DEVELOPMENTAL CHANGES IN THE DISTRIBUTION AND DIET OF NUCELLA LAPILLUS (L.) FROM A MUSSEL-DOMINATED SHORE

J. HARRIS

Ph.D. 1988
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DEVELOPMENTAL CHANGES IN THE DISTRIBUTION AND
DIET OF NUCELLA LAPILLUS (L.)
FROM A MUSSEL DOMINATED SHORE

by

Jean Harris

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No material contained in this thesis has been accepted or is concurrently being submitted for any other academic award.

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date

This is to certify that the work submitted here was carried out by the candidate herself. Due acknowledgement has been given to any assistance received.

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date

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Supervisor of studies

date
Developmental changes in the distribution and diet of *Nucella lapillus* (L.) from a mussel dominated shore.

by

Jean Harris

Aspects of the developmental biology of an intertidal predatory gastropod, *Nucella lapillus* were investigated for a population located on a mussel dominated shore at Whitsand Bay, Cornwall.

A field sampling programme revealed that the centre of abundance of small *Nucella* (<3.4mm) occurred at lower shore levels than that of all larger individuals and the egg capsules. Laboratory studies demonstrated that hatchlings are both negatively geotactic and phototactic, directing them upshore and into crevices.

The relative profitabilities of four different sized mussels to four developmental stages of *Nucella* were investigated using both ability to promote growth and energy gain per unit handling time (E/T) as measures of prey value. The response curves were similar in that proportionately large and small prey were less profitable than medium sized prey with the optimal prey size increasing with predator size. However the most profitable size according to the E/T model was larger than in the growth rate model because large meals appeared to be less efficiently utilized.

An ontogenetic shift in prey size selection was demonstrated in laboratory and field, the results of which were more accurately predicted by the growth rate model of prey value. Predatory events in the field were investigated using borehole dimension as an index of predator size.

The feeding and growth of *Nucella* were investigated at differing periods of tidal emersion. Growth rates were substantially reduced at emersion periods of above 30%, but these could not be wholly attributable to reduced feeding rates.

Field growth trials demonstrated that a mature size could be reached in 19-21 months, that growth does not cease at maturity, and that juveniles grow throughout the year. A strong correlation existed between growth rate and environmental temperature. Growth rates in the field were about 75% those in the laboratory, suggesting few constraints on foraging in the field.
Acknowledgements

I am indebted to many people for their assistance throughout the conduct of this work.

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Financial support was provided by Devon County Council.

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CHAPTER 1 INTRODUCTION

The predatory whelk, Nucella lapillus (L.), is common intertidally on rocky shores, where it feeds predominantly on other molluscs and barnacles. Like most marine snails the embryos are enclosed in capsules which, for this species, are attached to hard surfaces in the intertidal zone. Unlike the majority of marine snails in British waters development is direct, the young emerge from the capsule as small snails without an intermediate planktonic veliger stage. As the entire life cycle occurs on the shore, the developmental biology of this species can be studied, in situ, from the time of emergence from the capsule, as a 1mm hatchling, to maturity, when the mean length can range from 17.0 to 47.6mm (Crothers, 1985).

Although adults of the species have been studied quite extensively, (for reviews see Crothers, 1985; Fretter & Graham, 1985), there is relatively little information regarding the juvenile stage. This is somewhat surprising as the juvenile phase is not short-lived, having an estimated duration of two to two and a half years (Feare, 1970a).

The developmental responses of predators have been largely over-looked yet an increased knowledge of the factors influencing the biology of juveniles can be viewed as critical to achieving a greater understanding of a species as a whole and to the role it plays in the community.

As a contribution towards an understanding of the ontogenetic changes in the life of a predator, this study investigates the developmental changes in the distribution and diet of Nucella, from hatchling to adult, as it occurs on an exposed rocky shore in conjunction with one of its major prey, the mussel Mytilus edulis L.

Since the young and adults of a species might be expected to have
differing demands on, and tolerances to, their environment, we might expect them to be separated spatially. Among intertidal gastropods, intraspecific size gradients along vertical transects of the shore have been shown to be of common occurrence (Vermeij, 1972). Such size gradients may result from differential growth rates at different shore levels (Seed, 1968; Sutherland, 1970) or from size dependent mortality which varies with height on the shore (Green & Robson, 1970; Connell, 1961). For mobile species size gradients may result from active migration of size classes within a population (Frank, 1965; Paine, 1969; Edwards, 1969; Chow, 1975).

Intraspecific shore level size gradients among mobile rocky shore gastropods were considered by Vermeij (1972) to be the result of juveniles being adapted to inhabit the shore level of minimal mortality within the range of the species. He argued that such adaptation could arise from a predictable vertical gradient in the nature and intensity of juvenile mortality in the intertidal zone. The dominant causes of juvenile mortality were considered to be physical stress in the upper intertidal and biotic factors, particularly predation, in the lower intertidal.

An alternative explanation was forwarded by Bertness (1977) who suggested that a predator-prey size selection advantage would provide a feasible explanation for the evolution of shore level gradients in two species of the predatory whelk, Thais.

In addition to shore level size gradients, the topological complexity provided by a rocky shore, with spatial refuges for small snails in crevices, may result in small-scale size-specific differences in distribution patterns.

Previous descriptions of intraspecific shore level size gradients in Nucella have been conflicting (see chapter three for review) and a
re-examination of the effect of shore height on the size composition of
*Nucella* forms part of this study (chapter 3).

The egg capsules are large (1cm long), conspicuous and easy to count
and the lack of a dispersive planktonic phase means that young are
probably recruited locally. Thus by monitoring the number and
distribution of egg capsules, along with that of the hatchlings, early
behaviour patterns on the shore may be elucidated (chapter 3).

Before they can grow, developing organisms must acquire sufficient
energy to exceed their maintenance requirements, and in general the
rate at which an animal feeds governs the rate of development. Thus
effective feeding behaviour can be considered a crucial requirement
during ontogeny. Among invertebrate predators the time spent procuring
prey items can range from being almost instantaneous, e.g. filter
feeding bivalves, to being prolonged, e.g. web spinning spiders and
caddis fly larvae. *Nucella* falls into the latter category.

When feeding on mussels *Nucella* has to drill through the shell to
gain access to the flesh, a method of attack employed by all size
classes. The time spent drilling can be considerable, and depends on
the thickness of the mussel shell and on whelk size. The drilling
period represents a considerable investment in each predatory event,
and whilst drilling the whelk gains no reward for the effort expended.

Return from a predatory event, in terms of amount of mussel flesh
ingested, will also depend on the size of the prey relative to predator
size. The flesh content of a mussel increases with size, but the extra
effort expended in the drilling process of a relatively large mussel
may be wasted if all the flesh is not available to the consumer.

Thus from a foraging efficiency viewpoint all mussel sizes would not
be expected to be equally profitable to a given size of *Nucella*. Since
the mechanical properties of the drilling and ingesting apparatus will
develop considerably on growing from a 1mm hatchling to a 30mm adult, the same mussel size would not be expected to remain equally profitable throughout the developmental phase.

The present predator-prey system provides an excellent opportunity to study the changing foraging conditions as an animal develops without the complexities of varying prey species. Moreover, although laboratory studies have looked at the developmental response of invertebrate predators on a single species of prey (e.g. Thompson, 1975), it is unusual to find a situation where the predator is exposed to, and feeds almost exclusively upon, a single major prey type in the field. Aspects of prey profitability have been studied for adult Nucella (Hughes & Dunkin, 1984; Dunkin & Hughes, 1984), but little attention has been paid to the changes that occur during development for this, or any other species.

According to optimal foraging theory (as reviewed, for example, by Stephens & Krebs, 1986) selective pressures act upon predators to result in the evolution of optimal foraging decisions. One such decision, which has received considerable attention, is that of which prey items should be included in the diet. Given that not all prey items are equally profitable to the predator, and provided that the predator can recognise different prey items and rank them according to some benefit measure, prey choice should be governed by optimality criteria. In most optimal diet studies prey profitability has been defined as the net energy reward per unit handling time (Krebs, 1978).

During ontogeny it might be expected that the optimal prey size would increase. This effect was investigated for developing Nucella feeding on mussels, using two measures of prey value. In the first instance, working with juveniles provided an opportunity not afforded by studies with mature animals; that of taking prey value as the
potentiality of the prey to promote consumer growth (chapter 4).

Reasoning that in juveniles increased growth rates lead to an increase in fitness (for review see chapter 4), the most profitable prey size will be that which yields maximum growth rates. Provided that no energy is partitioned to reproductive effort, energy uptake in excess of maintenance demand will be channelled into growth. Although a breakdown of the costs and benefits of consuming a given size of prey remain unknown, growth rates provide a direct measure of the value of a prey item.

The second measure of prey value was taken as the more usual energy gain per unit handling time (chapter 5). This latter measure requires the determination of times required to handle prey items of varying size (the drilling and ingestion times), and the yield from those prey items. In building a model for a single size of predator information need only be gained on the mean drilling and ingestion rates and the mean reward from a given prey size. For a developmental response, in addition the functional relationships between both drilling and ingestion rates and predator size are required.

If as Nucella develops the mussel prey size providing the maximum return is constantly changing, there would need to be a continuously modified foraging response to prey size if the predator is to forage optimally. A developmental change in foraging behaviour requires that during ontogeny the snail can recognise the dimensions of its prey and respond accordingly, updating its responses as it grows.

In this study I test for a developmental response in prey size selectivity in simple laboratory experiments, and compare it with the spectra of prey profitability defined both as the ability to promote growth and as the energy yield per unit handling time (chapter 6).

However it has been recognised (McFarland, 1977) that foraging
decisions resulting in optimal foraging behaviour may have to be modified in order that other facets of an animal's life are simultaneously optimized. Where conflicting demands on an animal's overall behaviour exist, foraging decisions studied in isolation can appear sub-optimal.

Prey size selection decisions in the artificially benign conditions of the laboratory may, in the field, be modified by the need of the predator itself to avoid being preyed upon, by the risk of being washed off, or by the dangers of temperature and desiccation stress. The influence of constraints in the field on the developmental foraging response can be investigated using this predator-prey system. Permanent records of field predation by *Nucella* are provided by the boreholes, which are characteristic of the species (Fretter & Graham, 1962). Provided a functional relationship between predator size and borehole dimension exists, predatory events in the field can be attributed to given sizes of *Nucella* to test for developmental changes in prey size choice in the field (chapter 6).

Since constraints on foraging behaviour may also be expected to result in less than maximal growth in the field, the growth rates of a marked population of developing *Nucella* were monitored for one year on the shore and compared with laboratory maxima (chapter 3).

Finally it was anticipated that one constraint, that of tidal level, may act to alter the optimal foraging solution of prey size selection. This effect was investigated in a tidal tank regime (chapter 7).

It is the interrelations between juvenile *Nucella* feeding responses, growth and distribution on the shore that form the body of this work.
CHAPTER 2 BACKGROUND AND GENERAL TECHNIQUES

2.1 The Animals

2.1.1 Nucella lapillus

Nucella lapillus is a muricid gastropod that lives on rocky intertidal shores on both sides of the North Atlantic. Its geographical distribution ranges from Norway (71°N) to Portugal (37°N) on the European coastline (Cooke, 1915) but on the eastern American coast its range is more limited, extending from Southern Labrador (51°N) to New York (41°N). Moore (1936) related the northern limit of N. lapillus to the -1°C winter isotherm and the southern limit to the 19°C summer isotherm. Although not very tolerant of strongly estuarine conditions (Moore, 1936; Fretter & Graham, 1985) Nucella have been found in salinities as low as 20-28% in the Severn Estuary (Boyden et al., 1977).

On the shore Nucella are commonly found between MHWN and MLWS (Moore, 1936; Moyse & Nelson-Smith, 1963; Peare, 1970a; Hughes, 1972; Coombs, 1973; Crothers, 1976) and are most abundant around midtide level (Moore, 1938b; Moyse & Nelson-Smith, 1963). Although rarely found below ELWS, Moore (1936) reported occasional specimens recovered sublittorally. Connell (1961) suggested that the upper shore limit to its range was governed by intolerance to increased exposure to air while its lower limit reflected a decrease in the population density of its prey.

Within the tidal zone normally inhabited by Nucella lapillus age-specific differences in vertical distribution have been reported and variously related to physical disturbance (Moore, 1938b), predation pressure (Peare, 1970a) and desiccation tolerance (Coombs, 1973).

Nucella are most abundant on shores of intermediate exposure, in
extreme exposure it is scarce and confined to crevices while on extremely sheltered shores it is absent or rare (Moore, 1936; Ballantine, 1961; Moyse & Nelson-Smith, 1963).

The species is predatory, commonly feeding on barnacles and mussels (Colton, 1916; Moore, 1938b; Connell, 1961; Largen, 1967a) although a wide variety of molluscs may occasionally be eaten (reported diet listed in Hughes & Dunkin, 1984; Crothers, 1985). Prey may be detected at a distance by olfaction, particularly if the prey are damaged (Morgan, 1972a), but recognition of single prey items is probably through tactile stimuli (Hughes & Dunkin, 1984).

*Nucella* attack mollusc prey by boring a hole through the shell using rasping movements of the radula and chemical dissolution through activities of the accessory boring organ (Fretter & Graham, 1962; Chetail & Fournié, 1969; Webb & Saleuddin, 1977). The flesh of the prey is ingested through the borehole using the proboscis. Drilling of barnacles may occasionally occur although more usually access to the flesh is gained by forcing apart the opercular valves of the prey (Connell, 1961).

The sexes are separate (Fretter & Graham, 1985) and fertilization is internal (Fretter, 1953). The eggs are laid in vase-shaped capsules which are securely attached to rock surfaces, generally in crevices, on overhangs or on the underside of stones (Fretter & Graham, 1962). Each capsule originally contains 500 to 600 eggs (Pelseneer, 1935) most of which are nurse eggs, providing nourishment for the few embryos that develop (Fretter & Graham, 1985). The embryos pass through a reduced veliger stage within the capsule (Fretter & Graham, 1985) and after approximately four months (Pelseneer, 1935) juvenile snails hatch from the capsules. The number of embryos within each capsule to complete development have been variously reported as ten to twelve (Colton,
1916), five to forty (Pelseneer, 1935), thirteen to thirty-six (Feare, 1970a) and twelve to fifteen (Crothers, 1977).

The newly hatched snails feed on small mussels (Colton, 1916) or Spirobranchus borealis (Moore, 1938b), although small specimens of a considerable number of barnacle and mollusc species can form part of their diet (Largen, 1967a).

Growth to maturity takes approximately two and a half years (Moore, 1938a; Feare, 1970a), with adult longevity estimated at five to six years. Nucella fall prey to a variety of predators, mainly crabs, birds and fish (see Connell, 1961 and Crothers, 1985 for references therein).

2.1.2 Mytilus edulis

The lamellibranch mollusc, Mytilus edulis is a widely distributed species of the Northern hemisphere. It occurs in Arctic waters extending south to California and Japan on the Pacific coasts and to North Carolina and North Africa on the Atlantic coast (Seed, 1976). The northern limits of the species are closely paralleled by the summer limits of the pack ice (Barnes, 1957) and the southern limit coincides approximately with the maximum surface isotherm of 27°C (Seed, 1976).

Mytilus edulis is found in littoral and shallow sublittoral waters. It is a sessile, filter feeding organism which can live on a variety of substrata, from rock and stones to compacted mud and sand. It often forms a dense covering. The species can flourish in exposed conditions (Lewis, 1964) but does not tolerate sheltered fucoid-dominated open coasts. It is able to withstand a wide range of salinities, living both in open water and brackish estuaries.

The species exhibits erratic distribution patterns (Lewis, 1964) which although possibly due to differences in the physical environment are thought more likely to result from variations in recruitment
patterns, competition, predation and detachment (Seed, 1969a). In particular the downward extension of the species on the shore is thought to be controlled by predators (Seed, 1969b) while the upper limit is set by physical factors (Baird & Drinnan, 1957).

The almost cosmopolitan distribution of *Mytilus edulis* in the northern hemisphere has been attributed to tolerance of a wide range of environmental conditions and high reproductive output (Seed, 1969b). The sexes are separate, spawning of gametes occurs into the surrounding water where fertilization occurs. During larval development, which takes place in the plankton, dispersion can occur over great distances. Bayne (1964) recognised that the larvae undergo two separate settlements. The primary settlement takes place after 3 to 5 weeks of planktonic existence and occurs on filamentous substrates, where the larvae remain for approximately four weeks (Seed, 1969a). Following the primary settlement the larvae pass through another migratory phase and are transported by water currents to their secondary settlement site, often existing mussel beds.

The growth rate of *Mytilus edulis* is very variable, differing between and within localities. In favourable conditions growth can be as high as 57mm/year (Mason, 1971) or in adverse conditions as low as 1.5mm/year (Seed, 1969b). The single most important factor affecting growth rate is probably food supply (Seed, 1976) but other factors influence growth, e.g. temperature (Richards, 1946), population structure (Seed, 1969b) and level on the shore (Baird, 1966).

Predation contributes significantly to the mortality of *M. edulis* (Seed, 1976), the major predators being gastropods (Kitching et al., 1959) crabs (Ebling et al., 1964), starfish, fish (Dare, 1976) and birds (Milne & Dunnet, 1972). Although tolerant of a range of environmental conditions physical factors, for example storm damage,
extremes of temperature and excessive silt, can contribute to the mortality of *Mytilus edulis* (Seed, 1976).

2.2 The Site

An initial survey was made of potential field sites along the south coast of England stretching from Looe in Cornwall to Hopes Nose near Torquay in Devon. The rocks at Whitsand Bay (National Grid reference SX 3952) supported the highest density of *Nucella lapillus*. Other sites were characterised by low densities (less than one per square metre) of adults and a conspicuous lack of juveniles and egg capsules.

Bryan et al. (1985) have since shown that populations of dogwhelks in south-west England have been adversely affected by antifouling paints containing tributyltin compounds, and that near centres of boating and shipping activity organotin exposure causes imposex in adult female whelks. Although all dogwhelks in the region exhibit imposex, the degree varies with organotin exposure; at high concentrations the females are unable to lay egg capsules (Gibbs & Bryan, 1986). At the time of this study the animals at Whitsand Bay were at the "intermediate" stage (Gibbs & Bryan, 1986) so that some reproductive success was still possible.

Whitsand Bay in South Cornwall (plate 1) was chosen as the site for all fieldwork and the collection of animals for laboratory experiments. The bay stretches approximately 7.5km from Portwrinkle (National Grid reference SX 360538) in the west to Queener Point (National Grid reference SX 415490), (Fig. 1). It is a south-west facing sandy beach enclosed by high cliffs of Dartmouth Slate of lower Devonian origin with outcrops of near vertical rock protruding from the sand. The outcropping rocks have a south-east facing side that is sloping, generally smooth, with a dense cover of *Mytilus* and a few adult *Nucella*. The north-west facing side is nearly vertical, more ragged,
Figure 1. Map showing location of Whitsand Bay, Cornwall.
has considerable gaps in the mussel bed and has a higher density of *Nucella*, both young and adult. Egg capsules are almost exclusively laid on this north-west facing side and it supports a greater variety of marine life. Appendix 7 provides a list of the most abundant species found within the *Nucella* zone.

2.3 Experimental Systems

2.3.1 Continuous Immersion System

Most of the experimental laboratory work was carried out in a system of recirculating sea-water in which the animals were continuously submerged. This will be referred to as the "continuous immersion system" (Fig. 2).

Circulation and cleansing were maintained by an Eheim external filter and power unit (model 1026, Peter Golding Ltd.) with an output of 12 litres per minute. Four experimental tanks, white plastic trays of dimensions 650mm x 390mm x 155mm, were set up with parallel circulation. Each tank had an input flow rate of approximately 0.8 litres per minute, providing a complete change of water every 30 minutes. A temperature of 15°C, equivalent to summer and early autumn sea temperatures in south-west England (section 3.4), was maintained using two channels of a triple coil icebank cooler (model 20116, M.K. Refrigeration) and a 200 watt immersion heater controlled by a separate electronic thermostat (C. Ellson & Co. Ltd.).

The system was filled with natural sea-water from Plymouth Sound which was maintained at 34% by dilution. The water was completely renewed at approximately two monthly intervals.

As the continuous immersion system was housed in a general laboratory no attempt could be made to control day-length. The laboratory lighting most closely approximated to a summer regime.
Figure 2. Diagram of continuous immersion system.
2.3.2 Experimental Arenas

From the outset it was felt desirable to be able to determine individual responses to an experimental situation. Therefore containers for individuals were needed within the experimental tanks. Since I was concerned with snails from 1mm hatchlings to 30mm adults the nature of the containers had to be suited to the size of the predator and its prey. Two types of containers were used.

i) For hatchlings

In experiments the hatchlings were accommodated in individual wells of a multi-well plate. From hatching to 4mm length a 96 well, flat bottomed plate (Sterilin Ltd.) was used. Each snail and its prey were contained in a cylindrical compartment 7mm diameter by 8mm high. The animals were prevented from escaping by a fine mesh gauze held in place by a tightly fitting perspex frame. Only every alternate compartment, both horizontally and vertically, was used. The entire apparatus was submerged in the experimental tank below the inlet to encourage water circulation within each well. Although this system was successful for very small snails and prey, once the mussels were 4mm length they could move from one compartment to another. Therefore the apparatus was modified by replacing the gauze top with a 3mm thick sheet of perspex drilled with 13 holes (0.5mm diameter) over each experimental compartment (Fig. 3). This system prevented escape but caused higher mortality among the young Nucella.

ii) For juvenile Nucella

Individuals above 4mm in length were housed in a cylindrical container which was made from two 50mm diameter plastic petri-dish bases acting as lid and base to a 50mm high tube of stiff plastic gauze. Where 5mm Nucella or Mytilus were involved the tube was made from nylon filter gauze (Henry Simon Ltd.) with a mesh size of 1mm.

-16-
Figure 3. Isometric exploded drawing of apparatus used to house hatchling *Nucella* in feeding experiments.
The cut edges of the gauze were sealed with silicone rubber sealant (Dow Corning) and sewn into a tube. For all larger animals green plastic Netlon with a mesh size of 3mm formed the body of the cylinder. These "pots" allowed free circulation of water, provided a surface suitable for snails to walk on and for mussels to attach to. Observation was easy through the transparent lids. A clear glass microscope slide placed on top stopped them floating. In one experiment, where 60mm mussels were involved, large pots of the same basic design were constructed using the bases of 85mm diameter petri-dishes, and Netlon sewn into a tube 46mm high. Apart from life history individuals (appendix 1) there were no mortalities of whelks within any of these pots.

2.4 Measurements

The length of mussels was taken as the maximum anterio-posterior dimension of the shell and the size of whelks as the length of the shell between the apex and the tip of the siphonal canal. These measurements were recorded to within 0.1mm using vernier calipers. Initial size classes quoted below are all ± 1mm, with the exception of 60mm mussels, which were ± 2mm, because of their scarcity at Whitsand Bay. Weighings of mussel flesh were carried out using a Sartorius electronic balance to within 1mg.

2.5 Analysis

Most of the statistical analyses were performed using Minitab release 5.13 on a Prime mainframe. Where other statistical packages were used these are referred to in the text.
CHAPTER 3 DISTRIBUTION AND GROWTH OF NUCELLA ON THE SHORE

3.1 Introduction

Age-specific differences in the vertical distribution of *N. lapillulus* on the shore have been reported in the literature. Moore (1938b) found that although capsules were laid at the same level as adults (from MTL to MHWN) the youngest animals occurred at much lower levels, around MLWS. Following emergence from the capsule hatchlings were thought to be washed downshore by water movements, where they remained to feed and grow, migrating upshore to the adult zone at a size of 8 to 10mm.

In contrast Feare (1970a) found hatchlings at the same shore level as adults, where they remained for their first winter. In the following summer the juveniles were reported to migrate upshore and return to their original level during their second year. The upshore migration of juvenile whelks had the effect of protecting the vulnerable small size groups from crab predation.

A contradictory age-related distribution pattern was observed by Coombs (1973). *Nucella* of less than 16mm were generally found at lower tidal levels than larger whelks and were thought to migrate back upshore at about one year old. Coombs related this pattern to the observation that small whelks, although more tolerant of fluid loss, lost water more rapidly than adults. The natural zonation levels were thought to reflect the age-dependent ability of the whelks to withstand exposure to desiccating conditions.

A year long sampling programme was conducted at Whitsand Bay with the aim of detecting seasonal and size-specific changes in the density of *N. lapilllus* in relation to its vertical shore position.

For the same rocks the temporal and spatial distribution of egg capsules were monitored to identify possible movement patterns of the
young snails following hatching. Some preliminary behavioural studies were conducted on newly hatched Nucella and related to their observed distribution on the shore.

There are few reports in the literature of the growth of N. lapillus on the shores of the British Isles, although some measures originate from the east coast of North America (Colton, 1916; Hughes, 1972; Osborne, 1977). In Britain Moore (1938a) estimated growth of marked second year individuals both in Plymouth Sound and at Port Erin, but due to the difficulties of recovering small snails, estimates of growth for first year whelks were made in the laboratory. The major work on field growth rates comes from that of Feare (1970a) at Robin Hoods Bay, Yorkshire, in which, owing to the restricted breeding season, growth rates were estimated from successive size-frequency distributions.

Growth rates of marked Nucella at Whitsand Bay were monitored for a period of one year to provide a basis of comparison with previous reports and with rates obtained in laboratory conditions (section 4.3).

3.2 Field Surveys at Whitsand Bay

3.2.1 Methods

3.2.1.1 Sampling design for occurrence of Nucella and mussels

The sampling programme was subject to two constraints. First the sampling had to be destructive, because although adult Nucella were generally clearly visible in or on the mussel bed, or aggregated in rock crevices the young were often found within or beneath the mussel bed. Removal of the entire mussel mat and underlying sand necessarily limited the area that could be removed without severely affecting the remaining ecosystem. Second the sampling had to be achieved within the two hours that the base of the rocks was exposed at spring low tides and as live animals were required, the initial processing of the samples had to be completed within a maximum of two days from the time...
of collection.

The two rocks that were selected for the survey lay just to the east of Sharrow Point, National Grid reference SX 393521), a promontory that lies about mid-way along Whitsand Bay (Fig. 4). The rocks themselves (plate 2) provided the following advantages. They were low on the shore and each was isolated being surrounded by sand thus the migration of Nucella from neighbouring areas was limited. They were fairly inaccessible and thus unlikely to be disturbed by the holidaying public. The rocks were of similar size, position and orientation to the sea, and together provided an area sufficient for the sampling requirements. On both rocks there was a high density of egg capsules and so, presumably, young Nucella.

Samples were taken from five vertical heights on the rock, the lowest being about 30cm above the base of the mussel bed and the uppermost one being above the limit of Nucella, as determined from a preliminary sampling exercise carried out in November 1984. This allowed for 5 sampling heights each 30cm apart, ranging approximately from just below MLWN to just above MLL. Six replicate transects (A-F) were set up (A, B & C on one rock, D, E & F on the other) providing thirty samples in all (Fig. 5). The rocks were not homogeneous along their length, thus in order to eliminate confounding the effects of horizontal rock position and time of year the sampling was randomised. Each transect was considered to be made up of a 5x5 spatial array, the (i) variable being the vertical height and the (j) variable being the horizontal position. The ij position from which each monthly sample was taken was determined by the randomised latin square technique. Thus over each five month period, each level(i) would be sampled from each horizontal area of rock(j). Each ij position contained three sampling sites, random number tables were used to select the order in
Figure 4. Map showing location of rocks from which samples were taken at Whitsand Bay.
Plate 2. View of sample rocks from the cliff top, Whitsand Bay. (Note footprints in the sand for scale).
Figure 5. Sampling positions on one rock (transects A, B, & C) at Whitsand Bay.
which these three should be taken. Each transect and each set of three was randomised separately.

A theodolite was used to equalise heights along the length of each rock and between rocks. Owing to the shifting nature of the sand permanent markers were required. At both ends of each transect and at each height nails were driven into the rock wherever possible, and the position marked with brightly coloured paint.

To locate the position on the rock from which the sample was to be taken, a string 5m long, with numbered tags every 30cm was attached to the nails. Although the rock surface showed considerable irregularities the method proved to be sufficiently accurate and robust.

3.2.1.2 Treatment of samples

Each sample consisted of the area contained within a 10 x 10cm quadrat. Broadly speaking there were four types of surface covering; mussels, *Balanus perforatus* Bruguiere, small barnacles and bare rock. Areas of mussels or *B. perforatus* were cleared completely whereas patches of small barnacles and bare rock were searched for inconspicuous individuals, particularly those located within empty barnacle shells. Samples were removed with a trowel, care being taken to minimise damage to the individual mussels. Underlying sand was also collected and the whole transferred to polythene bags, returned to the laboratory and stored at 10°C until processed.

Each sample was washed under a continuous flow of tapwater into a 2mm sieve underlain by a 0.5mm sieve. The mussels were washed free of sand and the byssus threads broken. The contents of the 2mm sieve were examined and the following noted for each sample. The wet weight of *Mytilus* and *Balanus perforatus*. The length (to nearest 0.1mm) of all live and dead *Nucella*. The length (to nearest 1mm) of all dead and...
drilled whole and half Mytilus shells, and similarly the length of all dead and undrilled whole and half Mytilus shells. The number of Mytilus shell fragments with a drill hole, and the frequency with which complete Mytilus shells had a single drill hole, or a drill hole on each valve of the shell.

The drilled Mytilus shells were saved for bore-hole size analysis (see section 6.4). The thirty samples for each month were processed in this way within 48 hours of collection. The contents of the 0.5mm sieve were transferred to small labelled petri-dishes, covered in a fine gauze and placed in the continuous immersion system (section 2.3.1). Within a further two days these samples were searched using a binocular microscope for the presence of small live and dead Nucella. No sub-sampling was employed throughout.

3.2.1.3 Mapping of Nucella egg capsules

Mapping of Nucella egg capsules on the Whitsand Bay sampling rocks was carried out at roughly two monthly intervals beginning in early March 1985 continuing until February 1986. No sampling was possible in January 1986 as high seas prevented access to the rocks. The area mapped included all the sample area plus 30cm above level five, 30cm below level one and 1m out from the edges of transects A, C, D & F, providing an area of approximately 61m².

Egg capsules are laid in fairly discrete clusters, an egg capsule site was defined subjectively as a group of egg capsules that were moderately continuous. The following characteristics of each egg capsule site were noted; the number of capsules per cluster, where capsules were in inaccessible positions or covered by adult whelks an estimate of the number was made. The number of capsules from which the young had hatched, characterized by the lack of an apical plug and a complete loss or reduced number of visible young within the capsule.

-26-
Thirdly, the co-ordinate position of the centre of each cluster, defined in relation to the vertical level and horizontal distance along each transect as established for the monthly sampling programme (section 3.2.1.1).

Following the report of reproductive failure in female Nucella caused by tributyltin contamination (Gibbs & Bryan, 1986), egg capsule numbers on the same rocks at Whitsand Bay were determined for September and November 1987.

3.2.2 Results

Sampling continued from February 1985 to February 1986 with the omission of January 1986 when high seas prevented access to the rocks. On most occasions it was possible to acquire all samples, however the data for transect B were incomplete owing to spring and autumn storms washing away the sand at the base of the rock and also to the nature of the rock at that transect which presented a slight overhang.

3.2.2.1 Live Nucella

The mean number of live Nucella per 100cm² sample was 2.54, variance 13.35, indicating the aggregated nature of the population. Of the 334 samples taken a high proportion (38%) had no live Nucella thus in all the analyses the data from the replicate transects were pooled. Even so, the counts were still too low and variable to permit the analysis of interaction between the three variables of interest: level on the shore, month and Nucella size. General trends could only be elucidated when data from either one or two of these variables were pooled.

As Nucella cannot easily be aged (but see Feare, 1970a; Berry & Crothers, 1968; Coombs, 1973), the present work was concerned solely with the sizes found. The size frequency distribution of all live Nucella (Fig. 6) illustrated that although there were large numbers of hatchlings the numbers in each mm size category remained relatively
Figure 6. Size frequency distribution of all live *Nucella* (*n* = 847) found in 334 samples collected from Whitsand Bay for the period February 1985 to February 1986, (mm size class categories).
stable until the adult size was reached. A linear combination of size classes was unsatisfactory for the present analysis since the emphasis was put on the adults, so an exp 0.6mm size class interval was employed, giving the categories:

<table>
<thead>
<tr>
<th>size class (mm)</th>
<th>size range (mm)</th>
<th>approximate stage of life</th>
</tr>
</thead>
<tbody>
<tr>
<td>$e^0 - e^{0.6}$</td>
<td>1.0 - 1.8</td>
<td>hatchlings</td>
</tr>
<tr>
<td>$e^{0.6} - e^{1.2}$</td>
<td>1.9 - 3.3</td>
<td>post-hatchlings</td>
</tr>
<tr>
<td>$e^{1.2} - e^{1.8}$</td>
<td>3.4 - 6.0</td>
<td>young 1st. years</td>
</tr>
<tr>
<td>$e^{1.8} - e^{2.4}$</td>
<td>6.1 - 11.0</td>
<td>older 1st. years</td>
</tr>
<tr>
<td>$e^{2.4} - e^{3.0}$</td>
<td>11.1 - 20.0</td>
<td>2nd. years</td>
</tr>
<tr>
<td>$&gt; e^{3.0}$</td>
<td>$&gt; 20.0$</td>
<td>adults</td>
</tr>
</tbody>
</table>

This provided (Fig. 7) a more even distribution of frequencies within each size class with the emphasis on the young. The age of the size classes approximate those found by Feare (1970a). These size classes are generally used throughout the following discussion.

The total number of live *Nucella* (Fig. 8) was relatively constant for the months February to June with an increase in July and particularly in August. The seasonal effect on the size-frequency distribution of the three smallest size groups (Fig. 9) showed that although trickle hatching occurred throughout the year the peak of hatching was between July and August.

The numbers found at each level illustrated a peak in the middle of the sampling range (level three) and although samples could not be taken lower than level one owing to sand cover, at the upper region adult *Nucella* were seen to occur above the highest sampling level so this does not represent the upper limit of their vertical range.

Both size and level on the shore significantly affected the distribution of all live *Nucella* for all months combined. While the
Figure 7. Size frequency distribution of all live Nucella (n = 847) found in 334 samples collected from Whitsand Bay for the period February 1985 to February 1986, (e0.6 mm size class categories).

Nucella size classes:

1 = 1.0 - 1.8 mm
2 = 1.9 - 3.3 mm
3 = 3.4 - 6.0 mm
4 = 6.1 - 11.0 mm
5 = 11.1 - 20.0 mm
6 = > 20.0 mm
Figure 8. Seasonal variation in the numbers of live Nucella found in samples from Whitsand Bay. (Transect B has been omitted to equalize number of samples for each month).
Figure 9. Seasonal variation in the numbers of live *Nucella* in the three smallest size classes, sampled from Whitsand Bay.
two smallest size classes peaked at level two (Fig. 10), all larger whelk size groups peaked at level three. There was a significant difference in the vertical distribution of whelks smaller than 3.3mm and those larger than 3.3mm (Kolmogorov-Smirnov test, $D_{\text{max}} = 0.12$, $P<0.005$).

At all times of year the whelks were not dispersed at random (Fig. 11a). Seasonal changes in Morisita's index of dispersal indicated that for all sizes combined the individuals were less aggregated in the summer than in the winter. Since hatchlings originate from a point source their distribution is forced to be aggregated, with removal of hatchlings (whelks < 1.9mm) from the calculation, the seasonal trend becomes more apparent (Fig. 11b).

3.2.2.2 Dead Nucella

Over 40% of all samples contained one or more dead Nucella. During the winter and spring the numbers of dead Nucella found were generally low, death of hatchlings in August and post-hatchlings in September and October (Fig. 12) contributed largely to the increase in numbers of deaths in late summer and early autumn.

The ratio of dead : dead + alive Nucella was consistent for levels one to four but rose slightly at level five (Fig. 13a). Size dependent death was fairly constant from 1-11mm, declining sharply for whelks larger than 11mm (Fig. 13b) and the seasonal trend (Fig. 13c) can be accounted for by the high mortality of hatchlings.

3.2.2.3 Drilled Mytilus

For each sample the size frequency distribution of drilled mussel shells and drilled half shells was noted. Since it was not known how frequently a mussel would be drilled on both valves it was necessary to establish the likelihood that a single mussel valve with a drill hole was the result of only one predation event. One thousand complete
Figure 10. Distribution of live *Nucella*, classified according to size, in relation to shore level at Whitsand Bay, (level 1 is the lowest shore level).

*Nucella* size classes:

- O-----O 1.0 - 1.8 mm
- •-----• 1.9 - 3.3 mm
- △-----△ 3.4 - 6.0 mm
- ▲------▲ 6.1 - 11.0 mm
- □------□ 11.1 - 20.0 mm
- ●-------● > 20.0 mm
Numbers live Nucella

Shore level

-34-
Figure 11. Seasonal variation in Morisita's index of dispersion for samples collected from Whitsand Bay.

a) for all live *Nucella*

b) for live *Nucella* >1.9 mm.
Figure 12. Seasonal variation in the number of dead *Nucella*, in the three smallest size classes, sampled at Whitsand Bay.
Figure 13. Proportion of dead *Nucella* to total *Nucella* found in all samples from Whitsand Bay in relation to a) shore level, b) *Nucella* size, c) month of year. (*Nucella* size classes as defined in figure 7).
shells with at least one hole, collected from the field, yielded only 4.7% with a drill hole on both valves, so levels of predation are taken to be the numbers of complete and half shells combined. The number of drilled mussels per level closely reflected the number of Nucella present (Fig. 14a). The most frequent size class was 21-25mm (Fig. 14b).

While large drilled mussels (>25mm) were evenly distributed between the five shore levels (Fig. 15), small (<16mm) mussels were found significantly more frequently at lower levels than medium-sized mussels (16-25mm), (Kolmogorov-Smirnov test, $D_{max} = 0.151, P<0.001$). The mean wet weight of mussels per sample, for all transects and all months combined (Fig. 16) increased linearly with height on the shore. The number of drilled mussel shells per kg wet weight of mussels was calculated as an approximate index of predation pressure. On a seasonal basis, feeding pressure was highest in May, declined through the summer and rose again in autumn (Fig. 17a). Feeding intensity was high at levels one and two and fell sharply with increasing height on the shore (Fig. 17b).

3.2.2.4 Egg capsules

The seasonal occurrence of egg capsules at each shore level are given in figure 18. Since capsules remain on the rocks for 3-4 months between being laid and hatching (Pelseneer, 1935) data for successive bi-monthly samples overlap to some extent. Unfortunately only transects A, B & C were counted in July, but as the numbers found at each level agreed closely with those found in the same transects in September, it can be considered that the overall trend for July would have reflected that for September.

With the frequencies re-scaled to account for the number of transects taken (Fig. 19) it can be seen that a major spawning occurred
Figure 14. Total number of drilled mussel shells sampled from Whitsand Bay for the period February 1985 to February 1986, according to a) shore level (dashed line is the distribution of live Nucella, and b) mussel length.
Figure 15. Distribution of all drilled mussel shells, classified according to size, in relation to level on the shore. (Figures to the right of each line refer to mussel length in mm).
Figure 16. Effect of shore level on the mean (+ S.E.) wet weight (g) of mussels per 100cm² sample, collected from Whitsand Bay, for all months combined. (Each point is the mean of ≥ 60 samples).
Figure 17. a) Seasonal variation in the mean number of drilled mussel shells per kg wet weight mussel bed, for all levels combined, collected from Whitsand Bay.
b) Effect of level on the shore on the mean number of drilled mussel shells per kg wet weight mussel bed, for all months combined, collected from Whitsand Bay.
Figure 18. Seasonal variation in the occurrence of *Nucella* egg capsules on the sample rocks at Whitsand Bay, in relation to height on the shore. (Level 1 is the lowest shore level).
(number of transects counted)

- Total egg capsules
- Number hatched

Shore level

March 1985
May 1985
July 1985
September 1985
November 1985
February 1986

Number egg capsules

[Graph showing data for different months and years]
Figure 19. Seasonal changes in the number of egg capsules counted on an area of 61m² of rock at Whitsand Bay. Numbers have been adjusted to take account of the number of transects counted.
between early May and early July, by early September most of these capsules were empty. Between early September and early November another major spawn had taken place, with spawning continuing throughout the winter, and by February 1986 roughly a third of the autumn spawned capsules had hatched. The discrepancy between the March 1985 and February 1986 data suggest a similar large spawn did not occur in the autumn of 1984.

The proportion of capsules at each level indicated that the spring spawn was low on the shore (in May more than 95% of capsules were below level three) with spawning sites becoming progressively higher on the shore as autumn approached. By November, when a major new spawning had been initiated, less than 34% of capsules were below level three.

Egg capsule numbers in September 1987 were one sixth of those found in September 1985, and in November 1987 the number of capsules represented only 4% of the number found in November 1985 (Fig. 19).

3.2.3 Discussion

In common with other *N. lapillus* populations (Feare, 1970a; Hughes, 1972; Crothers, 1985), when considering the population larger than 5mm, the largest size classes were of highest frequency, suggesting high juvenile mortality and longevity of adults. Age specific mortality rates, calculated as the number dead as a percentage of total whelks in each size group, were consistently lower than those determined by Feare (1970a) from counts of survivors in successive years;

<table>
<thead>
<tr>
<th></th>
<th>Present study</th>
<th>Feare</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st. year mortality</td>
<td>37.5%</td>
<td>&gt;90%</td>
</tr>
<tr>
<td>2nd. year mortality</td>
<td>11.5%</td>
<td>52%</td>
</tr>
<tr>
<td>3rd+ year mortality</td>
<td>0.4%</td>
<td>27%</td>
</tr>
</tbody>
</table>

However the present study recorded only those whelks that died and
remained within the mussel bed, no account was taken of whelks washed off the rocks by wave action or taken in predation.

Hatchling survival can be estimated from the observed density of live hatchlings and observed density of hatched egg capsules, taking a mean of twelve live embryos per capsule (section 2.1.1). Within approximately the first month of life, of those potentially present, 90.0% of hatchlings died in September 1985 and 90.2% in February 1986 (table 1). Since Feare's (1970a) estimate of first year mortality did not account for hatchling mortality during the first two months of life, overall mortality during the young juvenile stages must considerably exceed 90%. The observed density of dead hatchlings in the samples accounted for only 3% in September and 2.7% in February of all hatchlings potentially present. Combining the observed dead with those found alive results in the majority of hatchlings (87% in September and 87.5% in February) unaccounted for. Their most likely fate was that they were washed off the rocks, either into the sand or into the sea. Additionally the polychaete **Eulalia viridis** (Muller), common on the mussel beds at Whitsand Bay and reported to prey upon capsule contents (Feare, 1970a), may have contributed to hatchling mortality.

Juvenile *Nucella* shells were often found deep within the mussel mat, sometimes entangled by byssus threads, but there was no evidence that this provided a significant source of mortality for adults as suggested by Petraitis (1987). Complete drill holes indicated that some deaths of juveniles could also be attributed to intra-specific predation. Damaged juvenile shells, indicative of crab predation (Feare, 1969), were not found in the mussel bed samples suggesting that although juvenile *Carcinus maenas* (L.) were present they did not contribute significantly to the mortality of juvenile *Nucella*.

-46-
<table>
<thead>
<tr>
<th></th>
<th>Sept.'85</th>
<th>Feb.'86</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number observed egg capsules in $61.2m^2$</td>
<td>13089</td>
<td>6881</td>
</tr>
<tr>
<td>Number potential live embryos hatched</td>
<td>157068</td>
<td>82572</td>
</tr>
<tr>
<td>\hspace{1cm} (at 12 embryos/capsule)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density of potential hatchlings/$m^2$</td>
<td>2566</td>
<td>1349</td>
</tr>
<tr>
<td>Number observed live hatchlings</td>
<td>77</td>
<td>33</td>
</tr>
<tr>
<td>Area sampled for hatchlings ($m^2$)</td>
<td>0.3</td>
<td>0.25</td>
</tr>
<tr>
<td>Density observed live hatchlings/$m^2$</td>
<td>257</td>
<td>132</td>
</tr>
<tr>
<td>Observed hatchling survival of all potential hatchlings (%)</td>
<td>10.0</td>
<td>9.8</td>
</tr>
<tr>
<td>Number observed dead hatchlings</td>
<td>23</td>
<td>9</td>
</tr>
<tr>
<td>Density observed dead hatchlings/$m^2$</td>
<td>77</td>
<td>36</td>
</tr>
<tr>
<td>Percentage of all potential hatchlings found dead</td>
<td>3.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Percentage of hatchlings unaccounted for</td>
<td>87.0</td>
<td>87.5</td>
</tr>
</tbody>
</table>

Table 1. Values used to estimate hatchling mortality.
Field observations provided evidence of adult mortality from at least two sources. Following severely stormy weather sand surrounding the rocks were strewn with adult *Nucella*. On one occasion approximately fifty such whelks were collected and returned to the laboratory, the majority were dead. Menge (1978a) similarly found wave shock to be a source of mortality for *N. lapillus* at exposed sites. On at least three occasions there was evidence of recent *Nucella* predation by birds. Groups of adult whelks (as many as forty), surrounded by bird footprints, were found turned over in the sand with their operculum and part of the body contents removed. This method of attack coincides with that of oystercatchers (Feare, 1971b) which were frequent visitors to Whitsand Bay from September to February in the winters of 1985-6 and 1986-7. Although adult *Nucella* were frequently seen with attempted drill holes in their shells, particularly noticeable in May 1985, only one was found that had completely penetrated, indicating that intra-specific predation was an unimportant source of mortality for adults.

Reports in the literature of the frequency and timing of spawning periods for *N. lapillus* accord in essence with the results presented here but differ in detail, possibly reflecting climatic variation between locations and from year to year. As at Whitsand Bay, some populations spawn throughout the year (Moore, 1938a; Pelseneer, 1935; Crothers, 1966), and the spring spawning occurred sometime between early May to early July, somewhat later than reported elsewhere; winter to spring (Moore, 1938a), from January to April (Pelseneer, 1935), in April and May (Feare, 1970b), end of February to late April (Boyden et al., 1977) and February to March (Crothers, 1974).

At Whitsand Bay the second autumn spawn, which occurred between September and November of one year, was as large as the spring spawn.
Similarly Crothers (1985) reported occasional spawning activity in August, Pelseneer (1935) quotes September and Moore (1938a) related a sharp drop in body dry weight between October and November to another possible major spawning period. From a histological study of the gonads, Feare (1969) noted that in each of two years Nucella displayed a second peak of gametogenesis, but it only resulted in a second spawning in July and August of one year. From this Feare (1969) suggested that the potential for a second spawning may only be realised when climatic conditions are suitable.

Capsules laid between May and July were almost all empty by early September coinciding with a peak in the number of juveniles present on the rocks in August. Thus development time within the capsule, for the spring spawning, was a maximum of three months, shorter than the four months quoted for temperate latitude whelks (Pelseneer, 1935, Feare, 1970a). Development time for the autumn laid capsules was longer, only 37% had hatched after a minimum of three months. The hatching of young Nucella in August coincided with the major mussel settlement at Whitsand Bay. Bi-monthly sampling of the mussel population on the other side of the rocks from which the Nucella were sampled here, shows that the main spat fall occurred between July and September (Fig. 20, data kindly supplied by C. Worrall, Plymouth Marine Laboratory). The temporal synchrony between Nucella hatching and mussel spat-fall results in there being an ample supply of young mussels for the newly hatched Nucella to feed on.

Annual female whelk fecundity can be estimated from the present data as the density of egg capsules for September and February combined (since these were two distinct spawns), divided by the density of adult whelks (>25mm). Assuming an equal proportion of males and females within the adult population, a value of twenty capsules per female per
Figure 20. Seasonal changes in the number of mussels of less than 5mm length occurring in a 0.15m² sample of mussel bed. Samples taken from the S.E. facing side of the rocks from which Nucella sampled in the present study at Whitsand Bay. (Data supplied by C. Worrall, Plymouth Marine Laboratory).
year was calculated. This estimate is considerably lower than one made in the last century of 200 capsules/female/year (Cooke, 1895, cited Colton, 1916) and is less than half of a more recent estimate of forty-seven capsules/female/year for a population in Nova Scotia (Hughes, 1972). This apparent reduction in fecundity may represent the beginnings of reproductive failure following exposure to tributyltin contamination (Gibbs & Bryan, 1986). The dramatic drop between 1985 and 1987 in the numbers of egg capsules laid on the shore supports the view of Gibbs (pers. comm.) that during this time the population of Nucella at Whitsand Bay was transitioning between the 'intermediate' and 'late' stages of imposex (Gibbs & Bryan, 1986).

Although throughout the year whelks show some degree of an aggregated dispersal pattern, this was most marked in the winter. Summer aggregations, of the type found by Feare (1971a) were not evident, probably due to the topography of the rock offering some protection from water movement. In Yorkshire the pre-breeding aggregation was found to merge with the non-feeding winter aggregation; egg capsules were laid between April and May and emergence from aggregation sites occurred in May and June (Feare, 1971a).

There was circumstantial evidence that the timing of these two events may differ in South-West England. In the present study the concomitant drop in the Morisita's index of dispersal and the rise in predation intensity occurring between mid-April and mid-May suggests that during this period whelks were emerging from their winter aggregation and commencing to feed. This apparent increase in activity was substantiated by field observations, which in early May noted that whelks were out and actively foraging. Yet at this time few egg capsules had been laid.

Two explanations can be forwarded. Firstly since female gastropods
are able to store sperm (Fretter & Graham, 1962; Palmer, 1984), they may be fertilized within the winter aggregation, undertaking a period of foraging before spawning. Alternatively the increase in foraging activity and reduction in the dispersal index may have been due to the activities of the males only, leaving the females within the aggregation sites to spawn. The latter explanation would seem the less energetically viable since it requires the females to expend their maximum reproductive effort at the end of a period of reduced feeding activity.

Although the present sampling programme covered a narrow vertical range compared to that inhabited by Nucella on other shores (section 2.1.1) some comments can be added to observations cited in the literature concerning developmental changes in the vertical distribution of this whelk.

There was no evidence to support the view that first year whelks migrate upshore of the adults as shown by Feare (1970a) at Robin Hood's Bay, or that they are found lower on the shore than adults as at Blackrock, Sussex (Coombs, 1973). At Whitsand Bay the only significant age-specific difference in vertical distribution was that small Nucella (<3.3mm) were found lower on the shore than all larger whelks. Movement of hatchlings following emergence from capsules can be inferred from data concerning the spring spawn. The relative abundance of hatchlings (<3.3mm) at a given level in the July and August 1985 samples combined, most closely reflected the number of hatched capsules in September 1985 in the area immediately above that level (Fig. 21).

The present results can be interpreted in the same way as the observations of Moore (1938b) (section 3.1), that newly hatched whelks are washed to lower levels, and crawl upshore at a later period. However, whereas Moore believed the snails to be 8 to 10mm when they
Figure 21. Effect of shore level on the number of *Nucella* hatchlings (3.3mm) found in samples for July and August 1985 combined, and the number of hatched egg capsules in September 1985 sampled at the same rocks at Whitsand Bay. (Number of hatchlings were surveyed at each level and number of egg capsules between levels).
migrated upshore, here all snails larger than 3.4mm had the same centre of distribution. A similar shore-level size gradient was found at Rhossili (appendix 4) where small whelks (<7mm) formed a greater proportion of the population at low tidal levels than at high tidal levels. Since hatchlings display negative phototactic and negative geotactic responses (section 3.3), their behavioural characteristics tend to ensure that they regain height on the shore and lead them into crevices, protected from water movement.

3.3 Behaviour of Hatchlings in the Laboratory

3.3.1 Method

A limited series of experiments were carried out to monitor the movements of individual unfed hatchling N. lapillus in an artificial environment. Capsules containing ripe embryos were collected from Whitsand Bay and maintained in the continuous immersion system (section 2.3.1). Within three days of emergence hatchlings were removed, their shells allowed to dry and marked with coloured felt tip pens to facilitate tracking of individuals. Each hatchling was placed in the centre of a square plastic dish (43cm x 43cm) containing sea water to a depth of approximately 12mm. The transparent dish overlay mm graph paper so that the co-ordinate position of the hatchlings could be monitored.

The position of hatchlings were recorded at regular intervals (either every 2 or 5 minutes) until they reached the edge of the tray or became quiescent. To ensure that hatchling behaviour would not be affected by the vicinity of others, single individuals were added to the experimental arena only when all others were at least 15cm from the centre of the tray. Three ambient temperatures were employed (18°C, 21°C and 24°C), and at 21°C, two light regimes, non-directional and directional light.
3.3.2 Results

In all the movements of twenty-seven individuals were monitored, divided between the different temperature and light regimes as follows:

<table>
<thead>
<tr>
<th>Temp. °C</th>
<th>Non-directional light</th>
<th>Directional light</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n individuals</td>
<td>time-interval</td>
</tr>
<tr>
<td>18</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>21</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>24</td>
<td>8</td>
<td>2</td>
</tr>
</tbody>
</table>

Following transference to the centre of the dish most animals (n=16) had moved by the first reading, the others remained quiescent for between two and thirty minutes (mean = 7 minutes, S.D. = 5.3). A Fortran program was written to convert the successive co-ordinate positions into length of walk and angle of turn between successive time intervals (appendix 8).

For each whelk the mean rate of crawling and the mean angular deviation was found for the period between the start of movement to either arrival at the edge of the dish or until the animal became inactive. The mean rate of movement was not affected by temperature within the range used here nor upon the presence of directional or uni-directional light (table 2a & c). The overall mean rate of crawling was 6.4 mm/min (S.D. = 1.9) and on average it took the hatchlings 1 hour 5 minutes to reach the edge of the dish (range 30 minutes to 2 hours 15 minutes, depending on the tortuosity of path).

The tracking records of individuals at 21°C in non-directional light (Fig. 22) suggested that the path taken by the whelks was initially more tortuous than subsequently. Plots of angular deviations with time (Fig. 23) support this view, most individuals changed direction frequently during the first 15 minutes or so, after which the whelks followed a fairly straight path. The mean angular deviation was not
### Non-directional light

**a) Crawling rate (mm/min)**

<table>
<thead>
<tr>
<th>Temp. °C</th>
<th>mean</th>
<th>S.D.</th>
<th>n</th>
<th></th>
<th>mean</th>
<th>S.D.</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>5.8</td>
<td>1.5</td>
<td>9</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>21</td>
<td>7.2</td>
<td>1.3</td>
<td>6</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>24</td>
<td>6.0</td>
<td>2.6</td>
<td>8</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**b) Angular deviation (°)**

<table>
<thead>
<tr>
<th>Temp. °C</th>
<th>mean</th>
<th>S.D.</th>
<th>n</th>
<th></th>
<th>mean</th>
<th>S.D.</th>
<th>n</th>
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</thead>
<tbody>
<tr>
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<td>-</td>
</tr>
<tr>
<td>21</td>
<td>41.1</td>
<td>10.1</td>
<td>6</td>
<td></td>
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<td>17.1</td>
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</tr>
<tr>
<td>24</td>
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<td>12.8</td>
<td>8</td>
<td></td>
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<td>-</td>
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</tbody>
</table>

**c) t test to compare means**

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Crawling rate</th>
<th>Angular deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>d.f.</td>
</tr>
<tr>
<td>18°C Non vs 21°C Non</td>
<td>1.92</td>
<td>13</td>
</tr>
<tr>
<td>21°C Non vs 24°C Non</td>
<td>1.10</td>
<td>12</td>
</tr>
<tr>
<td>18°C Non vs 24°C Non</td>
<td>0.18</td>
<td>15</td>
</tr>
<tr>
<td>21°C Non vs 21°C Uni</td>
<td>0.14</td>
<td>8</td>
</tr>
</tbody>
</table>

**d) Final position of hatchlings**

<table>
<thead>
<tr>
<th>Temp. °C</th>
<th>above water</th>
<th>at air-water surface</th>
<th>still</th>
<th>became</th>
<th>quiescent</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>6</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>21</td>
<td>10</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<tr>
<td>24</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

Table 2. Effect of temperature and light regime on
a) the mean rate of movement (mm/min) and
b) mean angular deviation (°) shown by hatchling Nucella on a horizontal surface whilst submerged.
c) t tests to compare means (Non=non-directional light, Uni=uni-directional light).
d) Effect of temperature on the number of hatchlings found at different positions at the end of each experimental run.
Figure 22. Tracks of *Nucella* hatchlings released from a central point at 21°C in non-directional light. 

○ = position as noted at 2 minute intervals.
Successive readings at 2 min intervals

Figure 23. Successive angular (°) turns (readings taken at 2 minute intervals) of six Nucella hatchling individuals at 21°C in non-directional light, in the laboratory.
affected by the light regime but was significantly more tortuous at 24°C than at 21°C (table 2b & c). Unlike whelks at 21°C those at 24°C did not settle down to a straight path (Fig. 24) but continued to have a high rate of change of direction.

The final position of hatchlings are shown in table 2d. Only three individuals, all at 24°C, became quiescent on the base of the dish after a mean time of 1 hour 42 minutes. All other individuals (n=24) on reaching the edge of the dish crawled up the sides. Two whelks (both at 18°C) continued walking horizontally around the dish under the meniscus and were stopped more than three hours later. The most usual response however was to crawl straight to the air-water interface, where three individuals came to rest. The remaining nineteen hatchlings crawled above the surface of the water, surrounded by a drop of water and became inactive at a mean height of 8.7mm (S.D. = 4.2) above the water level. The ten individuals at 21°C that became quiescent above the water level were left over-night and their positions re-examined the following morning. None had moved and after re-immersion in sea water for a further six hours all were found to be dead.

Whereas in uniform light the individuals dispersed in random directions (Fig. 22) in directional bright light (provided by a sky light on a sunny day) the hatchlings showed a definite negative phototactic response (Fig. 25). When the directional light stimulus was removed the whelks undertook a more meandering path.

The observed tendency for the animals to show a negative geotactic response was tested on a separate batch of thirty newly hatched Nucella. The animals were transferred to the base of a 100mm high measuring cylinder containing sea water and their position noted at five minute intervals. After thirty minutes sixteen snails were at the
Sucessive angular (°) turns (readings taken at 2-minute intervals) of three Nucella hatchling individuals at 24°C in non-directional light in the laboratory.
Figure 25. Tracks of *Nucella* hatchlings released from a central point at 21°C in directional light. 
- ○ = position as noted at 2 minute intervals.
- †† = removal of directional light source.
top of the cylinder, nine were still climbing and five remained at the base. Those at the top came to rest either at the air-water interface or above the water level.

3.3.3 Discussion

The limited observations on the behavioural responses of newly hatched *N. lapillus* can be compared with a larger study on the closely related species, *Urosalpinx cinerea*, by Carriker (1957). As hatchlings both species showed a strong negative geotactic response, with a marked tendency to crawl through the meniscus and come to rest above the water level. As the film of water surrounding the animals evaporated, the animals retracted into their shells and died of dehydration. However Carriker found that the number of young drills that died following such emergent behaviour was greatly reduced if a heavily fouled substrate was substituted for glass or a lightly fouled shell. After 6.2 hours of exposure 71% of hatchlings survived on a heavily fouled surface compared with 100% death rate after three hours on glass. Thus on the shore, an intertidal surface overgrown with sessile organisms may retain sufficient moisture to prevent death of hatchlings by dehydration.

The observed emergent behaviour may be in response to continual immersion since Moore (1938a) reported that the emergent tendency of newly hatched *N. lapillus* was prevented if a tidal regime was supplied and that the duration of the tide was unimportant. Thus the emergent behaviour may be a reaction to prolonged immersion, exhibited for example by hatchlings in a rock pool or at sublittoral levels. When the animals crawl out of the water and dehydrate it is noticeable that they are difficult to re-sink. Conceivably on the shore, the return of the tide would have the effect of transporting the floating animals to different, and possibly more suitable, areas. Carriker (1957)
considered that hatchling *U. cinerea* could be dispersed great distances by floating on the surface film or attached to debris and similarly populations of *N. lapillus* may not be so isolated as has been previously thought (Berry & Crothers, 1968).

Carriker (1957) studied the behavioural response of newly hatched drills to directional light of differing light intensity. As with young *Nucella*, the young drills showed a negative phototactic response to the intense light of full outdoor illumination but were positively phototactic in moderate illumination. Thus on sunless days the combination of negative geotactic and positive phototactic responses would have the effect of directing the animals upshore, so that hatchlings washed downshore (section 3.2.3) have the potential to regain their original shore height.

In bright sunlight, with the concomitant dangers of dehydration, the negative phototactic response would direct the animals into the shade where conditions would also be more moist. The observed mean rate of crawling at 6.4mm/minute for young *Nucella* was similar to that of newly hatched *U. cinerea*, for which the mean rate of movement of the seven most active individuals was measured as 8mm/minute (Carriker, 1957). Without allowing for the topological complexities of the shore, at this rate the young whelks would be able to regain their downward vertical displacement (section 3.2.3) in under two hours, assuming immersion time to be 50% of total time. Since the upward crawling behaviour of young whelks only occurs when immersed, the length of time available to them for upward migration would be a negative function of their tidal height. Conceivably the combined effect of continually being washed downshore and crawling up again would be for the hatchlings to maintain an intermediate position on the shore.

In general the initial response of the young whelks following the
disturbance of being transferred to the experimental arena was to follow a zig-zag path as if sampling the environment, and then to follow a more direct path. A reduction in the amount of turning has the effect of taking animals more quickly into new areas, behaviour which has been shown to be associated with hunger in adult Nucella (Hughes & Dunkin, 1984).

The behaviour of hatchlings at 24°C differed from that at lower temperatures in that the animals turned more, it appeared that there was no reduction in the tortuosity of path with time and three of the individuals at the higher temperature became quiescent on the base of the tray. It is possible that at 24°C the hatchlings suffer heat trauma, Largen (1967b) having shown that adult Nucella became torpid at 25°C and entered heat coma at 27°C.

3.4 Field Growth Rates
3.4.1 Method

Growth rates in the field were estimated by monthly mark-recapture of uncaged N. lapillus on a specific rock complex at Whitsand Bay. The animals were first put out in September 1986 and a final collection made in October 1987. The rock complex, although not isolated, was separated by sand on all sides from other rocks, the nearest being about 30cm. The complex consisted of a vertical rock face (approximate dimensions 6m wide by 3m high) and an adjoining series of undulating rock ridges at one side (approximately 1.25m high by 2m wide).

The vertical distribution of encrusting organisms was typical of the rocks at Whitsand. Due to shifting sand the base of the rocks were largely devoid of marine life. The vertical rock face had a fairly continuous mussel bed about 1m deep, above which the remaining metre or so was barnacle encrusted. The tops of the rock ridges were largely mussel covered with barnacles and bare rock below. Resident Nucella
were largely found in or below the mussel bed zone and on the north-west facing side of the rock. Other species present were as described in appendix 7.

At the outset the whelks were given identification numbers using quick-drying cellulose paint but, due to abrasion in the field, these markings were not very permanent. So once the shells were large enough their numbers were engraved on the shell and paint applied in the grooves. Small specimens were gently filed to remove imbrications prior to painting. As the animals grew their numbers became obscured by the new growth and so fresh markings were applied to the outermost whorl.

An initial batch of 132 measured snails, ranging in size from 6.1 to 34.7 mm, were put out in September 1986 on the north-west facing side of the rock complex. Snails were placed on the rock at the beginning of low tide to allow them maximum time for attachment before the incoming tide threatened them with being washed off. As far as possible resident snails of a given size were replaced, into the same position, by numbered snails of a similar size.

During the following year the site was re-visited at monthly intervals, coinciding with spring tides. Each month a thorough search (a minimum of two man-hours) was made for the marked snails, concentrating on the north-west facing side but including also the south-east facing side and the surrounding rocks. Recovery of small snails was particularly low and, as they grew, the average size of the marked population increased. To maintain a wide range of sizes, each month an average of twenty-eight immatures were collected at the same time as the recaptures. Initially the immatures were taken from the rock complex, but as they became increasingly scarce, collections were made from other rocks at Whitsand. All animals were transferred to the
laboratory and maintained, without food, in the continuous immersion system (section 2.3.1).

In the laboratory recaptures were re-measured in length and re-marked. Individuals with undecipherable numbers were counted, their remaining paint removed and returned to the shore unmarked. New immatures were processed as for the initial batch.

All animals were returned to the field site within 48 hours of removal. Another intensive search was made of the rock complex and surrounding rocks (minimum of one man-hour) and newly recovered individuals measured and re-painted in the field. Snails were placed on the rock in positions typical of their size category. Total recaptures plus new individuals provided a minimum of 100 snails put out each month.

3.4.2 Results

Out of a total of 463 marked snails, 343 (74%) were recovered alive at least once. Only seven (1.5%) dead snails were found while sixty-one (13%) had to be removed from the experiment due to undecipherable markings. The majority of the snails were found on the first visit to the rock each month, out of a total of 1538 recaptures, only 125 (8%) were recovered at the second visit. A monthly breakdown of these figures is provided in table 3.

Immature snails (<15mm) were the most difficult to recover, not only because of their small size but also because of their tendency to live deep within the mussel bed. In contrast the adults were quite conspicuous, aggregating in crevices devoid of mussels, or when feeding, being on the surface of the mussel bed. As the year progressed the proportion of adults in the marked population increased, the majority of them being found each consecutive month.

On the whole recaptures were made from the area of rock complex
<table>
<thead>
<tr>
<th>Month</th>
<th>Total recovered</th>
<th>New young</th>
<th>Total out</th>
<th>Found after 48h</th>
<th>Found dead</th>
<th>Unclear markings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept.</td>
<td>-</td>
<td>-</td>
<td>132</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>70</td>
<td>39</td>
<td>109</td>
<td>8</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
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<td>117</td>
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<td>0</td>
<td>3</td>
</tr>
<tr>
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<td>111</td>
<td>14</td>
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<td>2</td>
</tr>
<tr>
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<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Feb.</td>
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<td>10</td>
<td>107</td>
<td>8</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
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<td>109</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Apr.</td>
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<td>25</td>
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<td>0</td>
<td>4</td>
</tr>
<tr>
<td>May</td>
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<td>19</td>
<td>139</td>
<td>12</td>
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<td>7</td>
</tr>
<tr>
<td>June</td>
<td>143</td>
<td>23</td>
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<td>1</td>
<td>4</td>
</tr>
<tr>
<td>July</td>
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<td>28</td>
<td>171</td>
<td>13</td>
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<tr>
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<td>25</td>
<td>195</td>
<td>11</td>
<td>1</td>
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<td>6</td>
</tr>
<tr>
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<td>-</td>
<td>-</td>
<td>6</td>
<td>0</td>
<td>2</td>
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</tbody>
</table>

Table 3. Summary of the numbers of Nucella individuals used to determine growth rates on the shore at Whitsand Bay for the period September 1986 to October 1987.
where they had been put out but each month about ten (mainly adult) snails were found on the other side of the rock and there were always a few, about five, snails found on surrounding rocks. Occasionally recaptures were made from more distant rocks, one from 22m distance, one from 40m and one from a rock 150m away to the east.

Increase in shell length plotted as a function of initial size for September to October 1986 (Fig. 26) was distinctly humped, consistent with a sigmoid growth function, however for other months (Fig. 27) the relationship was more nearly linear, possibly due to the recovery of fewer small snails. In each month there were some snails that did not grow and others, more noticeable in the winter, that showed negative growth as a result of erosion of the shell apex.

From mid-December through to mid-April animals larger than 25mm did not grow, as illustrated by the January to February sample in figure 27. Growth of snails greater than 25mm commenced in the period April to May and continued through the summer and autumn. During the period mid-July to mid-August mean growth rate of snails larger than 25mm was 0.6mm/month (n=70, S.D.= 0.45).

The monthly mark-recapture data was used to estimate the growth parameters $L_\infty$, a constant representing the asymptotic length, and $K$, a constant representing the rate at which the asymptotic length is approached, for the von Bertalanffy, logistic and Gompertz growth equations (Yamaguchi, 1975; Ricker, 1979; Causton, 1983).

From the non-sigmoid von Bertalanffy growth equation the instantaneous growth rate at a given size can be given by

$$\frac{dL_t}{dt} = K L_\infty - K L_t$$

where $L_t$ is size at time $t$. Thus instantaneous growth rate is a linear function of size with slope $-K$ and intercept $KL_\infty$. For the logistic growth equation, the instantaneous relative growth rate at a given size
Figure 26. Growth (mm/month) of *Nucella* individuals in relation to initial length, on the shore at Whitsand Bay for the month September to October 1986.
Figure 27. Effect of season on the growth (mm/month) of *Nucella* individuals in relation to initial length, on the shore at Whitsand Bay.
is given by

$$\frac{dL_t}{L_t} \, dt = K - \left( \frac{KL_t}{L_\infty} \right)$$  \hspace{1cm} \text{eqn 2}

thus instantaneous relative growth rate is a linear function of size with slope $-\frac{K}{L_\infty}$ and intercept $K$. From the Gompertz growth equation, instantaneous relative growth rate is a linear function of \ln size

$$\frac{dL_t}{L_t} \, dt = K \ln L_\infty - K \ln L_t$$  \hspace{1cm} \text{eqn 3}

with slope $-K$ and intercept $K \ln L_\infty$.

As an approximation, the instantaneous growth rates were taken as the observed growth rates based on the increments in length between two successive months. No account was taken of the differing number of days within an observation period (range 27-30 days) or that a few whelks were measured on the second visit to the shore each month. For each month separately, least squares regression analysis was used to determine the growth parameters $K$ and $L_\infty$, for each of the three growth equations using the relationships defined in equations 1 to 3. The initial marking of snails took several days to complete, during which time the snails were starved. Considering that a longer period of starvation would affect subsequent growth rates in the field, data for September to October 1986 have been omitted.

For each month the correlation coefficients were consistently higher for the sigmoid logistic and Gompertz growth equations than for the von Bertalanffy model (Fig. 28). For each month the estimated asymptotic length was largest under the von Bertalanffy model and smallest using the logistic growth equation (Fig. 29), although all values fell within the range 25 to 32mm. From the size frequency distribution (Fig. 6) the most common adult size was 28mm, which was more consistent with the values derived from the Gompertz and logistic equations, where the average asymptotic length for each month was used to derive overall means of 28.5 and 27.5 mm respectively.

-71-
Figure 28. Monthly correlation coefficients for the relationships described by equations 1 to 3 used to fit growth equations to observed growth of *Nucella* on the shore at Whitsand Bay.

Growth equations:

- **von Bertalanffy**
- **Gompertz**
- **logistic**
Figure 29. Monthly estimates of asymptotic length provided by equations 1 to 3 from growth equations used to describe growth of *Nucella* on the shore at Whitsand Bay.

Growth equations:

- ○ ○ von Bertalanffy
- □ □ Gompertz
- △ △ logistic
Each model provided the same seasonal pattern in the growth parameter $K$ (Fig. 30). Distinctly lower growth rates were found for the period mid-January to mid-April. There was a sharp rise in growth rates between April and May, reaching a peak from mid-June to mid-August. The three months with the lowest values of $K$ coincide with those of lowest correlation coefficient for the relationships defined in equations 1 to 3.

A comparison can be made between the calculated values of $K$ and environmental temperature (Fig. 31). Sea temperatures were kindly supplied by staff of the City of Plymouth Environmental Health Officer. The temperature of the water in Plymouth Sound is taken two or three a week at a depth of approximately 2 metres at the end of the outer pier at Millbay Docks, some 8km from Sharrow Point at Whitsand Bay. From this data the mean monthly sea temperature was calculated for periods corresponding to those of successive growth rate readings. For the same periods the mean monthly air temperatures were derived from records of the daily maxima and minima air temperatures recorded at Plymouth Polytechnic’s meteorological station, 10km distance from Sharrow Point.

For most of the year there was a good correlation between the growth parameter $K$ and the environmental temperature. However there were exceptions. The particularly cold spell of January 1987, when daily mean temperatures did not rise above freezing point for six consecutive days, occurred at the end of the December to January growth period. This cold spell was reflected in a sharp drop in growth rates the following month. Although growth rates dropped between August and September 1987, temperatures, particularly air temperatures, were still high.

From the calculated values of $K$ and $L_{oo}$ for each month the expected
Figure 30. Seasonal variation in the growth parameter $k$, provided by equations 1 to 3 from growth equations used to describe growth of Nucella on the shore at Whitsand Bay.

Growth equations:

- $\circ\circ$ von Bertalanffy
- $\Box\Box$ Gompertz
- $\triangle\triangle$ logistic
Figure 31. Seasonal variation in the growth parameter $k \ (\square-\square)$ derived from the Gompertz growth equation used to describe growth of *Nucella* on the shore at Whitsand Bay and both air (○-○) and sea (●-●) temperatures recorded at stations nearby.
growth patterns of *N. lapillus* on the shore can be obtained for individuals hatching at particular times of the year. Using the von Bertalanffy model, assuming that age is zero when length is zero, the length at the end of the first month can be calculated from

\[ L_t = L_\infty \cdot (1 - e^{-k_1 t}) \]

where \( t \) = one month. Rearrangement of equation 4 provides the age (or time) at which that length would have been achieved in the second month by;

\[ t = \frac{-1}{k_2} \cdot \ln(1 - (L_t/L_\infty)) \]

Substituting the calculated value of \( t + 1 \) into equation 4, using \( K_2 \) and \( L_\infty \), gives the size at the end of the second month, (Fig. 32).

Similarly, using the Gompertz growth equation, and assuming that time is zero when the length is one mm, the age (or time) at which a given length is achieved can be found from

\[ t = \frac{-1}{K} \cdot \ln(1 - (\ln L_t/\ln L_\infty)) \]

Figure 33 provides the growth patterns calculated in this way for hatchlings emerging in August or March. Under the von Bertalanffy growth model, taking into account seasonal variation in growth rate and under-estimating the initial size, the whelks reach a length of 25mm in thirteen months if hatching occurs in August and 14.5 months if hatching in March. Under the Gompertz model, which provided a better fit to the observed growth data, individuals would take an average of 20 months if hatching in August, or 17 months if hatching in March, to reach 25mm length.

### 3.4.3 Discussion

The high recovery of marked snails indicated that the whelks did not move far from their release point. Previously *Nucella* have been shown to move only a few metres during a feeding season (Hughes, 1972), but may move further (33cm/day) in search of food (Morgan, 1972b).
Let length at $t_1 = L_{t_1}$. Using the growth parameters of the first month ($L_{\infty 1}$ and $k_1$) the length one month later (at $t_2$) = $L_{t_2}$.

To move to the second month consider that the length $L_{t_2}$ would represent snails of nominal age $t_3$, which one month later (at $t_4$) would measure $L_{t_3}$, using the growth parameters ($L_{\infty 2}$ and $k_2$) of the second month.

**Figure 32.** Summary of method used to determine the seasonal growth pattern of *Nucella* on the shore using the monthly growth parameters $L_{\infty}$ and $k$ provided by the von Bertalanffy and Gompertz growth equations used to describe observed growth at Whitsand Bay.
Figure 33. Predicted growth pattern of *Nucella* determined from the monthly growth parameters, $L_\infty$ and $k$, according to the von Bertalanffy (○—○ ●—●) and Gompertz (□—□ ■—■) growth equations, for hatchlings emerging in August (open symbols) or March (closed symbols).
Although occasionally adult whelks were seen crawling across sand, the ones found on distant rocks were thought to have been transported by water movement.

Non-linearity for the relationship between linear increment and initial dimension, in which growth rate increases initially and then declines, has been reported for other gastropod species, (Yamaguchi, 1977; Hughes, 1980; Williamson & Kendall, 1981). In the present study, the sigmoid growth functions were better descriptions of observed growth in the field than the non-sigmoid von Bertalanffy growth equation. The relationship between linear increment over a growing period of five months and initial size was found to be linear for two Nova Scotian populations of *Nucella* (Hughes, 1972).

However Yamaguchi (1977) has shown that growth rates obtained from a sigmoid curve may appear as if they are derived from a non-sigmoid growth function if small individuals are not represented and if the observation period is long in relation to growth rates. Detection of non-linearity is important, since interpreting early growth as linear leads to a substantial over-estimate of size at a given age, especially in the early stages of growth.

At Whitsand Bay some growth occurred throughout the year, unlike populations in Nova Scotia (Hughes, 1972) where growth ceased from October to April. Peare (1970a) reported that for a Yorkshire population of *Nucella* the main growth period was from June to November, whereas in the warmer south-west growth was only substantially reduced for three months in the winter (mid-January to mid-April). Growth in the winter was confined to whelks of less than 25mm length. Similarly, Peare (1970a) reported that slow growth of juveniles occurred during the winter due to intermittent feeding.

There was a strong correlation between growth rates and temperature.
Largen (1967b) found in laboratory conditions that the feeding rate of *Nucella*, on both mussels and barnacles, was dependent on water temperature. Feeding did not cease completely until the temperature was below 3°C, but that above this temperature feeding rate more than tripled for each 10°C rise, reaching a maximum at 20°C. Mean monthly sea temperatures at Whitsand Bay for the winter of 1986-7 did not fall below 5°C, and as this is above the critical threshold temperature for feeding found by Largen, feeding was possible throughout the winter.

If growth rates are dependent on temperature, via feeding rates, a delay would be expected between changes in temperature and changes in growth rate. By introducing a lag of two weeks (Fig. 34) growth rate is seen to be closely related to temperature, with air temperature providing a closer fit than sea temperature. However, for two months of the year growth rates were lower than expected. The mild weather of October 1986 (mean monthly air temperature of 12.3°C) did not result in correspondingly high growth rates but it may have coincided with a large November spawn. Unfortunately no data are available to test this. The second month to deviate from the general trend was August 1987, for which the drop in growth rate remains inexplicable. At high temperatures an increase in temperature did not result in increased growth rates, asymptotic growth rate was achieved at 13°C.

In the present study animals up to 31mm length displayed some growth in the field. The generally held view (Fretter & Graham, 1985) is that adult *Nucella* do not grow. The onset of maturity in *Nucella* is difficult to assess from external features. Moore (1936) stated that when *Nucella* reach sexual maturity growth at the shell lip ceases and that instead the region near the lip thickens and a row of 'teeth' are laid down along the inside margin of the aperture. Later studies (Cowell & Crothers, 1970; Berry & Crothers, 1970) demonstrated that
Figure 34. Relationship between the monthly growth parameter k derived from the Gompertz growth equation used to describe growth of Nucella on the shore at Whitsand Bay and the air (o) and sea (●) temperatures recorded at stations nearby.
during prolonged cessation of growth juveniles laid down 'teeth' and that thickened animals with 'teeth' did re-commence growth, but these animals were not thought to be mature. Hughes (1972) confirmed that thickened animals continued growing. However from histological studies Feare (1970b) concluded that adults with ripe gonads had renewed growth after maturity.

At Whitsand Bay there was clear growth of thickened individuals, but no attempt was made to determine the size at which sexual maturity was reached. However since nearly all whelks above 25mm length displayed some growth (Fig. 27), especially in the summer months, it would be unlikely that these were all immatures. Therefore it must be concluded that growth does not cease at maturity.

If adult status is arbitrarily assigned to individuals of 25mm length, using the Gompertz growth equation hatchlings emerging in August could spawn in May to June of their second year (some 21 months later), while those hatching in March could spawn in October to November of their second year (19 months from hatching).

The estimated time taken to reach maturity was shorter on the shore at Whitsand Bay than for other populations reported in the literature. On the Yorkshire coast young *Nucella* that hatched in September 1966 had grown to a mean length of 13mm a year later, and animals with a mean length of 13mm in September 1966 grew a mean of 7mm in their second year (Feare, 1970a). Sexual maturity was reported to occur at the age of 2 to 2.5 years. By contrast on the Cornish coast, at Whitsand Bay, individuals hatching in August were calculated to reach a mean of 19mm within one year. The milder weather in the south-west cannot be the sole reason for more rapid growth since, from growth studies on Drakes Island in Plymouth Sound, Moore's (1938a) estimated age at maturity agrees with that of Feare (1970a).
The growth patterns of *N. lapillus* have been reported to depend on shore type and the availability of prey. Hughes (1972) noted that a wave-exposed population with an excess of small mussels as prey grew faster, to a larger size and reached sexual maturity at a greater shell length than a population from a wave-sheltered shore where food was scarce. Moore (1936) also reported that *Nucella* fed on mussels, rather than barnacles, attained sexual maturity at a greater size although no details were given of the relative rates at which sexual maturity was reached. In Massachusetts, *N. lapillus* from a wave-exposed shore feeding on mussels had an earlier age of first reproduction (1.8 years), but were smaller, than those from a wave-sheltered shore (2.3 years) where food was more limited (Osborne, 1977).

That higher growth rates and earlier age of first reproduction in exposed situations may not be dependent solely on the greater availability of prey is suggested by the work of Menge (1978b). Menge showed that exposed-phenotype *Nucella* had an overall intrinsically higher rate of feeding on mussels than the sheltered shore phenotype.

At Whitsand Bay the combination of exposed-phenotype snails, an abundant food supply, as mussels, and the mild weather allowing growth of juveniles throughout the year, has resulted in more rapid growth rates than previously reported for this species.
CHAPTER 4 FEEDING AND GROWTH OF JUVENILE WHELKS

4.1 Introduction

This section explores the use of growth rates as a measure of prey profitability to developing Nucella. If growth rates are to be used as a measure of fitness, we need to establish that increased rates of growth confer increased fitness on the organism.

For animals that can reproduce at any time of year an increased growth rate reduces the age of first reproduction, as shown by Vadas (1977) for sea urchins and Palmer (1983) for both Thais emarginata and T. canaliculata. By the compound interest law the sooner an animal commences reproduction the greater its total reproductive output (Calow, 1977).

For an animal that has a limited reproductive season, increased growth rates result in larger size at first reproduction. That larger females tend to produce a larger number of offspring has been found for many invertebrates including gastropods (e.g. Palmer, 1983; Spight & Emlen, 1976; Hughes & Roberts, 1980).

If juvenile mortality is high more rapid development, by reducing the time spent by organisms in the vulnerable small stages of the life cycle, increases the chance of reaching maturity and hence breeding. Juvenile mortality in N. lapillus has been estimated to be at least 90% in the first year reducing to 27% by the third year (Feare, 1970a). The adults are long-lived, estimated at 5-6 years (Feare, 1970a), resulting in populations that are dominated by adults (Hughes, 1972; Crothers, 1985; Feare, 1970a).

More rapid juvenile growth can increase the probability of survival to adulthood for N. lapillus in a number of ways. Sheltered shore N. lapillus are at great risk from crab predation (Kitching et al., 1966).
with smaller snails being more vulnerable (Hughes & Elner, 1979). Exposed shore whelks are in most danger of being swept off the rocks by rough seas (Kitching et al., 1966) and wave shock is potentially a major source of mortality (Menge, 1978a). The pull required to dislodge a whelk is dependent on its size (appendix 3) which might be expected since foot area correlates positively with shell weight (Kitching et al., 1966). Although larger whelks present a larger surface area on which water movement can have an impact, an increase in size may result in an increased ability of N. lapillus to withstand wave action on an exposed shore. Mortality from desiccation is potentially important for intertidal animals. Coombs (1973) has shown that small N. lapillus lose water more rapidly than larger animals, and suggests that young animals are more likely to suffer mortality from desiccation.

Finally, an increase in animal size may increase the range of potential food, both by type and size, so that in times of food shortage larger animals are more likely to find something to eat (e.g. Wilson, 1973, 1975; Griffiths, 1980; Jenkins, 1987).

Thus increased growth rates not only lead to an increase in fecundity but also greater size confers reduced vulnerability to adverse physical conditions, food shortages and predation.

Provided that an animal is not reproducing, growth rates represent a biologically meaningful measure of the value of a food source. Although there may be differential costs and benefits associated with the acquisition and processing of various food sources, these do not need to be measured, since the final outcome, a net balance of energy and materials, results in growth.

The use of growth rates as a measure of fitness in studies of optimal diet relies upon differential growth rates being achieved on
different types and sizes of prey. There is some prior evidence that
growth rate does vary with diet in gastropods. The type of prey
offered to gastropods has been shown to affect growth rate in field
experiments (Moran et al., 1984) and in culture conditions (Ansell,
1982b). A few studies have quantified the effect of prey size on
growth. In extended field trials of caged Thais species feeding on
barnacles and mussels, Palmer (1983) found some evidence that prey size
affected predator growth rate. Similarly, rate of growth and ultimate
size, both in laboratory and field experiments were reported to be
affected by size of prey for the pteropod mollusc Clione limacina
(Conover & Lalli, 1972). The size of oysters as prey influenced the
rate of growth of Bupleura caudata (MacKenzie, 1961). By analysis of
the energy budget of Thais haemastoma canaliculata, Garton (1986) found
that small drills displayed higher scope for growth on small oysters
than on large but there was no effect of prey size for large drills.

Perhaps the biggest drawback to using growth as an index of fitness
lies in its measurement. Growth may be defined as a permanent change
in the amount of protoplasm and its normal secretions (Vines & Rees,
1972). For practical purposes it is necessary to measure some quantity
which is, as nearly as possible, proportional to true growth.
Various methods have been used to assess growth in molluscs (Wilbur &
Owen, 1964). Destructive methods include dry weight changes and
micro-growth bands of the shell (Ekaratne & Crisp, 1982).
Non-destructive methods are limited to changes in wet weight or some
linear measurement of the shell. There are however limitations to
these non-destructive techniques, especially when applied to molluscs.
Wet weight changes will be profoundly affected by the amount of
extra-visceral fluid present, estimated by Coombs (1973) to be 30% of
total fluid weight of adult N. lapillus. The weight of the shell alone
can be estimated by weighing the animal in water (Havinga, 1928, cited Wilbur & Owen, 1964) and extended to include estimates of body weight by weighing in air after extrusion of extra-visceral water (Palmer, 1982). However during field growth experiments on three species of Thais, Palmer (1983) attributed some deaths of the experimental animals to the trauma of handling using this method. More significantly T. lamellosa displayed recurrent negative growth (when measured as % body weight change) which Palmer attributed to the problems of removing extra-visceral water in a repeatable manner.

Increase in shell length, because of its ease of measurement and its repeatability, has been a favoured criterion of mollusc growth. Weight \(w\) and length \(l\) are related by a power relationship of the form:

\[ w = a l^b \]

where \(a\) and \(b\) are fitted constants. If weight and length are transformed to logarithms equation 5 becomes:

\[ \log w = \log a + b \log l \]

a straight line for which regression analysis provides the values of the slope \(b\) and the intercept \(\log a\). Thus body weight can be estimated from shell length provided that there is a direct relationship between the two variables over the whole size range.

Changes in gastropod shell length however may not always be concomitant with changes in body size and **vice versa**. Morton (1986) reported that, following hatching, *Hemifusus tuba* displays a period of rapid shell growth which is not reflected in body growth, after which there is a phase of rapid body growth with only a slight increase in shell length. Erosion of the shell apex has been shown to occur in mature gastropods (Spight, 1973; Yamaguchi, 1977) and in juveniles with repeated handling (Morton, 1986). Decrease in body weight, without a decrease in shell length, can occur during periods of starvation.
(Emerson, 1967; Stickle & Duerr, 1970; Stickle, 1971; Russell-Hunter & Eversole, 1976), and reproductive adults will show fluctuations in body weight not associated with changes in shell size.

However juvenile *N. lapillus* do not appear to show differential partitioning of growth to shell and body tissue (R. Kirby, Plymouth Marine Laboratory, per. comm.), and since the present study is concerned only with active growth in juveniles, the problems associated with starvation and reproduction do not apply.

Finally some gastropods, for example *Thais lamellosa* (Spight, 1973) and *Hemifusus tuba* (Morton, 1986a), display growth checks that appear to be intrinsic. During these periods shell length and tissue weight remain constant but total weight increases due to shell thickening. Periods of inherent 'non-growth', if not carefully accounted for, could limit the use of growth as a measure of prey value. However growth of *N. lapillus* in culture appears to be continuous (Crothers, 1980; life-history studies, appendix 1)

By using increment in shell length as a measure of growth in *N. lapillus* the benefits (of ease, repeatability and lack of trauma) seem to outweigh the possible disadvantages. Throughout this study shell lengths were recorded and converted to dry body weight as required.

4.2 Feeding and Growth of Hatchlings

4.2.1 Introduction

The mussel beds at Whitsand Bay contained several mollusc species of a size suitable for predation by newly hatched *Nucella*. Trials were set up to determine if some of these potential prey species could be eaten by young *Nucella* (section 4.2.2) and if the growth rate of hatchlings was affected by type and size of prey (section 4.2.3).
4.2.2 Acceptable Diet

4.2.2.1 Method

Egg capsules of *Nucella lapillus* containing well developed embryos were collected from the Whitsand Bay rocks and transferred to the laboratory. Here they were kept in perspex dishes with a fine mesh gauze top in the continuous immersion system (section 2.3.1). Only newly hatched individuals (less than 3 days old), without prior feeding experience, were used in the feeding trials. The prey were obtained by washing samples of mussel bed in a continuous stream of tap water, collecting the sand and small animals in a 0.5mm sieve.

A microscopic examination of washed samples from the mussel bed showed that potential prey, by virtue of their small size, included *Lasaea rubra* (Montagu), *Otina ovata* (Brown), *Odostomia scalaris* Macgillivray, *Cingula cingillus* (Montagu), *Rissoa parva* (da Costa) and small *Mytilus edulis*. Of these only *L. rubra*, *O. scalaris* and *M. edulis* were sufficiently abundant to set up and maintain the feeding experiments and common enough to form an important part of the diet of whelks in the field. Initially mussels of 2mm (+0.5mm) length were used, later the trials were extended to include 3mm (+0.5mm) and 4mm (+0.5mm) mussels. The average length of *Lasaea rubra* individuals, although not accurately measured, was marginally smaller than 2mm, whilst the *Odostomia* were generally between 2 and 3mm.

Individual *Nucella* hatchlings were set up with ten items of one potential prey type in separate compartments of a multi-well plate (section 2.3.2) with a gauze top. To ensure that only live animals were provided in the feeding trials each prey item was only included once it was seen to have extended its foot. Control compartments, containing just ten prey or one predator, were set up alongside the others. Each prey type was replicated several times (see table 4).
### Table 4. Feeding and growth of newly hatched *N. lapillus* on various prey. 

#### a) Individual feeding responses of hatchlings to 3 prey types common at Whitsand Bay. 

<table>
<thead>
<tr>
<th>Days</th>
<th>No.</th>
<th>Outcome</th>
<th>Days</th>
<th>No.</th>
<th>Outcome</th>
<th>Days</th>
<th>No.</th>
<th>Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>0</td>
<td>D</td>
<td>22</td>
<td>4</td>
<td>E</td>
<td>20</td>
<td>6</td>
<td>D</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>E</td>
<td>22</td>
<td>22</td>
<td>E</td>
<td>30</td>
<td>35</td>
<td>S</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>E</td>
<td>22</td>
<td>9</td>
<td>E</td>
<td>30</td>
<td>12</td>
<td>E</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>E</td>
<td>35</td>
<td>5</td>
<td>D</td>
<td>38</td>
<td>61</td>
<td>S</td>
</tr>
<tr>
<td>34</td>
<td>0</td>
<td>S</td>
<td>38</td>
<td>45</td>
<td>S</td>
<td>38</td>
<td>52</td>
<td>S</td>
</tr>
<tr>
<td>34</td>
<td>0</td>
<td>S</td>
<td>42</td>
<td>63</td>
<td>S</td>
<td>55</td>
<td>74</td>
<td>S</td>
</tr>
</tbody>
</table>

#### b) Comparison of mean feeding and growth rates by hatchlings on the three prey types.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Trials</th>
<th>Mean Number Eaten/day (S.E.)</th>
<th>Mean Growth Rate mm/day (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Odostomia</em></td>
<td>6</td>
<td>0.000</td>
<td>0.00</td>
</tr>
<tr>
<td>2mm <em>Mytilus</em></td>
<td>7</td>
<td>1.10 (0.20)</td>
<td>0.055 (0.009)</td>
</tr>
<tr>
<td><em>L. rubra</em></td>
<td>5</td>
<td>0.58 (0.21)</td>
<td>0.042 (0.014)</td>
</tr>
</tbody>
</table>

(E=escaped, S=trial stopped, D=died)
Every four or five days the length of the dogwhelk was measured to within 0.1 mm using a binocular microscope and graduated eye-piece. The number of drilled and consumed prey was recorded and these replaced by fresh individuals. Non-predatory deaths were also recorded. The intention was that the experiment would continue until the whelks reached at least 4 mm length or until a minimum of 30 days had passed. Unfortunately the gauze top did not restrict the Nucella and their prey to just one compartment and the experiment had to be terminated early. As the replicates were set up on different days the replicates had run for different lengths of time at the end of the experiment (table 4a).

4.2.2.2 Results

Two Nucella hatchlings, acting as controls, survived 30 days without food and did not grow. A direct comparison of the recorded non-predatory death rate in the experimental and control batches was made difficult by the different periods of time for which each ran. No mussels, of any size, either experimental or control, died during the course of the experiment. There were no deaths of L. rubra other than by predation, in the five experimental runs and two deaths in the control run within 30 days. Odostomia were less vigorous, in the six experimental runs there were five deaths by day 25 and in the controls three deaths.

The feeding and growth responses of individual Nucella hatchlings to the three potential prey types are given in table 4. Although hatchlings would drill and consume small mussels and Lasaea rubra they would not feed on Odostomia, even after 30 days of starvation. Comparing the hatchlings fed on 2 mm mussel or the similarly-sized Lasaea rubra (table 4 b), there was no significant difference in the mean feeding rate ($t=1.76$, d.f. = 10, NS) nor the mean growth rate ($t=0.66$, d.f. = 10, NS). Most of the Nucella which escaped, did so on
the same day, suggesting that the cause lay with some external factor unrelated to prey type.

4.2.3 Growth Rate of Hatchlings on Variable Prey

4.2.3.1 Method

Three size classes of mussels were used, 2mm, 3mm and 4mm (all \( \pm 0.5\) mm) and in addition Lasaea rubra of approximately 2mm length. The experimental procedure was similar to that used in the acceptable diet trial (section 4.2.2) with the following modifications. The gauze top was replaced by a solid sheet of perspex (section 2.3.2) to prevent the animals escaping. In order to equalize the probability of encounter with the mussels of different sizes, an attempt was made to equalize the total surface area of prey within each compartment. An estimate that the surface area of small mussels equals the square of the length was used to provide the densities given in table 5 a. The higher density of twenty-four Lasaea rubra or 2mm Mytilus obviated a problem encountered in the acceptable diet experiment, where larger Nucella individuals, those approaching 4mm, sometimes ate nearly all the ten available prey in 4 days. Four replicates of each prey type were set up in randomised positions in the multi-well plate. Observations, measurements and timings were the same as in the acceptable diet trial. Two replicates of each prey regime were set up without Nucella as controls.

4.2.3.2 Results

Within the control replicates only two prey deaths were recorded over the 30 days, one each of a 2mm mussel and a Lasaea rubra. Of the sixteen experimental trials six hatchlings had died before or shortly after day 30, three of these from the 4mm mussel regime, two from the 2mm mussels and one from the 3mm mussels. It was considered that the modified lid, although preventing escape, did not provide sufficient
Table 5.  a) Numbers of each prey type provided in growth rate experiment to equalize total surface area of prey.
b) Mean growth rate (mm/day) (S.E.) of hatchlings provided with different prey regimes, over the first 20 days of feeding.
water circulation for the young predator. Individual growth rates were variable within each treatment (Fig. 35) with several animals not growing at all during the experiment. However it is clear from figure 35 that looking only at the Nucella that did grow, there is little difference between the growth rates on the different prey. Mean growth rates over the first 20 days of feeding (table 5 b) were not significantly affected by type or size of prey (ANOVA, $F = 0.71$, d.f. = 3,12, NS).

4.2.4 Discussion

Feare (1970a) suggested that following hatching the first requirement of the young Nucella was to find shelter rather than food. That they can survive considerable periods, at least one month, without feeding was shown here. Largen (1967a) showed that hatchlings were able to feed on a wide variety of prey, including Lasaea rubra and small mussels. He suggested that almost any shelled species of a suitable size might form the diet of hatchlings. However in the present trials, young Nucella did not eat Odostomia which, as an ectoparasite on mussels, were abundant on the mussel beds at Whitsand Bay.

The reason for ignoring Odostomia as a potential food source is not clear. Odostomia is not particularly active yet on no occasion were the young Nucella seen in close contact with them. Nor were any incomplete drill holes found on the shells of Odostomia ruling out an inability on the part of the young whelks to penetrate the shell. In sand samples from which the prey were obtained there were frequent examples of drilled shells of Lasaea rubra, Otina ovata and small mussels, but none were seen of Odostomia.

Preliminary trials to detect cannibalism indicated that intraspecific predation by hatchlings did occur. Empty drilled Nucella
Figure 35. Individual growth curves of *Nucella* hatchlings fed pure diets of *Mytilus edulis* of differing length (i-iii) or *Lasaea rubra* (iv). Solid symbols represent death of the predator. (see also overleaf).
Figure 35 continued.

- iii) 4mm mussels
- iv) Lasaea rubra
shells were also found in the sand samples. Similarly Ansell (1982b) found that hatching juveniles of Polinices catena in culture conditions fed by cannibalism on other members of the same brood if no suitable alternative food was provided. Young Nucella on the mussel beds at Whitsand Bay showed a clumped distribution (section 3.2) and as Largen (1967a) suggested, during the period immediately following hatching, intraspecific predation may be a common occurrence. Morton (1987) found that in Hemifusus tube sibling cannibalism, although occurring during the first two weeks following hatching, was insignificant compared to the amount of bivalve tissue consumed. He suggested that cannibalism may enhance survival during the time needed to discover and learn to feed on natural prey. In the present study since small mussels were abundant in the field samples throughout the year and since they were the most frequently drilled shells found in the sand samples it is suggested, that on an exposed shore of this type, small mussels form the bulk of the hatchlings diet.

Newly hatched Nucella included in their diet mussels in the length range 1.5 to 4.5mm. However differences in growth rate of hatchlings, dependent on type and size of prey, could not be detected by the methodology employed. The shells of the young predator were too small and fragile to be measured with calipers. However, under a binocular microscope, the movement of hatchlings resulted in inaccurate measurements relative to the small increments in growth that occurred. Given a sufficiently long growth period this problem would have been partially overcome, but the system of housing individuals proved inadequate to maintain the Nucella in a healthy condition for long enough. Alternatively, several hatchlings could have been housed in a larger container, but such a system would have exposed the animals to possible intraspecific predation and provided no information on the
the relation between growth and predation rates. For these reasons it was not considered worthwhile to study the feeding and growth responses of the hatchlings any further.

Though limited, these trials have shown that young Nucella can achieve a growth rate of up to 2.5mm/month when fed on a diet of small mussels or Lasaea rubra, prey which are abundant in the mussels beds throughout the year.

4.3 Feeding and Growth of Juveniles

4.3.1 Introduction

The aim of this section was to determine the effect of mussel prey size on the growth and feeding behaviour of juvenile N. lapillus. The initial experiment (section 4.3.2) involved four sizes of mussels up to 20mm in length. The results from this trial suggested that larger prey should be considered (section 4.3.3). During the experiment on large prey there were visible signs that, whilst the whelks were still feeding, decomposing flesh was leaching from the mussel shell. The third experiment (4.3.4) was aimed at detecting the timing and extent of such losses for prey of intermediate size.

The method and results for each experiment are described separately with the results brought together in section 4.3.5 and discussed in section 4.3.6. Throughout the results and discussion sections, size of whelk refers to the initial size.

4.3.2 Small to Medium Size Prey

4.3.2.1 Methods

Nucella and Mytilus were collected from Whitsand Bay one day before the start of each replicate experiment. The mussels were washed clear of sand and debris and held without food in the sump of the continuous immersion system (section 2.3.1) until required. Throughout each run the whelks were housed in the continuous immersion system in separate
pots so that individual responses to prey size could be monitored.

Following collection from the field the dogwhelks were starved for one week to eliminate the effect of previous feeding on growth and to initialize hunger levels. They were measured before and after this period.

Four size classes of juvenile dogwhelks (5, 10, 15 & 20mm, all ±1mm) were allowed to feed for 28 days. This feeding period should be as long as possible to allow the whelks to reach a steady state of feeding and growing. However a period longer than 28 days would incur the risk that one size class would grow into the next since, under these laboratory conditions, growth rates can exceed 1mm per week.

One individual whelk from each size class was presented with a single size class of mussels. Four size classes of mussels were used; 5, 10, 15 or 20mm (all±1mm). As encounter rate might be expected to be a function of prey surface area the number of each mussel size offered was adjusted so as to equalize total surface area. The required number of mussels to equalize surface area was calculated from appendix 5, viz.

<table>
<thead>
<tr>
<th>Prey size (mm)</th>
<th>Numbers used</th>
<th>Total surface area (mm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>100</td>
<td>3402</td>
</tr>
<tr>
<td>10</td>
<td>30</td>
<td>3488</td>
</tr>
<tr>
<td>15</td>
<td>14</td>
<td>3465</td>
</tr>
<tr>
<td>20</td>
<td>8</td>
<td>3422</td>
</tr>
</tbody>
</table>

At each of these densities the predator would be feeding at the plateau of its functional response curve (appendix 2). Therefore prey would be sufficiently abundant to minimize search time.

Each treatment was inspected weekly to ensure that uneaten prey were always available to the predator. Provided that the dogwhelk was not
feeding its length was recorded. The mussel clump was dissociated and each mussel examined microscopically for the presence of boreholes. Detailed examination was most important when small Nucella were feeding on large prey as the adductor muscles of drilled Mytilus were frequently left intact with the shell staying closed. Any mussel flesh remaining in the shell was removed, oven dried for 24 hours at 100°C and weighed.

The number of dead, undrilled, uneaten mussels was recorded as non-predatory deaths. Dead prey were replaced with live mussels of the same size to re-establish the initial densities. A dogwhelk was deemed to be feeding if it remained sat on a mussel for at least one hour following removal of the pot from the tank. A dogwhelk that was feeding was left for a further day to finish its meal before the weekly recordings were taken.

After the 28 days of feeding the dogwhelks were left for a further week without food and re-measured. During this final week of starvation the whelks would continue to grow utilising the food already consumed. By including growth in this final week with growth over the 28 days of feeding, a measure can be gained of the efficiency with which a given amount of food is converted to growth.

A dogwhelk of each size was starved throughout as a control and measured at weekly intervals. Also a control set of each mussel size, without Nucella, was used to determine the death rate due to factors other than predation. The control mussels were inspected weekly, the dead mussels counted, removed and replaced by live ones.

Five replicates were carried out between January and July 1986, (for dates see table 9).

The relation between dry flesh weight and mussel length was determined for each seasonal replicate by two methods:
i) oven-drying; the mussel flesh was dissected, oven dried at approximately 100°C for 24 hours and weighed (length range 10-20mm).

ii) freeze-drying; the posterior adductor muscle was cut, the whole animal deep frozen for 24 hours and freeze dried for 48 hours before weighing. The dried flesh was removed from the shell and discarded. Dry flesh weight was taken as the difference between the weight of the whole animal and shell weight (length range 5-20mm).

Both methods were thought necessary since it was impracticable to dissect the flesh of 5mm mussels for oven-drying, hence only freeze-drying was suitable for the entire size range. However, for logistic reasons, the dry flesh weight of partially eaten prey could only be achieved by oven-drying.

4.3.2.2 Results

a) Controls

Deaths of mussels in pots without Nucella were very low (eleven deaths out of a total of 608 individuals over 28 days). However this figure was five times higher than the number of undrilled, uneaten, dead mussels recorded in the experimental runs (table 6). The discrepancy was probably due to the difference in the average length of time spent by individual mussels within the pots. In comparison to the control set of mussels, the ones in the experimental runs were being continually eaten and replaced by fresh individuals.

An alternative explanation is that non-predatory deaths were counted as predatory deaths. One conceivable way in which this could have occurred was by taking a chipped mussel shell as a marginal borehole (see Fig. 67). Mis-identification of the cause of death would result in an over-estimate of predation rate. A measure of the error can be obtained with death rate expressed as mean deaths per pot run of 28 days. The difference between mean non-predatory death rate in the
<table>
<thead>
<tr>
<th>Mussel size (mm)</th>
<th>Experimental groups</th>
<th>Controls</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Predatory</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>1258</td>
</tr>
<tr>
<td>10</td>
<td>20</td>
<td>521</td>
</tr>
<tr>
<td>15</td>
<td>20</td>
<td>226</td>
</tr>
<tr>
<td>20</td>
<td>20</td>
<td>130</td>
</tr>
</tbody>
</table>

Table 6. Comparison of recorded mussel deaths in experimental and control groups. Values given for the experimental group are total losses for the four sizes of *Nucella* and five replicates combined. Values for the control group are total deaths in the four replicates combined. All are for periods of 28 days.
control and experimental groups provides a value for the
over-estimation of predation rate. Even when represented as a
proportion of all recorded predatory deaths, this over-estimate was
less than 4% for all mussels sizes (table 7), and can, therefore, be
ignored. Feeding rates given are those that were recorded as predatory
deaths.

The control Nucella (n = 20) all survived the six weeks without
food. Following the week of starvation one individual showed a slight
increase in length (of 0.4mm) thirteen whelks stayed the same and six
showed a slight loss (of up to 0.2mm). The latter was probably due to
erosion of the shell apex during handling. No account of this loss has
been made in the experimental group. Thus it could be assumed that, in
the experimental group, the growth achieved after the initial period of
starvation was due to the benefit of feeding in the laboratory.

b) Feeding rate

Each size of whelk (5-20mm) was able to feed on the range of mussel
sizes offered. The logarithm of the number of mussels eaten over the
28 days of feeding was dependent on both predator and prey size (see
two-way ANOVA below and Fig. 36).

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>m.s.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nucella size</td>
<td>3</td>
<td>0.9126</td>
<td>49.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mussel size</td>
<td>3</td>
<td>3.7653</td>
<td>203.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>9</td>
<td>0.0403</td>
<td>2.2</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Error</td>
<td>64</td>
<td>0.0185</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

As would be expected fewer large than small mussels were eaten by
all sizes of Nucella. The two largest sizes of whelk showed a
reduction in numbers eaten with increasing size of mussel throughout
the range of prey sizes used. However the mean feeding rate by 5mm
Nucella remained the same for both 15 and 20mm mussels, whilst 10mm
Mean number of mussel losses (deaths/pot/28 days)

<table>
<thead>
<tr>
<th>Mussel size (mm)</th>
<th>Experimental group</th>
<th>Control</th>
<th>%error</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pred. (a)</td>
<td>Non-pred. (b)</td>
<td>Non-pred. (c)</td>
</tr>
<tr>
<td>5</td>
<td>62.9</td>
<td>0.30</td>
<td>1.75</td>
</tr>
<tr>
<td>10</td>
<td>26.0</td>
<td>0.15</td>
<td>0.75</td>
</tr>
<tr>
<td>15</td>
<td>11.3</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>20</td>
<td>6.5</td>
<td>0.00</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Table 7. Calculation of possible error in recording non-predatory losses as predatory deaths.

\[ \%error = \frac{(c-b)}{a} \times 100 \], where \( a, b, c \) are expressed as mean number of deaths per pot per 28 days. Pred = recorded predatory deaths, non-predatory = recorded non-predatory deaths.
Figure 36. Effect of mussel prey size (mm ± 1mm) on the feeding rate (mussels/28 days) of juvenile *Nucella* of four different initial sizes. (Plots are means (± S.E.) of 5 replicates).
Nucella only showed a slight decrease on the larger prey. These observations could account for the marginally significant interaction effect.

c) Ingested ration

For each replicate, and for both oven dried and freeze dried methods, the dry flesh weight of mussels (mg) was related to length (mm) using least squares regression analysis following logarithmic transformation. Covariance analysis showed that for each replicate there was no significant difference between the methods (table 8) so the data from each method were combined to determine the predicted dry flesh content of mussels in each replicate (table 9). The values given in table 9 were used to determine the total ingested ration for each whelk from the numbers eaten, taking into account the weight of any remaining flesh.

In general the consumption of mussel flesh over the 28 days of feeding increased as the size class of the predator increased and was also significantly greater with larger prey (see two-way ANOVA below on log transformed data and Fig. 37).

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>m.s.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nucella size</td>
<td>3</td>
<td>1.646</td>
<td>118.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mussel size</td>
<td>3</td>
<td>1.316</td>
<td>94.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>9</td>
<td>0.033</td>
<td>2.4</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Error</td>
<td>64</td>
<td>0.014</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

However there were exceptions to these general relationships leading to a weak interaction effect. The mean consumption of mussel flesh by 5mm Nucella increased only marginally when feeding on 20mm mussels compared with 15mm ones, and 20mm Nucella showed a decrease in mean consumption rate between 15 and 20mm prey.

The amount of flesh eaten (taken as the difference between predicted
<table>
<thead>
<tr>
<th>Rep.</th>
<th>M</th>
<th>a</th>
<th>b</th>
<th>rss</th>
<th>d.f.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>O</td>
<td>-2.22</td>
<td>3.01</td>
<td>0.1649</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-2.11</td>
<td>2.98</td>
<td>0.2430</td>
<td>23</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-1.84</td>
<td>2.72</td>
<td>0.2902</td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.6981</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-1.97</td>
<td>2.84</td>
<td>0.7880</td>
<td>66</td>
<td>1.996</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td>2</td>
<td>O</td>
<td>-2.38</td>
<td>3.10</td>
<td>0.0844</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-2.31</td>
<td>3.08</td>
<td>0.1695</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.2539</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-2.26</td>
<td>3.01</td>
<td>0.2790</td>
<td>40</td>
<td>1.878</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td>3</td>
<td>O</td>
<td>-2.49</td>
<td>3.14</td>
<td>0.0697</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-2.07</td>
<td>2.80</td>
<td>0.1359</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.2056</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-2.13</td>
<td>2.85</td>
<td>0.2321</td>
<td>40</td>
<td>2.449</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td>4</td>
<td>O</td>
<td>-1.94</td>
<td>2.92</td>
<td>0.1664</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>-1.69</td>
<td>2.75</td>
<td>0.1245</td>
<td>19</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.2909</td>
<td>37</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-1.68</td>
<td>2.71</td>
<td>0.3181</td>
<td>39</td>
<td>1.730</td>
<td></td>
<td>NS</td>
</tr>
</tbody>
</table>

Table 8. Comparisons of regression equations relating length and dry weight in mussels by oven and freeze drying. 
a and b are constants in the equation: log_{10}\text{dry weight(mg)} = a + b \cdot \log_{10}\text{length(mm)}. (M = method of drying: O = oven dried, F = freeze dried, C = combined, P = pooled, Rep. = replicate, rss = residual sum of squares).
<table>
<thead>
<tr>
<th>Replicate</th>
<th>Dates</th>
<th>Mussel size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5mm</td>
</tr>
<tr>
<td>1</td>
<td>20.1.86 - 3.3.86</td>
<td>1.0</td>
</tr>
<tr>
<td>2</td>
<td>25.2.86 - 8.4.86</td>
<td>0.7</td>
</tr>
<tr>
<td>3 &amp; 4</td>
<td>8.4.86 - 20.5.86</td>
<td>0.7</td>
</tr>
<tr>
<td>5</td>
<td>23.5.86 - 7.7.86</td>
<td>1.6</td>
</tr>
</tbody>
</table>

Table 9. Predicted dry weight flesh content (mg) of mussels calculated from the combined regression equations in table 8.
Figure 37. Effect of mussel prey size (mm ± 1mm) on the consumption rate (mg dry weight mussel flesh/28 days) of juvenile *Nucella* of four different initial sizes (mm ± 1mm).

(PLOTS are means (± S.E.) of 5 replicates).
mussel weight and weight of remaining flesh) was calculated for each mussel eaten. The mean size of meal increased as prey size increased, with the exception that 5mm Nucella did not consume more flesh from a 20mm mussel than they did from one of 15mm (Fig. 38 a).

The amount of flesh taken by each predator from each mussel meal was expressed as a percentage of the meal size available. All sizes of whelk consumed the contents of 5mm mussels. The mean percentage of flesh consumed from the larger prey fell as mussel size increased and as Nucella size decreased (Fig. 38 b).

d) Growth rate after collection

The amount of linear growth achieved by the juvenile whelks during the first week of starvation following collection from the field was very variable (mean growth rate was 0.38mm/week, S.D. = 0.337, n = 100). The mean growth rates over this period for each Nucella size and for each replicate are given in Table 10a. Two-way analysis of variance (Table 10 b) showed that the amount of linear shell growth was independent of whelk size but the seasonal variation was just significant, being lowest in the January replicate and highest in May.

e) Effect of prey size on juvenile growth rates

The growth rates recorded in these experiments could be presented in two ways. Either as the observed increase in shell length or, by taking the initial and final shell lengths, as the equivalent increase in dry weight. The latter is the preferred measure since it does not underestimate the extent of increase of the fastest growing individuals, and has been used for comparisons of growth rates within one size class of whelk. However comparisons of growth rate between predator size classes have been made on observed shell length increases. The variances associated with linear increments of the shell were not significantly different between the various size classes.
Figure 38. Effect of mussel prey size (mm ± 1mm) on 
a) mean meal size (mg dry flesh weight) consumed, 
b) mean % of available mussel flesh removed,  
by juvenile Nucella of 4 different initial sizes. 
(Error bars are S.E., ones omitted for clarity 
were smaller than the ones given).
**Table 10.**  

a) Growth achieved by *N. lapillus* during the week of starvation following collection from the field. Each value is the mean (+S.D.) growth in mm/week for *n=5* individuals.  

b) Two-way ANOVA on the above data.
of Nucella. Use of dry weight equivalents would result in large differences in the variances requiring data transformation before analysis.

In the experimental group (n = 80) only one individual - a 20mm whelk feeding on 5mm mussels - did not grow. Two way analysis of variance was performed on the growth rate (mm/week) with predator size and prey size as main effects (see below).

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>m.s.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nucella size</td>
<td>3</td>
<td>0.8463</td>
<td>11.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mussel size</td>
<td>3</td>
<td>0.7425</td>
<td>10.06</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>9</td>
<td>0.2512</td>
<td>3.40</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Error</td>
<td>64</td>
<td>0.0738</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The significant interaction effect indicates that there was a contrasting growth response, to the size of mussel prey, by the different sizes of juvenile whelks. Figure 39 illustrates the effect of mussel prey size on the linear growth (mm/week) of the four size classes of Nucella. The 5mm Nucella showed an initial rise in growth rate as prey size increased from 5mm to 10mm, then a decline in growth rate on the larger prey. Similarity in growth response to prey size was shown by 10 and 15mm whelks. Each had a comparatively low growth rate on 5mm mussels which rose, and appeared to continue to rise, although more slowly, on the larger prey. 20mm Nucella again exhibited slow growth on 5mm prey, which rose to a peak on 15mm mussels but surprisingly declined on 20mm mussels.

As there was a significant interaction effect between Nucella size and prey size, separate analyses of variance had to be performed for each predator size to determine if prey size was having a significant effect on growth rate.

Lengths were converted to flesh dry weights according to the
Figure 39. Effect of mussel prey size (mm ± 1mm) on mean shell growth rate (mm/week) of juvenile *Nucella* of four different initial sizes (mm ± 1mm). Plots are means (± S.E.) of 5 replicates.
regression equation

$$\log_{10} W = 0.925 + 3.14 \log_{10} H$$

where \( W \) = dry flesh weight in mg, \( H \) = shell height in cm (Bayne & Scullard, 1978a), and the analysis of variance performed on these values (table 11 a). Only 10mm whelks showed no significant difference in growth rate on the various prey sizes. For the other three size classes of Nucella the multiple range test (Snedecor, 1966) was used to identify significant differences among means (as mg growth/28days) obtained on the four sizes of prey (table 11 b).

5mm Nucella grow significantly faster on 10mm mussels than they do on 20mm, but there is no difference between the other prey size classes. Both 15 and 20mm snails grow significantly less well on 5mm mussels than on all larger sizes but there is no difference within the three larger size classes of prey.

Two way analysis of variance was used to assess the effect of season and prey size on the dry weight increment for each predator size separately. Only for the 10mm whelks was there any indication of a seasonal effect on growth rate (\( F = 4.00, d.f. = 4,12, P<0.05 \)), the January-February replicate showed a mean growth rate half that of the other replicates.

f) Final growth

The mean growth rate (mm/week) of developing Nucella in the week following the cessation of laboratory feeding (Fig. 40 a) was independent of Nucella size but was significantly dependent on the size of prey that they were eating. Combining data from all Nucella size classes (Fig. 40 b) indicates that growth in the final week increases as prey size increases possibly reflecting gut fullness at the start of starvation.
a) Separate ANOVAs to test for significant differences in growth rate (as mg/28 days) of juvenile whelks feeding on different prey sizes.

<table>
<thead>
<tr>
<th>Nucella size(mm)</th>
<th>Source</th>
<th>d.f.</th>
<th>m.s.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>Prey size</td>
<td>3</td>
<td>19.21</td>
<td>3.98</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>16</td>
<td>4.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Prey size</td>
<td>3</td>
<td>100.0</td>
<td>1.50</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>16</td>
<td>66.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Prey size</td>
<td>3</td>
<td>805</td>
<td>7.00</td>
<td>&lt;0.01</td>
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<tr>
<td></td>
<td>Error</td>
<td>16</td>
<td>115</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>Prey size</td>
<td>3</td>
<td>1776</td>
<td>6.51</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>16</td>
<td>273</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

b) Results of multiple range test to compare means in growth rate (as mg/28 days) of juvenile whelks feeding on 4 prey sizes. (NS= not significant, * = significant at 5% level).

<table>
<thead>
<tr>
<th>Comparison between mussel size classes (mm)</th>
<th>Nucella size(mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 vs. 10</td>
<td>NS</td>
</tr>
<tr>
<td>5 vs. 15</td>
<td>NS</td>
</tr>
<tr>
<td>5 vs. 20</td>
<td>NS</td>
</tr>
<tr>
<td>10 vs. 15</td>
<td>NS</td>
</tr>
<tr>
<td>10 vs. 20</td>
<td>NS</td>
</tr>
<tr>
<td>15 vs. 20</td>
<td>NS</td>
</tr>
</tbody>
</table>

Table 11. a) Separate ANOVAs to test for significant differences in growth rate (as mg/28 days) of juvenile whelks feeding on different prey sizes. b) Results of multiple range test to compare means in growth rate (as mg/28 days) of juvenile whelks feeding on 4 prey sizes. (NS= not significant, * = significant at 5% level).
Figure 40.

a) Mean growth rate (mm/week), in the week of starvation following four weeks of feeding on four different mussel prey sizes (mm ± 1mm), of juvenile Nucella of four different initial sizes (mm ± 1mm).
(Each point is the mean of 5 replicates).

b) Effect of previous mussel prey size (mm ± 1mm) on the growth (mm/week) of all juvenile Nucella combined, in the week of starvation following four weeks of feeding.
(Each point is the mean (± S.E.) of 20 replicates).
4.3.2.3 Discussion

As predators grow their demand for food increases. The present data confirm the observations of Ansell (1982b) and Garton (1986) that when predatory gastropods are provided with a constant size of prey the predation rate increases as predator size increases. Alternatively, for a given size of predator, an increase in the size of prey results in a decrease in the rate of predation, since the predators can in general acquire a greater ration per prey item eaten. However it might be expected that there exists some limit to the amount of flesh that a Nucella can consume from one meal, due either to constraints imposed by gut capacity or the physical inability of the predator to reach all the flesh contained in the prey. Such a limit was illustrated by the insignificant rise in meal size of 5mm Nucella feeding on 15 and 20mm mussels.

In theory since the length of the proboscis in Nucella is approximately equal to its body length (Crothers, 1985) then, depending on drill site, Nucella should be able to reach all the flesh in a mussel which is less than or equal to its own body length (with an end drill hole) or, up to twice its own length (mid-point drill hole). In reality, although the percentage of flesh removed increased as the size ratio between predator and prey was raised, complete consumption of flesh was only noted when the predator was considerably larger than the prey.

That predatory gastropods do not eat all the flesh available to them is a common occurrence, eating first the softer parts of the body (Chew & Eisler, 1958; Gunter, 1979). Polinices duplicatus ate 80% of the available tissue when preying upon Mya arenaria, leaving the siphon and mantle fringes (Edwards & Huebner, 1977). Hughes and Dunkin (1984) estimated that adult Nucella lapillus eat 90% of available tissue from
10mm mussels but only 60% from 40mm mussels. As was also noted in the present study, when the majority of the flesh was eaten, the uneaten portions consisted mainly of edges of mantle tissue and the foot.

Significant differences in growth rate, on the prey size range offered, were achieved for all but the 10mm whelks, with an indication of an ontogenetic shift in prey value. Smaller prey were more profitable for small predators while larger mussels produced more rapid growth for the two larger classes of whelk. In the light of the results obtained for 5mm whelks, where growth rate declined on large prey, a similar response may occur for large whelks if provided with proportionally large prey.

It is important to note that for 5mm *Nucella* the ingested ration continued to increase as prey size increased but that this was not reflected in a concomitant increase in growth rate. Also, for the three larger predators, in general growth rates were on a plateau for the three largest prey sizes, but ingested ration continued to increase. These observations will be discussed more fully in section 4.3.6.

The majority of small *N. lapillus* collected from the intertidal region of Whitsand Bay displayed some degree of shell ornamentation in the form of imbrications (over 80% of 5 and 10mm *Nucella*), whilst the majority of large whelks had smooth shells (70% of 15mm and 96% of 20mm *Nucella*). Abrasion by wave action has been invoked to explain the lack of imbrication on older specimens (Moore, 1936). However that so many young whelks had imbrications is surprising since the imbricated form has been thought to be largely sublittoral (Moore, 1936; Rees, 1949) or, if intertidal, confined to relatively sheltered shores (Largen, 1971). During the growth experiments it was particularly noticeable that individuals with imbrications when collected from the field, had
none on the new shell growth formed in the laboratory, suggesting that active feeding and growth do not coincide with the formation of imbrications. However the opposite was found by Largen (1971); previously smooth individuals secreted lamelllose shell when kept in sheltered laboratory conditions and fed on mussels. Although both imbricate and smooth forms breed true in the laboratory (Largen, 1971) there is clearly some plasticity in response to environmental conditions.

4.3.3 Large Prey

4.3.3.1 Introduction

The aims of this experiment were threefold. First to determine the growth rate of juvenile N. lapillus on large mussels as an extension to the experiment on small and medium sized prey (section 4.3.2). Second to ascertain if, by increasing the size of mussel offered as prey, an upper asymptotic meal size would be reached with large Nucella similar to that shown by 5mm Nucella feeding on 15 and 20mm mussels (section 4.3.2.2). Third, to determine the time sequence of feeding and inter-feeding phases.

4.3.3.2 Method

After starving for one week Nucella in the size classes 10, 15 & 20mm were initially presented with one individual mussel which was either twice or three times the snail's own length. The mussel shells were scraped clean of barnacles. Ten dogwhelks of each size class were allowed to feed on each of the two mussel sizes in a single run in January 1987. Each whelk and its prey were kept in separate pots in the continuous immersion system (section 2.3.1).

Each treatment was inspected at least daily and a note made of the time and date that feeding commenced and finished. When a dogwhelk had ceased to feed both predator and prey were removed and measured. The
dry weight of any remaining mussel flesh was determined and a fresh mussel of the same size was provided. The whelks were allowed a minimum of 28 days for feeding. If they were not feeding at the end of this time the whelks were measured, starved for a further week and re-measured. Whelks engaged in feeding at 28 days were observed daily until they moved off the mussel whereupon they received the same final treatment. The relationship between length and dry flesh weight of the prey was determined from the same batch of mussels using individuals in the size range 17-63mm (n = 50).

4.3.3.3 Results

The feeding and growth responses of juvenile Nucella on the large prey are shown in table 12. A summary of the significance tests comparing responses of each size of whelk to the two prey sizes is given in tables 13 a & b. Predation rates by 10 and 15mm Nucella were significantly higher on the smaller mussels but independent of prey size for 20mm whelks. Figure 41 illustrates how individual whelks partitioned their time between feeding and non-feeding periods. Days spent between the beginning of the experiment and the initiation of feeding was significantly longer for the 15mm Nucella feeding on the larger mussels but independent of prey size for both 10 and 20mm whelks. For each size of whelk, the time spent feeding on a prey item was significantly longer on the larger prey but, for whelks consuming more than one prey, the time between cessation of feeding on one mussel and commencement on another, was independent of prey size. Mean values for consecutive feeding and inter-feeding periods are shown in figure 42.

Mussel dry flesh weight (mg) was related to length (mm) according to the least squares regression equation:-

\[ \log_{10}\text{dry flesh weight} = -2.18 + 2.94 \log_{10}\text{length} \]
<table>
<thead>
<tr>
<th>Nucella size (mm)</th>
<th>Prey size (mm)</th>
<th>Number Nucella eating/10</th>
<th>Mean number mussels eaten</th>
<th>Mean ingestion rate (mg/28days)</th>
<th>Mean growth rate (mm/week)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>20</td>
<td>10</td>
<td>3.9(0.18)</td>
<td>121(6.1)</td>
<td>0.99(0.10)</td>
</tr>
<tr>
<td>10</td>
<td>30</td>
<td>10</td>
<td>2.8(0.25)</td>
<td>180(24.7)</td>
<td>0.74(0.08)</td>
</tr>
<tr>
<td>15</td>
<td>30</td>
<td>10</td>
<td>2.6(0.27)</td>
<td>199(30.7)</td>
<td>0.58(0.11)</td>
</tr>
<tr>
<td>15</td>
<td>45</td>
<td>6</td>
<td>1.3(0.33)</td>
<td>278(28.4)</td>
<td>0.45(0.09)</td>
</tr>
<tr>
<td>20</td>
<td>40</td>
<td>9</td>
<td>1.9(0.28)</td>
<td>355(50.3)</td>
<td>0.40(0.08)</td>
</tr>
<tr>
<td>20</td>
<td>60</td>
<td>9</td>
<td>1.4(0.22)</td>
<td>545(32.6)</td>
<td>0.43(0.08)</td>
</tr>
</tbody>
</table>

Table 12. Feeding and growth response of juvenile *Nucella lapillus* on large mussel prey (values in parenthesis are S.E.). Mean ingestion and growth rates are only for those whelks which fed. Number of mussels eaten is the mean number of mussels on which feeding started within 28 days, for all ten whelks.
Table 13 a). Comparisons of predation rate and timing of feeding sequences of juvenile *N. lapillus* feeding on mussels either twice or three times their own length.

| Size(mm) Nucella | Size(mm) Mussels | Mann-Whitney U Test |  
|-----------------|-----------------|-------------------|---|
| i) Number of mussels eaten | | | |
| 10 | 20 v 30 | 10 | 10 | <0.01 |
| 15 | 30 v 45 | 10 | 10 | <0.02 |
| 20 | 40 v 60 | 10 | 10 | NS |

| ii) Days to first meal | | | |
| 10 | 20 v 30 | 10 | 10 | NS |
| 15 | 30 v 45 | 10 | 10 | <0.005 |
| 20 | 40 v 60 | 10 | 10 | NS |

| iii) Days feeding on each mussel | | | |
| 10 | 20 v 30 | 39 | 28 | <0.001 |
| 15 | 30 v 45 | 26 | 12 | <0.005 |
| 20 | 40 v 60 | 19 | 14 | <0.0001 |

<p>| iv) Days between meals | | | |
| 10 | 20 v 30 | 29 | 18 | NS |
| 15 | 30 v 45 | 16 | 6 | NS |
| 20 | 40 v 60 | 10 | 5 | NS |</p>
<table>
<thead>
<tr>
<th>Size(mm)</th>
<th>Size(mm)</th>
<th>t-test</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nucella</td>
<td>Mussels</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

v) Mg flesh consumed/28days

<table>
<thead>
<tr>
<th></th>
<th></th>
<th>2.32</th>
<th>18</th>
<th>&lt;0.05</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>20 v 30</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>30 v 45</td>
<td>1.73</td>
<td>14</td>
<td>NS</td>
</tr>
<tr>
<td>20</td>
<td>40 v 60</td>
<td>3.17</td>
<td>16</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

vi) Mean meal size (mg)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th>5.30</th>
<th>65</th>
<th>&lt;0.001</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>20 v 30</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>30 v 45</td>
<td>2.43</td>
<td>36</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>20</td>
<td>40 v 60</td>
<td>3.87</td>
<td>31</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

vii) Mg growth/28days

<table>
<thead>
<tr>
<th></th>
<th></th>
<th>1.76</th>
<th>18</th>
<th>NS</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>20 v 30</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>30 v 45</td>
<td>0.96</td>
<td>14</td>
<td>NS</td>
</tr>
<tr>
<td>20</td>
<td>40 v 60</td>
<td>0.18</td>
<td>16</td>
<td>NS</td>
</tr>
</tbody>
</table>

Table 13 b). Comparisons of feeding and growth responses of juvenile *N. lapillus* feeding on mussels either twice or three times their own length.
Figure 41. Feeding (——) and non-feeding (······) sequences of individual juvenile Nucella of three different initial sizes (mm ± 1mm), supplied with mussel prey of twice or three times the length of the whelk.
Figure 42. Feeding and non-feeding sequences of juvenile *Nucella* of three different initial sizes preying upon mussels.

- ◼️ mean number of days to start of first meal
- ◻️ mean number of days feeding on consecutive meals
- □️ mean number of days between consecutive attacks

Numbers above each figure refer first to the initial length of *Nucella* (mm ± 1mm), and second to the length of mussel provided as prey (mm ± 1mm, or ± 2mm for 60mm mussels). (Variable number of replicates since not all whelks fed or ate the same number of prey).
Number consecutive meals
An estimate of the amount of flesh ingested was determined by predicting initial dry weight from mussel length and subtracting the weight of remaining flesh. Several of the whelks which began feeding just prior to the 28 day deadline took a considerable time to complete this meal, up to a further 14 days. Values of ingested ration (table 12) have been adjusted to 28 days. In contrast to their response on smaller prey some whelks did not feed on these large mussels.

For those whelks that fed, both 10 and 20mm Nucella consumed significantly more flesh when feeding on the larger mussels, consumption rate was independent of prey size for 15mm whelks (table 13 b). For all Nucella sizes mean meal size was significantly greater on the larger prey (table 13 b). Mean growth rates (as mg dry flesh weight increase/28 days), for those whelks that fed, were not significantly affected by prey size (table 13 b).

Comparisons between the two Nucella sizes (10 and 15mm) feeding on 30mm mussels are summarized in table 14. The only response significantly affected by predator size was days between meals, for which 15mm Nucella spent significantly longer.

4.3.3.4 Discussion

Bayne and Scullard (1978a) report that for N. lapillus the time spent drilling and ingesting a mussel was independent of predator size since the larger predators preyed upon larger mussels. This seems an over-simplification since for a given size of predator they did not relate feeding time to size of prey. That total handling time is a function of prey size was shown here for juvenile N. lapillus and by Hughes and Dunkin (1984) for the adults.

The inter-feeding interval did not depend on prey size. This suggests that, if some hunger threshold initiates feeding, at the end
Mann-Whitney U test

| a) Number of mussels eaten | 10 | 10 | NS |
| b) Days to first meal       | 10 | 10 | NS |
| c) Days feeding on each mussel | 28 | 26 | NS |
| d) Days between meals      | 18 | 16 | <0.05 |

t-test

| e) mg flesh consumed/28days | 0.48 | 18 | NS |
| f) Mean meal size (mg)     | 1.20 | 52 | NS |
| g) mg growth/28days        | 1.47 | 18 | NS |

Table 14. Comparisons of the feeding and growth responses of 10 and 15mm *N. lapillus* feeding on 30mm mussels.
of the shorter feeding period on smaller prey, the whelks were at the same satiation level as when feeding on larger prey. Overall a greater proportion of a whelk's total time was spent feeding when eating the larger prey.

Definitive values for mean consumption rate and mean meal size cannot be given since occasionally some mussel flesh, particularly coloured gonadal tissue, visibly leached into the surrounding water. This was particularly noticeable towards the end of a long feeding period on the largest prey (45 and 60mm). Unfortunately no record was kept of which individuals were affected. Thus the question of an upper asymptotic meal size, as prey size increases, cannot be resolved with certainty from these data.

However to test whether the values obtained for mean meal size of whelks feeding on large, potentially leaky, prey are unrealistically high it is possible to compare them with the amount of flesh that can be theoretically reached (as outlined in section 4.3.2.3).

Consider a mussel of length (Lmm) to be a prolate spheroid of volume \((4\pi ab^2)/3\) where \(a = L/2\) and \(b = L/4\) since the height of mussels is approximately half the length (appendix 6). From the length:dry weight relationship of mussels, the volume required to occupy 1mg dry flesh weight can be calculated as 23.3mm\(^3\) (table 15 a). The hemispherical volume of mussel flesh that can be reached by a whelk is dependent on its proboscis length, and hence on body length. A whelk of length \(L\) mm can reach, within the mussel, a volume of \(2/3.\pi L^3\) mm\(^3\). This equates to \(2/3.\pi L^3.23.3^{-1}\) mg dry mussel flesh, and provides the maximum meal size that a whelk of given size can physically obtain. These theoretical maxima are compared with observed mean maximum meal size (table 15 b). For the two largest class of whelk, for which leaching may have been important, mean maximum meal size are half those
### a) Mussel Volume mg.dry vol/wt

<table>
<thead>
<tr>
<th>size (mm)</th>
<th>Volume (mm$^3$)</th>
<th>weight</th>
<th>ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>16.37</td>
<td>0.70</td>
<td>23.38</td>
</tr>
<tr>
<td>10</td>
<td>130.95</td>
<td>5.62</td>
<td>23.30</td>
</tr>
<tr>
<td>15</td>
<td>441.96</td>
<td>19.06</td>
<td>23.19</td>
</tr>
<tr>
<td>20</td>
<td>1047.62</td>
<td>45.30</td>
<td>23.13</td>
</tr>
</tbody>
</table>

### b) Theoretical vs. As observed

<table>
<thead>
<tr>
<th>Nucella length (mm)</th>
<th>volume can reach (mm$^3$)</th>
<th>weight can reach (mg)</th>
<th>approx. Nucella (mm)</th>
<th>Mean max. meal size (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>262</td>
<td>11</td>
<td>5-10</td>
<td>15</td>
</tr>
<tr>
<td>10</td>
<td>2095</td>
<td>90</td>
<td>10-15</td>
<td>69</td>
</tr>
<tr>
<td>15</td>
<td>7071</td>
<td>304</td>
<td>15-20</td>
<td>156</td>
</tr>
<tr>
<td>20</td>
<td>16762</td>
<td>720</td>
<td>20-25</td>
<td>380</td>
</tr>
</tbody>
</table>

Table 15 a). Calculation of volume required to occupy 1mg dry flesh weight of mussel tissue. Regression equation relating length of mussel (L mm) to dry flesh weight (W mg) used: $\log_{10} W = -2.26 + 3.01 \log_{10} L$.

b) Comparison between the dry weight of mussel flesh theoretically reachable by whelks of a given size, and the maximum mean meal size observed during growth experiments.
calculated to be available to them, and therefore probably not unrealistically high. From the above calculations it appears that the larger whelks do not exploit larger prey to the same extent as smaller whelks.

That whelks can perceive the size of prey available to them is shown by the time taken to initiate feeding. For example, when presented with large mussels (40 and 60mm) the 20mm whelks took a mean of 9.4 days to commence feeding, yet within the first week of the small-medium prey experiment the same size of whelk had consumed a mean of 5.8 15mm mussels and 2.2 20mm mussels. Similarly, both Thais haemastoma canaliculata (Garton, 1986) and Eupleura caudata (MacKenzie, 1961) were shown to be 'reluctant' to feed on large oysters.

The six whelks which failed to feed on the large prey were, at the end, each given the opportunity to feed on a 20mm mussel. They all initiated feeding within one day suggesting that their earlier lack of feeding was, in some way, due to the large size of the prey offered and not to a lack of hunger.

4.3.4 Leaching of Mussel Flesh

4.3.4.1 Introduction

In the first experiment of section 4.3, where Nucella were fed on small or medium sized prey, there was often some delay between a whelk finishing feeding on a mussel and the mussel being removed from the tank for dry weight measurement of its flesh remains. If during this period there were significant losses of mussel flesh by leaching, the consumption rate would be over-estimated. This experiment was designed to test the conditions under which leaching might have contributed significantly to loss of mussel flesh in the small-medium prey experiment.

The state of a mussel at the end of a feeding period by a whelk can
be crudely related to the relative sizes of the predator and its prey as follows;

<table>
<thead>
<tr>
<th>Mussel condition</th>
<th>Predator/Prey size relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Entire contents eaten, shell gapes.</td>
<td><em>Nucella</em> &gt;&gt; <em>Mussel</em></td>
</tr>
<tr>
<td>2) Mostly eaten, often only damaged adductor muscles and edge of mantle tissue remaining, shell gapes.</td>
<td><em>Nucella</em> &gt; <em>Mussel</em></td>
</tr>
<tr>
<td>3) Sufficient eaten to cause death and gaping of mussel shell.</td>
<td><em>Nucella</em> &lt; <em>Mussel</em></td>
</tr>
<tr>
<td>4) Insufficient eaten to cause death during feeding, shell remains closed.</td>
<td><em>Nucella</em> &lt;&lt; <em>Mussel</em></td>
</tr>
</tbody>
</table>

Leaching seemed most likely to occur in mussels left in condition 3 where the *Nucella* ate enough flesh to kill their prey but did not consume it all.

4.3.4.2 Method

Mussels in the size range 19-21mm were collected from Whitsand Bay in May 1987, one day before the start of the experiment. They were stored in the sump of the continuous immersion system (section 2.3.1), without food, until required. The mussels were subjected to one of the following three treatments:

a) A hole was drilled through the centre of one valve of the mussel shell using a burr giving a hole diameter of approximately 1mm, this being equivalent to a hole drilled by an adult whelk (section 6.3.1). The rotating burr was inserted into the mussel flesh for a depth of 1-2mm to damage the underlying mantle tissue, thus simulating a mussel left in condition 4 (above).

b) The posterior adductor muscle was severed to cause death of the mussel and to facilitate leaching of mussel flesh from the gaping
shell. This treatment would most closely simulate mussels left in condition 3 and to a lesser extent those in condition 2 (above).

c) Mussels with no manipulation as controls.

The mussels were placed separately in pots in the continuous immersion system. To determine the time course of leaching the mussels were left in the tank for a fixed period ranging from one to seven days with a daily increment. Thus seven time periods were employed with eight replicates for each of the three treatments. All the experimental animals within one time period were set up on the same day but the starting day of the time periods was randomised. All trials were started within one week of collection. At the end of the allocated time period the mussels were removed, their lengths measured and the dry weight of their remaining flesh determined.

4.3.4.3 Results

The variation in dry flesh weight content of the mussels as a function of their length, treatment and period of immersion is shown in figure 43. ANCOVA (GLIM 3.12) was performed to determine which of these variables were significantly contributing to the variance. The analysis also explored the interaction between treatment and time immersed (see below).

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>1</td>
<td>18.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>23.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Days</td>
<td>6</td>
<td>4.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction, Days:Treatment</td>
<td>12</td>
<td>3.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>146</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The significant interaction effect showed that the treatments were responding differently with differing times of immersion. Control mussels of 19mm length on day 1 were used as a reference point. Under
Figure 43. Effect of time and treatment on the individual dry flesh weight content (mg) of mussels in the experiment to determine the conditions under which leaching of mussel flesh may occur.

△ = controls,

□ = mussels with a hole drilled through one shell valve,

■ = mussels in which the posterior adductor muscle had been severed.
Mussel dry weight (mg)

Mussel length (mm)
the fitted model for predicting dry weight, estimates were given for
the mean deviation (±S.E.) of each separate parameter from the
reference point. Overall there was no significant loss of flesh from
mussels which had either a drill hole or a cut adductor muscle. Nor
were the values for any one particular day significantly lower than the
reference point. Considering all possible combinations of
treatment:day interaction effects, the only significant losses of dry
weight were found to occur for mussels with a cut adductor on day 5
(one tail t-test, $t = 1.83$, d.f. $= 146$, $P<0.05$) and more significantly
on day 7 (one tail t-test, $t = 3.72$, d.f. $= 146$, $P<0.001$). Reference to
figure 43 shows that by day 7 mussels with a cut adductor muscle had
lost, on average, half of their body flesh weight.

4.3.4.4 Discussion

These results illustrate that significant loss of flesh by leaching
would occur only if a mussel was left for over 4 days after the damage
had occurred and then only through a gaping shell (condition 3 above).
The presence of a drill hole alone did not facilitate leaching. In the
experiment on small-medium size prey (section 4.3.2) the predator-prey
regimes most likely to suffer from leaching are those where the whelk
would have taken some days to drill and consume its meal. Hence the
time gap between the cessation of feeding and the weekly observation
would be unlikely to exceed 4 days. Consumption rates here can be
regarded with confidence.

One interesting feature to emerge from this experiment was the
ability of the mussels to repair their shell after being drilled. Of
the eight mussels that had been drilled and left for 7 days, four had
new shell material partially occluding the hole, while in the remaining
four it formed a complete covering. The repair was made from material
less dense than normal shell, it extended beyond the boundary of the
hole, was dome shaped on the inside and had a rough surface. Repairs of this type had been noted in mussel shells collected from the field (section 6.4), typically on large shells with small drill holes. This suggests that even if a small Nucella can drill a large mussel successfully and feed, the mussel has some ability to recover.

4.3.5 Combined Results

By comparing the results of the experiments on small-medium prey (section 4.3.2) and large prey (section 4.3.3) the growth response of juvenile Nucella can be judged against the full size range of mussels likely to be encountered at Whitsand Bay. Growth rates were converted from mm increment in shell length to their body dry weight equivalent as in section 4.3.2.2.

Figure 44 illustrates the effect of prey size on the growth (as mg dry flesh weight increase/week) of juvenile whelks. Inclusion of the large prey has resulted in the same overall shape in the growth response for each of the four Nucella sizes, with reduced growth on proportionally small and large prey, although not all these differences are significant. T-tests for planned comparisons were used to compare growth on 'large' prey with the values obtained on 'small-medium' prey. For both 15 and 20mm whelks the growth rate on the large prey was significantly lower than that found on the plateau. Prey size had no significant effect on growth rate for the 10mm Nucella, however these whelks show the same overall growth response to prey size.

For the one predator:prey size regime that was replicated in the two experiments, 10mm Nucella feeding on 20mm mussels, the mean growth rates were equal.

The amount of mussel flesh ingested (mg/28days) did not consistently continue to rise as prey size increased (Fig. 45). The replicated 10mm whelks consumed significantly less flesh ($t = 4.64, \text{d.f.}=13, P<0.001$)
Figure 44. Effect of mussel prey size (mm ± 1mm, or ± 2mm for 60mm mussels) on growth rate (mg dry flesh weight increase/week) of juvenile *Nucella* of four different initial sizes (mm ± 1mm). Plots are means (± S.E.) of 5 replicates from the small-medium prey experiment (●) and of 6-10 replicates from the large prey experiment (○). Vertical bars to the right of each figure connect means among which there are no significant differences.
Mussel size class mm

Growth mg/7 days

5mm Nucella

10mm Nucella

15mm Nucella

20mm Nucella
Figure 45. Effect of mussel prey length (mm) on the consumption rate (mg dry flesh weight/28 days) of juvenile Nucella of four different initial length (mm). Points are means (±S.E.) for 5 replicates of the small-medium prey experiment (●) and for 6-10 replicates of the large prey experiment (○). Dashed lines connect to trials where leaching may have influenced observed consumption rates.
when part of the large prey experiment than when part of the small-medium prey. Mean meal size continued to rise as prey size increased (Fig. 46).

Gross growth efficiency (k1), defined as mg increase in predator dry body weight during the feeding period plus seven days, divided by the mg dry flesh weight of mussel flesh ingested during the feeding period, was calculated for each whelk that fed. Mean gross growth efficiency for the two smaller Nucella size classes was a decreasing function of prey length (Fig. 47). For the two larger whelk sizes, mean k1 values initially rose as prey size increased and then declined on the larger mussels.

4.3.6 Discussion

It is recognised that some caution must be exercised in combining the growth data from the experiments on small-medium prey (section 4.3.2) and large prey (section 4.3.3) since the experimental designs were not identical. The differences in procedure most likely to contribute to variation in response were a) a reduction in the total surface area for all but the 60mm mussels and hence a possible reduction in encounter rate in the large prey experiment, and b) whereas the small-medium prey experiment was replicated at different times of year to overcome possible inherent seasonal variation in growth rate, all replicates of the large prey experiment were carried out simultaneously.

Variations in the growth rate of molluscs are brought about by the interaction of an array of exogenous and endogenous factors. The present study was aimed at detecting the effect of a single factor, namely, prey size. Following I.B.P. terminology (Ricker, 1968) the net energy exchange of an individual organism with its environment is described by the standard energy budget equation.
Figure 46. Effect of mussel prey length (mm) on the mean meal size (mg dry flesh·weight) taken by juvenile *Nucella* of four different initial lengths (mm ± 1mm). Dashed lines connect to trials in which leaching may have over-estimated meal size.
Figure 47. Effect of mussel prey size (mm $\pm$ 1mm, or $\pm$ 2mm for 60mm mussels) on the gross growth efficiency of juvenile *Nucella* of four different initial sizes (mm $\pm$ 1mm). Gross growth efficiency defined as mg dry flesh weight increase during 4 weeks of feeding plus one week of starvation, divided by mg dry weight of mussel flesh consumed. Plots are means ($\pm$ S.E.) of 5 replicates from the small-medium prey experiment (●) and 6-10 replicates of the large prey experiment (○).
where $C$ is the energy content of the food consumed, $F$ is the unabsorbed energy lost as faeces, $U$ the absorbed energy lost as excretory products, $R$ is energy equivalent of metabolic heat loss and $P$ is production, the energy incorporated into growth and reproduction. Growth can only occur when energy acquisition exceeds energy expenditure. The rate at which energy is made available for growth and reproduction, scope for growth (Warren & Davis, 1967), is derived from equation 6.

$$SPG = aC - (R + U)$$
eqn 7

where $SPG$ is scope for growth, normally expressed as energy per unit time, and $a$ is the absorption efficiency, such that $a = (C - F) / C$. That scope for growth, when estimated as an analysis of the energy budget, provides a reasonable predictor of growth as observed has been shown for mussels (Bayne et al., 1979; Bayne & Worrall, 1980). For *Nucella lapillus*, Stickle and Bayne (1987) showed that $SPG$, predicted from physiological measurements, was positively correlated with change in body energy content (determined from changes in shell length).

Using growth rates as a measure of fitness, the value to be optimized as a result of the foraging strategy is $P (=SPG)$, which will depend on the rate at which resources can be acquired and the efficiency with which they can be utilized. All of the processes involved in the energy budget equation are capable of variation in response to environmental changes. It is the interaction of these processes, in the context of previous studies on physiological adaptation, that I now wish to explore in an attempt to explain how changes in prey size bring about changes in growth rate.

One measure of efficiency, gross growth efficiency, ($k1$), is the capacity of an animal to convert food into flesh. Recorded absolute
values of $k_1$ for gastropod predators have shown in some instances to decline with age. Broom (1982) quotes that for Natica maculosa and Thais carinifera, $k_1$ values decline steadily from a maximum of 26% for small individuals to 0.4% for large ones. Similarly, for Polinices duplicatus the value fell from 48% for 1-2 year olds to 16% for 3-4 year old animals (Edwards & Huebner, 1977). Although gross somatic efficiency in Polinices alderi declined from values of 20-30% with age (Ansell, 1982c), when reproductive production was included overall gross growth efficiency remained constant at 38-42%.

In the present study $k_1$ values were in the range 4-24%, variations of which were more dependent on prey size than on predator size, with the possible exception that 20mm Nucella displayed a lower maximum value than the three smaller sizes. Bayne and Scullard (1978a) calculated scope for growth for a range of N. lapillus sizes (10-35mm shell length) and from their data (table VI) gross growth efficiency can be calculated as $\text{SFG} \times 0.66 \times \text{assimilated ration}^{-1}$. There was no effect of whelk size on $k_1$, all values fell within 43-49%. The determination of scope for growth, by physiological measurement of the energy budget, is independent of the differential partitioning of resources to somatic growth and reproduction. The lack of any correlation between $k_1$ values and size from the SFG measurements, but the indication here that 20mm Nucella have lower gross growth efficiencies, suggests that the latter organisms, although not reproductively active, may be partitioning some energy into preparation for reproduction. The values of $k_1$ calculated from Bayne and Scullard's data (1978a) are twice the maximum found in the present context.

In a later study Stickle and Bayne (1987) report that the maximum mean gross growth efficiency of 23.4% for Nucella lapillus in the size
range 23-28mm feeding on 15-20mm mussels occurred at 15°C, 30°/oo and under constant immersion. These environmental conditions correspond closely to those in the present study where the equivalent k1 value for 20mm whelks was 11-13%. The above value quoted by Stickle and Bayne was derived from scope for growth estimates, and although actual growth correlated positively with scope for growth, when calculated on the basis of observed growth, k1 for the same set of animals falls to 0.7%. Clearly reported values of k1 for predatory gastropods are very variable and encompass the range found in the present study.

The pattern of gross growth efficiency as a function of prey size varied for the different sizes of whelk. In general maximum k1 values were found to occur at an increasing mussel size as whelk size increased. A similar response was found for mussels with an increasing available ration (Thompson & Bayne, 1974). Since k1 values were all positive, consumption of mussel flesh, for all predator-prey combinations, was sufficient to cover metabolic costs. For the two largest sizes of whelk, small mussels were concomitant with reduced ingestion rates and lower k1 values, indicating that on small prey a greater proportion of the ingested ration was required for metabolic demands.

Paloheimo and Dickie (1966) showed that for a number of fish species log k1 was inversely linearly related to the amount of food consumed (the k-line), however since k1 is zero at maintenance ration it must increase before it can decrease (Kerr, 1971). In figure 48, log k1 is plotted as a function of daily ration for each predator-prey combination. The efficiency with which food is utilised for growth does depend on consumption rate, but there are some interesting exceptions. For the encircled pairs of data, a comparison can be made between whelks of a given size which consumed a roughly equivalent
Figure 48. Mean gross growth efficiency ($k_1$) plotted as a function of mean consumption rate (mg dry weight mussel flesh/28 days) for *Nucella* of 4 different initial sizes (mm ± 1mm): (*—*•) = 5mm, (•—•) = 10mm, (▲—▲) = 15mm, (■—■) = 20mm. Mussel prey size classes (mm) given alongside each point. Points are means of 5 replicates from small-medium prey trials (solid symbols) and of 6-10 replicates from large prey trials (open symbols). Encircled points link values where a given size of whelk consumed approximately equal amounts from different size prey. In each case $k_1$ values were higher on the smaller prey.
amount of flesh, but from different sized prey items. In each case $k_1$ was lower on the larger prey item, indicating that $k_1$ depends not only on daily ration, but also on meal size, the amount of flesh eaten at one sitting, which is directly related to prey size.

To understand further the relationship between growth rate and prey size consideration should be taken of the other energy demands that are made upon the ingested ration and the efficiency with which the food is utilized, as summarized by equation 7.

For all predator sizes reduced growth rates on proportionately small prey can be attributed to lower ingestion rates, but those found on large prey are less easily explained. In general consumption rates on large prey were equal to or greater than those on medium-sized prey, yet growth rates were significantly lower. From the SFG equation it follows that reduced growth from an increased ration could occur if a) proportionately more energy were required for the metabolism of excretory products and for the production of mucus, i.e. an increase in $U$ on high consumption rates; b) high consumption rates resulted in an increase in respiratory rate ($R$), either for the acquisition of the extra food or for its subsequent processing; or c) a decrease in absorption efficiency ($a$) with an increase in consumption rate and/or with increasing food-packet size.

Which of these processes, or any combination, is responsible for the observed drop in growth rate on large prey cannot be resolved from the present data. There is a lack of energy budgets reported in the literature for animals eating different-sized packets of food, but several reports of growth potential in relation to ration size, mainly for filter feeders. For example, Thompson and Bayne (1974) found a similar response to the amount of energy available for growth and reproduction in mussels fed on a range of algae ration sizes. The
optimum ration for SFG occurred at intermediate ration levels. The single most significant factor causing SFG to drop at high rations was the reduction in assimilation efficiency which fell from 0.9% on low ration to 0.2% on the highest ration.

An estimate of assimilation efficiency can be obtained from the present data, using estimates of the other energy requirements reported in the literature. From \( P = aC - (R + U) \), assimilation efficiency, \( a \), becomes \( R + U + P / C \), of which only \( P \) and \( C \) have been measured. Mollusc losses due to excretion are often ignored as being negligible, estimated by difference in the energy budget equation e.g. 7% of ingested energy for Navanax inermis (Paine 1965) or guessed at e.g. as 7% for Tegula funebralis (Paine, 1971) and 15% for three species of opisthobranch (Carefoot, 1967). Where measurements have been made of the energy losses due to excretion there is evidence that this component of the energy budget may make up a significant proportion of the total energy loss, particularly if the animal produces mucus for locomotion, feeding or faeces production. For example, as a percentage of total energy intake, energy losses due to \( U \) made up 11-19% for Hydrobia ventrosa (Kofoed, 1975) and 4% for adult N. lapillus (Stickle & Bayne, 1987). In freshwater gastropods the percentage of absorbed energy for total excretory losses was as high as 13-32% (Calow, 1974).

None of the above studies reported that a proportionately greater amount of energy was required for excretion with increasing ration size, so by taking this component of the energy budget to be a mean value of 10% of the ingested ration, the amount is dependent solely on consumption rate.

Respiratory losses often form a major component of the energy losses as a proportion of that absorbed. From a survey of marine molluscs of all feeding types, a mean value of 64% (S.D. = 19.3%) is reported.
Although metabolic energy expenditure can be affected by a wide range of environmental and endogenous factors, the effect of body size and temperature rank as the most important (Bayne & Newell, 1983). The relationship between body size and metabolic rate has been described by the allometric equation:

$$ Y = a X^b $$

where $Y$ is the metabolic rate, $X$ is body size and $a$ and $b$ are fitted constants. To estimate the energy required for metabolism by the present whelks, the trapezoidal rule was applied to the lengths of individual snails as measured weekly, and converted to body dry weight equivalents. The amount of mussel flesh required to meet the metabolic demands of animals of this size were calculated by data supplied by Bayne and Scullard (1978a). The conversion equations are summarized in table 16.

It has been assumed that the metabolic demand depends only on the size of whelk and not on the prey size. Although there is evidence to suggest that metabolic energy demands fall during periods of starvation in *N. lapillus* (Bayne & Scullard, 1978b), or on low ration in mussels (Thompson & Bayne, 1974) the latter study reported that once the optimal ration had been reached respiratory costs did not increase further with increasing ration. Furthermore, Garton (1986) found no difference in total energy losses (via oxygen consumption, primary amine or ammonia excretion) between oyster drills feeding on small or large oysters, although differences in SFG were established.

Mean assimilation efficiencies, calculated from observed consumption and production rates, and from estimated rates of energy loss due to excretion and metabolism, are plotted as a function of prey size in figure 49. For all predator-prey size combinations estimated assimilation efficiencies fell largely within the range 30 to 70%.
length of *Nucella* converted to weight

\[ \log_{10} W = 0.925 + 3.14 \log_{10} H \]

where \( W \) = mg dry flesh weight

\( H \) = length in cm

oxygen consumption related to size (16°C)

\[ \log_{10} V_{O_2} = 0.709 + 0.511 \log_{10} W \]

where \( V_{O_2} \) = uls O₂ consumed/hr

\( W \) = mg dry flesh weight

conversion of oxygen consumption to calories consumed

4.8 calories/ml O₂

calorific value of mussel flesh

5.2 cal/mg flesh

Table 16. Calculation of metabolic requirements of developing *N. lapillus* (all data from Bayne & Scullard, 1978a). Final value provided in mg of mussel flesh for comparison with amount consumed.
Figure 49. Estimated assimilation efficiency in juvenile *Nucella* of four different initial sizes (mm ± 1mm) as a function of mussel prey size, (mm ± 1mm, or ± 2mm for 60mm mussels). Plots are means (± S.E) of 5 replicates from the small-medium prey experiment (●) and of 6-10 replicates from the large prey experiment (○). Dashed lines connect to points where leaching may have over-estimated observed consumption rates.
Aquatic carnivores tend to have high assimilation efficiencies, a range of 30 to 90% was quoted by Welch (1968). Assimilation efficiencies among *Thais* species have been variously reported as 66% for *N. lapillus* (Bayne & Scullard, 1978a), 2-59% for *N. lapillus* (Stickle, 1985) and 86-91% for *Thais haemostoma canaliculata* (Garton, 1986), although the latter study did not take losses due to mucus production into account.

However for an animal faced with a variable food supply, it is the variability in assimilation efficiency which is more important than the absolute mean value. For each predator size, assimilation efficiency dropped from a maximum value of approximately 70% on small prey, which provided a low ration, and came in small packets, through intermediate values on medium sized prey to a lower plateau level of approximately 30% on large prey. An inverse relationship between ingestion rate and assimilation efficiency has been noted for *Ancylus fluviatilis* and *Planorbus contortus* (Calow, 1975a), mussels (Thompson & Bayne, 1974; Widdows, 1978), *Daphnia magna* (Schindler, 1968), *Diaptomus gracilis* (Schindler, 1971), *Daphnia pulex* (Richman, 1958) and an oligochaete (Streit, 1978).

However in some animals assimilation efficiency remains constant over a wide range of feeding rates (see Lawton, 1970 and references therein).

From a physiological viewpoint the negative correlation between assimilation efficiency and both consumption rates and meal size can be attributed to the relative size of the consumed meal and gut capacity. Increased assimilation efficiency on small meals could be brought about by more efficient mixing of gut contents and gut secretions thus allowing a greater surface area of the ingested food contact with digestive enzymes. Concurrently there may be an increased residence time within the gut. Calow (1975b) has shown that for two freshwater
gastropods, satiated animals showed an increase in gut emptying rate over starved animals. In particular, for starved animals there was a reduced rate of passage though the hepatopancreas, the major site of digestion and absorption.

Whilst accepting Calow's (1977) homeostatic viewpoint that fitness is ultimately proportional to the rate at which useful energy is gained by the predator and that hence a flexibility in metabolic adaptation will be of considerable survival value with a fluctuating food resource, it is not clear why assimilation efficiencies should actually drop on large prey. With a constant or even increasing consumption rate it might be expected that the animal would be able to maintain a constant flow of energy over the gut wall. The crucial element may lie in the size of the meal. If absorption rates are initially high when the gut is comparatively empty but then decline with increasing fullness of gut to some lower asymptotic value, when gut emptying equals food intake rate, then for a given amount of food consumed, a few large meals would result in less overall food absorbed than would a series of smaller meals.

Low growth rates on large prey is not in itself of adaptive significance. The whelks were faced with two alternatives, either to feed on the large prey or not to feed at all. Having invested a considerable amount of resources into gaining access to the large meal, the animal does not then only consume sufficient to provide for maximum efficiency.

Such apparently wasteful behaviour has been highlighted by Branch (1981). From his study of limpets Branch draws a distinction between 'conserver' and 'exploiter' species which have differing metabolic strategies that depend on food supply. 'Conservers', which experience food shortages, conserve energy resources by efficient absorption and a
reduction in both metabolic and excretory energy demands. Conversely, 'exploiters', which have an abundance of food, have high rates of metabolism and mucus production and low absorption efficiencies. Within an individual species of limpet, some degree of variability in the pattern of food utilization was noted.

One specific example of metabolic adaptation in the face of a variable food supply was provided by the present study. At low prey density, 10mm whelks feeding on 20mm mussels ate fewer mussels, consumed less flesh, yet by having a higher assimilation efficiency grew as much as whelks at a prey density eight times higher. A similar response was found by Ansell (1982b) in that Polinices catena ate fewer and grew less on low prey density but conversion efficiencies (as mean total weight increment per prey item consumed) were increased.

A few previous studies on predatory gastropods have attempted to relate some aspect of growth to prey size. Palmer (1983) used net growth as a measure of prey value for three thaidid species feeding on, among others, three sizes of mussel (size range 20.0 to 52.5mm). In only seven of eighteen instances were growth rates significantly affected by mussel size, but in each of these there was a decrease in growth rate on the largest mussels, as found here. Increase in predation and consumption rates were responsible for increased growth rates of Clione limacina when feeding on large Spiratella retroversa (Conover & Lalli, 1972).

In contrast to the present study, Garton (1986) found that consumption rates of oyster drills were higher on a small oyster diet than on a large oyster diet. Since there was no difference in energy losses between the two groups, significantly increased SPG was found on small oysters. However the efficiency with which the consumed food was used, both gross and net gross efficiencies, were significantly higher.
on the large prey diet. This Garton attributed to the observed
reduction in absorption efficiency with higher consumption rates in the
small oyster diet group. So in the case of the oyster drills, large
meal size did not reduce assimilation efficiency as has been suggested
for the whelks in the present study.
CHAPTER 5 HANDLING COSTS AND DETERMINATION OF RATE OF ENERGY GAIN

5.1 Introduction

The optimal foraging theory predicts the behaviour of animals while they are foraging. The energy maximization hypothesis states that, faced with a choice of food, a predator should choose items that maximize reward, usually defined as the net energy gain per unit feeding time (Schoener, 1971).

The energy gain from an item of prey is strictly the net energy assimilated from a food item, i.e. gross energy extracted minus energy costs of handling and digesting the food (Townsend & Hughes, 1981). In practice handling and digestive costs are usually assumed to be equal for the different prey items, and energy gain is made equivalent to energy intake (Elner & Hughes, 1978; Hughes & Elner, 1979; Cook & Cockrell, 1978; Kitchell et al., 1981; Dunkin & Hughes, 1984; Hughes & Dunkin, 1984; Bence & Murdoch, 1986). Energy value of a prey item becomes energy intake from that item divided by the time taken to handle that prey item.

This approach was adopted in the determination of energy value of different size mussels, as prey, to juvenile N. lapillus. The present chapter is concerned with the determination of the functional relationships between handling costs and predator and prey size. From these relationships, energy gain per unit handling time (E/T_h) has been determined. Inspection time has not been included, handling costs are considered only as drilling and ingestion time.

5.2 Drilling Rates

5.2.1 Method

The rate at which dogwhelks can penetrate mussel shells was determined by interruption of the drilling process. Single mussels,
housed in experimental pots (section 2.3.2) were left in the continuous immersion system (section 2.3.1) overnight to allow them time to attach. Whelks of varying size (range 5.3 to 31.9 mm) were added singly to each pot the following morning. The size of mussel allocated to each whelk was generally once to twice the length of the whelk, to ensure that the time required for complete penetration of the shell exceeded the time allowed for drilling.

A drawing was made of the position of each whelk in relation to its prey every 30 minutes for the next 8 hours. At the end of this period any whelks which were in close contact with a mussel in a potential feeding position, and had been stationary for at least one hour, were left undisturbed. Other whelks were removed from the pots. Drilling time was taken as the time from a settled feeding position to the time that the whelks were removed (range 15 to 23 hours later). For large whelks depth of borehole was determined by taking four measurements of mussel shell thickness around the hole to obtain a mean and subtracting the depth of remaining shell at the hole site. The use of a pointed anvil micrometer allowed accurate shell thickness measurements (to within 0.005 mm) of all parts of the curved mussel shell. For smaller whelks the diameter of the hole was less than that of the points of the micrometer, so hole depth was measured directly using a Zeiss standard 14 as a travelling microscope (again to within 0.005 mm). As a check of consistency between the two methods, some holes were measured by both techniques.

5.2.2 Results

The two methods of measuring hole depth, by micrometer and microscope, did not yield significantly different values (t-test for paired comparisons, t = 0.024, d.f. = 8, NS). The rate of drilling (mm/hour) as a function of whelk size displayed considerable variation.
(Fig. 50). Some of this variation may be explained by the experimental procedure. Initiation of drilling was taken as the beginning of the sequence in which no further change in whelk position was noted. However a static predator on a prey item provides no guarantee of boring activity, so recorded boring rates may be an under-estimate of actual rates. Furthermore, since the observations were limited to half hourly intervals, error in the time of a settled position could have been ± 30 minutes. However this timing error is negligible (+3%) compared with the average total time allowed for drilling.

The relationship between Nucella size (x mm) and drilling rate (y mm/hour) was explored by MLP (maximum likelihood program). An exponential function of the form

\[ y = A - B e^{-kx} \]  

eqn 8

provided a significantly better fit \( F = 9.0, \text{d.f.} = 1,62, P<0.01 \) than least squares linear regression. The fitted parameters of the exponential function were;

<table>
<thead>
<tr>
<th>Parameter</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.01505</td>
</tr>
<tr>
<td>B</td>
<td>0.02233</td>
</tr>
<tr>
<td>K</td>
<td>0.20048</td>
</tr>
</tbody>
</table>

Observed measurements, along with the fitted function, are given in figure 50.

5.2.3 Discussion

Drilling rate of Polinices duplicatus on Mercenaria were independent of predator size (range 23.5 to 57mm) and time elapsed since the initiation of boring (Kitchell et al., 1981). Anala (1974, cited Crothers, 1985) found no correlation between the size of Nucella lapillus and the time taken to penetrate the shells of mussels or barnacles (predator size range and number of readings unknown). In
Figure 50. Functional relationship between *Nucella* length (mm) and drilling rate (mm/hour). Curve relates drilling rate \( (y) \) to *Nucella* length \( (x) \) according to the exponential function:

\[ y = 0.01505 - 0.02233 \ e^{-0.20048x} \]
contrast the present data suggest that drilling rate increases rapidly up to a size of approximately 12mm although it is effectively independent of size for whelks over 12mm.

Penetration of the prey shell is a repeated combination of chemical dissolution by activity of the accessory boring organ (Chetail & Pournie, 1969; Webb & Saleuddin, 1977) followed by scraping of the softened material by the radula (Fretter & Graham, 1962; Carriker, 1981). It might be envisaged that rate of shell dissolution, being chemical, is independent of whelk size but that the scraping phase, being mechanical, is more efficiently performed by larger whelks.

The mean rate of drilling found in the present study is in close agreement with other estimates for muricid gastropods, which appear consistently lower than for naticids (table 17). The average asymptotic value provided by the exponential function above gives a daily drilling rate of 0.36mm, exactly the value estimated for adult N. lapillus by Hughes & Dunkin (1984), although at the lower temperature of 12°C.

5.3 Mussel Shell Thickness
5.3.1 Method

All the drilled mussel shells collected from Whitsand Bay, as part of the field survey (section 3.2), in March, September and October 1985 were examined for shell thickness and position of boreholes. The thickness of the shell at the borehole site was estimated as the mean of four measurements around the hole. Shell thickness was measured (to within 0.01mm) with a pointed anvil micrometer.

The maximum length (L mm) and height (H mm) of each shell was recorded. For shells larger than about 10mm shell dimensions were measured with vernier calipers, smaller shells were measured using a binocular microscope and graduated eye-piece (both to within 0.1mm).
<table>
<thead>
<tr>
<th>Predator (Naticid Muricid)</th>
<th>Temp. °C</th>
<th>n</th>
<th>Predator size range (mm)</th>
<th>Method</th>
<th>Mean rate drilling mm/day</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lunatia nitida (N)</td>
<td>?</td>
<td>1</td>
<td>8.0</td>
<td>?</td>
<td>0.60</td>
<td>Ziegelmeier, 1954</td>
</tr>
<tr>
<td>Polinices duplicatus (N)</td>
<td>20</td>
<td>18</td>
<td>23.5 -57.0</td>
<td>a)</td>
<td>0.54</td>
<td>Kitchell et al., 1981</td>
</tr>
<tr>
<td>Murex erinaceus (M)</td>
<td>10-15</td>
<td>2</td>
<td>25.0 -26.0</td>
<td>a)</td>
<td>0.30</td>
<td>Pieron, 1933</td>
</tr>
<tr>
<td>Urosalpinx cinerea (M)</td>
<td>?</td>
<td>36</td>
<td>?</td>
<td>?</td>
<td>0.40</td>
<td>Federighi, 1931</td>
</tr>
<tr>
<td>Urosalpinx cinerea (M)</td>
<td>?</td>
<td>?</td>
<td>adults</td>
<td>?</td>
<td>0.50</td>
<td>Galtsoft et al., 1937</td>
</tr>
<tr>
<td>Urosalpinx cinerea (M)</td>
<td>19-20</td>
<td>2</td>
<td>36.5 -37.3</td>
<td>b)</td>
<td>0.32</td>
<td>Carriker &amp; Van Zandt, 1972</td>
</tr>
<tr>
<td>Nucella lapillus (M)</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>0.34</td>
<td>Ziegelmeier 1954</td>
</tr>
<tr>
<td>Nucella lapillus (M)</td>
<td>12</td>
<td>20</td>
<td>adults</td>
<td>c)</td>
<td>0.36</td>
<td>Hughes &amp; Dunkin, 1984</td>
</tr>
<tr>
<td>Nucella lapillus (M)</td>
<td>15</td>
<td>65</td>
<td>5.0 -31.9</td>
<td>a)</td>
<td>0.32</td>
<td>Present study</td>
</tr>
</tbody>
</table>

Table 17. Drilling rates of boring gastropods.

Method a) = interrupted drilling, b) = microhydrophone recordings of radular movements and c) calculated from total feeding time minus estimated ingestion time.
Hole position was quantified as the horizontal distance of the borehole from the anterior end of the shell (A mm) and from the ventral surface (B mm), (Fig. 51). Measurements were made to within 0.5 mm, again using calipers or microscopic examination, as appropriate, care being taken to avoid parallax errors.

5.3.2 Results

The best fit functional relationship between mussel shell thickness (Y mm) and the three separate variables, shell length (L mm), distance from the anterior end of the shell (A mm) and distance from the ventral surface (B mm) were:

\[
\begin{align*}
\log_{10} Y &= a_1 + b_1 \log_{10} L \\
\log_{10} Y &= a_2 + b_2 \log_{10} \frac{L}{A} \\
\log_{10} Y &= a_3 + b_3 \log_{10} \frac{H}{B}
\end{align*}
\]

For each month separately, stepwise regression analysis was performed on the transformed data to determine if all three variables were contributing significantly to shell thickness (table 18). The partial regression coefficient of \( \log_{10} \frac{H}{B} \) was not consistently different from zero, so to simplify the relationship this variable was removed from the model and a new multiple regression equation fitted. In the reduced model the partial regression coefficients associated with both mussel length and position on the shell in relation to the anterior end, were consistently and highly significantly different from zero. Consequently the reduced model was deemed appropriate.

Analysis of covariance (method in Zar, 1984, p347) revealed that there was a significant difference between the months (F = 3.9, d.f. = 6,456, P < 0.001), and that March was different from the other two months. Plausibly this inconsistency resulted from the difference in the size frequency distribution of the mussels measured. Whereas in March mussels of less than 10 mm length made up only 3% of the total, in
Figure 51.

a) Measurements used to determine position on the mussel shell from which shell thickness dimensions were taken.

b) Qualitative effect of position on the thickness of a mussel shell. Arrows point to regions of increasing thickness.
<table>
<thead>
<tr>
<th>Date</th>
<th>Variable</th>
<th>b</th>
<th>Sb</th>
<th>d.f.</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L</td>
<td>0.8591</td>
<td>0.0451</td>
<td>179</td>
<td>19.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L/A</td>
<td>0.2554</td>
<td>0.0212</td>
<td>179</td>
<td>12.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>log&lt;sub&gt;10&lt;/sub&gt; H/B</td>
<td>-0.0852</td>
<td>0.0238</td>
<td>179</td>
<td>-3.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>a = -1.6513</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L</td>
<td>0.9236</td>
<td>0.0499</td>
<td>91</td>
<td>18.53</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L/A</td>
<td>0.1487</td>
<td>0.0404</td>
<td>91</td>
<td>3.69</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>log&lt;sub&gt;10&lt;/sub&gt; H/B</td>
<td>-0.0463</td>
<td>0.0595</td>
<td>91</td>
<td>-0.78</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>a = -1.7088</td>
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<td>October</td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L</td>
<td>1.0404</td>
<td>0.0302</td>
<td>183</td>
<td>34.47</td>
<td>&lt;0.001</td>
</tr>
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<td></td>
<td>log&lt;sub&gt;10&lt;/sub&gt; L/A</td>
<td>0.1486</td>
<td>0.0193</td>
<td>183</td>
<td>7.70</td>
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<td>log&lt;sub&gt;10&lt;/sub&gt; H/B</td>
<td>-0.0677</td>
<td>0.0258</td>
<td>183</td>
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<td>a = -1.8375</td>
<td></td>
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</tr>
</tbody>
</table>

Table 18. Statistics provided by the multiple regression analysis of mussel shell thickness (Y) in relation to mussel shell length (L) and position on the shell (L/A and H/B), according to the model

\[ \log_{10} Y = a + b_1 \log_{10} L + b_2 \log_{10} L/A + b_3 \log_{10} H/B \]

(A and B defined in Fig. 51). Sb = standard deviation of coefficient.
September and October they made up 28% and 27% respectively. To ensure that all mussel sizes were represented the data from the three samples were combined and an overall multiple regression analysis performed, giving:

\[ y = -1.80 (+0.027) + 0.977 (+0.022) x_1 + 0.161 (+0.013) x_2 \]

\[ \text{eqn 9} \]

where \( y = \log_{10} \text{shell thickness (mm)} \)

\[ x_1 = \log_{10} \text{shell length (mm)} \]

\[ x_2 = \log_{10} \text{shell length / distance from anterior end,} \]

\( F = 1047, \text{d.f.} = 2,462, P<0.001 \) (values in parentheses = S.D.).

5.3.3 Discussion

Mussel shell thickness varies with location, slower growing intertidal mussels possess thicker, heavier shells relative to their length than subtidal populations (Fox & Coe, 1943; Baird & Drinnan, 1957). For the intertidal population under study shell thickness was directly proportional to length of mussel, modified by position on the shell. The shell was thickest at the anterior end, in the oldest part, becoming progressively thinner towards the outer margin in the region of newest growth. The tendency for the shell to be thicker towards the dorsal surface was due to the particularly thickened ridge at the hinge region. Within any one area of shell variation occurred on a small scale, with thickened ridges that have variously been attributed to annual growth rings (Seed, 1973) or to disturbances caused by exposure to wave action (Harger, 1970).

5.4 Ingestion Rates

5.4.1 Introduction

Ingestion rates were determined using mussels in which the posterior adductor muscle had been cut, allowing whelks easy access to the flesh. This procedure produced a far higher feeding response rate from whelks than provision of intact mussels. Although rates of ingestion from a
gaping mussel may differ from those through a borehole, the alternative
was to allow whelks to drill and then consume, applying mean drilling
rate to estimate the transition point between drilling and ingestion.
By this method variation in drilling rate would have added to variation
in measured ingestion rate.

5.4.2 Comparison of Methods to Assess Amount Ingested

5.4.2.1 Introduction

Measurement of ingestion rate by Nucella requires an assessment of
the amount of mussel flesh consumed, an estimate of which can be gained
by the difference between initial and final weight of the prey. The
usefulness of dry weight and wet weight differences was explored by
comparing the results with a known amount removed.

5.4.2.2 Method

The posterior adductor muscle was cut in twenty mussels of varying
size (range 10.4 to 28.3mm). The gaping shell of each mussel was
stood, dorsal side uppermost, on absorbent paper to allow the mantle
cavity fluid to drain out. The shell surface was blotted dry and the
entire animal weighed. Each mussel was placed in a separate pot in the
continuous immersion system (section 2.3.1) for four hours, after which
the drying and draining procedure was repeated.

A portion of the mussel flesh was removed, the amount varied
randomly but included gonad and digestive gland first to simulate the
feeding preference of a whelk. The wet weight of the removed portion
was determined and the dry weight found after 24 hours of oven-drying
at approximately 90°C. These weights represented the real amount
'eaten' against which the values estimated by the two separate methods
could be judged.

Mussels from which the portion had been removed were blotted dry and
drained as previously described. A wet weight value for these
mutilated mussels was found, the remaining flesh removed, weighed, oven-dried and re-weighed. Figure 52 provides a flow diagram of the method and the values computed.

To assess the amount of flesh ingested by the dry weight method, the dry weight of the flesh remains was subtracted from the predicted initial dry weight for a mussel of that size. The predicted values were gained from a length:dry weight least squares regression analysis performed on log transformed data of a separate sample of mussels from the same batch (n = 30),

\[
\log_{10} \text{mg dry weight} = -2.30 + 3.10 \log_{10} \text{mm length}, \quad F = 1368, \quad \text{d.f.} = 1,28, \quad P<0.001. 
\]

Amount ingested by the wet weight method, was taken as the difference between initial wet weight and wet weight following mutilation. Wet weight of flesh was converted to its dry equivalent from a wet:dry weight conversion factor established on the same mussels. The mean wet:dry ratio used was 5.45 (S.E. = 0.16), one data point was removed completely since it gave a spurious wet:dry ratio of 11.1.

5.4.2.3 Results

The differences in total animal drained wet weight before and after the 4 hour immersion period, expressed as a percentage of the first weighing, varied from +4 to -14\% (mean = -5.7\%). A t-test for paired comparisons showed that the mean difference between the pairs of data was significantly different from zero (t = 5.2, d.f. = 18, P<0.001). The overall reduction in wet weight could have been due to an actual loss of organic material from the damaged mussels or to low reproducibility of the draining procedure. The first hypothesis can be tested. Since the total dry weight of each animal was known (dry weight 'eaten' + dry weight flesh remains) these could be compared with
WHOLE MUSSEL

cut adductor muscle,
drain and weigh — — — → wet weight 1
(A)
leave 4 hrs in sea-water

drain and re-weigh — — — → wet weight 2
(B)
remove portion of flesh ('eaten')

'EATEN'

wet weight ← — — wet weigh 'eaten'
(F)
drain & weigh — — → wet weight entire animal — whole mussel remains
(C)

ovendry 24 hrs

'dry weight ← — — weigh 'eaten'
(G)
remove flesh — → wet weight flesh remains
(D)

ovendry 24 hrs

weigh — — — → dry weight flesh remains
(E)

length/dry weight relationship (H)

Real amount 'eaten' = G

Amount eaten by dry weight method = H - E

Amount eaten by wet weight method = (A - C) / (D / E)

Figure 52. Flow diagram to assess amount ingested by dry and wet weight methods.
weights predicted by the length:dry weight regression. The mean difference between actual and predicted dry weight represented a mean loss of only 0.6mg, which was not significant (paired comparisons t-test, t = 0.22, d.f.= 18, NS). It must be concluded that there was no actual loss of flesh by leaching but that there was incomplete draining of mantle cavity fluid in the initial weighings.

To determine which of the two methods provided the best estimate of the amount 'eaten' the dry weight values of each method were compared with those of the actual amount removed. An accurate method would provide a ratio of real loss:predicted loss close to unity. The mean ratio for the dry weight method was 0.99 (S.D.= 0.37) and for the wet weight method 0.65 (S.D.= 0.15) The paired comparison t-test showed that the mean of the differences between the real and estimated amount 'eaten' was not significantly different from zero in the dry weight method (t = -0.22, d.f.= 18, NS) but was significantly different for the wet weight method (t = -4.77, d.f.= 18, P<0.001).

5.4.2.4 Discussion

There was no apparent loss of mussel flesh, by leaching, during the 4 hours of immersion. An accurate prediction of the average amount of flesh removed was provided by the dry weight method, although the results were highly variable. The dry weight method will be sensitive to variability in flesh content of mussels of a given size because the initial dry weight has to be estimated from an average dry weight:length relationship. However when the results are pooled, the average response is close to the real one.

By contrast the wet weight method did not accurately predict the real value, it consistently over-estimated the amount removed, due to lack of reproducibility of the draining procedure from one occasion to another. The method was, however, less variable, since it was not
subject to inherent variation in flesh content.

To procure an average real value of the amount of flesh ingested the dry weight method should be employed, while to obtain the overall response, the wet weight method will provide less variable results.

5.4.3 Time Course of Ingestion

5.4.3.1 Introduction

When feeding on a single prey item the ingestion rate of insect predators has been shown to be a declining function of the time spent feeding (Cook & Cockrell, 1978). An analogous response would be expected for *Nucella* since at one sitting it can consume at least twice its own body weight in mussel flesh, a process taking several days. To determine the effect of time since the commencement of feeding on the amount of flesh ingested, whelks were monitored for a range of time intervals.

5.4.3.2 Method

Both wet and dry weight methods were used to estimate the amount of flesh consumed as in section 5.4.2. Animal size was standardized, *Nucella* were in the range 14 to 16mm and mussels in the range 19 to 21mm. There were two experimental runs, one month apart, the first in October 1986. A fresh batch of whelks was collected from Whitsand Bay for each run and they were starved for 2 weeks prior to each experiment. In the first run fifty-four whelks were accommodated in separate pots in the continuous immersion system (section 2.3.1), supplied with a single gaping mussel and allocated a feeding period of either 2, 4, 8, 16, 20 or 24 hours. For the first fourteen hours the whelks were observed every 15 minutes to determine the time at which feeding commenced and to check for continuous feeding. Within this time the regimes 2, 4 and 8 hours were complete; however for the longer time regimes monitoring did not continue overnight.
In the second run the whelks were monitored for a continuous period of 28 hours, the observation interval being increased to every 30 minutes from mid-night to 06.00 hours. A total of fifty-six starved whelks were employed with random allocation of a time regime of either 2, 4, 8, 12, 16, 20 or 24 hours.

A separate length: dry weight relationship for the mussels was carried out for each run to provide predictions of initial dry weight content. Also, for each run, a separate wet: dry weight ratio was calculated and used to convert estimated wet flesh weight eaten to dry weight.

5.4.3.3 Results

Of the 110 whelks set up nineteen did not feed. The whelks that came off during the night in the first experiment could not be included in the analysis, nor, on reflection, could the ones allocated more than 8 hours feeding time, since it was not certain that they had fed continuously. These two categories accounted for twenty-three whelks. Of the remaining sixty-eight, fifty whelks were removed at the allotted time and the remaining eighteen came off of their own accord. Figure 53 shows how each method predicted the amount of flesh ingested for each experimental run, categorized into those taken off and those finishing before time.

The data from both runs were pooled since there was no apparent tendency for one run to produce consistently higher values than the other. All the whelks left some flesh uneaten, the mean dry flesh weight content of a 20mm mussel was 51.8mg. The wet weight method provided significantly higher estimates of the amount ingested than the dry weight method (t-test for paired comparisons, t = 4.9, d.f. = 67, P<0.001).

The effect of time on the mean consumption of mussel flesh for only
Figure 53. Consumption of mussel flesh (mg dry weight) by individual *Nucella* (14-16mm length) feeding on gaping mussels (19-21mm length) in relation to time allowed for feeding, using a) dry weight and b) wet weight methods to assess consumption.

○ = 1st run, whelks removed; ● = 1st run, whelks came off; ○ = 2nd run, whelks removed; ■ = 2nd run, whelks came off.
those individuals removed, for both methods, is shown in figure 54. Although the data for these curves were derived from the same source, they show distinctly different trends and some compromise is required. Whereas the wet weight method shows a steady decline in consumption rate with time, the dry weight method has a marked discontinuity at 12 hours. The apparent drop in the amount consumed at 16 and 20 hours shown by the dry weight method might be attributable to the fact that those whelks still left feeding (n = 3 & 4 respectively) were slow consumers. The mean amount consumed by whelks which left of their own accord during the 12 to 20 hour period was 25.63mg (S.E. = 2.4mg) which represents a slight increase on the 12 hour value of 23.3mg.

5.4.3.4 Discussion

The wet weight food extraction curve is similar to those found by Cook and Cockrell (1978) for insect predators. As an approximation, and for the purposes of the E/n^m model, it was considered that the ingestion curve consisted of two straight lines, an initial high rate of ingestion followed by a slower rate. The transition point needs to be established for each size of whelk. For the 14 to 16mm whelks used in the time course experiment the inflection point was considered to occur at 12 hours. Using the dry weight method values, and removing one spuriously low value, the mean amount consumed in 12 hours was 27mg. Since a 15mm whelk has a body weight of approximately 30mg, for simplicity it was considered that the transition point occurs when a whelk has consumed the equivalent of its own body weight in mussel flesh.

5.4.4 Effect of Nucella Size on Ingestion Rate

5.4.4.1 Method

Sixty-two whelks in the size range 6.6 to 28.5mm were starved for 2 weeks following collection from the field. Each whelk was provided
Figure 54. Ingestion curves for 14-16mm *Nucella* feeding on 19-21mm mussels, using wet weight (•••••) and dry weight (0—0) methods. Values are means (±S.E.) of the individuals removed at the allotted time.
with a gaping mussel of approximately its own length. Each predator along with its prey were accommodated in separate pots in the continuous immersion system (section 2.3.1) and checked every 15 minutes to determine the time at which the whelks commenced to feed and to monitor for continuous feeding. After a mean period of 7.2 hours (S.D. = 1.2 hours) the whelks were removed and the dry weight of remaining mussel flesh determined. Thus data were collected for the determination of ingestion rate by the dry weight method.

5.4.4.2 Results

Of the initial sixty-two whelks, fifty fed continuously on the flesh of the gaping mussels. The other twelve either did not feed or fed intermittently, data for these are not included in the analysis. The rate of ingestion of mussel flesh was a function of Nucella length, (Fig. 55) and can be related by the least squares regression equation:

\[ y = -2.91 (+0.34) + 2.74 (+0.28) x \]

where \( y = \log_{10} \) ingestion rate in mg/hr and \( x = \log_{10} \) Nucella length in mm.

(Values in parenthesis are S.D.). \( F = 97.1, \) d.f. = 1,48, \( P<0.001 \). The time allowed to feed did not significantly affect the rate of ingestion (ANOVA, \( F = 2.4, \) d.f. = 1,47, NS).

5.4.4.3 Discussion

Feeding rates have commonly been found to be proportional to the power of body weight i.e.

\[ Y = ax^b \]

where \( Y \) represents feeding rate, \( X \) the body weight and \( a \) and \( b \) fitted constants. In the present study the exponent relating ingestion rate to Nucella length was 2.74, and that relating length to dry weight 3.14 (Bayne & Scullard, 1978a), thus providing an exponent of 0.87 relating ingestion rate to body weight. Other estimates for molluscs of varying
Figure 55. Effect of Nucella length (mm) on ingestion rate (mg/hour). Curve relates ingestion rate ($y$) to Nucella length ($x$) according to the function:

$$\log_{10} y = -2.91 + 2.74 \log_{10} x$$
feeding types (table II, Bayne & Newell, 1983) are lower than this value, indeed Bayne and Scullard (1978a) found the exponent to be 0.555 for N. lapillus. Since ingestion rates might be expected to be proportional to the cross-sectional area of the feeding apparatus the value of 0.67 has been predicted for the exponent relating ingestion rate to body weight (Hughes, 1986). However that the exponent can be higher than the theoretical value has also been shown for Polinices duplicatus at 0.81 (Edwards & Heubner, 1977), for Patella vulgata at 0.94 (Wright & Hartnoll, 1981) and for Natica maculosa at 1.01 (Broom, 1982).

5.5 Determination of Rate of Energy Gain (E/T^h)

5.5.1 Introduction

To determine the ontogenetic changes in the effect of mussel size on prey profitability knowledge of mean costs, in terms of handling time, and mean benefits, in terms of energy gain per prey item eaten, were required for each predator-prey regime. The selection of mussel sizes against which the predictions of the E/T^h model were to be judged, were determined over a period of 28 days feeding (section 6.2), during which time the whelks grew approximately 5mm. All values calculated in the model are based upon the expected mean size during the four weeks of feeding (i.e. for 7.5, 12.5, 17.5 and 22.5mm whelks).

5.5.2 Method

Handling time was taken as the sum of drilling time and ingestion time. Drilling time was calculated as mussel shell thickness at the central point of a valve (eqn 9, section 5.3) divided by drilling rate (eqn 8, section 5.2). Drilling rate was considered independent of depth of hole.

From the time course experiment (section 5.4.3) the amount of flesh ingested was regarded as a rectilinear function of ingestion time, the
point of inflection occurring once the whelk had consumed its own body weight in mussel flesh. Rate of ingestion during the second phase was slower than in the initial phase (Fig. 56).

For the purposes of the E/T\textsubscript{n} model the functional dependence of ingestion rate on 	extit{Nucella} size during the initial phase was taken as the rate determined in section 5.4.4. Rate of ingestion during the second phase was considered some function of the initial rate, irrespective of whelk size. To determine the functional relationship between initial rate and final rate of ingestion, detailed observations of each predatory event by 10mm whelks feeding on 20mm mussels in the large prey experiment (section 4.3.3) were utilized. For each mussel eaten (n = 39) the following parameters were known; a) the size of whelk just prior to feeding and hence drilling and ingestion rates, b) the size of mussel drilled and the thickness of the shell at the borehole site, thus drilling time, c) the amount of mussel flesh ingested and d) total time for the whelk to feed, i.e. the observed handling time.

The predicted time to drill and ingest each prey item was calculated by taking the second rate of ingestion as different functions of initial rate, until the geometric mean regression (Sokal & Rolf, 1981) of observed handling time against predicted handling time yielded a slope of unity.

A slope of 1.03 was obtained when the second phase of ingestion was one third of the initial rate. Thus total ingestion time was calculated as the time required to ingest a meal of up to the predator's own body weight at the initial rate, plus, if consuming more than its own weight, the time taken to consume the rest at one third the initial rate.

Return, in terms of dry mussel flesh weight gain per prey item
Figure 56. Estimated flesh extraction curve for *Nucella* feeding on mussels, as used in the model to predict energy gain per unit handling time on different sizes of prey. The transition point A occurs when whelks have, at one sitting, consumed the equivalent of their own body weight in mussel flesh.
eaten, was derived from the mean meal sizes observed for each predator-prey regime during the growth rate experiments (sections 4.3.2 & 4.3.3). The mean meal sizes obtained represented those consumed by whelks during the course of growing from some initial size to some final size. For each mussel size, mean meal size was plotted as a function of mean size of *Nucella* during the feeding period, and the values required for the model (i.e. 7.5, 12.5, 17.5 and 22.5mm) obtained by linear interpolation.

5.5.3 Results

Prey profitability was defined as the ratio of mean dry weight mussel flesh ingested to mean handling time. The functional dependence of prey profitability, as derived from the E/T^h model, on prey size, for the four sizes of juvenile *Nucella*, is shown in figure 57. Maximum E/T^h values occurred on larger mussels with increasing *Nucella* size. For all sizes of whelk, 5mm mussels were the least profitable. Profitability rose rapidly until the maximum was reached and thereafter fell slowly as prey size increased. Larger whelks displayed consistently higher E/T^h values than smaller whelks.

5.5.4 Discussion

Kitchell et al. (1981) determined cost:benefit functions for *Polinices duplicatus* feeding on a variety of prey types of different size in which handling costs were considered only as drilling times. For each prey type the largest prey were the most profitable, until the prey were too large to be manipulated or the shells too thick to be drilled, at which point benefits dropped to zero. An upper limit to the mechanical ability of *N. lapillus* to drill mussels was not reached in the predator-prey size regimes considered here.

Similarly prey profitability for adult *N.lapillus* feeding on a range of mussel sizes was found to increase as prey length increased to
Figure 57. Relationship between mussel length (mm) and their predicted value to four sizes of juvenile *Nucella*. Prey value calculated as (dry weight of mussel flesh ingested)/(drilling plus ingestion time).
the maximum length of mussel used, i.e. 40mm (Hughes & Dunkin, 1984). In the latter study Hughes and Dunkin comment that profitability may be expected to decrease on prey larger than 40mm, as drilling time continues to increase but meal size may reach an asymptote. Although asymptotic meal size was not built into the present model, the handling costs associated with the larger prey were not offset by the increase in dry flesh mussel weight gain, and the predicted drop in $E/T_h$, although slight, was noted for each predator size.

A comparison of the absolute values of dry mussel weight gain per unit handling time, show that the present figures are roughly double those of Hughes and Dunkin (1984), with the expectation that if adults had been included in the present model values would have been higher still. Part of the discrepancy between the two absolute values can be explained by the inclusion of inspection time in total handling time by Hughes and Dunkin. Inspection time was found by them to be independent of mussel length, at approximately 2 hours. Inclusion of a two hour inspection period in the present model reduces overall $E/T_h$, but only substantially for meals of short duration, for example, for 20mm Nucella feeding on 5mm mussels $E/T_h$ reduces by 25% of its stated value, but only by 1% when feeding on 60mm mussels.

Predictions from the $E/T_h$ model, along with those of the growth rate model, are compared with observed selection of mussel size in section 6.2.
CHAPTER 6 PREY SIZE SELECTION

6.1 Introduction

Models of optimal diet require that predators can distinguish between different prey items and that they are able to rank them according to some benefit measure. For Nucella it has previously been shown (Bayne & Scullard, 1978a; Hughes & Dunkin, 1984) that they neither forage at random, nor make foraging decisions on a density dependent basis, thus at least the first criterion is met. The decision rules that govern prey selection are less easily determined.

The two models of prey profitability, that of growth rate potential (section 4.3.5) and that of rate of energy gain (section 5.5) had some common characteristics. Both agreed that for a given size of Nucella not all mussels were equally profitable, that proportionally small and large mussels were the least profitable and that the optimum size of prey increased as predator size increased. However they differed in that the most profitable mussel size, as defined by rate of energy gain, was larger, sometimes considerably, than that providing greatest growth potential. Accordingly discrepancies exist between the predictions of each model as to how predators should behave when selecting food items.

Where conflict exists between observed behaviour and predicted optima the most usual explanations are as follows. First, that since organisms are integrated units, most behavioural characters cannot be considered in isolation. The many behavioural components that have to be maximised if overall fitness is to be maximised, may impose constraints on the optimal foraging strategy. Second, lack of agreement between predicted and observed behaviour may be due to the nature of the model, either in the setting up of inappropriate goals on
which natural selection might be expected to act, or that all the costs and benefits within the optimality model have not been accounted for or accurately measured. Third, that the rate of environmental change exceeds the rate of optimal strategy evolution (Cody, 1974).

The present chapter aims to explore the mussel size selection by developing *Nucella* in both the laboratory (section 6.2) and the field (section 6.4) and to compare observed patterns of choice to the predictions generated by the two models of prey profitability.

### 6.2 Laboratory Choice Experiments

#### 6.2.1 Method

The experimental procedure was the same in all respects to that of the juvenile growth rate experiment on small to medium prey (section 4.3.2.1) except that rather than feeding on a pure diet of one mussel size the whelks were supplied with mussels of two sizes. The number of each prey size provided was halved to maintain overall prey surface area equal to that in the growth rate experiment. One individual from each of the four size classes of whelk was provided with one of the following pair-wise combinations of mussel size; 5 + 10mm, 5 + 15mm, 5 + 20mm, 10 + 15mm, 10 + 20mm or 15 + 20mm. This constituted one replicate. Four replicates of each combination of prey sizes were performed, between January and July 1986, concurrently with the growth rate experiment.

#### 6.2.2 Results

The number of each prey size eaten, over the 28 days of feeding, for each size of *Nucella* in the four replicates are given in table 19. The log-likelihood ratio test (Sokal & Rholf, 1981) was applied to each replicate separately and to the pooled frequencies.

Since the total surface area of each prey size was equal, the expected frequencies were based on the null hypothesis of a 1:1 ratio
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Table 19. Numbers of each mussel size eaten when offered in pair-wise combinations to juvenile *N. lapillus* of initial length a) 5mm, b) 10mm, c) 15mm, d) 20mm. Feeding period was 28 days. Significance levels are given for G-statistic for each of four replicates separately; $G_H = G$ for heterogeneity, d.f.=3; $G_P$ = pooled value of $G$, d.f.=1; $G_T$ = total $G$, d.f.=4. (tables 19 b, c & d overleaf)
### b) 10mm *Nucella*

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### c) 15mm *Nucella*

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d) 20mm *Nucella*

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of numbers of each prey size eaten, presupposing that encounter rate is dependent on surface area. An overall significant departure from a 1:1 ratio was only accepted if total G was significant and the pooled value for G more significant than G for heterogeneity. The null hypothesis could not be accepted simply because G for heterogeneity was significant, since a significant value for heterogeneity can occur when there is a consistent trend within the replicates differing only in magnitude (see e.g. 15mm Nucella feeding on 5 V 10mm mussels, table 19 c). Relative significance levels must be regarded with some caution since, as larger prey took longer to handle, it would be more difficult for a predator to eat significantly more large than small prey in the time available.

Based on the results of the four replicates combined the following selection of mussel sizes occurred. Of the significant results, 5mm whelks always chose the smallest of each pair, i.e. chose 5mm in preference to 15 and 20mm mussels, and 10 and 15mm in preference to 20mm mussels. However they did not discriminate significantly between 5 and 10mm mussels or between 10 and 15mm mussels, although eating between two and three times the number of smaller prey.

10mm Nucella ate significantly more 5 and 10mm than 20mm mussels, so again selecting the smaller prey.

The only overall significant result for the 15mm whelks was that they chose 10mm in preference to 5mm mussels. 20mm Nucella selected all three larger sizes in preference to 5mm mussels and ate more 10mm than 20mm mussels.

The general trend was for the smallest Nucella to eat the smaller of the prey pair offered, whilst the largest whelks discriminated heavily against the smallest prey. The ontogenetic shift in mussel size selection is more clearly seen in figure 58, as might be expected there
Figure 58. Numbers of each mussel size eaten (mm ± 1mm) by juvenile *Nucella* of four different initial sizes (mm ± 1mm) during 28 days of feeding in the laboratory. Trials are grouped according to the prey pair-wise combinations that were offered to the whelks. Values are the pooled frequencies of four replicates. G-statistic significance levels, to test for a significant selection of one mussel size over the other are; * p < 0.05, ** p < 0.01, *** p < 0.001.
was a lack of discrimination, by all *Nucella* sizes, where larger prey differed by only 5mm.

6.2.3 Profitability Versus Selection

6.2.3.1 Introduction

The profitability of different sizes of mussels to juvenile *N. lapillus* was defined in two ways. First as the ability to promote growth during a period in which the predator grew approximately 5mm (section 4.3.2) and second, the energy intake per unit handling time of each prey size by predators at the mid-point of each size range (section 5.5.3). These measures of prey value are compared with observed size selection, based on the numbers of each prey size eaten, during the time it takes the predator to grow approximately 5mm.

Whilst significant levels can be attached to differences in growth rate by a given size of predator on different prey sizes, no measure of variation was associated with the values of energy gain per unit handling time so it cannot be stated with certainty that one prey size was more or less profitable than another. Thus demonstration of size preference can only be judged against the general trends in prey profitability.

6.2.3.2 Results

For each predator size separately the two measures of prey profitability were scaled to equalise the range of observations and presented on a comparative scale (Figs 59 to 62). No weight is attached to the relative positions of the two measures, only to the comparative effect of prey size on profitability. For ease of comparison the observed selection of mussel sizes by each whelk size is shown alongside the profitability curves.

The growth rate model predicts that 5-10mm *Nucella* should select 5mm in preference to 15 and 20mm mussels, whilst the E/T model predicts
Figure 59.

Upper figure - comparative profitabilities of different sizes of mussel to juvenile *Nucella* of 5mm (± 1mm) initial length, according to energy gain per unit handling time (E/Tₜ) and growth promoting potential.

Lower figure - numbers of each mussel size (mm) eaten, when offered in pair-wise combinations, by juvenile *Nucella* of 5mm (± 1mm) initial length over 28 days of feeding. (Figures in the boxes refer to mussel size class (mm ± 1mm)). Values are the pooled frequencies of 4 replicates. Significance levels for G-statistics:

* p > 0.05,
** p > 0.01,
*** p > 0.001.
Figure 60.
Legend as for figure 59, for juvenile *Nucella* of 10mm (± 1mm) initial length.
Figure 61.
Legend as for figure 59, for juvenile *Nucella* of 15mm (± 1mm) initial length.
Figure 62.
Legend as for figure 59, for juvenile *Nucella* of 20mm (± 1mm) initial length.
that 5mm mussels, by being less profitable than all other sizes, should be excluded from the diet. By eating more 5mm prey than all other sizes these small whelks were behaving in accordance with predictions from the growth rate model but not the E/T\textsubscript{n} model. Within the three larger prey sizes, whelks eat the smallest of each pair, predictions provided by both models.

For 10-15mm Nucella, both models predict that 5mm mussels should be excluded from the diet where larger prey are available. However in the selection experiments, although showing an insignificant tendency to select 10mm rather than 5mm mussels, the smallest mussels are the preferred prey in combination with the three larger mussels, behaviour that contradicts the predictions of both models. Within the three largest prey sizes, growth rates were independent of prey size and thus this model would predict that no selection would occur. The E/T\textsubscript{n} model suggests that 15mm mussels are the most profitable and should be selected in preference to 10 and 20mm mussels. Although the significant preference for 10 over 20mm mussels conflicts with the predictions of both models, that no selection occurred between 10 and 15mm or between 15 and 20mm prey, is in accordance with the growth rate model but not the E/T\textsubscript{n} model.

The only significant selection exhibited by the 15-20mm Nucella was that for 10 over 5mm mussels, a prediction provided by both models. However both models also predict that 15 and 20mm mussels should be eaten in preference to 5mm, but there was no evidence that this occurred. Whereas growth rates were independent of mussel size in the three largest prey groups, and no selection should occur between them, the E/T\textsubscript{n} model predicts that the largest prey of each pair should be selected. That no significant selection occurred between the three largest prey sizes suggests that prey profitability defined by the
The prey profitability curves for the 20-25mm whelks followed closely that of the 15-20mm Nucella. In agreement with both models, that 5mm mussels, being less profitable, should be excluded from the diet when larger prey are available, significant preference was shown in each case for the larger prey. Although significant differences in growth rate could not be detected on the three largest prey, and thus no selection should be evident between them, the \( E/T_h \) model again predicts that the largest of each pair, being more profitable, should be the preferred prey. That there was no selection between 10 and 15mm mussels or between 15 and 20mm prey again conforms more closely to the growth rate model than the \( E/T_h \) model of prey profitability. The significant selection of 10mm over 20mm mussels was the only instance not predicted by the growth rate model.

6.2.3.3 Discussion

The size preferences of juvenile \textit{N. lapillus} as demonstrated in the laboratory experiments do not conform, in their entirety, with the predictions of either model of prey profitability. However the growth rate model of prey value more closely predicted the animals choice of prey than did the energy intake per unit handling time model. It was apparent that the only cases where the \( E/T_h \) model accurately predicted the predators size preference was when both models predicted the same outcome. The whelks either consistently selected smaller prey than the \( E/T_h \) model predicted, or failed to select large prey where the \( E/T_h \) model indicated them to be more profitable. This point will be returned to in section 6.5.

6.3 Borehole Analysis

6.3.1 Introduction

The size of boreholes made by predatory gastropods has previously
been shown to be a function of predator size in Polinices duplicatus (Wiltse, 1980; Kitchell et al., 1981) and Urosalpinx cinerea follyensis (Carriker & Van Zandt, 1972), but not for Dicathais aegrota (Black, 1978). The functional dependence of borehole dimension on predator size has been used to investigate predator-prey size relationships in both recent (Wiltse, 1980) and fossil (Kitchell et al., 1981) shell assemblages. The same approach was used in the present study for juvenile N. lapillus feeding on Mytilus edulis. The functional relationship between Nucella size and borehole dimension was established (section 6.3.2) and measurements of bored field collected mussels used to investigate predator-prey size relationships (section 6.4).

6.3.2 Method

Nucella in the size range 1.5 to 30.4 mm were housed individually in pots (section 2.3.2) with a mussel that was between one half and three times its own length, in the continuous immersion system (section 2.3.1). The lengths of predators were measured before feeding and separated into mm size categories (i.e. 1.5-2.4 mm ... 29.5-30.4 mm). Drilled shells were collected and borehole dimensions determined (to within 2 x 10^-2 mm) using a Kyowa binocular microscope and calibrated eye-piece.

Boreholes drilled by Nucella are fairly uniform in structure, they resemble a truncated cone (plate 3) with the widest part of the cone on the external surface of the shell, and are drilled perpendicular to the shell surface (Fig. 63). Holes are not perfectly circular, so to determine which parameter(s) of hole size would provide the best predictor(s) of predator size, the following six measurements were made. 1) The maximum outer diameter (plate 4 & Fig. 64), where the periostracum was worn away this dimension was judged as the outer edge
Plate 4. Scanning electron micrograph of a borehole drilled by a 3mm Nucella in the shell of a mussel, showing the clearly defined inner hole boundary and the less well defined outer hole boundary. (Magnification: x220).
Figure 63. Diagrammatic L.S. of a **Nucella** borehole drilled through a mussel shell.
A-B maximum outer diameter
C-D diameter at right angle to maximum

Figure 64. Diagram of surface view of a *Nucella* borehole drilled in a mussel shell (drawn from plate 4) to illustrate the dimensions measured as outer borehole diameters.
of the bevel. 2) The diameter of the outer hole at right angles to the maximum diameter called, for convenience, the minimum outer diameter. 3 & 4) The maximum inner diameter and the one at right angles to it (minimum inner diameter). 5 & 6) The maximum diameter at the junction of the blue prismatic and white nacreous shell layers and the one at right angles to it; however these latter measurements were later abandoned since in some shells this line could not be determined. The length of mussel was measured for a sub-set of the data.

6.3.3 Results

A total of 502 observations was made, within twenty-nine size classes of predator. Normality of the distribution of the four borehole dimensions for each size class of predator was tested using the probability plot correlation coefficient test (Filliben, 1975). In 110 of the 116 distributions (P = 0.05) there was no evidence to contradict normality (i.e. the expected 5%).

For comparison with work on other predatory gastropods borehole dimensions were related to Nucella size by least squares regression analysis following logarithmic transformation. Each of the four borehole dimensions was highly significantly dependent upon Nucella size.

\[
\begin{align*}
\text{max. outer diameter} & : y = -0.875 + 0.778 x, \quad r = 0.979, \quad P < 0.001 \\
\text{min. outer diameter} & : y = -0.914 + 0.784 x, \quad r = 0.977, \quad P < 0.001 \\
\text{max. inner diameter} & : y = -1.010 + 0.705 x, \quad r = 0.982, \quad P < 0.001 \\
\text{min. inner diameter} & : y = -1.050 + 0.707 x, \quad r = 0.979, \quad P < 0.001
\end{align*}
\]

where \( x = \log_{10} \text{Nucella length (mm)} \), \( y = \log_{10} \text{borehole dimension (mm)} \).

To predict the size of whelk responsible for a predation event from evidence of borehole dimensions the functional dependency of Nucella size on borehole size is required. The relationships between mean
Nucella length and the four parameters of borehole dimension are shown in figures 65 and 66. Variation in Nucella size increases with increasing borehole dimension, truncation at the upper end is due to whelks over 30mm not being included.

Multiple least squares regression analysis, following logarithmic transformation, was carried out to investigate the effect of the four parameters of borehole size on Nucella size. Analysis of covariance (table 20) revealed that minimum outer diameter did not contribute significantly to the regression and so was removed. Further ANCOVA on the reduced model indicated that the three remaining borehole dimensions all made a significant contribution to the regression and were retained. The relationship was;

\[ y = -.879 + 0.489x_1 + 0.490x_2 + 0.351x_3 \]

where \( y = \log_{10} \) Nucella length (mm)
\( x_1 = \log_{10} \) maximum outer diameter
\( x_2 = \log_{10} \) maximum inner diameter
\( x_3 = \log_{10} \) minimum inner diameter

(Borehole dimensions are given in eye-piece units, where 45 e.p.u. = 1mm) \( r = 0.987, F = 5602, \) d.f. = 3,498, \( P<0.001 \)

Mussel length did not contribute significantly to the relationship between Nucella size and the three borehole dimensions (ANOVA, \( F = 2.07, \) d.f. = 1,106, NS; table 21).

In the case of some field holes (section 6.4) only outer borehole dimensions could be measured. Nucella size was functionally dependent on outer borehole dimensions according to the least squares regression equation;

\[ y = -0.904 + 0.816x_1 + 0.416x_2 \]

where \( y = \log_{10} \) Nucella length (mm)
\( x_1 = \log_{10} \) maximum outer diameter
Figure 65. Maximum borehole dimensions (mm) in relation to the mean (±S.D.) size of Nucella (mm) responsible for the drilling event.
Figure 66. Minimum borehole dimensions (mm) in relation to the mean (±S.D.) size of *Nucella* (mm) responsible for the drilling event.
Table 20. ANCOVA to investigate the effect of removing each variable of borehole dimension separately from the full multiple regression model relating borehole size to *Nucella* size. Maxout - maximum outer diameter, maxin - maximum inner diameter, minout - minimum outer diameter, minin - minimum inner diameter.

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<td>NS</td>
</tr>
<tr>
<td>Error</td>
<td>106</td>
<td>0.144</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 21. ANCOVA to investigate the effect of mussel length on the reduced least squares multiple regression equation (eqn 10) relating *Nucella* size to three parameters of borehole dimension.
\[ x_2 = \log_{10} \text{minimum outer diameter} \]

\( (F = 6217, \text{d.f.} = 2,499; P<0.001). \) (Borehole dimensions are in eye-piece units, 45 e.p.u. = 1mm).

6.3.4 Discussion

With one exception (Black, 1978), the relationship between predator length (\( x \) mm) and borehole diameter (\( y \) mm) has been shown to be highly significant for gastropod drills (table 22), and can be described by the power function \( y = a + x^b \). Calculated values of \( b \) fall between 0.46 and 0.86 indicating that the drilling apparatus does not grow isometrically with shell length. Carriker and Van Zandt (1972) reported a weak correlation between radula width and borehole diameter, concluding that, compared with the accessory boring organ, the radula plays an insignificant part in shaping the boreholes. In common with other studies (Wiltse, 1980; Kitchell et al., 1981), prey length, and hence shell thickness, did not affect the relationship between predator length and borehole diameter, thus permitting estimation of predator size and predator-prey size relationships from measurements of bored shells.

6.4 Field Predation

6.4.1 Introduction

Studies of predator-prey size relationships in the field are restricted to those prey that have undigestible body parts, for example the analysis of predator gut contents or faecal pellets for arthropod exoskeletons. With molluscs as prey and boring snails as predator, predation rates and predator-prey size relationships have been inferred from analyses of field collected bored shells (Ansell, 1960; George, 1965; Green, 1968; Franz, 1977; Griffiths, 1981b). Most field studies of boring gastropod predation have concerned soft sediment assemblages or beached collections which may not provide a faithful record of
<table>
<thead>
<tr>
<th>Predator</th>
<th>Size-range</th>
<th>n</th>
<th>Method</th>
<th>Regression</th>
<th>r</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urosalpinx cinerea</td>
<td>14.0 -42.0</td>
<td>88</td>
<td>a)</td>
<td>-1.150 0.861</td>
<td>.86</td>
<td>Calculated from Carriker &amp; Van Zandt, 1972</td>
</tr>
<tr>
<td>Polinices duplicatus</td>
<td>3.5</td>
<td>36</td>
<td>c)</td>
<td>0.504</td>
<td>.95</td>
<td>Wiltse, 1980</td>
</tr>
<tr>
<td>Polinices duplicatus</td>
<td>25.0</td>
<td>77</td>
<td>d)</td>
<td>-0.372 0.552</td>
<td>.89</td>
<td>Kitchell et al., 1981</td>
</tr>
<tr>
<td>Nucella lapillus</td>
<td>1.5 -30.4</td>
<td>502</td>
<td>d)</td>
<td>-0.894 0.781</td>
<td>.98</td>
<td>Present study</td>
</tr>
</tbody>
</table>

Table 22. Relationships between predator size (x mm) and borehole dimension (y mm), where a and b are fitted constants in the equation: 
\[ \log_{10} y = a + b \log_{10} x. \]

Diameters measured were a) maximum outer borehole, b) minimum outer borehole, c) maximum at junction of prismatic and nacreous shell layers, d) mean outer borehole and e) mean inner borehole.

Wiltse (1980) found a linear relationship \( y = 0.298 + 0.049 x \), the quoted exponent b calculated by Kitchell et al. (1981).
predation. Using artificial valves, Lever and Thijssen (1968) demonstrated that, under the influence of waves and water currents, there was differential transportation of valves according to their size, symmetry, presence or absence of boreholes and even position of borehole. Thus both predation rate and origin of shells cannot be ascertained with certainty for shell assemblages exposed to water movement.

By contrast, intertidal drilled mussel shells remain attached to rocks by byssus threads. Although differential detachment, according to mussel size, also precludes the use of mussel shell collection for the analysis of predation rate, the system can identify certain feeding patterns within a specific location. One pattern, that of predator-prey size relationships, depends on the mussel shells remaining relatively intact, free from abrasion by sea and sand. This was the case at Whitsand Bay, the shells became detached from the rocks before their condition deteriorated.

6.4.2 Method

As part of the field sampling programme (section 3.2) drilled mussel shells were collected from six replicates of five tidal heights. A detailed examination was carried out on the bored shells sampled in March, September, October and November 1985. For each entire specimen or valve, the maximum length, maximum height and position of borehole(s) were measured as detailed in figure 51. The position of the borehole, either on the left or right valve, was also noted.

Boreholes were characterised qualitatively as being either complete, where the hole extended to the inner boundary of the bevelled edge; partial, where penetration of the shell was restricted to a small circular area within the major depression; or incomplete, where a bevelled edge indicated drilling activity but the mussel shell remained
intact (Fig. 67). In all these categories the hole was drilled through the body of the shell, but further holes were drilled so close to the edge of the shell that part of their circumference was interrupted by the shell margin (plate 5), here called marginal holes.

The four borehole dimensions (as detailed in section 6.3) were measured for all complete holes while for partial and incomplete holes only outer borehole dimensions could be recorded. Due to the proximity of marginal holes to the shell edge often only a small segment had been drilled out of the shell, so measurements were taken of the maximum hole diameter parallel to the shell edge (d) and the perpendicular distance from the shell margin to the outer hole edge (w) (Fig. 68). For the purposes of estimating borehole dimensions marginal holes were considered to be perfectly circular. Where w was more than half the value of d, the maximum and minimum outer borehole diameters were taken to equal d (Fig. 68 a). Where w was less than d/2 (Fig. 68 b), outer borehole diameter was calculated by simple geometry (Fig. 68 c).

6.4.3 Results

Of a total of 845 holes inspected only one was drilled from the inside out. Drill holes were equally common on left (n = 439) and right (n = 406) valves ($X^2 = 1.21$, d.f. = 1, NS). The frequency of each hole type, in the four separate months, is shown in table 23. In all months complete holes were the most common with marginal holes being the next most abundant in the autumn three months.

The appearance of partial holes suggested that they had been formed by whelks drilling mussel shells that were already empty, with the impression that the tiny inner hole was just large enough to permit chemosensory investigation of the internal contents of the mussel. Alternatively they may represent an interruption, by some external factor, of the boring process at the point of shell breakthrough. The
Figure 67. Characteristics of the four types of *Nucella* borehole found drilled on mussel shells collected from Whitsand Bay.
Plate 5. Scanning electron micrograph of a Nucella borehole drilled at the margin of a mussel shell. (Magnification: x83).
Figure 68. Estimation of outer borehole dimensions for marginal holes.

a) where $w > d/2$, $d$ = maximum & minimum outer diameters.

b) where $w < d/2$, calculation of $d$ by geometric method, see c) and below.

Since radius $= a + w = \sqrt{(d/2)^2 + a^2}$

Then $a + w = \sqrt{(d/2)^2 + a^2}$

From which $a = \frac{(d/2)^2 - w^2}{2w}$

Then $2(a + w) = d$ = maximum & minimum outer diameters.
<table>
<thead>
<tr>
<th></th>
<th>Marginal</th>
<th>Complete</th>
<th>Partial</th>
<th>Incomplete</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>10</td>
<td>182</td>
<td>18</td>
<td>21</td>
<td>231</td>
</tr>
<tr>
<td>September</td>
<td>29</td>
<td>95</td>
<td>4</td>
<td>12</td>
<td>140</td>
</tr>
<tr>
<td>October</td>
<td>55</td>
<td>187</td>
<td>15</td>
<td>44</td>
<td>301</td>
</tr>
<tr>
<td>November</td>
<td>44</td>
<td>96</td>
<td>11</td>
<td>22</td>
<td>173</td>
</tr>
<tr>
<td>Total</td>
<td>138</td>
<td>560</td>
<td>48</td>
<td>99</td>
<td>845</td>
</tr>
</tbody>
</table>

Table 23. Number of each borehole type found on the drilled mussel shells collected from Whitsand Bay in March, September, October and November 1985.

<table>
<thead>
<tr>
<th>Shells with partial holes</th>
<th>Rest of shells</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Double</td>
</tr>
<tr>
<td></td>
<td>valve</td>
</tr>
<tr>
<td>No other hole</td>
<td>4</td>
</tr>
<tr>
<td>Other hole(s)</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>465</td>
</tr>
</tbody>
</table>

Table 24. Frequency of partial holes on shells with and without other boreholes compared with all other shells having one or more boreholes.
first hypothesis gains support from the frequency of occurrence of partial holes in shells with other holes compared with shells with no other hole (table 24). Partial holes occurred eight times more frequently on entire shells with another hole. However for the set of all other shells, double drilling was relatively uncommon, only one in ten had two or more drill holes. On single valves, partial holes occurred equally frequently on those with or without another hole, while for all other single valves less than 9% had two or more successful drill holes. Thus, while some partial holes may arise from the interruption of a whelk during the feeding period, the more likely explanation for the majority of partial holes is that they represent errors by the whelk, the drilling of a mussel previously eaten.

The size of Nucella responsible for each predation event was estimated according to equation 10 for complete holes and according to equation 11 for partial, incomplete and marginal holes.

The frequency of each hole type, expressed as a percentage of all predatory attempts, for each size class of whelk (Fig. 69) shows that the drilling of partial holes remains fairly constant throughout the life of the predator, at under 10%. The percentage of predatory attempts that resulted in incomplete boreholes was highest among the smallest whelks (34%) and dropped steadily as whelks grew. However this result may have been biased by the sampling procedure, involving only an inspection of shells with at least one visible borehole (section 3.2.1.2). Larger whelks may have attempted, unsuccessfully, to drill larger shells that were not included in the sample.

Marginal holes formed a small proportion of total holes for both the smallest and largest size group of whelks, peaking at 34% for 10 to 15mm whelks. The trend, for medium-sized whelks to drill edge holes in a high proportion of cases, depends on the accuracy with which the
Figure 69. Effect of estimated *Nucella* size class on the frequency of each borehole type (expressed as % of all predatory attempts) on mussel shells collected from Whitsand Bay for March, September, October and November 1985 combined.

*Nucella* size classes:

1 = < 5 mm  
2 =  5 - 10 mm  
3 = 10 - 15 mm  
4 = 15 - 20 mm  
5 = 20 - 25 mm  
6 = > 25 mm

Borehole types: c = complete, p = partial, ic = incomplete, m = marginal.
dimensions of marginal holes can be used to estimate Nucella size from the relationship provided by complete holes. It might be conceivable for whelks to drill smaller (or less likely, larger) holes on the thinner edges of a mussel shell than through the body of the shell, thus under-estimating (or over-estimating) Nucella size. A separate functional relationship between Nucella size and marginal hole dimensions would provide a more accurate prediction of the size of whelk responsible for these marginal predatory events.

For each size of whelk complete holes were the most common type, with the tendency that, of all holes, complete holes formed a greater proportion the larger the whelk.

The effect of predator size on mean size of mussel drilled, for all hole types separately and combined, is shown in figure 70, with summary statistics in table 25. For all hole types there was a clear tendency for larger whelks to drill larger mussels. For a given size of whelk, marginal holes tended to be drilled on mussels smaller than the average size attacked, with only a slight increase in mussel size as Nucella size increased. The mean size of mussel with a partial hole was close to that of complete holes for most Nucella sizes. There was a consistent tendency for incomplete holes to be drilled on mussels larger than the average size attacked.

For each month separately the dimensions of complete holes were used to estimate Nucella size and related to the size of mussel drilled (Fig. 71). In March the mean size of mussel drilled was independent of Nucella size, however in September, October and November there was clear evidence of an ontogenetic shift in prey size selection, although becoming less apparent at larger predator sizes. The variance of mussel size eaten remained fairly constant for all Nucella size classes, suggesting that whelks are neither more or less selective at
Figure 70. Effect of estimated Nucella size class on the mean length (mm) of drilled mussels collected from Whitsand Bay for the months March, September, October and November 1985 combined. Nucella size classes as defined in figure 69. Error bars omitted for clarity, S.D. given in table 25.

Borehole types:
- complete,
- partial,
- incomplete,
- marginal,
- all types combined.
### Table 25. Analysis of Nucella drill holes found on mussel shells collected from Whitsand Bay for the combined months March, September, October and November, 1985. For each estimated size class of Nucella are given n, the number of mussel shells attributed to that size class and the mean (and S.D.) of the length (mm) of mussel drilled. Hole types are defined in Fig. 67.
Figure 71. Effect of estimated *Nucella* size class on the mean length (mm ± 95% confidence interval) of drilled mussel shells collected from Whitsand Bay in March, September, October and November 1985. *Nucella* size classes as defined in figure 69. The number of mussel shells is given below the corresponding mean.
any particular age. Least squares regression analysis, following logarithmic transformation, yielded significant relationships between predator size and prey size for the three autumn months (table 26), with relatively constant regression coefficients. The predator:prey relationship for each individual predatory event resulting in a complete borehole for the four months combined (Fig. 72) shows that both maximum and minimum prey size increased as predator size increased.

The position of each complete borehole, defined by the co-ordinates mussel length divided by distance from the anterior end (L/A) and mussel height divided by distance from the ventral surface (H/B) (as defined in section 5.3) is illustrated in figure 73. Whilst all areas of a mussel shell were drilled, the highest concentration of holes formed a band running in an anterior-posterior direction located towards the dorsal surface. Marginal holes (Fig. 74) were concentrated at the posterior end of the mussel shell.

There was evidence to suggest that size of whelk affected the position of complete holes. In figure 75 the solid line represents the mean distance from the anterior end of the mussels drilled within each size class. If no selection for drill site occurred this line would represent the relationship between expected mean hole position and mussel size. Whelk size classes have been coded from the smallest to the largest (1 to 6) and the mean distance from the anterior end of the mussel of holes drilled by each predator:prey size combination entered by code number. Smaller whelks drilled closer to the anterior end of the mussel than would be expected by chance, whilst larger whelks drilled further towards the posterior end.

6.4.4 Discussion

The ontogenetic shift in prey size selection demonstrated in
<table>
<thead>
<tr>
<th>Month</th>
<th>a</th>
<th>b</th>
<th>F</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>1.140</td>
<td>0.104</td>
<td>3.0</td>
<td>1,180</td>
<td>NS</td>
</tr>
<tr>
<td>September</td>
<td>0.592</td>
<td>0.572</td>
<td>151.4</td>
<td>1,93</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>October</td>
<td>0.627</td>
<td>0.519</td>
<td>155.9</td>
<td>1,185</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>November</td>
<td>0.623</td>
<td>0.524</td>
<td>90.4</td>
<td>1,94</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 26. Results of least squares regression analysis relating length of mussel (mm) eaten in the field to size of whelk (mm), for complete holes only. a and b are constants in the equation

$$\log_{10} \text{mussel length} = a + b \log_{10} \text{Nucella length}$$
Figure 72. Relationship between estimated *Nucella* length (mm) and length (mm) of mussel drilled with a complete borehole. Mussel shells were collected from Whitsand Bay in March, September, October and November 1985.
Figure 73. Position of all 560 complete boreholes drilled on mussels sampled from Whitsand Bay in March, September, October and November 1985.

Ratio length = $L/A$

Ratio height = $H/B$, as defined in fig. 51.
Figure 74. Position of all 138 marginal holes drilled on mussels sampled from Whitsand Bay in March, September, October and November 1985.
Ratio length = \( \frac{L}{A} \)
Ratio height = \( \frac{H}{B} \), as defined in fig. 51.
Figure 75. Position of complete boreholes in relation to mussel and *Nucella* size. Solid line represents the mean distance (mm) from the anterior end of mussels within each size class (1-6). Numbers on the plot refer to size class of *Nucella* and are located at the mean borehole distance from the anterior end of mussels within each mussel size class. Drilled mussels were sampled from Whitsand Bay in March, September, October and November 1985.

Mussel and *Nucella* size classes:

1 = <5mm, 2 = 5 - 10mm, 3 = 10 - 15mm,
4 = 15 - 20mm, 5 = 20 - 25mm, 6 = >25mm.

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laboratory experiments (section 6.2) has been shown to hold for *N. lapillus* feeding on mussels in the natural environment.

Two explanations can be forwarded for the observation that, for a given size class of whelk, incomplete holes were found to occur consistently on mussels larger than those drilled successfully. Firstly, that when whelks attacked relatively large mussels, with thicker shells, the increased drilling time resulted in a higher probability of being dislodged by wave action and/or an increased tendency by the whelk to abandon drilling. Accordingly successful predatory events may be restricted at the upper range of mussel sizes. Alternatively, the mussels may have grown since the unsuccessful attack. Which explanation is correct cannot be resolved from the present data. If the first explanation is true, then, since incomplete holes were in general drilled on larger mussels by larger whelks, the ontogenetic shift in prey size selection still stands, only increasing the range of prey attacked by a given size of whelk.

It was occasionally noticed that small holes, on relatively large mussels, were occluded on the inside by re-growth of the mussel shell, as found in section 4.3.4. These were counted as complete holes since they had penetrated the shell, but as they did not cause the death of the prey, the mussel could have grown between that predation event and the one that eventually killed it. Inclusion of these holes has increased the mean size of mussel successfully drilled by the smaller whelks.

Marginal holes made up a significant proportion (20%) of all successful predatory attacks in the field, and may represent an alternative feeding strategy. By forming only part of a complete hole and by being drilled through the thinnest part of the mussel shell, marginal holes would require less investment in drilling time. However
most marginal holes were drilled at the posterior margin of the mussel shell, and combined with restrictions of predator proboscis length, a whelk would only have access to all the flesh if the mussel were less than the predator's own length. Thus from an investment:reward viewpoint marginal holes should be confined to mussels smaller than the average, which was the observed response. Without detailed knowledge of the costs and benefits involved in marginal hole drilling, a comparison cannot be made between the profitabilities of the two alternate drilling strategies - drilling through the body of the shell or from the edge.

A seasonal change in prey size selection was indicated by the field data; whereas in the autumn three months there was a positive correlation between predator and prey size, no such relationship occurred in March. Lack of information on the length of time dead mussel shells remain attached to rocks renders interpretation of seasonal events more difficult. However some tentative explanations can be forwarded. First there were few recorded predatory attacks by small whelks in March compared with the autumn months. The major hatching period occurred in August 1985 (section 3.2), reflected in the large numbers of shells drilled by whelks of less than 5mm found in the September 1985 sample. However in March, with only a sample size of one for whelks of less than 5mm, this data point was essentially absent. Second since *Nucella* have been shown to have reduced feeding rates in the winter months (Feare, 1970) they might be expected to be hungrier, and so less selective, in the early spring. Finally, due to the seasonal spawning of mussels, relatively fewer small mussels were available in January 1985 than in November 1985 (Fig. 76).

However comparisons of what an animal eats with what is potentially
Figure 76. Size frequency distribution of live mussels sampled within the *Nucella* zone at Whitsand Bay in January (-----) \((n = 2446)\) and November (-----) \((n = 2249)\), 1985.
available, based solely on relative abundances, ignores the complexities of the natural environment. Small mussels were frequently buried in sand and debris, or located deep in the mussel bed, thus effectively unavailable to surface foraging predators. If encounter rate is dependent on surface area then encounter probability becomes the product of frequency and size. Small scale changes in mussel size frequency distributions can occur, e.g. due to the availability of sites for larval settlement, which may or may not coincide with the distribution of the Nucella population.

The distribution of drill holes also reflects restrictions imposed by the natural environment. On the whole mussels are orientated so that either their dorsal surface or their posterior regions are presented to the surface of the mussel bed. Larger whelks tended to aggregate around patches of mussels, thus drilling from the side of the mussel, or to forage over the surface of the bed, thus restricting drilling to those regions that are accessible to them.

By contrast, small drill holes were found predominantly at the anterior end of the mussel shell which correlates with the observation that small whelks were found deep within the mussel bed, often in pockets formed by mussels becoming detached from the rocks. From this position the small whelks are forced to drill from beneath the mussel mat.

If the frequency of partial holes reflects mistakes by Nucella drilling already empty shells, then mistakes occurred relatively infrequently, in less than 7% of all predatory attacks. Part of the inspection time, reported by Hughes and Dunkin (1984) to be approximately two hours, may be used to discern if the mussel has already been drilled.
6.5 Discussion - Profitability versus Selection

When presented with a single size of mussel, *Nucella* could feed on a wide range of prey sizes (e.g. a span of 5 to 60mm mussels were eaten by 20mm whelks) thus behavioural rather than structural characters limit their preferred size range when a spectrum of prey sizes are available. It was evident, that in addition to the mean, both the maximum and minimum prey size selected in the field increased as predator size increased as found by Leviten (1976), and Paine (1965, 1976). There is no evidence that large *Nucella*, when feeding on mussels in the field, expand their diet width although they have the mechanical ability to do so.

A positive correlation between size of predatory boring gastropod (other than *N. lapillus*) and size of a single species of prey has previously been shown under laboratory (Griffiths, 1981b; Broom, 1982; Ansell, 1982b) and field conditions (Pieron, 1933; Ansell, 1960; Green, 1968; Edwards, 1974; Edwards & Heubner, 1977; Kitchell et al., 1981; Vignali & Galleni, 1986). For *N. lapillus* an ontogenetic shift in mussel size selection in laboratory experiments has been both substantiated (Bayne & Scullard, 1978a; Hughes & Dunkin, 1984) and refuted (Stickle et al., 1985).

For each size of whelk the mean mussel size selected in the field corresponded with that found to provide maximum growth rates in the laboratory (section 4.3). For the smallest whelk class the chosen mussel size also coincided with the most profitable prey size as defined by energy gain per unit handling time. In contrast, for the three largest whelk size classes, maximum prey value, defined as $E/T_h$, occurred on mussels considerably larger than those selected in the field. Comparisons between the predictions provided by the two measures of prey profitability and the observed selection in the field,
closely correspond to those found in the laboratory experiments (section 6.2.3).

The lack of selection of large mussels may have been a response imposed upon the whelks by a shortage of large mussels in the field or a positive discrimination against the larger prey. An examination of the size frequency distribution of the mussel population from which the whelks made their prey choices (Fig. 76) reveals that mussels greater than 30mm length were indeed rare. However, support for positive selection of mussels smaller than the optimum predicted by $E/T_h$ when larger prey are available, can be gained from the literature.

From laboratory experiments Bayne and Scullard (1978a) report a similar hyperbolic relationship between predator and prey size (Fig. 77), although for a given size of whelk the preferred mean mussel size was lower than that observed from the Whitsand Bay field data. In a further experiment 20mm whelks, provided with mussels in the range 5 to 52mm, selected a mean size of 18.2mm (S.D. = 4mm) (Bayne & Scullard, 1978a). Additionally when presented in the laboratory with mussels in the range 10 to 35mm, the preferred mussels size class for three size classes of N. lapillus (Hughes & Dunkin, 1984) were in close agreement with the field response reported here (Fig. 77). Thus there is considerable agreement between these separate reports of the Nucella-Mytilus size relationship, irrespective of the availability of larger prey.

Previously, prey profitability defined as energy gain per unit handling time, has been determined for 20mm Nucella (Bayne, 1981) and for adult Nucella (Hughes & Dunkin, 1984) feeding on different sizes of mussel. Both studies also report that whelks preferred smaller individuals than those found to be of optimal value. Hughes and Dunkin (1984) suggest that the profitability of larger mussels may be reduced.
Figure 77. Effect of *Nucella* length (x) on the preferred size of mussel (y) as prey, according to:

1) \[
y = \frac{x}{0.46 + 0.36x}
\]
determined by Bayne & Scullard (1978a).

2) \[
\log_{10} y (\text{mm}) = 0.623 + 0.524 \log_{10} x (\text{mm}),
\]
determined from November field data in the present study (table 26).

3) \[ \rightarrow \rightarrow \rightarrow \] the preferred size range, Hughes & Dunkin (1984).
by intruding whelks or that Nucella may act as a time minimiser (Schoener, 1971) thus keeping to a minimum the risks involved in foraging.

The combined results of the present study suggest that constraints acting to alter the optimum foraging strategy do not need to be invoked, but rather that the basic definition of the energy maximization premise be examined carefully.

Emlen (1966) considered the net energy gain to a predator from a food item to be the product of calorific content of the food and the efficiency with which it is utilized, minus the energetic costs of capturing and consuming the prey item. In most $E/T_h$ models the rate of energy utilization during handling is considered independent of both predator and prey size. Provided that prey size does not affect the proportion of time required for the different handling activities, and provided that during these handling activities the rate of energy expenditure is equal, then prey size will not affect overall handling energy costs. The inclusion of the energetic costs of searching and handling is necessary when comparing the energetic intakes of foragers of different body size since the rate of energy utilization will be a function of body size. By assuming these costs to be equal comparisons can be made within one size class of predator, but not between size classes.

More importantly, previous $E/T_h$ models have assumed that energy intake is equivalent to useful energy gain by the predator. The efficiency with which ingested food is converted to usable energy for growth has previously been shown to be a function of the ingested ration and meal size (section 4.3.6). Since there was a positive correlation between energy intake and prey size, the $E/T_h$ model, by taking net energy gain to the predator as the ingested ration,
over-estimated the relative value of large prey. By contrast, using
growth rates as a direct measure of prey value to the predator,
predictions concerning the optimum foraging behaviour have been largely
verified. Other studies which have similarly reported that marine
invertebrates select food items that have the highest growth potential
to the predator include Carefoot (1967), Conover & Lalli (1972),

From the findings presented here it would appear that in studies of
optimal diet which include large differences in prey size, growth rate
would provide a more appropriate measure of prey value to juveniles
than $E/T_h$. For non-growing adult predators some caution should be
exercised in interpreting results where $E/T_h$ is the measure of prey
profitability.
CHAPTER 7  EFFECT OF IMMERSION TIME ON FEEDING AND GROWTH OF NUCELLA

7.1 Introduction

The benign conditions under which growth of juvenile *N. lapillus* was measured in the laboratory (section 4) might be expected to yield unrealistic estimates of growth as it occurs in the demanding environment of the intertidal zone of exposed shores as at Whitsand Bay. Indeed the temperature and salinity regime provided in the laboratory experiments were similar to those found to promote maximum scope for growth of *N. lapillus* feeding on mussels under continuous immersion (Stickle & Bayne, 1987).

Intertidal organisms however are subjected to the semi-diurnal rise and fall of the tide resulting in periodic exposure and immersion and to complex fluctuations of air and water temperatures. Sources of physical stress for intertidal animals arise from extremes of temperature and desiccating conditions while emersed and wave shock on exposed shores whilst immersed. These stresses may be expected to act as constraints on the foraging behaviour of *N. lapillus* and to result in lower growth rates in the field than observed in the laboratory.

The effect of one such constraint on the feeding and growth responses of juvenile *N. lapillus* that can be easily investigated in the laboratory is that of degree of aerial exposure. The following experiment was designed to investigate the feeding and growth rates of two sizes of juvenile *Nucella* on diets of four mussel sizes at four tidal heights. The mussel sizes used corresponded to those of the small-medium prey experiment (section 4.3.2) and the large prey experiment (section 4.3.3). It is conceivable that prey size and tidal level may have an interactive effect on growth rates, such that some prey sizes are more conducive to growth at certain tidal heights. For

-236-
example, small prey, with shorter handling times, may provide comparatively faster growth rates at higher tidal levels than large prey.

7.2 Method

A simple tidal tank system was constructed based upon the design of Evans (1964) in which the water level in the tank followed a sine curve with time. Reproduction of the shape of natural tides was achieved by having the water outlet at the end of a perspex arm that rotated once every twelve hours, with the water level in the tank corresponding to the position of the outlet throughout the rotation, (Fig. 78).

The tank itself was constructed of glass, it measured 1m long by 500mm wide and 410mm deep. Within the tank four shelves were built at different heights to provide four tidal levels with submersion for 90%, 70%, 50% and 30% of the time (levels 1 to 4 respectively). To reduce the weight of water held in the tidal tank at high tide and the volume required in the sump at low tide, the space below the shelves was sealed so that water was restricted to the upper portion only. The system was supplied with natural sea water from Plymouth Sound, circulation and cleansing were maintained by an external pump and filter (Eheim, model 2013). To ensure consistency between outlet level and tank level the input flow rate had to be carefully adjusted, a flow rate of 800ml/minute was suitable. On each shelf was placed a nylon coated steel rod tray, with 25mm mesh, which accommodated twenty-four experimental pots (section 2.3.2), lain on their sides and held in position by elastic cord. Water entered the tidal tank above level four and at low tide flowed over the surface of the shelves, below the experimental pots, so that although not moistened with water, the animals would have generally experienced a high humidity throughout the tidal cycle. The system was housed in a constant temperature room at
Figure 78. Diagrammatic representation of the tidal tank system. Levels 1 to 4 provided immersion times of 90%, 70%, 50% and 30% respectively.
15°C with a summer lighting regime.

Two initial sizes of Nucella were used, 5 and 15mm. Animals were collected from Whitsand Bay just prior to each experimental run and starved for one week in the continuous immersion system (section 2.3.1). On transference to the tidal tank the 5mm snails were provided with pure diets of one mussel size, either 5, 10, 15 or 20mm, for four weeks. 15mm snails were fed on pure diets of 10, 20, 30 or 45mm mussels (see table 27 for numbers provided and total surface area of prey). After four weeks the whelks were transferred back to the continuous immersion system and kept for a further week without food.

The length of each whelk was measured at the time of collection, after one week of starvation, weekly for the period in the tidal tank and again after the final week of starvation. During the feeding period in the tidal tank a weekly record was kept of the number of prey that had been eaten and the number of dead, uneaten mussels. Dead mussels were replaced by live animals of the same size. If the mussels were partially consumed the dry weight of the remaining flesh was determined.

One replicate consisted of each predator-prey size combination at each tidal level. Five replicates were conducted during the period 2 February to 11 May 1987. For the first, third and fifth replicates one Nucella individual of each size was kept at each level in the tidal tank for four weeks without food. For the same periods one control set of each mussel size, without Nucella, was housed on each tidal level to determine death rate due to factors other than predation.

7.3 Results

Of the twenty-four control snails only one grew after the first week of starvation (by 0.1mm) and three 5mm snails died during the six week period without food (two at level three and one at level four). Of the
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Table 27. Prey density and total surface area of prey in tidal tank experiment.
initial eighty 5mm whelks in the experimental group, seven died (one at level two, two at level three and four at level four). Death generally occurred early in the experimental run and so fresh individuals were used, however for four of these replacement snails growth and feeding was monitored for a period of only three weeks. There were no deaths among either control or experimental 15mm snails.

There was no significant difference between the mean number of dead, undrilled mussels per pot per 28 days in the control or experimental groups (t test for paired comparisons, t = 1.01, d.f. = 23, NS), (Fig. 79). Initially the death rate of mussels in the tidal tank was high because when deaths occurred this led to a loss of water quality and further deaths. The problem was controlled to some extent by daily observation to detect, remove and replace gaping mussels.

For a given size of whelk the mean weekly predation rates dropped as mussel size increased and there was a general tendency for predation rate to be lower at higher tidal levels (Fig. 80). (ANOVA on log_{10} numbers eaten, table 28).

The length-dry weight relationship of mussels was determined on two occasions, once at the beginning of the experimental period (January 1987) and again over half way through (early April 1987). The least squares regression equations on log transformed data from the two occasions were significantly different (ANOVA, \( F = 25.73, \) d.f. = 2,96, \( P<0.001 \)). As mussels were used continuously and since there was no way of determining at which point a transition between the two models occurred, the data from both estimates were combined to provide an overall mean length-dry weight relationship, as below:

\[
\log_{10} \text{dry weight (mg)} = -2.12 + 2.86 \log_{10} \text{length (mm)}
\]

(\( F = 2151, \) d.f. = 1,98, \( P<0.001 \)). Using the above relationship the weekly consumption rate of dry mussel flesh was calculated for each
Figure 79. Comparisons of mean number of mussel deaths, due to factors other than predation, per pot per 28 days in the tidal tank, in control and experimental runs. (Tidal level 4 had the longest period of aerial exposure). Dimensions above each plot refer to the mussel length.
Figure 80. Effect of tidal level and prey size on the mean predation rate (number/week) by juvenile *Nucella* feeding on mussels in the tidal tank. Each point is the mean of 5 individuals, for ANOVA see table 28.
### 5mm *Nucella*

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### 15mm *Nucella*

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Table 28. Two-way analyses of variance to test for the effect of prey size and tidal level on mean weekly $\log_{10}$ numbers of mussels eaten by juvenile *Nucella* in the tidal tank experiment.
whelk from the number of prey eaten minus the dry weight of flesh remaining in the mussels.

For each predator size mean consumption rates (mg dry weight mussel flesh consumed/week) increased with increasing prey size (Fig. 81). ANOVA detected a significant effect of tidal level on consumption rate for 15mm Nucella but not for 5mm whelks (table 29). However on closer examination of the data for 5mm Nucella (Fig. 81), when feeding on the three smallest prey sizes (5, 10 & 15mm) mean consumption rates clearly declined with increasing exposure, but there was no clear pattern when feeding on 20mm mussels.

Snail shell lengths were converted to body dry weight using the relationship reported by Bayne and Scullard (1978a) (see section 4.3.2.2). Growth rate during the four weeks of feeding in the tidal tank was significantly affected by both prey size and tidal level (Fig. 82 and table 30) for each predator size.

Gross growth efficiency was calculated for each whelk as mg dry weight increase during the four weeks of feeding in the tidal tank and the final week of starvation, divided by the mg dry weight of mussel flesh eaten during the four weeks of feeding. For both predator sizes mean gross growth efficiency decreased with increasing size of prey and was significantly affected by tidal level (Fig. 83 and table 31). Overall mean gross growth efficiency (for all prey sizes combined) was highest at level two and decreased through level one, level three to level four for each predator size.

A comprehensive picture of the effect of tidal height and prey size on growth for the six week period of the experiment can be gained by plotting mean cumulative increase in dry weight of predators against time (Figs 84 & 85). In addition to the effects already noted, of particular interest is the growth response during the final week of
Figure 81. Effect of tidal level and prey size on the mean consumption rate (mg dry flesh weight/week) of juvenile Nucella feeding on mussels in the tidal tank. Each point is the mean of 5 replicates, for ANOVA see table 29.
Table 29. Two-way analyses of variance to test for the effect of prey size and tidal level on mean weekly consumption of dry weight of mussel flesh (mg) by juvenile *Nucella* in the tidal tank experiment.
Figure 82. Effect of tidal level and prey size on the mean growth rate (mg dry flesh weight/week) of juvenile *Nucella* feeding on mussels in the tidal tank. Each point is the mean of 5 individuals, for ANOVA see table 30.
Table 30. Two-way analyses of variance to test for the effect of prey size and tidal level on mean growth rates (as mg dry flesh weight /week) of juvenile *Nucella* in the tidal tank experiment.
Figure 83. Effect of tidal level and prey size on the gross growth efficiency of juvenile *Nucella* feeding on mussels in the tidal tank. Gross growth efficiency defined as mg dry flesh weight increase during 4 weeks of feeding in the tidal tank plus one week of starvation in the continuous immersion system, divided by mg dry weight of mussel flesh consumed. Each point is the mean of 5 individuals, for ANOVA see table 31.
Table 31. Two-way analyses of variance to test for the effect of prey size and tidal level on mean gross growth efficiency of juvenile *Nucella* in the tidal tank experiment.
Figure 84. Effect of tidal level and prey size on the mean cumulative increase in mg dry flesh weight of 5mm (± 1mm) Nucella during the six weeks of the tidal tank experiment. Whelks were starved for one week in the continuous immersion system (S1), fed for four weeks in the tidal tank (F) and starved for the final week in the continuous immersion system (S2). Each point is the mean of 5 replicates.

Mussel prey sizes: △ = 5mm, ▲ = 10mm,
□ = 15mm, ■ = 20mm, all ± 1mm.
Figure 85. Legend as for figure 84 using 15mm (± 1mm) Nucella and prey sizes;  
△ = 10mm, ▲ = 20mm, □ = 30mm, ■ = 45mm (all ± 1mm).
starvation in the continuous immersion system. At level four (with only 30% immersion time) growth rate during the period in the tidal tank was low, especially so for 15mm whelks, but increased considerably during the week of starvation under continuous immersion. A similar effect was noted at level three.

This effect can be investigated by comparing growth rates during the period in the tidal tank with those during the final week in the continuous immersion system. However as snails grow their expected increase in dry weight increases exponentially with time, thus a comparison of the dry weight increments at the end of each feeding sequence with those that came before confounds the effects of snail initial size and whether exposed or submerged. For the present purposes a better measure of growth would be increment in shell length which has been shown to be approximately linear with time (appendix 1).

The change in growth rate on transference to the continuous immersion system was taken as the difference between shell growth rate in the final week of starvation and the mean weekly shell growth rate during the time in the tidal tank. For each predator size the mean difference was not affected by prey size, but was significantly affected by tidal level (ANOVA, table 32). The overall mean difference (for all prey sizes combined) was below zero for levels one and two, indicating that growth rates were lower in the period of starvation under continuous immersion than when feeding in the tidal tank (Fig. 86), but increasingly positive at levels three and four.

7.4 Discussion

The observed feeding and growth responses of juvenile Nucella in the tidal tank corroborate the overall relationships determined in the continuous immersion system of the effect of prey size (section 4.3). These include that for the given sizes of predator and with increasing

-254-
### 5mm Nucella

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### 15mm Nucella

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**Table 32.** Two-way analyses of variance to test for the effect of prey size and tidal level on the mean difference in growth rate during the final starvation week in the continuous immersion system and the mean growth rate of juvenile *Nucella* during the 28 days of feeding in the tidal tank. Growth rate expressed as mm increase in shell length/week.
Figure 86. Effect of tidal level on the difference in juvenile Nucella growth rate during the final week of starvation in the continuous immersion system and the mean for the four weeks of feeding in the tidal tank. Growth rate expressed as mm shell length increase/week. Each point is the mean of 20 individuals.
prey size, the predation rate decreases, ingestion rate of mussel flesh increases and that gross growth efficiency decreases. The rank order of prey size for promoting growth remained the same for 15mm Nucella (i.e. 20mm > 10mm > 30mm > 45mm) whereas for 5mm whelks there was a reversal of the first two mussel sizes (i.e. in the tidal tank 5mm > 10mm > 15mm > 20mm, in the continuous immersion system 10mm > 5mm > 15mm > 20mm).

The lack of interaction effects between prey size and tidal level on the feeding and growth of juvenile Nucella demonstrate that the snails do not have contrasting responses to the different prey sizes according to their degree of aerial exposure. Since the effect of prey size has been previously discussed (section 4.3.6) comments here will be restricted to a consideration of the effect of tidal level.

Juvenile Nucella ate significantly fewer mussels as the period of aerial exposure increased. Overall feeding rates at level four dropped to approximately 60% of those observed at level one for both predator sizes, although over the same tidal range the period of immersion fell by one third. Thus the time emersed does not have a proportionate effect on the number of prey consumed. Other muricid gastropods that have been shown to have significantly reduced feeding rates on barnacles at higher tidal levels when kept in cages on the shore include Thais lamellosa (Palmer, 1981) and Morula marginalba (Moran, 1985). A negative correlation between feeding rate and degree of aerial exposure could be brought about by either an increased handling time for each prey item eaten or a reduced overall proportion of time devoted to feeding with increasing tidal height.

Since the consumption of one mussel takes approximately one tidal cycle for the smallest prey offered to each of these predator sizes, (i.e. 5mm Nucella feeding on 5mm mussels and 15mm Nucella feeding on
10mm mussels each take about 12 hours, section 5.5) feeding cannot be restricted to just one state of the tide. However initiation of feeding may be confined to one period as shown by Menge (1974) for the whelk Acanthina punctulata. Initiation of feeding by A. punctulata only occurred at low tide, and if not already involved in feeding at high tide whelks retreated to crevices which had the effect of reducing the risk of dislodgement by wave action. In a similar way it is conceivable that Nucella only initiate feeding during periods of immersion, having the effect of reducing the risk of desiccation, however no data are available to test for this pattern of foraging behaviour.

The overall drop in consumption rate (dry weight mussel flesh/week) with increasing aerial exposure could be explained by either the whelks eating fewer prey or a combination of a reduced predation rate and reduced amount of flesh taken per mussel eaten at the higher tidal levels. To test the latter possibility, for each whelk the mean consumption of flesh per mussel was calculated from the mean consumption rate and mean predation rate. Tidal level had no effect on the mean amount of flesh consumed per mussel. Thus it can be concluded that tidal level affected consumption rates directly via reduced predation rates. For a population of Nucella lapillus on the east coast of the United States, Menge (1978b) found significantly reduced consumption rates of mussel flesh at the higher of two tidal levels.

In contrast, in laboratory experiments Stickle et al. (1985) reported increased consumption by N. lapillus with 83% submersion compared with those continually submerged and on the basis of this finding suggest that aerial exposure as a stress factor for intertidal fauna be re-evaluated. However it can be argued that such short exposure times may not be expected to have a detrimental effect on
feeding activity.

Previous reports show conflicting growth patterns of molluscs in response to tidal height. A reduction in growth rate with increasing shore level has been well documented for filter feeding bivalves (Baird, 1966; Seed, 1968; Griffiths, 1981a) and has been attributed to the reduced time available for feeding. Level on the shore has been shown to affect growth rates in grazing limpets (Sutherland, 1970; Creese, 1980; Underwood, 1984) and *Littorina saxatilis* (Berry, 1961).

In the above examples the effects of degree of aerial exposure were confounded with the abundance of food, but where the two factors were separated (Sutherland, 1970; Creese, 1980) increased aerial exposure did result in reduced growth rates. In the present study prey densities were constant at each tidal level, hence lack of prey availability cannot explain the observed differences in growth rate. A similar observation was made for caged *Thais lamellosa* on the shore, Palmer (1981) found significantly reduced growth at the higher of two tidal levels.

As we have seen there is a behavioural component to reduced growth rates at higher tidal levels in that the juvenile whelks ate fewer mussels, but there was also a physiological component. The efficiency with which the ingested food was converted to growth also depended on tidal level, there was a general tendency for gross growth efficiency to be highest at level two (70% submersion) and a definite trend for a decrease in gross growth efficiency at higher tidal levels. This result contrasts with the physiological adaptation shown by many bivalve species in response to increasing periods of aerial exposure. Bivalves have been shown to adapt by reducing metabolic energy demand with increasing exposure (Morton et al., 1957; Elvin & Gonor, 1979; Griffiths, 1981c), and assimilation efficiency is either unaffected by
tidal height (Griffiths & Buffenstein, 1981), or increases with increasing periods of exposure (Elvin & Conor, 1979).

A possible explanation for the observed drop in gross growth efficiency with increasing tidal height is that since measurements were made only of shell length, tissue growth could have proceeded at a greater rate than shell growth at the upper shore levels. Although no information is available on comparative rates of body and shell growth in juvenile Nucella under these conditions, Palmer (1981) found in Thais lamellosa a reduction of 22.6% and 25.2% for shell and tissue growth respectively, at the higher tidal level, suggesting that for this species there was no differential partitioning of growth between shell and body tissue dependent on tidal level.

If the same growth pattern holds for N. lapillus, the rapid increase in observed growth during the final period in the continuous immersion system following four weeks feeding at the upper tidal levels, suggests some limiting factor to shell growth during long periods of emersion. Since the calcium required for shell deposition is derived mainly from sea-water (Wilbur & Jodrey, 1952) the limiting factor could be decreased time available for calcium absorption. Alternatively as the shell is secreted by the mantle (Fretter & Graham, 1962) a process that is interrupted if the mantle is withdrawn, as for example in air, lack of growth may simply reflect the reduced time available for active shell secretion. Growth checks have been demonstrated to occur in Nucella at each period of tidal emersion, which are visible as micro-growth bands on the shell (Ekaratne & Crisp, 1982).

If shell growth is limited to periods of immersion a positive linear relationship might be predicted between growth rate and period of submersion. Such a relationship existed for submersion periods between 70% and 30% (Fig. 87) but there was little or no decrease in mean
Figure 87. Effect of tidal level on the mean growth rate of juvenile *Nucella*. Growth rate expressed as mg increase in dry flesh weight/week for 5 mm *Nucella*, and x10 this value for 15 mm *Nucella*. Each point is the mean of 20 individuals.
growth rate between 90% and 70% submersion time. These results suggest that if juvenile whelks experience less than 70% submersion time, tidal height will have a deleterious effect on growth rate, not through a proportionate decrease in feeding rate but through a decrease in shell secretion rate. At tidal levels providing more than 70% submersion time, tidal level has little effect on growth rate.

On the shore at Whitsand Bay mussel density increased with tidal height (section 3.2.2) so for juvenile Nucella there would exist a conflict between increased encounter rate with prey at higher shore levels but reduced submersion time for shell secretion, and hence less efficient use of the food ingested. For non-growing adult Nucella however the increased abundance of food at higher shore levels could lead to increased reproductive effort, the conflict now possibly being between increased consumption rates and the risk of desiccation.
CHAPTER 8 CONCLUDING REMARKS

Throughout the present text the results have been discussed at the end of each chapter. It only remains to reiterate and synthesise some of the findings as they reflect upon various aspects of the biology of Nucella as it develops on a mussel dominated shore. The aspects I will consider are diet breadth in relation to the optimality models, the possible effects of Nucella predation on the community and finally the possible role of constraints on altering the optimal foraging strategy of the developing predator.

Irrespective of the currency, either as gross energy gain per unit handling time or as net energy gain per unit time (growth potential), profitability was found to be a function of mussel prey size for developing Nucella. Additionally the optimal prey size range, that maximizing net rate of return, showed a general tendency to increase during ontogeny.

According to optimal foraging theory evolutionary selective pressures would be expected to have acted to maximize foraging efficiency thus resulting in an ontogenetic shift in prey size selection. That such a shift occurred, in both laboratory and field conditions, demonstrates that Nucella can detect the dimensions of its prey and make appropriate adjustments to its foraging decisions during development. It was further noted that the ontogenetic shift was not the result of the predator being restricted to certain prey size classes by morphological constraints.

Previous models relating profitability to prey size have often formed peaked curves (e.g. Davies, 1977; Elner & Hughes, 1978) with profitability falling sharply outside a fairly narrow range. This pattern was only evident for small Nucella size classes where changes
in prey size were large compared with predator size. For the larger predators both models predicted that a relatively broad range of prey sizes would be equally profitable.

These results pose some interesting questions about diet choice in predators. I would like to consider the questions, what are the causes and consequences of a broad plateau of optimally sized prey, why do the plateaus occur in different places for the two models and how should this affect the way we view previous foraging models using $E/T_h$ as the measure of fitness?

For the growth rate model significantly reduced growth rates were identifiable only at the extremes of the prey size range. Since at the lower prey sizes consumption rate was a function of prey size, the smallest prey provided only sufficient energy to cover metabolic requirements with a small proportion available for growth, thus overall gross growth efficiency was low. Turning now to the plateau; as prey size increases, at the low end of the plateau, although the relatively high handling costs still resulted in a low rate of gross return, the high efficiency with which the food was utilized rendered these food items profitable for growth. Towards the upper prey sizes, but still on the plateau, although consumption rate had increased the reduced efficiency of the use of these larger meals rendered these prey items no more profitable than smaller items. In general the largest prey, representing large meals, provided both reduced efficiency and little further increase in consumption rate. There may be physiological adaptive mechanisms in response to consumption rate and meal size which change the efficiency of food processing. The consequences of these mechanisms appear to be largely responsible for the plateau of the observed relationship between prey size and net energy gain per unit time.
The shape of the response curves to prey size derived from the gross energy gain per unit handling time model, although resembling those gained from growth studies, differed in that the drop in profitability on large prey was far less marked, particularly for the largest two predator sizes. Small prey were of low value because although they required relatively short handling times, the return in mussel flesh was also low. As prey size increases increased handling times are more than offset by the exponential rise in mussel flesh content, until the plateau is reached. When feeding on still larger prey handling costs continue to rise but the amount consumed per meal rises less rapidly due either to constraints on gut capacity or limitations to assessability, or both. These processes are included in the growth rate model but the latter includes the extra component of efficiency of food use. A further complicating factor in relating the two models to each other and to the foraging behaviour of Nucella is the temporal spacing between meals.

In the E/T\textsubscript{h} model, for the two smallest predator size classes, proportionately large prey dropped in value from the maximum achieved, but for the two largest size classes there was only an insubstantial drop in predicted profitability of the largest prey in the size range tested, thus providing a broad plateau of equally profitable prey.

Can the shape of the profitability curves themselves be considered capable of modification by natural selection? It is conceivable that there would not be strong selective pressures to become efficient on a narrow range of prey sizes since time spent searching for these would reduce overall profitability. In addition for a non-visual predator like Nucella, where detection of prey size depends on tactile stimuli, inspection time, from initial contact with a prey item to either initiation of feeding or abandonment, can be a lengthy process (Hughes
& Dunkin, 1984). A narrow prey size range of high value and acceptability would increase total inspection time and so reduce overall profitability from a foraging bout (Hughes, 1979). As we have seen the relatively broad plateau of equally profitable prey for growth could have resulted from modification of the physiological responses to meal size.

The range of prey sizes forming the plateau of high profitability did not coincide for the two models for all Nucella size classes. For the smallest predator size there was fairly close agreement between the two models, but for the largest two predator sizes in particular the plateau of the E/T^n model was shifted towards larger prey. The discrepancy arises as a result of equating gross energy intake with value to the consumer, which has been shown not to be the case for Nucella. It was of no surprise then that growth rate of pre-reproductive Nucella provided the closest correspondence between predicted and observed foraging behaviour since growth rates reflect the net value of a food item to the consumer.

Some previous studies on prey size selection in relation to profitability based on E/T^n have similarly shown that predators select prey smaller than the predicted optimum (Elner & Hughes, 1978; Hughes & Dunkin, 1984) while others have shown a close correspondence between predicted and observed behaviour (e.g. Kislalioglu & Gibson, 1976). It would not be expected that the disparity between the two models of profitability as shown in this study would be of critical importance in all prey size selection situations. Where all meal sizes within the range of prey sizes under consideration are small compared with the digestive capacity of the predator, for example with planktivorous fish, it would be unlikely to obtain such a dramatic drop in gross growth efficiency with increasing prey size as was witnessed here.
In the present predator:prey regime the quantification of the growth value of different mussel sizes for developing Nucella provides an insight into not only prey selection behaviour but also the effect of the predator on the observed distribution of prey. The distribution of prey species has been shown previously to be radically affected by the predatory behaviour of muricean gastropods (Connell, 1961; Menge, 1978a, 1978b; Suchanek, 1978). Relatively large mussels, which were less profitable in growth terms, were less readily consumed by Nucella than smaller prey. Reluctance to feed on large mussels suggests that Mytilus may achieve a size refuge from predation by Nucella, as indicated to occur for the prey of other drilling gastropods (Ansell, 1960; George, 1965; Taylor, 1970; Dayton, 1971; Adegoke & Tevesz, 1974; Franz, 1977; Edwards & Heubner, 1977; Palmer, 1983).

The existence of an upper prey size, above which the probability of predation is small, might act to stabilize single predator:prey interactions since those prey individuals, which by virtue of their of size are relatively immune to attack, have a significantly greater reproductive output than smaller individuals.

The absence of relatively large mussels within the zone inhabited by Nucella may reflect a high predation intensity, few mussels survive to a size affording predation immunity. Environmental limitation to mussel size is precluded by a comparison of the size frequency distributions of mussels on various areas of the same rock. The S.E. facing slopes of the rocks at Whitsand Bay supported a low density of Nucella, due probably to high temperatures and desiccating conditions during emersion. Similarly on the N.W. facing rock surface, although there was not a clear demarcation line, Nucella density was low on the higher reaches of the rock. The visual impression that within these two areas mussels achieved a greater size than within the Nucella zone.
was confirmed by sampling the mussel population from the three contrasting regions (Fig. 88).

Thus it appears that where predation intensity is high a size refuge for mussels is rarely achieved, but a spatial refuge for the breeding population can be gained by the mussels being more tolerant of high temperatures and desiccating conditions than their predators.

In regions of mussel bed inhabited by *Nucella* the effects of their predatory activity may be viewed as advantageous to their survival and growth of the population. Whereas above the *Nucella* zone the mussels formed extensive tightly packed beds, within the *Nucella* zone areas cleared of mussels, as a result of whelk predation, resulted in patches of bare rock. Such patches provide space for egg capsule deposition and are available for mussel recruitment thereby providing food of a suitable size for young whelks. Additionally the patchy distribution of mussels afford some protection from wave action for the adult whelks which aggregate around the periphery of mussel clumps, particularly when feeding. High predation intensity on mussels also has the effect of preventing mussels from growing to their size refuge, ensuring that the majority of the prey population are within an optimum size range for the consumer.

However should the predation intensity increase sufficiently to exclude mussels locally, as appears to have happened on some rocks at Whitsand Bay, barnacle and limpets, alternative prey for *Nucella*, recolonize the area. The behaviour of the predator, to switch to the new prey type or migrate in 'search' of mussels, their preferred prey (Hughes & Drewett, 1985), would affect the subsequent fate of the area. If *Nucella* remained in the patch feeding on barnacles, but then switched back to mussels as they became re-established, behaviour that might be expected from the work of Hughes and Drewett (1985), there
Figure 88. Comparison of the size frequency distribution of mussels from different areas of the same rock at Whitsand Bay.

1) on the N.W. facing side, within the Nucella zone, 12 samples, total surface area = 0.12 m², n = 2246, sampled January 1985.

2) on the N.W. facing side, above main Nucella zone, 12 samples, total surface area = 0.12 m², n = 4596, sampled March 1988.

3) on the S.E. facing side, same tidal level as 1), 1 sample of 0.15 m², n = 3602, sampled March 1985.

(Data for 3) supplied by C. Worrall, Plymouth Marine Laboratory).
would be little opportunity for the mussels to become dominant again. Only where the population density of the predator showed a considerable decline might one expect mussels to be able to re-establish.

Although little of the work presented here was concerned specifically with identifying constraints that might act to alter the optimal foraging strategy of Nucella in the field, some observations can be invoked to address this question.

The high proportion of hatchlings that were unaccounted for in the field study and their low degree of tenacity suggest that wave action poses a real threat to their survival. Most predatory attacks by the young juveniles were made through the anterior, and hence thickest, part of the mussel shell as if drilled from beneath the mussel bed. Moreover, the diet breadth of young Nucella equalled that of larger individuals, with a general tendency for the small individuals to consume prey in the field which were larger than the optimum. (In the laboratory however, in the absence of constraints, large prey were rarely eaten). One possibility is that from their sheltered position under the mussel mat the detection of prey size was made more difficult and mistakes more likely to occur.

These observations suggest that the constraint of being washed off the rock has been a more powerful selective pressure than the need to increase foraging efficiency by selecting the thinnest part of the mussel shell or the most profitable prey size. The pronounced negative phototactic response could have evolved as a mechanism for avoiding micro-habitats exposed to wave action.

Mortality of late juvenile and adult whelks was low, as evidenced by the repeated recapture of marked individuals in the field. Apart from the occasional activity of oystercatchers there was little evidence of predatory pressure upon the larger Nucella, and the realization of the
potential risk of dislodgement was witnessed only during severely stormy weather. Furthermore for the older whelks there was no evidence that the activity of feeding rendered them more likely to dislodgement by wave action than non-feeding activities. Indeed, if anything, the whelks were more difficult to dislodge when engaged in feeding. At what size dislodgement ceases to be a real danger was not determined but it would be interesting to see if it correlates with an ontogenetic decline in the negative phototactic response.

The physical rigours of intertidal life, with alternating periods of submersion and emersion, might be thought to act as a constraint on the foraging behaviour of Nucella and hence result in reduced growth rates in the field compared with those obtainable in laboratory conditions.

When, in the laboratory, Nucella were provided with emersion periods longer than those experienced within the normal distribution range of the species, growth rates were significantly reduced. Lower growth rates with increasing aerial exposure were shown not to be entirely the result of reduced feeding rates, but rather the inability to produce shell and hence less efficient use of the food consumed.

It was surprising to find that where comparisons could be made between laboratory and field growth rates the latter, although reduced, were in some cases approaching the maximum observed in the laboratory.

For example, mean linear shell increment of juveniles collected from Whitsand Bay and starved for one week was 0.38 mm/week (section 4.3.2), compared with the asymptotic mean growth rate of 0.42 mm/week for snails during the week of starvation following ad libitum feeding in the continuous immersion system (Fig. 40). Less strikingly, mean growth rates of 5 to 20 mm whelks whilst feeding in the laboratory on a range of prey sizes was 0.85 mm/week (n = 80, S.D. = 0.39 mm/week) (section 4.3) compared with mean growth rates achieved in the field from July to
August for whelks up to 20 mm length of 0.62 mm/week (n = 39, S.D. =
0.24 mm/week) (section 3.4). Thus growth rates in the field were 73% of
those observed in the laboratory at a similar water temperature.

These two observations suggest that, with the exception of the
smallest *Nucella* and where food, as mussels, is relatively abundant,
the physical rigours of intertidal life experienced by the whelks at
their normal tidal range do not, in themselves, impose significant
constraints on the foraging and growth activity of juveniles of this
species.
REFERENCES


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APPENDIX 1  LIFE HISTORY GROWTH STUDIES

The pattern of growth over the life of seven individual Nucella lapillus fed ad libitum on mussels in the laboratory was recorded.

Method

Ripe egg capsules collected from Whitsand Bay were kept in the continuous immersion system (section 2.3.1) until hatching occurred. The feeding and housing regimes provided for the whelks changed as they grew. From hatching to 4 mm length the snails were maintained in separate wells of a multi-well plate (section 2.3.2) and provided with ten mussels in the range 1.5 to 2.5 mm length. At 4 mm the whelks were transferred to small glass vials (measuring 35 mm by 22 mm diameter) escape being prevented by a gauze top and provided with ten mussels in the range 4 to 5 mm length. From 8 to 24 mm the whelks were housed in separate small green pots (section 2.3.2) and given twelve mussels in the length range 10 to 11 mm. Once larger than 24 mm the whelks were transferred to large green pots (section 2.3.2) and provided with five 23 to 25 mm mussels as prey. Throughout the trial the animals were housed separately and accommodated in the continuous immersion system.

Every four to five days the length (to within 0.1 mm) of the developing snails was determined using a binocular microscope and graduated eye-piece for snails too fragile to handle, and subsequently vernier calipers. Consumed prey were counted and replaced with fresh mussels.

Results

All snails grew for at least four months during which time growth was fairly continuous, and lived for at least six months (Fig. 89). For all snails there was a fairly abrupt cessation of feeding, and hence growth, sometime before death occurred. Only two of the seven
Figure 89. Growth of individual *Nucella* in the continuous immersion system, fed *ad libitum* on mussels, and measured every 4-5 days. Vertical bars denote death of the whelks, trials were discontinued in March 1986.
snails reached 25mm length, an adult size, before dying. Following hatching the majority of snails showed increasing increment of shell length with time until a size of approximately 6mm was reached, after which growth rate was constant until either feeding stopped or the whelks reached approximately 20mm length. In general growth rate declined beyond a length of 20mm. Mean growth rate of the seven individuals for the period from 6 to 20mm length (or maximum size) was 1.13mm/week (S.D.=0.16mm). The two individuals that grew beyond 25mm length took 22.4 and 26.3 weeks to grow from hatching to 25mm.

Comments
1. Growth rates of *N. lapillus* under laboratory conditions (15°C, 34%) are sufficiently rapid to enable adult size to be reached in six months.
2. However after four to six months of continual submersion both feeding and growth ceased.
3. Whelks continued to live for at least two months following the cessation of feeding.
APPENDIX 2 FUNCTIONAL RESPONSE OF NUCELLA FEEDING ON MUSSELS

Most invertebrate predators show a type II functional response (Holling, 1959). An investigation was conducted into the effect of prey density on the feeding rate of juvenile Nucella to ensure that during subsequent feeding trials the densities used would be at the asymptote of a possible functional response curve.

Method

In each of four experiments, spanning a range of predator sizes, five prey densities (8, 12, 16, 24 & 32) were established in the experimental pots in the continuous immersion system (section 2.3.1). One Nucella was introduced to each pot and allowed to feed for between 9 and 14 days. After the allotted period drilled prey were removed and counted, but there was no replacement of prey during the experiment.

Results

The feeding rate is given in table 33. Feeding rate was independent of prey density (ANOVA, F= 0.70, d.f. = 4,15, NS) so at these densities the whelks are not limited by encounter rate.

Comment

The surface area of prey in the growth (section 4.3.2) and selection (section 6.2) experiments fell above or within the range presented here.
<table>
<thead>
<tr>
<th>Nucella size (mm)</th>
<th>Prey size (mm)</th>
<th>Days of feeding</th>
<th>Feeding rate number/day</th>
<th>Prey density</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1 - 4.8</td>
<td>4 - 6</td>
<td>9</td>
<td>0.56 0.56 0.67 0.44 0.56</td>
<td></td>
</tr>
<tr>
<td>14.3 - 16.0</td>
<td>13 - 15</td>
<td>14</td>
<td>0.43 0.21 0.28 0.50 0.36</td>
<td></td>
</tr>
<tr>
<td>14.8 - 15.8</td>
<td>14 - 16</td>
<td>12</td>
<td>0.25 0.42 0.50 0.58 0.50</td>
<td></td>
</tr>
<tr>
<td>17.9 - 19.1</td>
<td>18 - 20</td>
<td>12</td>
<td>0.50 0.42 0.25 0.58 0.67</td>
<td></td>
</tr>
</tbody>
</table>

Table 33. Effect of mussel prey density on the feeding rate of juvenile *Nucella lapillus*. 

-A5-
APPENDIX 3 TENACITY OF NUCELLA

The effect of Nucella size on an artificial measure of tenacity was determined. An estimate was gained of the relative risk of dislodgement of snails whilst submerged, emerged and feeding.

Method

Whelks in the size range 8.6 to 29.0mm were collected from Whitsand Bay, numbered with quick drying cellulose paint and their total shell length and aperture length (Crothers, 1974) measured. To each snail was attached a terry clip of an appropriate size to grip the shell firmly but not to impede movement.

Experiment 1: Effect of whelk size on tenacity whilst submerged.

Equipped with their terry clips, the snails were allowed to attach themselves to a slate tile submerged in the continuous immersion system (section 2.3.1). After a period of not less than 5 minutes the snails were lightly tapped to allow them to secure a grip of the substratum and a spring balance was carefully hooked under the clip and a steady upwards force applied. The force required to dislodge the snail from the tile was recorded. The range and accuracy of the balance used depended on whelk size. For large snails a spring balance in the range 0 to 500 grams was used, readings taken to the nearest 10 grams, for smaller snails the balance was in the range 0 to 100 grams, readings being possible every 5 grams. Six measurements were thus made for each of sixty-eight snails, with a period of at least ten minutes between trials for any one whelk.

Experiment 2: Effect of whelk size on tenacity at simulated low tide.

The same batch of snails was fitted up as above and allowed a minimum of thirty minutes for attachment whilst submerged. The slate tile was then gently lifted out of the water and held vertically to
dislodge unattached snails. The whelks remaining on the slate were left exposed in the laboratory for one hour to simulate low tide, after which time the surface of the slate was dry. The force required to detach the whelks from the slate was measured as in experiment 1.

Experiment 3: Effect of size on tenacity whilst feeding.

Clumps of mussels were scattered at random on the submerged slate and the whelks, with their clips, allowed to forage. After a period of approximately 18 hours, for those whelks positioned on mussels in a potential feeding position, measurements were made of the force necessary to detach them whilst submerged. Microscopic examination of the mussel shell at the point of whelk contact revealed if the whelks had been inactive, drilling or ingesting.

Results

There was considerable variation in the force required to dislodge whelks whilst submerged, both between individuals of a given size and within the six trials for any one individual. The mean force of the six trials for each individual is shown in figure 90 as a function of Nucella size. Clearly the tenacity of N. lapillus increases exponentially with increasing size, and can be described by the least squares regression equation;

$$\log_{10} f = -1.33 + 2.52 \log_{10} L$$

where \( f \) is force in grams, \( L \) is length of Nucella in mm. (\( F = 636.5, \) d.f. = 1,66, \( P<0.001 \)).

The maximum force increased in the same manner with increasing Nucella size and can be described by the least squares regression equation;

$$\log_{10} \text{max}f = -1.26 + 2.59 \log_{10} L$$

where \( \text{max}f \) is the maximum force in grams of six trials, \( L \) is length (mm) of Nucella. (\( F = 545.3, \) d.f. = 1,66, \( P<0.001 \)).
Figure 90. Effect of Nucella length (mm) on the mean (of six trials) force (g) required to dislodge snails from the substratum whilst submerged.
The force required for dislodgement following a simulated low tide of one hour was determined for thirty snails, each snail having one or two trials. Out of a total of forty-six trials, twenty-one fell above the range displayed by the whelks whilst submerged, twenty-two were within the range and three were below (Fig. 91).

Only six trials on six separate snails were conducted to determine the tenacity of *Nucella* whilst feeding. In five of these trials the force required to dislodge the whelks fell above the range exhibited whilst submerged (Fig. 91), these snails were all either drilling or ingesting. For one individual the force required whilst feeding fell below its submerged range, this whelk was drilling a marginal hole.

The mean ratio of shell length (*L*) to aperture length (*Ap*) was 1.55 (S.D.=0.08), *L/Ap* increased with increasing size of *Nucella*, (Fig. 92).

**Comments**

1. Both whilst submerged and emerged the force required to dislodge *N. lapillus* increased exponentially with shell length.
2. In general tenacity of snails after one hours exposure to air was greater or equal to their tenacity in water.
3. In general the tenacity of snails was greater whilst feeding than when attached to rocks under water.
4. The experimental procedure was not a good simulation of the major cause of dislodgement in the natural environment, namely water movement. Since water movement would generally exert its force on the side of the snail, larger snails would offer more resistance than smaller snails. To what extent the increase in surface area of the foot, and hence tenacity, would be offset by the increase in shell surface area for the force of water movements to act upon cannot be judged. Ideally some form of 'water tunnel' is required but in the laboratory it is difficult to generate the necessary forces. Despite
Figure 91. Forces (g) required to dislodge individual *Nucella* under varying conditions. Vertical bars represent the range of forces (g) for individuals whilst submerged, n = 6 trials. ○ = force required after one hour in air. • = force required whilst feeding. The *Nucella* are arranged in ascending length order, sizes (mm) are given for every fifth individual.
Figure 92. Effect of *Nucella* length (mm) on the ratio shell length: aperture length.
this drawback the results suggest that for a given size of snail neither the activity of feeding nor short periods of emersion constitute a greater risk of dislodgement than when whelks are submerged.

5. The mean value for the ratio total shell length to aperture length was high compared with those reported by Crothers (1974) for exposed shores.
APPENDIX 4 SIZE-FREQUENCY DISTRIBUTION OF NUCELLA ON ROCKS AT RHOSILI

The size-frequency distribution was determined for a population of Nucella lapillus on cliffs between Kitchen Corner and Rhossili (National Grid reference SS 403876) on the Gower, South Wales in September 1985. The cliffs are nearly vertical, the pitted surface of the limestone rock providing shelter for a dense population of whelks.

Method

Samples of N. lapillus were collected from three separate rock faces at two heights, 2.4m apart vertically. The upper sample was taken from a region with virtually 100% cover of live and dead barnacles, while the lower sample had approximately 50% barnacle cover, 35% cover of small mussels and 15% of bare rock. Each of the six samples consisted of the first one hundred Nucella individuals from a 10cm deep horizontal band selected at random from the appropriate area. All the whelks collected were measured in length to the nearest 0.1mm.

Results

Data from the three rocks were combined to provide the size-frequency distribution for both lower and upper shore positions (Fig. 93). Over one half of the whelks (180 out of a total of 302) found at the lower site were less than 7mm in length, with generally progressively fewer in each size category as size increased, less than 2% were over 16mm in length. In contrast the upper shore distribution was roughly tri-modal, with peaks at lengths of 5mm, 10 to 11mm and 22mm. Overall there was a greater proportion of larger snails at the upper shore position.

Comments

1. At the time of sampling no egg capsules were visible on the rocks, so movement of hatchlings following emergence could not be established.
Figure 93. Size frequency distributions of *Nucella* collected from rocks at Rhossilli, in relation to height on the shore, during September 1985.
2. Maximum size of whelk and size of whelks in the 'adult' peak were smaller than observed at Whitsand Bay.

3. As at Whitsand Bay there was a greater proportion of small snails on the lower shore than on the upper shore.
APPENDIX 5  SURFACE AREA-LENGTH RELATIONSHIP OF MUSSELS

Since the shell shape of mussels shows considerable plasticity in response to environmental conditions (Seed, 1968), the relationships between length and surface area and between length and height (appendix 6) were determined for mussels from Whitesand Bay.

Method

The surface area of a range of mussel sizes was determined by wrapping cling film around one valve and drawing on the cling film at the edges of the shell. The area enclosed by the outline thus obtained was determined by superimposing the cling film on graph paper.

Results

Surface area (S mm$^2$) was related to length (L mm) by the least squares regression equation;

\[ S = (0.883 + 0.99 L)^2 \]

\( (F = 3064, \text{ d.f.} = 1,8, P<0.001). \)
APPENDIX 6 LENGTH-HEIGHT RELATIONSHIP OF MUSSELS

Method

The length and height of drilled mussel shells collected from the field in March, September, October and November 1985 (section 3.2) were measured to within 0.1 mm.

Results

For each month separately the height (H mm) of mussel shells was related to their length (L mm) by least squares regression analysis - see below.

\[
\begin{array}{cccc}
& r & F & \text{d.f.} & P \\
\hline
\text{March} & H = 1.37 + 0.43 L & 0.98 & 3993 & 1,181 < 0.001 \\
\text{September} & H = 1.06 + 0.44 L & 0.99 & 3766 & 1,93 < 0.001 \\
\text{October} & H = 1.04 + 0.44 L & 0.99 & 9627 & 1,185 < 0.001 \\
\text{November} & H = 0.97 + 0.45 L & 0.99 & 4242 & 1,94 < 0.001 \\
\end{array}
\]

Comment

Under these models the height is approximately half the length, with mussels getting relatively 'slimmer' as length increases. Calculated heights (in mm) at sample lengths are given below.

<table>
<thead>
<tr>
<th>Mussel length</th>
<th>10mm</th>
<th>20mm</th>
<th>30mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>5.7</td>
<td>9.9</td>
<td>14.2</td>
</tr>
<tr>
<td>September</td>
<td>5.5</td>
<td>9.9</td>
<td>14.3</td>
</tr>
<tr>
<td>October</td>
<td>5.5</td>
<td>9.9</td>
<td>14.3</td>
</tr>
<tr>
<td>November</td>
<td>5.5</td>
<td>10.0</td>
<td>14.5</td>
</tr>
</tbody>
</table>
APPENDIX 7. SPECIES FOUND IN THE SAME ZONE AS NUCELLA AT WHITSAND BAY

<table>
<thead>
<tr>
<th>PHYLUM</th>
<th>SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porifera</td>
<td>Halichondria panicea (Pallas)</td>
</tr>
<tr>
<td></td>
<td>Scypha compressa (Fabricius)</td>
</tr>
<tr>
<td></td>
<td>Myxilla sp.</td>
</tr>
<tr>
<td>Coelenterata</td>
<td>Actinia equina L.</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>Electra pilosa (L.)</td>
</tr>
<tr>
<td>Annelida</td>
<td>Spirobranchus borealis Daudin</td>
</tr>
<tr>
<td></td>
<td>Pomatoceros triqueter (L.)</td>
</tr>
<tr>
<td></td>
<td>Bulalia viridis (O.F. Muller)</td>
</tr>
<tr>
<td></td>
<td>Perinereis cultrifera (Grube)</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>Balanus perforatus Bruguiere</td>
</tr>
<tr>
<td></td>
<td>Semibalanus balanoides (L.)</td>
</tr>
<tr>
<td></td>
<td>Chthamalus montagui Southward</td>
</tr>
<tr>
<td></td>
<td>Gammarus sp.</td>
</tr>
<tr>
<td></td>
<td>Idotea viridis (Naylor)</td>
</tr>
<tr>
<td></td>
<td>Cancer pagurus L.</td>
</tr>
<tr>
<td></td>
<td>Carcinus maenas (L.)</td>
</tr>
<tr>
<td></td>
<td>Nymphon gracile Leach</td>
</tr>
<tr>
<td>Mollusca</td>
<td>Palio dubia (M. Sars)</td>
</tr>
<tr>
<td></td>
<td>Acanthochitona crinitus (Pennant)</td>
</tr>
<tr>
<td></td>
<td>Lepidochitona cinereus (L.)</td>
</tr>
</tbody>
</table>

-A18-
Mollusca
(continued)

- Patella vulgata L.
- Patella depressa (Pennant)
- Gibbula umbilicalis (da Costa)
- Monodonta lineata (da Costa)
- Littorina littorea (L.)
- Rissoa parva (da Costa)
- Cingula cincillis (Montagu)
- Nucella lapillus (L.)
- Odostomia scalaris Macgillivray
- Onchidella celtica Forbes & Hanley
- Mytilus edulis L.
- Hiatella arctica (L.)
- Lasaea rubra (Montagu)

Rhodophyta

- Palmaria palmata
- Ceramium flabelligerum
- Ceramium shuttleworthianum
- Porphyra umbilicalis
- Corallina officinalis
- Lomentaria articulata
- Gigartina stellata
- Laurencia pinnatifida
- Lithophyllum incrustans
- Rhodymenia pseudopalmata
- Polysiphonia sp.

Phaeophyta

- Fucus serratus
- Dictyota dichotoma
- Cladostephus spongiosus
Phaeophyta
(continued)
Leathesia difformis
Ralfsia sp.

Chlorophyta
Ulva lactuca
Enteromorpha linza
Cladophora sp.

Visited by:
Turnstones
Herring gulls
Oystercatchers

1. The keys used in the identification of the seaweeds (Hiscock, 1979, 1986) did not provide authorities.
APPENDIX 8. FORTRAN PROGRAM TO DETERMINE LENGTH OF WALK AND ANGULAR DEVIATIONS FROM CO-ORDINATE DATA.

C DISTANCES AND ANGLES MOVED BY HATCHLINGS
C X(I), Y(I) = COORDINATE POSITIONS
C DX(I), DY(I) = DISTANCES MOVED ALONG X AND Y AXES ON WALK (I)
C D(I) = ACTUAL DISTANCE MOVED ON WALK (I)
C A(I) = ANGLE MOVED WITH RESPECT TO POSITIVE X AXIS ON WALK (I)
C C(I) = ANGLE OF TURN AT BEGINNING OF WALK (I) IN RADIANS
C DEG(I) = ANGLE OF TURN AT BEGINNING OF WALK (I) IN DEGREES
REAL X(0:100), Y(0:100), DX(0:100), DY(0:100), D(0:100), A(0:100)
REAL C(0:100), DEG(0:100)
CALL READIN (X,Y,N)
A(0)=0
DO 20, I=1,N
   DX(I)=X(I)-X(I-1)
   DY(I)=Y(I)-Y(I-1)
C TO CALCULATE DISTANCE MOVED
   D(I)=SQRT((DX(I)*DX(I))+(DY(I)*DY(I)))
C TO CALCULATE ANGLE OF WALK (I) WITH RESPECT TO POSITIVE X AXIS
   IF (DX(I).GT.0) THEN
      A(I)=ATAN (DY(I)/DX(I))
   ELSE IF (DX(I).LT.0 .AND. DY(I).GE.0) THEN
      A(I)=ATAN (DY(I)/DX(I))+2*ASIN(1.0)
   ELSE IF (DX(I).LT.0 .AND. DY(I).LT.0) THEN
      A(I)=ATAN(DY(I)/DX(I))-2*ASIN(1.0)
   ELSE IF (DX(I).EQ.0 .AND. DY(I).GT.0) THEN
      A(I)=ASIN(1.0)
   ELSE IF (DX(I).EQ.0 .AND. DY(I).LT.0) THEN
      A(I)=ASIN(-1.0)
   ELSE IF (DX(I).EQ.0 .AND. DY(I).EQ.0) THEN
      A(I)=0
   END IF
C TO CALCULATE ANGLE OF TURN AT BEGINNING OF WALK (I)
   IF (A(I).NE.0) THEN
      C(I)=A(I)-A(I-1)
      IF (C(I).GT.2*ASIN(1.0)) THEN
         C(I)=C(I)-4*ASIN(1.0)
      ELSE IF (C(I).LT.2*ASIN(-1.0)) THEN
         C(I)=C(I)+4*ASIN(1.0)
      END IF
   ELSE IF (A(I).EQ.0) THEN
      C(I)=0
      A(I)=A(I-1)
   ENDIF
   IF (I.EQ.N) THEN
      PRINT *, 'PROGRAM COMPLETE'
      PRINT *, 'PROGRAM COMPLETE'
   ENDIF
20  CONTINUE
DO 40, I=1,N
   DEG(I)=(C(I)/(2*ASIN(1.0)))*180
40  CONTINUE
DO 30, I=1,N
   WRITE(6,600) I, X(I), Y(I), D(I), A(I), C(I), DEG(I)
600  FORMAT (13,2X,5(F6.2,2X),F6.1)
30  CONTINUE
STOP
END