The Population Structure of Late Pliocene and Early Pleistocene Neptunea angulata, Gastropoda and an Investigation into Bias in the Fossil Record and Museum Collections

En undersökning av populationsstrukturen hos Neptunea angulata under sen Pliocen och tidig Pleistocen samt snedfördelning inom fossilfynd och museisamlingar

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Abstract

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The fossil population structure of the gastropod Neptunea angulata from the late Pliocene and Early Pleistocene was investigated in this project in order to contribute to a wider study on the influence of predation on populations and the evolutionary history of organisms. Over time, predator-prey relationships can drive evolution in a way similar to the Red Queen Hypothesis. However, before the effects of predation can be understood one must determine how the population dynamics functioned without the influence of predation. There are a number of problems that arise when determining population dynamics for fossil assemblages. These are usually caused by missing fossil data and the uncertain nature of their absence. Bias is rife within fossils at various stages from post-mortem processes to when they are present in museum collections. One way to estimate these biases is to investigate the population structures of the fossils both directly from the fossil record and from museum collections.

The variation in oxygen isotopes found in N. angulata shells corresponded to yearly cycles which then were counted to determine the age of the specimen at time of death. Measuring the length of the spiral at yearly intervals provided the growth rate for the organism while it was alive. The growth rates were then used to determine the ages of specimens based on their size. The resulting ages were organized into an age distribution graph which was used to determine any museum bias. Bias in the preservation was also investigated by measuring the taphonomic damage of organisms of different size and then determine the distributions of size vs taphonomy.

The ages of three specimens were found to differ even though the organisms had similar whorl lengths. As a result the growth equations differed and so different age distributions were calculated from each growth equation. All the age distributions demonstrated that the museum collections did show some bias against the smaller sized and thus younger specimens. There also appeared to be a size bias towards small N. angulata within the fossil record, with the extremely small individuals missing. The majority of the smallest specimens found in the field collections were not actually N. angulata specimens. A major problem with the results was a lack of data and a small sample size and it is highly recommended that an extensive collection and review of material be undertaken to fully determine the population structure present in the fossil assemblages. Other parts of the study, for example, the growth rates also require larger data sets in order for the confidence of the data to be improved.

Keywords: Bias, age distributions, taphonomy, population structure

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Populärvetenskaplig sammanfattning

En undersökning av populationsstrukturen hos *Neptunea angulata* under sen Pliocen och tidig Pleistocen samt snedfördelning inom fossilfynd och museisamlingar

*Thomas Owen*

I detta projekt studerades snäckpopulationer (*Neptunea angulata*) från Pliocen och Pleistocen för att besvara bredare frågeställningar om predation och dess inflytande på populationer och evolution. Innan man kan fastställa effekten av predation så behöver man förstå hur populationen betedde sig utan predationstryck. Flertalet problem uppstår när man studerar fossila populationer: tillgången på data kan vara begränsad och det kan vara svårt att se vad som saknas och varför. Information från fossil förloras från tiden som organismen dör fram till att de återfinns i museisamlingar. Ett sätt att uppskatta informationsförlusten är att studera fossil såväl i fossilbäddar som i museisamlingar.

Genom att använda sig av den observerade cyklika skillnaden i stabila syreisotoper mellan olika tillväxtzoner i skalen av *Neptunea angulata* var det möjligt att uppskatta åldern på en organism vid en viss längd. Hastigheten med vilken snäckan växte beräknades genom att mäta förändringen i växt mellan olika åldrar. Genom att beräkna hur snabbt en snäcka växte så var det möjligt att använda storleken på fossilerna för att uppskatta dess ålder då den dog. Fossilen organiserades efter ålder för att visa populationsstrukturer. Förfluster av fossil efter deposition uppskattades undersökt genom att bestämma om mindre storleksgrupper var mer skadad än större storleksgrupper.

Den varierade tillväxten hos olika snäckor användes för att beräkna dess åldrar. Det upptäcktes att museisamlingar tenderade att inneha större och äldre individer. Det tycktes också finnas färre små fossil av *Neptunea angulata* inom opartisk samling. Några av de extremt små individerna saknades helt och majoriteten av de minsta fossilerna var inte ens *Neptunea angulata*. Skador på fossilen var större ju mindre individerna var. Mängden data inverkade negativt på denna studie och därför rekommenderas en omfattande genomgång av de tillgängliga samlingarna för att bättre kunna besvara frågor kring denna population i framtiden.

**Nyckelord:** Snedfördelning, åldersfördelning, tafonomi, populationsstrukturer

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1 Introduction

This project is part of a broader study on the effect of predation on the evolutionary history of an organism. The investigation will take place on specimens belonging to the extinct gastropod *Neptunea angulata* (Wood, 1848), which is one of a few left handed species of marine gastropod. The left handedness may be the result of predatory selection as crabs and other peeling predators are more efficient predators of right handed gastropods (Dietl and Hendricks, 2006). This makes *N. angulata* an interesting organism to study when investigating the evolutionary effects of predation.

Shelly organisms that are predated by means other than boring tend to get completely destroyed and thus are no longer present in the population. Therefore the organisms that are left in the fossil record are ones that were not predated and that died from a variety of other factors such as disease, old age and starvation. This makes it extremely difficult to estimate what proportion of the population was predated and to determine what the most common occurrence of death was. As it is likely that the great majority of organisms eventually fall victim to predation, a paradox thus arises in which the fossil record, from which all inferences about predation must be drawn, is largely drawn from the rare organisms that did *not* die from predation.

The project will specifically focus on the population of structures of organisms that survive or avoid predation. To begin investigating predation’s effect on populations of organisms, the predatory death rate must be differentiated from the normal base rate of death from other causes. Determining age distributions and survivorship curves are the best way to study the mortality rate excluding death from predation. Once this is done the data can be used in models attempting to determine predatory influences. However, there are a variety of factors that can influence population structure which need to be determined. Using size distributions have been carried out for many extinct and extant populations, and the investigations as to why certain distributions exist have been extensively studied (Fagerstrom, 1964; Bitner, 2002).

Using a sample of a large amount of specimens it is possible to determine the age frequency distributions of the populations. Age frequency distributions can be used for two purposes: the first would be to determine the (non-predatory) mortality rate of the organisms at different ages and; the second would be to record the percentage of the population of a particular age that is attacked by predators. Size frequency distributions are able to demonstrate how much transport the death assemblage has undertaken, with normal distributions allegedly indicating some transport and right-skews indicating no transport (Fagerstrom, 1964). They could also show which parts of the population are being removed by taphonomic processes and thus can indicate how biased and incomplete the fossil record investigated is. In addition it could indicate which age groups are removed from the fossil record by disruptive predatory attacks.

*N. angulata* is a good organism to investigate with regards to age distributions because of its easy identifiability as well as abundance in both museum collections and in the geological record. There has
been a great deal of research on extant *Neptunea* species which can be used for better palaeoecological inferences and can allow the comparison of population structures in extant populations and the extinct populations in order to estimate potential biases in the fossil record (Pearce and Thorson, 1967, Fujinaga and Nakao, 1996).

In order to determine the age of *Neptunea* gastropods for age distributions the use of statoliths or opercula are required (Miranda et al., 2008, Richardson et al., 2005). Unfortunately these are not usually preserved with the shell and as such the use of another method is required. Even if such structures were preserved it would be quite an arduous task measuring all of them to calculate the age of individual specimens. As a result another source of age data is needed. One source could be isotope data, as the seasonal variations of the $^{18}$O isotopes could be counted to estimate the age (Urey et al., 1951). Using the age and size of the organism it would be possible to calculate the growth rate, which, if linear, implies a direct relationship between size and age. Regardless, the equation of the growth rate can then be used to calculate the age of specimens using their size.

Determining fossil populations is a difficult task; there is a significant loss of data through taphonomy and lack of preservation. There are several types of bias that occur in the fossil record which makes it difficult to accurately determine the effect of predation on populations. Before biases in different assemblages can be discussed, some definitions must be explained. A life assemblage is an assemblage when the fossils are preserved in situ. A death assemblage occurs when the fossils were initially transported to the site of deposition (Boucot, 1953). One bias can occur in the death assemblage where the preferential transport of certain sizes can remove specimens. Further bias can occur when specimens are lost from the death assemblage during preservation owing to their mineralogy or size (Kidwell and Bosence, 1991). The fossil record is naturally also heavily biased towards the preservation of shelly organisms. Smaller organisms with weaker shells tend to be broken and do not appear in the fossil record (Craig and Hallam, 1963). By bulk sampling random parts of the sediment it is possible to determine how much taphonomy the organisms experienced and at what size the taphonomic effect reduces. Estimating the amount of taphonomic damage to the shells could allow the estimation of the number of shells that were present in the death assemblage before any destruction.

One source of data that could be used to calculate predation rates is museum material. However, there is a suspicion that the museum material is heavily biased in terms of size of specimen and taphonomical quality of specimen. Therefore this bias in the data source will need to be investigated before applying any patterns determined in these collections to the entirety of the fossil assemblage. For example one could suggest that predation greatly affected the smaller organisms. However, this would be an erroneous conclusion to draw as the true size distribution of the fossil population is still not known. One way to eliminate this bias is to randomly sample material from the same formation where the museum collection was collected from and attempt to see any size and age differences between the two samples. Taphonomy (in the guise of biostratinomy, ie pre-burial damage) also needs
to be investigated. Obviously this is required because museum collections will rarely contain heavily
damaged specimens. By working out the taphonomic bias in the collections as well as the amount of
damage that may occur, the initial undamaged death assemblage may be estimated and so it could be
possible to estimate how many organisms would survive predation.

There are many aspects to investigate when trying to model predation in fossil populations, for
example the age distributions of organisms that survive predation and the mortality rate in different
age groups. There is also a need to determine which data is missing in order to estimate the extinct
population. Once these aspects of the population dynamics have been determined, a more focused look
on the effect of predation can begin. Another student is studying the rate of predation by counting the
number of attacks that have occurred on organisms which have survived.

2 Aims

The aim of this thesis is to investigate the population structure of *Neptunea angulata*, specifically the
age distribution, and to compare this distribution in museum and field collections. All specimens
studied will have originally come from the Red Crag in the South East of England. The project will
use isotopic data from *N. angulata* fossil shells to calculate the age of the organisms at the time of
death. Their ages at certain whorl lengths will then be used to calculate the snails’ growth rates. The
growth models can then be used to calculate the ages of shells using the relationship between whorl
length and age. The ages of measured shells from existing collections and unbiased material can then
be used to determine the age distributions within ancient populations of *N. angulata*. The populations
recorded in museum collections and in the fossil record should show different structures. This project
will also attempt to answer the question as to why the populations are structured the way they are and
why they may differ from one another. This can then be used to estimate the impacts of predation on
the ancient population by removing the effects of general mortality from the models.

3 Background

3.1 *Neptunea angulata*

The organisms studied in this project belong to the species *Neptunea angulata*. It belongs to the family
Buccinidae within the clade Neogastropoda (Rafinesque, 1815, Thiele, 1929). Organisms belonging to
the genus *Neptunea* are commonly found in many arcto-boreal, outer neritic-inner benthic faunas from
the late Cenozoic. They have short to moderately elongate fusiform shells and are dextrally coiled with
spiral structures. Only three known species are sinistrally coiled, one of which is *N. angulata* (Nelson
and Pain, 1986). It is very similar to the extant species *N. contraria* (Linnaeus, 1771). *N. contraria*
arose during the Pliocene during a migration of Pacific fauna into the Atlantic. A right handed species
known as *N. lyrata* is believed to have provided the lineage from which *N. contraria* is derived (Vermeij, 2002). A species that is found in similar environments to the ancient *N. angulata* is the species *N. antiqua* (Linnaeus, 1758). The feeding habits of this species focus on scavenging (Pearce and Thorson, 1967). Since most whelks are either predators or scavengers it is fair to assume that *N. angulata* was also a scavenger. Studies on Buccinidae species have demonstrated that *Neptunea* species appear to have some of the greatest life spans with *N. lyrata* (Gmelin, 1791) living up to 18 years (Borulya and Bregman, 2002). In regards to the geology of the South East of England, *N. angulata* is only found in the Red Crag (Fig. 1) and has never been found in the older Coralline Crag (Baden-Powell, 1960).

### 3.2 The Red Crag Formation

The Red Crag is a 5 m thick series of shallow marine sediments found in East Anglia, England (Fig. 2) which were laid down along the western margin of the southern North Sea (Mathers and Zalasiewicz, 1988). They are dated from the upper Pliocene to lower Pleistocene including the Pliocene-Pleistocene boundary, and are the only sequence of this age in Britain (Zalasiewicz et al., 1988). The sequence overlays the London Clay and in places the Coralline Crag (Dixon, 2011). The rocks found in the south are considered the oldest from the formation. These include the rocks from Walton-on-the-Naze which have been dated between 2.9 and 2.6 Ma using a variety of techniques (Head, 1998). Species of benthic foraminifera and molluscs suggest that the climate at the time of deposition was a warmer period compared to the rest of the Red Crag which was deposited during the time of a cooling trend that began at 2.55 Ma (Wood, 1866, Harmer, 1900, Funnell and West, 1977). The fossils in the Red Crag suggest that the material was transported before burial and as a result have been time averaged. Two mollusc assemblages have been identified, AS-Mol 1 and AS-Mol 2 which are both from the Pleistocene. AS-Mol 1 contains many species that are typical for the Red Crag (Zalasiewicz et al., 1988). The sheer abundance of *N. angulata* specimens in the Red Crag meant it would provide at least some specimens within a limited collection time. Three collections of Red Crag material exist at the University of Cambridge and are the Philip Cambridge Collection, the

![Figure 1. An image of a *Neptunea angulata* shell. The specimen is from the Red Crag.](image-url)
Sedgwick Museum Collection and the Cannon and Brooks Collection. These collections were used in this study.

**Figure 2.** Map of the distribution of the Red Crag. Altitude of the Red Crag shown using m O.D. (ordnance datum). Taken from Zalasiewicz et al., 1988 (Fig. 1). Reproduced within the fair use policy.

### 3. 3 Isotopes

Oxygen has three stable isotope, $^{16}\text{O}$, $^{17}\text{O}$ and $^{18}\text{O}$. $^{16}\text{O}$ is the most common and has an abundance ratio of 500:1 with $^{18}\text{O}$. Owing to their differing number of neutrons, the isotopes exhibit slightly different kinetic properties (Bowen, 2013). They therefore become incorporated into carbonate minerals at slightly different rates depending on temperature. The first evidence that the ratios between
the isotopes $^{16}$O and $^{18}$O could change at different temperatures was noticed by Urey (1948), who found that calcium carbonate crystallizing at $0^\circ$C would have a ratio of 1.026:500 and at $25^\circ$C a ratio of 1.022:500. As a result he concluded that fossils could be used as a palaeothermometer by using the temperature coefficient for the abundance of the oxygen isotope. Since then improvements to the method have allowed palaeotemperatures to be calculated.

Isotopes may be affected by a variety of environmental factors that may disrupt the accuracy of estimated palaeotemperatures. Fluctuations of $\delta^{18}$O values have been correlated with ice sheet changes and so it is important to make corrections in order to accurately measure palaeotemperatures (Mook, 1971). Influxes of freshwater on organisms in shallower seas can also affect the oxygen isotope values since freshwater has lower $^{18}$O values (Goodwin et al., 2003). Other studies on isotope palaeontology have suggested that variation of isotopic ratios within single shells could be the result of changes in depth habitat, timing of growth change in feeding, reproduction and metabolic activities (Wefer and Berger, 1991).

Post-depositional effects may also come into play, for example $^{18}$O depleted water could cause isotope shifts in deposited calcium (Urey et al., 1951). It would also be possible that diagenesis could affect the carbonate isotope values (Hoefs, 1980). The problem of the diagenetic effect on $^{18}$O/$^{16}$O ratios therefore increases the uncertainty in isotopic data from fossil carbonate shells; the problem is greater in Palaeozoic material (Lowenstam, 1961). The problem is especially common in aragonite because of its instability; as a result it often recrystallizes to calcite and so loses its primary isotopic record (Urey et al., 1951).

There have been discussions as to whether the isotopes within biogenic calcium carbonate are actually in equilibrium with the ambient sea water in which it is deposited. The possibility that this could be the result of a vital effect was first noticed by Urey et al. (1951). The vital effect does not allow oxygen isotopes in carbonate deposition to be in equilibrium with seawater. It is believed that the kinetics of the uptake for rapidly laid down material is the most out of equilibrium. Further study on the mechanics of biomineralization suggests that vesicles take up the ions directly from sea water and transport it to the site of deposition and so it would be fair to assume that the ions are in equilibrium with sea water (Weiner and Dove, 2003). Most of the literature suggests that the isotope ratios within mollusc shells are in equilibrium with the sea water isotope ratios and as a result can accurately reflect palaeotemperatures especially in the Cenozoic (Emiliani, 1966; Weiner and Dove, 2003; Mook, 1971).

Oxygen isotopes have also been used to determine the ecology and life histories of organisms. Belemnites from the Jurassic have shown seasonal variation in the isotope values throughout their shell and with counting the number of seasons the age has been calculated (Urey et al., 1951). Jones et al., (1983) has noted that the yearly periodicity within $\delta^{18}$O variation could be used to estimate age of the organisms and perhaps even determine growth rate.
3.4 Growth Rates

Growth is simply the measurable increase in body weight and/or size (Von Bertalanffy, 1938). It can be controlled by a variety of factors that include environmental conditions and genetics. Growth occurs when assimilated food or energy is incorporated into the organism’s biomass (Kideys and Hartnoll, 1991). There are many types of growth patterns that can be seen in a variety of organisms. The two main divisions between growth pattern types are determinate growth and indeterminate growth. The former growth pattern causes the organism to stop growing at a certain point, usually at sexual maturity. Indeterminate growth means that the organism continues to grow during its lifetime and only stops during death or stress, but can resume when the stress is over (Sebens, 1987). The body size and age can be correlated as a result (Lincoln et al., 1982). Most marine invertebrates demonstrate plastic asymptotic growth which is an indeterminate growth pattern. This is similar to type II habitat-dependent determinate growth, but the asymptotic size can vary dramatically (Sebens, 1987). This size is usually dependent on food availability and other factors, such as environmental temperatures, that affect the physiology of the organism. Energetic costs of poikilotherms can be dependent on temperature and so metabolic rates can increase with temperature (Sebens, 1987). Previous work on another buccinid genus investigated as to whether buccinid shells experienced indeterminate growth or determinate growth. It was found that the species *Buccinum isoatakii* may have indeterminate shell growth (Ilano et al., 2004). Borulya and Bregman (2002) demonstrated that shell height increments decreased with age in *Neptunea* species and in some did not exceed 5mm per year. However, growth was fastest in the younger years.

There are a variety of ways to calculate growth rates. The most commonly used is the absolute growth rate which is the absolute increase in weight or length during a period of time. However, it has some limitations in that it relies on the fact that the growth rate is constantly linear. Another commonly used function is the Von Bertalanffy model which has two simple functions in relation to weight and length (Hopkins, 1992). Other models that are often used are the Gompertz growth model and the logistic growth model (Miranda et al., 2008). The three models can calculate the growth constant and size at infinite age. The Gulland and Holt plot is based on a linear relationship between the rate of increase in length to average length (Hopkins, 1992). However, most of these models are used for calculating fish growth in fisheries. This project used the Von Bertalanffy model and the Gulland and Holt plot, the equations used are shown in the methods section.

3.5 Population Structures

There are several ways to demonstrate population structures. The clearest to use are size or age frequency distributions, which demonstrate how many individuals at different ages exist. The dynamics of the population could be shown through life tables and survivorship curves in which mortality rate could be calculated (Deevey, 1947). Both require the use of cohorts to be created.
Cohorts are a group of individuals in a species born at the same time. Survivorship curves are a visual way to show the number of survivors within a cohort over time: the y-axis shows the number or percentage surviving and the x-axis the time period (Dodd and Stanton, 1981). There are three types of curves that are produced. Type I curves have an upwardly convex shaped and show an accelerating mortality rate (so-called senescence). Type II curves are straight lines that demonstrate a constant mortality rate through time. Type III curves are concave upwards and demonstrate high juvenile mortality. This is commonly seen in invertebrates. However, in reality many organisms, including humans, show a sigmoidal curve with high mortality rates in juveniles followed by a constant death rate in adulthood that accelerates when old age is reached. The data source for these curves could come from size or age distributions. However, age distributions must be utilized for fossil populations, and the age class is the number of individuals that reached that age. The youngest class is assumed to have no mortality and is marked as 100% of the population. Fossils tend to show normal population structures which can be converted to survivorship curves since age distribution is a function of survivorship (Dodd and Stanton, 1981). However, such distributions are difficult to explain for a variety of reasons.

Survivorship curves for fossil populations rarely represent the true population unless a catastrophic event causes the appearance of a census population (Dodd and Stanton, 1981). Before fossilization remains of organisms undergo pre-burial and post-burial effects. Pre-burial effects can involve the selective removal of loose shells (Fagerstrom, 1964). These tend to affect smaller shells which are removed by waves and currents. Studies on this problem have suggested that the absence of small shells is not just due to collection bias (Craig and Hallam, 1963). Missing these smaller organisms can cause marine invertebrates which survive the high larval mortality rate to exhibit survivorship curves similar to higher organisms (Craig and Hallam, 1963). Post-burial effects can include selective leeching, replacement and crushing of shells (Fagerstrom, 1964). However, a method in order to investigate how transported a fossil assemblage has been discovered. Size distribution curves can indicate the amount of transport that has occurred. Transported assemblages exhibit bell-shaped distributions as smaller organisms have been lost and non-transported assemblages show a right skew as smaller specimens remain (Fagerstrom, 1964). Time averaging should also have an effect on the survivorship curves producing more uniform population structures in death assemblages than in life assemblages (Olszewski and West, 1997). Time averaging can also remove abundance spikes that may occur during the life assemblage (Cummins et al., 1986). Many short term fluctuations should be removed by time averaging and so time averaged assemblages have less noise (Kowalewski, 1996).

In relation to gastropods and other benthic animals, it is very possible that the survivorship of *N. angulata* is like other invertebrates that demonstrate a large mortality rate in the larval stages giving rise to strongly concave survivorship curves. It could also demonstrate a sigmoidal curve if the larval stages are excluded (Hallam, 1972).
4 Methodology

4.1 Material Collection

Material was collected in the south east of England from exposures of the Red Crag (Fig. 3). The material was used both for studies on taphonomy and to determine any collection bias. The material was bulk sampled at random sites along shelly layers of the Crag. In some outcrops the sediment could be removed using a spade and in places where it was harder, a hammer and chisel were used. Samples were taken from slumped material where there was no permission to dig into the sediment.

Samples were taken from seven sites. Two of these were around the village of Butley and were Broom Covert (TM 36680 49392) and Neutral Farm (TM 37150 51050). The other sites were Buckanay Farm Pit at Alderton (TM 35621 42421), a quarry at Waldringfield (TM 25840 44547), Walton-on-the-Naze (TM 26581 23525), Bawdsey Beach (TM 35472 39641) and a locality near the Ramsholt Arms, Ramsholt (TM 30686 41527). The material collected at all sites was treated as one entire population and was labelled as the unbiased collection.

4.2 Material Preparation

The material was washed in the Sedimentological Laboratory at the University of Cambridge. 4 mm sieves were used as any material less than 4 mm in diameter were shelly fragments that were deemed to have no value to the present study.

Three *Neptunea* specimens were selected for mass spectrometry analysis. One came from Buckanay farm and two came from Walton-on-the-Naze. First the height of the shell and spiral length

![Figure 3](image-url)
were measured. Measurements of whorl length were taken using a piece of twine string wrapped around the spiral and then measuring the length of the string between the two marked ends. The samples were polished with sand paper and then washed with deionized water to remove contaminating materials. 5 mm intervals along the whorl length were marked out to indicate where material would be taken for mass spectrometry analysis. Samples were removed from the shell using a Newwave Micro mill machine from ESI which held the drill bit in place and would control the speed of its rotation. The *Neptunea* shell was moved underneath the drill bit to remove material along the growth lines. The material dropped on to a piece of card fashioned into a triangular dish. The sample was then placed into a tube and sealed ready for analysis. Shell 1 had 33 samples taken from it, shell 2 had 37 samples taken and shell 3 had 30 samples, resulting in a total of 100 samples.

### 4.3 Mass Spectrometry

The samples were sent to the Godwin Laboratory for Palaeoclimate Research for mass spectrometry. Approximately 50-200 micrograms of dried homogenised sample was transferred in to Exetainer® vials and sealed with silicone rubber septa using a screw cap. The samples were flushed with CP grade helium then acidified with 104% orthophosphoric acid, left to react for 1 hour at 70 degrees Celsius and then analysed using a Thermo Gasbench preparation system attached to a Thermo Delta V Advantage mass spectrometer in continuous flow mode. Each run of samples was accompanied by 10 reference carbonates (Carrara Z) and 2 control samples (Fletton Clay). Carrara Z has been calibrated to VPDB using the international standard NBS19. The results are reported with reference to the international standard VPDB and the precision is better than +/- 0.08 per mil for 12C/13C and +/- 0.10 per mil for 16O/18O.

### 4.4 Analysis of Isotope Ratios

To begin to determine the ages of the organisms, sites along the shell spiral where samples were taken for mass spectrometry were marked and their position along the spiral length was measured. A graph was then plotted with the spiral lengths of the sample sites on the x-axis and the $\Delta^{18}O$ values taken from sites at the same spiral lengths on the y-axis. The variations in the temperature represented seasonal changes and could then be counted to determine the ages of the three specimens.

Palaeotemperatures ($t$) were calculated using the isotope ratio values. The temperature equation developed by Epstein et al., (1953) and improved by Craig and Gordon (1965) was used to calculate temperatures and is shown in equation 1. Previous studies have shown that the gastropods isotopes are in equilibrium with the isotope values of seawater. Isotope corrections for the sea ice coverage during the Piacenzian had to be made for specimen 2 and 3 of 0.2‰ and were based on corrections suggested by Krantz (1990).

$$t = 16.9 - 4.2\Delta O^{18} + 0.13(\Delta O^{18})^2$$

(1)
4.5 Growth Equations of the three *Neptunea angulata* Specimens

To calculate absolute growth equation, the years of age of the shell were plotted on the x-axis and the spiral length at the different years was plotted on the y-axis (Fig. 4). The graph produced a line with an equation similar to \( y=mx+c \), where \( m \) was the absolute absolute growth rate.

Two growth models were used to calculate the growth equations of the shells. These were a Gulland and Holt plot (Fig. A1) and a Von Bertalanffy plot (Fig. 5). The Gulland and Holt plot required the plotting of values of \( \Delta L/\Delta T \), where \( \Delta L \) is the change in length of spiral and \( \Delta T \) is the change in time, on the y-axis and the mean length (\( L^*t \)) values on the x-axis. \( L^*t \) values were calculated with the formula

\[
L^*t = \frac{L(t+\Delta t)+L(t)}{2}
\]

The plot should produce a linear trend line and using the equation of the line, \( y = mx + c \), the negative value of variable \( m \) is equal to the growth rate from the Gulland and Holt plot.

The Von Bertalanffy plot required an estimation of \( L_\infty \), which is the length of the organism’s spiral at infinite age. This was estimated at twice the maximum length of the spiral from the largest specimen measured in the collections at the University of Cambridge. This came to a length of 950mm. The plot required \( t \) (year) on the x-axis and on the y-axis was the value derived from \( -\ln(1-L(t)/L_\infty) \). The plot should again produce a linear trend line with the a linear equation corresponding to \( y = mx + c \). The rate constant, \( k \), is equivalent to the m value of the linear equation. In order to calculate ages using this equation the value \( t_0 \) is needed, this is equal to \( c/m \).

4.6 Age Distribution of *Neptunea angulata*

To calculate the age distribution the ages at time of death for each specimen must first be calculated. The ages were calculated by using the size-age relationships determined by the previously described growth plots and required the spiral lengths of specimens. The age distributions were determined for the unbiased collection and the material from the three museum collections, the Philip Cambridge collection, the Sedgwick Museum collection and the Cannon and Brooks collection. Ages were calculated with both the absolute growth plot and the Von Bertalanffy plot. This meant that each collection had six age distributions, Each of the three specimens had two size-age relationships.

As the absolute growth plot had produced a linear relationship, the equation of the graph could be rearranged to find \( x = \frac{y-c}{m} \). For ages calculated using the Von Bertalanffy growth parameters equation 2 was used. \( L(t) \) is the age at the measured length. \( T_0 \) and \( k \) are parameters calculated from the Von Bertalanffy plot. The rearrangement of the Von Bertalanffy equation is shown below.

\[
L(t) = t_0 - \left( \frac{1}{k} \times \ln \left( 1 - \frac{L}{L_\infty} \right) \right)
\]

The age distributions were determined using the histogram function in Microsoft© Excel©.
4.7 Survivorship Curves

Survivorship curves (Fig. 7, Figs. A10 and A11) for age estimates from the unbiased collection calculated using the absolute growth equations of specimen 1, 2 and 3 were created in Microsoft© Excel©. Survivorship curves for the museum collection material were not done due to the bias discovered in the collections. Age categories were created to estimate the number of individuals who had survived until that stage and the number of individuals who had died within the age category. The percentage of surviving organisms was calculated using the number of organisms remaining and the total number of organisms. The survivorship curve was plotted with age on the x-axis and the percentage of organisms surviving was plotted on the y-axis with a log scale. To calculate the error for the survivorship curves the percentage of surviving organisms can be used to estimate the probability of the number of organisms surviving at a particular age which is p. For example if 40% of organisms survive to a particular age then the probability of survival is 0.4. Using the error estimate the standard error (SE) was calculated as \(SE = \sqrt{\frac{p(1-p)}{N}}\), where N is the number of specimens. To fit the standard error to the log curve it is necessary to use the equation:\(\left(1 \div p\right) \times \text{standard error}\). The value derived from this is then doubled and plotted either side the corresponding point (R. Mann 2016, pers. comm., 18 April).

4.8 Taphonomic Distribution

In an attempt to calculate how much data was lost during the preservation of the unbiased collection, the sizes of specimens were measured along with their degree of taphonomic degradation. These measurements included other \(Neptunea\) sp. due to a lack of smaller \(N. \text{angulata}\) specimens. Taphonomy was measured on a scale of 1-5, 5 being perfect or museum quality, 4, slightly broken, 3, quite broken, 2, mostly broken and 1 was a fragmentary piece. The measurements were plotted in a histogram to show whether there was differences in taphonomy among different size groups. Specimens assigned with a grade of 1 or 2, were too damaged to properly measure and so three size categories were created, small with a whorl length of 0-80 mm, medium which was 80-150 mm and large which was \(\geq150\) mm. The number of specimens falling into these classes were recorded.

5 Results

5.1 Sites of the Red Crag Visited

The sites where material was collected differ greatly in quantity and quality of fossils. The Broom Covert pit at Butley had very few \(Neptunea\) visible before collection. There were many more specimens of the bivalve \(Glycymeris\ glycymeris\) (Linnaeus, 1758) visible. The sediments at the pit were divided into alternating layers of large shelly fragments and layers with smaller fragments.
Neutral Farm pit, also at Butley, appeared to have less shelly fossils in the sediment and there was no visible evidence of *Neptunea* specimens. Both of these sites represent the top of the Red Crag Formation (Daley and Balson, 1999). The Buckanay Farm pit at Alderton was much richer in fossils than other outcrops collected from, with many large sized *Neptunea* visible. There were thick layers (approximately 5 dm thick) of larger fossils (Fig. 4a) which were surrounded by layers with smaller shell fragments (approximately 1 dm thick). The outcrop at Bawdsey Beach was also investigated, most of the outcrop had been covered with recent landslides and vegetation growth. However, a small number of samples were collected from a place with some exposure. The quarry at Waldringfield was visited and samples were collected from a pile of material labelled “Red Crag as raised”: as a result a lot of the material had been mixed. Walton-on-the-Naze was a beach outcrop and a number of large *Neptunea* specimens were visible. Material was taken from mixed slumps due to the lack of permission to dig in to cliffs and as a result a large amount of the London clay was collected. The locality at the Ramsholt Arms outside of Ramsholt had a roughly 10 cm layer of small shelly fragments and was much poorer in quality than the rest of the outcrops visited (Fig. 4b). Additional outcrop images can be seen in the appendix (Figs. A1-A3).

5.2 Growth Rate

The growth rates calculated from the absolute growth plots for the three specimens differed significantly. Specimen 1 had a growth rate of 20.8 mm year\(^{-1}\), specimen 2 had a growth rate of 44.8 mm year\(^{-1}\) and specimen 3 had a growth rate of 61.5 mm year\(^{-1}\). As the error for the measured whorl length was estimated to be ±2mm, the error for the growth rates were estimated to be ±2mm year\(^{-1}\). Specimens 2 and 3 had a growth rate that was more than double the growth rate for specimen 1. The plot can be seen in figure 5.
The Von Bertalanffy plot and Gulland and Holt Plot showed similar patterns. In the Gulland and Holt plot the growth constant for specimens 2 and 3 are twice as much as the growth constant for specimen 1. The growth constant for specimen 2 is 0.1 year\(^{-1}\) and the growth constant for specimen 3 0.1 year\(^{-1}\), the growth constant for specimen 1 is 0.05 year\(^{-1}\). Unfortunately, the Gulland and Holt plot created did not show a particularly linear relationship, as a result it was deemed unwise to use the values derived from the plot to calculate age estimates. The Gulland and Holt plot and additional information can be found in the appendix (Fig. A4, Table A1).

![Figure 5. The absolute growth plot for the measured specimens of *N. angulata*. Specimen 1 has a slower growth rate compared to specimens 2 and 3. Specimens 2 and 3 have growth rates which are similar to each other than to specimen 1.](image)

Von Bertalanffy growth constants were 0.02 year\(^{-1}\) with an estimated error of ±0.006 year\(^{-1}\) for specimen 1. Specimen 2 had a growth constant of 0.05 year\(^{-1}\) with an error of ±0.005 year\(^{-1}\) and specimen 3 had a constant of 0.0736 year\(^{-1}\) with an error of ±0.002 year\(^{-1}\). The K values and \(t_0\) values were used as well as spiral length to determine the age of the snail. The Von Bertalanffy plot can be seen in figure 6.
Figure 6. The Von Bertalanffy Plot for the measured specimens of *N. angulata*. Specimen 1 has a lower growth constant compared to specimens 2 and 3. Specimens 2 and 3 have growth constants which are similar to each other than to specimen 1.

5.3 Age Distributions

Each of the three *Neptunea* specimens studied had both an absolute growth equation and a Von Bertalanffy growth equation meaning that a total of six age distributions were calculated for each collection studied. The age distribution calculated from the absolute growth plot for specimen 1 will be labelled absolute age 1. As a result the age distribution for the absolute growth plot for specimen 2 will be labelled absolute age 3. Specimen 3 will have an age distribution labelled absolute age 3. Collectively they will be referred to as the absolute age distributions. In regards to the age distributions calculated from the Von Bertalanffy growth equations, they will be labelled VB 1, VB 2, and VB 3 in accordance to the specimens they were derived from. Collectively these will be referred to as the Von Bertalanffy age distributions.

The absolute age distributions for the museum collections had a normal (bell-like) distribution. Age extremes were underrepresented and there were a large proportion of the median ages (Fig. 7a). In contrast, the age distribution of unbiased shells had no such bell shaped distribution but had a more polymodal distribution (Fig. 7b). There appears to be a larger proportion of younger organisms in the unbiased data set. The museum collection distribution in Figure 7 is from the Philip Cambridge collection and was one of the collections that clearly demonstrated the normal distribution Figure 7 used the age distribution from absolute age 3. Other distributions from the other museum collection did not have as clear a normal distribution can be found in the appendix (Figs. A7, A9, A11). The age distributions for absolute age 2 and 3 can also be found in the appendix (Fig. A5). The error in the age estimates for absolute age 1 was ±0.002 years, the error estimated for absolute age 2 was ±0.8 years and error estimated for absolute age 3 was ±0.7 years.
The Von Bertalanffy age distributions showed a similar pattern to the absolute age distributions. There were normal distributions for museum collection material (Fig 8a, Figs. A8, A10, A12). The unbiased material had a more polymodal pattern (Fig 8b, Fig. A6). The Von Bertalanffy curves (Fig. 8) were slightly more skewed to the left but had a larger frequency distribution in older ages. The error in the age estimates for VB age 1 was ±0.2 years, the error estimated for VB age 2 was ±0.9 years and error estimated for VB age 3 was ±0.8 years.
5.4 Survivorship Curves

The survivorship curves were created from the unbiased collection since museum material was most likely to be biased in size as the younger shells were missing from the age distributions. The survivorship curve for the absolute age 1 distribution was mostly linear before turning concave downward at the end (Fig. 9). The curve appears to be a mixture between the type I and type II survivorship curves. For the absolute age 2 distribution the survivorship curves shows a clear concave line that looks particularly like the typical type I survivorship curve (Fig. A13). The survivorship curve from age estimates 3 has a somewhat similar structure to the age 2 survivorship curve although the curve has a much shorter length and the concave structure has a smaller angle (Fig. A14). The other survivorship curves can be found in the appendix (Figs. A13, A14).

5.5 Taphonomic Distributions

Comparing the taphonomic distributions of different size classes it is possible to suggest that the smaller the specimens are the more likely they are to be damaged. However, the ratio of severely broken to slightly broken shells could be seen as roughly 50/50 between all the size classes (Fig. 10). There were more specimens of the taphonomic grade 1 and 2 in the smaller size class (between 0-
80mm) compared to the larger size classes. Many of the smaller specimens were damaged, although there were some small specimens which were of good taphonomic quality. These were *Neptunea* sp. and not actually *N. angulata*. The higher taphonomic grades showed a less clear pattern.

**Figure 9.** The survivorship curve for the absolute age 1 distribution. Error bars are shown.

**Figure 10.** A comparison of the number of specimens of different size with the taphonomic grades of 1 and 2 and 3, 4 and 5. The size classes are small (0 – 80 mm), medium (80 – 150 mm) and large (≥150 mm).
5.6 Temperature from Isotopic Ratios

The palaeotemperatures were calculated from isotopic values. When plotted together the temperatures from specimens 2 and 3 appeared to be higher, especially during the summer months (Fig. 11). However, this could also be due to a larger range of temperatures experienced. The calculated palaeotemperatures appeared to match the trend of cooling seen at the end of the Piacenzian and the start of the Gelasian as the younger specimen 1 had a lower temperature than the older specimens 2 and 3. The mean temperature from specimen 1 is 7.8°C, for specimen 2 is 8.9°C and for specimen 3 it is 9.0°C. To further determine whether there was a statistically significant difference between the temperatures found from specimen 1 and specimens 2 and 3 a t-test was employed. The values derived from the t-test suggested that the differences between the mean temperature values for all specimens were not statistically significant. The t-test also revealed that the temperatures calculated from specimen 1 were much less varied than the temperatures from specimens 2 and 3 (Table A2, 3, 4). Specimen 1 had a variance of 7.9 whereas specimen 2 and 3 had a variance of 20.0 and 15.4 respectively. The error for the palaeotemperatures was ±0.33°C.

Figure 11. The palaeotemperatures recorded in all three specimens are plotted together to visualize the differences in temperature. Specimens 2 and 3 appear to have a large amount of variation in the recorded temperatures. Whereas specimen 1 has less temperature variation.
6 Discussion

6.1 Growth Rates of *Neptunea angulata*

The growth rates for each specimen were calculated in three ways, using a plot of whorl length vs age, the Von Bertalanffy plot and the Gulland and Holt plot. The Gulland and Holt plot did not show a linear relationship like the other plots. As a result the rate constants calculated from this plot were not used. It is possible that the time intervals for the plot were too large as it tends to work best for smaller time intervals and younger specimens (Sparre and Venema, 1998).

The absolute growth plot was linear, contrary to what would be expected as the growth rate would decrease as the organisms got older causing the growth rate to begin to plateau. The age estimates of the measured *Neptunea* specimens ranged from 4-8 years. It is therefore possible that the organisms could still be considered young. Compared to the age estimates of the larger specimens found in the collections they were certainly younger. An age estimate study carried out by Richardson et al. (2005) suggested that individuals belonging to the species *N. antiqua* could live to 12-17 years. Another study by Borulya and Bregman (2002) showed that the species *N. lyrata* were found to have lived up to 18 years old. Other studies on different molluscs show that growth rates decrease with age (Ivany et al., 2003, Jones and Allmon, 1995, Jones et al., 1978). Therefore it is fair to assume that the organisms had a fairly constant growth rate owing to their young age and were yet to reach the age in which the growth rate begins to decrease. The growth rate may also be linked to weight and/or size. It has been noted that as weight and size increases metabolic rate and thus growth rate can decrease (Von Bertalanffy, 1957). It is then possible that they were not large enough to cause the change in metabolism which causes a slowing of growth rates.

The growth rates predictably differed between the three specimens. Specimen 1 had a distinctly slower growth rate compared to specimens 2 and 3. It was noted that the first specimen came from Buckanay Farm and the other two came from Walton-on-the-Naze. Buckanay Farm had been identified as belonging to the Gelasian Stage (Early Pleistocene) and the rocks from Walton-on-the-Naze were dated to the older Piacenzian Stage (Late Pliocene) (Head, 1998). The Early Pleistocene was marked by a distinctive cooling trend so palaeotemperatures recorded in the shells’ isotope data were calculated to see if the temperatures experienced by the shells during the organism’s life times differed. The mean temperature calculated from specimen 1 was roughly 1º C less than the other two shells. The variation in temperatures within the seasons for specimen 1 was much lower than the other two specimens suggesting that the growth periods for the organism were shorter and less productive. This can then be suggested to be the cause of the slower growth rate.

Predation could have influenced the growth rates of the specimens. Crowl and Covich (1990) demonstrated that fresh water snails that shared environments with predators experienced slower growth rates than those that did not. They also took longer to reach sexual maturity and lived longer in...
Other effects of predation could be due to the result of behavior. As nutrient in-take directly influences growth rate, predation pressure could also influence growth rate by reducing the ability of the *Neptunea* snails to feed (Abrams et al., 1996). Several studies have shown that organisms reduce their feeding habits to reduce the risk of being predated. Therefore in relation to the specimens studied, it suggests that specimen 1 could have experienced higher predation pressure than the other two specimens. Since the beds at Buckanay farm were quite rich with fossils it is fair to assume the environment in which the shells were transported from were quite high nutrient and energy environments and so predators should be quite common.

In addition to food shortages caused by predation avoidance, food shortages due to the environment can have a distinct effect on growth rate. With malnourished organisms having a slower rate of growth compared to organisms living in nutrient rich environments. However, survival can depend on the plasticity of the growth rate. When an organism’s growth rate is not able to change the organism may starve as faster growth rates can use up more resources than are available (Gotthard et al., 1994). This could also explain the differences in age seen between the specimens. If it is assumed that the growth rate of *N. angulata* is not plastic then the younger specimens could have starved to death during a time period with food shortages. However, the specimen 1 which had the lower growth rate was able to survive such shortages as it would be more likely to survive periods of starvation and thus did not experience the cost of fitness associated with higher growth rates.

It is also possible that the growth rates between organisms could be due to natural variation found between different individuals of the same species. A study by Janson (1983) on *Littorina saxatilis* (Olivi, 1792) suggested that the growth rate was at least partly controlled by genetics although Janson suggested the greatest influence came from the environment. In another study on *Littorina saxatilis*, it was demonstrated that a lot of size variation was controlled genetically (Johannesson et al., 1997). As a result it could be inferred that the growth rates of *Neptunea* are also controlled genetically. The study noticed that the growth rate varied between organisms of the same morph which were also found in the same environment. This could explain the differences between the specimens 2 and 3 as they most likely inhabited a similar environment and so differences in growth rate were genetic.

Sexual dimorphism could be the cause of the differences in growth rate. Since extant whelk species do have larger females and some ornamentation in buccinid snails can be indicative of sex, it could be possible to determine the sex of the shells (Power and Keegan, 2001). However, it is difficult to actually investigate whether the differences in growth rate are due to sexual dimorphism as morphological differences need to be correlated to genitals which are not preserved with the shells.

Parasitism can also have an effect on growth rates. *Littorina littorea* (Linnaeus, 1758) individuals infected with trematodes had a slower growth rate than uninfected individuals (Mouritsen et al., 1999). There are two problems with this suggestion. The first is that parasitism is very hard to prove without physical evidence and currently there are no indications that the snails studied had been infected with parasites. The second is that it would be reasonable to assume that an infected individual would have a
shorter life span than uninfected individuals. As with specimen 1, it had a lower growth rate but a longer life span which causes the parasite hypothesis major problems.

6.2 Isotopic Ratios

As the isotopic ratios showed clear variations it was fairly easy to determine the age of the specimens at time of death. There were no parts missing in the record so it would be fair to assume no recrystallization had occurred. However, there were some anomalous values from specimen 2. It suggested that one of the summers was extremely warm. This could have been the case. Although it is possible that a large influx of freshwater changed the ambient water isotopic ratios causing much lighter oxygen values to be incorporated into the organism’s carbonate (Goodwin et al., 2003). A third possibility is that there was a significant amount of contamination in the sample that caused the low $\Delta^{18}O$ values that contributed to the higher temperature estimates.

The effect of diagenesis could also be a concern. However, the trace elements present in the fossils need to be analysed to determine whether diagenesis has taken place and this has not been done in this project. Mainly manganese (Mn), Iron (Fe) and Strontium (Sr) are used to identify diagenesis, with the enrichment of Mn and Fe and the depletion of Sr being indicative of diagenesis (Popp et al., 1986). The main effect of diagenesis is the reduction of $^{18}O$ values making them more negative and thus temperatures will be calculated as warmer than they actually were (Sharp et al., 2000). Therefore the effect of diagenesis is one concerning the palaeotemperatures calculated from them and should not affect the age and thus growth rates calculated using them. If the temperatures of specimen 1 had been shifted by diagenesis the temperature differences may have been greater than observed and thus could explain why the growth rates between specimen 1 and specimens 2 and 3 differed greatly. Analysis into whether diagenesis has occurred needs to be done to validate this speculation. However, it is possibly unlikely that diagenesis did occur since the specimens are from young sediments, they were not deeply and compactly buried, many still have an aragonitic layer and they are not damaged in ways that suggest diagenesis has taken place.

6.3 Ages of the Specimens

The snails measured also differed in age as well as growth rate. The peculiar thing is that all three reached similar sizes, although the smallest was specimen 1. Since there was no obvious damage to the shells that indicated predation another cause must be the case. There are a variety of different causes of death. These can include disease, parasitism, starvation and environmental catastrophe. An environmental catastrophe is more likely to damage the shell. However, underwater sand slides could bury the snails killing them without leaving a trace. This is unlikely since the Red Crag is composed of transported material (Zalasiewicz et al., 1988). For specimens 1 and 2, the possibility of death due to
abnormally cold temperatures during winter can be ruled out as the temperatures at the end of the whorl corresponded to the summer months. In studies of the Neptune whelk (N. arthritica) it was found that mortality in the populations increased during periods of food shortages and abnormally low water temperatures (Fujinaga and Nakao, 1996). The true cause of death is difficult to prove since there are no details on the shell that can indicate the cause of death. It is possible for both disease and parasites to leave no mark on the shell and starvation would not be very visible either. Therefore the cause for mortality can only be speculated. In modern populations N. antiqua and N. arthritica both sexes can die off after spawning and so this may have caused the deaths in the younger specimens (Fujinaga 2003).

**6.4 Age Distribution of Neptunea angulata**

Due to the transportation of the shells prior to burial and fossilization, the specimens collected can be regarded as a normal population and cannot be regarded as a census population (Zalasiewicz et al., 1988; Dodd and Stanton, 1981). Untransported fossil assemblages are commonly found to have right skewed age distributions (Fagerstrom, 1964). Population structures in existing populations have been found to show a normal distribution with only a few organisms becoming quite old in comparison to the rest (Fahy et al., 1995; Narvarte et al., 2008). Other studies showed that size distributions of gastropod species tend to show a normal distribution (Konar et al., 2014; Kideys, 1996). These match the size and age distributions of the collection specimens, but do not match the distributions of the unbiased specimens. There are some explanations for this. The first could be that the sample sizes between the collections and unbiased material are just so large that the comparison between the two would be erroneous. The number of unbiased specimens is 35 and so it is very possible it is too small a number to accurately represent the ancient population. The sample sizes for the previously referenced studies also had a much larger sample size than our own. A study involving Miocene brachiopods produced meaningless histograms when the sample size was too small and as a result it concluded that large sample sizes produced the most meaningful histograms (Bitner, 2002). A study involving gastropods from the Triassic also demonstrated the pitfalls of a small sample size where comparing size-distributions of two different species of gastropod was fairly meaningless. One gastropod had a sample size of 143 and the other had a sample size of 13. This produced one histogram with a clear distribution and the other was missing size categories and had a very small distribution. This would cause any conclusions drawn from the comparison of the two to be fairly speculative (Brayard et al., 2010). Therefore, further samples need to be taken and analysed to provide more meaningful histograms to compare to the unbiased material.

A sampling bias for the collection specimens may also be to blame, since the smaller specimens would have been overlooked and so left behind. Damage may occur more often in smaller specimens and so they would be left behind. This is suggested since there is a higher proportion of younger specimens in the unbiased samples than the samples from the collections. This is not applicable to all
the collections and the Philip Cambridge collection appears to be the most biased. The other museum collections have smaller and thus younger specimens which are not much different to the unbiased collection. There are some problems with this argument for collection bias since it cannot be employed for the modern investigations into gastropod population structures since trawling and traps were used to collect individuals and measures were taken to ensure no bias took place (Konar et al., 2014, Narvarte et al., 2008). However, due to time averaging’s effect on short term fluctuations the structures of modern populations can produce a misleading prediction for how the fossil assemblage population structure should appear. Therefore there could be some other explanation for the differences in population structure. However, when searching the unbiased samples it appears that they are also missing some of the smallest shells. Tiny gastropod shells were found in some sites but did not belong to \textit{N. angulata}.

Due to the fact that the growth rates between the three specimens differed, three different age estimates using the absolute growth plot were produced and three age estimates using the Von Bertalanffy plot were produced. At the moment it is undecided which growth rate is best to use for the age estimations and so the most convenient are used. One way to improve the age estimations would be to sample more growth rates from more shells and determine a statistically significant mean growth rate, and use that growth rate to calculate age estimate closer to the true values to look at the age distributions.

\textbf{6.5 Taphonomic Distribution}

After investigating the distribution of taphonomic degradation among differently sized specimens, a few questions have been raised. It is still not entirely clear as to whether there is a significant difference between the proportion of very broken and slightly broken shells. However, many of the smaller specimens that were preserved did not actually belong to \textit{N. angulata} as they were dextrally coiled. So the actual breakage proportions for \textit{N. angulata} are unknown. The question as to why the small shells have preserved for other species but have not for \textit{N. angulata} needs to be addressed. It could be due in part to different minerology (Kidwell and Bosence, 1991). However, the mineralization between the different species needs to be tested in order to determine how much the mineral composition differs in order to infer how much of an effect it had. It is possible that the structures of the shells at young ages differed in strength and contributed to differences in preservation. But the fact that most of the larger specimens and more complete specimens are \textit{N. angulata} is even more puzzling. It is possible that the strange populations could be due to differences in habitat for juvenile and adult gastropods. Studies on \textit{Strombus gigas} (Linneaus, 1758) showed that juveniles would tend to grow in different habitats and areas compared to adults. And so populations would have a bias towards juveniles in one place and a bias towards adults in other areas (Stoner et al., 1988; Peel and Aranda, 2012). The size distributions of gastropods can differ according to depth as was shown by Takada (1996). Therefore the source of the transported material could be from areas
where low numbers of the smaller organisms may have lived. As with many problems that have arisen with this project, more samples and data are needed to begin to fully understand what is happening to the fossil assemblage. It may also be of interest to try and differentiate the size and taphonomic distributions of the species according to site. Since the deposits at different sites are separated by several thousands of years, changes in habitats and behaviours may show different distribution patterns. Other sites of the Red Crag around the North Sea could also be investigated in order to determine if the difference is ecological or taphonomic. It must also be noted that the size distributions are not necessarily perfect as some specimens that would belong to the large category were damaged in such a way that a large part of the whorl length would be measured as much shorter than it would be if the specimen was perfectly preserved.

6.6 Survivorship Curves

The fact that the age estimates differed in survivorship curves is most likely due to the different age ranges caused by the different growth rates. Age 1 estimates were calculated from the growth rate of the older specimen which had a slower growth rate and so the age of organisms varied much more, whereas the age ranges for the other estimates were much smaller and these produced more concave curves.

The fact that the curves vaguely represent type 1 growth curves is extremely interesting. It suggests that there is an increasing mortality rate within the population. This is contrary to the survivorship curves seen in invertebrates which demonstrate a high juvenile mortality rate which then decreases with age. In reality due to the missing data the survivorship curve is most likely to have a sigmoidal shape, which is the most common type of survivorship curve seen in nature (Dodd and Stanton, 1981). It is very likely that there was a large population of juvenile organisms present initially, in both pre-larval stage and post-larval stage. Many of these would have died off before they reached the age of 1 year and, due to the lack of a shell, would not preserve. The early death rate and an increasing death rate towards the end of their life would produce a sigmoidal curve. Miranda et al., (2009) demonstrated massive juvenile mortality in brood stocks, which was sometimes as high as 87%. The mortality decreases after age 1, therefore there should be much higher amount of the youngest specimens entering the death assemblage (Smith et al., 2011).

Since the taphonomic processes have not removed the smallest shells of other species there should be small *N. angulata* fossils present in the unbiased curves. It is very possible that the absence is due to low mortality as shown in the survivorship curves (Cadée, 1982). The low mortality could be caused be two things. The first could be that the environment in which the organisms lived preferentially caused death to the older gastropods. For example, a rocky shore which contains small crevices in which the smaller gastropods can take shelter can improve the likelihood of survival for the smaller gastropods. Whereas the larger gastropods cannot take shelter and are thus exposed to elements that might increase mortality (Takada, 1996). The second possibility is that the shells were...
absent from the original environment and have lived and died in an area which was not affected by the currents that transported the material to site of the Red Crag deposition (Zalasiewicz et al., 1988, Stoner et al., 1988).

Unfortunately due to the missing data the survivorship curves cannot be of much use and only show the mortality rate of organisms that have been preserved. The lack of data for certain age classes in the collections meant that the survivorship curves were not calculated for the museum data.

7 Conclusion

Using the isotopic data from three \textit{N. angulata} shells, the age and growth rates for the organisms were calculated. The three specimens that were studied each demonstrated different growth rates. However, it is not known which rates are closest to a universal growth rate. Therefore, for the time being all three were used until an average growth rate is found. Using these rates, age estimates for a large number of specimens from museum collections and field samples were calculated and age distributions were organized. From these age distributions, it was revealed that there was a large amount of bias against younger specimens seen in the museum collections relative to the field collections, specifically the Philip Cambridge Collection. The other collections did not appear to have such an obvious bias.

There was an absence of the smallest \textit{N. angulata} shells in the supposed unbiased field samples. The survivorship curves were influenced by this absence as they suggested that there was very little juvenile mortality, which was unexpected. However, the presence of small specimens from other gastropod species including other \textit{Neptunea} species suggested that the absence may not due to taphonomical effects.

From this study there are many questions left unanswered due to time and resource deficiencies. For example, there are a variety of possible reasons as to why the smallest shells were removed from the fossil assemblage and so it is important to study which mechanism may have caused the distributions discovered. This would require a much larger collection of material and perhaps even a systematic look at each outcrop to determine any differences between them. Further large sized shells are required to investigate the growth rates further in order to calculate a more universal growth rate which can result in age distributions that would more closely reflect the populations of \textit{N. angulata}.

8 Acknowledgements

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9 References


10 Appendix

10.1 Sites Visited

Figure A1. An image from the site visited at Waldringfield Quarry

Figure A2. An image from the site visited at Broom Covert.
Figure A3. An image from the site visited at Buckanay Farm.
10.2 Gulland and Holt Plot

Figure A4. Gulland and Holt plot calculated for specimens 1, 2 and 3.

Table A1. The equations derived from the Gulland and Holt plot for all three specimens. Also included are the $R^2$ squared values and rate constant.

<table>
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<th>Equation</th>
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<td>1</td>
<td>$y = -0.049x + 9.7069$</td>
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<td>0.05</td>
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<tr>
<td>2</td>
<td>$y = -0.1178x + 26.395$</td>
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<td>$y = -0.0964x + 31.894$</td>
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</table>
10.3 Age Distributions Using the Other Age Estimates

**Figure A5.** The age distributions calculated from the unbiased collection using the age estimates determined by the absolute growth plots for specimen 1 and 2

**Figure A6.** The age distributions calculated from the unbiased collection using the age estimates determined by the Von Bertalanffy growth plots for specimen 1 and 2
Figure A7. The age distributions calculated from the Philip Cambridge collection using the age estimates determined by the absolute growth plots for specimen 1 and 2.

Figure A8. The age distributions calculated from the Philip Cambridge collection using the age estimates determined by the Von Bertalanffy growth plots for specimen 1 and 2.
Figure A9. The age distributions calculated from the Cannon and Brooks collection using the age estimates determined by the absolute growth plots for specimen 1, 2 and 3.

Figure A10. The age distributions calculated from the Cannon and Brooks collection using the Von Bertalanffy growth plots for specimen 1, 2 and 3.
Figure A11. The age distributions calculated from the Sedgwick Museum collection using the age estimates determined by the absolute growth plots for specimen 1, 2 and 3.

Figure A12. The age distributions calculated from the Sedgwick Museum collection using the Von Bertalanffy growth plots for specimen 1, 2 and 3.
### 10.4 T-test Results

**Table A2.** The t-test results for Specimen 1 and Specimen 2

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**Table A3.** The t-test results for Specimen 1 and Specimen 3

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**Table Appendix 4.** The t-test for Specimen 2 and Specimen 3

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10.5 Survivorship Curves of the Other Age Estimates

**Survivorship Curve Unbiased Age 2**

Figure A13. The survivorship curve calculated for the unbiased collection. Based on age estimates calculated from the absolute growth plot for specimen 2.

**Survivorship Curve Unbiased Age 3**

Figure A14. The survivorship curve calculated for the unbiased collection. Based on age estimates calculated from the absolute growth plot for specimen 3.