action on rocky shores of the Western Atlantic (Dayton, 1971), where it partly determines the degree of domination of space by algae (Lubchenco and Menge, 1978). An increase in the harshness of physical conditions reduces the importance of predation in this region by reducing the effectiveness of predators (Menge and Sutherland, 1987).

Nucella predation can sharply reduce barnacle and mussel abundance and increase the amount of free space in the North-Western Atlantic (Waser and Price, 1981), and in the mid-intertidal regions of protected locations in the North-Eastern Pacific (Berlow and Navarrete, 1997). When these predators are excluded, interspecific competition occurs between barnacles and mussels on exposed shores, with mussels usually monopolizing the substrata from late summer to winter (Menge, 1976b), as they apparently did at Llanfairfechan where mussels outcompeted all other primary space occupants, especially on tops of boulders, and so monopolised lower-mid to mid upper levels. At more sheltered locations communities are already structured around competitive interactions, as space becomes limiting (Dayton, 1973). Similar results were also seen on vertical surfaces at the two exposed shores. Here, barnacle coverage, and the percentage of dead barnacles were significantly higher on vertical surfaces at Porth Nobla than Porth Defaid. Conversely, the availability of bare space was significantly higher at Porth Defaid, a reflection of the disparity in wave-action, and the resultant barnacle and dogwhelk densities that occur betweeen these two locations.

Comparison of boulder fields to vertical surfaces.

Results for all treatments showed that at the exposed shore (Porth Nobla), there was no difference between substratum types, but at the very exposed Porth Defaid, vertical surfaces had significantly higher coverages of live barnacles. At both shores, the percentage of dead barnacles was significantly higher on vertical surfaces (non-isolated) than boulders (isolated), and the amount of algal coverage was significantly higher on boulders than on vertical surfaces. There was only a difference (more on boulders) in bare rock at Porth Defaid in treatments 1 (*Nucella* exclusion) and 4 (control). The easier and more frequent settlement of barnacles on the lower boulders compared to the more elevated vertical faces, the greater accessibility of vertical faces to dogwhelks, and the concurrent higher efficiency of limpet removal on boulders, explain the differences in coverage of live barnacles, dead barnacles and algae respectively.

The effect of barnacle density on Nucella lapillus foraging numbers.

The numbers of *Nucella* foraging on different prey patches was directly proportional to barnacle densities on all shores except for Defaid where the correlation was more tenuous. This suggests that dogwhelks are actively drawn to concentrations of prey in densities that are roughly related to adult barnacle densities. It is very difficult to ascertain any causal relationships between predator and prey from x-sectional density measurements (Frank and Leggett, 1985; Pepin, 1987), so repeated counts of both were taken on a weekly basis on several replicated sites. Food does not seem to be a the limiting factor for *Nucella lapillus* on the shores of North Wales, as there are so many barnacles (except for Porth Defaid perhaps) in relation to the numbers of foraging whelks. It is more likely that the time available for foraging could be more important. There is evidence from previous studies that variation in prey density does account for the results of this experiment, since dogwhelks moved away from rocks stripped of barnacles, and towards boulders rich in them in research by Connell (1961b). Futhermore, the settlement of *Semibalanus balanoides* onto a shore where it had previously been uncommon, quickly induced settlement of *Nucella lapillus* as observed by Morgan (1972a).

Dogwhelks and other related intertidal carnivorous gastropods show a positive reaction to feeding conspecifics (Crisp, 1969; Trott and Dimock, 1978; Palmer, 1984), they stop amongst more abundant prey, and aggregate with other feeding individuals. An even more complex behaviour has been demonstrated in *Urosalpinx cinerea*, in the laboratory, which are repelled by starved conspecifics, but moved towards other conspecifics which had been fed (Pratt, 1976). This will tend to increase foraging efficiency by directing snails away from unproductive areas, and towards their prey, and contributes to the reationship between experimentally controlled barnacle densities and resultant *Nucella* foraging numbers seen in the experimental results.

Summary.

The effects of *Nucella lapillus* and *Patella vulgata* on the coverage of sessile organism assemblages were basically the same on both boulders and vertical surfaces, on all shores. Dogwhelks and limpets both kill barnacles in significantly large numbers, although only limpets had a sufficient impact to reduce the overall coverage of live barnacles. Again, only *Patella* (by grazing) keeps the distribution and abundance of algae low on these North Wales shores. Neither the predator nor the herbivore had any significant influence on the amount of bare space apart from *Patella vulgata* at Porth Defaid whose removal premoted a significant decrease in bare space on boulders.

Remarkably little intrinsic differences were seen between the shores in their sessile organism coverage or in the amount of bare space on boulder fields, despite their geographical separation or variation in exposure to wave-action. Only Porth Defaid had significantly lower barnacle coverage, and only the two most exposed shores (Porth Nobla and Porth Defaid) had significantly less algae, and significantly more bare space, than all the rest. Manipulative exclusions affected the sessile communities on the different shores to different extents (excluding Porth Defaid whose relative position in the hierarchy remained unchanged). Barnacle coverage at Red Wharf Bay (moderately exposed) became significantly less than on more sheltered shores, greater than on the most exposed shores, and algal coverage followed the same pattern. Finally bare space at Llanfairfechan (notably the shore without algae) was significantly lower than on other shores. Fronds of algae can be torn off during violent storms taking away much of the understory coverage (barnacles) with them in the process on the other study shores, a common process of disturbance, often producing large swathes of bare substratum at unpredictable intervals.

In Britain, a complex suite of both positive and negative interactions occurs between *Fucus vesiculosus*, *Patella vulgata*, and *Semibalanus balanoides* (Hawkins et. al., 1992). The *Nucella*-barnacle predator-prey system is widespread on our rocky shores, but there is little evidence that it is a crucial determinant of community structure, since other mortality factors and compensatory mechanisms could explain the observed changes in barnacle numbers. In fact, Connell (1961a), deduced that predation has little influence on space utilization, and that interspecific competition is the main influence on the observed distribution and abundance patterns of sessile invertebrates. Moreover, although biological interactions may directly structure many communities, the actual intensities and directions of these interactions are fundamentally shaped by underlying physical factors (Hawkins et, al., 1992).

Therefore unlike the situation on the New England coast, where there appears to be an inverse relationship betweens the influence of competition between sessile organisms, and predation in structuring the community (Menge, 1976b; Menge and Sutherland, 1976), that is dependent on the amount of activity of *Nucella lapillus* (Menge, 1978a; 1978b), *Nucella lapillus* does not function as a "keystone predator" in the studied areas on the West coast of Britain. The influence of *Nucella lapillus* predation on community structure in North Wales is somewhat limited, unlike the effects of *Patella vulgata* on sessile organisms and community structure which are far more extensive here.

The spatial (and temporal) variation of both these species does have some influence on other components of the complex "environment" of intertidal sessile organisms (Jernakoff and Fairweather, 1985). The classic theory of Paine (1966; 1974), that removal of consumers can lead to reduced diversity, whilst intermediate levels of grazing or predation lead to enhanced diversity, has been recently challenged, but not necessarily disproved by Lohse (1993), and it is still feasible that *Nucella lapillus* may actually determine the "trajectory"followed during community succession on these shores in North Wales. Successional sequences can depend heavily on predation (Lubchenco and Menge, 1978), and at the end of the two year exclusion experiments, major changes in sessile organism coverage were just starting to appear. Longer, more intense exclusions, may yet detect more substantial influences on community structure by *Nucella lapillus*.

CHAPTER 7
GENERAL DISCUSSION.

From field observations and field experimentation on the distribution, dispersal, foraging activity, microhabitat utilisation, and community interactions of *Nucella lapillus* on six North Wales shores, there were easily discernible trends in relation to the size of whelks, in different seasons, with changing shore level, and on different shores.

Size of Nucella lapillus.

The mean size and most frequent shape of dogwhelks tended to be related to the habitat they occupied at the time of sampling. Larger individuals (>30mm in length, > 20mm in width) were more often found in the open, moderately-large whelks under boulders and algal canopy, with the smaller cadres predominately in small refuges such as crevices and pits. Concurrent size changes occured between shore levels, and on different shores. Large adults and smaller juveniles dominated lower regions, effectively partitioning different growth stages along the vertical extent of the shore. Shape was also related to height on the shore, with those animals found on the low shore being longer and wider than those in the upper shore. Short squat forms dominated exposed shores, as larger forms (>30mm length; >20mm shell width) can be swept off by the high amounts of wave action, and are restricted by the decreased availability of small refuges in these locations. Both smaller whelks (<24mm) and very large individuals (30-41.9mm in shell length), were more common in sheltered areas.

There were often wide variations in shell size and shape within populations of *Nucella lapillus*, but most conformed to majority trends related to habitat, shore level and shore. Size gradients were related to size-specific mortality, as mortality rates increased in smaller animals, particularly at higher shore levels (elevated tidal height). The lower regions of sheltered shores, where *Carcinus maenas* predators were particularly common, exhibited a greater mean size in dogwhelk adults, as smaller *Nucella lapillus* were more susceptible to these crabs (personal observation).

Size determined the dispersal distance, the proportion of whelks feeding at one time, the length of the feeding bout, as well as the size of prey selected. For all of these parameters, values were higher in adults than in subadults, reduced in larger juveniles and smallest for early juveniles. Larger whelks dispersed further, foraged in greater proportions, fed for longer, and chose larger prey. Adults are able to move further than juveniles, due to a larger foot, but also did so because they are generally less restricted by potentially limiting environmental factors (chiefly desiccation). (Menge, 1978a). The mean size of individuals engaged in different activities, was also different. Those spawning were largest, then those foraging in the open, which in turn were longer than whelks foraging within refuges, and finally refuging animals were the smallest. These trends were consistent for all shore levels on all shores. Within these various activities, whelks on the low shore were generally larger than those in the mid shore, which in turn were larger than individuals in the upper shore, a reflection of the general trends of size in relation to tidal height. Larger whelks also prefered to occupy larger prey patches (where the mean barnacle size tended to be greater) and for longer (increased patch residence time). In addition, the size of the whelk and the size of refuge they occupied were clearly related, whelks increased in size as the size of refuge (maximal width), also progressively increased. Dogwhelk size and microhabitat utilisation (and concurrent activity) were closely matched, and distinct. However, these differences in size related activity and use of microhabitat become less progressively towards the upper shore, and on the very exposed shore Porth Defaid there were virtually no differences within or between shore levels.

Seasonal trends.

There were clear seasonal changes in vertical distribution in relation to desiccation, and on exposed shores in relation to periods of heavy wave action. Population size-frequency distributions decreased (mean size) following periods of spawning, and increased following both the Winter and the Summer, for during these periods mortalities of small individuals was particularly high. Spawning was particularly seasonal, being high in May and June (and occurred all year round in sheltered locations). Mean weekly dispersal figures revealed marked seasonal differences in activity. The main reasons for the observed trends were desiccation (related to air temperatures, insolation and submersion times) and wave action (related to fetch distance, wave height and wave force).

From April to October most foraging excursions took place in the open, when conditions were favourable. Conversely from June to August, a high amount of foraging in refuges was apparent, and overall dispersal activity was minimal from December to February. Only whelks at Porth Defaid showed any deviations from these trends, exhibiting relatively substantial foraging during the Summer, and even lower activity than other shores during the winter, when wave action was particularly severe. There were clear differences in seasonal patterns of dogwhelk movement (distance moved and direction of vertical migration), and degree of dispersion (aggregation), between sheltered and exposed locations (summarised in Table 7.1), reflecting changing exposure to desiccation and wave action.

Table 7.1. Seasonal trends in dispersal, migration and aggregation on different shore types.

	Dispersal		Migration		Aggregation	
	Sheltered	Exposed	Sheltered	Exposed	Sheltered	Exposed
Winter	minimal	very low	down	Low, mid up, upper down	aggregated	very highly aggregated
Spring	very high	very high	low, mid down, upper up	low,mid down, upper up	dispersed	dispersed
Summer	very low	moderate	down	down	very highly aggregated	aggregated
Autumn	high	moderate	no obvious trend	limited upward	dispersed	dispersed

Information presented show relative degrees of dispersal, migration and aggregation (subjective assessment of quantitative data).

The proportion of animals engaged in the four main identified activities was also related to type of shore and to the different seasons (Table 7.2). Spawning took place all year round on sheltered shores, being more discontinuous in other locations, especially in the upper level. Foraging in the open occured all year round on sheltered shores, but ceased at mid and upper shore levels for part of the Winter. The number of whelks foraging within refuges was inversely related to seasonal wave action and positively related to increased temperatures, especially on sheltered shores. Refuging was universely high during the winter and again very common at sheltered locations in the Summer, where desiccation effects became a particular problem. Dogwhelk mortality also varied noticably with the changing season. On sheltered and moderately-exposed shores mortality was high during the Winter and Summer, and lower in Spring and Autumn.

On exposed shores, Winter mortalities were very high, relatively lower in Summer, Spring and Autumn when compared to other environments.

Table 7.2. Summary of proportion of *Nucella lapillus* in activity in relation to season.

Activity	Shore type	Winter	Spring	Summer	Autumn
spawning	sheltered	moderate	high	low	moderate
	semi-exposed	very low	moderate-high	low	moderate-high
	exposed	moderate	low-mod	low	moderate
	very exposed	very low	low-mod	very low	low
foraging in open	sheltered	very low	high	low-mod	low-mod
	semi-exposed	very low	high	moderate	moderate-high
	exposed	very low	very high	high	high
	very exposed	extremely low	moderate	high	moderate
foraging in refuge	sheltered	low-moderate	high	high	high
	semi-exposed	low-moderate	high	high	high
	exposed	low-moderate	moderate	moderate	moderate-high
	very exposed	moderate	high	moderate	moderate-high
refuging	sheltered	very high	very low	moderate	very low
	semi-exposed	very high	low	moderate	low
	exposed	very high	low	low	low
	very exposed	very high	low-moderate	low-moderate	moderate-high

Information presented show relative degrees of activity (subjective assessment of quantitative data).

There were also marked seasonal changes in the coverage of sessile organisms on both boulders and vertical rock faces in the study area. Barnacle coverage was highest from April to July, a period when the percentage of dead barnacles was lowest. Algal coverage reached a maximum from April to September, (and was much reduced from January to March); which was the antithesis of the amount of primary space available at these times as might be expected.

Changes with shore level.

Desiccation, actual wave action experienced, and therefore the time available for foraging all change with the degree of submersion, which is governed by an individual's position (vertical distribution) on the shore. Dogwhelk dispersal and foraging changed with shore level, both being greater in the lower shore where whelks are submerged for longer. The one exception was the very exposed shore Porth Defaid, where foraging was often higher in the mid shore than lower. Feeding bout increased with tidal height, on all shores, particularly in adult whelks, and within each size class, individuals selected larger prey at higher tidal heights, reflecting the reduced opportunity for foraging at those levels. The overall degree of aggregation was generally highest in the upper shore, apart from the two most exposed shores (Porth Nobla and Porth Defaid,) where it was even more pronounced in the lower shore during the winter, when these areas are subject to very strong wave action.

The relative proportion of dogwhelks engaged in different activities (spawning, foraging, refuging), clearly varied with shore level. The numbers (and proportion) spawning (predominantly in lower levels at sheltered locations) increased up the shore with increasing wave action (from Menai to Nobla inclusive), except for Porth Defaid, which though very exposed, had a higher proportion of whelks spawning in the lower shore. This is obviously related to desiccation effects (on sheltered shores), and increasing wave momentum (at more exposed sites), that sequentially change along the wave-exposure gradient. The proportion of dogwhelks foraging tended to be higher in the lower shore, and lowest higher up the shore, particularly foraging in the open. Foraging in the open, was greatest in the upper shore, reduced in the lower shore, during bad (stormy) weather at Porth Defaid. Foraging in refuges increased with tidal height, noticably more so on the three more exposed shores. The proportion refuging was greatest on the upper shore at all times, on all shores, except again for Porth Defaid, where most refuging occurred in the lower reaches of the shore in response to heavy wave action. Overall whelk density decreased with tidal height (but was modified periodically by seasonal migration patterns), whereas mortality rates increased with tidal height, even on sheltered shores where predation is higher on the lower reaches of the shore.

The coverage of barnacles was intrinsically greatest in the lower shore, gradually decreasing with tidal height on all shores, except for the two most exposed shores, which showed a fairly uniform abundance of barnacles with changing height in the boulder field. The percentage of dead barnacles was highest in mid shore (on all shores). Algal coverage did not generally change with shore level, except for Red Wharf Bay where it decreased noticeably with tidal height. The availability of bare space increased significantly with tidal height on all shores. These observed patterns in coverage are related to recruitment, desiccation, wave action and community interactions, but it would require further field investigations to determine the relative importance of each factor in time and space.

Lighter coloured dogwhelks were more common in the mid and upper shore (which is subject to longer periods of emersion and hence insolation, during day time low tides), than in the lower shore at all locations, but especially on sheltered shores. Many darker morphs were found in the middle shore of Llanfairfechan associated with the extensive mussel beds in that area, an environment in which their colour pattern rended them substantially more cryptic.

Changes with shore.

Wave exposure changed sequentially on all six shores from Menai (very sheltered) to Porth Defaid (very exposed) inclusive. Differences in topography and microhabitat on these shores influenced within shore distribution and activity of dogwhelks, the distribution of sessile organisms, and the intensity of wave action they were subjected to. Both the frequency of whelks with teeth and the number of teeth per individual (indicators of environmental stress) increased with wave exposure, indicating that exposed shores constitute a more difficult environment for dogwhelks. As an indication of this, density decreased as wave exposure increased, due in part to higher overall mortality rates on these exposed shores.

Monthly dispersal distances varied more markedly at the three more exposed shores, which showed higher weekly migrated distances, particularly in Spring and Autumn. In Winter, wave action was more severe on the exposed shores, often making foraging in the open unsafe due to a greater risk of dislodgement. The frequency (and extent) of passive dispersal episodes, were certainly greater on the more exposed shores at this time. Dispersal and foraging behaviour changed significantly with shore type, which can be explained by wave action reducing the efficiency of foraging at these locations. As a result of this, feeding bout length increased with wave exposure, as dogwhelks needed to forage longer to attain and consume sufficient prey items. *Nucella lapillus* is an opportunistic feeder on exposed shores where the time available for foraging is often restricted by large waves. So whelks in this situation tend to forage (disperse) further and for longer, and when conditions are favourable (less than severe wave-action).

The overall proportion of *Nucella lapillus* involved in different activities at any one time also changed from shore to shore. Overall spawning was greatest on sheltered shores, followed by moderately-exposed to exposed shore, lowest on the extremely exposed shore Porth Defaid. Overall foraging in the open occurred more on the three most exposed shores, whilst foraging in refuges was inversely related to wave exposure. A higher overall proportion of whelks was found refuging at Llanfairfechan (no algal coverage), and Defaid (very exposed to wave action) during the two year period, followed by the two most sheltered shores. Refuging was comparably lower at Red Wharf Bay and Porth Nobla.

Space utilisation was clearly different on shores subject to different degrees of wave action, and dogwhelks showed clear trends in their microhabitat utilisation. There was a shift from horizontal surfaces to vertical surfaces as wave exposure increased (apart from the very exposed Defaid where this trend was reversed), as well as an increase in the occupation of small refuges such as pits and crevices. The use of under boulders spaces decreased with increased wave impact. More dogwhelks were found in empty shells and in the spaces between barnacle shells on moderately-exposed shores, compared to both sheltered and exposed locations.

The exclusion experiments revealed interesting facets of the relationship between sessile organisms consumers *Nucella lapillus* and *Patella vulgata*. Before exclusion, barnacle coverage and the percentage of dead barnacles were not significantly different between shores (except for Porth Defaid). Algal coverage was basically the same at sheltered and moderately-exposed locations, and lower at the two exposed shores. Bare space did not vary significantly between sites (apart from Defaid). After *Patella vulgata* exclusions, barnacle coverage increased significantly on all shores, increases being significantly greater on the three most sheltered shores than the three more exposed.

The positive effect of limpet removal on barnacle coverage, showed that their bulldozing effects have a greater negative effect on barnacles cyprids and metamorphosed larvae, than the positive effect they have by keeping algal growth to a minimum (reducing competition for space). *Patella* removals led to a significant increase in algal coverage on all shores (except for Llanfairfechan where macroalgae was completely absent). Algal cover increases were greatest on sheltered shores, and least on the two exposed shores. After *Nucella lapillus* exclusions, the percentage of dead barnacles decreased on all shores, changes being more extensive on the two most sheltered shores, again less so at the exposed experimental sites. Decreases in primary space, that followed *Patella vulgata* exclusions were greatest on the three most sheltered shores, less pronounced at the three more exposed locations.

It appears that the importance of these two consumers (based on the magnitude of changes in coverage), is much greater on the more sheltered shores, as barnacle density, algal cover, and availability of bare space were affected differentially in those locations, in relation to wave exposure. The studied shores were different in community structure. An increase in physical harshness had important effects, reducing the impact (intensity) of predation of *Nucella lapillus* (by reducing time for foraging, reducing efficiency), as well as (to a lesser extent) the movement and foraging activity for *Patella vulgata*. Generally speaking, environmental conditions govern the behaviour (foraging, refuging, migration) of *Nucella lapillus* on the shores of North Wales. Prey (barnacles) are usually in ample supply, and the numbers of whelks in one place at one time were not high enough for intraspecific interference (competition) to become significant. Even at Porth Defaid, where barnacle densities are relatively low compared to foraging dogwhelks, the extreme conditions still determined the everyday activities of these carnivores. Moreover, there were considerable differences in slope, wave-exposure, topography, microhabitat availability, as well as the structure of the sessile community on the different shores. All of these factors played a part in the different observed patterns of dogwhelk foraging and prey selection, refuging, and migration, as well as in the variation in the shape and size-frequency distributions of populations in these locations. Similar trends in dogwhelk behaviour did occur on all the shores, but clearly detectable differences were seen at Porth Defaid, which is at one extreme of the wave-exposure gradient.

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APPENDIX 1.

PHOTOGRAPHS OF FIELD WORK.

Figure 1.1. *Nucella lapillus* exclusion on boulder field at Red Wharf Bay (mid shore, June 97).

Figure 1.2. *Patella vulgata* exclusion on boulder field at Red Wharf Bay (mid shore, June 97).

Figure 1.3. *Nucella lapillus* and *Patella vulgata* exclusion on boulder field at Red Wharf Bay (mid shore, June 97).

Figure 1.4. Control treatment (no exclusions) on boulder field at Red Wharf Bay (mid shore, June 97).

Figure 1.5. Microhabitat utilisation experiment showing one 4m^2 study area (mid shore, Red Wharf Bay).

Figure 1.6. Microhabitat utilisation experiment showing one $4m^2$ study area (upper shore, Porth Nobla).

Figure 1.7. Vertical surfaces used in experiments at Porth Defaid.

Figure 1.8. Tagged *Nucella lapillus* foraging in dense barnacle bed (mid shore, Red Wharf Bay).

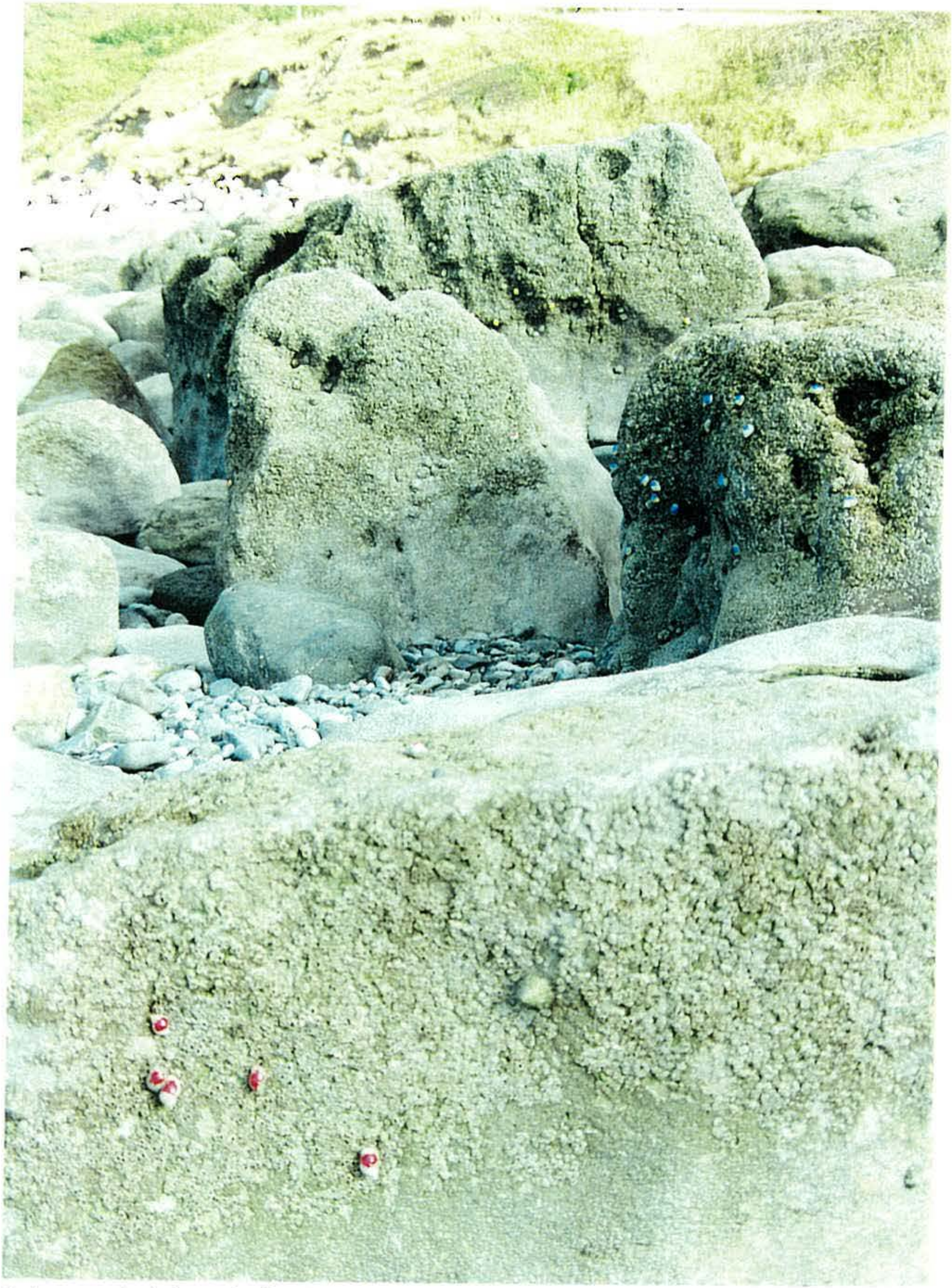


Figure 1.9. Colour coded dogwhelks in dispersion (aggregation) experiment (Red Wharf Bay).

Figure 1.10. Maximum wave-force measuring equipement (low shore, Red Wharf Bay).

Table 2.1 Horizontal Distribution of Dogwhelks, including mean size, shape, microhabitat and relative density.

Key.
N = Number collected.
L = Length of Shell (mm).
Sp = Spire Length (mm).
Map Ref. = Co-ordinates on Anglesey.
L/Ap = Length/Aperture length ratio.
WapxAp = Aperture Area x 2.
RD = Relative Density (N/3 mins).
L/W = Length/Width ratio.

Key to Microhabitat Types.
AFTBS = Artificial fish trap boulders on sand
BE = Boulder, exposed site
BFP = Boulder field, protected site
BH = Boat hull (derilict)
C = Crevice in rock
CSO = Crevice, sheltered outcrop
DBM = Dispersed boulders, mud
DMS = Dispered mussels, flat sand
DSBM = Small dispersed boulders, mud
EO = Exposed outcrop
IP = Irregular rock platform
IRO = Irregular rock outcrop
IROC = Irregular rock outcrop in crevice
L = Ledge
LBM = Large boulder, mud
LROS = Large rock outcrop, sand
P = Rock platform
PS = Rock platform, sheltered site
PIER = Rock substrate under pier
POT = Pot-holed rock substrate
RMUSS = Rock covered in mussels
RP = Rock, protected site
RAMPS = Shelterd site on slipway
ROE = Rock outcrop, exposed site
SBM = Small boulder, mud
SBSC = Small boulder in sheltered cove
SRM = Small rock, mud
SRO = Small rock outcrop
SS = Small stones
Slate = Slate rock slabs
TR = Trench (gulley)
VRO = Vertical face on rock outcrop
VC = Vertical sided steep channel
B = Boulder
BF = Boulder field
BRO = Boulder on rock outcrop
Bridge = Rock substrate under bridge
CEO = Crevice, exposed outcrop
CAVE = Substrate in cave
DBS = Dispersed boulders, sand
DSB = Small dispersed boulders
DSBS = Small dispersed boulders, sand
EOS = Exposed outcrop, sheltered site
IR = Irregular rock
IROS = Irregular rock outcrop, sheltered
ISRO = Island of rock outcrop
LB = Large boulder
LBF = Large boulder field
MBF = Medium boulder field
PE = Rock platform, exposed site
PC = Rock platform, in crevice
PIPE = On sewage pipe (mussels)
R = Rock
RMB = Rock on mussel bed
RAMP = Concrete slipway
RO = Rock outcrop
ROS = Rock outcrop, sheltered site
SBP = Small boulder protected site
SBFS = Small boulder field, sand
SRS = Small rock, sand
STIRO = Steep irregular rock outcrop
SSS = Small stones, sand
SJ = Stone Jetty
V = Verticle face
VROE = Exposed vertical face on outcrop

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
1a	532814	SBF	10	0.2	24.50	1.538	1.408	10.45	156
1b	533816	SBF	22	0.1	28.50	1.524	1.373	9.42	170
2	533818	L	10	0.2	29.22	1.506	1.401	9.63	166
3a	572811	DBS	20	10	27.44	1.489	1.414	8.69	149
3b	574813	DBS	26	10	27.54	1.507	1.303	9.13	156
4	575814	BF	23	10	30.45	1.474	1.339	9.99	208
5	576815	BF	20	10	30.68	1.598	1.394	10.69	175
6	577818	BF	30	10	29.28	1.529	1.395	9.87	173
7a	578818	EO	20	15	24.50	1.446	1.364	7.27	111

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
7b	579819	EO	20	15	29.64	1.482	1.371	7.39	167
8	580820	EO	20	15	24.67	1.438	1.387	6.96	132
9	583822	BF	20	30	26.43	1.467	1.385	7.97	136
10	585823	BF	20	30	26.22	1.469	1.389	7.88	138
11	587823	BF	20	30	26.82	1.504	1.369	8.11	143
12a	589824	BF	20	35	29.94	1.461	1.363	8.13	155
12b	590824	BF	20	35	26.98	1.555	1.386	8.32	137
13	593824	LBF	20	40	28.87	1.513	1.395	9.27	165
14a	642814	EOS	20	13	28.60	1.581	1.478	9.66	144
14b	642815	EOS	20	12	28.32	1.614	1.422	10.48	150
14c	641815	EOC	24	10	28.03	1.575	1.376	11.79	183
14d	641815	EOC	21	10	27.39	1.554	1.382	11.69	177
14e	641814	EO	20	10	25.51	1.463	1.345	9.84	175
15	640814	EOS	22	15	27.53	1.509	1.288	10.10	151
16	637814	EOS	20	13	25.96	1.532	1.359	8.14	129
17	636815	EOS	20	10	31.11	1.585	1.455	13.93	220
18	635815	EO	20	10	24.94	1.493	1.321	11.59	180
19	635816	EO	23	13	24.76	1.467	1.324	6.63	139
20a	634816	BH	21	15	27.04	1.539	1.343	8.39	151
20b	633816	SBF	20	17	27.15	1.476	1.323	8.54	170
21	631817	V	20	12	25.84	1.494	1.409	6.95	131
22a	630818	EO	23	10	25.68	1.486	1.405	6.86	126
22b	628818	EO	23	10	23.67	1.478	1.359	6.47	116
23a	627817	EO	20	10	23.19	1.479	1.269	6.86	114
23b	627816	EOS	23	15	26.74	1.525	1.292	9.08	147
24a	626817	EO	22	12	24.36	1.506	1.242	7.46	127
24b	623816	EO	20	13	27.52	1.506	1.309	8.69	165
25	624816	R	20	13	24.42	1.476	1.328	7.19	117
26	623815	RO	20	20	26.46	1.589	1.385	8.12	124
27	622815	C	20	18	29.07	1.662	1.397	10.05	147
28	621815	BF	21	20	28.61	1.527	1.404	9.21	170
29a	620815	RAMP	20	17	27.38	1.544	1.336	9.24	156
29b	620815	RAMP	20	18	27.96	1.487	1.345	9.45	171
30a	619816	SBFS	20	18	29.38	1.573	1.491	14.17	213
30b	619816	SBFS	20	15	29.70	1.558	1.472	13.40	210
30c	619817	SBFS	20	15	29.49	1.608	1.519	13.70	193
31	533819	L	20	1	27.78	1.513	1.373	10.78	199
32	532821	L	20	1.5	28.87	1.575	1.487	8.77	156
33a	531821	DSBS	20	7	27.98	1.541	1.457	8.57	148
33b	532822	DSBS	20	10	28.59	1.618	1.519	9.92	154
34	528823	DSBS	20	10	29.19	1.614	1.447	12.42	196
35	526824	DSBS	20	11	27.82	1.561	1.457	9.25	150
36	524825	DBS	20	22	28.52	1.621	1.533	10.17	163
37	524827	PIPE	20	2.5	33.50	1.485	1.377	10.55	191
38	522830	SBF	20	17	27.00	1.523	1.427	12.83	208
39a	523831	SBF	20	15	28.69	1.597	1.486	12.95	185
39b	523832	SBF	20	15	28.44	1.601	1.511	12.90	185
39c	523833	SBF	20	15	29.77	1.519	1.445	13.12	234
40	522834	POT	20	10	25.22	1.487	1.389	10.50	166
41	619815	SJ	20	12	27.65	1.559	1.427	11.87	195

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
42a	618816	TR	20	20	25.34	1.534	1.358	10.79	157
42b	617816	TR	20	19	25.76	1.511	1.397	11.07	170
43	615817	TR	20	23	26.35	1.539	1.367	10.92	176
44	613817	B	20	18	28.70	1.589	1.436	12.70	193
45a	610818	PC	20	13	27.78	1.626	1.398	12.43	180
45b	609818	PC	20	12	28.34	1.601	1.298	12.75	196
46a	609819	CAVE	20	21	24.53	1.466	1.281	9.57	172
46b	609819	CAVE	20	20	24.14	1.435	1.302	9.08	166
47	608818	V	20	25	24.67	1.504	1.359	10.44	162
48	607818	BF	20	20	24.05	1.395	1.317	9.02	179
49	606819	RO	20	23	28.08	1.497	1.525	11.51	204
50	605820	RO	26	18	24.48	1.427	1.375	9.85	178
51	604822	ROE	20	17	23.20	1.445	1.348	8.49	155
52	603823	ROS	20	20	28.14	1.568	1.389	12.33	192
53a	602823	RO	20	12	27.05	1.459	1.354	10.82	196
53b	601823	RO	20	15	27.39	1.548	1.371	11.62	191
54a	597823	BF	20	13	27.34	1.643	1.407	12.36	164
54b	595824	BF	23	13	27.60	1.582	1.414	12.10	178
55	642813	P	20	7	30.04	1.498	1.378	12.50	232
56	642812	C	20	7	29.53	1.529	1.379	12.43	224
57	642812	C	20	8	29.47	1.591	1.378	13.35	196
58	642811	SBF	20	5	29.55	1.606	1.406	13.28	195
59	642811	SBF	20	4	29.77	1.619	1.398	13.42	188
60	641811	SJ	20	5	30.00	1.681	1.438	13.81	188
61	639810	ROS	20	17	29.15	1.678	1.448	13.34	169
62	639808	ROS	24	18	29.81	1.582	1.411	13.42	212
63	638806	RO	20	12	28.62	1.584	1.401	12.70	198
64	637805	SBF	20	3	31.57	1.573	1.439	14.73	249
65	635805	LB	23	5	27.84	1.749	1.501	13.28	159
66	631804	DSBS	20	2.5	27.68	1.687	1.497	12.55	156
67a	632798	DBS	20	1.5	30.60	1.771	1.523	12.60	135
67b	631797	DBS	21	3	28.47	1.701	1.587	13.35	159
67c	631797	DBM	20	3.5	29.10	1.723	1.449	11.87	144
68a	630796	DBM	20	5	29.98	1.597	1.444	13.56	199
68b	630796	DBM	20	3.5	27.75	1.565	1.401	11.92	184
68c	629796	DBM	20	2	28.20	1.586	1.437	12.34	180
69	628795	V	22	5	27.41	1.599	1.409	12.16	171
70	627795	DSBM	26	6	27.60	1.769	1.456	13.14	148
71	627794	DSBM	20	3	27.42	1.721	1.497	12.21	152
72	626793	DSBM	20	2.5	28.85	1.651	1.382	10.90	151
73	626792	DSBM	20	2.5	29.20	1.692	1.477	13.39	166
74a	625792	DSBM	20	4.5	27.02	1.662	1.464	11.99	155
74b	625791	DSBM	20	4	24.11	1.598	1.441	10.24	126
75	624790	DSBM	20	4	26.31	1.653	1.479	11.71	136
76	623789	DSBM	20	3.5	28.72	1.631	1.475	12.60	168
77	622786	DSBM	20	3.5	31.21	1.709	1.543	14.03	185
78	622785	DSBM	20	2	28.47	1.824	1.474	13.65	140
79	619784	SBM	20	1	27.56	1.888	1.566	13.44	120
80	618781	SBM	20	5	30.46	1.686	1.477	14.90	191
81	618778	SBM	20	5	28.93	1.707	1.471	12.86	159

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
82	616777	SBM	20	7.5	27.57	1.551	1.459	12.43	187
83	615776	SBM	20	5	27.75	1.625	1.503	12.15	244
84	612774	SBM	20	6	28.28	1.584	1.557	13.72	196
85	612771	SSM	20	5	31.73	1.602	1.501	15.56	231
86	611768	SSM	20	7.5	31.37	1.634	1.508	15.37	219
87	611765	SSM	20	10	31.81	1.684	1.484	15.76	216
88	610763	SSM	20	17	30.94	1.651	1.497	15.34	211
89	606758	PIER	20	10	33.44	1.507	1.511	14.56	287
90	599751	SBM	23	4.5	27.74	1.617	1.482	11.98	150
91	595750	SBM	20	1	35.05	1.749	1.447	17.09	259
92	594749	SBM	20	4	30.28	1.599	1.409	13.12	208
93	593748	SBM	20	2	32.00	1.561	1.397	13.10	242
94	592748	SBM	20	2	30.48	1.584	1.486	13.26	206
95	590747	SBM	20	1.5	29.95	1.618	1.474	12.85	199
96	589746	LBM	20	1	32.53	1.547	1.469	13.74	245
97	581741	IRO	20	1	32.41	1.546	1.411	13.45	244
98a	522835	LBF	20	17	26.07	1.478	1.323	9.59	180
98b	522836	LBF	21	20	27.52	1.529	1.337	11.03	200
98c	522837	LBF	20	20	27.14	1.519	1.301	10.66	199
99a	521838	LBF	40	22	26.49	1.559	1.377	9.25	149
99b	521838	LBF	20	23	28.40	1.616	1.376	11.34	171
100a	521839	LBF	22	25	26.47	1.546	1.355	8.28	147
100b	521839	LBF	22	22	29.51	1.527	1.403	12.43	226
100c	520840	LBF	20	30	28.18	1.573	1.362	9.85	166
101a	520841	LBF	20	23	27.04	1.495	1.403	10.47	192
101b	520842	LBF	42	30	28.09	1.605	1.36	10.21	164
102	520843	LBF	25	20	28.32	1.558	1.394	10.24	164
103	520845	P	41	26	27.09	1.569	1.387	9.76	156
104	520846	P	26	21	28.65	1.558	1.355	9.92	173
105	520847	P	31	20	29.81	1.551	1.438	12.61	209
106a	519848	LBF	22	17	28.24	1.593	1.389	11.28	183
106b	519848	LBF	20	20	27.14	1.528	1.378	10.59	183
106c	519848	LBF	20	20	29.10	1.549	1.389	11.68	196
106d	519848	LBF	20	16	28.40	1.541	1.367	11.77	210
107a	518848	P	20	14	27.11	1.609	1.429	11.02	168
107b	518848	P	20	13	27.78	1.556	1.386	11.08	191
108a	518847	DBS	21	18	26.91	1.517	1.405	10.18	180
108b	518847	DBS	49	18	29.22	1.594	1.407	11.36	180
108c	518847	DBS	40	20	28.64	1.639	1.448	11.88	175
109a	516847	IROS	20	11	31.53	1.538	1.379	13.70	231
109b	516848	IROS	20	12	29.41	1.564	1.397	11.94	192
110a	514850	SRO	20	15	26.87	1.581	1.401	10.61	176
110b	514851	SRO	20	15	29.83	1.581	1.437	11.64	190
110c	515851	TR	22	13	28.05	1.576	1.386	11.09	186
111	516852	IP	25	12	28.30	1.594	1.413	11.46	178
112	518853	IP	24	14	27.33	1.542	1.405	10.53	186
113	518853	IP	30	16	29.76	1.609	1.428	12.86	210
114	517854	IP	20	19	28.55	1.571	1.401	11.72	195
115	517854	IP	20	17	29.60	1.611	1.434	12.69	186
116	517855	C	20	22	28.99	1.656	1.413	12.23	180

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
117	517856	IP	20	16	26.17	1.594	1.386	9.79	157
118	516857	IP	20	14	23.91	1.576	1.368	10.37	158
119	515857	P	20	17	28.27	1.624	1.419	11.57	182
120	514857	P	20	16	27.70	1.581	1.386	11.02	182
121	514858	B	20	13	26.41	1.619	1.451	10.47	150
122	514859	RO	20	18	27.28	1.551	1.353	10.51	182
123	514860	RO	20	19	26.93	1.521	1.345	11.50	190
124	513863	V	39	24	28.07	1.661	1.467	12.28	176
125	514864	MBF	22	20	27.77	1.639	1.418	11.89	168
126	514865	MBF	27	25	27.98	1.643	1.407	11.61	172
127	515865	RAMP	30	18	26.83	1.611	1.407	11.17	162
128	515865	RAMPS	40	24	28.06	1.641	1.389	11.48	165
129	516866	MBFS	30	15	28.44	1.674	1.456	11.90	163
130	517867	ROE	20	5	23.61	1.499	1.319	7.98	143
131	517868	BS	20	10	29.56	1.716	1.448	12.68	177
132	517869	BS	26	14	28.67	1.723	1.439	12.57	162
133	516869	BS	26	16	30.06	1.712	1.418	13.12	178
134	515869	RMB	38	19	26.68	1.583	1.383	10.07	160
135	514868	LBF	23	15	31.00	1.672	1.422	13.74	202
136	513868	LBF	31	17	30.29	1.613	1.419	12.52	201
137	511869	LBF	24	16	30.59	1.639	1.416	13.22	206
138	509871	MBF	36	21	29.74	1.627	1.441	11.26	190
139	508871	MBF	20	20	27.82	1.496	1.373	10.53	192
140	508872	MBF	20	19	25.99	1.498	1.359	11.38	161
141	507872	MBF	25	22	26.96	1.533	1.325	10.66	182
142	506873	MBF	20	18	26.02	1.501	1.346	8.99	169
143	506872	MBF	20	19	29.28	1.675	1.451	12.45	180
144	506872	MBF	20	19	30.55	1.548	1.372	12.26	221
145	505872	MBF	20	22	27.51	1.556	1.345	10.67	177
146	505872	MBF	20	20	30.94	1.587	1.407	13.11	223
147	505872	MBF	25	18	28.39	1.687	1.381	12.59	174
148	504872	MBF	20	17	29.50	1.693	1.474	12.67	173
149	504872	MBF	20	19	28.79	1.612	1.411	11.99	177
150	504872	MBF	20	18	29.85	1.527	1.365	11.96	221
151	503872	IROC	20	13	29.66	1.588	1.393	12.08	189
152	503872	IROC	20	15	20.90	1.514	1.384	11.38	161
153	505875	IROC	20	20	25.79	1.615	1.417	11.75	146
154	504873	IROC	20	17	28.09	1.612	1.381	11.46	166
155	503873	IROC	20	15	27.09	1.537	1.339	10.33	174
156	502873	B	29	20	26.81	1.598	1.403	10.17	136
157	501872	AFTBS	20	10	31.02	1.668	1.478	13.42	197
158	500873	AFTBS	20	7.5	30.39	1.646	1.454	12.86	186
159	494877	IROS	20	14	26.65	1.532	1.408	9.49	158
160	495878	IROS	65	22	25.15	1.571	1.352	8.89	136
161	494879	IROS	22	15	25.62	1.569	1.334	9.39	138
162	495880	IROS	23	16	25.81	1.597	1.344	9.90	145
163	494880	IROS	47	19	26.53	1.571	1.309	10.39	160
164	494881	LROS	20	17	27.15	1.599	1.396	11.28	175
165	494883	LROS	20	7.5	27.71	1.599	1.396	11.97	154
166	496883	SRS	20	8	28.86	1.581	1.428	11.58	191

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
167	493883	SRS	29	22	29.03	1.641	1.421	12.13	173
168	493884	SRS	20	20	26.32	1.625	1.359	11.02	147
169	489887	LROS	20	19	28.10	1.659	1.381	11.77	169
170	490888	LROS	35	18	27.19	1.651	1.383	11.37	159
171	489888	LROS	20	10	26.90	1.558	1.416	9.74	159
172	490889	LROS	28	16	30.04	1.612	1.432	12.62	200
173	489890	LROS	28	21	27.44	1.565	1.407	11.47	171
174	488888	LROS	20	10	28.53	1.609	1.414	11.60	179
175	487895	R	20	10	27.62	1.609	1.437	10.59	160
176	490898	SLATE	20	10	27.49	1.669	1.426	11.25	148
177	491900	B	46	23	27.40	1.583	1.347	12.40	162
178	493902	P	31	10	30.05	1.639	1.444	12.68	170
179	492904	P	20	8.5	27.98	1.589	1.358	10.66	174
180a	492906	LBF	35	15	26.01	1.649	1.395	10.02	136
180b	492907	LBF	20	10	23.10	1.585	1.404	8.03	109
181	457937	STIRO	20	9	23.19	1.452	1.274	7.46	131
182	461936	STIRO	20	9	26.04	1.583	1.379	9.01	138
183	465935	STIRO	20	11	24.22	1.483	1.291	8.14	137
184	469932	STIRO	22	11	26.00	1.483	1.338	9.17	157
185	470933	STIRO	25	13	25.93	1.542	1.399	8.92	137
186	472933	STIRO	49	24	23.48	1.492	1.306	8.07	125
187	474933	STIRO	49	25	24.21	1.496	1.311	8.10	125
188	476932	STIRO	22	11	25.35	1.501	1.327	8.13	160
189	477931	STIRO	20	10	27.94	1.526	1.353	10.40	187
190	481933	RO	20	5	24.90	1.525	1.341	8.68	134
191	483932	RO	20	5.5	23.92	1.564	1.367	8.41	111
192	483930	RO	20	4.5	26.27	1.529	1.358	8.84	158
193	481934	RO	27	8	29.12	1.529	1.384	9.98	188
194	481935	RO	27	9	28.22	1.523	1.309	10.45	197
195	482936	RO	47	12	27.55	1.528	1.329	10.30	188
196	484929	P	26	10	26.30	1.587	1.404	12.28	202
197	484928	P	20	5	29.32	1.562	1.342	10.89	204
198	483927	P	24	6	30.82	1.588	1.381	11.81	206
199	478930	LBF	20	10	30.10	1.571	1.388	11.54	186
200	479931	LBF	23	11	26.24	1.462	1.321	8.26	171
201	479932	LBF	20	11	27.20	1.555	1.366	9.01	179
202	478934	VC	20	12	32.23	1.571	1.399	13.26	231
203	488920	VC	36	6	27.69	1.539	1.354	9.89	174
204	489920	VC	26	5	26.03	1.539	1.345	9.18	148
205	489919	VC	40	7	26.64	1.645	1.428	10.29	130
206	489918	VC	40	8	25.90	1.568	1.314	9.77	142
207	488917	SBP	20	5	26.94	1.601	1.368	9.52	131
208	488916	SBP	27	7	27.05	1.619	1.429	10.23	138
209	488915	RO	57	14	26.89	1.614	1.384	9.96	139
210	489914	RO	76	19	26.41	1.585	1.382	9.86	138
211	490914	RO	33	8.5	26.46	1.639	1.408	10.18	126
212	490913	RO	31	8	24.77	1.633	1.466	9.01	105
213	492912	B	33	16	25.90	1.606	1.441	9.02	126
214	492911	B	20	10	25.59	1.588	1.436	9.15	126
215	492910	B	25	12	26.02	1.608	1.412	9.45	127

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
216	492908	B	54	27	26.46	1.611	1.432	9.71	132
217	214796	SBSC	20	10	28.87	1.629	1.499	10.40	157
218	215796	CAVE	21	9.5	28.24	1.474	1.339	8.90	192
219	217798	V	20	9	22.85	1.511	1.372	6.99	108
220	218798	V	20	8	23.83	1.544	1.366	7.58	117
221	232799	IRO	20	7.5	23.80	1.499	1.389	7.12	117
222	233799	IRO	20	7	23.20	1.464	1.318	6.75	116
223	233796	ROE	20	5	25.11	1.424	1.321	7.03	125
224	242795	RO	20	5	27.60	1.527	1.368	9.64	152
225	242794	RO	63	8	24.42	1.511	1.379	7.60	129
226	240797	RO	20	10	24.48	1.451	1.372	7.67	140
227	248792	IRO	33	17	25.06	1.529	1.399	7.69	127
228	249791	IRO	20	10	22.47	1.415	1.335	6.28	117
229	250791	ROE	20	10	27.67	1.547	1.431	9.71	153
230	252790	ROE	20	9	25.24	1.547	1.421	8.47	129
231	254791	V	20	8.5	23.22	1.524	1.378	7.36	108
232	255787	P	20	12	24.56	1.494	1.355	7.61	121
233	254786	P	38	9.5	25.76	1.552	1.382	8.81	136
234	254786	RO	32	8	27.23	1.466	1.333	8.85	172
235	253786	RO	63	11	25.29	1.509	1.356	7.98	134
236	253786	ROS	49	5	27.19	1.521	1.364	9.11	161
237	253785	TR	20	20	27.99	1.503	1.345	9.50	182
238	254784	V	22	11	26.47	1.494	1.375	8.49	150
239	254783	RO	20	10	25.92	1.484	1.345	9.23	165
240	253783	ROS	22	11	26.22	1.499	1.399	7.91	140
241	252783	ROE	20	10	25.64	1.494	1.374	7.93	148
242	251782	ROE	44	11	26.64	1.471	1.355	8.19	162
243	251781	ROE	21	5.5	25.34	1.481	1.357	7.91	132
244	250780	ROE	30	7.5	24.92	1.449	1.294	7.34	147
245	250779	ROE	20	5	23.77	1.406	1.258	7.01	138
246	250779	ROE	36	9	24.35	1.391	1.243	6.86	155
247	253774	ROE	36	9	25.02	1.476	1.323	7.35	143
248	252777	ROE	44	11	25.37	1.469	1.334	7.36	143
249	251779	ROE	50	13	24.80	1.494	1.334	7.38	130
250	253772	ROE	20	5	26.74	1.424	1.321	7.40	176
251	256772	LROS	28	7	28.38	1.541	1.402	7.60	104
252	275748	RO	20	5	24.72	1.516	1.353	7.48	119
253	273749	RO	38	9.5	25.09	1.531	1.372	8.17	128
254	272750	RO	20	5	27.24	1.512	1.391	8.60	148
255	271746	BRO	20	5	27.98	1.521	1.354	9.34	169
256	270746	ROS	20	6	28.57	1.602	1.402	10.07	156
257	271747	V	20	6	25.75	1.587	1.372	8.44	126
258	269747	V	33	5.5	24.34	1.522	1.367	7.23	125
259	268747	TR	20	10	24.72	1.569	1.383	7.75	116
260	266748	ROE	20	5	26.19	1.513	1.316	8.54	150
261	263751	ROE	20	5.5	23.05	1.316	1.204	5.99	156
262	258754	RO	20	5	25.80	1.448	1.306	6.30	175
263	290750	ROS	20	4.5	24.75	1.421	1.221	7.65	163
264	292752	ROS	20	5	28.26	1.442	1.301	8.50	213
265	295751	LRO	20	5	24.70	1.449	1.304	6.20	133

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
266	309738	IROS	33	5.5	27.78	1.535	1.295	9.19	169
267	309739	IROS	20	5	26.95	1.522	1.283	8.68	162
268	308739	IROS	27	7	26.24	1.516	1.276	8.43	155
269	308740	IROS	20	5	25.77	1.451	1.271	7.89	160
270	307741	IROS	53	8	25.59	1.512	1.273	7.89	146
271	306741	IROS	20	10	24.74	1.461	1.274	7.64	149
272	306739	IROS	23	11	24.84	1.509	1.286	7.53	131
273	305736	TR	20	5	24.77	1.526	1.278	7.34	129
274	314731	RO	32	8	24.02	1.539	1.293	7.18	112
275	314729	RO	23	12	24.14	1.545	1.316	7.23	114
276	311729	RO	20	10	23.89	1.564	1.369	7.38	103
277	315727	C	33	16	24.43	1.573	1.367	7.64	106
278	315724	C	20	10	23.88	1.571	1.338	7.25	102
279	317723	RO	33	17	26.04	1.538	1.288	8.23	150
280	325719	ROS	29	15	24.01	1.539	1.341	7.23	105
281	328715	IRO	20	14	25.58	1.483	1.279	7.69	150
282	328713	IRO	20	10	23.23	1.406	1.268	5.83	124
283	329712	IRO	20	9.5	25.64	1.512	1.332	7.81	145
284	328710	IRO	20	11	25.45	1.484	1.326	6.73	146
285	332708	V	20	8.5	25.16	1.481	1.322	7.18	148
286	332708	V	20	11	23.84	1.445	1.251	6.59	135
287	331707	V	20	12	23.19	1.482	1.271	6.98	118
288	331707	V	20	13	24.52	1.443	1.254	6.73	146
289	330707	V	20	11	23.85	1.431	1.249	6.43	135
290	330707	V	20	5	25.69	1.483	1.261	8.11	137
291	328706	LB	20	12	26.61	1.521	1.272	8.33	164
292	328708	B	30	12	25.64	1.409	1.217	7.34	175
293	331705	B	35	16	27.22	1.461	1.256	8.46	184
294	331706	V	20	6	26.22	1.407	1.253	7.51	189
295	333683	RO	20	10	24.39	1.543	1.326	7.71	120
296	335683	RO	20	10	26.29	1.609	1.374	8.73	130
297	337682	RO	23	12	25.46	1.555	1.311	8.34	131
298	337680	RO	26	15	24.55	1.527	1.267	7.59	125
299	337678	RO	20	12	24.65	1.453	1.235	7.33	141
300	348677	RO	36	12	25.69	1.518	1.265	8.05	147
301	351678	RO	22	11	27.95	1.539	1.334	9.06	160
302	352677	RO	22	11	25.84	1.518	1.296	8.01	140
303	353676	RMUSS	76	19	25.98	1.516	1.266	7.97	154
304	356674	RMUSS	57	14	25.37	1.499	1.245	7.53	150
305	357673	RMUSS	56	15	25.75	1.491	1.243	7.82	158
306	358670	RMUSS	56	16	25.33	1.484	1.252	7.36	151
307	357668	SRO	50	12	24.81	1.529	1.259	6.92	147
308	358665	SRO	50	12	23.11	1.491	1.205	6.11	139
309	360665	SRO	90	20	26.01	1.546	1.266	7.58	160
310	361665	RO	20	5	22.48	1.509	1.221	6.08	123
311	362664	RO	40	10	22.41	1.468	1.201	5.24	129
312	362663	RO	60	14	22.13	1.527	1.211	5.83	114
313	363662	RO	50	12	23.61	1.534	1.219	6.64	135
314	362660	LRO	50	24	23.63	1.565	1.243	6.52	126
315	361657	LRO	100	25	23.11	1.512	1.231	6.52	125

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
316	363657	LRO	70	17	22.81	1.456	1.221	5.72	130
317	364655	LRO	80	20	25.11	1.497	1.233	7.79	157
318	366654	LRO	40	19	23.49	1.513	1.247	6.09	133
319	367653	LRO	60	17	23.36	1.475	1.226	6.06	142
320	390635	VRO	80	10	22.86	1.449	1.223	5.55	140
321	389634	VRO	80	11	25.58	1.458	1.216	6.52	177
322	388633	VRO	70	16	23.47	1.451	1.217	6.58	151
323	388632	VRO	50	23	23.31	1.409	1.218	5.46	150
324	387631	RO	20	19	22.34	1.471	1.229	5.62	132
325	387630	RO	20	21	23.11	1.412	1.182	5.41	149
326	386629	RO	20	19	23.64	1.444	1.208	5.87	151
327	386628	RO	20	22	25.56	1.445	1.218	6.57	172
328	386628	RO	20	21	23.69	1.465	1.245	6.18	148
329	385627	RO	30	29	24.46	1.468	1.289	6.88	145
330	385626	RO	20	20	24.53	1.551	1.299	6.67	136
331	384625	RO	20	21	22.51	1.454	1.222	5.23	130
332	396634	DMS	20	2	27.23	1.567	1.338	9.43	143
333	402630	DMS	20	2.5	30.63	1.569	1.344	11.47	201
334	406630	DMS	20	2.5	29.08	1.681	1.452	11.52	206
335	419622	DBS	20	2.5	27.71	1.502	1.341	7.31	175
336	422618	DMS	20	3.5	27.34	1.607	1.357	9.98	181
337	424617	DMS	20	3	26.81	1.474	1.311	8.59	171
338	426616	DMS	20	4	27.51	1.584	1.351	8.52	143
339	428616	DMS	50	5	30.61	1.589	1.367	10.86	189
340	434616	DMS	50	5	30.75	1.664	1.374	11.14	182
341	435615	DMS	30	2.5	32.44	1.605	1.369	12.19	221
342	437615	DMS	20	2	32.27	1.565	1.332	11.44	233
343	440614	DMS	40	2	29.62	1.541	1.321	9.86	204
344	443613	DMS	40	2.5	32.41	1.546	1.347	11.45	240
345	477647	PIER	40	10	29.62	1.721	1.429	10.97	157
346	487657	SSS	20	2	27.16	1.605	1.389	8.78	131
347	493663	SSS	20	2	26.29	1.652	1.399	8.78	128
348	500668	SSS	20	1.5	26.22	1.634	1.399	8.54	135
349	299890	P	20	11	26.49	1.476	1.314	7.66	166
350	299888	P	20	10	25.73	1.438	1.322	6.71	159
351	298887	PS	30	15	25.95	1.441	1.289	7.43	160
352	298887	PE	20	7.5	25.19	1.436	1.293	8.52	154
353	298886	PS	30	15	26.53	1.498	1.315	8.19	162
354	298886	PE	20	10	28.01	1.438	1.321	8.03	183
355	297885	SBS	20	11	26.41	1.508	1.339	8.59	124
356	297884	ROS	20	11	26.11	1.511	1.254	7.95	151
357	296883	ROE	20	20	24.43	1.411	1.234	6.34	156
358	295881	VRO	20	18	27.31	1.508	1.312	8.79	181
359	294878	BE	20	20	25.48	1.436	1.286	6.41	156
360	294877	B	100	13	23.43	1.476	1.294	6.37	122
361	293876	RO	80	19	24.27	1.468	1.292	6.54	135
362	292875	ROE	40	10	23.53	1.413	1.249	5.99	138
363	294874	VROE	40	12	23.82	1.424	1.259	6.25	141
364	291873	RO	50	13	25.07	1.447	1.272	6.42	146
365	292870	RO	50	14	24.24	1.449	1.278	6.58	140

Table 2.1 continued.

Sample	Map Ref.	Habitat	N	RD	L	L/Ap	L/W	Sp	WApxAp
366	291869	ROS	50	17	24.65	1.478	1.292	6.78	139
367	291867	ROE	50	12	24.82	1.416	1.281	6.51	152
368	555715	BRIDGE	50	13	32.34	1.695	1.418	13.09	199
369	536711	ROS	30	7.5	29.59	1.577	1.365	10.18	177
370	541712	BRIDGE	30	8	33.31	1.669	1.436	13.19	211
371	544715	ROS	30	8	33.62	1.635	1.417	13.17	225
372	290867	P	70	16	24.61	1.598	1.398	7.81	112
373	289866	SS	80	10	26.65	1.552	1.361	8.29	149
374	288864	TR	55	14	24.59	1.522	1.345	7.14	122
375	289863	TR	35	17	26.35	1.515	1.336	7.84	153
376	289863	B	50	13	24.51	1.559	1.363	7.24	113
377	290862	ROS	50	12	25.82	1.547	1.351	8.05	148
378	290862	VRO	40	10	24.72	1.496	1.331	7.15	127
379	291862	BE	50	12	25.62	1.469	1.329	7.66	158
380	291861	VRO	70	10	28.89	1.535	1.375	9.44	180
381	290860	PE	50	9	27.92	1.506	1.365	8.88	171
382	290860	PS	30	15	28.36	1.509	1.376	8.81	176
383	287859	ROS	70	17	24.36	1.509	1.345	7.26	126
384	287858	ROE	30	7.5	26.59	1.501	1.334	8.41	164
385	287857	C	20	10	26.37	1.452	1.285	8.71	173
386	287857	R	20	11	27.75	1.532	1.346	8.78	162
387	287856	ISRO	30	9	28.81	1.503	1.375	9.35	190
388	288856	RO	70	17	27.91	1.559	1.373	9.28	158
389	289855	ROS	40	19	25.92	1.591	1.376	8.23	134
390	287853	IROS	40	20	29.75	1.533	1.349	10.36	211
391	285850	V	50	15	26.81	1.445	1.292	7.72	181
392	284850	P	30	16	25.61	1.541	1.321	8.05	146
393	282851	VB	40	19	27.89	1.576	1.381	9.14	168
394	280848	VP	30	10	26.09	1.537	1.343	8.17	145
395	279846	BFP	40	11	25.35	1.541	1.359	7.48	137
396	280844	BFP	30	8.5	23.93	1.524	1.366	6.89	115
397	280842	BFP	30	9.5	25.11	1.505	1.319	7.51	143
398	280839	IP	30	7.5	25.84	1.473	1.305	7.41	154
399	282838	IP	30	8	26.22	1.498	1.319	7.43	154
400	283837	IP	30	8.5	25.51	1.497	1.304	7.62	142
401	299891	ROS	20	5	25.52	1.503	1.321	7.47	151
402	298891	VRO	20	5	24.76	1.484	1.311	6.78	135
403	298892	SS	20	5.5	27.12	1.449	1.325	7.72	183
404	297893	ROE	50	6.5	24.41	1.431	1.306	6.09	145
405	297894	BS	50	5	25.99	1.514	1.359	7.65	150
406	296895	VROE	25	7.5	24.75	1.436	1.297	6.35	143
407	295895	ROS	40	10	26.23	1.542	1.351	8.15	146
408	295895	PS	20	5	25.55	1.481	1.317	7.18	153
409	299896	VRO	20	10	25.69	1.469	1.344	6.97	153
410	298897	BF	30	15	25.82	1.518	1.356	7.59	148
411	295898	ROE	30	15	25.51	1.423	1.308	6.58	163
412	296900	LBF	30	14	26.39	1.478	1.323	7.45	161
413	293903	ROE	54	12	25.78	1.442	1.302	7.03	159
414	553717	ROS	40	4.5	32.76	1.552	1.324	11.72	248
415	292917	BE	40	2.5	25.89	1.433	1.517	10.25	189
416	295930	CPE	40	2.1	23.61	1.321	1.353	8.62	194

Table.2.2. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between months for Menai Bridge showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.428	< 0.001	0.309	< 0.001	0.250	< 0.001
1-3	0.281	< 0.001			0.166	< 0.001
1-4	0.219	< 0.001	0.185	0.002	0.312	< 0.001
1-5	0.387	< 0.001	0.239	< 0.001	0.196	< 0.001
1-6			0.451	< 0.001	0.108	< 0.001
2-3	0.147	0.003	0.348	< 0.001	0.416	< 0.001
2-4	0.647	< 0.001			0.563	< 0.001
2-5					0.446	< 0.001
2-6	0.355	< 0.001	0.759	< 0.001	0.358	< 0.001
3-4	0.499	< 0.001	0.225	< 0.001	0.146	< 0.001
3-5			0.278	< 0.001		
3-6	0.208	< 0.001	0.412	< 0.001		
4-5	0.605	< 0.001			0.116	0.003
4-6	0.292	< 0.001	0.636	< 0.001	0.205	< 0.001
5-6	0.313	< 0.001	0.689	< 0.001	0.088	0.020

Data presented are mean differences,with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table.2.3. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between months for Trwyn y Penrhyn showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2			0.167	0.033	0.115	0.002
1-4			0.645	< 0.001	0.113	0.003
1-5			0.597	< 0.001	0.267	< 0.001
1-6	0.234	< 0.001	0.735	< 0.001		
2-3					0.107	0.006
2-4			0.812	< 0.001	0.228	< 0.001
2-5			0.766	< 0.001	0.382	< 0.001

Table 2.3 continued.

2-6	0.207	< 0.001	0.902	< 0.001	0.098	0.050
3-4			0.685	< 0.001	0.121	0.001
3-5			0.639	< 0.001	0.275	< 0.001
3-6	0.232	< 0.001	0.776	< 0.001		
4-5					0.154	< 0.001
4-6	0.272	< 0.001			0.134	0.001
5-6	0.167	0.001			0.288	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.4. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between months for Llanfairfechan showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.081	0.021			0.227	< 0.001
1-3			0.195	0.002	0.108	< 0.001
1-4	0.229	< 0.001	0.325	0.001	0.457	< 0.001
1-5	0.161	< 0.001			0.327	< 0.001
1-6	0.268	< 0.001	0.191	0.013	0.101	0.001
2-3	0.073	0.043			0.119	< 0.001
2-4	0.147	0.001			0.230	< 0.001
2-5					0.100	0.042
2-6	0.186	< 0.001			0.126	< 0.001
3-4	0.220	< 0.001	0.519	< 0.001	0.349	< 0.001
3-5	0.152	< 0.001			0.219	< 0.001
3-6	0.259	< 0.001				
4-5			0.451	< 0.001	0.130	0.035
4-6			0.516	< 0.001	0.356	< 0.001
5-6	0.107	0.012			0.227	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.5. Post Hoc Bonferroni multiple comparisons of Topography, Microhabitat and Activity between months for Red Wharf Bay showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2			0.395	< 0.001	0.349	< 0.001
1-3	0.277	< 0.001	0.305	< 0.001		
1-4	0.207	< 0.001	0.194	< 0.001		
1-5					0.539	< 0.001
1-6			0.409	< 0.001	0.159	< 0.001
2-3	0.383	< 0.001			0.343	< 0.001
2-4	0.313	< 0.001			0.257	< 0.001
2-5	0.190	< 0.001	0.267	0.004	0.189	< 0.001
2-6	0.182	< 0.001			0.190	< 0.001
3-5	0.194	< 0.001			0.533	< 0.001
3-6	0.202	< 0.001			0.153	< 0.001
4-5					0.446	< 0.001
4-6	0.131	0.020	0.215	0.020		
5-6			0.280	< 0.001	0.380	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.6. Post Hoc Bonferroni multiple comparisons of Topography, Microhabitat and Activity between months for Porth Nobla showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.895	< 0.001			0.484	< 0.001
1-4	1.135	< 0.001	0.275	< 0.001	0.323	< 0.001
1-5	1.166	< 0.001	0.443	< 0.001	0.299	< 0.001
1-6	1.256	< 0.001	0.232	< 0.001		
2-3	0.898	< 0.001			0.432	< 0.001
2-4	0.240	< 0.001	0.369	< 0.001	0.161	< 0.001
2-5	0.271	< 0.001	0.537	< 0.001	0.184	< 0.001
2-6	0.360	< 0.001	0.325	< 0.001	0.436	< 0.001

2.6 continued.

3-4	1.138	< 0.001	0.339	< 0.001	0.272	< 0.001
3-5	1.169	< 0.001	0.507	< 0.001	0.248	< 0.001
3-6	1.258	< 0.001	0.296	< 0.001		
4-6	0.120	0.027			0.275	< 0.001
5-6			0.211	0.003	0.252	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values
Based on estimated marginal means

Table 2.7. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between months for Porth Defaid showing significant differences.

	Topography		Microhabitat		Activity	
Months	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.493	< 0.001			0.408	< 0.001
1-3			0.328	0.030	0.180	0.002
1-4	0.450	< 0.001	0.369	0.016		
1-5	0.303	< 0.001	1.162	< 0.001	0.353	< 0.001
1-6			0.389	0.012		
2-3	0.514	< 0.001			0.228	< 0.001
2-4			0.542	< 0.001	0.280	< 0.001
2-5	0.190	0.023	0.989	< 0.001	0.761	< 0.001
2-6	0.445	< 0.001	0.563	< 0.001	0.384	< 0.001
3-4	0.471	< 0.001	0.696	< 0.001		
3-5	0.324	< 0.001	0.834	< 0.001	0.533	< 0.001
3-6			0.717	< 0.001	0.157	0.008
4-5			1.531	< 0.001	0.481	< 0.001
4-6	0.403	< 0.001				
5-6	0.256	0.001	1.551	< 0.001	0.376	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means

The value of particular shore transect characteristics, namely: topopgraphy, microhabitat and activity of *Nucella* were all found to be significantly influenced by month on every shore (Table 2.8).

Table 2.8. Result of the Kruskal-Wallis test on Topography, Microhabitat and Activity between months.

	Topography		Microhabitat		Activity	
Shore	Chi square	Sig.	Chi square	Sig.	Chi square	Sig.
Menai Bridge	219.010	< 0.001	282.838	< 0.001	497.862	< 0.001
Trwyn y Penrhyn	86.665	< 0.001	457.672	< 0.001	212.867	< 0.001
Llanfairfechan	124.838	< 0.001	60.680	< 0.001	216.141	< 0.001
Red Wharf Bay	72.283	< 0.001	68.480	< 0.001	294.213	< 0.001
Porth Nobla	1818.156	< 0.001	129.618	< 0.001	420.547	< 0.001
Porth Defaid	105.493	< 0.001	81.832	< 0.001	198.303	< 0.001

Data presented are chi square values, with probabilities (P), which are all significant values.

Table 2.9. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Menai Bridge showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.435	< 0.001	0.023	1.000	0.010	1.000
1-3	0.430	< 0.001			0.188	< 0.001
1-4					0.214	< 0.001
1-5	0.323	< 0.001				
1-6	0.809	< 0.001			0.293	< 0.001
2-3					0.177	< 0.001
2-4	0.253	< 0.001			0.203	< 0.001
2-5	0.112	< 0.040	0.139	0.014		
2-6	0.374	< 0.001			0.283	< 0.001
3-4	0.248	< 0.001				
3-5	0.107	0.025			0.105	< 0.001
3-6	0.379	< 0.001			0.106	0.006
4-5	0.141	0.001	0.152	0.001	0.131	< 0.001
4-6	0.627	< 0.001	0.151	0.050		
5-6	0.486	< 0.001			0.211	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.10. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Trwyn y Penrhyn showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.346	< 0.001				
1-3	0.614	< 0.001				
1-5	0.397	< 0.001				
1-6	0.659	< 0.001			0.270	< 0.001
2-3	0.268	< 0.001				
2-4	0.244	< 0.001				
2-5					0.204	< 0.001
2-6	0.313	< 0.001			0.378	< 0.001
3-4	0.511	< 0.001				
3-5	0.235	< 0.001	0.158	0 .021	0.136	< 0.001
3-6					0.310	< 0.001
4-5	0.277	< 0.001			0.110	0.010
4-6	0.577	< 0.001			0.285	< 0.001
5-6	0.280	< 0.001	0.194	< 0.001	0.174	< 0.001

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.11 Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Llanfairfechan showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-4			0.331	0.002		
1-5	0.173	< 0.001				
1-6	0.192	< 0.001				
2-3			0.441	< 0.001		
2-5	0.125	< 0.001				
2-6	0.144	< 0.001				
3-4			0.569	< 0.001		
3-5	0.131	< 0.001	0.244	< 0.001		

Table 2.11 continued.

3-6	0.151	< 0.001	0.251	< 0.001		
4-5	0.107	< 0.001	0.325	< 0.001		
4-6	0.126	< 0.001	0.317	< 0.001		

Data presented are mean differences (md), with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.12 Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Red Wharf Bay showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-2					0.549	< 0.001
1-3					0.323	< 0.001
1-4	0.239	< 0.001	0.424	< 0.001	0.338	< 0.001
1-5	0.261	< 0.001			0.333	< 0.001
1-6	0.298	< 0.001	0.317	0.010	0.263	< 0.001
2-3			0.317	< 0.001	0.226	< 0.001
2-4	0.216	< 0.001	0.227	0.012	0.211	< 0.001
2-5	0.239	< 0.001	0.197	0.023	0.216	< 0.001
2-6	0.276	< 0.001			0.286	< 0.001
3-4	0.189	< 0.001	0.543	< 0.001		
3-5	0.212	< 0.001				
3-6	0.249	< 0.001	0.437	< 0.001		
4-5			0.424	< 0.001		
5-6			0.317	< 0.001		

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.13. Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Porth Nobla showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-2			0.383	< 0.001	0.190	< 0.001
1-3	0.221	< 0.001			0.199	< 0.001
1-4	0.192	0.002	0.453	< 0.001		
1-5	0.343	< 0.001	0.649	< 0.001		
1-6			0.294	0.002	0.154	0.001
2-3	0.188	< 0.001	0.297	< 0.001	0.390	< 0.001
2-4	0.225	< 0.001			0.240	< 0.001
2-5	0.376	< 0.001	0.266	< 0.001	0.256	< 0.001
2-6	0.187	< 0.001			0.344	< 0.001
3-4	0.413	< 0.001	0.367	< 0.001	0.150	< 0.001
3-5	0.564	< 0.001	0.563	< 0.001	0.131	< 0.001
3-6	0.375	< 0.001	0.207	0.001		
4-5	0.151	< 0.001	0.196	< 0.001		
4-6			0.159	< 0.001	0.104	< 0.001
5-6	0.189	< 0.001	0.356	< 0.001	0.085	0.004

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.14 Post Hoc Bonferonni multiple comparisons of Topography, Microhabitat and Activity between shore levels for Porth Defaid showing significant differences.

	Topography		Microhabitat		Activity	
Levels	*md*	*P*	*md*	*P*	*md*	*P*
1-2	0.215	0.002				
1-3	0.761	< 0.001	0.372	0.006		
1-4	0.308	< 0.001				
1-6	0.392	< 0.001				
2-3	0.546	< 0.001				
2-5	0.223	0.001			0.212	< 0.001
2-6	0.176	0.011			0.145	0.029

Table 2.14 continued.

3-4	0.453	< 0.001				
3-5	0.769	< 0.001				
3-6	0.370	< 0.001	0.520	< 0.001		
4-5	0.316	< 0.001			0.230	< 0.001
4-6			0.363	0.018	0.163	0.018
5-6	0.399	< 0.001				

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.15. Results of the Kruskal-Wallis test on Topography, Microhabitat and Activity between shore levels.

	Topography		Microhabitat		Activity	
Shore	Chi square	Sig.	Chi square	Sig.	Chi square	Sig.
Menai Bridge	153.699*	< 0.001	20.509*	< 0.001	118.921*	< 0.001
Trwyn y Penrhyn	54.408*	< 0.001	2.939*	< 0.001	4.299*	< 0.001
Llanfairfechan	61.668*	< 0.001	35.890*	< 0.001	2.795	0.247
Red Wharf Bay	6.835*	0.033	10.658*	0.005	88.477*	< 0.001
Porth Nobla	79.534*	< 0.001	53.199*	< 0.001	116.851*	< 0.001
Porth Defaid	99.792*	< 0.001	6.781*	0.034	3.337	0.189

Data presented are chi square values, with probabilities (P), * which are significant values.

Table 2.16. Results of the Kruskal-Wallis test on Topography, Microhabitat and Activity between shores at different levels.

	Topography		Microhabitat		Activity	
Level	Chi square	Sig.	Chi square	Sig.	Chi square	Sig.
1	308.215	< 0.001	193.315	< 0.001	111.900	< 0.001
2	584.779	< 0.001	718.867	< 0.001	219.901	< 0.001
3	1090.358	< 0.001	835.635	< 0.001	356.676	< 0.001
4	1182.068	< 0.001	1236.706	< 0.001	174.890	< 0.001
5	1583.676	< 0.001	1571.199	< 0.001	353.071	< 0.001
6	806.027	< 0.001	720.126	< 0.001	227.035	< 0.001

Data presented are chi square values, with probabilities (P), which are all significant values.

Table 2.17 Post Hoc Bonferonni multiple comparisons of size (shell length) showing significant differences between topography types.

Shore	Topography	mean difference	significance
Menai Bridge	1-2	4.024	0.001
	2-3	4.102	<0.001
Trwyn y Penrhyn	1-2	0.896	0.048
	1-3	0.964	0.034
Llanfairfechan	1-2	1.923	0.001
	1-3	2.115	< 0.001
Red Wharf	1-2	3.123	0.007
	2-3	2.940	< 0.001
Porth Nobla	1-3	4.529	< 0.001
	2-3	3.687	0.004

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.18 Post Hoc Bonferonni multiple comparisons of size (shell length) showing significant differences between microhabitat types.

Shore	Microhabitats	mean difference	significance
Menai Bridge	1-4	7.706	< 0.001
	2-4	8.598	< 0.001
	4-5	7.194	< 0.001
Trwyn y Penrhyn	1-2	1.491	0.024
	1-4	4.924	< 0.001
	2-4	6.414	< 0.001
	3-4	7.663	< 0.001
	4-5	4.899	< 0.001
Llanfairfechan	1-2	4.410	< 0.001
	1-3	3.377	0.020
	1-4	2.464	< 0.001
	2-4	1.946	< 0.001
Red Wharf Bay	2-4	2.390	< 0.001
Porth Nobla	1-2	4.732	< 0.001

Table 2.18 continued.

Porth Defaid	1-2	2.638	< 0.001
	1-5	1.494	0.034
	2-4	1.756	0.002

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.19. Post Hoc Bonferonni multiple comparisons of size (shell length) showing significant differences between *Nucella* activities.

Shore	Activities	mean difference	significance
Menai Bridge	1-2	8.328	< 0.001
	1-3	3.228	< 0.001
Trwyn y Penrhyn	1-2	3.751	< 0.001
	1-3	5.208	< 0.001
	2-3	8.958	< 0.001
Llanfairfechan	1-2	3.041	< 0.001
	1-3	5.156	< 0.001
	2-3	8.197	< 0.001
Red Wharf Bay	1-2	3.441	< 0.001
	2-3	5.507	< 0.001
Porth Nobla	1-2	3.159	< 0.00
Porth Defaid	1-2	1.031	0.003

Data presented are mean differences, with probabilities (P), which are all significant values.
Based on estimated marginal means.

Table 2.20. Post Hoc Bonferonni multiple comparisons of size (shell length) showing significant differences between shore levels.

Shore	Levels	mean difference	significance
Menai Bridge	1-5	2.515	0.041
	2-5	2.818	< 0.001
Trwyn y Penrhyn	1-2	3.891	< 0.001
	1-3	3.516	< 0.001
	1-4	3.430	< 0.001
	1-5	6.006	< 0.001
	1-6	4.655	< 0.001
	2-5	2.115	< 0.001
	3-5	2.490	< 0.001
	3-6	1.139	0.028
	4-5	2.576	< 0.001
	5-6	1.351	0.001
Llanfairfechan	1-2	1.565	0.009
	1-5	3.321	< 0.001
	1-6	4.587	< 0.001
	2-3	1.955	< 0.001
	2-5	1.755	< 0.001
	2-6	3.022	< 0.001
	3-4	1.508	< 0.001
	3-5	3.710	< 0.001
	3-6	4.976	< 0.001
	4-5	2.203	< 0.001
	4-6	3.469	< 0.001
	5-6	1.266	< 0.001
Red Wharf Bay	4-5	2.638	< 0.001
	4-6	2.608	0.001
Porth Nobla	1-5	4.154	0.047
	3-5	2.929	0.005

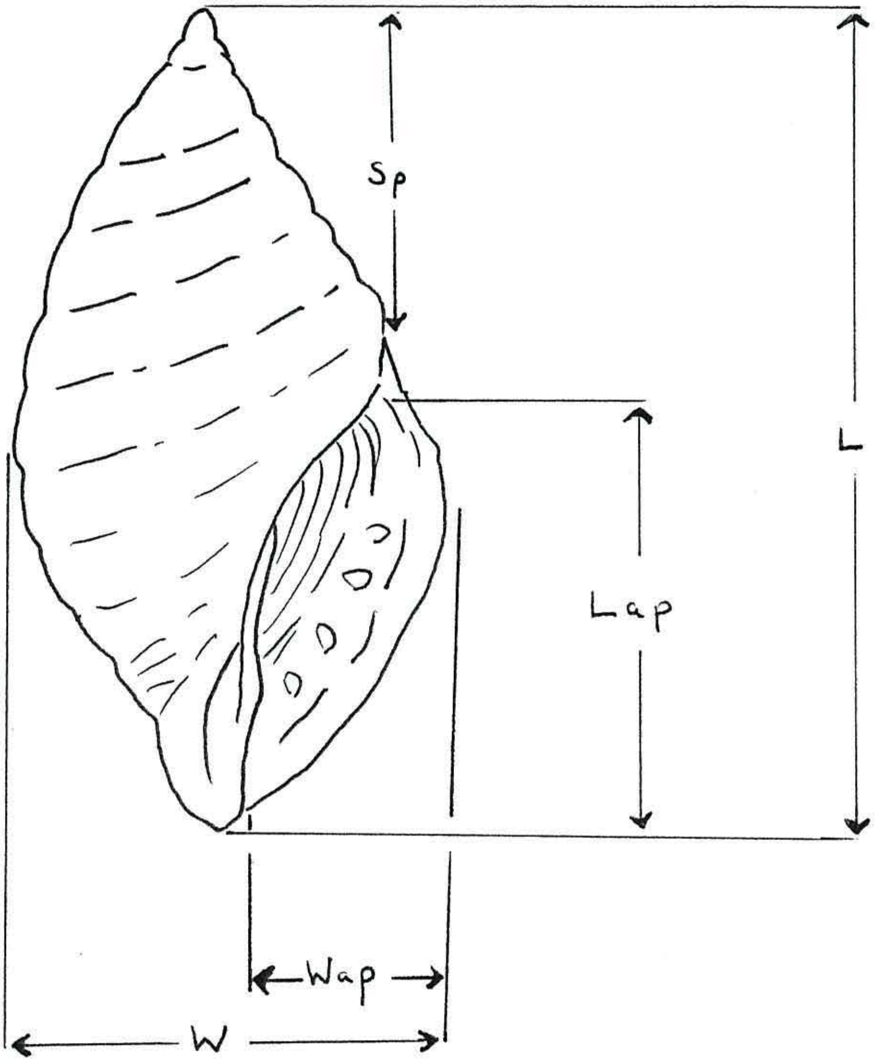
Data presented are mean differences, Based on estimated marginal means, all with significant probabilities (P).

Table 2.21.Result of Kruskal-Wallis test, showing significant differences in the percentage of particular size classes between different shores.

sizeclass	chi-square	significance
1	2.185	0.823
2	13.772*	0.017
3	13.338*	0.020
4	3.196	0.670
5	11.169*	0.048
6	10.454	0.063
7	11.989*	0.035
8	13.444*	0.020
9	12.462*	0.029
10	13.515*	0.019
11	6.524	0.259
12	7.573	0.181
13	9.882	0.079
15	11.339*	0.045
16	11.592*	0.041
17	9.004	0.109
18	12.787*	0.025
19	5.000	0.416
20	10.588	0.060

Data presented are chi square values, with probabilities (P), * which are all significant values.

Appendix 3.



Key to shell measurements:
L = length of shell
Lap = length of aperture
Wap = width of aperture
Sp = spire length
W = width of shell

Figure 3.1. Shell shape parameters of *Nucella lapillus*.

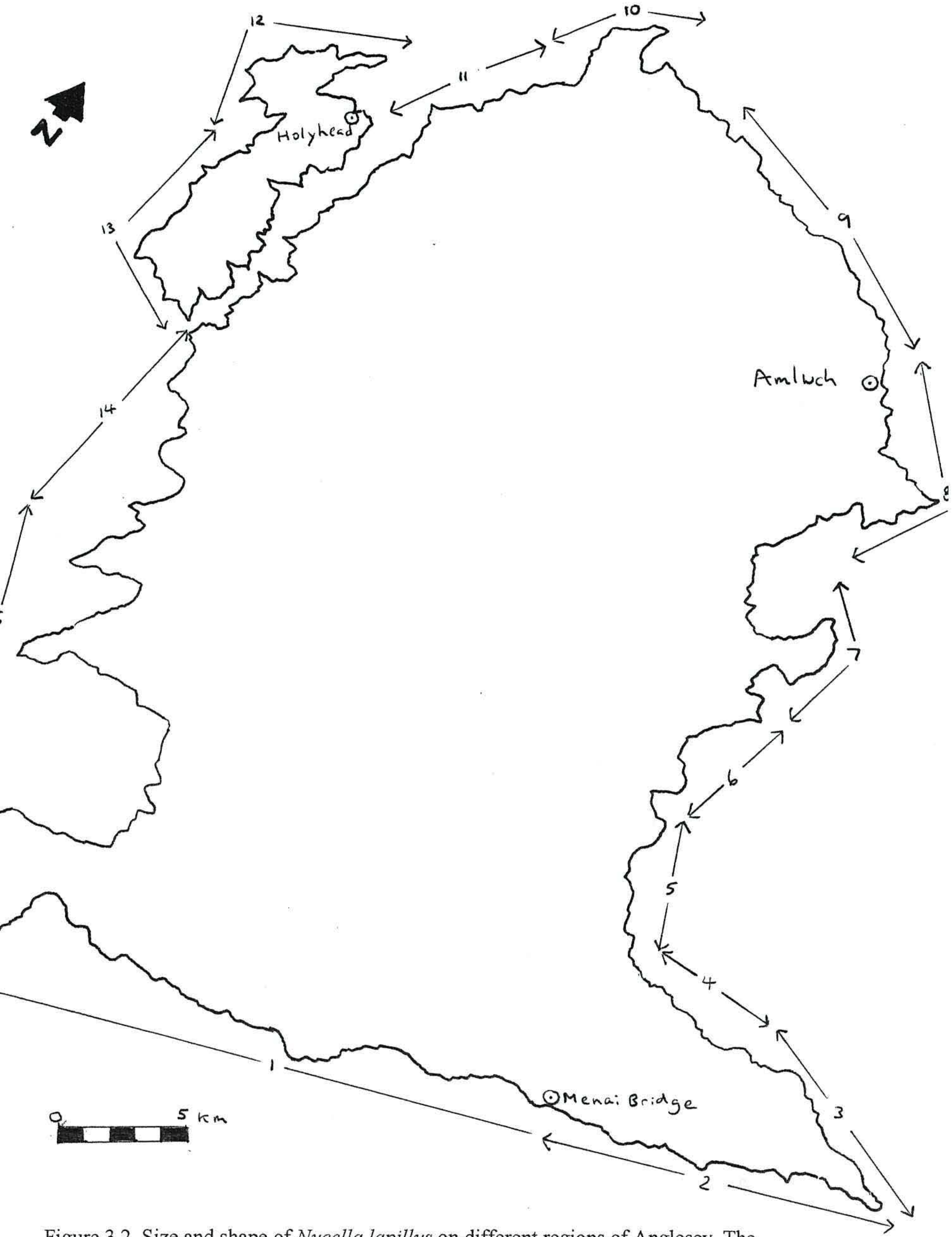


Figure 3.2. Size and shape of *Nucella lapillus* on different regions of Anglesey. The sixteen regions of Anglesey where dogwhelks were collected are marked on the map.

Figure 3.2. continued.

The size and shape of dogwhelks from 16 different regions of Anglesey in tabular forr

Region		Map Ref.	N	L	L/Lap	L/W	Sp	WapLap
Menai Strait	1	440620-599752	313	30.19	1.614	1.424	11.68	196
Beaumaris	2	599753-641813	816	29.08	1.649	1.464	13.16	183
North Coast	3	641814-618816	583	26.99	1.532	1.371	9.56	157
Red Wharf	4	618815-572810	688	26.14	1.511	1.375	9.98	168
Red Wharf	5	532814-523832	308	28.34	1.551	1.443	10.76	177
Penrhyn	6	523833-516867	1301	27.92	1.585	1.394	11.13	179
Lligwy	7	515865-487889	970	28.00	1.595	1.393	11.45	176
Porth y Aber	8	488896-488920	710	26.59	1.605	1.399	10.04	140
Lynas Point	9	483927-456937	561	26.75	1.529	1.348	9.59	166
Church bay	10	293903-292867	1109	25.46	1.463	1.303	7.16	152
Trefadog	11	290866-283836	1240	26.34	1.521	1.345	8.14	152
Treaddur	12	213794-256772	992	25.53	1.492	1.358	7.97	141
Rhoscolyn	13	258754-296751	311	25.79	1.496	1.332	7.88	148
Rhosneigr	14	206742-332705	711	25.14	1.495	1.288	7.53	141
Aberffraw	15	333683-368653	1194	24.53	1.515	1.256	7.14	139
Newborough	16	378653-444613	820	26.78	1.518	1.294	8.25	170

Key.
N = number of whelks sampled.
L = length of shell (mm).
L/Lap = shell length to aperture length ratio.
L/W = shell length to shell width ratio.
Sp = spire length (mm).
WapLap = aperture area (sqmm).

Appendix 3 Tables.

Table 3.1. Post Hoc Bonferonni multiple comparisons of Shell Shape Parameters (Shell Length, Aperture Length, Aperture Width, Spire, Shell Width), showing significant differences between shore levels.

Parameter	Shore levels	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
Shell length	1-2		0.010	0.007	<0.001		
	1-3		<0.001		<0.001	<0.001	
	2-3			0.001			
Ap. length	1-2		0.006	0.030	<0.001		
	1-3		<0.001		0.013		
	2-3			0.001			
Ap. width	1-2		0.003	0.021	0.003		
	1-3	0.031	<0.001				
	2-3			0.002			
Spire length	1-2		0.020	0.001	<0.001	0.002	
	1-3		<0.001		<0.001	<0.001	
	2-3			0.001			0.020
Shell width	1-2		0.010		<0.001		
	1-3		<0.001		<0.001		
	2-3			0.002			

Data presented are values of significance (P). Based on observed means.

Table 3.2. Post Hoc Bonferonni multiple comparisons of Shell Shape Ratios (Shell Length/Aperture Length, Aperture Area, Aperture Area/Length^2, Shell length/Shell Width), showing significant differences between shore levels.

Ratio	Shore levels	Menai	Trwyn	Llanfairfechan	Red Wharf	Nobla	Defaid
Length/length of aperture	1-2			0.001	0.009	<0.001	
	1-3				0.001	<0.001	0.036
	2-3			0.016			

Table 3.2 continued

Aperture area	1-2		0.006	0.005	0.001		
	1-3		<0.001		0.013		
	2-3		0.039	0.001			
shape	1-2		0.003	0.015	0.012	<0.001	
	1-3				<0.001	0.003	
	2-3					0.011	
Length/width	1-2			0.001		0.002	
	1-3						0.011

Data presented are values of significance (P). Based on observed means.

Table 3.3. Post Hoc multiple comparisons (Bonferroni test) showing significant mean differences in Shell Shape parameters between shores.

Shores	Shell length	Aperture length	Aperture width	Spire length	Shell width
1-2	<0.001	<0.001	0.002	<0.001	<0.001
1-3	<0.001	<0.001		<0.001	<0.001
1-4	0.040	0.001	0.002		<0.001
1-5		<0.001	0.002		0.001
1-6			0.003	0.018	
2-4	<0.001	<0.001	<0.001	<0.001	<0.001
2-5	<0.001	<0.001	<0.001	0.005	<0.001
2-6	<0.001	<0.001	<0.001		<0.001
3-4	<0.001	<0.001	<0.001	<0.001	<0.001
3-5	<0.001	<0.001	<0.001	0.017	<0.001
3-6	0.002	<0.001	<0.001		<0.001
4-5				0.014	
4-6				<0.001	0.030

Data presented are significant values (P), which are all significant.

Table 3.4. Post Hoc multiple comparisons (Bonferroni test) showing significant mean differences in Shell Shape ratios between shores.

Shores	Length/Aperture length	Aperture area	Shores	Length/Aperture length	Aperture area
1-2		<0.001	2-6	<0.001	<0.001
1-3		<0.001	3-4		<0.001
1-4		<0.001	3-5	<0.001	<0.001
1-5	<0.001	<0.001	3-6	<0.001	<0.001
1-6	<0.001	<0.001	4-5	<0.001	
2-4	0.056	<0.001	4-6	<0.001	
2-5	<0.001	<0.001			

Data presented are significant values (P), which are all significant.

Table 3.5. Mann-Whitney U test of comparisons of shell characteristics between light and dark morphs of *Nucella lapillus*.

	Teeth		LLAP		WAPLAP		SHAPE		LW	
Shore	Mann-W	sig.	Mann-W	sig.	Mann-W	sig.	Mann-W	sig.	Mann-W	sig.
Menai Bridge	1568*	0.004	1166*	< 0.001	1116*	< 0.001	1683	0.119	1661	0.099
Trwyn y Penrhyn	2022*	0.034	1718*	0.005	1944 *	0.044	2248	0.362	2062	0.113
LLanfairfechan	3858*	< 0.001	2931*	< 0.001	3065*	< 0.001	3770*	0.005	3512*	0.001
Red Wharf Bay	974	0.070	896	0.066	913	0.087	999	0.272	952	0.151
Porth Nobla	1711	0.391	1812	0.868	1808	0.854	1822	0.910	1730	0.564
Porth Defaid	60*	0.036	131	0.611	30*	0.003	111	0.335	106	0.299
All shores	67311*	< 0.001	73189*	0.003	60562*	< 0.001	80896	0.453	82507	0.775

Data presented are Mann-Whitney values, with probabilities (P), * which are significant values.

Table 3.6. Kruskal-Wallis test of comparisons of presence of teeth, shell colour and proportion of light and dark morphs between different shore levels.

	Teeth		Colour		Light/Dark morphs	
Shore	Chi square	sig.	Chi square	sig.	Chi square	sig.
Menai Bridge	1.297	0.523	7.616*	0.022	17.656 *	< 0.001
Trwyn y Penrhyn	3.332	0.189	0.289	0.866	4.298	0.117
Llanfairfechan	8.432*	0.015	48.321*	< 0.001	41.212*	< 0.001
Red Wharf Bay	0.053	0.053	7.981*	0.018	5.437	0.066
Porth Nobla	4.712	0.093	12.397*	0.002	8.998*	0.011
Porth Defaid	24.609 *	< 0.001	0.813	0.666	5.864*	0.048
All shores	16.294 *	< 0.001	0.203	0.904	6.050*	0.049

Data presented are Chi square values,with probabilities (P), * which are significant values.

Table 3.7. Kruskal-Wallis test of comparisons of shell characteristics between different coloured morphs (16 external colours) of *Nucella lapillus*.

	Teeth		LLAP		WAPLAP		SHAPE		LW	
Shore	Chi square	sig.	Chi square	sig.	Chi square	sig.	Chi square	sig.	Chi square	sig.
Menai Bridge	26.671*	0.014	31.037*	0.003	38.549*	<0.001	19.7.44	0.102	16.652	0.216
Trwyn y Penrhyn	54.194*	<0.001	50.105*	<0.001	35.419*	<0.001	18.971	0.062	6.972	0.801
LLanfairfechan	52.010*	<0.001	43.057*	<0.001	49.230*	<0.001	20.405	0.086	19.860	0.099
Red Wharf Bay	11.590	0.171	11.304	0.185	13.810	0.087	6.906	0.547	8.212	0.413
Porth Nobla	38.601*	<0.001	9.025	0.172	10.391	0.109	4.490	0.611	1.950	0.924
Porth Defaid	38.909 *	<0.001	4.409	0.621	15.846*	0.015	6.295	0.391	4.186	0.652
All shores	216.476	<0.001	70.296	<0.001	184.617	<0.001	99.833	<0.001	97.351	<0.001

Data presented are Chi square values,with probabilities (P), * which are significant values.

Table 3.8. The Frequency Diistribution of rarer Dogwhelk Colour Morphs on 16 Regions of Anglesey.

MORPH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
PY	116	17	20			13	5	74	27	301	153	74	56	154	158	152
Y	32	9	25	29		24	11	53		62	137	95	103	66	29	26
PO	12	5				6	3			57	20			25	14	20
O	32	12		15		14	4	7	7	16	14	32	23	33	20	24
OY	14	13			46	10		6.5				1.5		29	54	67
C	17	7				0.8	1	36	48	65	92	55	47	68	68	78
CY	9	9				2.5	2.5	5		37	35	10	11	23	11	14
YG	3					2.5	12	38	49	21	49	41	27	4	8	4
YW	34					2.5	10			20	2.5			1.5		
CW	6	4						0.5	2	8	6	6		1.4	2.5	8
WG						10	13		21	5.5		71		3.5	0.6	11
LG							12	13	35	9	3.5	21	52	23	23	11
G	3			3		7	98	43	59	19	8	47	72	14	38	54
DG								3	3			1.5		4	2	6
CG								2.5	1	2.5	3.5					
TAN	3	4					1.5							10	13.5	4
MUS													13	2	13	10
FAU	6					2			10	33	42	0.9		6	17	8
PIN						5	126	130	65			25		8.5		
MAU					36	8		21						2	0.4	4
PUR		15				11	22	52						3	2.5	
LBR	1					5	6		3	2.5		0.6	11	35	2.5	
BR	3	6				17	19	17	6	18	8.5	6	2	7	23	14
YBR	8						7	2.5		5.5		0.9	3.5	0.6	8.5	
CBR						1	3						5.5	4	2	
CHO	3					7	5	9				10		0.9	3	4
BAN	37					1	12.5	12	3	2.5	2.5	1.5	3.5	1.5	34	105
BLY	97	29														10
GRY	35	24				8	2.5	2.5				14		2		
WGR	15					2.5	3.5								0.3	
BL									1.5					0.9	2	70
OC								1.5								
GGR								5.5								
PURG							2									
WBR						1										
BLD												0.3				
OBR													3.5			
GBL															3.5	
PEA															1	
GR																3
BLBR															0.4	
BLTAN																20.5

The Numbers in the Table are Percentage (%) Frequency x10-3. PY - Pale Yellow Y - Yellow

PO - Pale Orange O - Orange OY - Orange-Yellow C - Cream CY - Cream/Yellow
YG - Yellow/Grey YW - Yellow/White CW - Cream-White WG -White/Grey LG - Light Grey
G - Grey DG - Dark Grey CG - Cream/Grey TAN -Tan MUS -Mustard
FAU - Faun PIN - Pink MAU - Mauve PUR - Purple LBR - Light browm
BR - Brown YBR - Yellow/Brown CBR - Chesnut Brown CHO - Chocolate BAN - Banded
BLY-Black Yellow Rim GRY - Green Yellow Rim WGR - White Green BL - Black OC - Orange/Cream
GGR - Grey Green PURG - Purple/Grey WBR - White/Brown BLD - Black Dots OBR - Orange/Brown
GBL - Grey/Black PEA - Peach GR - Grey/Red BLBR - Black/Brown BLTAN - Black/Tan

Appendix 4 Figures.

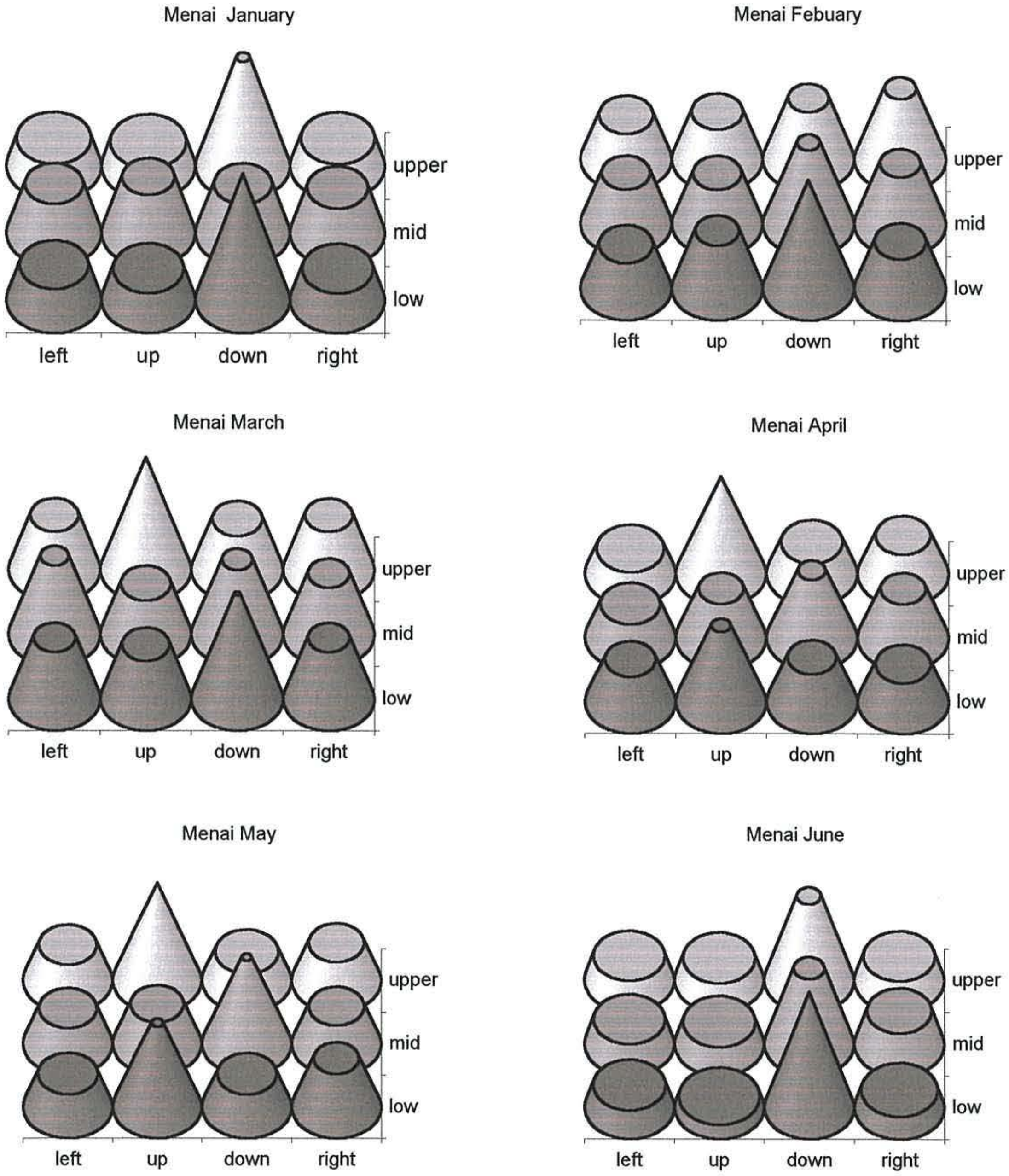


Figure 4.1.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

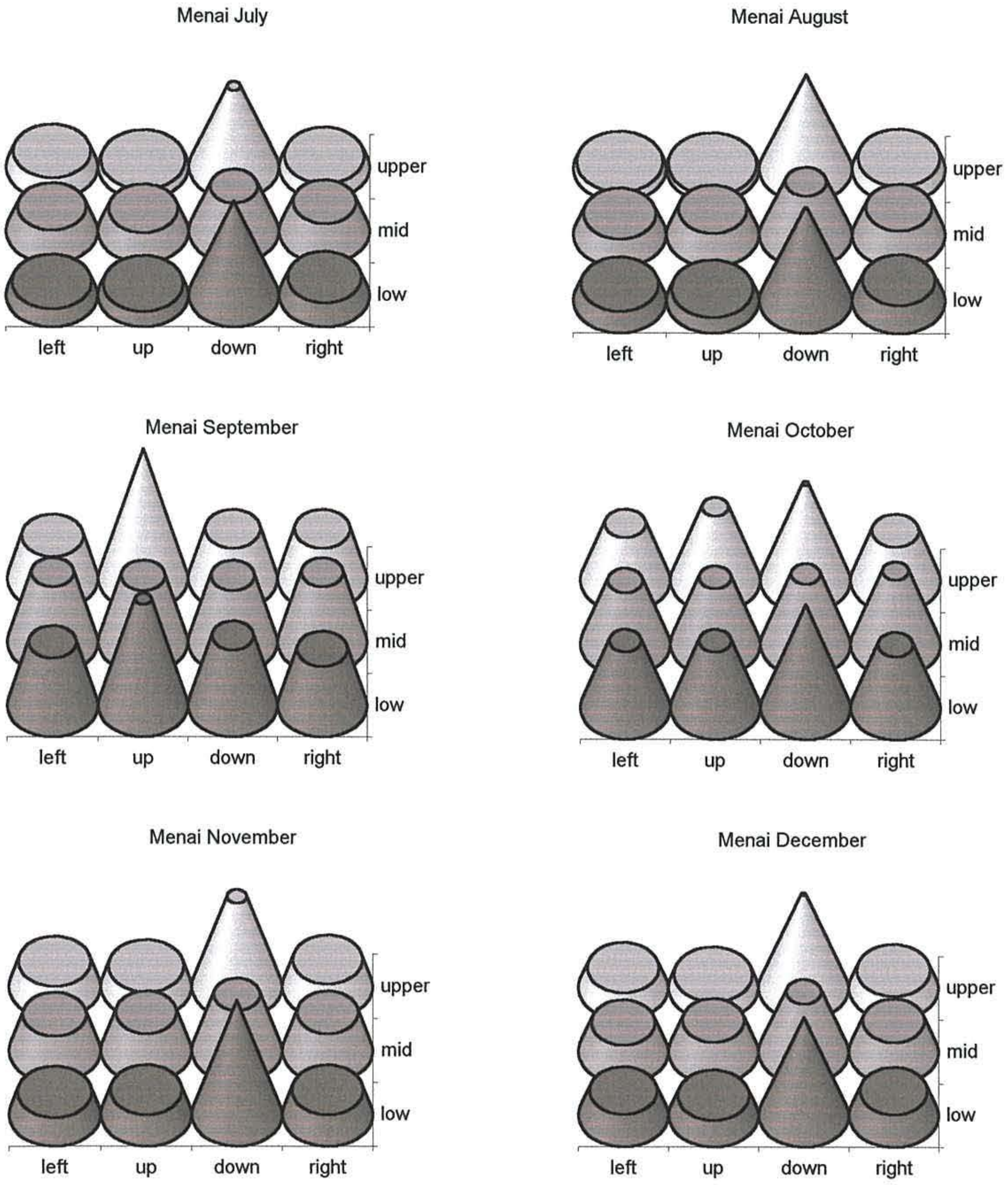
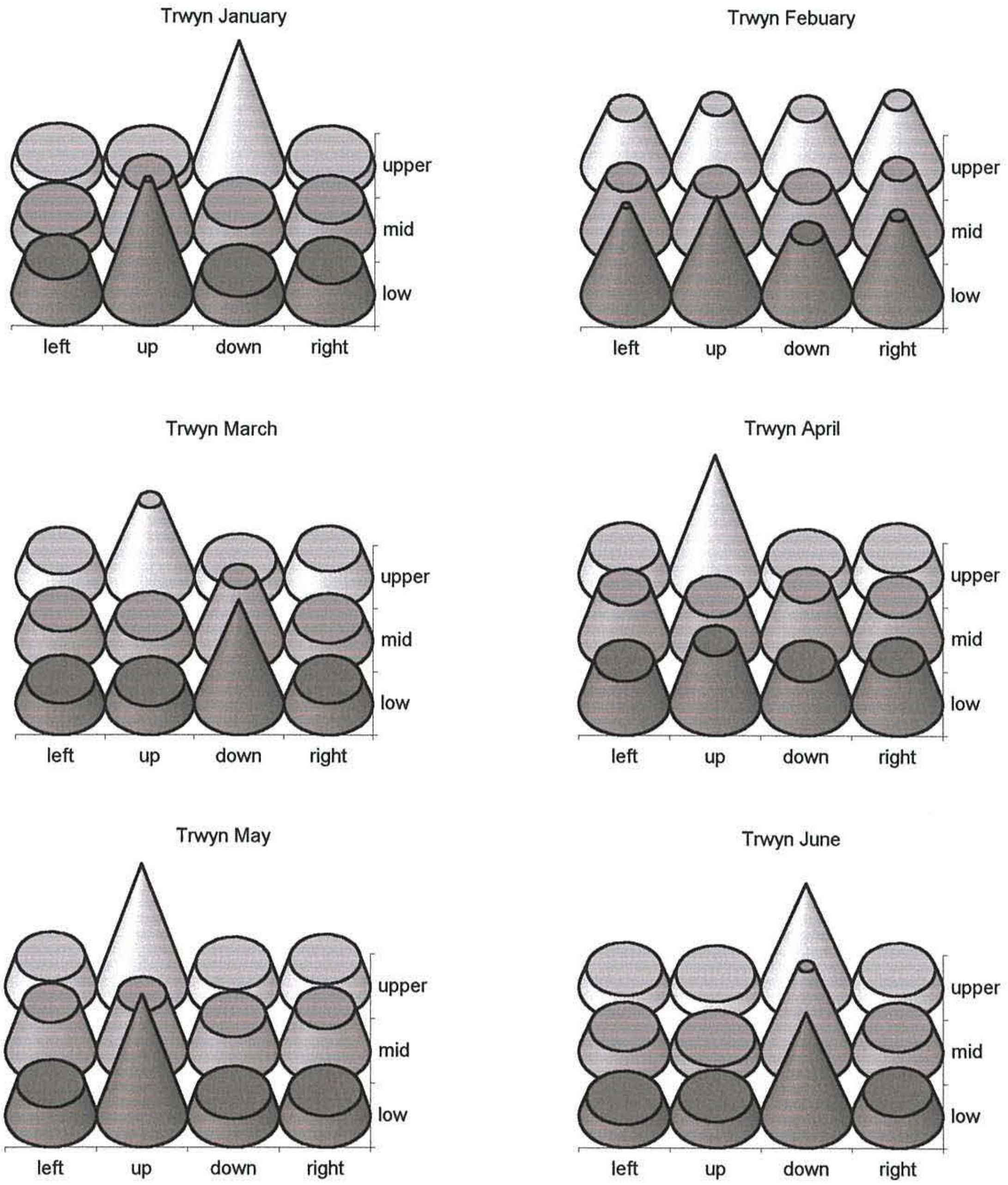


Figure 4.2.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.



Figures 4.3.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

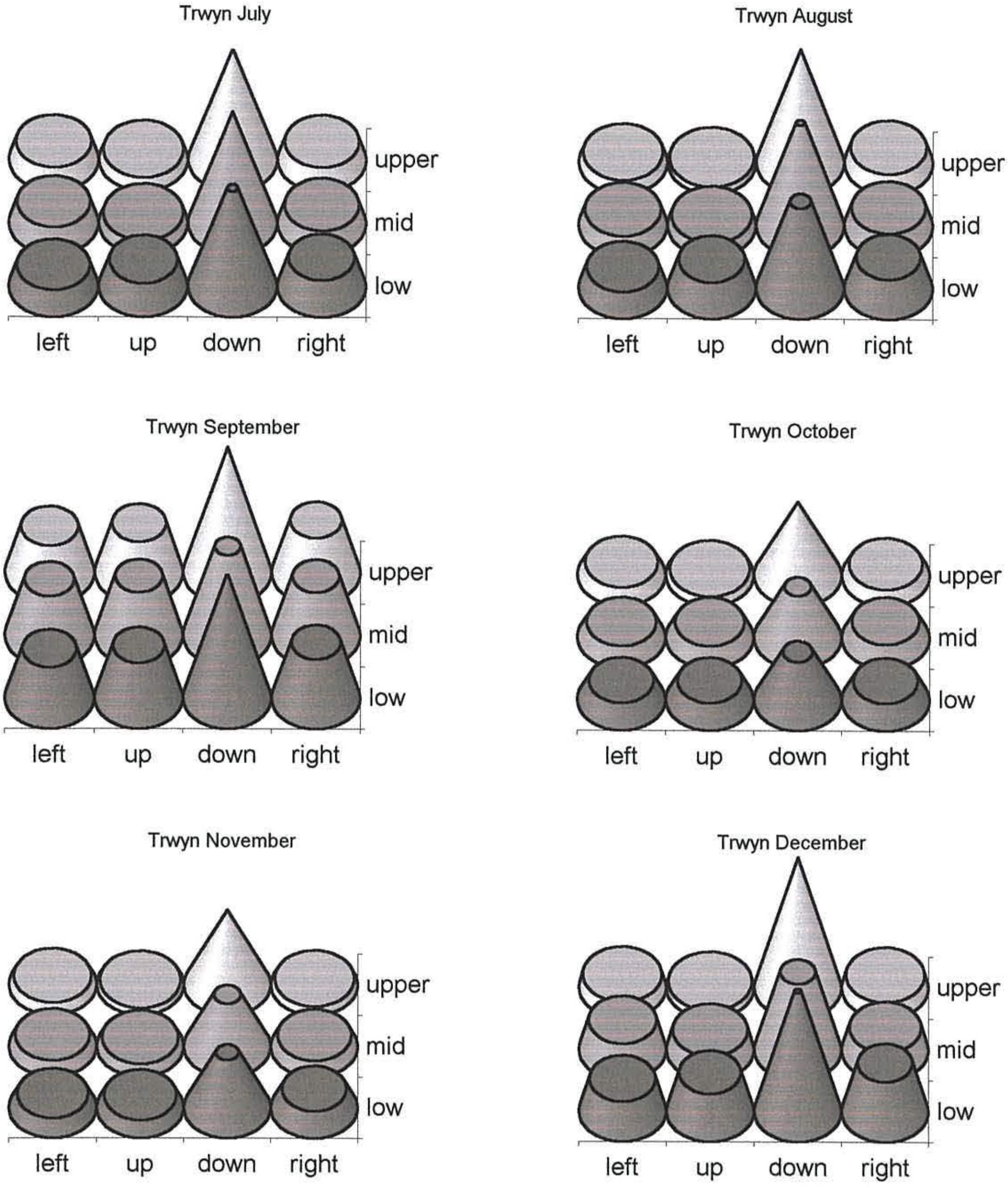


Figure 4.4.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

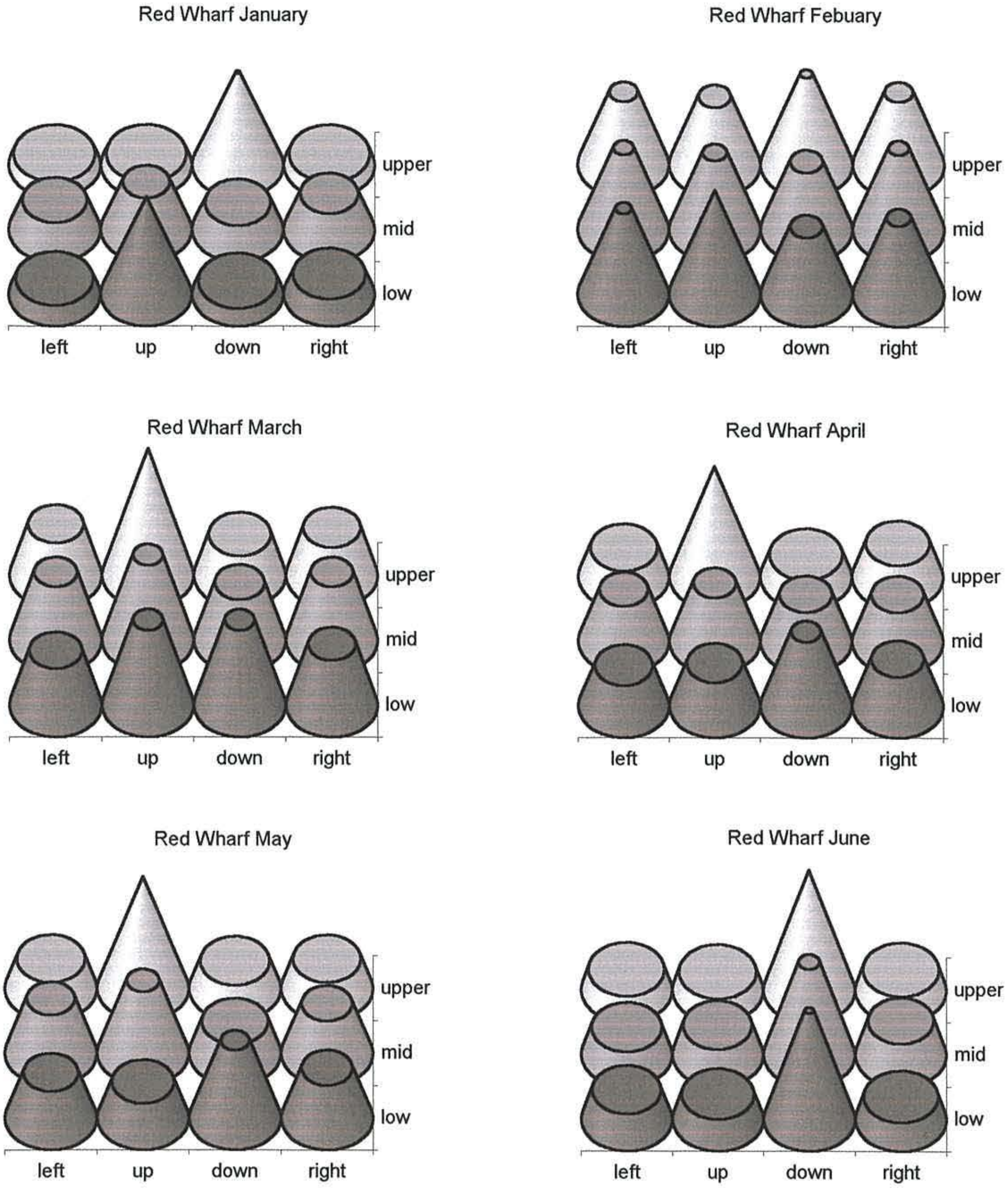


Figure 4.5. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

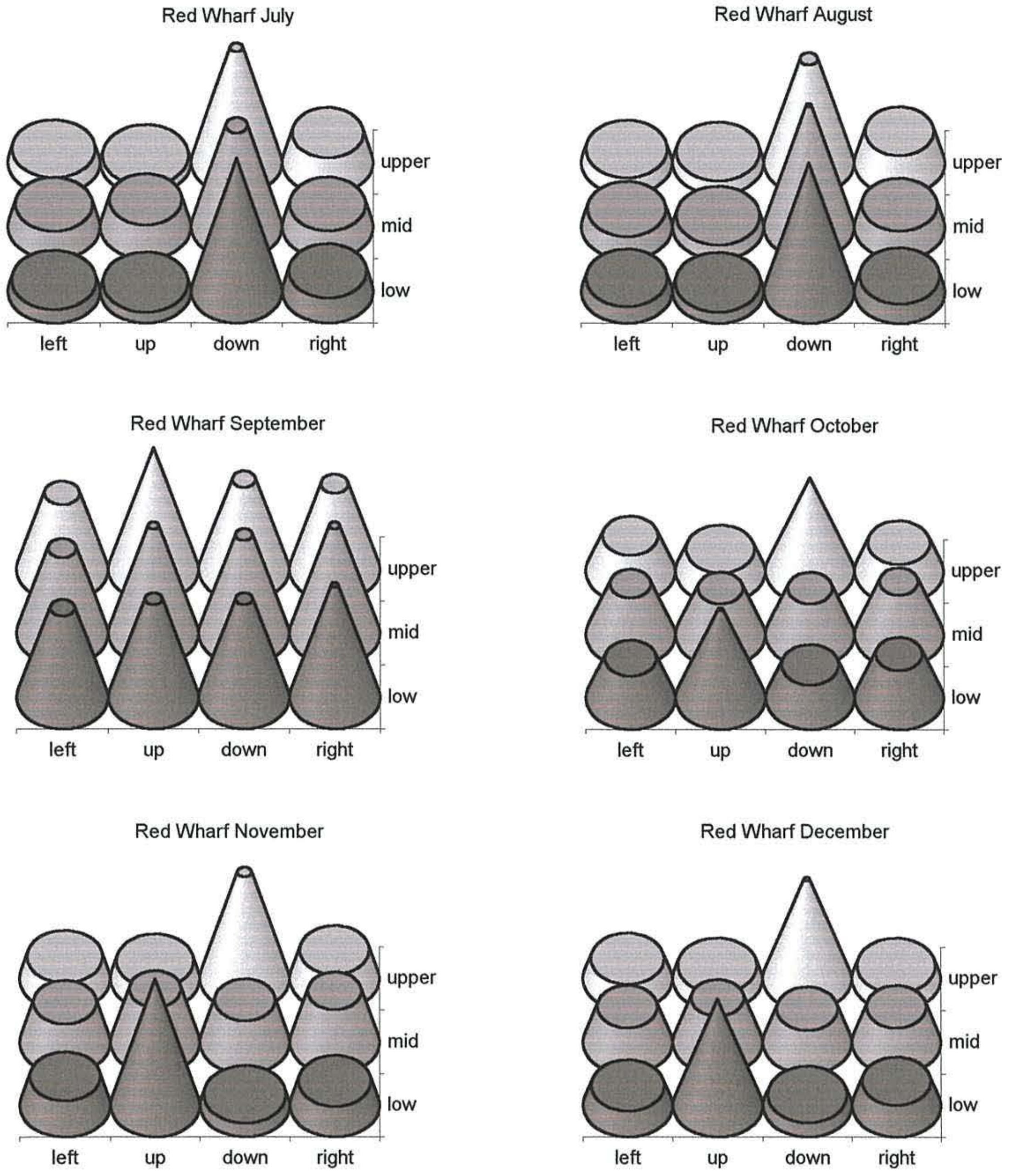


Figure 4.6. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

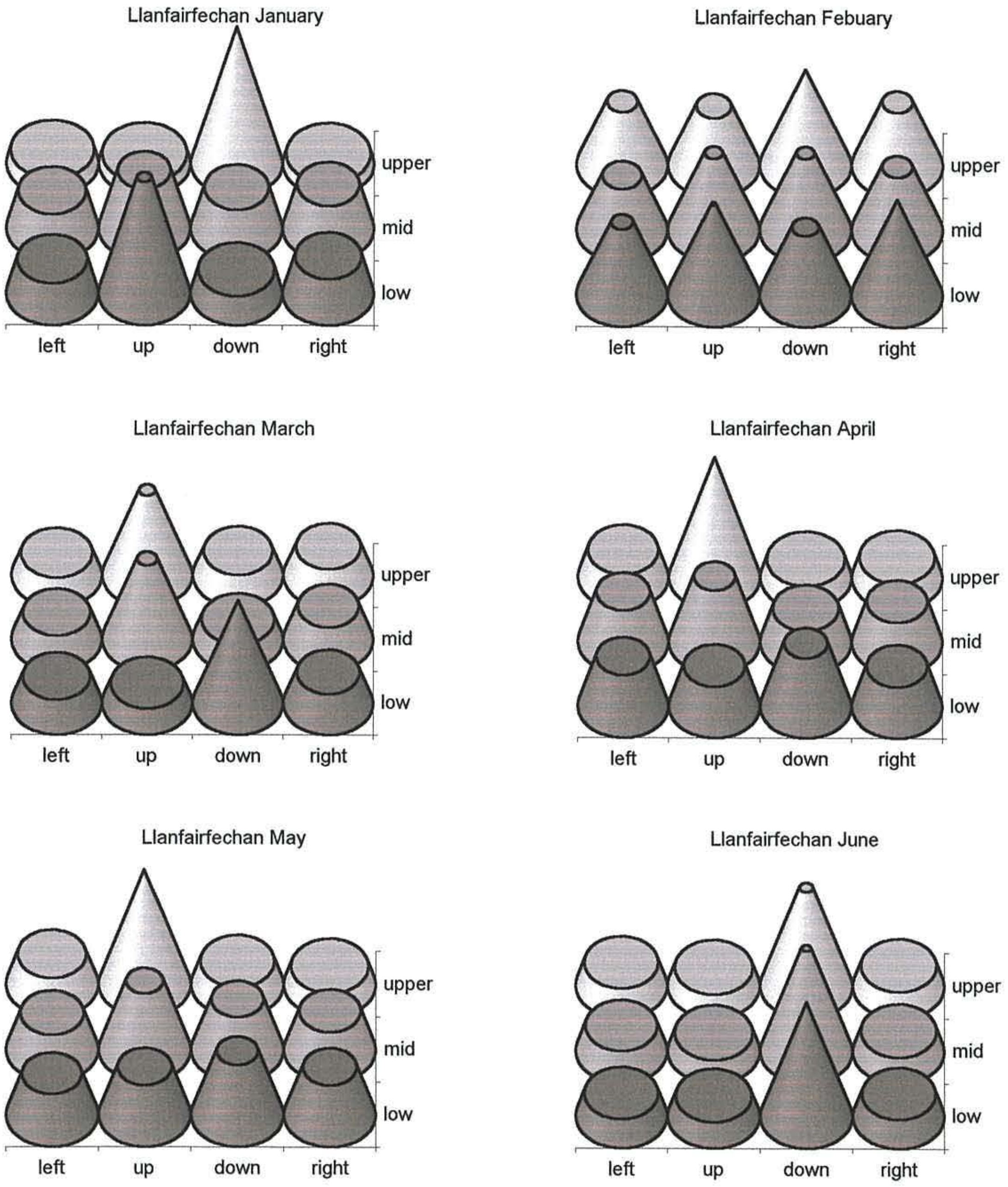


Figure 4.7. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

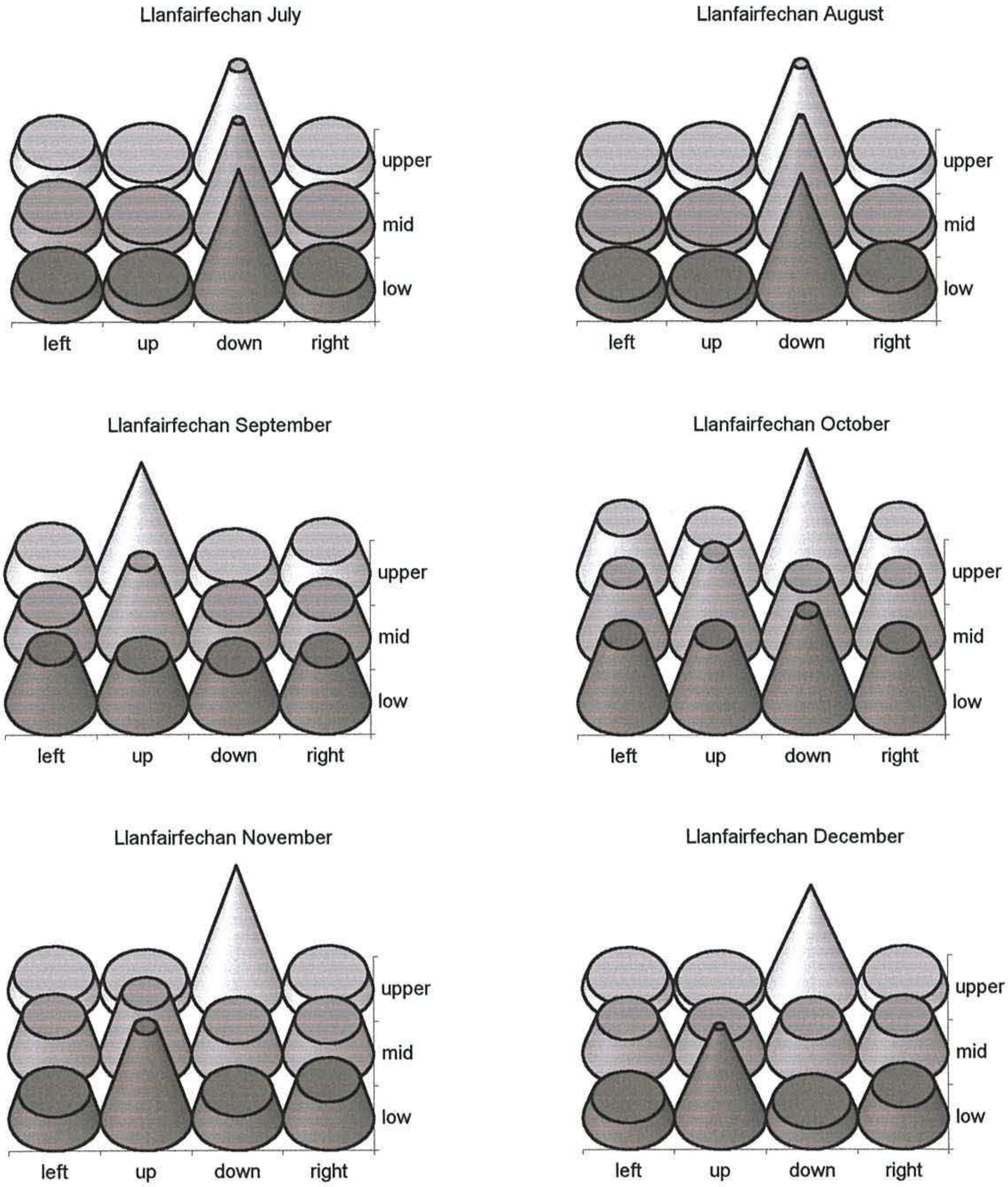


Figure 4.8. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

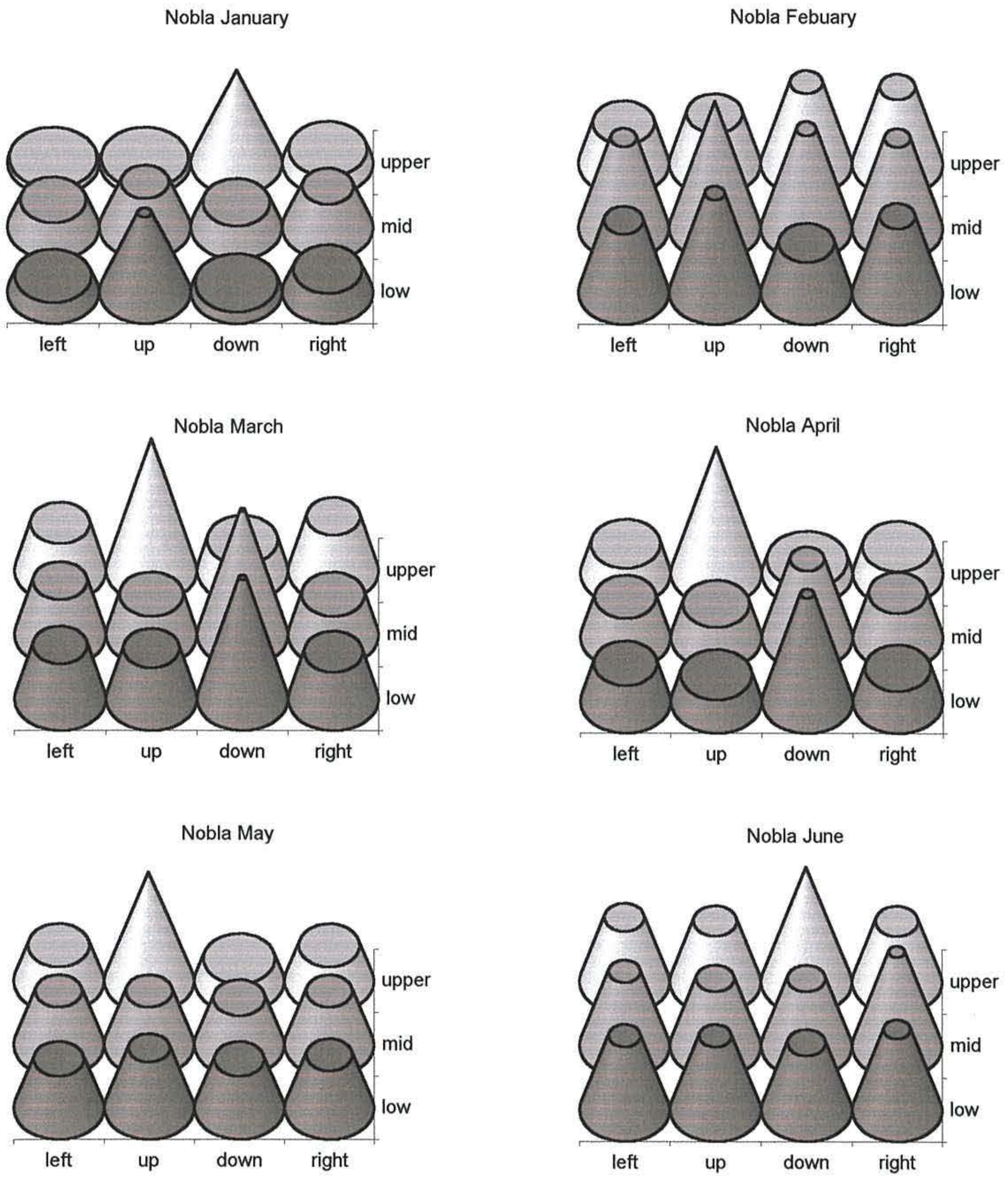


Figure 4.9.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

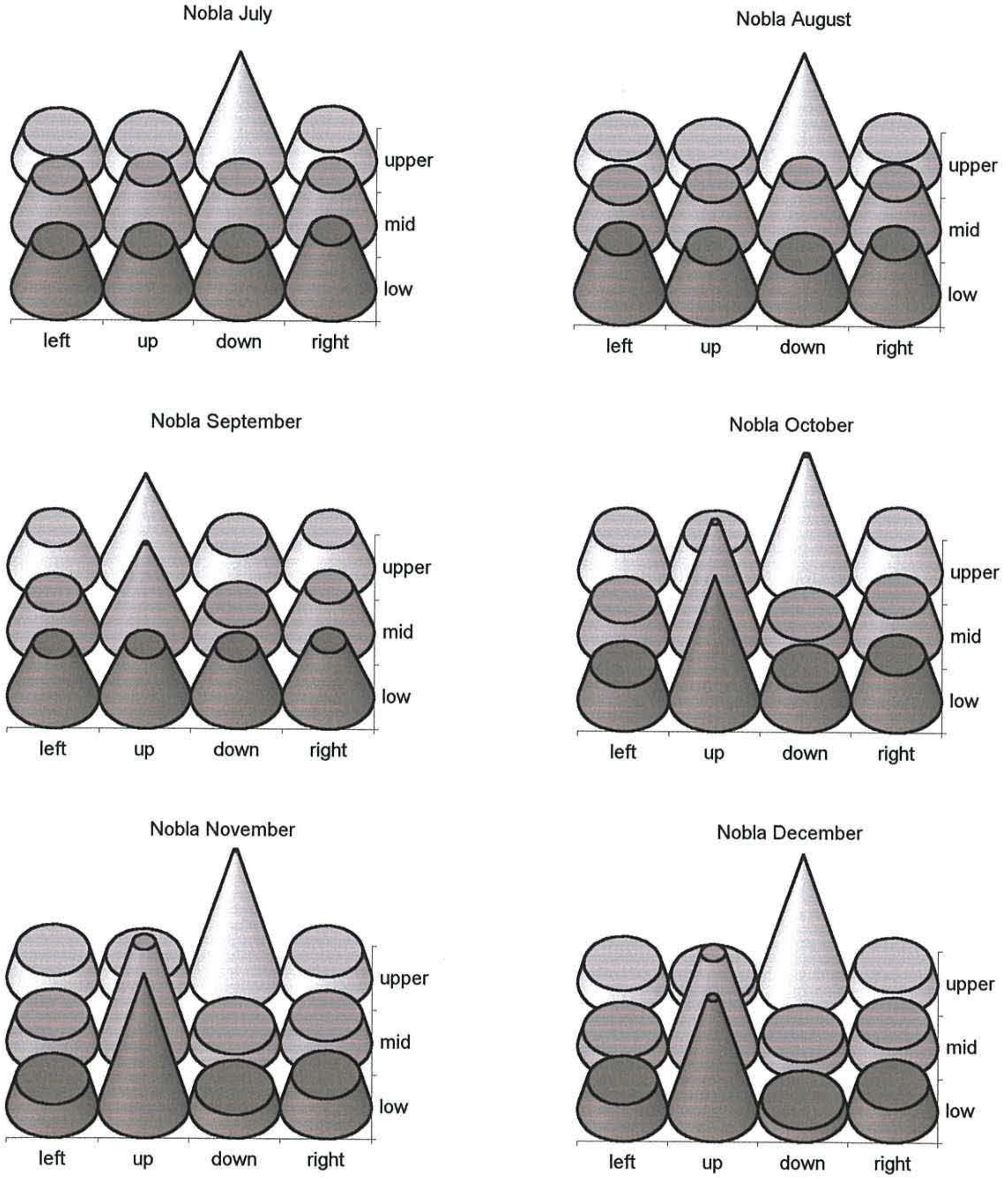


Figure 4.10. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

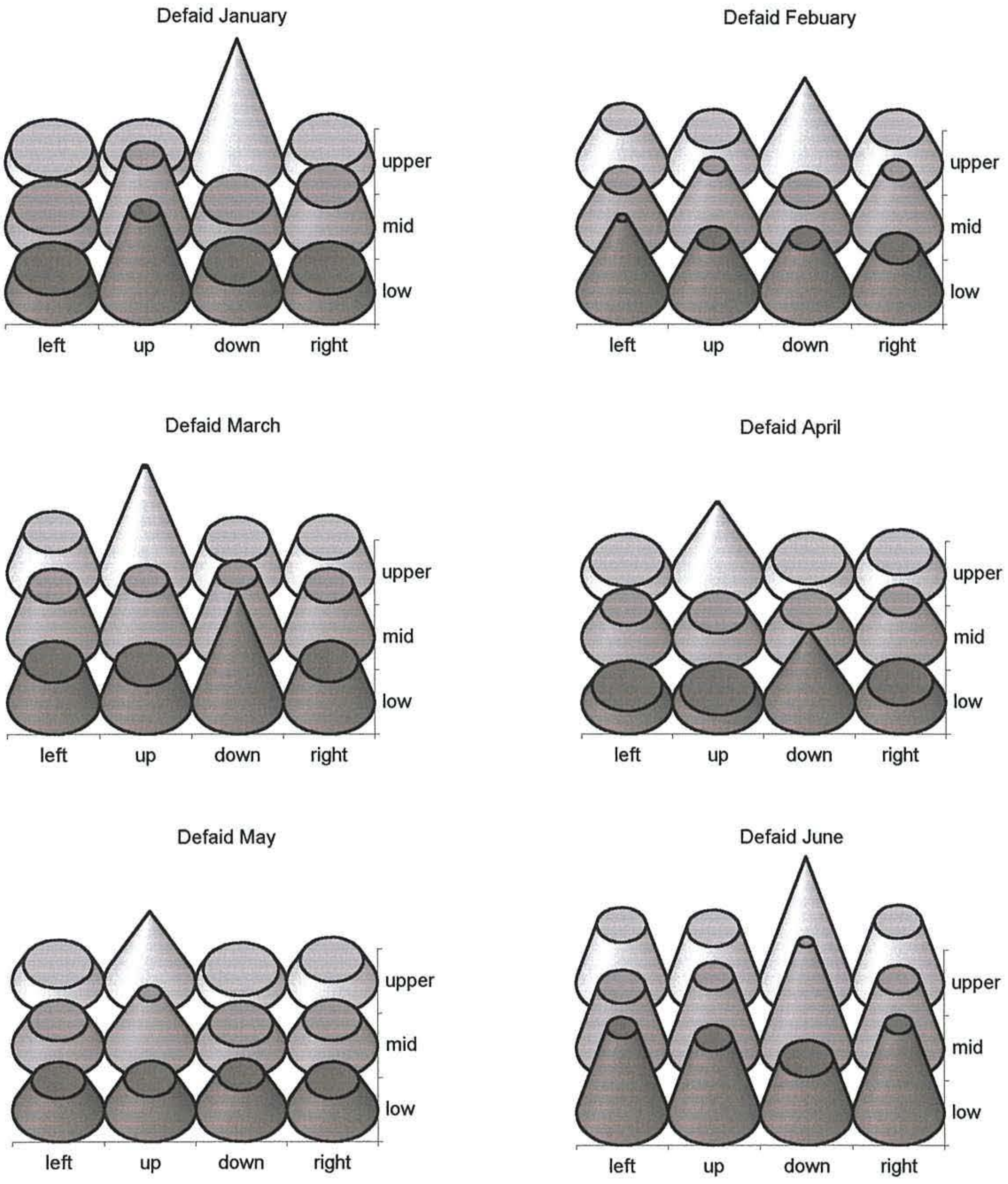


Figure 4.11.Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

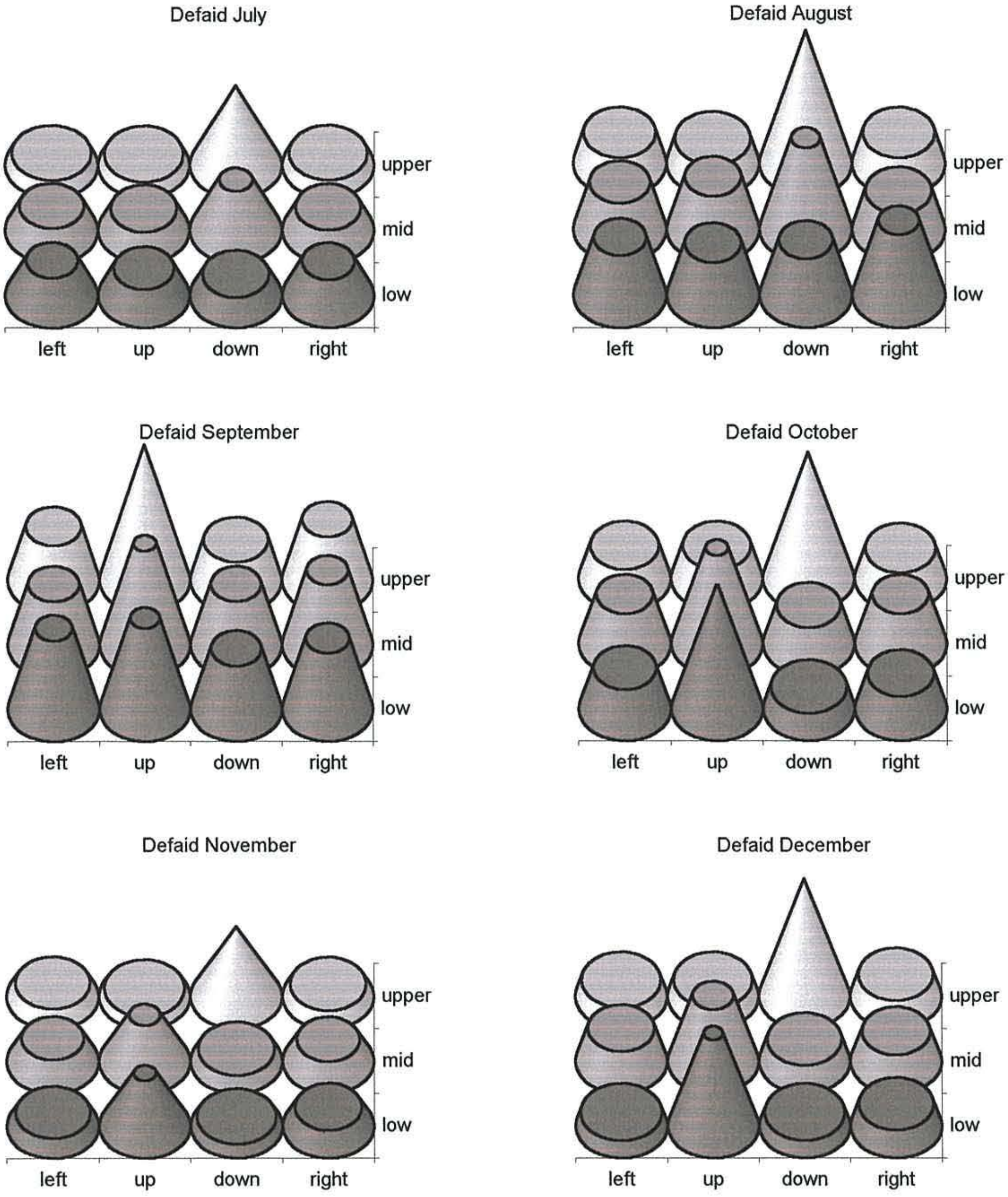


Figure 4.12. Monthly migration patterns of *Nucella lapillus* at different shore levels. Cones represent the relative numbers of whelks moving in specified directions.

Appendix 4 Tables.

Table 4.1. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Menai Bridge.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3			0.080	<0.001	0.060	<0.001
1-4	0.172	<0.001	0.165	<0.001	0.120	<0.001
1-5	0.319	<0.001	0.237	<0.001	0.178	<0.001
1-6			0.061	<0.001	0.049	0.001
1-9	0.172	<0.001	0.147	<0.001	0.134	<0.001
1-10	0.107	0.002	0.114	<0.001	0.104	<0.001
1-11	0.092	0.012	0.063	<0.001	0.046	0.004
2-3			0.058	0.001	0.044	0.010
2-4	0.130	0.001	0.143	<0.001	0.104	<0.001
2-5	0.277	<0.001	0.216	<0.001	0.162	<0.001
2-9			0.125	<0.001	0.118	<0.001
2-10			0.092	<0.001	0.087	<0.001
3-4			0.085	<0.001	0.064	<0.001
3-5	0.223	<0.001	0.158	<0.001	0.118	<0.001
3-7			0.074	<0.001	0.059	<0.001
3-8			0.078	<0.001	0.058	<0.001
3-9			0.067	<0.001	0.074	<0.001
3-12			0.069	<0.001	0.052	<0.001
4-5			0.073	<0.001	0.058	<0.001
4-6			0.104	<0.001	0.071	<0.001
4-7	0.165	<0.001	0.159	<0.001	0.120	<0.001
4-8	0.166	<0.001	0.163	<0.001	0.119	<0.001
4-10			0.052	0.005		
4-11			0.103	<0.001	0.074	<0.001
4-12	0.160	<0.001	0.155	<0.001	0.112	<0.001
5-6	0.245	<0.001	0.177	<0.001	0.129	<0.001
5-7	0.312	<0.001	0.231	<0.001	0.178	<0.001

Table 4.1 continued.

5-8	0.313	<0.001	0.236	<0.001	0.177	<0.001
5-9	0.188	<0.001	0.091	<0.001	0.044	0.003
5-10	0.212	<0.001	0.124	<0.001	0.172	<0.001
5-11	0.227	<0.001	0.175	<0.001	0.074	<0.001
5-12	0.307	<0.001	0.227	<0.001	0.132	<0.001
6-7			0.055	0.003	0.048	0.002
6-8			0.059	0.001	0.048	0.002
6-9			0.086	<0.001	0.085	<0.001
6-10			0.053	0.004	0.054	<0.001
6-12			0.050	0.010	0.041	0.022
7-9	0.124	<0.001	0.141	<0.001	0.133	<0.001
7-10			0.107	<0.001	0.103	<0.001
7-11			0.056	0.002	0.045	0.005
8-9	0.125	<0.001	0.145	<0.001	0.133	<0.001
8-10	0.101	0.005	0.111	<0.001	0.102	<0.001
8-11			0.060	<0.001	0.044	0.007
9-11			0.085	<0.001	0.088	<0.001
9-12	0.119	0.002	0.136	<0.001	0.126	<0.001
10-11			0.051	0.006	0.058	<0.001
10-12	0.094	0.047	0.103	<0.001	0.095	<0.001
11-12			0.052	0.006		

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.2. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Trwyn y Penrhyn.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.111	<0.001	0.086	<0.001	0.081	<0.001
1-4	0.237	<0.001	0.156	<0.001	0.138	<0.001
1-5	0.322	<0.001	0.247	<0.001	0.211	<0.001
1-6	0.116	<0.001	0.064	0.002	0.052	0.004
1-9	0.186	<0.001	0.162	<0.001	0.141	<0.001
1-10	0.137	<0.001	0.141	<0.001	0.117	<0.001
1-11	0.076	<0.001	0.062	0.002	0.066	<0.001
2-3	0.162	0.011	0.054	0.020	0.053	0.002
2-4	0.188	<0.001	0.124	<0.001	0.110	<0.001
2-5	0.273	<0.001	0.215	<0.001	0.184	<0.001
2-6	0.067	0.004				
2-9	0.137	<0.001	0.130	<0.001	0.114	<0.001
2-10	0.087	<0.001	0.109	<0.001	0.089	<0.001
3-4	0.126	<0.001	0.070	<0.001	0.057	<0.001
3-5	0.210	<0.001	0.160	<0.001	0.131	<0.001
3-7	0.092	<0.001	0.076	<0.001	0.068	<0.001
3-8	0.099	<0.001	0.076	<0.001	0.068	<0.001
3-9	0.075	<0.001	0.075	<0.001	0.060	<0.001
3-10			0.055	0.013		
3-12	0.080	<0.001	0.079	<0.001	0.072	<0.001
4-5	0.085	<0.001	0.090	<0.001	0.074	<0.001
4-6	0.121	<0.001	0.093	<0.001	0.086	<0.001
4-7	0.218	<0.001	0.146	<0.001	0.125	<0.001
4-8	0.225	<0.001	0.146	<0.001	0.125	<0.001
4-9	0.052	0.045				
4-10	0.101	<0.001				
4-11	0.161	<0.001	0.095	<0.001	0.071	<0.001
4-12	0.206	<0.001	0.149	<0.001	0.129	<0.001

Table 4.2 continued.

5-6	0.206	<0.001	0.183	<0.001	0.159	<0.001
5-7	0.303	<0.001	0.236	<0.001	0.199	<0.001
5-8	0.310	<0.001	0.236	<0.001	0.199	<0.001
5-9	0.136	<0.001	0.085	<0.001	0.070	<0.001
5-10	0.186	<0.001	0.105	<0.001	0.094	<0.001
5-11	0.246	<0.001	0.185	<0.001	0.145	<0.001
5-12	0.291	<0.001	0.239	<0.001	0.203	<0.001
6-7	0.097	<0.001	0.053	0.044		
6-8	0.104	<0.001				
6-9	0.070	<0.001	0.098	<0.001	0.089	<0.001
6-10			0.078	<0.001	0.065	<0.001
6-12	0.085	<0.001	0.055	0.016	0.043	0.049
7-9	0.167	<0.001	0.151	<0.001	0.128	<0.001
7-10	0.117	<0.001	0.131	<0.001	0.104	<0.001
7-11	0.057	0.026	0.052	0.041	0.054	0.001
8-9	0.173	<0.001	0.151	<0.001	0.129	<0.001
8-10	0.124	<0.001	0.131	<0.001	0.105	<0.001
8-11	0.064	0.009	0.051	0.047	0.054	0.001
9-11	0.110	<0.001	0.099	<0.001	0.074	<0.001
9-12	0.154	<0.001	0.154	<0.001	0.133	<0.001
10-11	0.060	0.011	0.079	<0.001	0.050	0.003
10-12	0.105	<0.001	0.133	<0.001	0.109	<0.001
11-12			0.054	0.014	0.058	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.3. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Llanfairfechan.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.131	<0.001	0.106	<0.001	0.091	<0.001
1-4	0.220	<0.001	0.181	<0.001	0.178	<0.001
1-5	0.380	<0.001	0.324	<0.001	0.266	<0.001
1-6	0.175	<0.001	0.163	<0.001	0.099	<0.001
1-9	0.216	<0.001	0.213	<0.001	0.175	<0.001
1-10	0.178	<0.001	0.187	<0.001	0.138	<0.001
1-11	0.093	<0.001	0.082	<0.001	0.072	<0.001
2-3	0.093	<0.001	0.081	<0.001	0.072	<0.001
2-4	0.183	<0.001	0.157	<0.001	0.158	<0.001
2-5	0.343	<0.001	0.299	<0.001	0.247	<0.001
2-6	0.137	<0.001	0.139	<0.001	0.079	<0.001
2-9	0.179	<0.001	0.188	<0.001	0.156	<0.001
2-10	0.141	<0.001	0.163	<0.001	0.119	<0.001
2-11					0.052	0.029
3-4	0.090	<0.001	0.075	0.002	0.086	<0.001
3-5	0.249	<0.001	0.218	<0.001	0.175	<0.001
3-7	0.099	<0.001	0.076	0.002	0.076	<0.001
3-8	0.108	<0.001	0.080	0.001	0.078	<0.001
3-9	0.085	<0.001	0.107	<0.001	0.084	<0.001
3-10			0.081	<0.001		
3-12	0.114	<0.001	0.092	<0.001	0.078	<0.001
4-5	0.160	<0.001	0.142	<0.001	0.089	<0.001
4-6					0.079	<0.001
4-7	0.188	<0.001	0.151	<0.001	0.162	<0.001
4-8	0.198	<0.001	0.155	<0.001	0.164	<0.001
4-11	0.127	<0.001	0.099	<0.001	0.106	<0.001
4-12	0.204	<0.001	0.167	<0.001	0.165	<0.001
5-6	0.205	<0.001	0.160	<0.001	0.167	<0.001

Table 4.3 continued.

5-7	0.348	<0.001	0.294	<0.001	0.251	<0.001
5-8	0.357	<0.001	0.298	<0.001	0.253	<0.001
5-9	0.164	<0.001	0.111	<0.001	0.091	<0.001
5-10	0.202	<0.001	0.136	<0.001	0.128	<0.001
5-11	0.287	<0.001	0.242	<0.001	0.195	<0.001
5-12	0.363	<0.001	0.309	<0.001	0.253	<0.001
6-7	0.143	<0.001	0.133	<0.001	0.084	<0.001
6-8	0.152	<0.001	0.137	<0.001	0.086	<0.001
6-9					0.076	<0.001
6-11	0.081	0.001	0.081	<0.001		
6-12	0.158	<0.001	0.149	<0.001	0.086	<0.001
7-9	0.184	<0.001	0.183	<0.001	0.160	<0.001
7-10	0.146	<0.001	0.157	<0.001	0.123	<0.001
7-11					0.056	0.015
8-9	0.194	<0.001	0.187	<0.001	0.162	<0.001
8-10	0.156	<0.001	0.161	<0.001	0.125	<0.001
8-11	0.071	0.008			0.059	0.009
9-11	0.123	<0.001	0.131	<0.001	0.104	<0.001
9-12	0.199	<0.001	0.198	<0.001	0.162	<0.001
10-11	0.085	<0.001	0.105	<0.001	0.066	<0.001
10-12	0.162	<0.001	0.173	<0.001	0.125	<0.001
11-12	0.077	0.001	0.068	0.008	0.059	0.006

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.4. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Red Wharf Bay.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.104	0.001	0.111	<0.001	0.081	<0.001
1-4	0.233	<0.001	0.221	<0.001	0.180	<0.001
1-5	0.459	<0.001	0.465	<0.001	0.334	<0.001
1-6	0.239	<0.001	0.167	<0.001	0.147	<0.001
1-7			0.071	0.021		
1-9	0.283	<0.001	0.229	<0.001	0.189	<0.001
1-10	0.306	<0.001	0.244	<0.001	0.209	<0.001
1-11	0.133	<0.001	0.135	<0.001	0.101	<0.001
2-3			0.075	0.011	0.055	0.021
2-4	0.205	<0.001	0.185	<0.001	0.153	<0.001
2-5	0.430	<0.001	0.430	<0.001	0.307	<0.001
2-6	0.210	<0.001	0.132	<0.001	0.121	<0.001
2-7	0.089	0.020				
2-9	0.255	<0.001	0.193	<0.001	0.162	<0.001
2-10	0.277	<0.001	0.208	<0.001	0.183	<0.001
2-11	0.105	0.001	0.096	<0.001	0.075	0.003
3-4	0.129	<0.001	0.110	<0.001	0.099	<0.001
3-5	0.355	<0.001	0.354	<0.001	0.253	<0.001
3-6	0.135	<0.001			0.061	0.001
3-8					0.0555	0.014
3-9	0.180	<0.001	0.118	<0.001	0.108	<0.001
3-10	0.202	<0.001	0.133	<0.001	0.128	<0.001
3-12			0.082	0.002		
4-5	0.226	<0.001	0.244	<0.001	0.154	<0.001
4-7	0.116	<0.001	0.150	<0.001	0.143	<0.001
4-8	0.174	<0.001	0.165	<0.001	0.154	<0.001
4-11	0.098	0.002	0.085	0.001	0.078	0.001
4-12	0.201	<0.001	0.192	<0.001	0.155	<0.001

Table 4.4 continued.

5-6	0.220	<0.001	0.298	<0.001	0.187	<0.001
5-7	0.342	<0.001	0.395	<0.001	0.297	<0.001
5-8	0.399	<0.001	0.409	<0.001	0.308	<0.001
5-9	0.175	<0.001	0.236	<0.001	0.145	<0.001
5-10	0.153	<0.001	0.221	<0.001	0.125	<0.001
5-11	0.325	<0.001	0.330	<0.001	0.233	<0.001
5-12	0.426	<0.001	0.436	<0.001	0.309	<0.001
6-7	0.122	<0.001	0.096	<0.001	0.111	<0.001
6-8	0.180	<0.001	0.111	<0.001	0.121	<0.001
6-10			0.076	0.004	0.062	0.045
6-11	0.106	0.001				
6-12	0.207	<0.001	0.138	<0.001	0.123	<0.001
7-9	0.166	<0.001	0.158	<0.001	0.152	<0.001
7-10	0.189	<0.001	0.173	<0.001	0.173	<0.001
7-11	0.172	<0.001	0.065	0.048	0.064	0.035
7-12	0.085	0.037				
8-9	0.224	<0.001	0.173	<0.001	0.163	<0.001
8-10	0.246	<0.001	0.188	<0.001	0.183	<0.001
8-11			0.079	0.003	0.075	0.002
9-11	0.150	<0.001	0.094	<0.001	0.088	<0.001
9-12	0.251	<0.001	0.199	<0.001	0.164	<0.001
10-11	0.172	<0.001	0.109	<0.001	0.108	<0.001
10-12	0.274	<0.001	0.215	<0.001	0.185	<0.001
11-12	0.101	0.002	0.106	<0.001	0.076	0.022

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.5. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Porth Nobla.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3					0.073	0.001
1-4	0.181	<0.001	0.206	<0.001	0.189	<0.001
1-5	0.427	<0.001	0.386	<0.001	0.290	<0.001
1-6	0.378	<0.001	0.252	<0.001	0.243	<0.001
1-7	0.175	<0.001	0.168	<0.001	0.123	<0.001
1-8	0.161	<0.001	0.099	<0.001	0.060	<0.017
1-9	0.181	<0.001	0.239	<0.001	0.214	<0.001
1-10	0.172	<0.001	0.150	<0.001	0.149	<0.001
1-11	0.074	0.043	0.079	0.004	0.067	0.002
2-3					0.064	0.046
2-4	0.188	<0.001	0.195	<0.001	0.180	<0.001
2-5	0.433	<0.001	0.375	<0.001	0.281	<0.001
2-6	0.384	<0.001	0.241	<0.001	0.234	<0.001
2-7	0.181	<0.001	0.158	<0.001	0.114	<0.001
2-8	0.167	<0.001	0.088	0.001		
2-9	0.187	<0.001	0.228	<0.001	0.205	<0.001
2-10	0.178	<0.001	0.139	<0.001	0.140	<0.001
2-11	0.080	0.015	0.068	0.037		
3-4	0.129	<0.001	0.134	<0.001	0.116	<0.001
3-5	0.375	<0.001	0.313	<0.001	0.217	<0.001
3-6	0.326	<0.001	0.180	<0.001	0.170	<0.001
3-7	0.122	<0.001	0.096	<0.001		
3-8	0.109	<0.001				
3-9	0.129	<0.001	0.167	<0.001	0.141	<0.001
3-10	0.120	<0.001	0.077	0.006	0.076	0.001
4-5	0.245	<0.001	0.179	<0.001	0.101	<0.001
4-6	0.197	<0.001				
4-7					0.066	0.010

Table 4.5 continued.

4-8			0.107	<0.001	0.129	<0.001
4-11	0.107	<0.001	0.127	<0.001	0.122	<0.001
4-12	0.154	<0.001	0.190	<0.001	0.178	<0.001
5-6			0.133	<0.001		
5-7	0.252	<0.001	0.217	<0.001	0.167	<0.001
5-8	0.266	<0.001	0.286	<0.001	0.230	<0.001
5-9	0.246	<0.001	0.146	<0.001	0.076	<0.001
5-10	0.255	<0.001	0.236	<0.001	0.141	<0.001
5-11	0.353	<0.001	0.306	<0.001	0.222	<0.001
5-12	0.399	<0.001	0.370	<0.001	0.281	<0.001
6-7	0.203	<0.001	0.084	0.002	0.120	<0.001
6-8	0.217	<0.001	0.153	<0.001	0.183	<0.001
6-9	0.197	<0.001				
6-10	0.206	<0.001	0.102	<0.001	0.094	<0.001
6-11	0.304	<0.001	0.173	<0.001	0.176	<0.001
6-12	0.350	<0.001	0.236	<0.001	0.232	<0.001
7-9			0.071	0.018	0.091	<0.001
7-11	0.100	0.001	0.089	0.001		
7-12	0.147	<0.001	0.153	<0.001	0.112	<0.001
8-9			0.140	<0.001	0.153	<0.001
8-10					0.089	<0.001
8-11	0.087	0.004				
8-12	0.133	<0.001	0.083	0.002		
9-10			0.089	<0.001	0.065	0.005
9-11	0.107	<0.001	0.160	<0.001	0.146	<0.001
9-12	0.153	<0.001	0.223	<0.001	0.202	<0.001
10-11	0.098	0.005	0.070	0.016	0.082	<0.001
10-12	0.144	<0.001	0.134	<0.001	0.138	<0.001

Data presented are mean differences (md), with probabilities (P) which are all significant values.

Table 4.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between months at Porth Defaid.

	low shore		mid shore		upper shore	
months	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.086	0.003	0.085	0.001	0.065	0.008
1-4	0.224	<0.001	0.199	<0.001	0.165	<0.001
1-5	0.467	<0.001	0.345	<0.001	0.271	<0.001
1-6	0.356	<0.001	0.281	<0.001	0.216	<0.001
1-7	0.217	<0.001	0.197	<0.001	0.149	<0.001
1-8	0.129	<0.001	0.125	<0.001	0.092	<0.017
1-9	0.184	<0.001	0.171	<0.001	0.139	<0.001
1-10	0.105	<0.001	0.115	<0.001	0.103	<0.001
1-11			0.066	0.034	0.067	0.004
2-3	0.076	0.018	0.074	0.011		
2-4	0.214	<0.001	0.189	<0.001	0.148	<0.001
2-5	0.457	<0.001	0.334	<0.001	0.254	<0.001
2-6	0.346	<0.001	0.271	<0.001	0.198	<0.001
2-7	0.206	<0.001	0.187	<0.001	0.132	<0.001
2-8	0.119	<0.001	0.114	0.001	0.074	0.001
2-9	0.174	<0.001	0.160	<0.001	0.122	<0.001
2-10	0.095	<0.001	0.105	<0.001	0.085	<0.001
3-4	0.138	<0.001	0.115	<0.001	0.100	<0.001
3-5	0.381	<0.001	0.259	<0.001	0.206	<0.001
3-6	0.270	<0.001	0.196	<0.001	0.150	<0.001
3-7	0.130	<0.001	0.112	<0.001	0.084	<0.001
3-9	0.098	<0.001	0.086	<0.001	0.074	<0.001
3-12	0.082	0.007	0.075	0.007		
4-5	0.243	<0.001	0.145	<0.001	0.107	<0.001
4-6	0.132	<0.001	0.081	0.007		
4-8	0.095	<0.001	0.075	0.008	0.073	0.001
4-10	0.119	<0.001	0.085	<0.001	0.062	0.011
4-11	0.185	<0.001	0.133	<0.001	0.098	<0.001

Table 4.6 continued.

4-12	0.220 <0.001	0.190 <0.001	0.152 <0.001
5-6	0.111 <0.001		
5-7	0.251 <0.001	0.148 <0.001	0.122 <0.001
5-8	0.338 <0.001	0.220 <0.001	0.180 <0.001
5-9	0.283 <0.001	0.174 <0.001	0.132 <0.001
5-10	0.362 <0.001	0.229 <0.001	0.169 <0.001
5-11	0.428 <0.001	0.278 <0.001	0.204 <0.001
5-12	0.463 <0.001	0.335 <0.001	0.259 <0.001
6-7	0.139 <0.001	0.084 0.002	0.066 0.005
6-8	0.227 <0.001	0.156 <0.001	0.124 <0.001
6-9	0.172 <0.001	0.110 <0.001	0.076 <0.001
6-10	0.251 <0.001	0.166 <0.001	0.113 <0.001
6-11	0.316 <0.001	0.214 <0.001	0.149 <0.001
6-12	0.352 <0.001	0.272 <0.001	0.203 <0.001
7-10	0.112 <0.001	0.082 <0.001	
7-11	0.177 0.001	0.131 <0.001	0.082 <0.001
7-12	0.212 <0.001	0.188 <0.001	0.137 <0.001
8-11	0.089 0.001		
8-12	0.124 <0.001	0.115 <0.001	0.079 <0.001
9-10	0.079 0.002		
9-11	0.144 <0.001	0.104 <0.001	0.072 <0.001
9-12	0.180 <0.001	0.161 <0.001	0.127 <0.001
10-12	0.101 <0.001	0.106 <0.001	0.089 <0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.7. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between size classes at Menai Bridge.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.174	<0.001			0.208	0.032
1-4	0.198	<0.001	0.159	0.029	0.287	0.001
2-3	0.132	<0.001	0.122	<0.001	0.132	<0.001
2-4	0.156	<0.001	0.148	<0.001	0.210	<0.001
3-4					0.078	<0.001

Data presented are mean differences (md), with probabilities (P) which are all significant values.

Table 4.8. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella* movement distance between size classes at Trwyn y Penrhyn.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.290	<0.001	0.443	<0.001	0.236	<0.001
1-4	0.311	<0.001	0.550	<0.001	0.273	<0.001
2-3	0.250	<0.001	0.307	<0.001	0.228	<0.001
2-4	0.271	<0.001	0.414	<0.001	0.266	<0.001
3-4			0.106	0.016		

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.9. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between size classes at Llanfairfechan.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.149	<0.001	0.123	<0.001	0.121	0.011
1-4	0.214	<0.001	0.175	<0.001	0.204	0.005
2-3	0.110	<0.001	0.082	<0.001	0.076	<0.001
2-4	0.175	<0.001	0.106	0.004	0.163	<0.001
3-4					0.086	0.005

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.10. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between size classes at Red Wharf Bay.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.136	0.002	0.134	<0.001	0.133	<0.001
1-4	0.207	<0.001	0.224	<0.001	0.273	<0.001
2-3	0.108	<0.001	0.043	0.018	0.075	0.001
2-4	0.179	<0.001	0.114	<0.001	0.166	0.001
3-4	0.079	<0.001	0.071	0.023	0.140	0.005

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.11. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between size classes at Porth Nobla.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.128	0.003	0.148	0.008	0.151	<0.001
1-4	0.143	0.001	0.225	<0.001	0.182	<0.001
2-3	0.093	<0.001	0.088	<0.001	0.102	<0.001
2-4	0.108	<0.001	0.165	<0.001	0.133	<0.001
3-4			0.076	0.049		

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.12. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* movement distance between size classes at Porth Defaid.

	low shore		mid shore		upper shore	
size classes	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-3	0.114	0.005	0.140	0.031	0.131	0.038
1-4	0.123	0.003	0.099	0.043	0.194	0.002
2-3	0.119	<0.001	0.117	<0.001	0.105	<0.001
2-4	0.145	<0.001	0.062	<0.001	0.168	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values

Table 4.13. Post Hoc multiple comparisons showing significant mean differences in *Nucella lapillus* migration direction within shore levels.

Shore	shore level	1-2	1-3	1-4	2-3	2-4	3-4
Menai	1	<0.001	<0.001	<0.001	0.040	1.000	0.024
	2	<0.001	<0.001	<0.001	0.163	0.104	1.000
	3	<0.001	<0.001	<0.001	<0.001	0.127	<0.001
Trwyn	1	<0.001	<0.001	<0.001	0.001	0.045	<0.001
	2	<0.001	<0.001	<0.001	1.000	1.000	1.000
	3	<0.001	<0.001	<0.001	<0.001	1.000	<0.001
Llanfairfechan	1	<0.001	0.002	<0.001	0.014	0.542	0.005
	2	0.001	1.000	<0.001	0.001	1.000	0.001
	3	<0.001	<0.001	<0.001	<0.001	1.000	<0.001
Red Wharf	1	<0.001	0.228	<0.001	<0.001	0.234	<0.001
	2	0.004	0.017	<0.001	0.274	0.184	0.021
	3	<0.001	<0.001	<0.001	0.005	0.316	0.002
Nobla	1	1.000	0.001	0.421	0.001	0.698	<0.001
	2	1.000	<0.001	0.007	<0.001	0.012	<0.001
	3	<0.001	0.002	<0.001	<0.001	0.761	<0.001
Defaid	1	0.243	0.013	0.264	0.003	1.000	0.003
	2	1.000	0.001	0.144	0.001	0.651	0.001
	3	<0.001	0.002	<0.001	0.001	1.000	0.001

Data presented are probabilities (P).

Table 4.14. Post Hoc multiple comparisons showing significant mean differences in *Nucella lapillus* migration direction between shore levels.

Shore	Direction	1-2	1-3	2-3	Direction	1-2	1-3	2-3
Menai	1	0.003	0.006	0.266	3	0.053	0.014	0.003
	2	0.020	0.136	0.006	4	0.022	0.021	0.003
Trwyn	1	0.001	0.633	0.001	3	<0.001	0.001	<0.001
	2	0.018	0.007	0.234	4	0.010	0.002	0.018
Llanfair.	1	0.001	0.050	0.001	3	0.335	0.062	0.330
	2	0.028	0.002	0.010	4	0.088	0.007	0.030
Red Wharf	1	0.008	<0.001	<0.001	3	0.006	0.010	0.701
	2	0.194	0.455	0.054	4	0.044	0.069	0.008
Nobla	1	0.075	0.001	0.001	3	0.040	0.004	0.025
	2	0.105	0.004	0.010	4	0.054	0.002	0.008
Defaid	1	0.105	0.001	0.001	3	1.000	0.036	0.050
	2	1.000	0.007	0.009	4	0.387	0.009	0.019

Data presented are probabilities (P).

Table 4.15. Post Hoc multiple comparisons showing significant mean differences in *Nucella lapillus* migration direction between shores.

Direction	Level	1-2	1-3	1-4	1-5	1-6	2-3	2-4	2-5
1	1	1.000	<0.001	0.001	<0.001	<0.001	<0.001	0.002	<0.001
1	2	1.000	0.004	<0.001	<0.001	<0.001	0.009	<0.001	<0.001
1	3	<0.001	<0.001	1.000	1.000	1.000	1.000	<0.001	<0.001
2	1	1.000	0.642	0.067	0.007	0.059	1.000	1.000	0.048
2	2	0.001	1.000	0.006	1.000	1.000	<0.001	0.151	0.001
2	3	0.076	0.394	0.010	1.000	1.000	0.005	1.000	0.088
3	1	0.062	<0.001	0.020	<0.001	0.001	0.001	1.000	0.001
3	2	0.001	0.007	0.002	<0.001	<0.001	<0.001	<0.001	<0.001
3	3	0.003	1.000	0.994	1.000	1.000	0.002	0.018	0.001
4	1	1.000	1.000	0.402	0.019	0.023	1.000	0.381	0.019
4	2	<0.001	1.000	0.001	0.812	1.000	<0.001	0.038	<0.001
4	3	0.169	0.778	0.074	1.000	1.000	0.014	1.000	0.089

Table 4.15 continued.

		2-6	3-4	3-5	3-6	4-5	4-6	5-6
1	1	<0.001	0.006	<0.001	<0.001	<0.001	<0.001	1.000
1	2	<0.001	0.018	<0.001	<0.001	<0.001	0.001	1.000
1	3	<0.001	<0.001	<0.001	<0.001	1.000	1.000	1.000
2	1	0.884	1.000	0.070	1.000	0.680	1.000	0.798
2	2	0.001	0.003	0.775	0.750	0.022	0.022	1.000
2	3	0.752	0.001	0.331	0.046	0.012	0.059	1.000
3	1	0.033	0.002	1.000	0.056	0.001	0.112	0.017
3	2	<0.001	1.000	0.001	0.002	0.002	0.008	1.000
3	3	0.002	0.373	1.000	1.000	0.138	0.707	1.000
4	1	0.022	1.000	0.043	0.053	0.489	0.639	1.000
4	2	<0.001	0.001	0.259	1.000	0.005	0.002	1.000
4	3	0.455	0.008	1.000	0.276	0.041	0.183	1.000

Data presented are probabilities (P).

Table 4.16. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* at Menai Bridge.

months	md	*P*	months	md	*P*	months	md	*P*
1-2	0.028	<0.001	3-8	0.043	<0.001	6-9	0.139	<0.001
1-3	0.038	<0.001	3-9	0.091	<0.001	6-10	0.099	<0.001
1-4	0.063	<0.001	3-10	0.050	<0.001	6-11	0.050	<0.001
1-5	0.074	<0.001	3-12	0.026	<0.001	6-12	0.022	0.001
1-9	0.129	<0.001	4-6	0.073	<0.001	7-9	0.143	<0.001
1-10	0.089	<0.001	4-7	0.077	<0.001	7-10	0.103	<0.001
1-11	0.040	<0.001	4-8	0.068	<0.001	7-11	0.054	<0.001
2-4	0.035	<0.001	4-9	0.066	<0.001	7-12	0.026	<0.001
2-5	0.046	<0.001	4-10	0.026	<0.001	8-9	0.134	<0.001
2-6	0.038	<0.001	4-11	0.023	0.001	8-10	0.094	<0.001
2-7	0.042	<0.001	4-12	0.051	<0.001	8-11	0.045	<0.001
2-8	0.033	<0.001	5-6	0.084	<0.001	9-10	0.040	<0.001
2-9	0.102	<0.001	5-7	0.088	<0.001	9-11	0.089	<0.001

Table 4.16 continued.

2-10	0.061	<0.001	5-8	0.079	<0.001	9-12	0.117	<0.001
3-4	0.025	<0.001	5-9	0.055	<0.001	10-11	0.049	<0.001
3-5	0.035	<0.001	5-11	0.028	<0.001	10-12	0.077	<0.001
3-6	0.048	<0.001	5-12	0.028	<0.001	11-12	0.028	<0.001
3-7	0.053	<0.001						

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.17. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* at Trwyn y Penrhyn.

months	md	*P*	months	md	*P*	months	md	*P*
1-2	0.048	<0.001	3-8	0.067	<0.001	6-8	0.042	<0.001
1-3	0.057	<0.001	3-9	0.110	<0.001	6-9	0.135	<0.001
1-4	0.069	<0.001	3-10	0.068	<0.001	6-10	0.092	<0.001
1-5	0.092	<0.001	3-12	0.046	<0.001	6-11	0.042	<0.001
1-6	0.033	<0.001	4-5	0.022	0.046	7-9	0.162	<0.001
1-9	0.168	<0.001	4-6	0.037	<0.001	7-10	0.119	<0.001
1-10	0.125	<0.001	4-7	0.064	<0.001	7-11	0.069	<0.001
1-11	0.075	<0.001	4-8	0.079	<0.001	8-9	0.177	<0.001
2-5	0.044	<0.001	4-9	0.098	<0.001	8-10	0.135	<0.001
2-7	0.043	<0.001	4-10	0.056	<0.001	8-11	0.085	<0.001
2-8	0.058	<0.001	4-12	0.058	<0.001	9-10	0.042	<0.001
2-9	0.119	<0.001	5-6	0.059	<0.001	9-11	0.093	<0.001
2-10	0.077	<0.001	5-7	0.086	<0.001	9-12	0.156	<0.001
2-11	0.027	0.002	5-8	0.101	<0.001	10-11	0.050	<0.001
2-12	0.037	<0.001	5-9	0.076	<0.001	10-12	0.114	<0.001
3-5	0.035	<0.001	5-10	0.033	<0.001	11-12	0.064	<0.001
3-6	0.025	0.012	5-12	0.080	<0.001			
3-7	0.052	<0.001	6-7	0.027	0.002			

Data presented are mean differences (md), with probabilities (P) which are all significant values.

Table 4.18. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* at Llanfairfechan.

months	md	P	months	md	P	months	md	P
1-2	0.031	0.001	3-5	0.037	<0.001	5-12	0.102	<0.001
1-3	0.101	<0.001	3-7	0.060	<0.001	6-9	0.103	<0.001
1-4	0.110	<0.001	3-8	0.068	<0.001	6-10	0.043	<0.001
1-5	0.139	<0.001	3-9	0.085	<0.001	6-12	0.046	0.001
1-6	0.083	<0.001	3-10	0.025	<0.032	7-9	0.146	<0.001
1-7	0.041	<0.001	3-12	0.064	<0.001	7-10	0.085	<0.001
1-8	0.033	<0.001	4-5	0.028	0.005	7-11	0.037	<0.001
1-9	0.186	<0.001	4-6	0.027	0.011	8-9	0.153	<0.001
1-10	0.126	<0.001	4-7	0.069	<0.001	8-10	0.093	<0.001
1-11	0.078	<0.001	4-8	0.077	<0.001	8-11	0.045	<0.001
1-12	0.037	<0.001	4-9	0.076	<0.001	9-10	0.060	<0.001
2-3	0.070	<0.001	4-11	0.032	0.001	9-11	0.108	<0.001
2-4	0.079	<0.001	4-12	0.073	<0.001	9-12	0.150	<0.001
2-5	0.107	<0.001	5-6	0.056	<0.001	10-11	0.048	<0.001
2-6	0.052	<0.001	5-7	0.098	<0.001	10-12	0.089	<0.001
2-9	0.155	<0.001	5-8	0.106	<0.001	11-12	0.041	<0.001
2-10	0.095	<0.001	5-9	0.048	<0.001	6-7	0.042	<0.001
2-11	0.047	<0.001	5-11	0.060	<0.001	6-8	0.050	<0.001

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.19. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* at Red Wharf Bay.

months	md	P	months	md	P	months	md	P
1-2	0.032	0.029	3-8	0.083	<0.001	6-9	0.158	<0.001
1-3	0.096	<0.001	3-9	0.144	<0.001	6-10	0.119	<0.001
1-4	0.138	<0.001	3-10	0.106	<0.001	6-11	0.042	<0.001
1-5	0.152	<0.001	3-12	0.052	<0.001	6-12	0.039	0.001
1-6	0.083	<0.001	4-6	0.055	<0.001	7-9	0.229	<0.001

Table 4.19 continued.

1-9	0.241 <0.001	4-7	0.126 <0.001	7-10	0.190 <0.001
1-10	0.202 <0.001	4-8	0.125 <0.001	7-11	0.113 <0.001
1-11	0.125 <0.001	4-9	0.102 <0.001	7-12	0.032 0.022
1-12	0.044 <0.001	4-10	0.064 <0.001	8-9	0.228 <0.001
2-3	0.064 <0.001	4-12	0.094 <0.001	8-10	0.189 <0.001
2-4	0.106 <0.001	5-6	0.068 <0.001	8-11	0.111 <0.001
2-5	0.119 <0.001	5-7	0.139 <0.001	8-12	0.031 0.036
2-6	0.051 <0.001	5-8	0.138 <0.001	9-10	0.038 <0.001
2-9	0.209 <0.001	5-9	0.089 <0.001	9-11	0.116 <0.001
2-10	0.169 <0.001	5-10	0.051 <0.001	9-12	0.197 <0.001
2-11	0.092 <0.001	5-12	0.107 <0.001	10-11	0.077 <0.001
3-4	0.042 <0.001	6-7	0.071 <0.001	10-12	0.158 <0.001
3-5	0.055 <0.001	6-8	0.069 <0.001	11-12	0.080 <0.001
3-7	0.084 <0.001				

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.20. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella lapillus* at Porth Nobla.

months	md P	months	md P	months	md P
1-2	0.051 <0.001	3-6	0.086 <0.001	6-7	0.057 <0.001
1-3	0.071 <0.001	3-9	0.233 <0.001	6-8	0.099 <0.001
1-4	0.101 <0.001	3-10	0.105 <0.001	6-9	0.147 <0.001
1-5	0.205 <0.001	3-11	0.081 <0.001	6-12	0.149 0.001
1-6	0.157 <0.001	3-12	0.063 <0.001	7-8	0.043 <0.001
1-7	0.099 <0.001	4-5	0.104 <0.001	7-9	0.204 <0.001
1-8	0.057 <0.001	4-6	0.057 <0.001	7-10	0.076 <0.001
1-9	0.304 <0.001	4-8	0.043 <0.001	7-11	0.052 <0.001
1-10	0.176 <0.001	4-9	0.203 <0.001	7-12	0.092 <0.001
1-11	0.152 <0.001	4-10	0.075 <0.001	8-9	0.247 <0.001
2-4	0.049 <0.001	4-11	0.051 <0.001	8-10	0.119 <0.001

Table 4.20 continued.

2-5	0.154	<0.001	4-12	0.092	<0.001	8-11	0.095	<0.001
2-6	0.106	<0.001	5-6	0.047	<0.001	8-12	0.049	<0.001
2-7	0.049	<0.001	5-7	0.104	<0.001	9-10	0.128	<0.001
2-9	0.253	<0.001	5-8	0.147	<0.001	9-11	0.152	<0.001
2-10	0.125	<0.001	5-9	0.099	<0.001	9-12	0.296	<0.001
2-11	0.101	<0.001	5-11	0.053	<0.001	10-12	0.168	<0.001
2-12	0.043	<0.001	5-12	0.197	<0.001	11-12	0.144	<0.001
3-5	0.134	<0.001						

Data presented are mean differences (md), with probabilities (P) which are all significant values.

Table 4.21. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean distances between individual *Nucella* at Porth Defaid.

months	md	*P*	months	md	*P*	months	md	*P*
1-3	0.124	<0.001	3-4	0.067	0.001	5-11	0.098	<0.001
1-4	0.191	<0.001	3-5	0.159	<0.001	5-12	0.261	<0.001
1-5	0.283	<0.001	3-6	0.101	<0.001	6-8	0.088	<0.001
1-6	0.225	<0.001	3-7	0.058	0.008	6-9	0.107	<0.001
1-7	0.182	<0.001	3-9	0.209	<0.001	6-12	0.204	0.001
1-8	0.137	<0.001	3-10	0.133	<0.001	7-9	0.150	<0.001
1-9	0.332	<0.001	3-11	0.061	0.004	7-10	0.075	<0.001
1-10	0.257	<0.001	3-12	0.102	<0.001	7-12	0.161	<0.001
1-11	0.184	<0.001	4-5	0.091	<0.001	8-9	0.195	<0.001
2-3	0.092	<0.001	4-8	0.054	0.023	8-10	0.120	<0.001
2-4	0.160	<0.001	4-9	0.141	<0.001	8-12	0.115	<0.001
2-5	0.251	<0.001	4-10	0.066	0.001	9-10	0.075	<0.001
2-6	0.194	<0.001	4-12	0.169	<0.001	9-11	0.148	<0.001
2-7	0.151	<0.001	5-6	0.057	0.004	9-12	0.311	<0.001
2-8	0.105	<0.001	5-7	0.100	<0.001	10-11	0.073	<0.001
2-9	0.301	<0.001	5-8	0.146	<0.001	10-12	0.235	<0.001
2-10	0.226	<0.001	5-9	0.049	0.011	11-12	0.163	<0.001
2-11	0.153	<0.001						

Data presented are mean differences (md), with probabilities (P), which are all significant values.

Table 4.22. Post Hoc multiple comparisons showing significant mean differences in *Nucella lapillus* density between shore levels.

	Menai		Trwyn		Llanfairfechan		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	250*	0.001	2707*	<0.001	217	0.109	113	0.127	115*	0.014
1-3	1113*	<0.001	2389*	<0.001	3744*	<0.001	775*	<0.001	60	0.289
2-3	863*	<0.001	318*	<0.001	3961*	<0.001	661*	<0.001	55	0.372

Data presented are mean differences (md), with probabilities (P), of which * are significant values.

Table 4.23. Post Hoc multiple comparisons showing significant differences in *Nucella lapillus* mortality between shore levels.

Shore	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	0.009	1.000	0.024	0.446	0.015	0.976	0.072	1.000	0.014	1.000	0.027	0.458
1-3	0.055*	<0.001	0.044*	0.026	0.044*	0.019	0.043*	0.032	0.027	1.000	0.022	0.730
2-3	0.046*	0.003	0.020	0.685	0.028	0.213	0.036	1.000	0.017	1.000	0.005	1.000

Data presented are mean differences (md), with probabilities (P), of which* are significant values.

Appendix 5.

Table 5.1. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Menai Bridge.

	low shore		mid shore		upper shore	
Activities	mean difference	P	mean difference	P	mean difference	P
1-2	1.196*	<0.001	1.725*	<0.001	0.614	1.000
1-3	4.895*	<0.001	6.455*	<0.001	3.088*	<0.001
1-4	6.309*	<0.001	7.225*	<0.001	4.022*	<0.001
2-3	3.699*	<0.001	4.730*	<0.001	2.474*	<0.001
2-4	5.113*	<0.001	4.730*	<0.001	3.408*	<0.001
3-4	1.414*	<0.001	0.771*	<0.001	0.934*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Table 5.2. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Trwyn y Penrhyn.

	low shore		mid shore		upper shore	
Activities	mean difference	P	mean difference	P	mean difference	P
1-2	0.726	1.000	0.706	0.245	0.851*	0.035
1-3	4.633*	<0.001	4.893*	<0.001	5.126*	<0.001
1-4	4.883*	<0.001	5.584*	<0.001	6.822*	<0.001
2-3	3.908*	<0.001	4.187*	<0.001	4.275*	<0.001
2-4	4.158*	<0.001	4.878*	<0.001	5.971*	<0.001
3-4	0.250	<0.001	0.691*	<0.001	1.696*	<0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Table 5.3. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Llanfairfechan.

	low shore		mid shore		upper shore	
Activities	mean difference	P	mean difference	P	mean difference	P
1-2	2.060*	< 0.001	1.583*	< 0.001	0.812	1.000
1-3	6.795*	< 0.001	4.213*	< 0.001	4.205*	< 0.001
1-4	8.271*	< 0.001	5.242*	< 0.001	5.022*	< 0.001
2-3	4.733*	< 0.001	2.630*	< 0.001	3.393*	< 0.001
2-4	6.211*	< 0.001	3.659*	< 0.001	4.210*	< 0.001
3-4	1.478*	< 0.001	1.029*	< 0.001	0.817*	0.035

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Table 5.4. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Red Wharf Bay.

	low shore		mid shore		upper shore	
Activities	mean difference	P	mean difference	P	mean difference	P
1-2	0.572	1.000	0.597	0.605	0.973	0.389
1-3	3.422*	<0.001	2.725*	<0.001	1.841*	<0.001
1-4	5.170*	<0.001	4.005*	<0.001	2.485*	<0.001
2-3	2.850*	<0.001	2.128*	<0.001	0.868*	<0.001
2-4	4.598*	<0.001	3.407*	<0.001	1.512*	<0.001
3-4	1.748*	<0.001	1.279*	<0.001	0.645*	<0.001

Based on estimated marginal means.*Mean difference is significant at the .05 level.

Table 5.5. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Porth Nobla.

	low shore		mid shore		upper shore	
Activities	mean difference	P	mean difference	P	mean difference	P
1-2	1.192*	0.002	0.407	1.000	0.839	0.119
1-3	2.591*	< 0.001	1.855*	0.002	2.995*	< 0.001
1-4	4.876*	< 0.001	2.324*	< 0.001	3.828*	< 0.001
2-3	1.399*	< 0.001	1.448*	< 0.001	2.156*	< 0.001
2-4	3.684*	< 0.001	1.917*	< 0.001	2.989*	< 0.001
3-4	2.284*	< 0.001	0.469*	0.018	0.833*	0.001

Based on estimated marginal means. *Mean difference is significant at the .05 level.

Table 5.6. Results of Post Hoc multiple comparison (Bonferroni test) showing significant mean differences in *Nucella lapillus* shell length between activities at Porth Defaid.

	low shore		mid shore		upper shore	
Activities	mean difference	*P*	mean difference	*P*	mean difference	*P*
1-2	0.799	1.000	1.181	1.000		
1-3	2.043*	0.005	1.589	1.000		
1-4	2.519*	< 0.001	3.089	0.377		
2-3	1.244*	< 0.001	0.407	1.000	1.458	0.296
2-4	1.720*	< 0.001	1.908*	0.005	1.812	0.055
3-4	0.476*	0.189	1.500*	0.010	0.354	1.000

Based on estimated marginal means.*Mean difference is significant at the .05 level.

n.b. no spawning individuals observed at the upper shore.

Table 5.7. Post Hoc multiple comparisons (Bonferroni test), showing significant differences in the monthly percentage of *Nucella lapillus* spawning between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	3.495*	0.024	3.435*	0.006	5.734*	0.006	3.609*	0.038	5.425*	0.006	0.379*	0.035
1-3	7.841*	0.002	5.345*	0.002	0.041	1.000	4.036*	0.028	1.170	0.352	1.380*	0.001
2-3	4.346*	0.013	1.909*	0.032	5.775*	0.005	7.465*	0.004	6.595*	0.003	1.000*	0.002

Based on observed means. Data presented are mean difference (md), and significance (P).

*Mean difference is significant at the .05 level.

Table 5.8. Post Hoc multiple comparisons (Bonferroni test), showing significant differences in the monthly percentage of *Nucella lapillus* foraging in the open between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	7.643*	0.047	2.235	1.000	2.207	0.655	0.986	1.000	0.614	1.000	2.139	0.451
1-3	5.983	0.091	7.131	0.124	0.426	1.000	7.583*	0.014	6.089*	0.039	1.748	0.642
2-3	1.660	1.000	4.895	0.299	1.780	0.898	6.597	0.020	6.704*	0.030	0.391	1.000

Based on observed means. Data presented are mean difference (md), and significance (P).

*Mean difference is significant at the .05 level.

Table 5.9. Post Hoc multiple comparisons (Bonferroni test), showing significant differences in the monthly percentage of *Nucella* foraging within refuges between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	3.957	0.758	0.025	1.000	3.044	0.344	4.320*	0.024	7.027*	0.049	4.332*	0.022
1-3	0.030	1.000	0.760	1.000	7.378*	0.038	7.120*	0.006	8.227*	0.024	6.604*	0.006
2-3	3.988	0.749	0.785	1.000	4.334	0.155	11.439*	0.001	14.434*	0.005	2.273	0.125

Based on observed means. Data presented are mean difference (md), and significance (P).

*Mean difference is significant at the .05 level.

Table 5.10. Post Hoc multiple comparisons (Bonferroni test), showing significant differences in the monthly percentage of *Nucella lapillus* refuging between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	15.062	0.123	5.623*	0.063	1.649	1.000	1.736	0.833	1.315	1.000	1.814	0.695
1-3	13.805	0.152	13.210*	0.006	6.611	0.621	4.498	0.125	13.145*	0.004	3.523	0.187
2-3	1.258	1.000	7.588*	0.028	8.260	0.416	2.762	0.378	14.459*	0.003	1.709	0.761

Based on observed means. Data presented are mean difference (md), and significance (P).

*Mean difference is significant at the .05 level.

Table 5.11. Post Hoc multiple comparisons (Bonferroni test), showing significant diiferences in the monthly density of *Nucella lapillus* between shore levels.

	Menai		Trwyn		Llanfairfechan		Red Wharf		Nobla		Defaid	
Shore levels	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*	md	*P*
1-2	94	0.172	239*	0.016	85	0.103	14	0.107	23	1.000	6	1.000
1-3	173*	0.035	182*	0.035	305*	0.003	10	0.266	82	0.118	28	0.057
2-3	79	0.259	58	0.514	219*	0.007	4	1.000	59	0.251	22	0.112

Based on observed means. Data presented are mean difference (md), and significance (P).

*Mean difference is significant at the .05 level.

Table 5.12. Monthly Microhabitat Activity (Percentage) on the Study Shores from May 97 to May 99.

Spawning	**May 97**	**June**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 98**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	11.8	11.67	5.68	2.17	8.01	9.02	6.87	9.94	11.02	11.69	15.64	12.12	11.25
Trwyn	10.16	14.18	6.19	7.6	16.89	14.64	10.82	12.23	13.73	6.22	7.72	4.05	11.71
RWB	3.83	0	0	5.87	5.97	20.95	7.63	0	9.76	2.5	3.97	4.21	4.55
Llanfair.	10.52	0	0	6.79	3.99	13.3	6.94	0	0	0	4.17	2.29	9.94
Nobla	10.78	7.06	0.35	0	7.14	9.32	9.29	10.2	12.25	7.87	6.29	0.84	2.8
Defaid	2.88	0	0	0	0.79	0	0.38	0	2.7	0	0.6	1.75	0
Foraging in Open													
Menai	23.87	13.62	10.71	9.47	6.87	6.76	7.5	3.31	0.32	1.81	9.39	15.73	20.5
Trwyn	37.18	23.53	18.81	12.03	15.77	6.83	4.72	2.87	2.62	3.21	11.42	25.05	27.83
RWB	49.84	30.3	16.67	15.09	38.02	15.37	9.02	1.44	1.13	10.81	24.79	30.75	45.24
Llanfair.	28.4	14.51	10.49	15.68	11.83	15.48	6.37	2.87	0.69	0.56	14.36	23.79	24.89
Nobla	50.42	43.99	32.37	27.3	47.91	22.85	13.17	4.67	0	9.55	39	44.81	50.02
Defaid	49.75	40.91	31.55	25.07	25.52	7.84	17.34	0	1.72	5.12	27.11	6.41	41.67
Foraging in Refuge													
Menai	53.4	57.85	63.04	67.55	68.68	59.85	53.04	38.08	5.07	16.69	33.04	50.27	49.44
Trwyn	36.15	45.31	45.52	54.22	43.02	37.43	38.69	19.93	12.36	21.5	27.47	45.9	36.27
RWB	36.82	49.52	47.26	53.07	43.29	47.91	51.5	44.59	26.98	21.76	44.07	44.58	35.51
Llanfair.	48.26	50.08	47.36	32.2	55.91	47.28	18.57	18.87	11.98	14.47	21.98	38.64	15.46
Nobla	23.22	26.32	37.35	39.28	25.61	38.13	47.22	25.64	9.88	29.87	27.46	37.96	31.52
Defaid	25.49	31.05	33.24	28.43	31.39	28.21	35.84	43.19	15.05	21.46	37.43	40.55	35.43
Refuging													
Menai	10.93	16.86	20.57	20.81	16.44	24.37	32.59	48.69	83.58	69.81	41.93	21.89	18.84
Trwyn	16.51	16.98	29.48	26.15	24.32	41.1	45.77	64.87	71.28	69.07	53.39	25	24.19
RWB	9.51	20.45	36.07	25.97	12.72	15.77	31.85	53.97	62.13	64.93	27.17	20.46	14.7
Llanfair.	12.82	35.41	42.15	45.33	28.27	23.94	68.12	78.25	87.33	84.96	59.49	35.28	49.7
Nobla	15.58	22.63	29.93	33.42	19.35	29.7	30.32	59.49	77.87	52.71	27.25	16.39	15.62
Defaid	21.88	28.04	35.21	46.5	42.3	63.95	46.44	56.81	80.53	73.42	34.86	51.29	22.9
Spawning		**June 98**	**Jul.**	**Aug.**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 99**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai		4.52	6.42	2.41	7.95	8.59	5.87	11.1	12.18	10.36	14.81	13.67	11.23
Trwyn		12.53	12.1	7.14	17.1	15.77	10.39	10.69	10.91	6.73	7.86	5.54	11.28
RWB		0	0	6.69	5.14	14.06	9.22	0	6.45	2.06	3.22	5.14	4.46
Llanfair.		8.05	3.3	5.81	3.29	11.37	7.88	0	0	0	3.14	3.61	7.87
Nobla		5.69	5.38	0	6.74	8.93	8.62	8.58	11.62	7.06	5.74	1.3	2.22
Defaid		0	3.01	0	1.19	0.32	0.11	0	2.56	0	0.66	2.11	0
Menai	**Forage**	4.7	6.34	8.32	7.08	5.53	7.36	2.04	0.08	1.18	7.23	15.71	22.79
Trwyn	**in the**	20.43	3.57	8.4	13.29	8.66	3.66	2.22	2.35	3.81	12.32	22.95	30.39
RWB	**Open**	36.34	24.95	20.7	25.69	14.76	5.55	0.92	0.66	9.09	22.09	33.45	43.33
Llanfair.		7.14	7.96	14.91	13.69	13.61	6.16	3.77	0.52	0.44	11.77	20.1	29.65
Nobla		43.7	33.04	29.69	46.57	23.55	12.11	5.27	0	7.03	33.91	46.5	56.38
Defaid		41.74	29.1	25.07	24.68	6.76	12.29	0	1.07	5.35	20.28	24.09	41.58
Menai	**Forage**	44.8	49.17	63.37	67.21	60.32	49.24	37.16	8.4	16.1	33.92	50.18	45.21
Trwyn	**in**	46.21	57.62	52.84	41.58	37.91	39.5	20.88	13.84	20.29	26.88	45.51	37.29
RWB	**Refuge**	48.32	48.18	52.61	45.25	46.46	51.21	45.24	28.92	21.62	42.98	43.54	34.26
Llanfair.		30.03	40.64	46.65	29.87	25.69	62.1	19.14	18.51	13.13	19.85	39.18	16.36
Nobla		30.65	34.24	37.52	26.95	35.46	42.41	24.24	10.62	28.63	28.25	37.23	29.13
Defaid		29.64	21.62	25.76	31.61	28.81	36.03	43.1	15.1	20.36	36.77	38.28	36.09
Menai	**Refuge**	45.98	38.07	25.93	17.76	25.56	37.85	49.69	79.34	72.35	44.04	20.44	20.57
Trwyn		20.81	26.7	31.62	28.02	37.66	46.45	66.21	72.86	69.17	52.95	26.01	21.05
RWB		15.34	26.54	19.99	20.59	24.71	37.36	53.84	63.97	67.22	31.71	17.86	17.94
Llanfair.		54.78	48.13	32.63	53.15	49.33	23.49	77.06	87.62	86.43	65.24	37.11	46.79
Nobla		20.29	27.26	32.79	19.74	32.06	36.86	61.9	77.76	57.28	32.1	14.97	12.27
Defaid		28.62	46.27	49.17	42.52	64.1	51.57	56.86	81.27	73.63	42.29	35.53	22.33

Table 5.12 continued. Monthly Spawning (Percentage) at different shore levels from June 97 to May 99.

% Spawning		**June 97**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 98**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	13.52	5.49	3.93	2.47	5.37	5.53	1.72	1.18	3.4	7.47	8.9	10.44
	Mid	5.51	3.29	2.57	14.69	16.49	10.95	10.58	12.89	11.02	9.99	10.13	10.65
	Lower	15.97	8.25	0	6.89	5.19	4.14	17.51	18.99	20.64	29.46	17.33	12.67
Trwyn	Upper	5.85	6.57	2.09	9.67	16.56	14.62	11.5	3.85	5.52	9.04	1.23	8.18
	Mid	30.24	4.54	2.49	15.11	12.01	8.57	8.65	7.91	4.68	5.43	4.78	13.02
	Lower	6.45	7.48	18.21	25.88	15.35	9.27	16.85	29.44	8.46	8.7	6.15	13.94
RWB	Upper	0	0	0	0	0	0	0	8.27	7.51	0	0	0
	Mid	0	0	14.63	6.2	54.22	22.88	0	17.36	0	0	0	0
	Lower	0	0	2.99	11.72	8.63	0	0	3.65	0	11.9	12.62	13.65
Llanfair.	Upper	0	0	20.38	0	0	0	0	0	0	2.86	0	3.42
	Mid	0	0	0	11.97	39.89	20.82	0	0	0	5.42	4.96	11.87
	Lower	0	0	0	0	0	0	0	0	0	4.22	1.92	14.54
Nobla	Upper	13.69	0	0	6.37	19.49	19.38	14.69	11.62	9.72	6.16	1.91	6.08
	Mid	0	0	0	3.67	2.55	0	2.99	7.78	2.26	0	0	2.42
	Lower	7.49	1.05	0	11.38	5.92	8.48	12.92	17.34	11.64	12.71	0.6	0
Defaid	Upper	0	0	0	0	0	0	0	0	0	0	0	0
	Mid	0	0	0	0	0	1.13	0	8.11	0	0	0	0
	Lower	0	0	0	2.36	0	0	0	0	0	1.8	5.26	0

% Spawning		**June 98**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 99**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	3.97	6.07	4.23	2.56	4.44	4.76	1.32	1.02	2.56	5.54	9.54	11.13
	Mid	3.94	3.88	2.46	11.65	14.32	9.32	13.43	15.76	9.76	8.02	9.05	9.56
	Lower	5.65	9.32	0.54	9.65	7.01	3.54	18.54	19.76	18.76	30.87	22.43	13.01
Trwyn	Upper	6.79	9.85	1.76	10.89	18.76	12.65	9.65	2.65	6.54	12.6	0.98	9.54
	Mid	20.98	16.01	3.65	16.98	13.89	7.54	7.87	6.54	5.54	4.43	6.98	12.76
	Lower	9.87	10.46	16.03	23.43	14.67	10.98	14.54	23.65	8.09	6.54	8.65	11.53
RWB	Upper	0	0	0	0	0	0	0	6.45	5.54	0	0	1.86
	Mid	0	0	16.54	4.67	34.22	27.65	0	12.89	0	0	0	0
	Lower	0	0	3.54	10.76	7.97	0	0	0	0.65	9.65	15.43	11.54
Llanfair.	Upper	6.93	0	17.43	0	0	0	0	0	0	1.56	2.43	2.54
	Mid	11.55	0	0	9.76	34.12	23.65	0	0	0	4.53	5.28	9.76
	Lower	5.67	9.8	0	0	0	0	0	0	0	3.33	3.12	11.32
Nobla	Upper	10.65	6.02	0	4.78	18.67	16.54	13.65	10.53	8.43	4.87	2.21	4.99
	Mid	0	2.15	0	2.67	3.34	1.67	1.56	8.67	1.98	0.78	0.45	1.67
	Lower	6.43	7.98	0	12.78	4.78	7.65	10.54	15.65	10.76	11.56	1.23	0
Defaid	Upper	0	0	0	0	0	0	0	0	0	0	0	0
	Mid	0	4.54	0	0	0	0.09	0	7.67	0	0	0	0
	Lower	0	4.48	0	3.56	0.97	0.23	0	0	0	1.97	6.32	0

Table 5.12. continued. Monthly Foraging in the Open (Percentage) at different shore levels from June 97 to May 99.

Foraging (Open)		**June 97**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 98**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	6.34	5.6	5.46	7.79	8.64	12.57	3.22	0	1.43	6.92	12.48	14.43
	Mid	6.1	5.26	3.38	2.5	3.62	5.09	0	0	0.96	5.13	13.22	19.54
	Lower	28.41	21.27	19.58	10.33	8.02	4.83	6.71	0.97	3.04	16.14	21.48	27.43
Trwyn	Upper	14.35	13.21	7.27	7.12	0.47	2.09	1.18	2.49	2.87	13.56	26.55	19.54
	Mid	25	26.13	16.86	15.23	3.59	3.98	2.37	1.62	2.45	9.82	22.97	36.54
	Lower	31.25	17.09	11.96	24.95	16.44	8.09	5.65	3.76	4.32	10.87	25.62	27.4
RWB	Upper	26.51	6.41	2.72	23.5	15.08	12.34	0	0	6.26	25.23	28.69	40.76
	Mid	31.68	21.66	17.07	53.1	8.76	7.71	0	0	12.57	23.32	29.45	50.54
	Lower	32.7	21.93	25.48	37.47	22.28	7.02	4.32	3.39	13.61	25.83	34.1	44.43
Llanfair.	Upper	4.64	4.44	23.85	12.43	26.36	16.41	6.13	0	0	2.85	14.97	29.65
	Mid	13.35	11.41	10	12.14	7.04	0.97	0.6	0	0	17.34	26.59	20.65
	Lower	25.53	15.63	13.2	10.92	13.04	1.73	1.89	2.08	1.69	22.89	29.81	24.37
Nobla	Upper	27.52	18.3	16.44	54.95	25.17	6.18	3.61	0	10.19	43.13	43.19	26.54
	Mid	48.94	33.44	27.37	53.94	27.7	15.76	6.09	0	9.95	33.34	45	60.08
	Lower	55.53	45.38	38.1	34.83	15.68	17.56	4.31	0	8.51	40.52	46.24	63.45
Defaid	Upper	37.05	29.39	20.12	10.69	7.73	38.68	0	5.15	7.74	28.13	4.32	24.1
	Mid	45.48	29.38	21.9	21.94	13.33	12.42	0	0	3.83	25.18	12.59	35.62
	Lower	40.2	35.88	33.18	43.94	2.45	0.92	0	0	3.79	28.03	2.31	65.29

Foraging (Open)		**June 98**	**Jul.**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 99**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	3.53	4.34	3.45	6.46	7.45	14.67	2.56	0	0.45	4.36	11.89	16.87
	Mid	2.34	0.91	4.98	3.1	2.67	3.76	0.56	0	0.32	3.54	10.67	22.34
	Lower	8.24	13.76	16.54	11.67	6.46	3.67	3.01	0.23	2.78	13.78	24.56	29.76
Trwyn	Upper	12.87	2.15	3.56	4.67	2.12	1.56	0.43	1.32	2.34	11.43	22.54	25.65
	Mid	22.87	5.06	11.98	14.65	5.32	2.87	1.78	2.76	3.34	11.76	17.54	32.32
	Lower	25.54	3.49	9.65	20.56	18.54	6.54	4.45	2.96	5.76	13.76	28.76	33.2
RWB	Upper	28.16	6.78	3.43	15.87	13.54	7.56	0.22	0	9.65	22.65	31.67	38.79
	Mid	45.11	42.5	25.12	40.43	14.43	4.54	0	0	6.87	16.87	30.65	44.69
	Lower	35.76	25.56	33.54	30.76	16.32	4.54	2.54	1.98	10.76	26.76	38.03	46.52
Llanfair.	Upper	2.16	3.76	21.65	15.86	22.64	14.87	8.32	0	0	1.23	11.87	32.65
	Mid	13.24	12.36	13.65	11.54	6.43	1.56	0.33	0	0	13.65	22.87	28.43
	Lower	6.02	7.77	9.43	13.67	11.76	2.06	2.66	1.56	1.32	20.43	25.56	27.86
Nobla	Upper	31.65	34.94	20.43	48.65	26.54	4.34	2.87	0	6.87	36.43	40.43	46.54
	Mid	47.43	33.87	30.54	57.31	30.34	18.66	8.96	0	7.45	28.77	48.54	56.55
	Lower	51.02	30.32	38.1	33.76	13.76	13.34	3.99	0	6.78	36.54	50.54	66.04
Defaid	Upper	44.36	31.82	20.12	13.22	9.43	25.78	0	3.21	9.43	18.65	22.43	27.89
	Mid	43.32	18.18	21.9	24.05	9.43	10.65	0	0	5.05	19.65	25.87	38.97
	Lower	37.54	37.31	33.18	36.77	1.43	0.43	0	0	1.56	22.54	23.96	57.88

Table 5.12 continued. Monthly Foraging in Refuge (Percentage) at different shore levels from June 97 to May 99.

Foraging (Refuge)		**June 97**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 98**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	48.11	55.69	58.41	71.23	61.12	51.58	49.37	4.9	15.64	38.64	53.97	48.54
	Mid	74.89	72.21	72.91	58.18	54.27	44.19	21.09	5.42	15.62	21.49	49.15	53.43
	Lower	50.94	61.23	71.34	76.63	64.17	62.57	43.77	4.9	18.81	38.98	47.68	46.34
Trwyn	Upper	41.93	43.73	58.39	40.4	23.76	46.73	17.71	11.17	17.31	31.07	44.51	40.54
	Mid	40.21	38.54	60.71	53.33	51.95	32.96	20.28	14.81	18.62	31.78	45.31	29.43
	Lower	53.79	54.28	43.57	35.35	36.57	36.39	21.81	11.1	28.57	19.56	47.88	38.85
RWB	Upper	52.16	40.39	68.06	61.32	71.44	66.78	55.09	16.24	19.21	43.89	47.9	49.54
	Mid	44.35	51.18	44.77	27.35	21.71	32.85	36.8	28.1	24.37	49.57	49.5	30.45
	Lower	51.24	50.21	46.39	41.21	50.57	54.86	41.89	36.61	21.71	38.75	36.35	26.54
Llanfair.	Upper	50.58	60.88	29.23	27.74	11.7	52.57	17.79	7.69	7.77	14.29	31.64	19.65
	Mid	38.91	38.96	38.57	23.08	22.56	63.6	19.04	11.54	20.64	27.1	47.1	15.43
	Lower	16.73	26.6	68.18	33.98	37.57	88.19	19.79	16.69	15.01	24.55	37.18	11.32
Nobla	Upper	12.25	31.79	25.68	11.95	16.91	35.12	20.62	13.03	34.01	10.46	33.48	35.1
	Mid	39.58	48.57	50.75	30.21	51.63	56	32.39	14.43	34.3	46.67	35.94	29.62
	Lower	27.13	31.68	41.4	34.69	45.84	50.53	23.9	2.19	21.29	27.26	44.47	29.85
Defaid	Upper	28.13	38.35	25.44	57.25	35.57	33.84	47.44	23.71	19.64	33.22	40.39	48.75
	Mid	26.91	36.45	28	18.51	28.6	32.28	46.08	11.46	32.51	45.65	42.28	36.93
	Lower	38.11	24.93	31.84	18.42	20.45	41.4	36.05	9.97	12.24	33.43	38.98	20.61

Foraging (Refuge)		**June 98**	**Jul.**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 99**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	49.15	58.98	62.23	68.54	56.65	49.34	44.53	14.55	16.54	41.56	55.67	42.43
	Mid	49.03	32.88	63.45	63.54	55.65	40.74	30.43	6.89	14.45	24.87	50.43	50.76
	Lower	36.21	55.65	64.33	69.54	68.65	57.65	36.54	3.77	17.32	35.34	44.45	42.43
Trwyn	Upper	44.34	49.85	56.54	36.78	29.65	49.54	20.43	15.43	15.56	28.65	47.65	41.65
	Mid	38.54	56.74	55.54	47.54	45.54	37.54	17.56	15.33	19.54	29.54	46.43	35.54
	Lower	55.76	66.28	46.43	40.43	38.54	31.43	24.65	10.76	25.77	22.45	42.45	34.67
RWB	Upper	48.76	42.5	66.76	57.54	64.43	69.54	50.43	17.9	16.54	45.87	46.54	44.34
	Mid	47.65	49.49	41.54	33.67	30.54	38.65	39.65	30.43	21.77	43.54	45.43	33.65
	Lower	48.54	52.54	49.54	44.54	44.43	45.43	45.65	38.44	26.56	39.54	38.65	24.78
Llanfair.	Upper	25.43	35.54	35.65	30.54	14.98	50.43	22.54	5.55	6.4	11.56	35.54	22.43
	Mid	38.03	44.32	33.54	28.54	19.65	60.32	17.54	12.45	19.55	25.87	42.78	13.87
	Lower	26.64	42.06	70.76	30.54	42.43	75.65	17.44	17.54	13.43	22.12	39.22	10.78
Nobla	Upper	18.76	20.48	22.43	16.43	19.65	39.32	25.43	16.54	29.68	12.76	31.56	32.65
	Mid	42.43	48.93	44.54	27.54	45.43	43.78	27.65	11.44	36.78	40.56	36.47	27.87
	Lower	30.76	33.51	45.6	36.87	41.32	44.13	19.65	3.87	19.43	31.43	43.65	26.87
Defaid	Upper	24.65	20.45	23.76	47.76	37.54	36.54	49.54	20.65	16.78	30.67	38.65	49.99
	Mid	29.95	25.01	25.87	25.43	31.56	31.55	44.43	13.87	29.54	42.78	39.65	34.65
	Lower	34.32	19.4	27.65	21.65	17.33	40.01	35.44	10.79	15.76	36.87	36.54	23.64

Table 5.12 continued. Monthly Refuging (Percentage) at different shore levels from June 97 to May 99.

Refuging		**June 97**	**July**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 98**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	32.03	33.22	32.2	18.51	24.87	30.32	45.96	93.92	79.53	46.97	24.65	26.59
	Mid	13.5	19.23	21.14	24.63	25.62	38.99	68.33	81.69	72.4	63.39	27.5	16.38
	Lower	4.68	9.25	9.08	6.15	22.62	28.46	32.01	75.14	57.51	15.42	13.51	13.56
Trwyn	Upper	37.87	36.49	32.24	42.81	59.21	36.56	69.61	82.49	74.3	46.33	27.71	31.74
	Mid	4.55	30.79	19.94	16.33	32.45	54.49	68.7	75.66	74.25	52.97	26.94	21.01
	Lower	8.51	21.15	26.25	13.82	31.64	46.25	56.29	55.7	58.65	60.87	20.35	19.81
RWB	Upper	21.33	53.2	28.22	15.18	13.48	20.87	44.91	75.5	67.02	30.88	23.41	9.7
	Mid	23.97	27.16	23.52	13.35	15.31	36.56	63.2	54.54	63.06	27.11	21.05	19.01
	Lower	16.06	27.86	25.14	9.6	18.52	38.12	53.79	56.35	64.48	23.52	16.93	15.38
Llanfair.	Upper	50.58	60.88	29.23	27.74	11.7	52.57	76.08	92.31	92.23	80	53.39	47.28
	Mid	38.91	38.96	38.57	23.08	22.56	63.6	80.36	88.46	79.36	50.14	21.35	52.05
	Lower	16.73	26.6	68.18	33.98	37.57	88.19	78.32	81.23	83.3	48.34	31.09	49.77
Nobla	Upper	46.39	49.91	57.88	26.73	38.43	39.32	61.08	75.55	46.08	40.25	21.42	32.28
	Mid	11.48	17.99	21.87	12.25	18.12	28.24	58.53	77.79	53.49	21.99	19.06	7.88
	Lower	9.95	21.89	20.5	19.1	32.56	23.43	58.87	80.47	58.56	19.51	8.69	6.7
Defaid	Upper	34.82	32.26	54.44	32.06	56.7	27.48	52.56	71.14	72.62	38.65	55.29	27.15
	Mid	27.61	34.17	50.1	59.55	58.07	54.17	53.92	80.43	63.66	29.17	45.13	27.45
	Lower	21.69	39.19	34.98	35.28	77.1	57.68	63.95	90.03	83.97	36.74	53.45	14.1

Refuging		**June 98**	**Jul.**	**August**	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Jan. 99**	**Feb.**	**Mar.**	**Apr.**	**May.**
Menai	Upper	43.35	30.61	30.09	22.44	31.46	31.23	51.59	84.43	80.45	48.54	22.9	29.57
	Mid	44.69	62.33	29.11	21.71	27.36	46.18	55.58	77.35	75.47	63.57	29.85	17.34
	Lower	49.9	21.27	18.59	9.14	17.88	35.14	41.91	76.24	61.14	20.01	8.56	14.8
Trwyn	Upper	36	38.15	38.14	47.66	49.47	36.25	69.49	80.6	75.56	47.32	28.83	23.16
	Mid	17.61	22.19	28.83	20.83	35.25	52.05	72.79	75.37	71.58	54.27	29.05	19.38
	Lower	8.83	19.77	27.89	15.58	28.25	51.05	56.36	62.63	60.38	57.25	20.14	20.6
RWB	Upper	23.08	50.72	29.81	26.59	22.03	22.9	49.35	75.65	68.27	31.48	21.79	15.01
	Mid	7.24	8.01	16.8	21.23	20.81	29.16	60.35	56.68	71.36	39.59	23.92	21.66
	Lower	15.7	21.9	13.38	13.94	31.28	50.03	51.81	59.58	62.03	24.05	7.89	17.16
Llanfair.	Upper	65.48	60.7	25.27	53.6	62.38	34.7	69.14	94.45	93.6	85.65	50.16	42.38
	Mid	37.18	43.32	52.81	50.16	39.8	14.47	82.13	87.55	80.45	55.95	29.07	47.94
	Lower	61.67	40.37	19.81	55.79	45.81	22.29	79.9	80.9	85.25	54.12	32.1	50.04
Nobla	Upper	38.94	38.56	57.14	30.14	35.14	39.8	58.05	72.93	55.02	45.94	25.8	15.82
	Mid	10.14	15.05	24.92	12.48	20.89	35.89	61.83	79.89	53.79	29.89	14.54	13.91
	Lower	11.79	28.19	16.3	16.59	40.14	34.88	65.82	80.48	63.03	20.47	4.58	7.09
Defaid	Upper	30.99	47.73	56.12	39.02	53.03	37.68	50.46	76.14	73.79	50.68	38.92	22.12
	Mid	26.73	52.27	52.23	50.52	59.01	57.71	55.57	78.46	65.41	37.57	34.48	26.38
	low	28.14	38.81	39.17	38.02	80.27	59.33	64.56	89.21	82.68	38.62	33.18	18.48

Table 5.12 continued. Monthly Density Estimates at different shore levels from June 97 to May 99.

Estimated density		June 97	July	August	Sept.	Oct.	Nov.	Dec.	Jan. 98	Feb.	Mar.	Apr.	May.
Menai	Upper	193.9	171.3	150	133.4	165.6	139.2	133.7	185.7	216.3	254.4	268.8	278.6
	Mid	221.3	207	198.2	187.2	154.6	235.7	250.5	195.5	243.9	306.2	362.3	426.4
	Lower	378.1	349.3	312.7	258.4	395.2	352.4	396.4	318.5	310.4	301.7	359.5	593.6
Trwyn	Upper	105.9	149.1	253.1	262.8	365.3	195.6	220.8	300.6	333.6	354.2	424.1	445.1
	Mid	57.2	90.3	168.5	327	298	464.5	410.2	420.9	478.4	387.7	445.8	466.4
	Lower	97.6	93.6	56	215.6	147.2	101.4	99	103.6	53.2	46.7	68.3	62.4
RWB	Upper	34.7	35.9	40.4	69.8	63	76.2	99.3	66.5	95.8	76.1	86.9	54.5
	Mid	80.5	63.7	69.7	125.8	64	40.2	31.8	36.3	50.9	57.9	65.8	92.5
	Lower	68.5	50.6	56.9	56.3	55.6	85.5	122.7	119.6	88.9	68.9	89.3	114.3
Llanfair.	Upper	109.9	49.6	26	34.6	40.2	39	32.6	26	19.3	35	35.4	63.6
	Mid	560.3	348.8	336	299	265.5	123.9	66.7	52	52.3	369	348.6	498
	Lower	503.7	415.3	396.7	227.2	245.4	127	185.4	287	141.9	664	485	602.1
Nobla	Upper	67.2	56.3	44.4	87.9	73.9	71.2	77.6	85.2	63.8	69.8	110.2	116.8
	Mid	99.3	90.6	85.5	147	123.5	125	103.4	94.4	97.4	160.5	193.1	210.7
	Lower	154.8	105.1	79	146.7	158.8	164.1	118.4	110.8	105.7	199.9	231.4	247.9
Defaid	Upper	35.9	27.9	16.9	13.1	19.4	39.3	21.5	19.4	16.8	29.5	25.5	52.3
	Mid	110.9	43.9	21	52.4	46.5	44.3	39.5	41.9	36.6	67.9	42.1	61.2
	Lower	71.9	39.3	22.3	63.5	57.2	54.1	45.5	31.1	58	66.7	60.8	75.2

Estimated density		June 98	Jul.	Aug	Sept.	Oct.	Nov.	Dec.	Jan. 99	Feb.	Mar.	Apr.	May.
Menai	Upper	206.7	159.9	144.8	168.4	158.4	147.5	140	160.1	240.4	263.5	277.9	285.6
	Mid	393.4	438.3	396.6	276.9	233.1	203.1	193.3	177.6	254.2	305.6	344.4	388.1
	Lower	578.6	516.6	423.8	355	337.3	299.3	245.4	255.9	325.1	331	356.8	437.7
Trwyn	Upper	349.9	325	296.3	313.6	324.1	223.5	188.6	190.2	265.8	342.7	363.5	383
	Mid	409	356	310.1	377.4	325.9	345.6	326.4	315.5	386	430.5	444	451.2
	Lower	73.3	86	63.2	147.8	133.7	107.9	101.2	84.3	96.6	101.4	105.4	122.2
RWB	Upper	57.5	59	42.5	77.5	65.4	77.4	64.4	71.4	98.5	123.4	106.5	93.9
	Mid	71.4	40	41.4	99.5	59.9	75.4	45.3	48.9	64.9	69.9	84.6	100.7
	Lower	77.9	62.2	53.6	65.7	57	63.7	76.9	88.8	80.6	93.8	111.4	127.2
Llanfair.	Upper	46.2	33.8	22.9	47.7	54.4	44.6	40.5	37.5	39.7	41.2	54.6	83.8
	Mid	342.1	278.2	257.4	306	271.3	148.7	88.3	58.8	76.4	264.2	297.5	353.6
	Lower	340.5	592	400.3	247.9	255.7	165.4	173.7	155.3	275.5	434.6	448.9	509.7
Nobla	Upper	96.5	83	66.3	90.2	81.2	74	68.5	62.7	77.9	84.4	93.9	100.7
	Mid	175	186	154.6	175.5	164.4	145.6	121.1	88.7	100.5	171.5	188.6	199.9
	Lower	234.6	188	139.7	185.9	173.1	179.6	135.5	106.2	123.3	218.7	232.3	247.7
Defaid	Upper	47.8	44	24.8	20.3	24.6	35.3	24.7	19.7	27.5	33.8	38.9	54.3
	Mid	54.5	44	27.5	32.4	43.5	40.7	37.6	34.7	44.7	58.4	63.7	89.6
	Lower	69.9	67	30.6	45.8	42.6	54.5	48.8	27.6	48.9	69.8	82.5	97.6

Appendix 6 Figures.

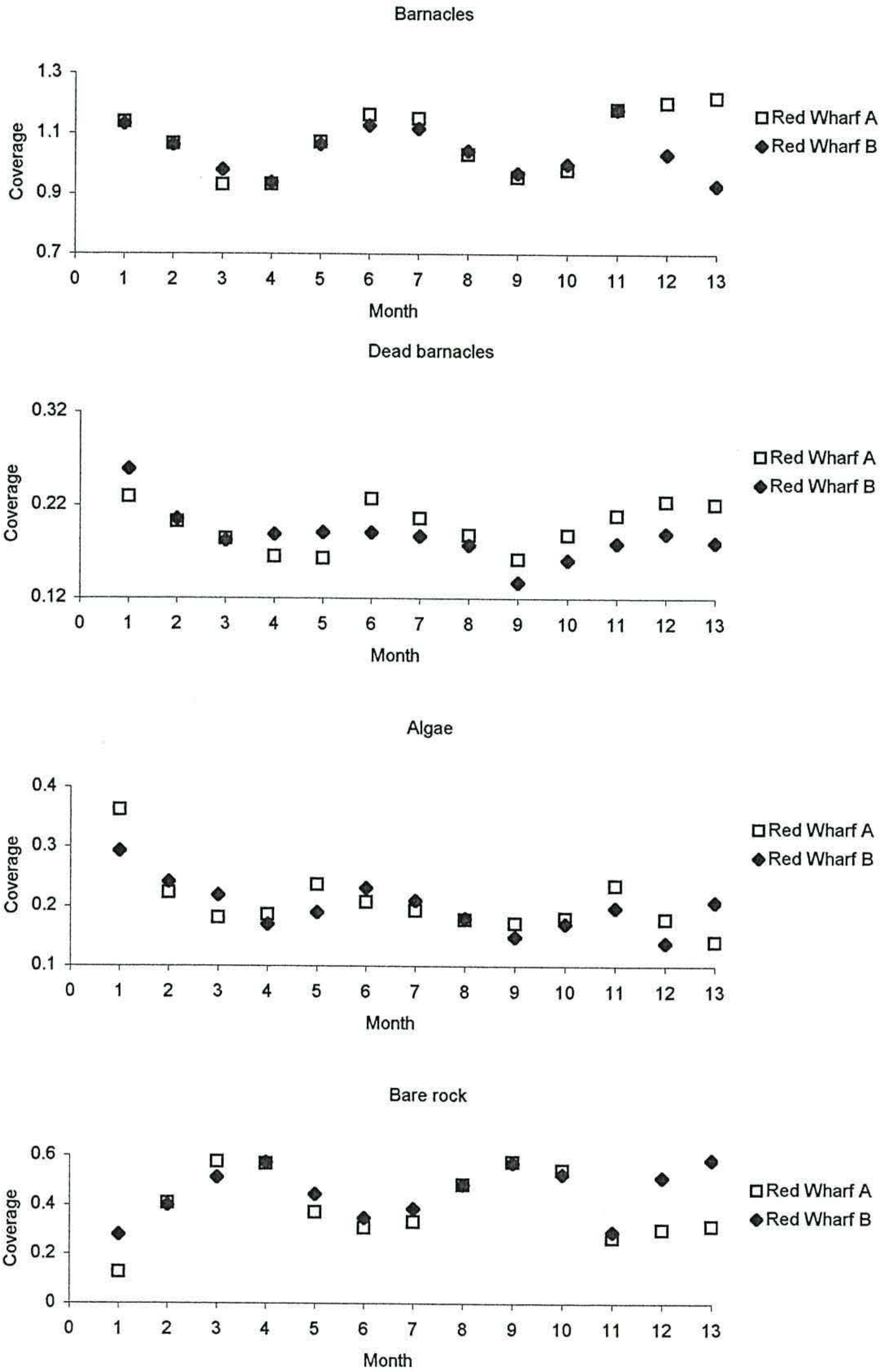
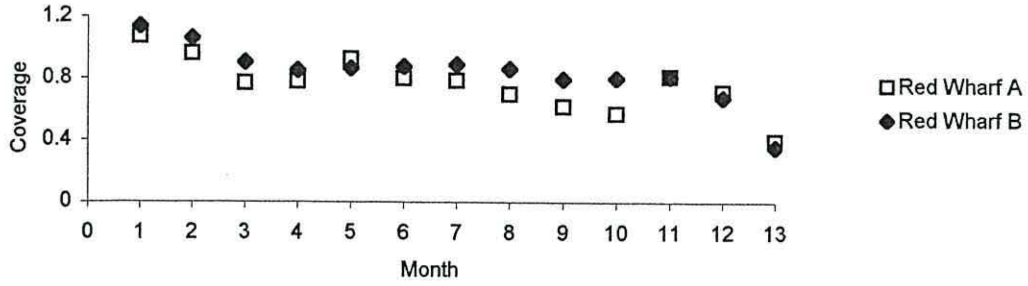
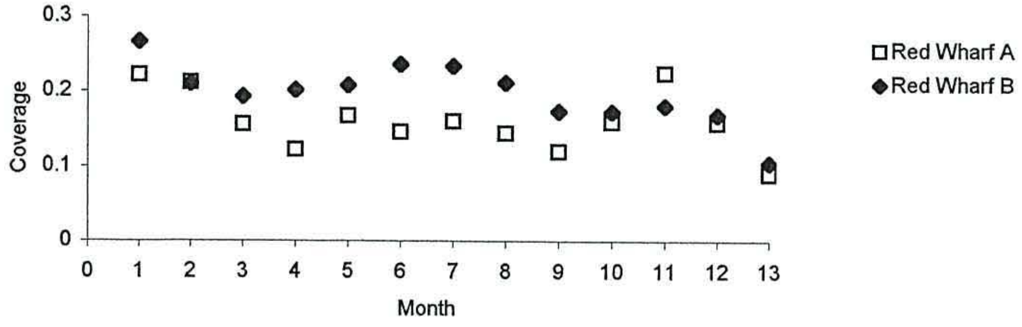
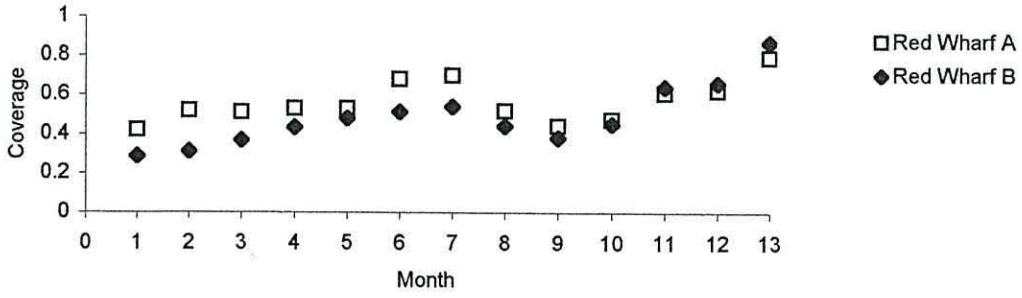


Figure 6.1. Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 1(*Nucella* removal).A comparison between Red Wharf A (experiment started in April) and Red Wharf B (started the subsequent September).


Barnacles


Dead barnacles


Algae

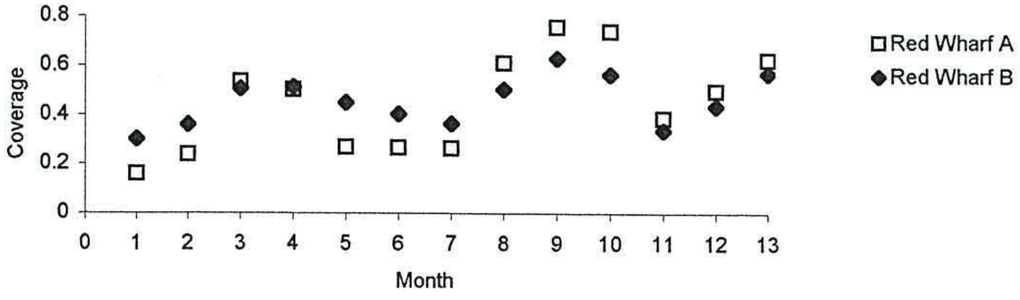

Bare rock

Figure 6.2.Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 2(*Patella* removal).A comparison between Red Wharf A (experiment started April) and Red Wharf B (experiment started in September).

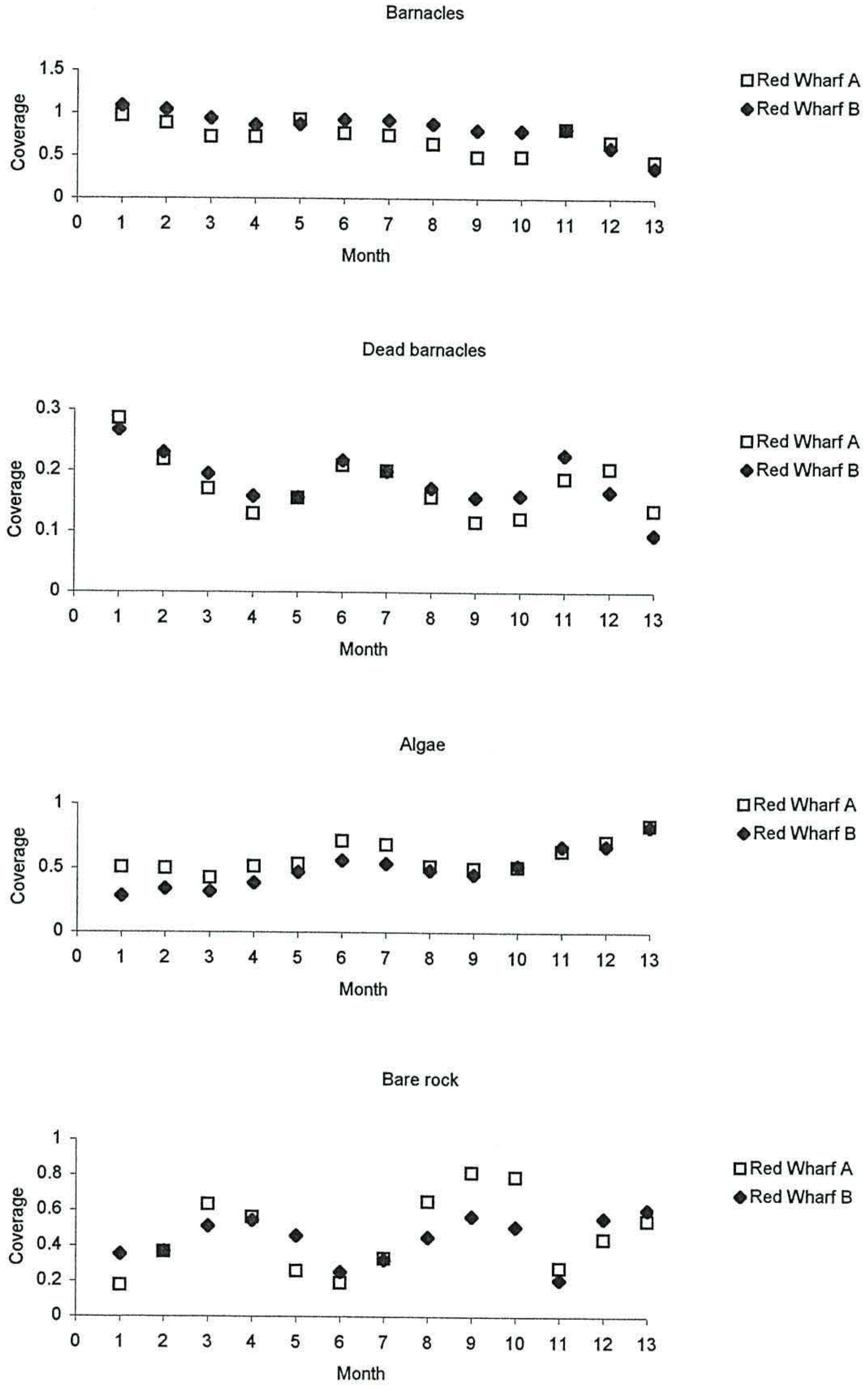


Figure 6.3.Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 3(*Nucella* and *Patella* removal). A comparison between Red Wharf A (started in April) and Red Wharf B (started in September).

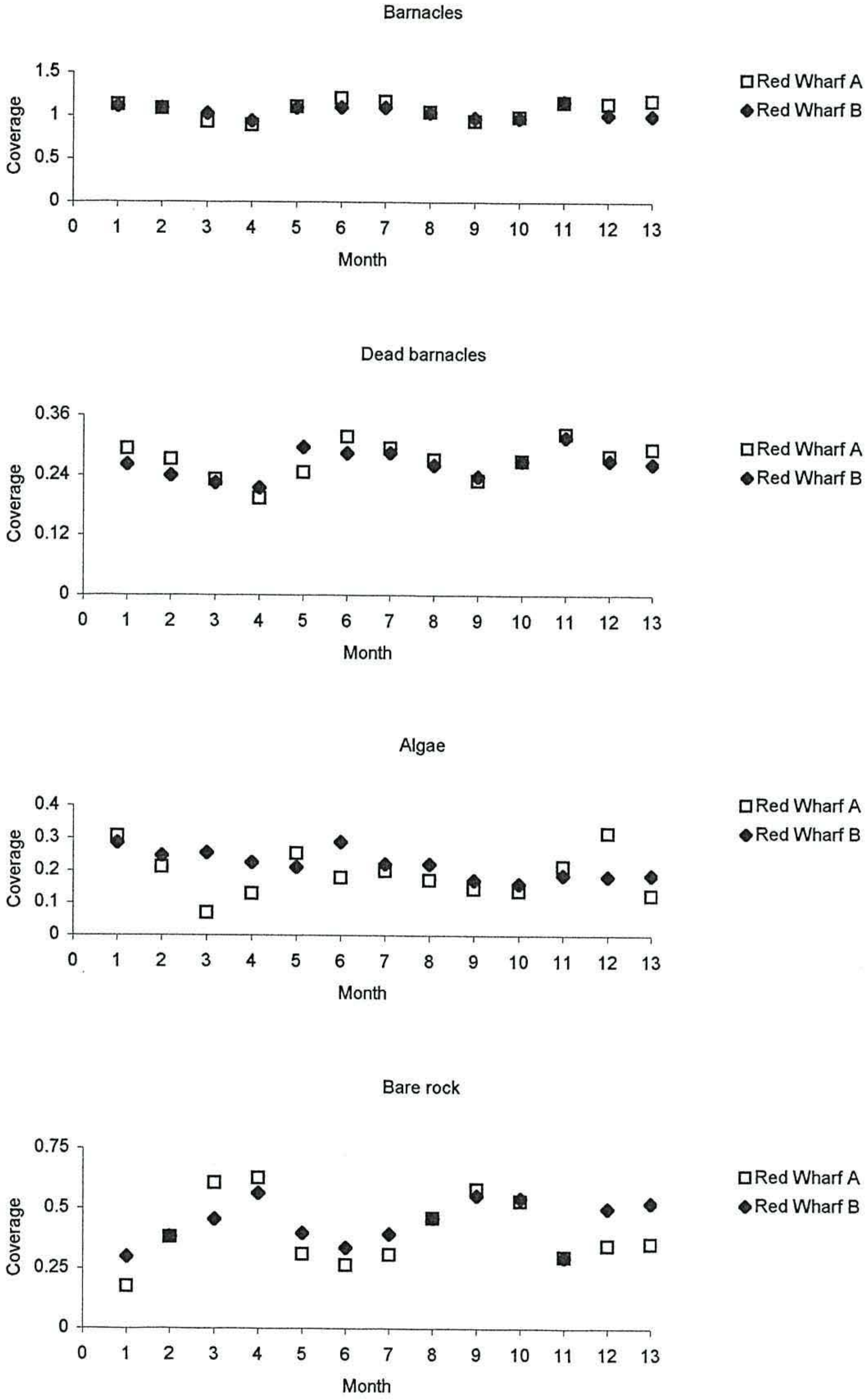


Figure 6.4.Percent coverage (arcsine transformed) of barnacles, dead barnacles, algae and bare rock following treatment 4(control). A comparison between Red Wharf A (started in April) and Red Wharf B (started in September).

Appendix 6 Tables.

Table 6.1. Results of Post Hoc multiple comparisons (Bonferroni test) showing significant overall mean differences in barnacle coverage between shores for all four experimental treatments.

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Shores	*P*	*P*	*P*	*P*
1-4		0.011	0.001	
1-7	<0.001	<0.001	<0.001	<0.001
2-3			0.035	
2-4		0.002	0.001	
2-5		0.014		
2-7	<0.001	<0.001	<0.001	<0.001
3-4		<0.001	<0.001	
3-5	0.017	0.002	<0.001	
3-7	<0.001	<0.001	<0.001	<0.001
4-6	0.040	0.002	<0.001	
4-7	<0.001	<0.001	<0.001	<0.001
5-6	0.005	0.019	0.003	
5-7	<0.001	<0.001	<0.001	<0.001
6-7	<0.001	<0.001	<0.001	<0.001

Data presented are probabilities (P), which are all significant values.

Table 6.2. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in dead barnacle coverage between shores for all four experimental treatments.

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Shores	*P*	*P*	*P*	*P*
1-3			0.001	
1-6	0.001		0.001	0.012
1-7	<0.001	0.001	<0.001	<0.001
2-3			0.001	
2-4		0.022		
2-6	0.002		<0.001	
2-7	<0.001	<0.001	<0.001	<0.001
3-4		0.014	<0.001	
3-5			<0.001	
3-6	0.028			
3-7	<0.001	0.002	<0.001	<0.001
4-6	0.005	0.006	<0.001	
4-7	<0.001	0.010	<0.001	<0.001
5-6	0.001		<0.001	
5-7	<0.001	0.001	<0.001	<0.001
6-7	<0.001	<0.001	<0.001	<0.001

Data presented are probabilities (P), which are all significant values.

Table 6.3. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in algal coverage between shores for all four experimental treatments.

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Shores	*P*	*P*	*P*	*P*
1-2		0.018		
1-4		<0.001	<0.001	
1-5		<0.001	0.002	
1-6	<0.001			0.026
1-7	<0.001	0.002		0.007
2-4	0.047	<0.001	0.002	
2-5	0.035	<0.001		
2-6	<0.001	0.011		0.002
2-7	<0.001			0.001
4-5		0.004		
4-6	<0.001	<0.001	<0.001	
4-7	<0.001	<0.001	0.001	0.014
5-6	<0.001	<0.001	0.002	0.012
5-7	<0.001	0.001	0.044	0.003
6-7		0.002		

Data presented are probabilities (P), which are all significant values.

Table 6.4. Results of Post Hoc multiple comparison (Bonferroni test) showing significant overall mean differences in availibility of bare space between shores for all four experimental treatments

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Shores	*P*	*P*	*P*	*P*
1-3	0.004			
1-7	<0.001	<0.001	<0.001	<0.001
2-3	0.007			
2-5	0.033			
2-7	<0.001	<0.001	<0.001	<0.001
3-4	0.003			
3-5	<0.001			
3-6	0.005			
3-7	<0.001	<0.001	<0.001	<0.001
4-7	<0.001	<0.001	<0.001	<0.001
5-7	<0.001	<0.001	<0.001	<0.001
6-7	<0.001	<0.001	<0.001	<0.001

Data presented are probabilities (P), which are all significant values.

Table 6.5. Coverage of sessile organisms: results of environmental manipulations.

May 96	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
RWB A	81.56	91.45	76.9	87.9	9.38	8.65	8.42	9.18	10.62	3.92	13.01	3.36	4.55	3.99	4.7	3.57

July 96	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
RWB A	86.94	78.67	71.68	88.96	6.48	7.61	10.43	9.86	7.85	8.98	15.98	5.15	0.87	10.46	7.29	1.21

September 96

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	76.58	79.61	74.85	72.39	7.86	9.43	7.81	9.38	14.56	13.21	11.76	12.45	8.86	7.18	13.39	15.16
Trwyn	79.56	81.26	84.23	80.35	8.97	9.34	10.76	11.46	9.24	9.33	8.76	10.45	11.2	9.41	7.01	9.2
Llanfair.	82.35	81.36	82.45	79.86	7.89	6.45	8.32	7.98	0	0	0	0	6.89	9.52	9.57	11.1
RWB A	84.23	74.57	68.86	83.86	5.87	4.32	12.15	10.8	10.45	22.43	26.86	9.12	1.65	1.37	0.83	3.16
RWB B	81.35	80.27	79.83	82.45	8.18	7.83	9.34	8.02	7.59	6.34	7.41	8.48	9.59	12.94	12.55	6.92
Nobla	80.48	81.47	79.89	81.26	11.56	12.35	12.45	11.98	9.98	8.98	7.76	9.82	9.54	9.55	12.35	8.92
Defaid	8.91	9.43	11.23	10.14	16.95	15.89	15.38	14.36	4.54	3.87	5.04	3.76	86.55	86.7	83.73	86.1

November 96

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	75.39	74.65	74.21	71.39	5.45	7.19	5.38	8.27	6.36	7.58	8.14	7.03	18.25	17.77	17.65	21.58
Trwyn	77.48	79.45	81.34	76.36	5.67	8.87	4.96	8.26	7.13	8.96	9.13	6.14	15.39	11.59	9.53	17.5
Llanfair.	80.43	80.03	85.34	80.45	4.44	6.06	4.67	7.13	0	0	0	0	9.5	10.5	8.37	9.97
RWB A	75.48	65.67	60.94	76.34	4.67	5.69	7.02	10.62	5.14	24.11	19.85	4.98	16.34	9.23	15.23	16.01
RWB B	77.84	74.54	75.37	80.37	5.93	6.25	6.06	7.26	5.27	9.83	10.58	6.03	14.86	14.5	13.1	11.64
Nobla	77.98	78.68	78.65	75.72	9.96	11.35	8.26	10.98	5.55	7.84	4.67	7.29	16.47	13.48	16.68	16.99
Defaid	8.34	9.02	10.67	8.87	11.45	12.16	9.97	14.03	2.86	3.56	4.17	3.14	88.8	87.42	85.16	87.99

January 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	74.35	72.72	73.56	70.41	2.97	4.57	3.38	5.93	3.26	4.98	2.34	5.14	22.39	22.3	24.1	24.45
Trwyn	75.68	77.45	79.56	72.65	5.56	6.11	4.69	5.22	6.62	8.45	9.95	5.43	17.7	14.1	10.49	21.92
Llanfair.	82.06	82.69	90.94	81.76	3.65	4.49	4.17	6.31	0	0	0	0	6.72	8.01	4.23	8.18
RWB A	62.45	49.65	41.45	60.85	4.56	5.24	6.98	7.47	2.87	24.2	14.23	0.53	32.09	25.67	40.16	37.22
RWB B	66.15	63.15	62.15	68.78	4.04	6.02	5.13	6.95	3.15	12.34	7.98	8.16	29.01	23.73	29.55	21.6
Nobla	75.76	73.27	80.02	70.83	6.83	8.18	5.78	10.8	2.02	1.95	4.35	4.85	22.22	24.78	15.63	24.32
Defaid	7.62	8.18	9.25	6.97	9.13	11.26	10.34	11.79	1.03	3.05	3.35	2.02	91.35	88.77	87.4	91.01

March 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	75.97	73.46	75.87	74.87	2.47	5.78	3.41	6.43	4.13	7.98	10.34	3.67	19.9	18.56	13.79	21.46
Trwyn	81.35	84.34	79.43	78.03	4.14	8.94	3.13	9.03	3.97	8.25	13.45	7.14	14.68	7.41	7.12	14.83
Llanfair.	81.78	80.67	88.46	82.34	2.82	7.34	4.21	6.86	0	0	0	0	7.88	9.88	5.67	8.32
RWB A	62.99	50.2	41.92	61.66	3.64	3.74	2.19	5.71	2.99	23.33	26.45	0.78	31.2	26.14	27.43	36.15
RWB B	64.24	59.23	60.06	66.37	4.11	6.93	4.87	6.43	3.31	15.68	12.46	5.68	30.62	24.66	27.24	26.72
Nobla	82.32	80.98	82.45	83.65	5.23	3.88	4.14	11.49	0.08	3.96	5.68	2.13	17.6	15.06	11.87	14.22
Defaid	12.34	5.97	8.14	8.65	7.27	10.67	12.47	8.76	0.23	7.22	8.95	0.02	87.43	86.81	82.91	91.33

Key to treatments: N: remove dogwhelks; P: remove limpets; B: remove dogwhelks and limpets; C: control.

Table 6.5. continued.

May 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	80.5	67	69	87.5	3.44	6.38	2.65	8.91	10	11.5	20.5	2.5	9.5	21.5	10.5	10
Trwyn	87.97	89.15	77.7	82.97	3.22	5.32	3.37	7.92	8.05	10.53	17.98	13.45	3.98	0.32	4.32	3.62
Llanfair.	85.74	86.5	83.34	82.31	2.28	4.35	3.13	6.02	0	0	0	0	7.9	5.86	9.23	7.26
RWB A	76.37	65.93	64.73	82.04	2.97	4.56	3.35	7.12	6.35	21.23	26.5	9.52	13.13	9.87	5.34	5.68
RWB B	77.38	62.39	62.47	78.45	3.86	8.87	5.15	9.17	4.45	19.34	22.45	5.35	17.6	18.06	15.08	14.99
Nobla	96.92	92.1	91.12	97.87	3.37	6.14	5.13	12.96	0	4.53	7.08	0	3.08	3.37	1.8	2.13
Defaid	17.49	3.67	7.07	11.94	5.87	14.96	16.86	5.91	0.42	14.49	19.92	0	82.09	81.84	73.01	88.06

July 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	80.52	66.55	69.22	84.25	3.16	2.83	7.38	5.1	10.09	11.34	23.75	10.24	9.39	22.11	7.03	5.51
Trwyn	82.18	89.89	74.78	82.17	5.33	7.15	12.3	10.03	11.84	6.75	17.74	11.85	5.98	3.36	7.48	5.98
Llanfair.	85.3	86.37	82.83	82.44	6.3	6.9	16.75	17.5	0	0	0	0	4.8	3.78	3.12	4.54
RWB A	87.42	47.38	42.3	88.08	5.87	4.32	12.15	10.8	4.92	43.16	45.6	3.43	5.98	9.46	6.77	6.37
RWB B	85.11	65.97	64.93	82.13	4.94	10.87	8.98	11.45	5.96	21.33	26.31	9.47	8.7	12.7	8.58	7.22
Nobla	92.72	78.4	88.52	91.12	6.83	8.18	12.15	10.8	0.02	10.1	5.18	0.3	7.26	11.5	6.3	8.58
Defaid	17.49	8.01	9.34	11.94	11.56	21.87	14.87	25.63	0.42	12.11	19.92	1.23	82.09	79.88	70.74	86.83

September 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	84.57	68.96	71.56	82.37	2.98	7.45	8.15	4.32	7.85	15.98	21.32	9.54	7.58	15.06	7.12	8.09
Trwyn	79.34	66.78	63.54	79.32	3.57	6.89	6.87	9.68	6.98	20.28	27.12	9.45	13.68	12.94	9.34	11.23
Llanfair.	79.64	85.98	81.69	82.39	5.01	9.12	10.78	12.45	0	0	0	0	7.48	7.95	11.07	8.23
RWB A	84.35	42.98	40.84	83.74	4.45	5.87	9.76	9.34	4.12	45.5	43.57	4.67	9.07	11.46	11.46	9.35
RWB B	82.96	64.75	63.66	80.23	4.67	9.45	6.54	10.36	4.43	24.37	24.41	4.04	12.35	10.88	11.93	14.59
Nobla	86.46	74.36	77.03	87.04	5.69	6.74	8.76	9.13	1.43	15.87	12.98	0.96	12.11	9.77	9.99	12
Defaid	9.23	2.34	3.51	6.83	10.17	11.17	22.36	25.23	1.22	33.67	46.84	0	89.55	63.99	49.65	93.17

November 97

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	80.34	69.34	73.59	83.21	3.45	6.84	6.48	7.48	5.79	11.24	10.98	5.47	13.87	19.42	15.43	11.32
Trwyn	73.48	61.35	54.34	71.39	3.48	6.48	4.56	8.26	5.57	12.98	14.48	6.85	20.95	25.67	31.18	21.76
Llanfair.	80.12	81.21	83.35	80.22	4.44	6.06	4.67	6.93	0	0	0	0	8.01	12.81	11.42	12.37
RWB A	73.84	37.59	34.28	73.28	4.67	5.69	7.02	10.62	3.63	23.56	26.79	3.17	20.56	38.44	35.85	21.07
RWB B	77.48	63.12	61.34	75.66	4.45	7.93	5.17	9.47	3.83	20.34	22.48	5.12	18.38	16.54	16.18	18.14
Nobla	83.41	71.13	72.05	82.98	4.42	9.94	5.58	10.05	0.96	14.23	13.69	0.54	15.63	14.64	14.26	16.48
Defaid	9.19	2.13	3.25	6.24	7.89	11.45	11.56	15.33	0.41	19.56	25.18	0	90.4	78.31	71.57	93.76

January 98

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	91.1	73.67	74.52	90.83	3.12	6.45	5.12	7.35	2.31	3.61	5.26	2.16	6.59	22.72	20.22	7.01
Trwyn	61.75	52.02	37.07	56.63	2.79	5.45	4.47	8.34	5.03	7.58	9.42	7.74	33.22	40.4	53.51	35.63
Llanfair.	79.64	85.98	81.69	82.39	4.23	7.59	8.9	9.67	0	0	0	0	8.8	8.9	11.96	9.63
RWB A	68.7	25.78	15.34	67.55	3.57	4.78	6.98	7.89	3.46	21.2	28.56	2.53	27.09	52.87	55.08	27.37
RWB B	70.47	53.38	51.44	73.91	2.84	6.04	5.01	8.73	2.99	16.45	24.38	3.26	25.8	30.03	24.18	21.91
Nobla	78.67	65.89	67.14	77.98	4.38	5.12	6.34	7.45	0.45	10.34	9.13	0.22	20.88	23.77	23.73	21.8
Defaid	8.24	2.26	3.09	5.61	7.23	9.45	11.47	12.45	0.12	15.87	17.93	0	91.64	81.87	78.98	94.39

Table 6.5. continued.

March 98

	live barnacles				percent dead barnacles				algae							
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	83.45	70.48	71.48	82.45	3.29	7.59	4.18	7.98	4.14	8.28	11.57	2.78	12.41	21.24	16.95	14.77
Trwyn	86.58	89.89	75.8	84.16	3.98	4.98	5.13	9.37	3.86	9.13	12.45	7.12	9.56	0.98	11.75	8.72
Llanfair.	82.06	82.68	90.94	81.76	4.57	6.89	7.54	8.96	0	0	0	0	6.72	8.01	4.23	8.18
RWB A	68.11	25.58	14.23	67.43	5.03	9.56	6.59	11.25	3.23	23.47	26.47	1.78	27.32	50.6	57.17	28.12
RWB B	67.85	50.12	47.36	66.63	3.23	5.44	4.78	9.48	3.36	21.95	27.82	2.42	27.56	27.61	24.61	29.39
Nobla	83.68	74.98	77.85	82.23	4.21	8.24	7.14	8.36	0.22	7.98	8.99	0	16.1	17.04	13.16	17.77
Defaid	10.48	4.59	5.1	8.27	8.08	13.12	10.12	17.65	0.04	15.92	18.16	0	89.48	79.49	76.74	91.73

May 98

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	81.49	65.56	67.78	87.51	3.84	5.65	4.14	7.14	10.01	11.89	21.58	2.86	8.5	22.55	10.64	9.63
Trwyn	87.42	87.51	76.21	85.72	5.22	10.26	4.47	12.35	7.43	11.45	16.94	13.43	5.15	1.04	6.85	0.85
Llanfair.	86.88	88.42	88.34	84.96	7.13	15.97	6.32	17.45	0	0	0	0	6.53	5.7	4.28	2.21
RWB A	83.47	50.19	60.45	84.75	4.64	10.98	6.1	13.32	5.84	36.79	34.32	7.01	8.92	12.98	2.85	5.99
RWB B	83.38	49.79	45.69	82.45	3.14	5.76	11.79	10.69	4.45	39.34	42.02	3.95	9.04	10.41	6.15	10.63
Nobla	96.32	81.63	90.15	95.96	9.12	12.56	11.96	9.02	0	5.27	7.26	0	3.68	13.1	2.59	4.04
Defaid	14.59	5.15	6.94	10.96	9.43	25.23	13.13	23.01	0.03	15.34	19.78	0	85.38	79.51	73.28	89.04

July 98

	live barnacles				percent dead barnacles				algae				bare rock			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	67.62	43.69	53.99	77.54	4.26	3.88	6.87	6.83	0.49	8.32	7.68	0.11	31.89	47.99	38.33	22.35
Trwyn	72.27	58.18	30.75	68.92	4.87	8.98	9.67	9.72	5.86	22.48	48.06	8.89	21.87	19.34	21.19	22.19
Llanfair.	72.75	69.03	61.74	75.5	6.8	8.54	11.29	14.98	0	0	0	0	14.93	19.6	26.07	14.72
RWB A	91.07	39.95	35.88	87.07	6.78	5.65	13.28	8.88	2.16	30.73	43.36	12.15	6.23	29.32	20.03	10.28
RWB B	67.47	35.46	23.87	74.19	5.36	8.83	11.02	10.05	1.47	36.63	37.79	4.03	31.06	17.91	38.3	21.06
Nobla	91.34	68.59	52.39	90.4	5.89	9.65	13.47	11.56	0.07	19.36	40.63	0	8.59	12.05	6.98	9.6
Defaid	13.23	0.39	0.81	6.01	13.56	17.87	16.98	28.97	0.22	29.85	35.96	0.57	86.55	69.76	63.23	93.42

September 98

	live barn				percent dead barnacles				algae				bare space			
	N	P	B	C	N	P	B	C	N	P	B	C	N	P	B	C
Menai	71.28	53.75	60.02	79.77	5.67	8.45	7.96	6.59	0.95	15.47	14.62	2.78	27.77	30.78	25.36	17.45
Trwyn	80.01	42.36	22.94	76.58	6.29	8.15	8.95	10.76	4.02	33.85	47.89	6.33	15.97	23.79	29.17	17.09
Llanfair.	74.39	70.92	54.66	73.87	7.72	9.35	9.71	12.01	0	0	0	0	16.35	18.23	33.03	14.19
RWB A	86.1	16.72	17.9	85.01	5.81	4.76	11.45	9.76	3.23	47.88	52.95	2.53	10.26	35.4	28.95	11.65
RWB B	67.35	18.41	14.75	78.66	4.99	8.77	6.65	9.33	2.32	57.21	52.25	1.49	30.33	24.38	33	19.64
Nobla	74.85	36.49	24.13	70.15	8.04	8.84	10.35	10.22	0	23.79	45.04	0	25.15	39.72	30.83	29.85
Defaid	5.75	0.78	1.58	5.71	13.42	13.47	16.11	18.76	0.21	37.08	39.17	0.54	94.04	62.14	59.25	93.75

Coverage of sessile organisms was determined at the end of every two months
figures in the table are (with the exception of dead barnacles) expressed as the percentage
of rock surface covered and therefore total 100%. coverage was obtained by the use of
quadrats subdivided into equal squares by string strung across the frame
the coverage of individual species was determined by placing perspex sheets over thses 10cm x 10cm
squares and tracing the outline of the individual or groups of individuals and determining area coverage
later in the laboratory. 4 full quadrats (= 4 x 25 10cmx10cm units) = 1 sq metre per boulder
were examined at random with equal weighting given to each side (seaward, leeward
side or top) to give a single value for the experimental unit.
In the laboratory area values were determined by placing the perspex sheets over graph paper