Bangor University

DOCTOR OF PHILOSOPHY

The ecology, age and growth of two muricacean gastropods from shores of Kuwait

Alsayegh, Lujain

Award date:
2015

Awarding institution:
Bangor University

PRIFYSGOL
BANGOR
UNIVERSITY

The Ecology, Age and Growth of Two Muricacean Gastropods from Shores of Kuwait

Lujain J. Alsayegh BSc, MSc
School of Ocean Sciences, University of Wales, Bangor, Marine Science
Laboratories, Menai Bridge, Anglesey, Gwynedd, Wales, LL59 5AB

Submitted in accordance With the requirements for the degree of Doctor of Philosophy

May 2015

Summary

Two predatory muricid gastropods, *Thalessa savignyi* and *Ergalatax junionae* commonly occur on the rocky intertidal shores of Kuwait. Three shores, Ra’s Ajūzah, Ra’s Eqaila and Ra’s al Qulay’ah between the north and south of Kuwait covering a distance of ~90Km, were studied to determine the geographical and seasonal abundance of these two muricids. *Thalessa savignyi* was absent from Ra’s Ajūzah in the north, but increased in abundance towards the south of Kuwait. By contrast the smaller gastropod *E. junionae* was present on the three shores but decreased in abundance towards the southernmost site, Ra’s al Qulay’ah. *Thalessa savignyi* prefers rocky platforms and associated fissures which are present on the southern shore whilst small boulders and crevices on the shores in the north of Kuwait were favoured by *E. junionae*. Egg laying by both species occurred in the laboratory in late June and these egg masses hatched ~30days later in late July. Intertidal recruitment of juveniles (<10mm) appeared into the populations at Ra´s Ajūzah and Ra´s Eqaila between October and January whilst no recruitment was observed at Ra´s al Qulay´ah. Polymodal size frequency distributions in some of the populations were separated into their component size (age) classes using the method of Bhattacharya. Using these estimates of the modal size and ages, Von Bertalanffy growth (VBG) curves were constructed to compare the growth of both species. *Thalessa savignyi* grew faster than *E. junionae* and both grew faster at Ra´s al Qulay´ah compared with the other two sites. Growth rings on the operculum and in the statoliths were used to estimate the age of *T. savingnyi* and *E. junionae*. Age estimates using whole and polished sections of the operculae were problematic because rings could not be seen through the thick and opaque operculum of *T. savignyi*. The operculum of *E. junionae* was thin and transparent but the number of rings counted was almost double those found in the statoliths. Operculae sections did not reveal clear growth rings. A latitudinal variation in the definition and the number of weak growth rings in the statoliths was observed. Generally rings in statoliths of both muricids from the northern sites in Kuwait were clearly defined and they contained less weak rings than statoliths from muricids from the southern site. These statoliths contained a wide variety of strongly and weakly defined rings. It was established from seasonal collections that statolith growth rings are deposited annually between November and January. A larval ring, deposited during the period of life in the egg and a settlement ring, formed at the time of metamorphosis from the plankton, were validated in developing *T. savignyi* larvae in egg masses and from newly hatched larvae. The age of both species was determined successfully using statoliths and VBG population growth curves constructed. *Thalessa savignyi* was found to be a faster growing species with a shorter longevity (4 years) than the smaller, longer-lived (5 years) and slower growing *E. junionae*. In the laboratory both muricids were found to be predators of the tube worm *Septibranchia krausii* and the mussel *Brachidontes variabilis*. A comprehensive seasonal survey of the three intertidal shores documented the tidal distributions of the macrofauna and macroalgae. No correlation between the presence of potential prey species and the distribution of *T. savignyi* and *E. junionae* was found.

Acknowledgments

As I started my PhD study I have passed so many wonderful experiences as well as heartbreaking. I am extremely lucky to have so many people there in each moment supporting me with all love, without them I wouldn't be here today writing the final words.

Mum and Dad, I am so blessed having you in my life. My words will never give back not even a tiny fraction of what you gave to me. My soul mate and much loved husband "Abdulaziz", the fruits have reaped today because of your support, patience, and understanding. My daughter Dhiya you are the most wonderful thing that I had in my life. It was the most challenging experience to have you while doing my PhD study, alone and far away from home and family. You filled my life with smiles that always motivates me and make me strong to achieve my goals. My best ever friend Zainab Al-Wazzan you were always there beside me encourage me when I am weak as well you helping me at field thank you from the bottom of my heart. Bushra and Najoud thank you for all your support.

This work would not be completed without the assistance of so many people. I would like to express my sincere gratitude at first to my supervisor Professor Chris Richardson, Head of the School of Ocean Sciences, for his continuous guidance in my research and all the precious hours that he spent with me helping and correcting my writing language. Thank you Dr Mohsen Al- Husaini, Fish ageing laboratory of Kuwait Institute for Scientific Research (KISR), for providing me working space and materials I needed for my experiments and thank you for all your support. A heartfelt thanks extends to Dr Salah Al- Mudhi, former General Director of Kuwait Environment Public Authority for all his support and encouragement. Thank you to Mr David Roberts for the help in taken photographs used in this thesis. My sincere gratitude goes to Dr Khaled Al-Salem, Coastal and Air Pollution Department (KISR); Captin Abdullah A. Al-Qallaf, Harbour Master of al Ahmadi port; Mrs Salma Marafie, Kuwait Ports Authority and Mr Hassan Abdullah Dashti, Head of the Department of Climate Kuwait at Meterological Center for providing me with the environmental data. Thank you to Dr David Ried and Ronald Houart for all the help with identification of the studied gastropods. Finally, my thanks goes to Mr. Jamal Al- Abdullah Manager of Sea Shells Resort at Ra's al Qulay ah for allowing me to access the resort during my field work.

Contents

CHAPTER ONE

General Introduction

1 General Introduction

The family Muricidae belong to the phylum Mollusca which is one of the largest group of marine organisms. The family constitute a highly diverse group of species, widely distributed in tropical and subtropical shallow waters. They are commonly known as “Murex snails” or “rock shells”. The Muricidae are the third largest group in the class Gastropoda, a taxonomically complex family consisting of around 1,502 species that are known worldwide (Bailly, 2012). According to Bouchet & Rocroi (2005), in the classification and nomenclature of gastropod families, this family is separated into 13 sub-families that are further subdivided into more than 90 genera. This classification is based largely on superficial shell and radular characters due to poor phylogenetic knowledge associated with this family (Claremont *et. al.*, 2013). The Muricidae belong to the order Neogastropoda which contain more than 10,775 estimated species and represent the largest order in the class Gastropoda, and comprise nearly 30,239 species. This is by far the largest among other molluscan groups in terms of the number of species and individuals (Radwin and D'Attilio, 1976; Bailly, 2012).

Members of the Muricidae can be generally distinguished from other neogastropod families by the presence of rows of protrusions or spines on their shells (Carpenter and Niem, 1998). Additionally, the shell sculpture is elongated possessing a long siphon canal, the operculum has either a marginal or lateral nucleus. Their eggs are usually laid in protective corneous capsules usually from which crawling juveniles hatch or more rarely planktonic larvae. The planktonic larval stages are economically important as food for pelagic fishes. The Muricidae group are carnivores that generally feeds on economically important molluscs as well as barnacles (Carpenter and Niem, 1998). The soft body of their prey is reached through a hole drilled by means of softening secretion and scraping of a toothed structure known as a radula. For the reason of their carnivores' mode, they are considered as pests, as they may cause substantial destruction in exploited natural beds and areas of cultured commercial bivalves.

Along the rocky seashores of Kuwait, marine snails offer the wide range of interesting projects; even so, the different species are not abundant in the area as elsewhere in the Indian Ocean. Carpenter (1997) suggested that the low number is possibly due to the harsh climate combined with a scarcity of suitable habitats e.g. rock shores. *Thalessa savignyi* (Deshayes, 1844) (formerly known as *Thais savignyi*) and *Ergalatax junionae* (Houart, 2008) are two common predatory snails, belonging to the family Muricidae that live on the intertidal rocky shores of Kuwait. *Thalessa savignyi* belongs to the subfamily Rapaninae (Gray, 1853) which was previously known as the Thaidinae (Jousseaume, 1888) until 1993, whereas *E. junionae* belongs to the subfamily Ergalataxinae. Both species are relatively common in the indo-pacific area and acknowledged to be fairly well known taxonomically. However, within these two genera there is considerable taxonomic confusion where both species were introduced with different names. For many years *Ergalatax junionae* was wrongly identified as *Morula martensi* (Dall, 1923), similarly, the name *Thais* (=*Thalessa*) *savignyi* was introduced as *Thais hippocastanum* (*non* Linnaeus, 1758). At the beginning of my study I began to suspect that what appeared to be small juveniles of *T. savignyi* were in fact a different species. I sought advice from Dr David Reid at the Natural History Museum in London and he confirmed the identity of two different species – *Thalessa savignyi* and *Ergalatax junionae*. This was later confirmed in correspondence with Dr Ronald Houart from Belgium; he confirmed my identification from photographs that I sent him by e-mail.

Thalessa savignyi is characterized by having a large shell reaching 50mm with strongly tuberculate ridges and fine spiral grooves between them (see figure 1.1). This species generally inhabits rocks from the middle tidal zone downwards to low shore (Jones, 1986). Ruwa (1984), studied the intertidal distribution of *T. savignyi* on two vertical rock cliffs in Mombasa, Kenya and compared their distribution to *T. savignyi*'s distribution in other parts of the Western Indian Ocean. Ruwa (1984) found a similar distribution to Jones (1986) and concluded that *T. savignyi* were abundant in the upper eulittoral zone. Eisawy (1974) found that this gastropod preferred shallow areas around the marine station at Al Ghrdaqa, where they were exposed to air during low tide. When Eisawy (1974) kept *T. savignyi* in cemented aquaria he found that they liked to live close to the water surface where water was entering the aquarium. The genus *Thalessa* is distributed in the Indo-Pacific region, it is also recorded from Gulf waters (see figure 1.4) and from the Red Sea. In a taxonomic review of the intertidal molluscan fauna of Saudia Ariabia, Hasan (1996) investigated seashore mollusc populations covering an area of ~250 km in the Gulf, between Jubayl to Salwa, Saudi Arabia. *T. savignyi* were present at 5 stations from a total of 12 surveyed. These stations were: Jubayl, Ra's Tanura, Dammam, King Fahad Bridge and Salwa. However Al-Khayat (1997) who list the benthic molluscs from the Qatari coastline did not record the presence of *T. savignyi* or *Ergalatax junionae*. Feulner and Hornby (2006) recorded *T. savignyi* in their list of intertidal molluscs from further south west in the Gulf in lagoons along the coastline of the United Arab Emirates (UAE). They found it occasionally on rocky intertidal cliffs adjacent to some of the lagoons, for example at Khor Hulaylah. *Thalessa savignyi* has also been recorded from the southern region of Iran in the southeast of the Gulf i.e. at Qeshem Island. This species has been recorded from Kuwaiti waters from Ra's al Ard in the north to Ra's az Zawr in the south (Al-Yamani *et. al.*, 2012).

The name *Ergalatax junionae* was proposed by Houart (2008) who described the morphology of this species and other close related *Ergalatax* genera i.e. *E. martensi* (see figure 1.2). Houart (2008) noted that *E. junionae* has a medium sized shell that can reach up to 29 mm in length at maturity. Almost nothing is known about the species in the Gulf and it may easily be confused with other species of similar size and shape *i.e. Cornia* (=*Drupella*) *margariticola*. I am therefore including a brief description of the shell of the species here to assist in identifying the species. Houart (2008) found that the length/width ratio for the species was 1.91– 2.03 and he observed that the shell is slender, lanceolate, heavy and nodose with a weakly sloping, concave shoulder. Shell colour is generally white or creamy white with dark brown or blackish patches, particularly at the primary spiral cords (P) and occasionally at the secondary spiral cord (s), between the second and third primary cords (s2) or between the third and fourth (s3) cords (see figure 1.3). The aperture is glossy white, large, narrow or ovate with a columellar lip that is smooth, entirely adherent, with low parietal teeth (see Houart, 2008). The siphonal canal is short, broad, dorsally recurved and broadly open. The operculum is dark brown, D-shaped, with a lateral nucleus in the lower right part of the operculum, up to 8 growth lines and a broad, callused rim that represents about 30–40% of the opercular width. The radula has a rachidian tooth bearing a long, slender central cusp, a small, short lateral denticle and a broad, long lateral cusp on each side. The lateral teeth are sickle-shaped, with a broad base and narrow end (Houart, 2008).

Figure 1.4 shows the distribution of *E. junionae* in the Gulf, Gulf of Oman, and the Arabian Sea, data taken form (Houart 2008). *E. junionae* is largely an intertidal species but it has been recorded subtidally down to depths of 4 m, where it occurs on and under rocks and stones (Houart, 2008). Following a coral bleaching event in the Gulf in 2007, *E. junionae* was observed by Saledhoust *et. al.* (2011) feeding subtidally in large numbers on the corals *Porites* and *Platygyra* at Kish Island at depths of 5 to7m.

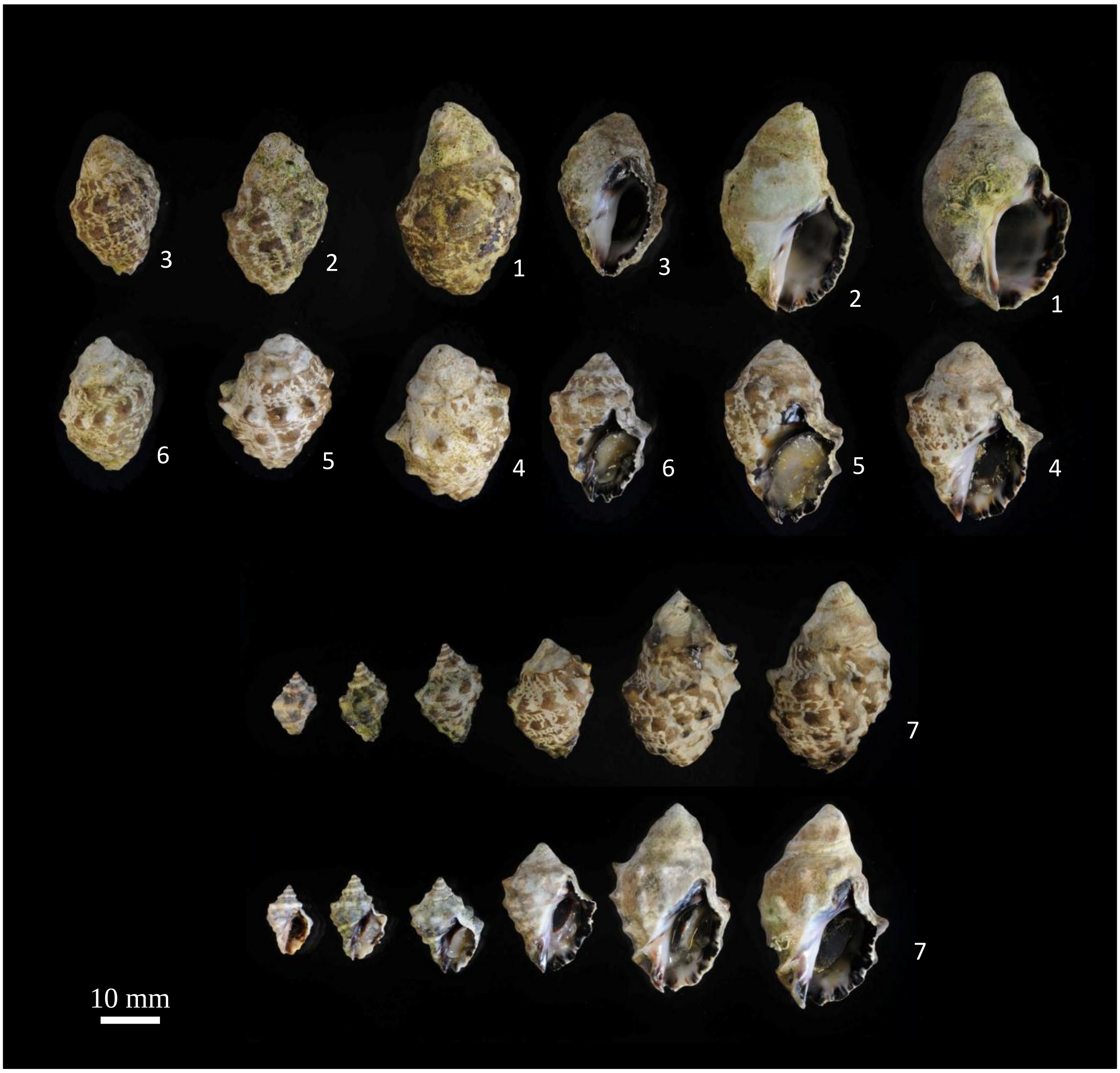


Figure 1.1. Variations in the outer shell shape and opercular openings of juveniles and adult *Thalessa savignyi* from the shores of Kuwait. (1-6) Ra´s al Qulay´ah and (7) Ra´s Eqaila.

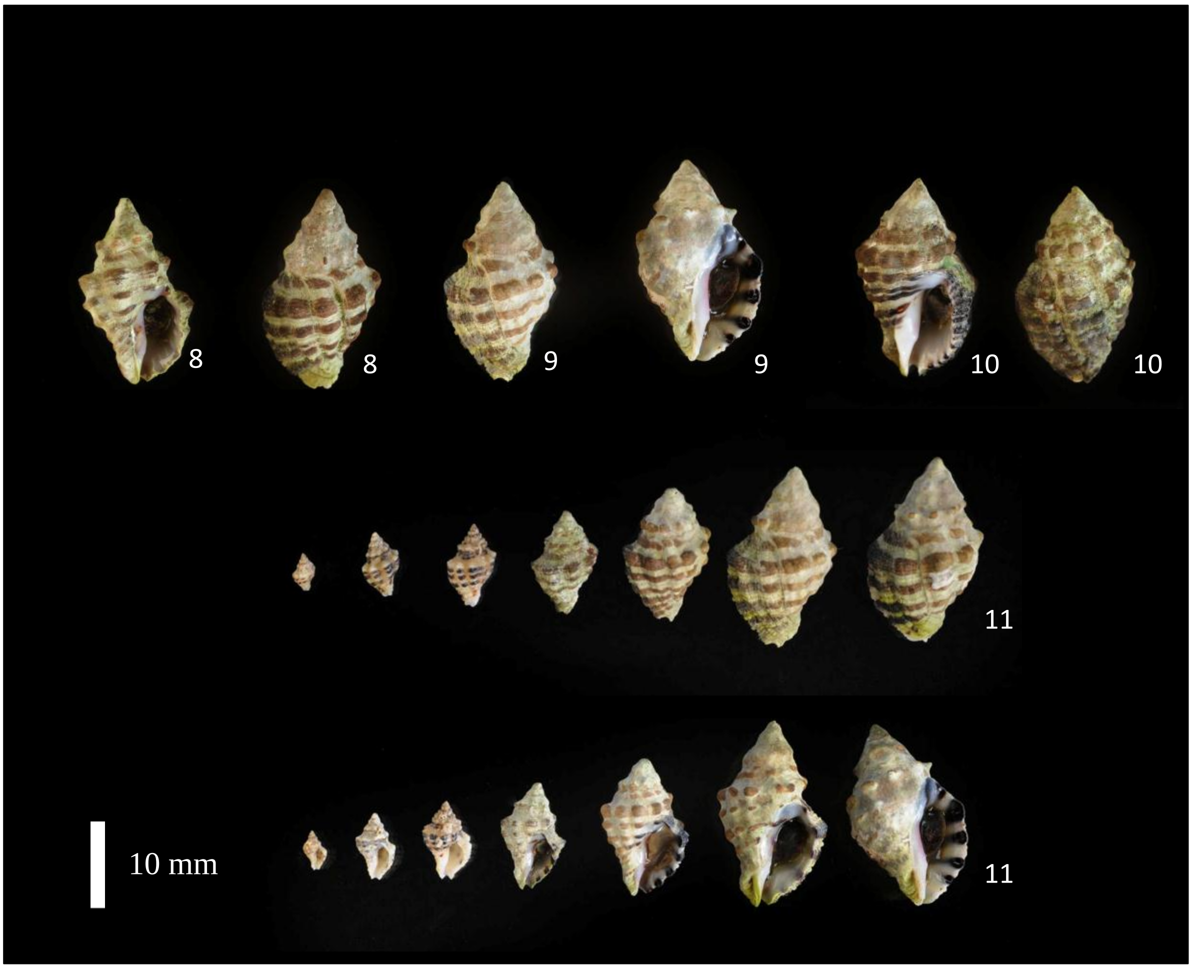


Figure 1.2 Variations in the outer shell shape and opercular openings of juveniles and adult *Ergalatax junionae* from the shores of Kuwait. (8) Ra´s Ajūzah (9 and 11) Ra´s Eqaila (10) Ra´s al Qulay´ah.

Figure 1.3 Spiral sculpture and opercular opening of *Ergalatax junionae*. SP: subsutural cord; P: Primary cord; s: secondary cord; P1: shoulder cord; P2-P6: Primary cords of convex part of the teleconch whorl; s1-s5: Secondary cords of convex part of the teleconch whorl; ID: infrasutural denticle; D2- D5: abapical denticle.

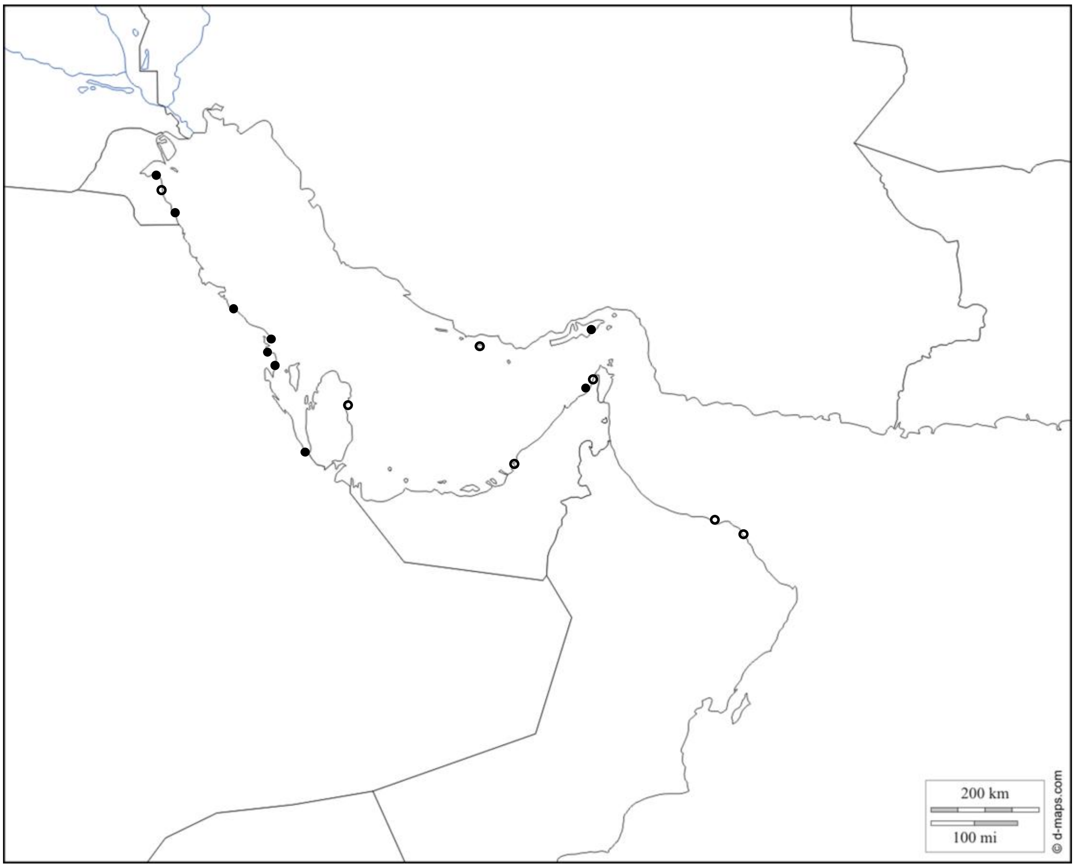


Figure 1.4 The distribution of *Thalessa savignyi* (•) and *Ergalatax junionae* (∘) along the Gulf as reported in the literature.

Saledhoust *et. al.* (2011) noted that *E. junionae* is unusual as it only consumes the coenchyme and the polyps are able to recover once feeding has stopped. This is in contrast to other corallivorous snails e.g. *Drupella rugosa* which eats all the coral tissues.

According to Soliman's (1987) scheme for classifying gastropod egg masses, he divides them into four different groups: (a) gelatinous egg masses where eggs are laid in a shapeless mass, or as an egg sheet, or globular mass, (b) a second category where egg capsules are laid, (c) as ribbons of eggs and (d) strings of eggs. Muricid gastropods are known to produce egg capsules with a variety of shapes and sizes. D'Asaro (1991) categorizes the very diverse forms of Muricid egg capsules into two major types, (1) vasiform capsules, which are deposited with the alignment of the suture nearly perpendicular to the anterior-posterior axis of the spawner's foot, and (2) ampulliform capsules, which are positioned with the alignment of the suture approximately parallel to the anterior-posterior pedal axis. The structure of the egg capsules produced by *T. savignyi* is vasiform and lingulate in shape. These egg capsules are usually attached to each other in an irregular mass (D'Asaro, 1991). Eisawy and Sorial (1974) found the spawning season for *T. savignyi* to be over a period, extending from August to November, at water temperatures ranging between 21°C to 30°C. Seawater temperature is known to greatly affect the development rate of the embryos (Eisawy and Sorial, 1974). These authors found that females deposited egg capsule in shallow niches in a solid substratum of dead coral or empty bivalve shells. Egg capsules, in all observed cases, were fixed to the lower surface of the substratum (shell) where they were exposed to diffuse sunlight. They noted that the animal took 15 minutes to produce each egg in the egg mass in August and 20 minutes in November. Additionally, the size of the eggs varied with the size of the individual as they stated that small individuals laid smaller capsules. They also found that the number of egg capsules that were laid by an individual ranged between 16 and 30 capsules and showed that groups of individuals may spawn in the same locality laying their capsules in the same area and this resulted in a large number of eggs (120 to 230) in each egg mass. The shape of the 3.5-3.7mm long, 3-3.2 wide, 0.5 thick egg capsules of *T. savignyi* were described as a broad flattened vase shape without a stalk (Eisawy and Sorial, 1974). Usually eggs capsules were fixed to the substratum by a broad base with a thin membrane to which were attached the neighboring capsules.

Thorson (1946) recognized three developmental patterns in marine benthic invertebrates particularly of prosobranch gastropods. The first form called planktotrophic larvae, involves a free drifting larvae swiming freely in the plankton for a specific period of time where it feeds on smaller planktonic organisms. The second type is a pelagic lecithotrophic larvae that spend periods of time in the planktonic phase but depends on yolk material stored in the egg for nutrition. The third form is a non-pelagic leithotrophic larva, which develops entirely in a benthic egg or is brooded by an adult. A fourth mode of larval development which Thorson (1946) did not mention in his study and has been proposed later by Mileikovsky (1971) is called a demersal larvae or a free-living benthic juvenile (Vance, 1973). The distribution of these different forms of larval development are comprehensively discussed by Thorson (1946 and 1950) as it has been thought to reflect a latitudinal pattern. Thorson's rule, named after Gunner Thorson by Mileikovsky (1971), stipulates that the proportion of species with pelagic larvae decreases with increase of latitude. Doubts have been voiced by Gallardo and Penchaszadeh (2001), where they point out other ecological conditions, i.e. bottom substrata and phylogenetical conditions and species composition in determining the developmental mode. In their work they indicated that no such patterns exist in the developmental mode of prosobranch gastropods from the Atlantic coast of South America. On the other hand, they see a clear latitudinal gradient along the Pacific coast.

A study by Gosselin & Rehak (2007) on *Nucella ostrina* juveniles has shown that offspring of a larger initial size have a greater ability to survive than smaller ones. They claimed that individuals with larger size are capable of surviving severe environmental conditions and determined the influence of exposure to waves and predation on hatching size. The average population hatching size did correlate with the degree of exposure where size increases with wave exposure. The intensity of wave action has a great influence on the level of desiccation stresses and thermal extremes. Thus wave protected-areas might be the most severe habitat for early juveniles to survive in and where the level of these stressors increase. On the other hand, they found that pressure of predation did not have that much importance in determining hatching size.

Spight (1976) pointed out that the chance of survival of a juvenile increases if it is able to grow among the adult (larger) muricides. He indicated that hatching size is dependent upon the surrounding macro- as well as micro-habitat. In other words, muricids hatch at a larger size in some habitats than in others. For instance, snails living on coral reef flats (e.g. *Murex incarnates*, 1.1-1.9 mm) or in subtidal habitat (e.g. *Murex angularis,* 0.6-2.5mm) are hatching in a larger size than those living on oyster reefs (e.g. *Ocenebra japonica* , 0.9-1.5mm) or on rocky intertidal shore (e.g. *Thais lapillus*, 0.6-1.3mm). Also, hatchling living in different microhabitat e.g. shore level have different chances to survive. The risk of death on the high shore, where exposure to air is longer than on the lower shore, makes them more susceptible to dehydration and overheating. While at low shore where long periods of submergence snails are more threatened to predators. This reveals that the chances of survival at various tidal levels are different. For example, at Friday Harbor, Washington in the USA the muricides *Thais emarginata, T. lima,* and *T. canaliculata*, on the upper shore all hatch at about

1.3mm shell length, while those that dwell on the lower shore hatch at a significantly smaller size of ~1.0mm (Spight, 1976).

The growth rate of an organism is an important feature of its life history (Etter, 1996). It can alter the fitness of an individual. For example when gastropods grow fast, they increase the chances of producing more offspring at a particular age. Also, with a higher growth rate organisms can reach a size refuge earlier in their life and reduce attacks from predators. A previous and earlier study by Etter (1988) on *Nucella lapillus* demonstrated that mortality due to predation was low when individuals reached a size of 15mm. Etter (1996) showed that there were growth rate differences amongst populations of the intertidal snail *N. lapillus* across an exposure gradient in the USA. The question asked by the author was whether this variation was due to the relative contribution of genetic differences or phenotypic plasticity induced by the surrounding environment. Etter (1996) conducted field and laboratory experiments to determine the extent to which these differences in growth rate are the result of genetic or environmental influences. Despite the fact that gastropods from shores of different wave gradient were reared under similar conditions in the laboratory they showed no visible differences in their rate of growth. Another experiment transplanted juvenile and adult dog whelks onto exposed and protected sheltered shores and their growth was subsequently followed. The results of this work demonstrated higher growth rates in dog whelks transplanted from exposed shores to sheltered shores compared with those moved from sheltered to exposed shores. It is known that exposed shores inhibit growth by limiting foraging time and efficiency. It is also known that the quantity and quality of prey can differ for each kind of shore. In Etter's (1996) experiment, the main diet for *N. lapillus* was the barnacle *Semibalanus balanoides* (L.) and mussels *Mytilus edulis* (L.), where mussels favour exposed shores and barnacles sheltered shores. Etter (1996) concluded that the growth rate of *N. lapillus* was extremely plastic and did not reflect any genetic differentiation but that differences in growth were related to environmental forces.

Various studies have demonstrated that different environmental factors result in different distributions of animal and macroalgae populations. According to Trudgill (1988), life on rocky shores is subject to a wide range of exposure to wave action and drying (see also Raffaelli and Hawkins, 1996) and these conditions influence the distribution of organisms and considerably affect the shape of the landforms on a shore. For example, rock pools, crevices, and rock pinnacles provide organisms with a wide variety of shelter and protection that encourages colonization in these areas and this results in local distributions of animals and macro algae that are influenced and controlled by their surroundings. Lewis (1964) was one of the first to study the distribution patterns of populations on two rocky shores that had a different exposure gradient to wave action and he noted an obvious succession of coloured belts (zones) that were naturally produced by the domination of specific organisms at each level. He was able to understand and describe differences between these two shores. He showed that exposed and sheltered shores have species that were common at the upper and lower margins. Macroalgae and macrofauna living on rocky shores are distributed in accordance to their ability to tolerate exposure conditions and their physiological adaptation, competition for food and living space along with a gradient of physical factors they encountered. Chapman and Underwood (1994) demonstrated that a combination of physical features of substratum, such as crevices and pits, and biological features, such as algal cover or sessile animals, plays an important role in the distribution of mobile intertidal creatures, such as gastropods, in providing them with different microhabitats. Trudgill (1988) commented that researchers usually focus on flora and fauna and neglect to consider the evolution of substrate morphology.

In this Thesis, the findings from a wide ranging investigation into the ecology and biology of *Thalessa savignyi* and *Ergalatax junionae* are presented. This chapter (Chapter 1) introduces the subject through a review of the literature. Chapter 2, describes the environmental setting, climatic features and environmental characteristics of the coastal waters around Kuwait and the physical features of the studied shores to understand the considerable environmental constraints that are placed upon organisms living on Kuwait's shores. The distribution, abundance and morphological differences between the two gastropod species are investigated latitudinally, seasonally and intertidally down the shore in relation to the various abiotic factors and are discussed in Chapter 3. In Chapter 4 the population structure of *T. savignyi* and *E. junionae* are separated into their component size classes using Bhattacharya's method and inter- and intra-differences in the growth of the two species determined. In Chapter 5 I explore the different methods for estimating the age and growth of both gastropod species and I develop an innovative method to investigate shell growth rates using the growth rings in the statoliths and operculae of adult *T. savignyi* and *E. junionae*. In Chapter 6 the distribution of fauna and flora across the studied shores is described and I give some relevant information on the feeding and reproduction of the two species that assisted in an understanding of the distribution of the two predatory gastropods. Finally, the results from all the chapters are drawn together and discussed in Chapter 7. All this information will assist in understanding where and how the two gastropod species are distributed both intertidally and latitudinally and whether there are any difference in abundance and growth rates along the shores of Kuwait.

1.1 REFRENCES

Al-Khayat, J. A. (1997). The marine mollusca of the Qatari waters, Arabian Gulf. Qatar University Science Bulletin, Vol. 17, pp. 479-491.

Al-Yamani, F. Y., Skryabin, V., Boltachova, N., Revkov, N., Makarov, M., Grinstov, V., & Kolesnikova, E. (2012). Illustrated Atlas on the Zoobenthos of Kuwait. Kuwait Institute for Scientific Research.

Bailly, N. 2012. Catalog of life 2012 annual checklist [online]. Available: http://www.catalogueoflife.org/annual-checklist/2012/browse/tree/id/2339548 [accessed 26 Febreuary 2013].

Bouchet, P., & Rocroi, J. P. (2005). Classification and nomenclator of gastropod families. *Malacologia*, Vol. **47**, pp. 1-397.

Carpenter, K. E. (1997). Living marine resources of Kuwait, eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates, pp. 45-48.

Carpenter, K. E., Niem, V. H. (1998). The Living Marine Resources of the Western Central Pacific: Seaweeds, corals, bivalves and gastropods, Vol. **1**, pp. 553-563.

Claremont, M., Reid, D. G., and Williams, S. T. (2008). A molecular phylogeny of the Rapaninae and Ergalataxinae (Neogastropoda: Muricidae), *Journal of Molluscan Studies*, Vol. **74**, pp. 215-221.

Claremont, M., Reid, D.G. & Williams, S. (2013). A molecular phylogenetic framework for the ergalataxinae (Neogastropoda: Muricidae), *Journal of Molluscan Studies*, Vol. **79**, pp. 19-29.

D'Asaro, C.N. (1991). Gunnar Thorson's worldwide collection of prosobranch egg capsules: Muricidae, *Ophelia,* Vol. **35**, pp. 1-101.

Eisawy, A.M. & Sorial, A.E. (1974). Egg Capsules and Development of Thais-Savignyi, *Bulletin of the Institute of Oceanography and Fisheries,* Vol. **4**, pp. 237-258.

Etter, R.J. (1996). The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.), *Journal of Experimental Marine Biology and Ecology,* Vol. **196**, pp. 341-356.

Etter, R.J. (1988). Physiological stress and color polymorphism in the Intertidal Snail *Nucella lapillus, Evolution,* Vol. **42**, pp. 660-680.

Feulner, G. R., & Hornby, R. J. (2006). Intertidal molluscs in UAE lagoons.*Tribulus*, Vol. **16**, pp.17-23.

Gallardo, C. S., Penchaszadeh, P. E. (2001). Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the southern hemisphere, *Marine Biology*, Vol. **138**, pp. 547-552.

Gosselin, L. A., Rehak, R. (2007). Initial juvenile size and environmental severity: influence of predation and wave exposure on hatching size in *Nucella ostrina , Marine Ecology Progress Series*, Vol. **339**, pp. 143-155.

Hasan, A. (1996). A taxonomic review of the bivalve and gastropod mollusc fauna along the Saudi intertidal zone of the Arabian Gulf. *Journal of King Abdulaziz University*, Vol. **7**, pp. 245-253.

Houart, R. (1996). On the identity of *Morula martensi* Dall, 1923 and description of a new species of *Ergalatax* from the Red Sea (Gastropoda: Muricidae: Ergalataxinae), *Nautilus,* Vol. **110**, pp. 12-16.

Jones, D. A. (1986). Field Guide to the Sea Shores of Kuwait and the Arabian Gulf, University of Kuwait. Blandford Press, Kuwait, pp. 123-129.

Laptikhovsky, V. (2006). Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules, *Marine Ecology Progress Series*, Vol. **27**, pp. 7-14.

Mileikovsky, S.A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation, *Marine Biology*, Vol. **10**,

Mohamed, S. Z. & Al-Khayat, J. (1994). A preliminary check-list of benthic Mollusca on the Qatari Coasts, Arabian Gulf. *Qatar University Science Journal*. Vol. **14**, pp.193-213.

Moreno, C., Reyes, A. & Asencio, G. (1993). Habitat and movements of the recruits of *Concholepas concholepas* (Mollusca; Muricidae) in the rocky intertidal of southern Chile, *Journal of Experimental Marine Biology and Ecology*, Vol. **171**, pp. 51-61.

Pechenik, J., Chang, S.C. & Lord, A. (1984). Encapsulated development of the marine prosobranch gastropod *Nucella lapillus*, *Marine biology Berlin, Heidelberg*, Vol. **78**, pp. 223-229.

Radwin, G.E., D'Attilio, A., & Mulliner, D.K. (1976). Murex shells of the world: an illustrated guide to the Muricidae, Stanford University Press, Stanford, California.

Raffaelli, D. & Hawkins, S.J. (1996) Intertidal ecology, Chapman and Hall, London.

Richardson, C.A. (2001). Molluscs as archives of environmental change, *Oceanography and Marine Biology Annual Review*, Vol. **39**, pp. 103–64.

Ruwa, R. (1984). Invertebrate faunal zonation on rocky shores around Mombasa, Kenya, *Kenya Journal of Sciences Series Biological Sciences*, Vol. **5**, pp. 49-65.

Saledhoust, A.; Negarestan, H.; Jami, M.J. and Brian Morton. (2011). Corallivorous snails: first record of corallivory by *Ergalatax junionae* (Gastropoda: Muricidae) in the Persian Gulf. *Marine Biodiversity Records*, Vol. **4**, pp. e99.

Soliman, G.N. (1987). The Egg Masses of Gastropods from the Northwestern Red Sea a Proposed Scheme of their Classification, *American Malacological Bulletin,* and Vol. **4**, pp. 109-110.

Spight, T. (1976). Ecology of hatching size for marine snails, *Oecologia*, Vol. **24**, pp. 283-294.

Thorson, G. (1946). Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound Oresund, *Medd Dan Fisk Havunders (Ser Plankton)*, Vol. **4**, pp. 1-529.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates, *Biological Reviews*, Vol. **25**, pp.1- 45.

Trudgill, S. (1988). Integrated geomorphological and ecological studies on rocky shores in southern Britain, *Field Studies*, Vol. **7**, pp. 239–279.

Vance, Richard R. (1973). On Reproductive Strategies in Marine Benthic Invertebrates, *The American Naturalist*, Vol. **107**, pp. 339-352.

CHAPTER TWO

Environmental Settings of the Studied Shores

Figure 2.1. Map of the State of Kuwait showing the location of sampling sites (★), weather forecast stations (1-4) (●) and tide prediction ports (a-c) (Δ) (map source: united nation cartographic section at http://www.un.org/Depts/Cartographic/english/htmain.htm)

2 Environmental Settings of the Studied Shores

2.1 INTRODUCTION

The purpose of chapter 2 is to describe the environmental setting, the main climatic features and environmental characteristics of the coastal waters around Kuwait and the physical features of the shores at the three sites that I selected to sample between 2012 and 2013.

Kuwait is a small desert area of about 17,818 km². It is located in southwest Asia lying at the western head region of the Persian Gulf which is locally known as the Arabian Gulf and recently has become increasingly commonly known in the media as "the Gulf". Kuwait is roughly lozenge in shape and it shares its borders with Iraq, in the north, and Saudi Arabia, to the west and south. Kuwait's coastline covers approximately 325 Km from the north of the Persian Gulf southwards (El-Baz & Al-Sarawi, 2000) (see figure 2.1). The average air temperature ranges between 10ºC and 20ºC in January (winter) to temperatures over 30º C in July (summer) (figure 2.2). The seasonal variation in seawater temperature mirrors the air temperature except in June and July when the seawater temperature is ~5ºC below the air temperature (figure 2.2). There is little rainfall in Kuwait with an average annual rainfall of <25cm so the salinity of the coastal waters is relatively stable (~40psu) throughout the year (figure 2.3). However in 2012 there were sudden falls (~38psu) in salinity in northern Kuwait during September and in southern Kuwait in early July. The wind roses for the period of study (figure 2.4) show that the winds are generally north westerly in direction so the impact upon the three study shores will be different because of the aspect of each shore. In the north the shore is northerly facing so any waves and swell will impact the shore directly from the north-west whereas the shores along most of the middle and southern regions of Kuwait will be less affected because the winds blow offshore so the impact of waves will generally be much less than at the north site.

The tides in the Gulf waters off Kuwait are mixed semi-diurnal tides indicating that one of the two low and high tides during the spring lunar cycle are of unequal amplitude (figure 2.5). Few parts of the Gulf region have a tidal range of over 1 to 1.5m (Sheppard *et.al.* 1992). However, the coastal waters around Kuwait have a moderately high tidal range and typically in Kuwait Bay a range of about 3.5m to nearly 4m between mean high water (MHW) and mean low water (MLW). The tidal range is greater in coastal waters in northern Kuwait (3.5m) compared to the south of Kuwait (2.0m) (see figure 2.4). The timing of low tides varies seasonally such that during summer (July) the lowest spring low tides are in the evening i.e. after 16.00 when air temperatures are cooling down after the heat of the day and in winter (December) the lowest spring tides occur in the early morning (07.00 to 11.00) when the air temperatures are only just beginning to warm at the start of the day. The frequency of aerial exposure during these two seasons and the timing of spring low tides plays an important part in controlling the communities of animals and macro-algae on the shores of the Gulf region (Jones, 1986). In order to sample the full extent of the shore it was necessary to sample during the lowest tides i.e. those low tides below 0.3m are the most suitable (figure 2.5). However in some months during the spring (March and April,) and late summer (August and September) the full extent of the low shore was not exposed sufficiently to allow sampling. For many of the months when it was possible to reach the lowest areas of the shore this was only possible during one spring cycle during the month (e.g. May. June and December). Kuwait’s climatic conditions can be described as generally hot, arid with scarce rainfall.

The selection of study sites along Kuwait’s 325Kms of coastline was constrained by the lack of suitable rock substrata, since only 70.8 Km of Kuwait’s shoreline is composed of cobble and/or boulders (3.1Km), beach rock outcrops (15.6km) and exposed bedrock platforms (52.1Km) and therefore there is a lack of suitable substrata for predatory gastropods and thei prey to live. The remaining areas of Kuwait's coastline are composed of sandy beaches in southern Kuwait and muddy shores in northern Kuwait. Also as a result of the 1990 war in Kuwait large areas of northern Kuwait's mud and rocky shores are "no go" areas because of the dangers of mines and unexploded bombs and missiles. The choice of shores for my study was based on providing as wide a latitudinal range as possible where the two gastropods *Thalessa savignyi* and *Ergalatax junionae* were present. After considerable searching and collecting, three shores (sites) were selected i.e. Ra´s Ajūzah north of Kuwait city, Ra´s Eqaila south of Kuwait city and Ra´s al Qulay´ah in southern Kuwait where there were sufficient numbers of the gastropods *Thalessa savignyi* and *Ergalatax junionae* present.

2.2 Study Areas

This section provides a general physical description of the three study sites to understand the differences in the habitats in order to explain any observed differences in the distribution and abundance of *T. savignyi* and *E. junionae* and its prey species. My study was conducted in three areas 1) Ra´s Ajūzah (29° 23'N, 47° 59'E) in the north, 2) Ra´s Eqaila (29° 10' N, 48° 7' E) in the middle part of Kuwait and 3) Ra´s al Qulay´ah (28° 52' N, 48° 17' E) in the south. The three sites are ~ 30 Km apart from each other (see figure 2.1).

Site 1: Northern Kuwait - Ra´s Ajūzah. This site is a continuation of a low headland that is located along the southeast margin of Kuwait Bay, west of Kuwait City and is composed of intertidal coral rock (Kana *et. al.*, 1986). The shore is shallow shelving and comprises small rocky cobbles (<25cm), boulders (>25cm), rock pools and exposed bed rock platforms (see Al-Sarawi *et. al.*, 1985) with patches of sand between (see later table 6.2 Chapter 6). Cobbles and boulders are spread across the upper part of the shore

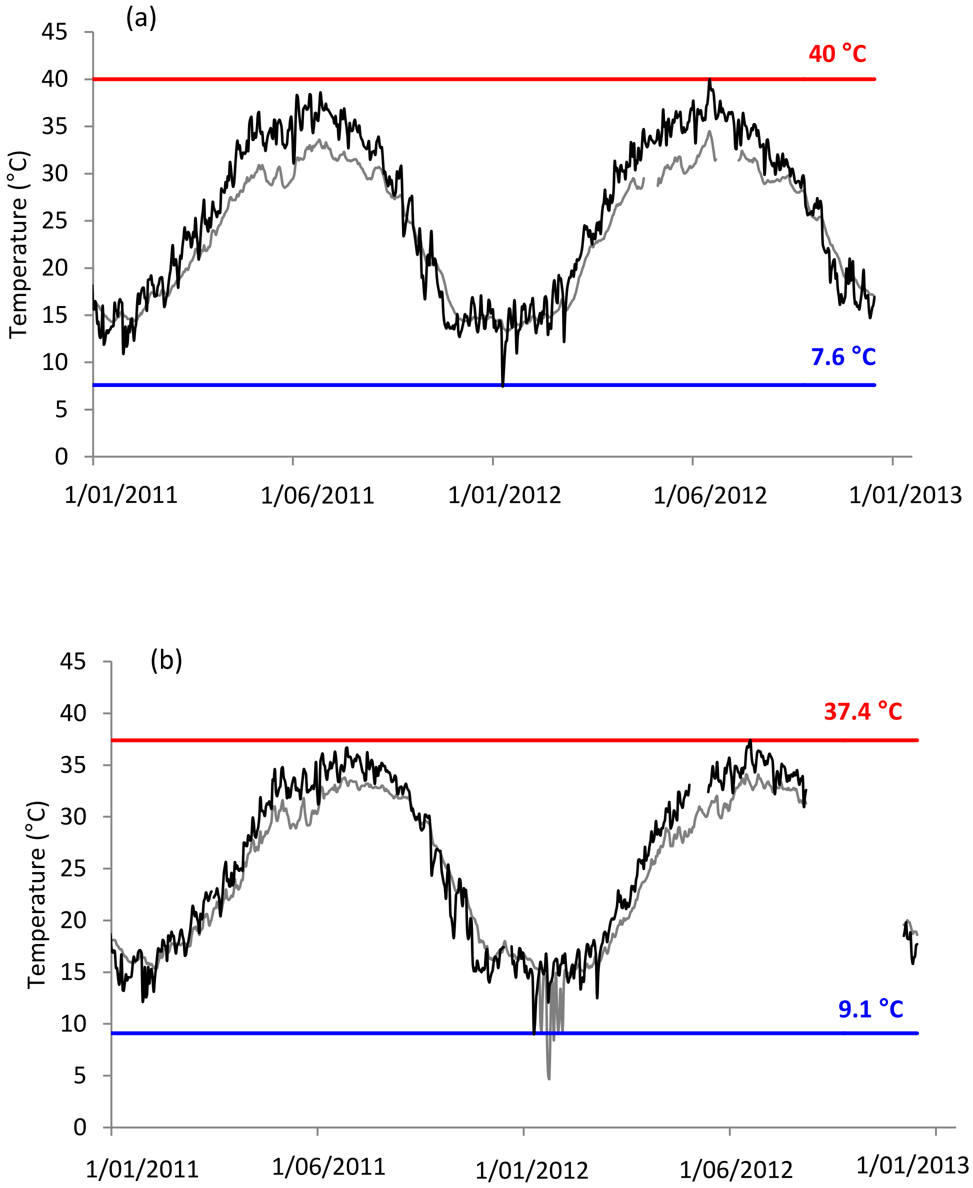
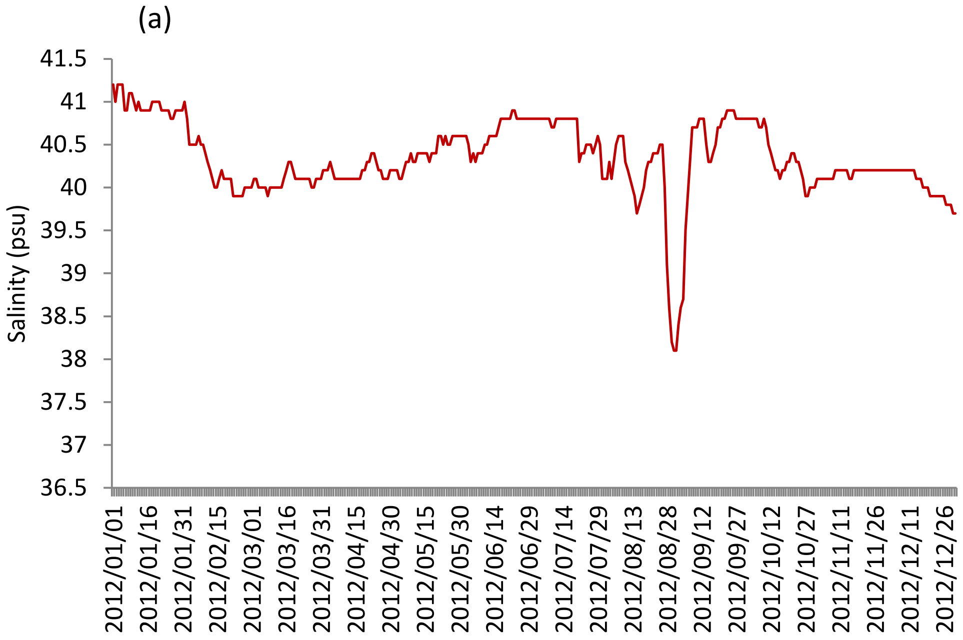


Figure 2.2. Daily mean air (black line) and sea-surface (grey line) temperature profiles between 2011 and 2012 to show the maximum range of air and seawater temperatures along the coastline of Kuwait. (a) in the north of Kuwait Bay (weather forecast station 1) and (b) in the south, Ahmadi oil pier/Ahmadi Port (weather forecast station 4). The daily mean temperatures are based on hourly records taken between 00:00 and 23:59 each calendar day. Upper red line indicates the summer (June 01 - October 08) maximum air temperature. Lower blue line indicates the winter (November 28 - February 12) minimum air temperature. No data were collected between September and December by weather forecast station 4 owing to a malfunction with a sensor. Figures plotted using data collected by weather forecast stations for the Kuwait Meterological Center, Directorate General of Civil Aviation – State of Kuwait.



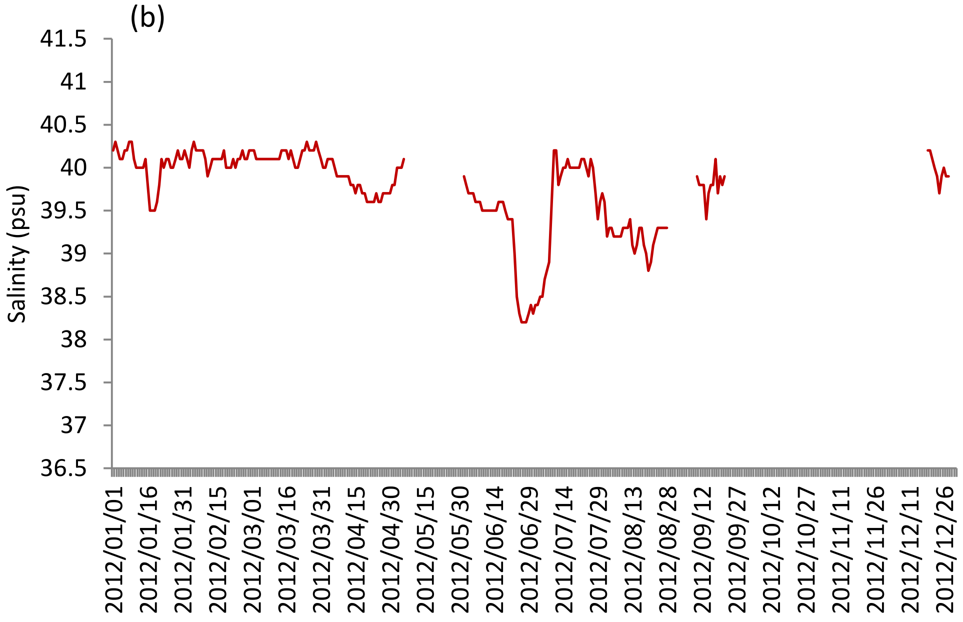


Figure 2.3. Daily average salinity profiles from (a) Kuwait Bay weather forecast station 1 and (b) Sea Island Buoy (opposite to Al-Fintâş) (weather forecast station 2) between 2012 and 2013. Daily average salinity based on hourly records taken between 00:00 and 23:59 each day. Some data are missing due to a malfunction of a sensor. Figures plotted using data collected by weather forecast stations for the Kuwait Meterological Center, Directorate General of Civil Aviation – State of Kuwait.

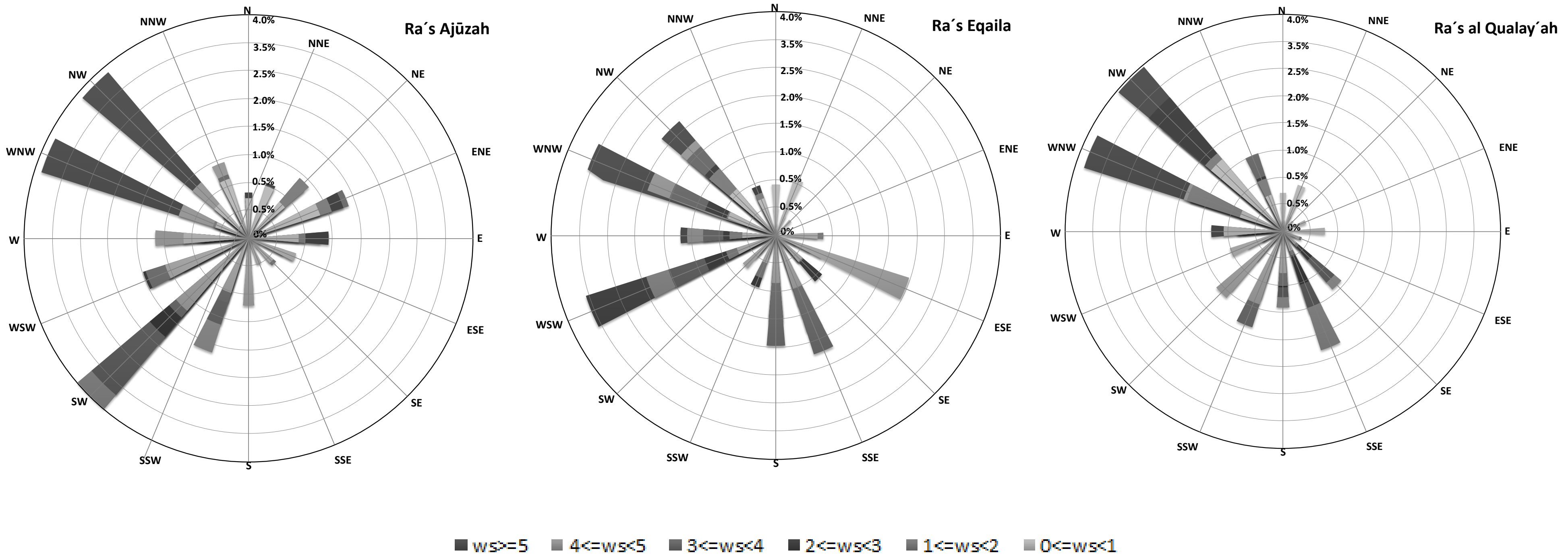


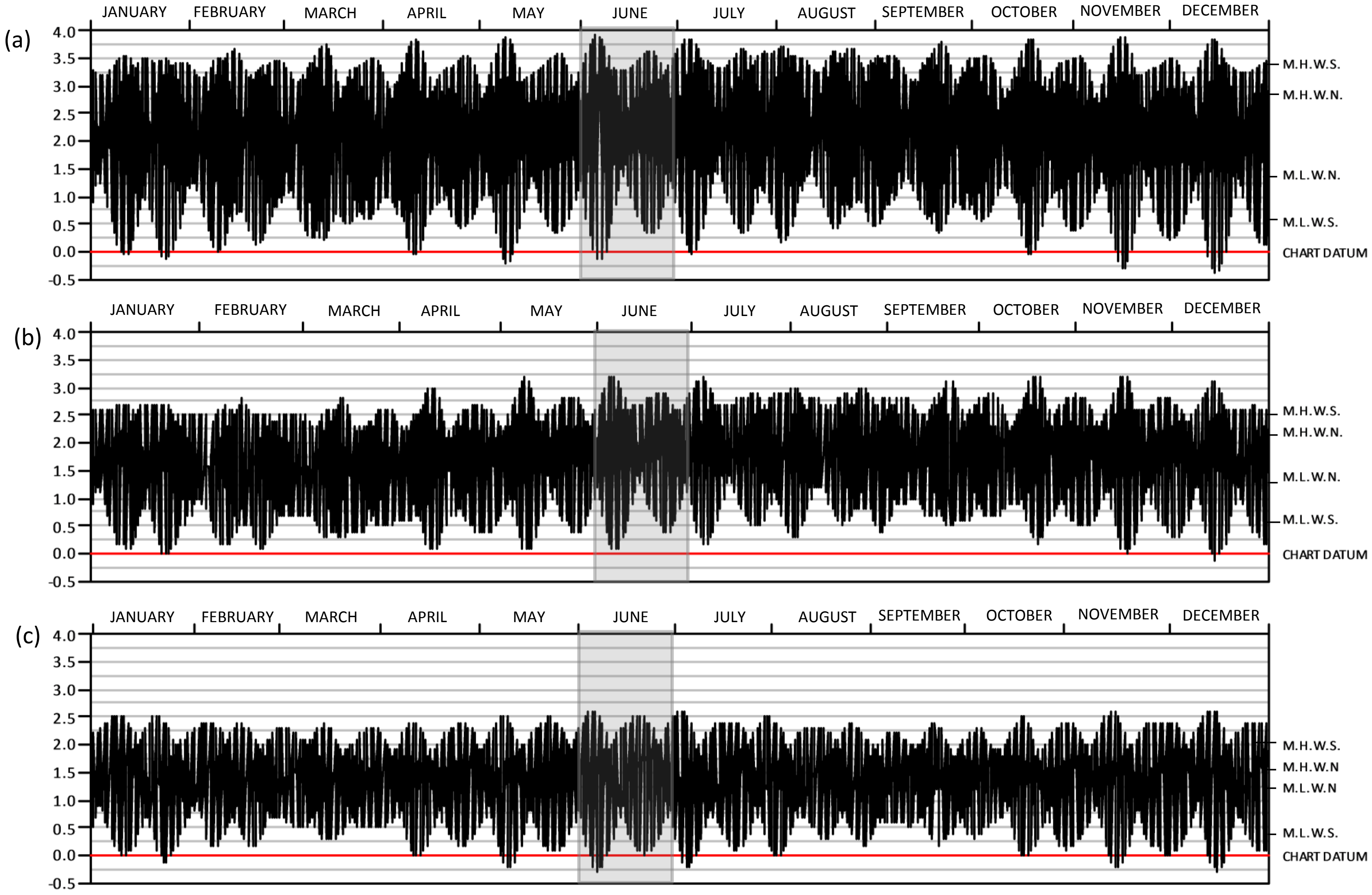
Figure 2.4. Wind roses to show the wind direction and speed (m s^{-1}) for 2009 at the three study sites. Constructed from data supplied by the Coastal and Air Pollution Department, Kuwait Institute for Scientific Research.

lying on sand. In the middle of the shore there is more sand with scarce numbers of scattered small boulders and it is usually covered partially with seawater. The lower shore is dominated by bed rock platforms surrounded by patches of small and large boulders with sand at the lowest point on the shore (figure 2.7 and 2.8, see also the description in Chapter 6, table 6.2). The shore is situated directly in front of a tourist spot - Kuwait Towers, which is the symbol of modern Kuwait and is positioned in Kuwait City (see figure 2.7). Kana *et. al.*, (1986) noted that due to the moderately high tidal range ~3.0 m between M.H.W.S. and M.L.W.S., the middle and upper levels of the shore were the most exposed parts to wave action.

Site 2: South of Kuwait City - Ra´s Eqaila. The shore at Ra´s Eqaila is located south of Kuwait City and is a popular swimming beach and comprises an upper eulittoral sandy beach, below which there are rock platforms and from the upper mid shore to low water the beach is strewn with boulders and stones of varying sizes that form a compact boulder shore interspersed with sand patches (see figure 2.9). The middle shore zone is narrower compared to the other two studied sites and is frequently covered with pools of seawater because of its topographic shape (see figure 2.10). Boulders and cobbles are widely distributed across this part of the shore. Flat rock platforms characterise the lower part of the shore interspersed with small and large boulders.

Site 3: Southern Kuwait - Ra´s al Qulay´ah. This is the most southern site surveyed and is adjacent to a holiday resort with a fine sediment sandy beach on the upper shore that gives way quickly to rapidly shelving beach rock outcrops and patches of fine sand (figure 2.11). In the upper part of the middle level of the shore there are small water pools with scattered cobbles and boulders then towards the lower part of this level rock platforms appear again with patches of sand. This feature continues toward the lower level of the shore, where larger pools have developed amongst the rock platforms

Figure 2.5. Seasonal variation in the amplitude of the spring-neap lunar cycle during 2012 at (a) Ash Shuwaikh (closest station to Ra´s Ajūzah) and (b) Al-Fintâş (closest station to Ra´s Eqaila) and (c) Ra’s al Qulay’ah, showing the regular alternation between high and low waters during neap and spring tides (re-drawn from predictions in Tide planner Tide Tables, Tucabo Ltd). M.H.W.S; mean high water of spring tides , M.H.W.N; mean high water of neap tides, M.L.W.N.; mean low water of neap tides , and M.L.W.S.; mean low water of spring tides. The shaded part of the figures in June are shown in more detail in figure 2.6.


(a)
(b)
(c)
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
M.H.W.S.
M.H.W.N.
M.L.W.N.
M.L.W.S.
CHART DATUM
M.H.W.N
M.L.W.N

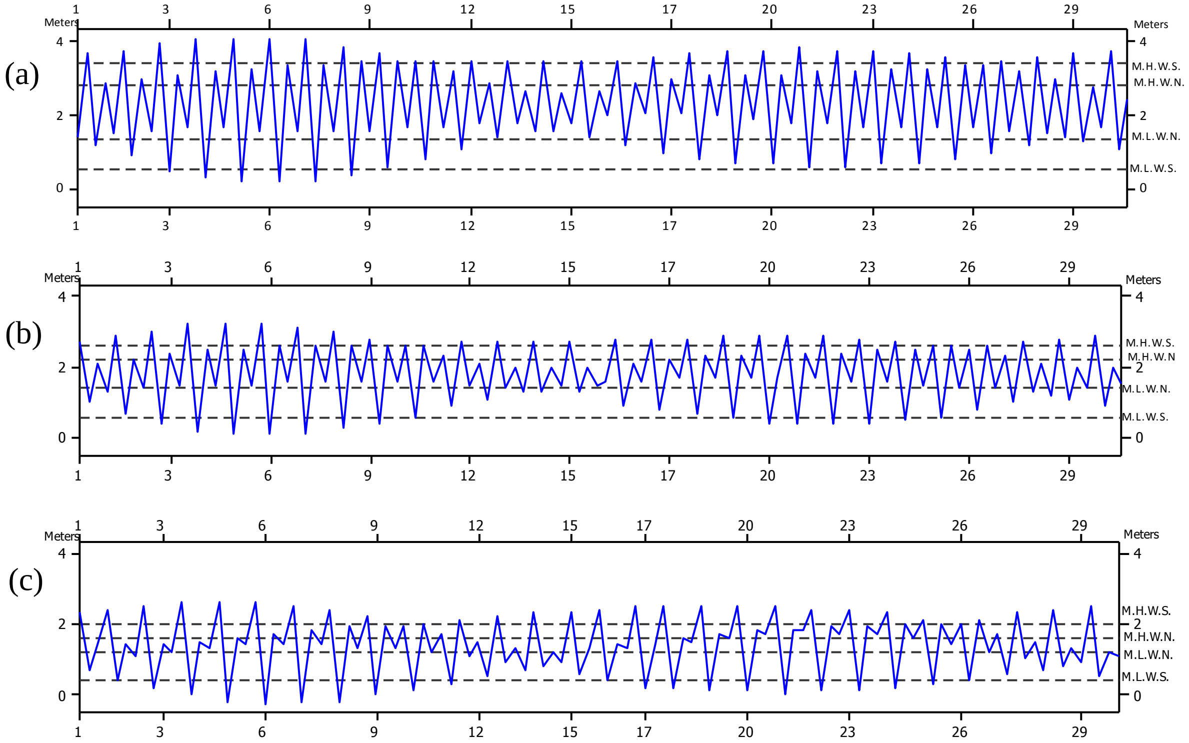


Figure 2.6. Mixed semi-diurnal tidal cycle during June 2012 to illustrate the diurnal variation in the height of low and high waters throughout the spring-neap tidal cycle at the three study sites (a) Ash Shuwaikh (closest station to Ra´s Ajūzah) and (b) Al-Fintâş (closest station to Ra´s Eqaila) and (c) Ra’s al Qulay’ah. (re-drawn from predictions in Tide planner Tide Tables, Tucabo Ltd).

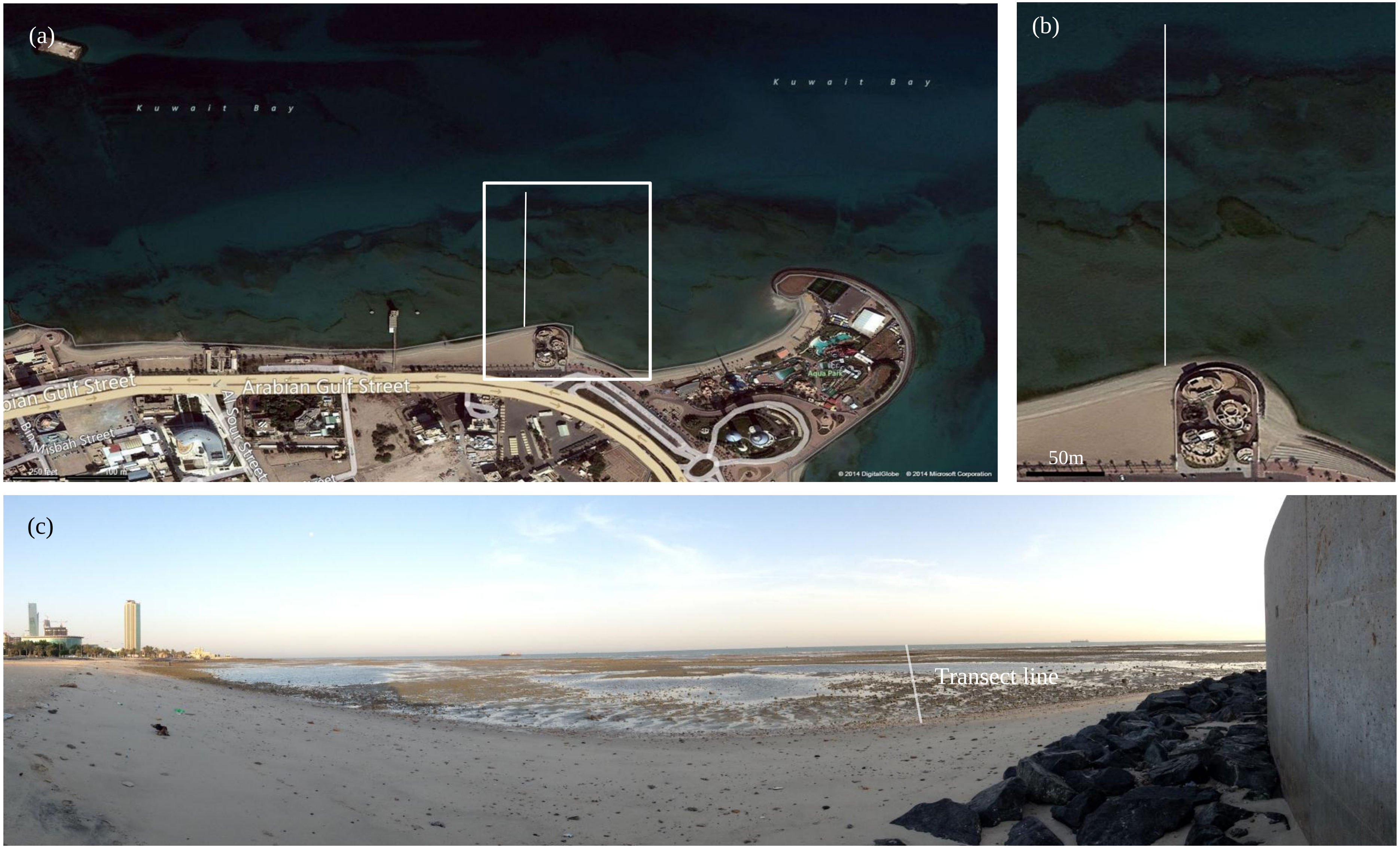
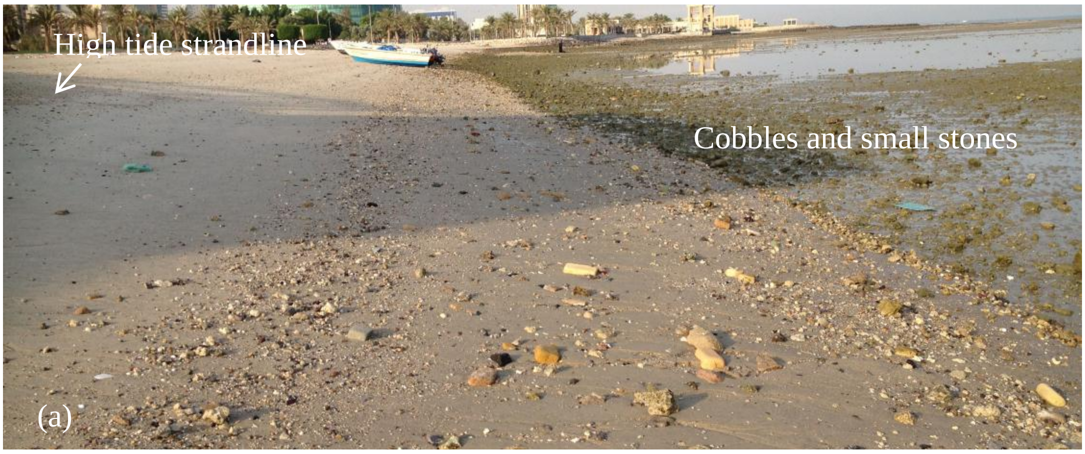
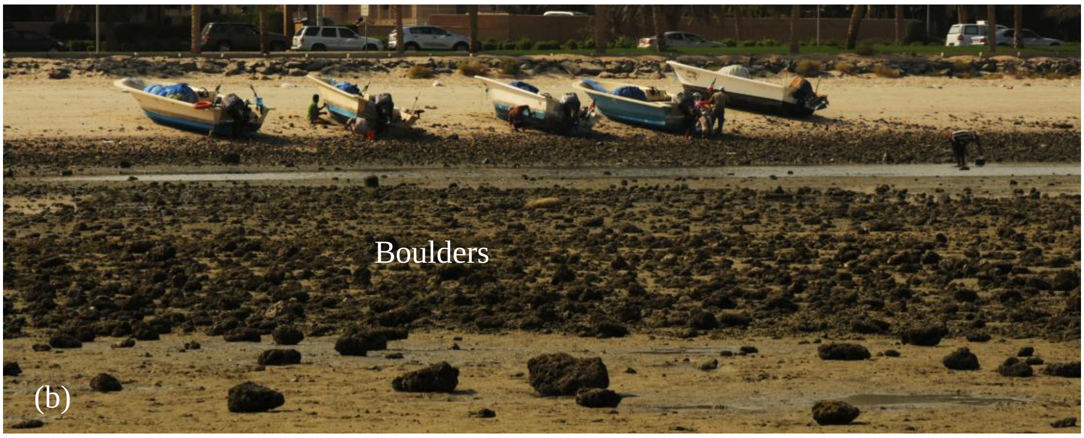
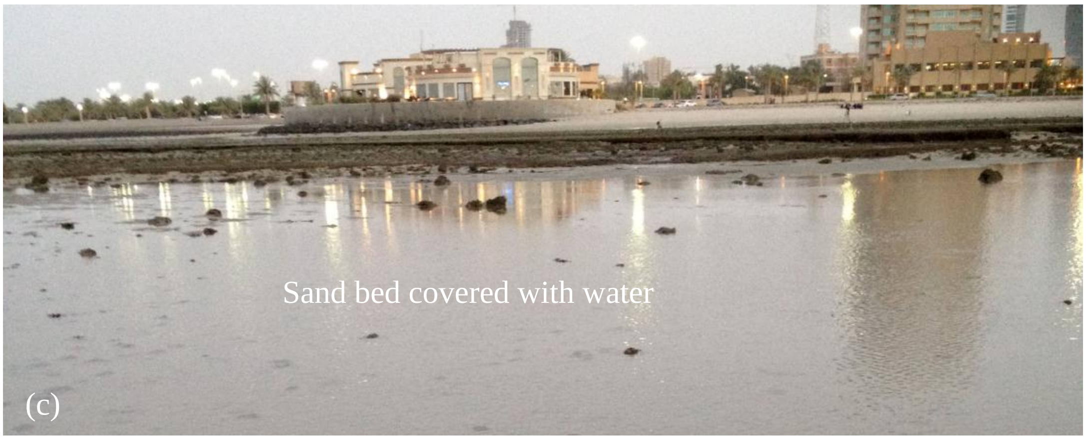


Figure 2.7. Site 1 Ra´s Ajūzah. (a) Aerial view of the general area of Ra´s Ajūzah adjacent to the shore (white line). The view was taken during high tide (www.Bing.com/maps/). The transect is shown, (b) A more detailed view of the shore and transect (white line) and (c) Panoramic photograph of the shore and position of the transect.


High tide strandline
Cobbles and small stones
(a)


Boulders
(b)


Sand bed covered with water
(c)


Flat rocky platforms with boulders and sand patches
(d)

Figure 2.8. Ra´s Ajūzah: the main features of the shore at different tidal heights (a) upper zone to (e) lower zone.

Figure 2.9. Site 2 Ra´s Eqaila. (a) Aerial view of the general area of Ra´s Eqaila adjacent to the shore. The view was taken during high tide (www.Bing.com/maps/). The transect is shown (white line), (b) A more detailed view of the shore and transect (white line) and (c) Panoramic photograph of the shore and position of the transect (white line).


(a)
Boulders and cobbles laying on sand bed
(b)
Intertidal pool
(c)
Bed rock platform
Sand patch
(d)

Figure 2.10. Ra´s Eqaila: the main features of the shore at different tidal heights (a) upper zone to (e) lower zone.

Figure 2.11. Site 3 Ra´s al Qulay´ah. (a) Aerial view of the general area of Ra´s al Qulay´ah adjacent to the shore. The view was taken during high tide (www.Bing.com/maps/). The transect is shown (white line), (b) A more detailed view of the shore showing removed parts of bed rock platform (see figure 2.13) and transect (white line) (c) photograph of the shore and position of the transect.

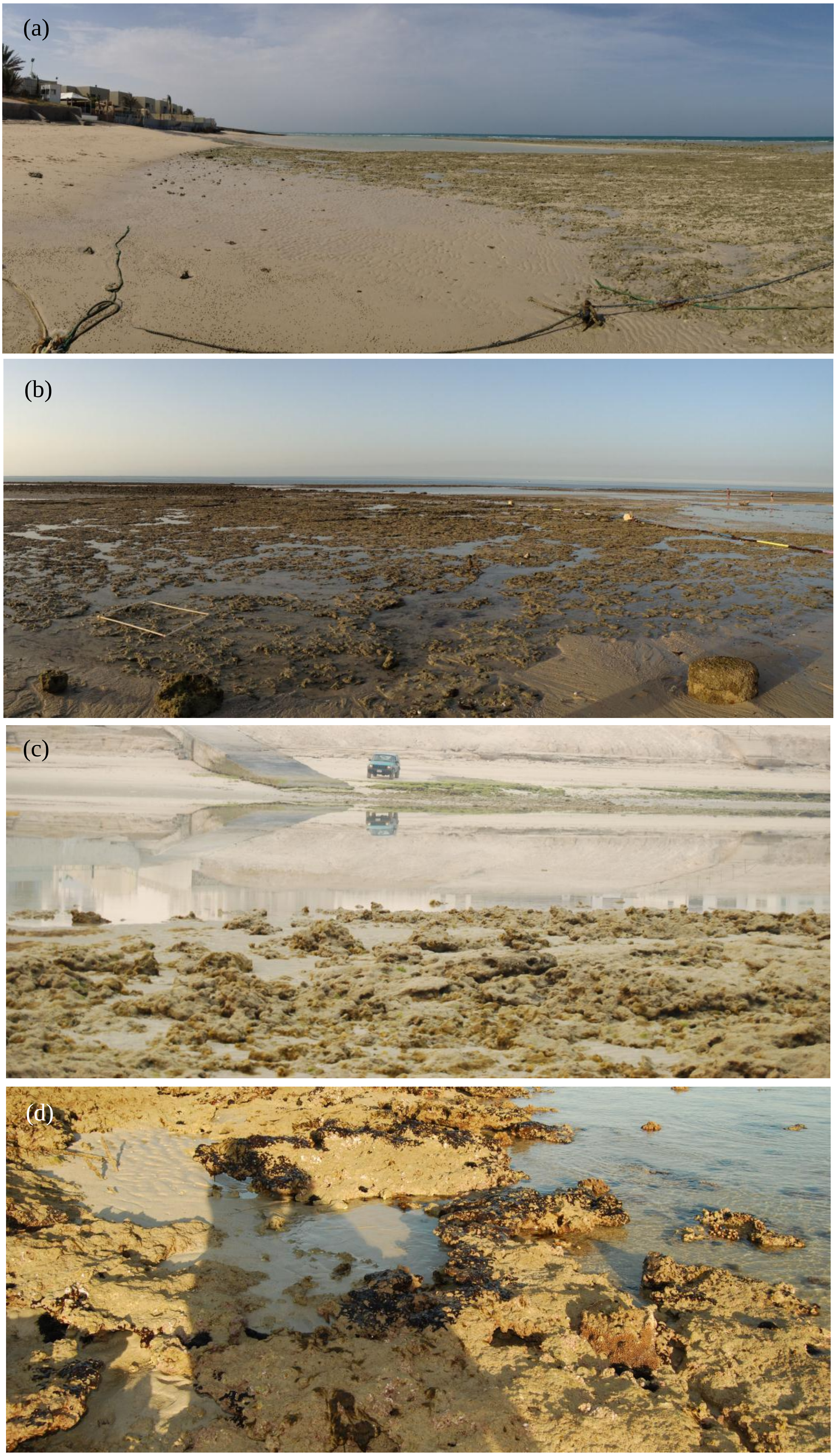

(a)
(b)
(c)
(d)

Figure 2.12. Ra´s al Qulay´ah: the main features of the shore at different tidal heights (a) upper zone to (e) lower zone. (images c, d and e supplied by Zainab Al-Wazzan).

Figure 2.13. Areas of the shore at Ra´s al Qulay´ah have experienced massive destruction and removal of bed rock platforms by the operator of the resort.

with sand substrata and scattered boulders (see figures 2.12 and 2.13). The biological communities of the three shores will be discussed later in chapter 6.

2.3 REFRENCES

Al-Sarawi, M., Gundlach, E. R., & Baca, B. J. (1985). *Kuwait: an atlas of shoreline types and resources*. Kuwait University, Kuwait.

Jones, David A. (1986). Field Guide to the Seashores of Kuwait and the Arabian Gulf. Blandford Press, Dorset.

El-Baz, F & Al-Sarawi, M. (2000). *Atlas of the State of Kuwait from satellite images*. Kuwait Foundation for the advancement of Sciences (KFAS), Kuwait.

Kana, T., Al-Sarawi, M., & Holland, M. (1986). Design and performance of artificial beaches for the Kuwait waterfront project. *Coastal Engineering Proceedings*, 1(20).

Sheppard, C., Price, A., & Roberts, C. (1992). Marine ecology of the Arabian region: patterns and processes in extreme tropical environment. The University Press, Cambridge, UK.

CHAPTER THREE

Distribution, Abundance and Morphology of *Thalessa savignyi* and *Ergalatax junionae* in Kuwait

3 Distribution, Abundance and Morphology of *Thalessa savignyi* and *Ergalatax junionae* in Kuwait

3.1 INTRODUCTION

Intertidal ecologists have long recognized that rocky shores are one of the most difficult habitats for organisms to inhabit. Early authors such as Lewis (1964) and Raffaelli and Hawkins (1996) and later Knox (2000), Murray *et. al.* (2006) and recently Little *et. al.* (2010) have documented a number of physical stressors through which intertidal macro-algae and macrofauna have developed various responses to cope with living under such complex conditions. For instance, Stephenson and Stephenson (1946) and Lewis (1964) recognized that the distribution of many intertidal species was limited to specific intertidal zones. Distinctive vertical zonation patterns of algae and invertebrates along rocky platforms were studied by Stephenson and Stephenson (1949). They observed zonation patterns in different regions around the world. They established the classic concept of three zones on British shores from the upper (1) supralittoral fringe inhabited by *Littorina neritoides,* (2) a mid-littoral balanoid e.g. *Semibalanus balanoides* zone and (3) an infralittoral fringe laminarian zone. Ellis (2003) has used the concept of zonation to monitor biodiversity development over a period of four years along rocky shores on the Pacific Coast of Canada. Guenther and Martone (2014) have shown that organisms have the ability to tolerate various abiotic stressors associated with periodic exposure to air during low tide emersion and high tide immersion in seawater. In their study of two common intertidal algal species, *Calliarthron tuberculosum* and *Corallina vancouveriensis* that occur at different shore levels along rocky shores at Vancouver Island, British Columbia Guenther and Martone (2014) explored the physiological responses of these algae. *Corallina* lives higher on the shore where high light and high air temperatures are experienced and where there is a high desiccation stress. *Calliarthron* were, however, more abundant subtidally under conditions of low light intensity and low seawater temperature. *Corallina* resisted desiccation, high light and high temperature environment, and recovered quickly when immersed again in seawater. This ability was absent in *Calliarthron*.

The thermal tolerance of 22 gastropod prosobranch species collected from the rocky shores of Hong Kong (0.5-3˚C higher) and Tanzania, including two species, *Plananxis scaltus* and *Lunella coronata* that are present on the shores of Kuwait have been investigated (Stirling, 1982). *Plananxis scaltus* and *Lunella coronata* are commonly found intertidally on rocky shores in Kuwait Bay (Al-Yamani *et. al.*, 2012). These two species, according to Jones (1986), occupy different zones on Kuwaits's rocky shores; *P. scaltus* inhabits the supralittoral zone slightly below a zone of small littorinid gastropods (e.g. *Echinolittorina arabica*), whilst *L. coronata* is more common from HWN (mean high water of neap tides) down to MWN (mean high water of neap tides). Jones (1986) agreed with Stirling's (1982) observations of the vertical distribution of both species in relation to their thermal tolerances. From data on the lethal temperature responses for both species collected from Dar AL Salam and Hong Kong, Stirling (1982) concluded that *L. coronata* were less able to tolerate higher air temperatures (43-46 ˚C). The study findings has showed that the relationship between vertical zonation and thermal tolerance were significant.

The dog whelk *Nucella lapillus* is a predatory gastropod found below mean tide level on British rocky shores and feeds on sedentary prey e.g. barnacles and mussels (Crothers, 1985). This snail is commonly found adjacent to its favoured prey and Crothers (1985) showed that the domination of *N. lapillus* depended in part on the distribution of its prey. *Echinolittorina arabica* (El Assal, 1990) (formally known as

Nodilittorina arabica (Williams *et. al.*, 2003)), is a grazing gastropod species that is widely distributed along tropical rocky shores, including Kuwaiti shores (Al-Yamani *et. al.,* 2012). It is usually abundant in the upper eulittoral and supralittoral zones (Williams and Reid, 2004). This intertidal snail inhabits exposed beach rocks along the United Arab Emirate (UAE) coastlines and is usually associated with blue-green algal species e.g. *Chroococcus membraninus* (Jones and George, 2005). Feulner and Hornby (2006) noted that *E. arabica* efficiently grazed micro-algae and cyanobacteria associated with exposed rock surfaces. The tropical species *Certhium scabridum* attains maximum abundances in the upper intertidal zone on rocky shores along the Indian coastline (Trivedi and Vachrajani, 2013) and in the Red Sea it has a preference for living in tidal rock pools where algal production is well developed (Ayal and Safriel, 1982). The species is also present on Kuwait's rocky shores (Jones, 1986; Alyamani *et al.*, 2012).

In a comprehensive study, Chambers and McQuaid (1994) reviewed the development characters of 26 species of intertidal pulmonate limpets, including *Siphonaria spp*. They postulated that zonation appeared to be influenced by the mode of larval development with most limpets that have a direct developing mode of reproduction common on the higher part of the shore whilst limpets that use a planktonic mode of dispersal greater on the middle and lower shores. For example, *Siphonaria kurracheensis* and *Siphonaria siphon,* two limpet species from the Persian Gulf have different developmental modes; *S.kurracheensis* has direct larval development and is found in greater numbers on higher shore levels (see also Black, 1979) whilst *S. siphon* lives between the middle and lower shores and has a planktonic larval stage (Chambers and McQuaid, 1994).

Christofoletti *et. al.* (2010) studied the role of tidal height and wave action (exposure) on the distribution of organisms on rocky shores in sub-tropical regions of the world. They investigated the role of the horizontal gradient of the shore and wave action on the distribution, composition and abundance of organisms on different shorelines. They demonstrated that the sublittoral fringe of sheltered subtropical areas is dominated by macroalgae, the low mid-littoral shores dominated by bare rock and barnacles, whilst exposed shores are dominated by filter-feeders. The role and influence of tidal range and wave exposure has been modelled by Bird *et. al.* (2013) and they have shown that the shoreline of the western Persian Gulf, and particularly the shoreline of Kuwait, is more affected by tidal range rather than exposure to wave action (figure 3.1). Little is known about the factors affecting the distribution of gastropods on the shores of the Arabian Gulf and although Jones (1986) and Jones and George (2005) has given a general review of the shores and species that inhabit them there is a paucity of data. This is the first study to investigate the distribution of two gastropod species on the shores of Kuwait along a latitudinal gradient from the north to the south of Kuwait.

In Chapter two I have listed and discussed the important environmental factors and potential stressors that intertidal organisms might experience on the shore of Kuwait e.g. tides, climate, shore topography, substratum etc. I have also highlighted the obvious heterogeneity of the physical structure of the rocky shores at each of my three study sites. In chapter 3 I investigate whether variations in the abiotic factors such as exposure to air, shore topography and substratum on the three shores affect the population structure of two common gastropods *Ergalatax junionae* and *Thalessa savignyi* inhabiting them? This will allow an understanding of how abiotic factors influence the zonal distribution of both species. I also investigate the distribution, abundance and morphological differences between the two gastropod species both latitudinally, seasonally and intertidally down the shore in relation to investigate how the various abiotic and biotic factors influence shell growth of both species.

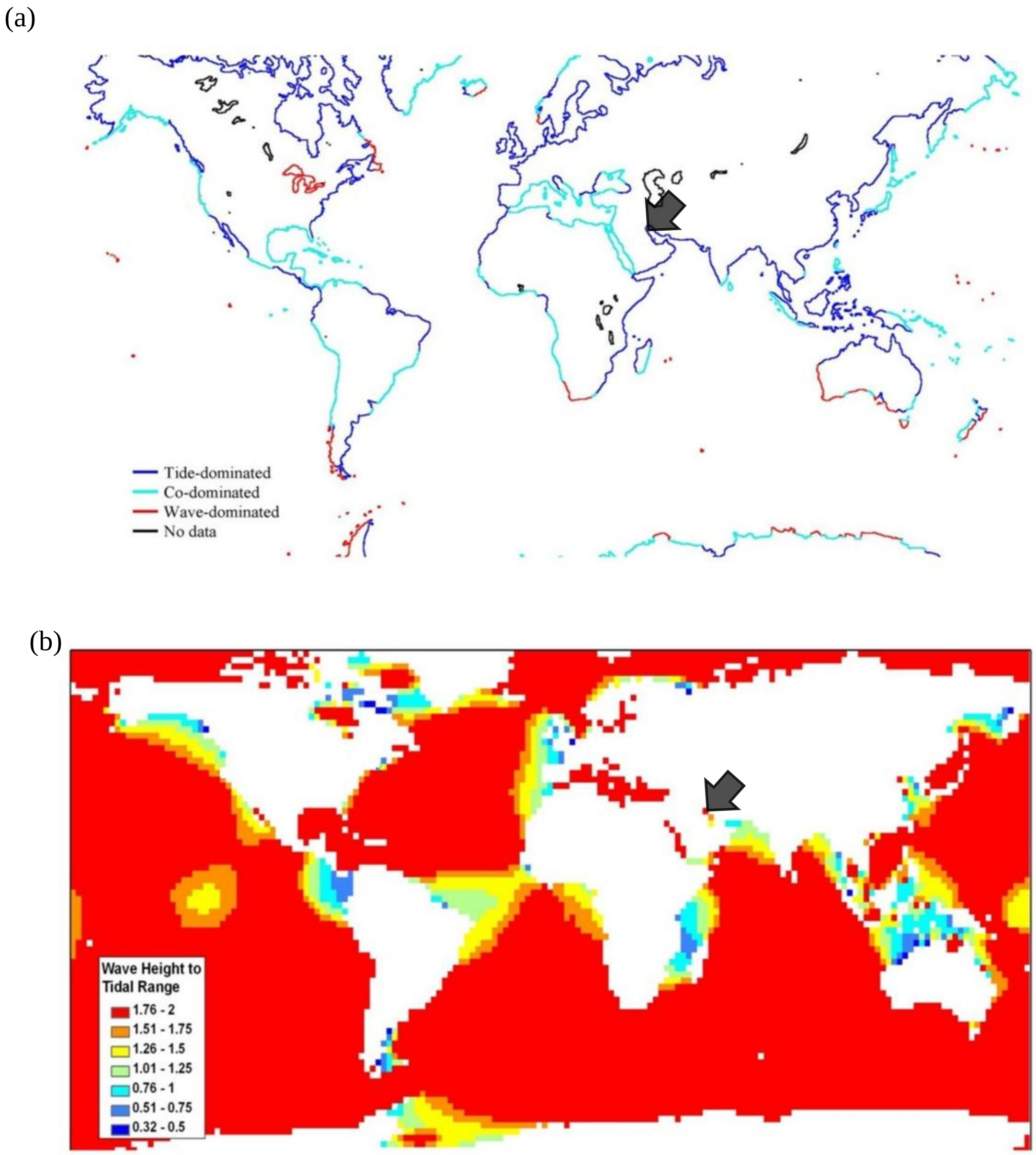


Figure 3.1. Global shoreline classification according to relative wave and tidal ranges. Arrow shows the study region of Kuwait. (a) Shorelines classified as tide-dominated (dark blue lines) (where mean diurnal tidal range is greater than mean wave height), co-dominated (cyan lines) (mean diurnal tidal range about equal to mean wave height), and wave-dominated (dark red lines) (mean wave height is greater than the mean diurnal tidal range), and no data (black lines). (b) Ocean area colour-coded by the ratio of wave height to tidal range. (After Bird *et. al.* 2013).

3.2 MATERIAL AND METHODS

3.2.1 Sampling the shore

The Present investigation was carried out between May 2012 and January 2013 at three locations on the coast of Kuwait, Ra´s Ajūzah (29° 23'N, 47° 59'E), Ra´s Eqaila (29° 10' N, 48° 7' E) and Ra´s al Qulay´ah (28° 52' N, 48° 17' E) (see Chapter 2 for details of each location). All surveys were conducted during low spring tides (water height below 0.3m above chart datum) and were studied and samples collected every three months to ensure that the two gastropod species were collected during the four seasons of the year. The seasons in Kuwait are defined as spring (February 13 - May 08); summer (June 01 - October 08); autumn (October 09 - November 27) and winter (November 28 - February 12) to cover the various periods of warm and cooler seawater temperatures. Samples of the two gastropod species were obtained at ~10 intervals (stations) along a transect (length ~160-400m) depending on the location and laid from above high water of neap tides (HWNT) to low water of spring tides (LWST).

The distance between the stations along each transect was initially pre-determined before sampling by subdividing the total distance of the transect by ten i.e. the number of stations that could be reasonably sampled during the period of spring low tides. However additional stations were sampled on the low shore later on when it became apparent during exceptionally low tides (May and January) that the tide had ebbed out further than expected beyond the lowest station (station 10). Thus at Ra´s Ajūzah three extra stations (11, 12, & 13) were sampled and at Ra´s Eqaila and Ra´s al Qulay´ah one extra station (11) was added at the low shore. The intertidal transects were surveyed perpendicular to the water’s edge. The starting point (station 1) was located just above the position of the highest marine organisms encountered, and the last point (station 11, 12 or 13) at the water’s edge.

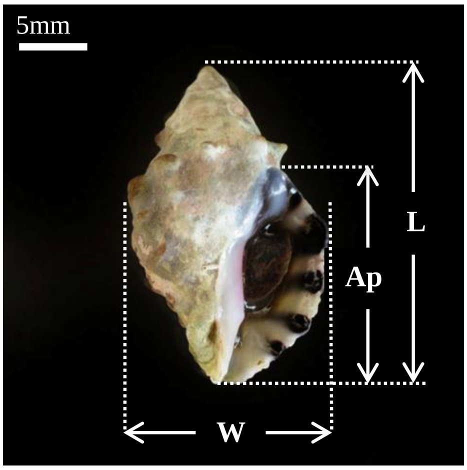


Figure 3.2. Measured dimensions of the shell that were used to describe the variation in morphology of *Ergalatax junionae* and *Thalessa savignyi.* L: shell length, W: shell width, Ap: Aperture length. Specimen shown is *E. junionae.*

Three 25 cm^2 quadrats were placed randomly at each station. The number of *E. junionae* and *T. savignyi* present in each quadrat was counted and removed and placed in labelled plastic bags for further investigation. Particular attention was paid to exploring under small rocks and crevices in the quadrat area to ensure that all individuals were removed. In reality it was occasionally impossible to remove the smallest *E. junionae* from a crevice, its normal habitat, because of access. However when they were seen this animal was recorded as being present and included in counting but not measured. During the quadrat survey it was soon obvious that the full picture of the distribution of the species could not be determined, so an additional timed search of 10 minutes duration was also undertaken within approximately a 5m radius of where the quadrats were sampled.

3.2.2 Morphological analysis

Due to time constraints, all the collected gastropods were placed in labelled plastic bags and returned to the laboratory where various biometric measurements were undertaken before the samples were frozen for later laboratory study and analysis. All measurements were taken to the nearest 0.1mm using vernier calipers. Measurements of the following shell dimensions were made: (1) the maximum distance from the apex to the outer shell (shell length (L)), (2) shell width (W), which is the greatest dimension at right angles to the shell length and (3) the aperture length (A) the maximum distance from the upper margin of the shell opening to the lower margin (see figure 3.2).

Possible differences in shell shape of the populations of *T. savignyi* and *E. junionae* were investigated to identify whether there was any morphological variation within and between each species. The morphological measurements (L, W & A) of between 40 & 76 individuals of each species from the different populations and covering the range from the smallest to the largest individuals (*T. savignyi* (11-45mm) and *E. junionae* (4-34mm) were made. Shell length, shell width and aperture length data were log transformed (logarithm base 10) using the statistical software package Minitab 16. The relationships between the various dimensions (dependent variables W & A) were linearly regressed against the independent variable, shell length (L) following a check of normality of data. Scatter plots were generated for the different dependent and independent dimensions for the shells from all locations. These data were then examined for evidence of differential growth by testing each pair of size variables x and y for their fit to the allomteric equation ($y = ax^b$) which, when logarithmically transformed, becomes ($\log_{10} y = \log_{10} a + \log_{10} x$) (see Seed & Richardson 1990; Richardson et al., 1995). Substitution of a value of slope (b) and variance (standard error of slope b) in the equation below where β equals 1 allowed a statistical t value to be calculated to indicate significant departure of the slope b from one i.e. isometry.

$$t\ (n\text{-}1\ df) = (b - \beta)/\text{s.e. of } b$$

Where: b=the slope of the regression line, s.e. of b is the standarad error of b, $\beta = 1$ and t is the student t test value for n-1 degrees of freedom (Richardson *et. al.*, 1995)

3.2.3 Shore profiling

The shore profile along one transect at each site was determined during October and November 2012 using a surveyor’s sight (Leica NA724), mounted on a tripod and a surveyors staff. Fore and back sight measurements were taken at various points (approximately every 20m to 30m depending on the site and the shore topography) along the transect and the fall and rise of the shore level calculated, from a position on the upper shore at the highest level where any organisms were observed to the lowest accessible point on the low shore using the method of Whyte & Paul (1985).

Measurements were taken every twenty meters at Ra´s Eqaila and Ra´s al Qulay´ah, and every thirty meters at Ra´s Ajūzah. On each shore the height above chart datum of the highest station along the transect was determined using the “Google Earth plugin”. The latitude and longitude of this station was obtained using a hand held GPS (GARMIN eTrex H to an accuracy of less than 3 m) and the co-ordinates entered into the “Google Earth Plugin” to determine the elevation of the station along the transect. Each transect station height was then corrected to a height above chart datum. In practice because of the wide error of the GPS (<3m) the position of the lowest station on each transect did not match exactly the position for the predicted height of low water shown for the day of measurement in the published tide tables. The likely reason for the difference is that the published data are not corrected because there are changes in barometric pressure each day; high pressures and the tide will ebb further out than predicted – low pressure will mean that low tidal height is higher than predicted. The times of low tide and high water and the height above chart datum (reference mark) are summarised in (table 3.1).

Table 3.1. Time of low tide and height above chart datum for shore profile field surveys.

Location	Date surveyed	Height above Chart Datum (m)		Time	
		high tide	low tide	high tide	low tide
Ra´s Ajūzah	23.10.2013	3.6m	0.4m	01:10	8:40
Ra´s Eqaila	25.10.2013	2.7m	0.6m	00:10	7:30
Ra’s al Qulay’ah	22.11.2013	2.2m	0.1m	22:30	6:00

3.2.4 Determination of tidal range and the timing of immersion and emersion at stations along the transects

Following on from the determination of the tidal height (above chart datum) of each station along each of the three transects, the length of time that animals at these stations

Table 3.2. Seasonal variation in the mean densities (no’s.m^{-2}) (± SE) of *Thalessa savignyi* and *Ergalatax junionae* on the three rocky shores. Shore zones are defined as upper zone (>50% time period exposed to air), mid zone (40-50% time period exposed to air), lower zone (< 20% of time exposed to air). Seasons are defined as spring (February 13 - May 08); summer (June 01 - October 08); autumn (October 09 - November 27) and winter (November 28 - February 12).

		Thalessa savignyi				*Ergalatax junionae*			
location	shore zone	spring	summer	autumn	winter	spring	summer	autumn	winter
Ra´s Ajūzah	upper	Absent				0	0	0	0
	mid					0.8 ± 0.6	5.3 ± 3.1	16.0 ± 9.96	0.0 ± 0.0
	lower					31.2 ± 6.0	47.0 ± 16.7	23.8 ± 5.25	41.3 ± 8.8
Ra´s Eqaila	upper	0	ND	0	0	0	ND	0	0
	mid	0	ND	1.3 ± 1.3	1.3 ± 1.3	5.3 ± 3.5	ND	22.7 ± 11.4	8.0 ± 0
	lower	1.8 ± 0.8	ND	2.2 ± 0.9	5.3 ± 1.8	35.6 ± 12.4	ND	33.3 ± 10.0	46.9 ± 11.9
Ra’s al Qulay’ah	upper	1.3 ± 1.3	2.7 ± 2.7	0	0	0	0	0	0
	mid	1.3 ± 1.3	4.9 ± 2.1	2.7 ± 0.9	3.1 ± 1.5	0	4.4 ± 3.0	3.1 ± 1.7	0
	lower	2.5 ± 0.8	1.0 ± 0.5	2.2 ± 0.7	2.5 ± 1.1	7.3 ± 2.5	2.0 ± 0.9	2.7 ± 0.9	4.0 ± 1.4

ND: no data collected

would be emersed/immersed was estimated. This was undertaken by estimating the time that each station was emersed during spring and neap tide low water using the versatile Smartphone application (App) “Tides Planner” ©Tucabo Ltd (see Chapter 2 figure 2.1). Using this “App” allowed access to plotted tidal data for various prediction ports along the Kuwaiti coastline. The nearest port where the tidal heights were available for each of the transects in this study was Ash Shuwaykh (29° 21'N, 47° 55'E) (data provided by the Proudman Oceanographic Laboratory (POL)) for site Ra´s Ajūzah, Al Fintas (29° 10'N, 48° 8'E) (tidal data from the UK Hydrographic Office (UKHO)) for Ra´s Eqaila whilst the port for the predicted tidal data at site Ra’s al Qulay’ah was based at this site (data provided by the National Oceanic and Atmospheric Administration (NOAA)). Inputting the tidal height of each station into the “Apps” predicted a tidal curve for each site, the time when the station was emersed (on the ebb tide) or immersed (on the flood tide) could then be estimated from the tidal curve to calculate the amount of time that organisms at each station were emersed.

3.1 RESULTS

3.1.1 Geographical distribution of *Thalessa savignyi* and *Ergalatax junionae*

Thalessa savignyi was completely absent throughout the year at the northern site, Ra´s Ajūzah but occurred at low densities at Ra´s Eqaila and in the south at Ra’s al Qualay’ah where it was present in the upper, mid and lower shores at the two locations at a range of average densities during the four seasons of the year of between 1.3 to 2.7.m^{-2}, 1.3 to 4.9.m^{-2} and 1.0 to 2.5.m^{-2} respectively (table 3.2). By comparison *Ergalatax junionae* was far more abundant attaining maximum densities on the low shore at Ra´s Ajūzah and Ra´s Eqaila of ~40.m^{-2} (table 3.2). Despite the collection of density data of the two species using quadrats, the method gave only a brief overview of abundances on the shore. The preferred method was to use timed searches as it allowed an investigation of the distribution of the two species under rocks and in crevices and covered a wide area of the shore at each station.

From data generated from the timed searches it was apparent that *Thalessa savignyi* was never found at Ra´s Ajūzah but occurred in numbers at Ra´s Eqaila and the southernmost site Ra's al Qulay'ah. Between May and July 2012 *T. savignyi* was prevalent between stations 5 and 10, particularly at Ra´s Eqaila where densities of up to 300ind.hr^{-1} were recorded. Abundances were generally similar at Ra's al Qulay'ah, although at this location *T. savignyi* extended further up the shore between stations 2 & 6. The tidal range at Ra´s Ajūzah is ~ 2.85m between mean low, low water (M.L.L.W.) to mean high, high water (M.H.H.W.) during spring tides (figure 3.3 a). There is little seasonal variation in the time emersed at stations 5-10, whilst 11-13 were only briefly emersed during low tide. On the upper shore (stations 1-4) there was ~ 15 % difference in the time emersed between seasons (figure 3.3 b).

At Ra´s Ajūzah, *E. junionae* was widely dispersed across the shore throughout the year from the upper shore stations (60% emersion) to the lower shore stations (10% emersion). Maximum numbers (up to 1200ind.hr^{-1}) were observed in crevices between stations 6 and 13 in May and July 2012 at the hottest time of the year (see chapter 2). In this area, rock boulders and crevices dominated the shore and this is where *E. junionae* was usually found (see chapter 2). *Ergalatax junionae* was particularly abundant at all of the stations in May and July 2012 with the highest densities (1,250ind.hr^{-1}) at station 7 in July. During October 2012 and January 2013 the counts of individuals dramatically declined to a maximum ~250 ind.hr^{-1} at station 4 in October 2012. *E. junionae* was absent between station 1 and 3 and was not as abundant on the shore as it was in May and July (Figure 3.3 c). Table 3.2 shows that *E. junionae* occur in higher densities below the middle of the shore during most of the year. However, they were more abundant on the lower shore (41.3 ± 8.8 ind.m^{-2} (± SE)) during the winter season. In October 2012 and January 2013 lower numbers of individuals, between 50-300 ind.hr-¹, were recorded with *E. junionae* displaying an apparent seasonal movement towards the upper part of the shore to stations 3, 4 & 5. During this period of the year the lowest air and seawater temperature ranges occurred (see chapter 2). Although the period of time that the *E. junionae* were emersed varied seasonally, the differences were however probably too small to influence the population density and distribution.

This trend in distribution was also apparent at Ra´s Eqaila with *E. junionae* widely distributed across the shore, particularly between July 2012 and January 2013. In May however, *E. junionae* had a low abundance with individuals mainly confined to the crevices of rocks at the lower shore stations (9-10). Overall the species was much less abundant than at Ra´s Ajūzah (peak abundances <400 ind.hr^{-1}). By contrast the abundance of. *E. junionae* at the southernmost location at Ra's al Qulay'ah was low (usually <100ind.hr^{-1}), although a peak in abundance (~400 ind.hr^{-1}) occurred on one occasion at station 5 in July 2012. No clear pattern of distribution could be seen, although abundances were higher in the upper shore stations (1-5) in May and July 2012 compared with the other seasons of the year. Ra´s Eqaila has a lower tidal range (~2m on spring tides) than Ra's Ajūzah, whilst the lowest tidal range observed at Ra's al Qulay'ah was ~ 1.6m. The upper shore at Ra's Eqaila is characterised by a large pool at station 2 during high water, although it drains quickly during the ebbing tide (25% of the time emersed) and few *E. junionae* were found here suggesting that the conditions might be too harsh at this station (figure 3.4). At Ra's al Qulay'ah the lowest densities of *E. junionae* were observed compared with the other two sites and they did not exceed 7.3 ± 2.5 ind.m^{-2} (± SE). *Thalessa savignyi* were completely absent from Ra's Ajūzah whereas at Ra´s Eqaila, they were

Figure 3.3. *Ergalatax junionae* distribution along the transect at Ra´s Ajūzah. (a) Shore profile and distribution of sampling stations. Black circles indicate the locations where levelling measurements were taken. Empty squares indicate the location of sampling stations. Mean low water (M.L.W), which occurred at 0.05 metres above Chart Datum, is also shown, as is Mean high water (M.H.W.), which occurred at 2.94 metres above Chart Datum. Dashed lines indicate the boundaries between different zones. The position of station 13 is not shown on the shore profile as it was covered when the shore was initially surveyed. (b) Estimated proportion of time emersed at each station during the four seasons, bars left to right: May 2012, July 2012, October 2012 and January 2013 and (c) abundance (ind.hr^{-1}) collected at stations during May, July and August 2012 and January 2013. No samples were collected at stations 12 and 13 in October 2012 as these stations were submerged.

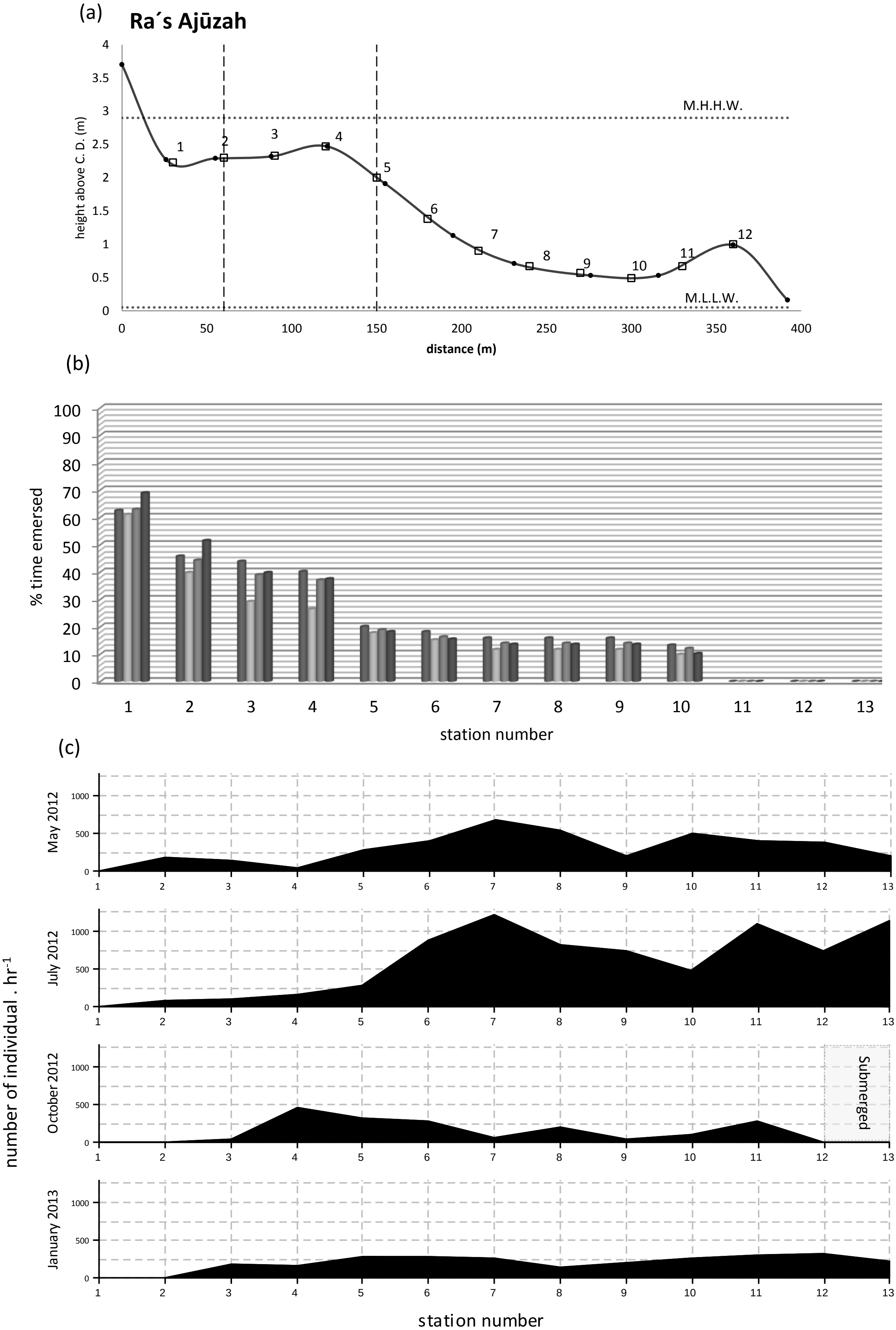
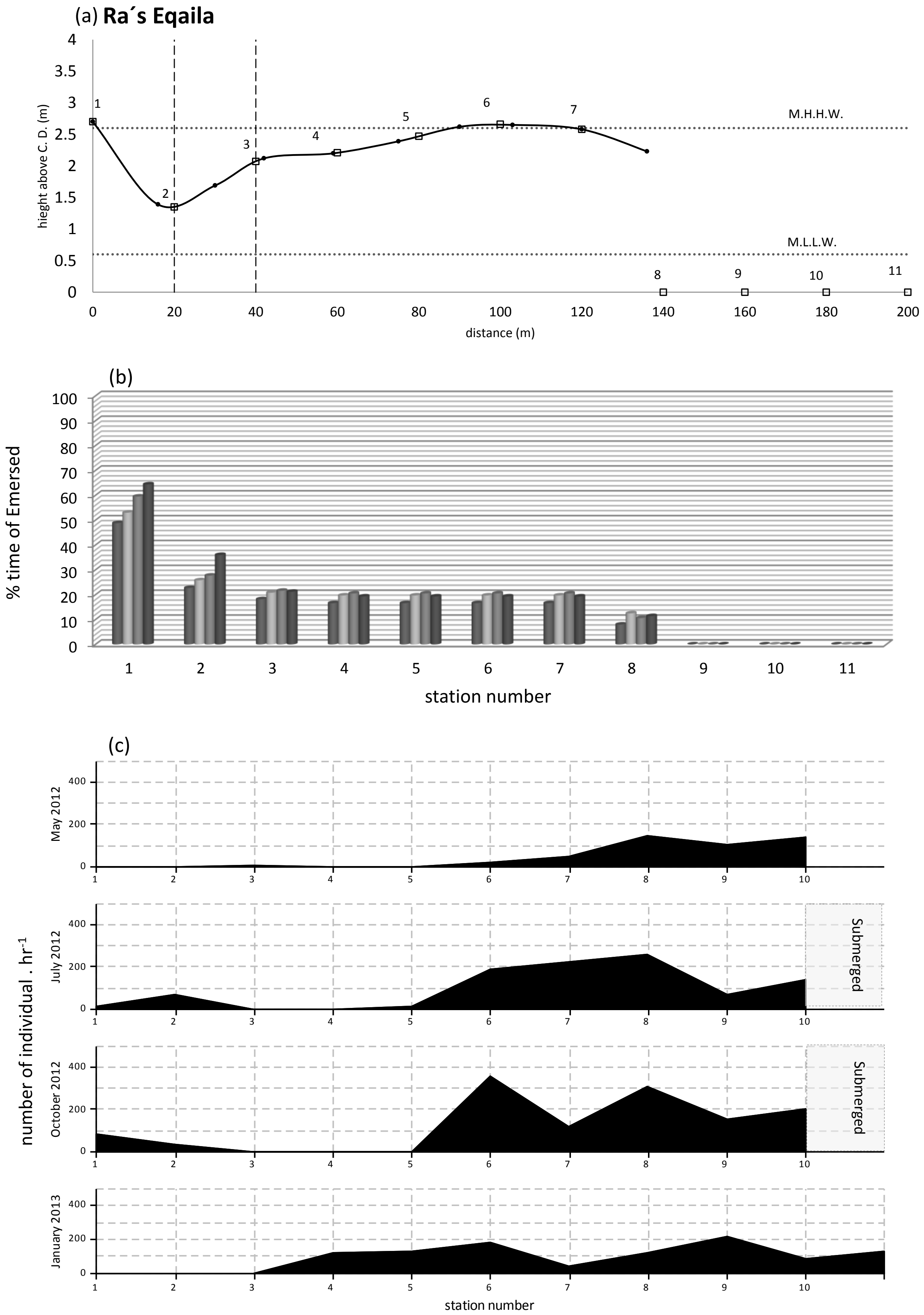
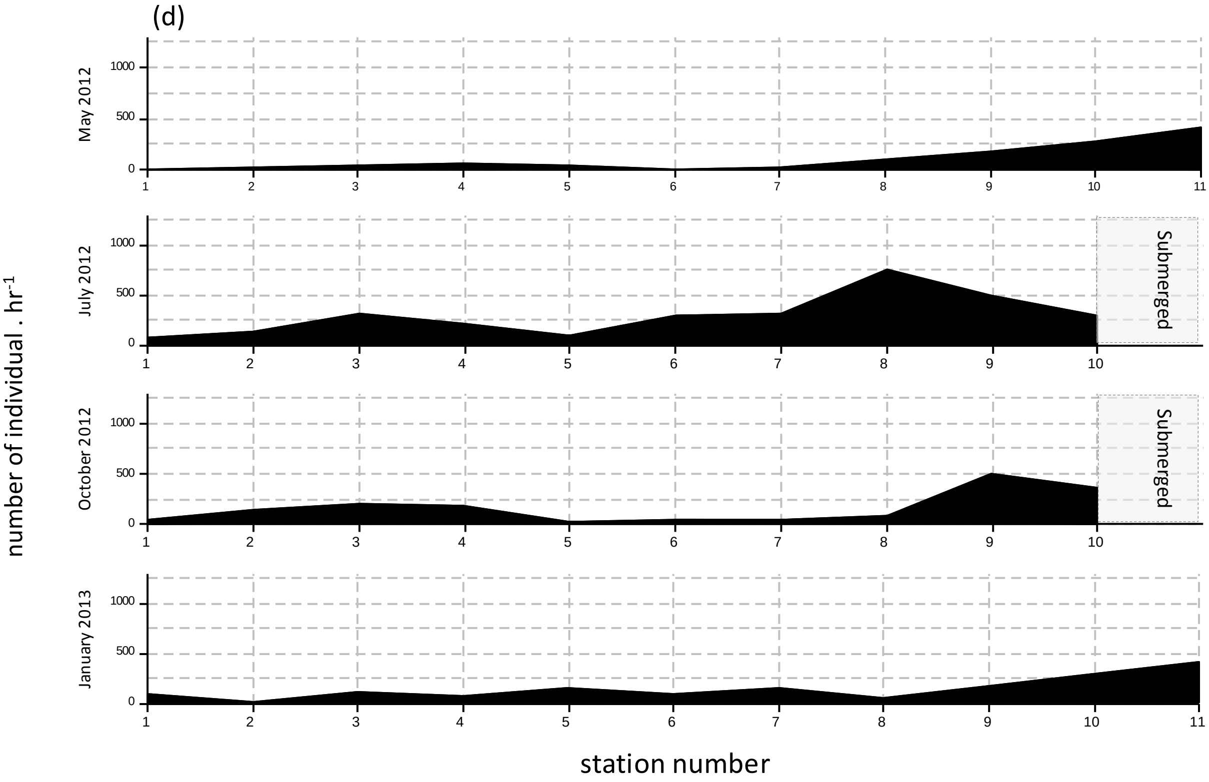

(a)
Ra´s Ajūzah
height above C. D. (m)
4
3.5
3
2.5
2
1.5
1
0.5
0
M.H.H.W.
M.L.L.W.
1
2
3
4
5
6
7
8
9
10
11
12
0
50
100
150
200
250
300
350
400
distance (m)
(b)
% time emersed
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
station number
(c)
number of individual . hr-1
May 2012
July 2012
October 2012
January 2013
1000
500
0
Submerged
1
2
3
4
5
6
7
8
9
10
11
12
13
station number

Figure 3.4. *Thalessa savignyi* and *Ergalatax junionae* distribution along the transect at Ra´s Eqaila. (a) Shore profile and distribution of sampling stations. Black circles indicate the locations where levelling measurements were taken. Empty squares indicate the location of sampling stations. Mean low water (M.L.W), which occurred at 0.6 metres above Chart Datum, is also shown, as is Mean high water (M.H.W.), which occurred at 2.6 metres above Chart Datum. Dashed lines indicate the boundaries between different zones. The position of stations 8-11 is not shown on the shore profile as it was covered when the shore was initially surveyed. (b) Estimated proportion of time emersed at each station during the four seasons, bars left to right: May 2012, July 2012, October 2012 and January 2013 and (c & d) abundance (ind.hr^{-1}) of *T. savignyi* and *E. junionae* respectively collected at stations during May, July and August 2012 and January 2013. No samples were collected at station 11 in July and October 2012 as these stations were submerged.


(a) Ra´s Eqaila
hieght above C. D. (m)
0
0.5
1
1.5
2
2.5
3
3.5
4
distance (m)
0
20
40
60
80
100
120
140
160
180
200
M.H.H.W.
M.L.L.W.
1
2
3
4
5
6
7
8
9
10
11
(b)
% time of Emersed
0
10
20
30
40
50
60
70
80
90
100
station number
1
2
3
4
5
6
7
8
9
10
11
(c)
number of individual . hr-1
May 2012
July 2012
October 2012
January 2013
0
200
400
Submerged
Submerged
station number
1
2
3
4
5
6
7
8
9
10


(d)
number of individual . hr^{-1}
May 2012
July 2012
October 2012
January 2013
0
500
1000
1
2
3
4
5
6
7
8
9
10
11
Submerged
station number

mainly distributed (~ 200-400 ind. hr^{-1}) on flat rock platforms and rocks below station 5 and were present in much lower densities than *E. junionae* attaining densities up to 750 ind.hr^{-1} and residing in the many crevices amongst the rocks. This contrasted with the distribution of *T. savignyi* at Ra's al Qulay'ah where individuals were distributed across the shore between stations 1 and 10. *Ergalatax junionae* were sparsely distributed across the shore although were present in greater numbers on the high shore during the spring (May) and summer (July) than in October and January (figure 3.5).

3.1.2 Analysis of shell morphology

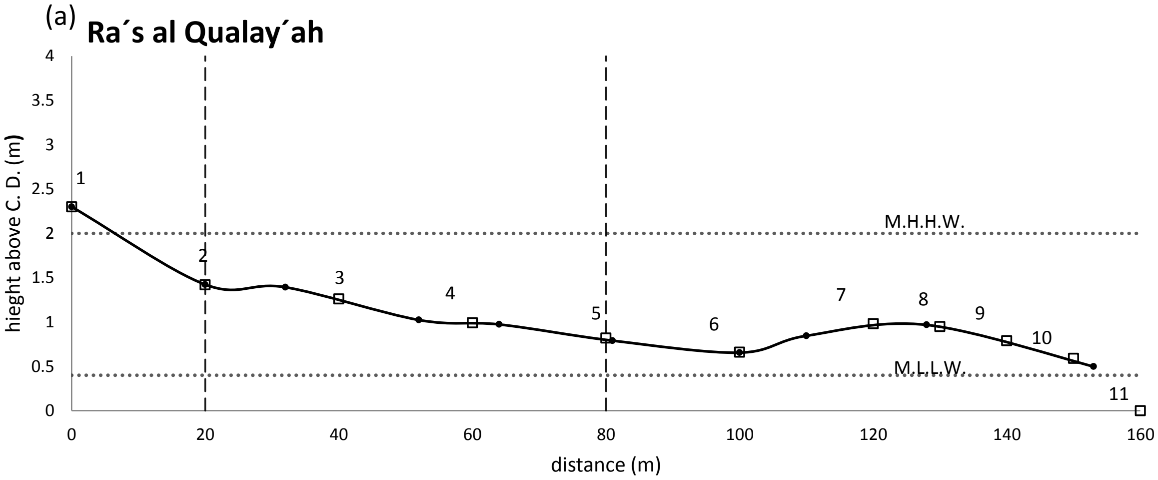
Shell width and shell length and aperture length and shell length are linearly related for *T. savingyi* and *E. junionae* and are shown in figure 3.6. Analyses of allometric growth and the departure of the slope b of the regression line from isometry i.e. a value of 1 are shown in (table 3.3). For *E. junionae* all the relationships between W, Ap and L were isometric except for the shells from Ra´s Eqaila where there was a negatively allometric relationship between Shell width and shell length (table 3.3). Similarly the relationships between these dimensions in shells of *T. savingyi* from Ra´s Eqaila were isometric but in those from Ra's al Qulay'ah the relationships were negatively allometric (table 3.3).

3.2 DISCUSSION

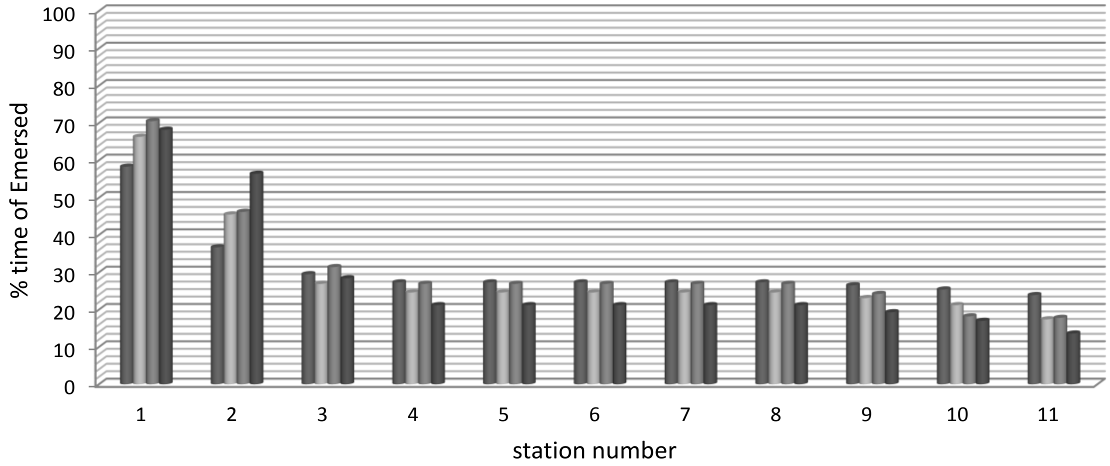
This investigation has shown that *Thalessa savignyi* was absent at Ra's Ajūzah in the north of Kuwait, but increased in abundance towards the south of Kuwait. By contrast the smaller gastropod *Ergalatax junionae* was present at all of the three studied shores but decreased in numbers towards the southernmost site, Ra's al Qulay'ah. Al Yamani *et. al.* (2012), in their general study of the occurrence of subtidal and intertidal macro benthic organisms along the coastline of Kuwait did not record the presence of

Figure 3.5. *Thalessa savignyi* and *Ergalatax junionae* distribution along the transect at Ra's al Qulay'ah. (a) Shore profile and distribution of sampling stations. Black circles indicate the locations where levelling measurements were taken. Empty squares indicate the location of sampling stations. Mean low water (M.L.W), which occurred at 0.4 metres above Chart Datum, is also shown, as is Mean high water (M.H.W.), which occurred at 2.0 metres above Chart Datum. Dashed lines indicate the boundaries between different zones. The position of station 11 is not shown on the shore profile as it was covered when the shore was initially surveyed. (b) Estimated proportion of time emersed at each station during the four seasons, bars left to right: May 2012, July 2012, October 2012 and January 2013 and (c & d) abundance (ind.hr^{-1}) of *T. savignyi* and *E. junionae* respectively collected at stations during May, July and August 2012 and January 2013. No samples were collected at stations 11 in July and October 2012 as these stations were submerged.

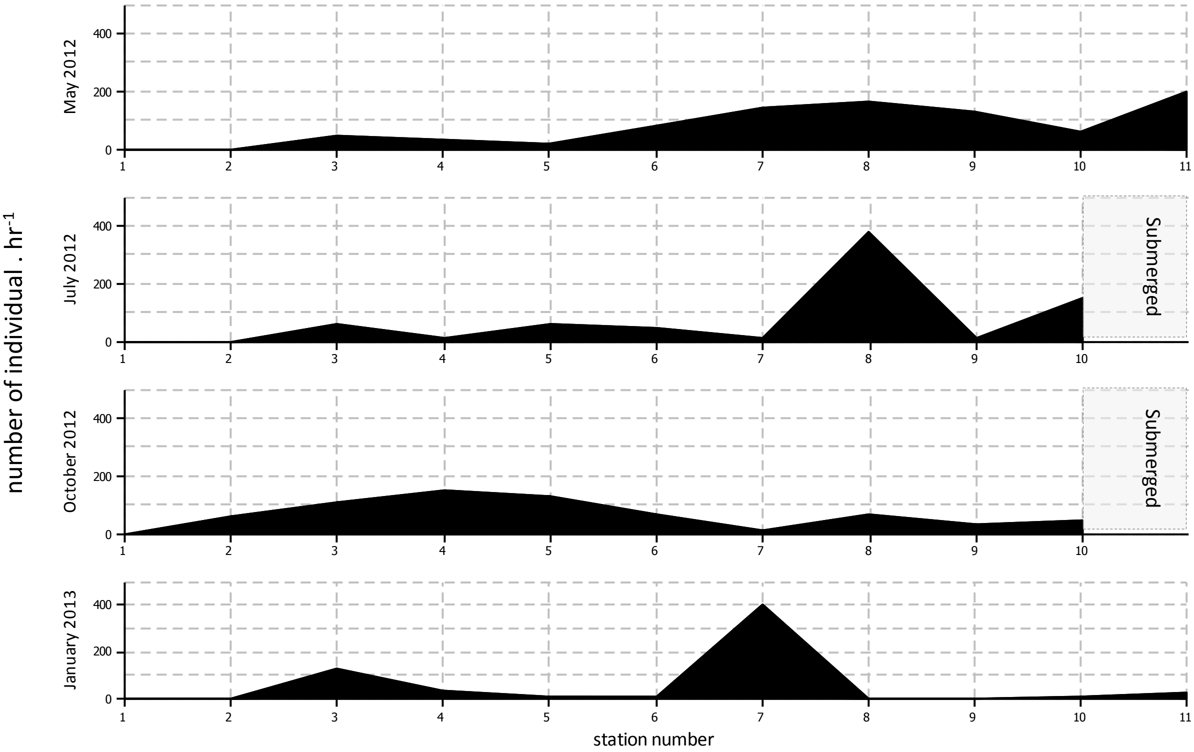
(a)

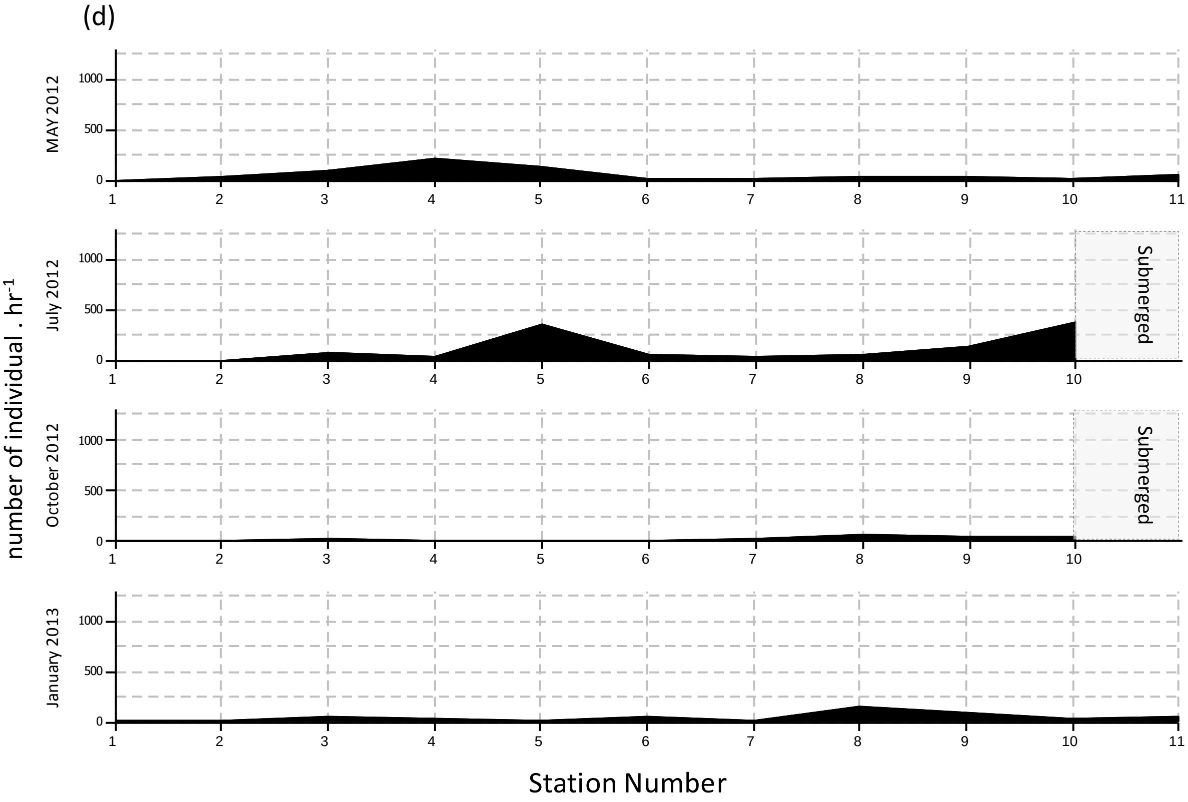

Ra´s al Qualay´ah
hieght above C. D. (m)
0
0.5
1
1.5
2
2.5
3
3.5
4
M.H.H.W.
M.L.L.W.
1
2
3
4
5
6
7
8
9
10
11
0
20
40
60
80
100
120
140
160
distance (m)

(b)


% time of Emersed
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
10
11
station number

(c)


number of individual . hr⁻¹
May 2012
July 2012
October 2012
January 2013
0
200
400
Submerged
Submerged
1
2
3
4
5
6
7
8
9
10
11
station number


(d)
MAY 2012
July 2012
October 2012
January 2013
number of individual . hr-1
0
500
1000
1
2
3
4
5
6
7
8
9
10
11
Submerged
Station Number

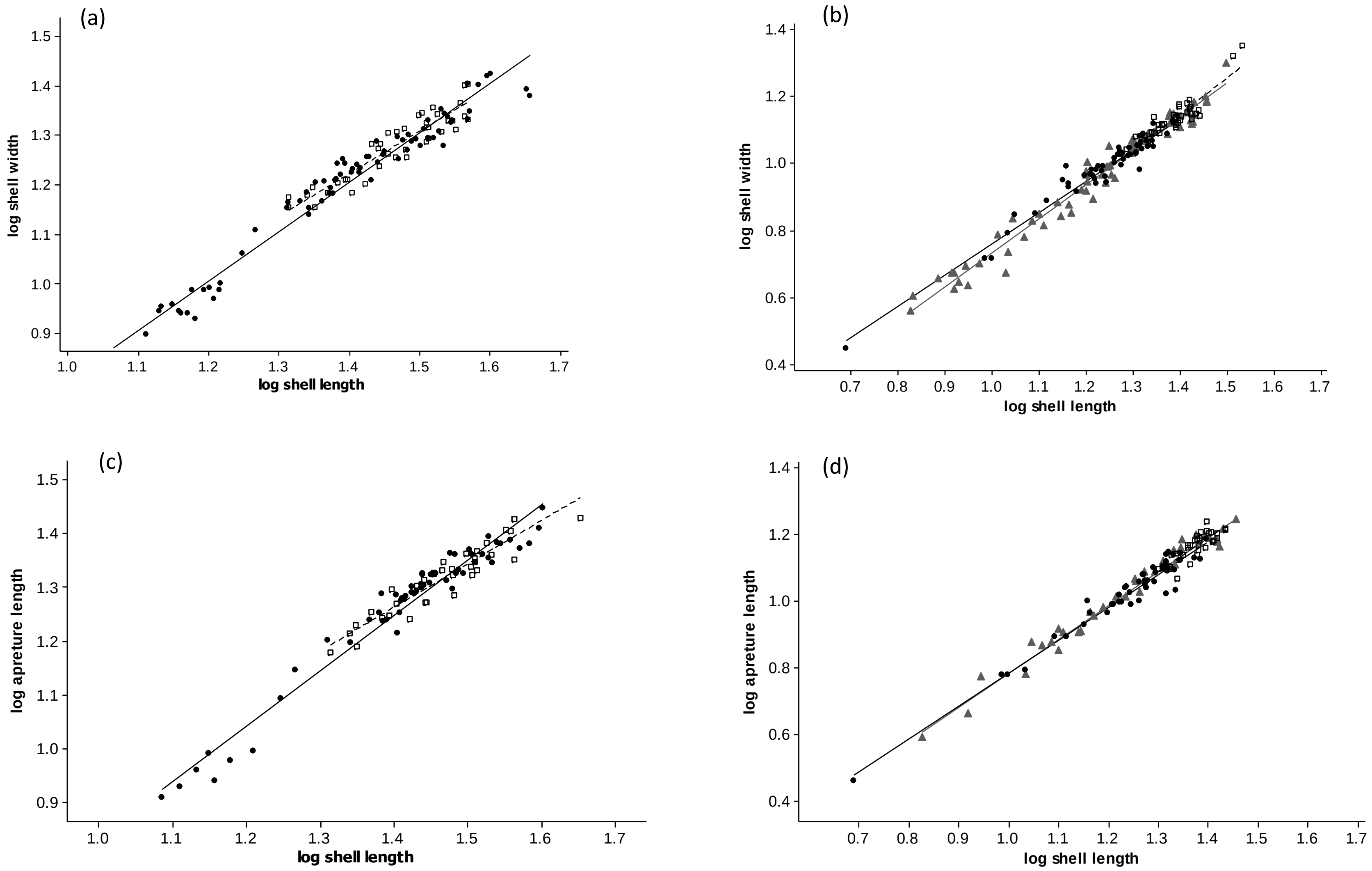


Figure 3.6. (a,b) $\log_{10}$ shell width/length and (c,d) $\log_{10}$ aperture length/shell length regression of (a & c) *Thalessa savignyi* and (b & d) *Ergalatax junionae* collections from three rocky shores (▲) Ra´s Ajūzah (●) Ra´s Eqaila and (□) Ra's al Qulay'ah.

Table 3.3. Regression constants for various combinations of size parameters in *Thalessa savignyi* and *Ergalatax junionae* from the three studied locations.

Site	Dependent variable (log$_{10}$)	Independent variable (log$_{10}$)	*Thalessa savignyi*						*Ergalatax junionae*					
			a	b	r^2	t	Sig.	A.R.	a	b	r^2	t	Sig.	A.R.
Ra´s Ajūzah	Shell Width	Shell length	No data available						-0.277±0.03	1.009±0.021	0.969	0.424	NS	Isometric
	Aperture length	Shell length							-0.233±0.033	1.017±0.027	0.976	-0.631	NS	Isometric
Ra´s Eqaila	Shell width	Shell length	-0.193±0.031	0.998 ± 0.022	0.963	0.069	NS	Isometric	-0.171±0.037	0.932±0.029	0.949	2.297	<0.05	Negative allometric
	Aperture length	Shell length	-0.195±0.042	1.031±0.030	0.957	-1.027	NS	Isometric	-0.205±0.039	0.989±0.032	0.954	0.339	NS	Isometric
Ra’s alQulay’ah	Shell width	Shell length	0.020±0.08	0.859±0.06	0.857	2.510	<0.02	Negative allometric	-0.344±0.114	1.065±0.082	0.812	-0.732	NS	Isometric
	Aperture length	Shell length	0.128±0.077	0.810±0.053	0.874	3.619	<0.001	Negative allometric	-0.243±0.170	1.025±0.123	0.698	-0.200	NS	Isometric

NS: Not significant at p>0.05

Note the –ve allometric relationship seen in *E. junionae* is probably the result of a smaller range of data.

T.savignyi in the north of Kuwait and found that this species only occurred between Ra's al Ard and Ra's az Zawr in the south. No records of *E. junionae* were made. In 2005, however, when this shore was investigated by this author a few *T. savignyi* were noted and interestingly, when shores further north than Ra's Ajūzah were surveyed during an investigation of the distribution of crabs by this author and Zainab Al-wazzan, only a few isolated specimens of *T. savignyi* were found. One possible reason to explain the low numbers of *T. savignyi* at Ra's Ajūzah in the North is the absence of suitable habitat for the species, such as the lack of large boulders, suitable cracks and fissures in which the species can gain protection. These kinds of habitat are commonly associated with the species' distribution in the southern sites. Large boulders are known to provide a more stable habitat for organisms e.g. barnacle species living on and under them (Gedan *et. al.*, 2011). The presence of large boulders at the southern sites could confer an advantage to *T. savignyi* in protecting them from the searing heat during tidal emersion; any advantage was not there at the northern site where large boulders were absent. These factors, together with the prevailing wind direction - north and south westerly winds (see chapter 2), *T. savignyi* inhabiting rocks at Ra's Ajūzah would be subject to onshore winds for a large proportion of the year and because of a lack of suitable habitat i.e. fissures and cracks they would likely be washed off the shore. In sites further south there is a larger area of suitable habitat available, e.g. fissures and cracks and offshore rather than onshore winds (north and south westerly direction), so less wave action (see Chapter 2) and a reduced danger of being washed away.

Ergalatax junionae's preference for small crevices, where its prey e.g. polychaetes live (see Chapter 6), likely influences the distribution of the species along Kuwait's coastline. In the North, where the abundance of *E. junionae* is highest the shore is dotted with small boulders and associated crevices, ideal habitat for *E. junionae*'s polychaete prey (chapter 6). Emson and Faller-Fritsch (1976) investigated the relationship between crevice size and *Littorina radius* density at sites on the Sussex coast. They found that crevice availability increased the population density and the size of crevice hole influenced the size of the snail inhabiting the crevice (see also Raffaelli and Hughes 1978 who studied *Littorina rudis* and *L.neritoides*.). Crevice dwelling has been shown to be beneficial in protecting gastropods from predators (e.g. Fairweather *et. al.*, 1984; McKillup snd McKillup, 1993; Catesby and Mckillup, 1998), from insolation and heat (Garrity, 1984; Harper and Williams, 2001) and for inducing aggregations of individuals for reproduction and harvesting of prey species (Pechenik, 1978; Tong, 1988; Benkendorff and Davis, 2004). In the south of Kuwait, although *E. junionae* present in large numbers, the lack of small boulders and associated crevices may account for its lower abundance at the southern sites compared with the northern site. *Ergalatax junionae* is also known to be a corallivore and it occurs at depths of up to 7m along the coastline of Iran where it feeds on coenchyme, the tissues surrounding coral polyps (Saledhoust *et. al.*, 2011). Corals were found more frequently subtidally and at extreme low water of spring tides at the southern Kuwait sites so *E. junionae* may be present amongst the coral polyps. However this study did not investigate the subtidal distribution of *E. junionae*.

The general distribution of both species of gastropod from high to low shore reflected the local topography of the shore. *Ergalatax junionae* was distributed across the shore at Ra’s Ajūzah in the north with the highest abundances on the low shore below station 5 and during May and July. The shore at Ra’s Eqaila is characterized by the occurrence of a large pool on the upper to mid-section of the shore during high water which partially drains during low tide. This pool and associated small boulders appeared to deter *T. savignyi* from the first 1-5 stations although a few individuals were found just below mean high water of neap tides. *E. junionae* by contrast was commonly encountered in the upper and mid parts of the shore and elsewhere further down into the lower part of the shore. Probably because of the presence of small boulders and crevices and its tolerance to living in shallow water that might become very warm during low tide. On the southernmost site the shore at Ra’s al Qulay’ah has a shallow topography and both species were distributed across the shore throughout the year.

The morphometric analysis revealed that *T. savignyi* exhibit isometric relationships between shell length and shell width and shell length and aperture length at two of the three studied sites, except Ra’s al Qulay’ah. The relationship at this latter site was negatively allometric between shell length and shell width and between shell length and aperture length. Similarly, *E. junionae* showed an isometric relationships for these dimensions except for those collected from Ra’s Eqaila where there is a negatively allometric relationship between shell length and shell width. Trussell and Etter (2001) in their review of gastropods have suggested that both genetic and environmental factors are responsible for the variations in phenotype with latitudinal and geographical variations.

Many studies demonstrate the various phenotypic responses in marine gastropods that are induced by predators (e.g. see Vermeij and Currey, 1980; Trussell and smith, 2000; Márquez *et. al*, 2015), wave action (Goodwin and Fish, 1977; Crothers, 1983; Etter, 1989; Fraser and Coleman, 2014) and water temperature (Philips *et.al.*, 1973; Irie, 2006). In the current investigation *T. savignyi* collected from Ra’s al Qulay’ah exhibited longer shells than those collected from Ra’s Eqaila and *E. junionae* shells from Ra’s Eqaila were longer than shells collected from Ra’s Ajūzah and Ra’s al Qulay’ah. Kemp and Bertness (1983) observed that where *Littorina littorea* on rocky shores in southern New England, USA were in high population densities (600-800 indv.m^{-2}) the shells tended to have elongate, cone shaped shells whilst at low population densities (< 25 indv.m^{-2}) the shells were more globose in shape. At high grazing density snails may be pressed close to each other and have more frequent interactions with individuals and this causes the shells to grow more along the length of the spire of the shell. At low densities there is likely to be little contact and the shells grow in width rather than along their spire length. The influence of density may be one possible factor that explains the difference in shape of the gastropods in this study. The density of predatory gastropods in my study is lower than those of other predatory gastropods in the U.K. e.g. Hughes *et al.* (2002) found densities of *Nucella lapillus* of 15.m^{-2} in crevices whilst on the open rock surfaces the densities were 9.2.m^{-2}. The average density of *T. savignyi* (4.9.m^{2}) at Ra’s al Qulay’ah throughout the year was similar to the density at Ra’s Eqaila (5.3.m^{2}) (see table 3.2). Likewise, *E. junionae* had similar densities at Ra’s Eqaila and Ra’s Ajūzah (e.g. on the lower shore 46.9.m^{2} and 47.m^{2} respectively) in comparison to the lower shore at Ra’s al Qulay’ ah in the south where the density of *E. juninae* was only 7.3.m^{2}.

Another possible reason suggested by Crothers (1983), is the level of wave exposure encountered by gastropods on rocky shores. He found that dog whelks, *Nucella lapillus* from exposed shores tended to have short squat shells which became more elongated on sheltered shores. Ra’s al Qulay’ah experiences more offshore winds which means less wave action in comparison to the northern site Ra’s Eqaila, where there are more on-shore winds and hence wave action (see chapter 2 and figure 3.). However whilst *T. savignyi* has a shape that might reflect the level of wave exposure, *E. junionae* has longer shells on the more wave exposed shore of Ra’a Eqaila than at Ra’s al Qulay’ah where densities are much lower. In *E. junionae* density therefore may be controlling shell shape rather than wave exposure. The habit of both species is different with *T. savignyi* inhabiting more open rock surfaces whilst *E. junionae* lives in crevices in cramped conditions so that space for individuals is restricted and this leads to an increase in length rather than width. Another difference in the shape of the two species is the length of the shell aperture. In *T. savignyi* from Ra’s al Qulay’ah the shell aperture is narrower compared to shells from Ra’s Eqaila. Narrow shell apertures and axial shell sculpture in gastropods have been shown to be architectural features that deter crab predation (Bertness and Cunningham, 1981). Márquez *et. al* (2015) found gastropods from intertidal habitats presented a low-spired shell and an expanded aperture which they suggest might allow better attachment to the bottom substratum, whilst subtidal individuals presented a slender and narrower shell shape. They also found that the number of scars on the shell attributed to crab attacks was significantly higher in shells from subtidal individuals. Many of the environmental factors and the interplay between individuals of each species may have led to differences in shell shape of the two species.

3.3 CONCLUSION

1) I have presented the various abiotic factors and described the population distribution, abundance and morphological differences for *Thalessa savignyi* and *Ergalatax junionae*.
2) The geographical distribution and the seasonal pattern in abundance and migration in the intertidal zone of both species have been identified and related to different physical factors.
3) *Thalassa savignyi* was absent from the rocky shore studied in the north and more abundant on shores in the south of Kuwait (e.g. June average density on the low shore 1.0 ± 0.5 .m^2). By contrast *E. junionae* was more abundant in the North of Kuwait and more abundant than *T. savignyi* (June average density on the low shore 47.0 ± 16.7 .m^2).
4) Within each species there was little difference in the intertidal distribution or densities although there was wide variation in seasonal abundance.

5) The presence of large rocky platforms and associated fissures on the southern shore sites were related to the increased abundance of *T. savignyi*. Whilst small boulders and crevices on the shores of the northern sites were preferred by *E. junionae*.
6) The relationships between shell length, shell width and aperture length in *T. savignyi* were isometric except for *T. savigyni* from Ra´s al Qulay´ah where negative allometric relationships were observed. *Ergalatax junionae* shells similarly showed isometric relationships at all three studied sites except at Ra´s Eqaila.

The evidence presented in this chapter indicates that the studied variations in both species are directly related to environmental causes. We have come to the end of this chapter where useful information has been obtained but in the next chapters I use different approaches to get a clearer picture of the population dynamics of the two species.

3.5 REFRENCES

Al-Yamani, F. Y., Bishop, J., & Ramadhan, E. (2004). Oceanographic atlas of Kuwait's waters. Kuwait institute for scientific research, 4 films printing, Kuwait.

Al-Yamani, F. Y., Skryabin, V., Boltachova, N., Revkov, N., Makarov, M., Grinstov, V., & Kolesnikova, E. (2012). Illustrated Atlas on the Zoobenthos of Kuwait. Kuwait Institute for Scientific Research.

Ayal, Y., & Safriel, U. N. (1982). Role of competition and predation in determining habitat occupancy of Cerithiidae (Gastropoda: Prosobranchia) on the rocky, intertidal, Red Sea coasts of Sinai. *Marine Biology*, Vol. **70**, pp. 305-316.

Benkendorff, K., & Davis, A. R. (2004). Gastropod egg mass deposition on a temperate, wave-exposed coastline in New South Wales, Australia: implications for intertidal conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, Vol. **14**, pp. 263-280.

Bertness, M. D., & Cunningham, C. (1981). Crab shell-crushing predation and gastropod architectural defense. *Journal of Experimental Marine Biology and Ecology*, Vol. **50**, pp. 213-230.

Bird, C. E., Franklin, E. C., Smith, C. M., & Toonen, R. J. (2013). Between tide and wave marks: a unifying model of physical zonation on littoral shores. *PeerJ*, Vol. 1, e 154.

Black, R. (1979). Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *The Journal of Animal Ecology*, Vol. **48**, pp. 401-411.

Catesby, S. M., & McKillup, S. C. (1998). The importance of crevices to the intertidal snail *Littoraria articulata* (Philippi) in a tropical mangrove forest. *Hydrobiologia,* Vol. **367**, pp. 131-138.

Chambers, R. J., & McQuaid, C. D. (1994). A review of larval development in the intertidal limpet genus *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, Vol. **60**, pp. 415-423.

Christofoletti, R. A., Murakami, V. A., Oliveira, D. N., Barreto, R. E., & Flores, A. A. (2010). Foraging by the omnivorous crab *Pachygrapsus transversus* affects the structure of assemblages on sub-tropical rocky shores. *Marine Ecology Progress Series*, Vol. **420**, pp. 125-134.

Crothers, J. H. (1983). Variation in dog-whelk shells in relation to wave action and crab predation. *Biological Journal of the Linnean Society*, Vol. **20**, pp. 85-102.

Crothers, J. H. (1985). Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.). *Field Studies*, Vol. **6**, pp. 291-360.

Ellis, D.V. (2003). Rocky shore intertidal zonation as a means of monitoring and assessing shoreline diversity recovery. *Marine Pollution Bullettin*, Vol. **46**, pp. 305-307.

Emson, R. H., & Faller-Fritsch, R. J. (1976). An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. *Journal of Experimental Marine Biology and Ecology*, Vol. **23**, pp. 285-297.

Etter, R. J. (1996). The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, Vol. **196**, pp. 341-356.

Fairweather, P. G., Underwood, A. J., & Moran, M. J. (1984). Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series*, Vol. **17**, pp. 143-156.

Feulner, G. R., & Hornby, R. J. (2006). Intertidal molluscs in UAE lagoons.*Tribulus*, Vol. **16**, pp. 17-23.

Fraser, C. M., Coleman, R. A., & Seebacher, F. (2014). Trying to fit in: are patterns of orientation of a keystone grazer set by behavioural responses to ecosystem engineers or wave action?*Oecologia*, Vol. **174**, pp. 67-75.

Goodwin, B. J., & Fish, J. D. (1977). Inter-and intraspecific variation in *Littorina obtusata* and *L. mariae* (Gastropoda: Prosobranchia). *Journal of Molluscan Studies*,

Garrity, SD. (1984). Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology*, Vol. **65**, pp. 559-574.

Guenther, R. J., Martone, P. T. (2014), Physiological performance of intertidal coralline algae during a simulated tidal cycle. *Journal of Phycology*, Vol. **50**, pp. 310–321.

Harper, K. D., & Williams, G. A. (2001). Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. *Journal of Zoology*, Vol. **253**, pp. 293-300.

Irie, T. (2006). Geographical variation of shell morphology in *Cypraea annulus* (Gastropoda: Cypraeidae). *Journal of Molluscan Studies*, Vol. **72**, pp. 31-38.

Jones, D. A. (1986). Field Guide to the Sea Shores of Kuwait and the Arabian Gulf, University of Kuwait. Blandford Press, Kuwait, pp. 123-129.

Jones, D. & George, D. (2005). The Shore and Shallow seas, pp. 123-128 *in* Hellyer, P. and Aspinall, S. (Editors). The Emirates: a natural history. Trident Press, Abu Dhabi, UAE.

Kemp, P., & Bertness, M. D. (1984). Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proceedings of the National Academy of Sciences*, Vol. **81**, pp. 811-813.

Knox, G. A. (2001). The ecology of seashores. CRC Press, Florida, USA.

Lewis, J. R. (1964). Ecology of rocky shores. English Universities Press, London.

Little, C; Williams, G. A. (2010). The biology of rocky shores, Oxford University Press,

Chambers, R. J., & McQuais, C. D. (1994). A review of larval development in the intertidal limpet genus *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, Vol. **60**, pp. 415-423.

Márquez, F., Vilela, R. A. N., Lozada, M., & Bigatti, G. (2015). Morphological and behavioral differences in the gastropod *Trophon geversianus* associated to distinct environmental conditions, as revealed by a multidisciplinary approach. *Journal of Sea Research*, Vol. **95**, pp. 239-247.

McKillup, S. C., & McKillup, R. V. (1993). Behavior of the intertidal gastropod *Planaxis sulcatus* (Cerithiacea: Planaxidae) in Fiji: are responses to damaged conspecifics and predators more pronounced on tropical versus temperate shores? *Pacific Science*, Vol. **47**, pp. 401-407.

Murray, S. N.; Ambrose, R.; Dethier, M. N. (2006). Monitoring Rocky Shores. University of California Press, Berkley.

Pechenik, J. (1978). Adaptation to intertidal development: studies on *Nassarius obsoletus*. *Biololgical Bulletin*, Vol. **154**, pp. 282–291.

Phillips, B. F., Campbell, N. A., & Wilson, B. R. (1973). A multivariate study of geographic variation in the whelk Dicathais. *Journal of experimental marine Biology and Ecology*, Vol. **11**, pp. 27-69.

Raffaelli, David, Hawkins, S.J. (1996) Intertidal ecology, Chapman and Hall, London.

Stephenson, T. A. and Stephenson, A. (1946). The universal features of zonation between tide-marks on rocky coasts, *Journal of Ecology*, Vol. **37**, pp. 289-305.

Richardson, C. A., Seed, R., & Naylor, E. (1990). Use of internal growth bands for measuring individual and population growth rates in Mytilus edulis from offshore production platforms. *Mar. Ecol. Prog. Ser*, *66*, 259-265.

Richardson, C. A.; Seed, R.; Brotohadikusumo & Owen, R. (1995). Age, growth and allometric relationships in *Septifer virgatus* (Bivalvia: Mytilidae). Asian marine biology, Vol. **12**, pp. 39-52.

Saledhoust, A.; Negarestan, H.; Jami, M.J. and Brian Morton. (2011). Corallivorous snails: first record of corallivory by *Ergalatax junionae* (Gastropoda: Muricidae) in the Persian Gulf. *Marine Biodiversity Records*, Vol. **4**, pp. e99.

Stirling, H. P. (1982). The upper temperature tolerance of prosobranch gastropods of rocky shores at Hong Kong and Dar Es Salaam, Tanzania. *Journal of Experimental Marine Biology and Ecology*, Vol. **63**, pp.133-144.

Tong, L. K. (1988). The reproductive biology of Thais clavigera and Morula musiva (Gastropoda: Muricidae) in Hong Kong. *Asian Marine Biology*, Vol. **5**, 65-75.

Trussell, G. C., & Etter, R. J. (2001). Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail, pp. 321-337 *in Microevolution Rate, Pattern, Process*. Springer, Netherlands.

Trussell, G. C., Ewanchuk, P. J., & Bertness, M. D. (2002). Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecology Letters*, Vol. **5**, pp. 241-245.

Whyte, W. S. & Paul, R. E. (1985). Basic metric surveying (3rd ed), Butterworths, Essex, pp. 171-201.

Vermeij, G. J., & Currey, J. D. (1980). Geographical variation in the strength of thaidid snail shells. *The Biological Bulletin*, Vol. **158**, pp. 383-389.

Williams, S. T., D. G. Reid, and D. T. J. Littlewood. (2003). A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism and biogeography of the Southern Ocean. *Molecular Phylogenetics Evolution*, Vol. **28**, pp.60–86.

Williams, S. T., & Reid, D. G. (2004). Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution*, Vol. **58**, pp. 2227-2251.

Wilson, R.J.P. (1983). Land Surveying, Pitman Publishing, London, pp. 464- 465.

CHAPTER FOUR

Population Structure, Recruitment and Growth

4 Population Structure, Recruitment and Growth

4.1 INTRODUCTION

In the previous chapter I made a quantitative investigation of the density and distribution of two intertidal gastropods *Thalessa savignyi* and *Ergalatax junionae* on three shores along the coastline of Kuwait. I also investigated the different physical factors that may have a role in regulating the distribution and abundance of the populations of both species. Undoubtedly, extracting such abundance data has provided useful information about these two organisms and their ecology. However, abundance alone is insufficient to describe a population in a way that reflects precisely its dynamics (see Cerrato 1980; Murray 2006). Murray (2006) presumed that population parameters such as size and age classes distribution provide a clearer picture of population structure compared with the density alone. There is sufficient evidence from many studies (e.g. Feare, 1970; Seed, 1976; Kendall and Lewis, 1986; Kendall, 1987; Roach and Lim, 2000) that size frequency profiles amongst sites and over time are informative for population features such as age structure and recruitment patterns and can provide estimations of survival and growth rates for building population models. However these methods are not without their drawbacks. For example individual cohorts in length frequency distributions may not necessarily represent a year class without further validation and in larger (older) size classes the separation between individual cohorts may be blurred and underestimate the number of size (age) classes in the population.

In many instances, estimates of recruitment in gastropods is based on size-frequency observation. For example, McGrath (1992) studied intertidal populations of the blue-rayed limpet *Helcion pellucidum*, from south east Ireland between August

1976 to December 1978. He did not observe settlement in 1977 but found a domination of a 0-1mm size class after February 1978 where he recorded a first juvenile recruitment. He noted that recruitment mainly took place on the lower shore where the adults are found attached to *Laminaria* sp. Other gastropod species such as *Littorina africana knysnaensis* have shown a different recruitment pattern by which a continuous addition of small size classes was observed throughout the sampling period (McQuaid, 1981). Yet, periods of heavy settlement were also apparent to Mc Quaid (1981) in October 1976, and between May and June 1977, and in December 1977 through to January 1978. The intertidal gastropod *Morula marginalaba* from rocky shores in New South Wales, Australia displayed variable recruitment on spatial scales with intense recruitment observed on some shores studied whilst on most of the other shores investigated recruitment was insignificant (Moran *et. al.*, 1984). This variation was related to the species of prey present, both within a shore where a variety of prey were available, and among shores each dominated by a single species of prey e.g. oysters. Thus these authors concluded that *M. marginalaba* settled in abundance in areas where their prey, in this case oysters, settled in abundance. Delany *et. al.* (1998) studied the effect of recruitment on the population structure of two limpet species *Patella vulgata* and *Patella ulyssiponensis* from mid shore tide pools in Ireland. These two intertidal species have different distribution ranges with *P. vulgata* tolerating a wide exposure range (high wave-exposure to sheltered shore exposure). *Patella ulyssiponensis* has a more limited distribution preferring shores with more wave-exposed conditions and occupying the lower shore. These authors reported large *P. ulyssiponensis* (>20mm) were more abundant than smaller size classes in tide pools on upper shore levels whilst juveniles occupied the lower shore. By contrast large and small (< 20mm) *P. vulgata* were both more abundant than *P. ulyssiponensis* in these tide-pools.

Several authors have noted a gradient in size distribution with tidal height in many intertidal gastropods (e.g. Vermeij, 1972; Bertness, 1977; Pardo and Johonson, 2005). For example, large individuals of *Littorina saxatilis* were found inhabiting the lower zone of three transects extended across the southern shore of the St. Lawrence estuary, Canada (Pardo and Johonson, 2005). Gendron (1977) found that the largest *L. littorea* occupied higher tidal levels and that their distribution varied seasonally. A seaward (lower shore) migration occurred during the winter season where densities dropped from 69-111 ind.m^{-2} in October to 6-15 ind.m^{-2} in January and increased from 0 ind.m^{-2} in March to attain densities of 96-132 ind.m^{-2} in the summer (July). Saier (2000) confirmed a downward migratory behaviour in many intertidal organisms including *L. littorea* in the Wadden Sea and other coastal habitats. He claimed this adaptation was to escape from the severe winter weather conditions on the high shore. The vertical migration of the intertidal gastropod *Monodonta labio* was investigated using mark and recapture techniques for one year at Amakusa, Japan (Takada, 1996). The investigation found that vertical migration of this species occurred throughout the year. Also, a clear seasonal fluctuation was observed with a single size distribution mode in the population at mid shore levels in the winter season (December to February) whilst in summer (April-August) two modes appeared at the high and lower mid shore level (Takada, 1996). Tadaka (1996) concluded that juveniles recruited to the mid zone in winter and spring, a time when they grow, and also that some migrated upward reducing the density in the middle of the shore.

The purpose of the present chapter is to describe the population structure of the two studied gastropods *Thalessa savignyi* and *Ergalatax junionae* using Bhattacharya's method to analyse population length frequency distributions and to determine whether there are inter- and intra-differences in the growth of the two species.

4.1 MATERIALS AND METHODS

4.1.1 Length Frequency Data

All the *Thalessa savignyi* and *Ergalatax junionae* collected during the timed searches and quadrat sampling (see Chapter 3) were placed in labelled plastic bags and transported to the laboratory where they were sorted and washed to remove all debris and adhering organisms. Living individuals were separated from those shells inhabited by hermit crabs (approximately 5%) and *Thalessa savignyi* and *Ergalatax junionae* were identified using the morphological characteristics presented in Chapter 3. The number of each species was counted and the length measured using vernier calipers before being frozen for further investigation (see chapter 3). All the measurement data were entered into Excel, graphically analysed and then these data were entered into Minitab version 16 to plot length-frequency distributions for each studied site, season, and station.

During the sampling survey (see chapter 3) I noticed that there was an absence of small individuals (<10mm) from the three investigated shores. However, upon close examination of the rocks and boulders at Ra´s Eqaila I noted the presence of a few small individuals (< 8mm) inside boulder crevices in the upper and lower shore levels during the first surveyed autumn season. In order to investigate whether smaller individuals were inside the crevices of the boulders , 2-3 football size (>50 cm) boulders with large *E. junionae* attached were collected from each shore level and transferred to seawater aquaria and held overnight to confirm whether the crevices might contain small juveniles. After ~ 24 hours the boulder and sea water were examined and any gastropods were collected, identified and measured using vernier calipers. This was undertaken during two successive seasons (autumn and winter).

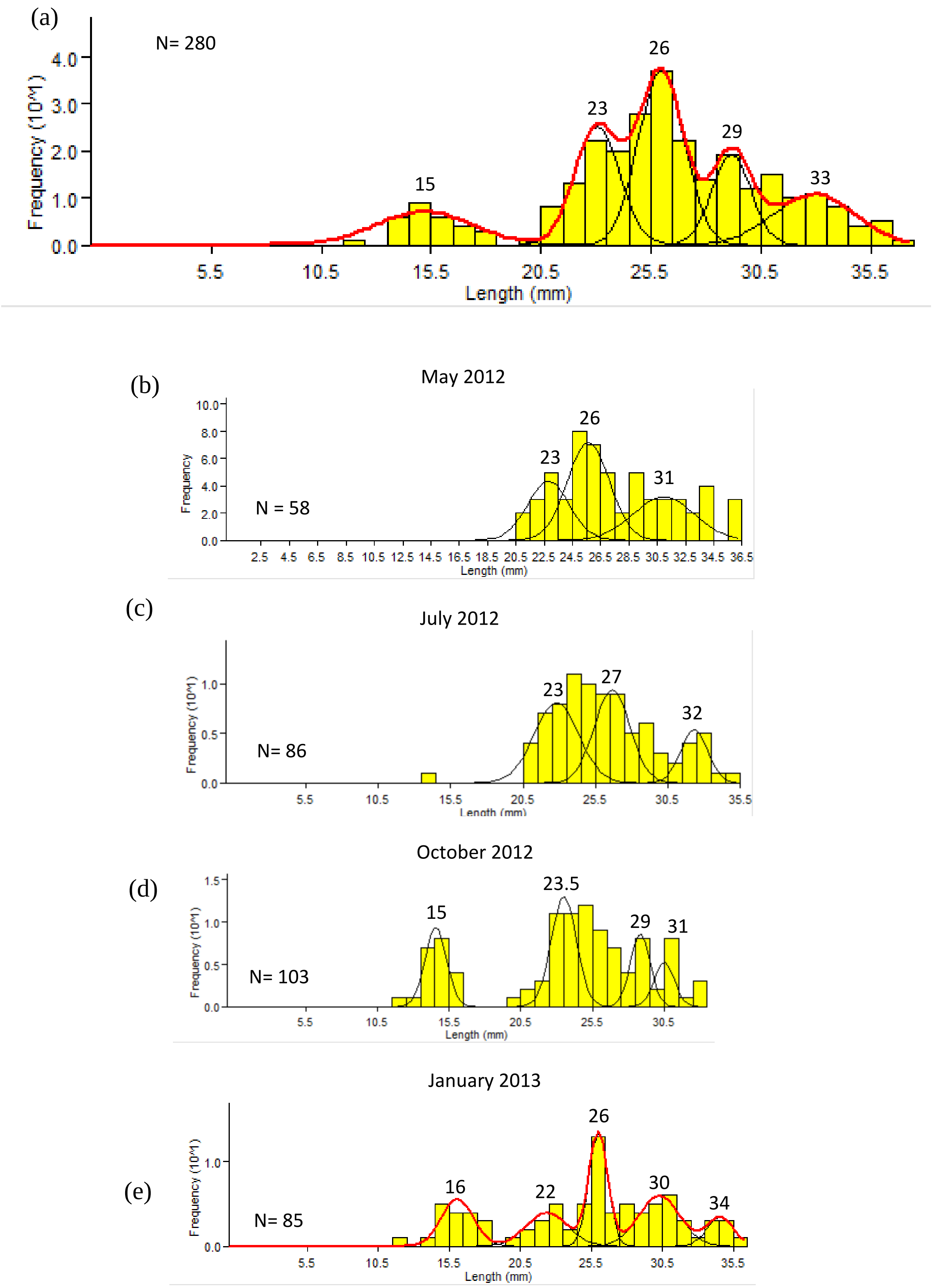


Figure 4.1. Graphical estimation of the modal size classes in size frequesncy distributions of *Thalessa savignyi* collected from Ra´s Eqaila using the method of Bhattacharya to separate the modal size classes. (a) all data collected between May 2012 and January 2013 conmbined into one plot and analysis, (b-e) individual analysis of the quarterly sampled seasonally collected data.

For some of the plots of the length frequency distributions only a few (<80 individuals) of *T. savingyi* and *E. junionae were* available for use in the analysis of the modal size class data using Bhattacharya's method in the Fisheries FiSat II program. The number of individuals in the analyses is usually >250. To maximise the Bhatacharya analyses, all the length frequency data for each of the four sampling periods could be combined into one annual length frequency distribution for each population, thus increasing the number of data points. However to ensure that the data for the quarterly samples gave a similar analysis of the modal size classes to that of the combined data, Bhattacharya's analyses were conducted on the quarterly seasonal samples and compared with the combined population size frequency. As an Example see figure 4.1. This approach was assessed by analysing each of the modal size frequency distributions of *T. savingyi* from Ra's Eqaila collected during the four sampling periods (January, October, May and July) in order to check that the estimated modal size classes were similar from the four samples and the combined population sample (see figure 4.1). Generally there was no difference in the estimated modal size classes between the four sample periods and the population sample, except for the appearance of a new modal size class in October and January as a result of recruitment of individuals into the population (see figure 4.1d & e). In the combined length frequency distribution this modal class was present. On the basis of these analyses each length frequency distribution for the combined population was plotted and separated into its modal length classes using the method of Bhattacharya. The estimated modal size (age) classes were tabulated for each species and shore and these length and modal size (age) class data were plotted graphically to produce growth curves. These data were further analysed using the Fishparm package and estimates of the Von Bertallanfy growth constants determined using the following equation:

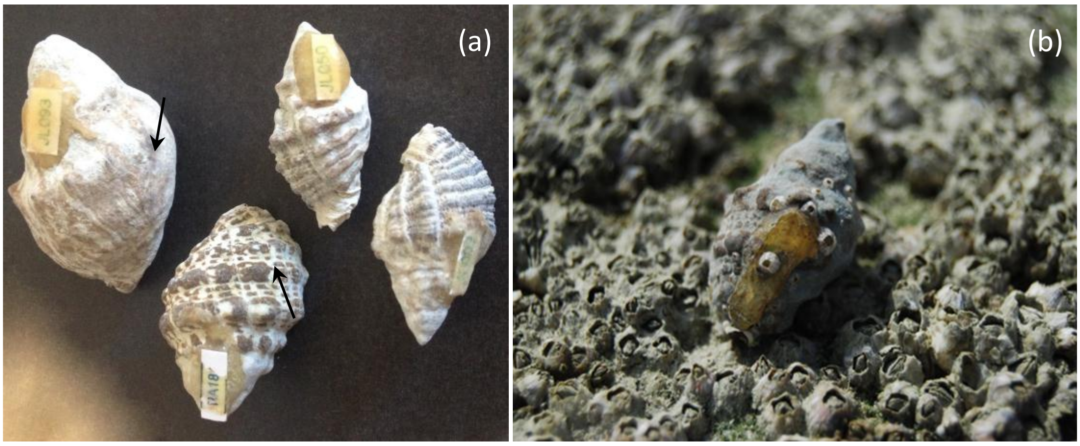


Figure 4.2. (a) Tagged individuals of *Thalessa savignyi* (arrows) and *Ergalatax junionae* before release into the natural environment. (b) an individual *Thalessa savignyi* that had been tagged and released at Ra´s Eqaila and was found later with only the resin mark on the shell.

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

Where Lt = Shell length at time (t), L∞ = the asymptotic maximum; K= the VBG growth constant and t_0 = the size at time (age) zero.

4.1.2 Age and growth

4.1.2.1Tagging

Traditionally some studies have employed the use of marked individuals to follow the growth of individuals in a population. For example Chatzinikolau & Richardson (2007) marked hundreds of individual netted whelks *Hinia* (= *Nassarius*) *reticulatus* in a lagoon at low water at Rhosneigr, Anglesey. They recaptured a few individuals on a number of occasions and these data helped to confirm the analyses of the age of the whelks from length frequency distributions and statoliths. On two occasions during my study (during May 2010) I marked 200 gastropods (200 *T. savignyi* and 200 *E. junionae*) with small tags glued to their shells with rapid setting Araldite (see figure 4.2). Four hundred gastropods were released onto the mid shore at Ra´s Eqaila throughout May. A further marking experiment was attempted later during October 2010 when 20 marked gastropods of each species were placed in mesh cages mounted on a stainless steel frame on the mid shore at the three sites. The cages were constructed with sharp spikes that allowed them to be hammered into the sediment in a similar manner to a Bedouin tent peg. At Ra´s Ajūzah only *E. junionae* was transplanted into the cage as *T. savignyi* is naturally absent from this shore.

4.1.2.2 Sclerochronology

Selected shells of *Thalessa savignyi* and *Ergalatax junionae* were scrubbed with gentle pressure from a small brush after defrosting to clean the surfaces prior to examination under a stereo-microscope for potential growth lines or rings. Following cleaning and examination the shells were then crushed using a small bench vice to remove the flesh and separate the operculum from the foot. In the case of *E. junionae* the operculum separated from the foot easily but in *T. savignyi* the operculum had to be pulled off using forceps with some force and in some cases pieces of attached flesh had to be removed following a brief 5 minute immersion in NaOH. The removed operculum was placed on a glass plate and a bright light was shone through it in an attempt to identify any rings. Following examination several different sized operculae were embedded in resin (Buehler resin) and sectioned using a diamond saw before grinding the cut surfaces on wet and dry trimite paper (400 and 1000 grit size) and polishing with diamond paste. An acetate peel replica of the resulting polished surface was made (see Richardson *et. al.*, 1979) and the peel viewed in transmitted light to investigate whether growth lines were present.

4.2 RESULTS

4.2.1 Length frequency distributions

On the basis of the analyses (above) there was no obvious difference in the estimated modal class lengths in the length frequesncy distribuitons estimated from the four sampling seasons and the combined data. Thus the analyses of the modal size classes and interpretations are based on the combined population samples. *Thalessa savignyi* is absent from the northern most site (Ra´s Ajūzah). At Ra´s Eqaila the population structure appears to be tri- or quadri-modal in structure with individuals ranging in shell length between 12.4 mm and 37mm. At Ra´s al Qulay´ah the population appears uni-modal in structure with individuals ranging in length from 20.6 to 45.4 mm. The population structure of *E. junionae* is unimodal in all three locations. In the northern most site (Ra´s Ajūzah) the size range lies between 6.8 and 25.9 mm, and a similar size range occurs at Ra´s Eqaila (5.1 to 27.6mm). In the southern site (Ra´s al Qulay´ah) the gastropods are much larger in length ranging in size from 19.9 to 32mm. In all the surveys of the population structure it was clear that small individuals (<10mm) were generally absent from most of the populations. When football size boulders (<50cm length) containing numerous crevices were collected from Ra´s Eqaila and transported back to the laboratory and placed into seawater aquaria overnight (>12h) they revealed that they were harbouring many small individuals of *E. junionae*. Overnight the small gastropods moved out of the crevices onto the base of the aquaria. When the length measurements of these individuals were additionally added to the population frequency of *E. junionae* the population structure was different with a reasonable proportion of small individuals present in the population (see figure 4.3).

Thalessa savignyi and *E. junionae* exhibited seasonal patterns in their length frequency distributions in the population. Figure 4.4 illustrate the arrival of new small individuals into the population at Ra´s Ajūzah and Ra´s Eqaila shores. Small sizes of *T. savignyi* appeared in the population at Ra´s Eqaila in October 2012 and January 2013. However there did not appear to be any seasonal recruitment of juveniles into the *T. savignyi* population at Ra´s al Qulay´ah which contained individuals > 20 mm. In the case of *E. junionae,* small sized individuals appeared into the population at Ra´s Ajūzah in October 2012 and January 2013. However, at Ra´s Eqaila small sized individuals appeared earlier into the population in July 2012 and there was no apparent recruitment in January 2013.

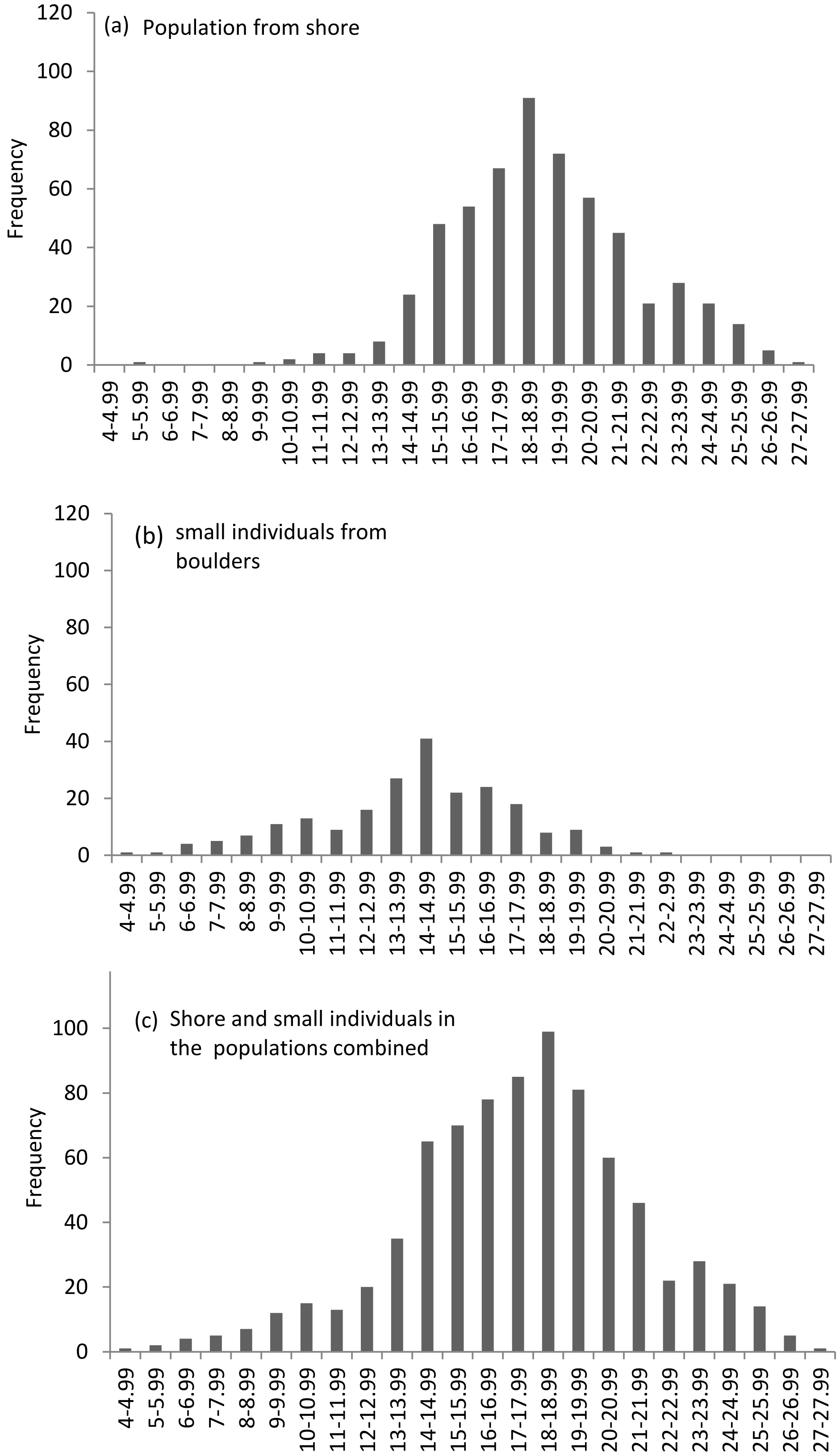


Figure 4.3. Population length-frequency distributions of *Ergalatax junionae* collected from Ra´s Eqaila a) shore population, b) small individuals collected from within boulders and c) combined data from the shore and boulder populations.

At Ra´s al Qulay´ah there was no evidence of recruitment into the population in any of the months and the size frequency distribution remained within a small size range (20-28mm) in the population throughout the year (figure 4.4). Figure 4.5 indicates the presence of two size gradients with shore level at two of the shores i.e. *T. savignyi* from Ra´s al Qulay´ah appeared to increase in shell size in a down shore direction (stations 2 to 9) but not to increase in size down shore at Ra's Eqaila whereas *E. junionae* from Ra´s Ajūzah increased in an up-shore direction (stations 9 to 1). At Ra's Eqaila and Ra's al Qulay'ah there was no apparent difference in size down shore at these two sites. Furthermore, small individuals showed preference for the colonization of specific areas of the shore. For example juveniles of *T. savignyi* were more abundant between stations 4 and 8 at Ra´s Eqaila, whilst at this site *E. junionae* preferred the upper (stations 2 and 3) and lower parts of the shore (stations 10 and 11). At the other sites there was no obvious preference for specific tidal zone by the smaller individuals of both species.

In statistically assigning modal size classes to the size frequency populations using Bhattachyra's method, 5 and 3 modal size classes respectively, were assigned to the size frequency distributions of *Thalessa savignyi* at Ra's Eqaila (see figure 4.6 a and table 4.1). A small mode around 10mm was apparent in the population from Ra´s Eqaila but not sufficiently large enough to be included in the analysis (figure 4.7). The first obvious mode occurred at ~15mm and the second modal class at ~23mm (table 4.1), the remaining population was devided into a further 3 modal size classes. The first apparent modal size group in the population from Ra´s al Qulay´ah (figure 4.6a) occurred around 26mm and this population appeared to contain 3 modal size classes. It is likely that the first modal size class is missing from the population at Ra´s al Qulay´ah and the first apparent modal class compares with the third modal class in the population from Ra´s Eqaila (see table 4.1).

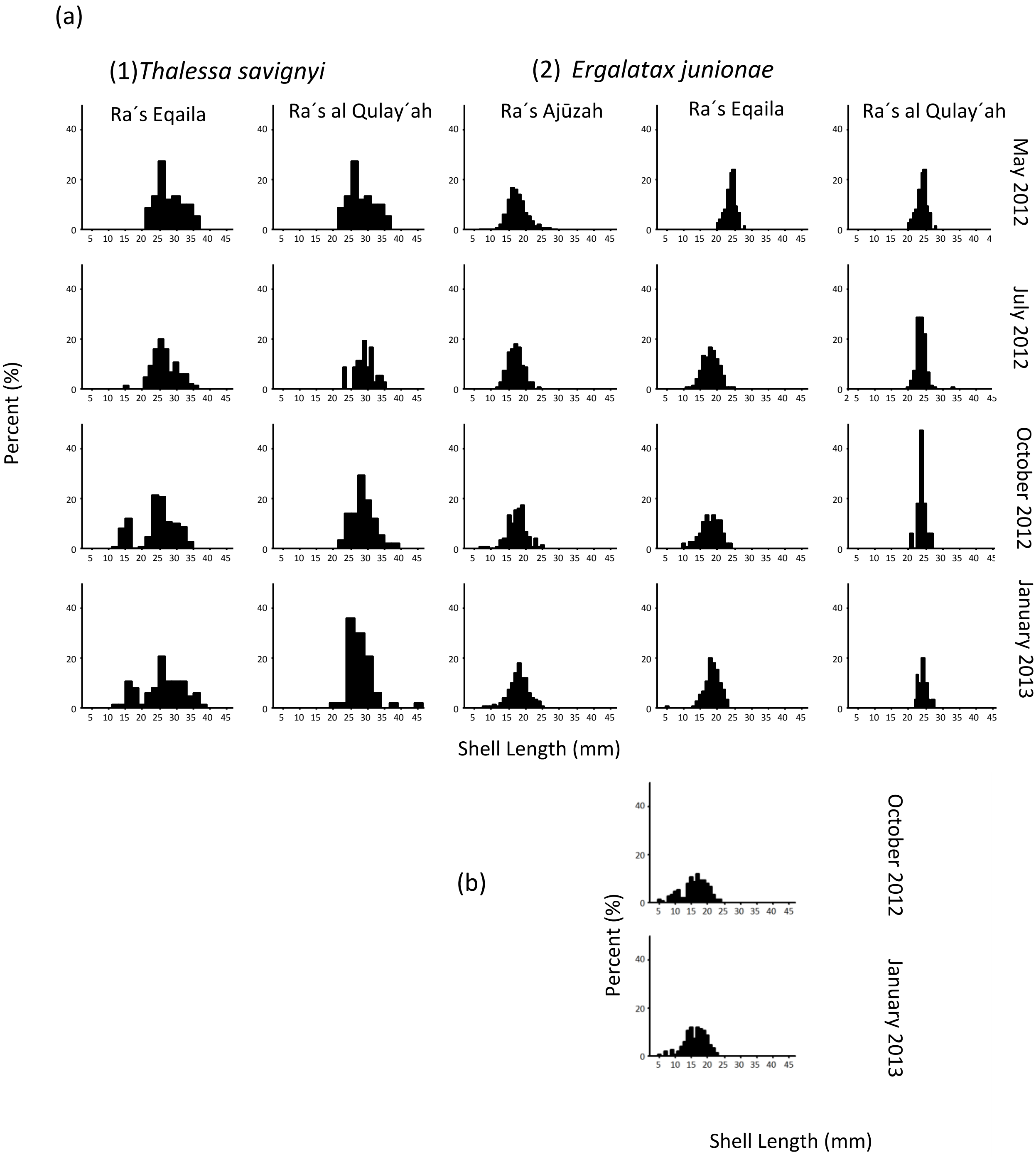


Figure 4.4 (a) Seasonal patterns (May, July, October 2012 and January 2013) in the length-frequency distribution of (1) *Thalessa sav*ignyi and (2) *Ergalatax junionae* from the shores investigated. (b) length-frequency distributions of *Ergalatax junionae* from Ra´s Eqaila including data from animals living within crevices in the boulders.

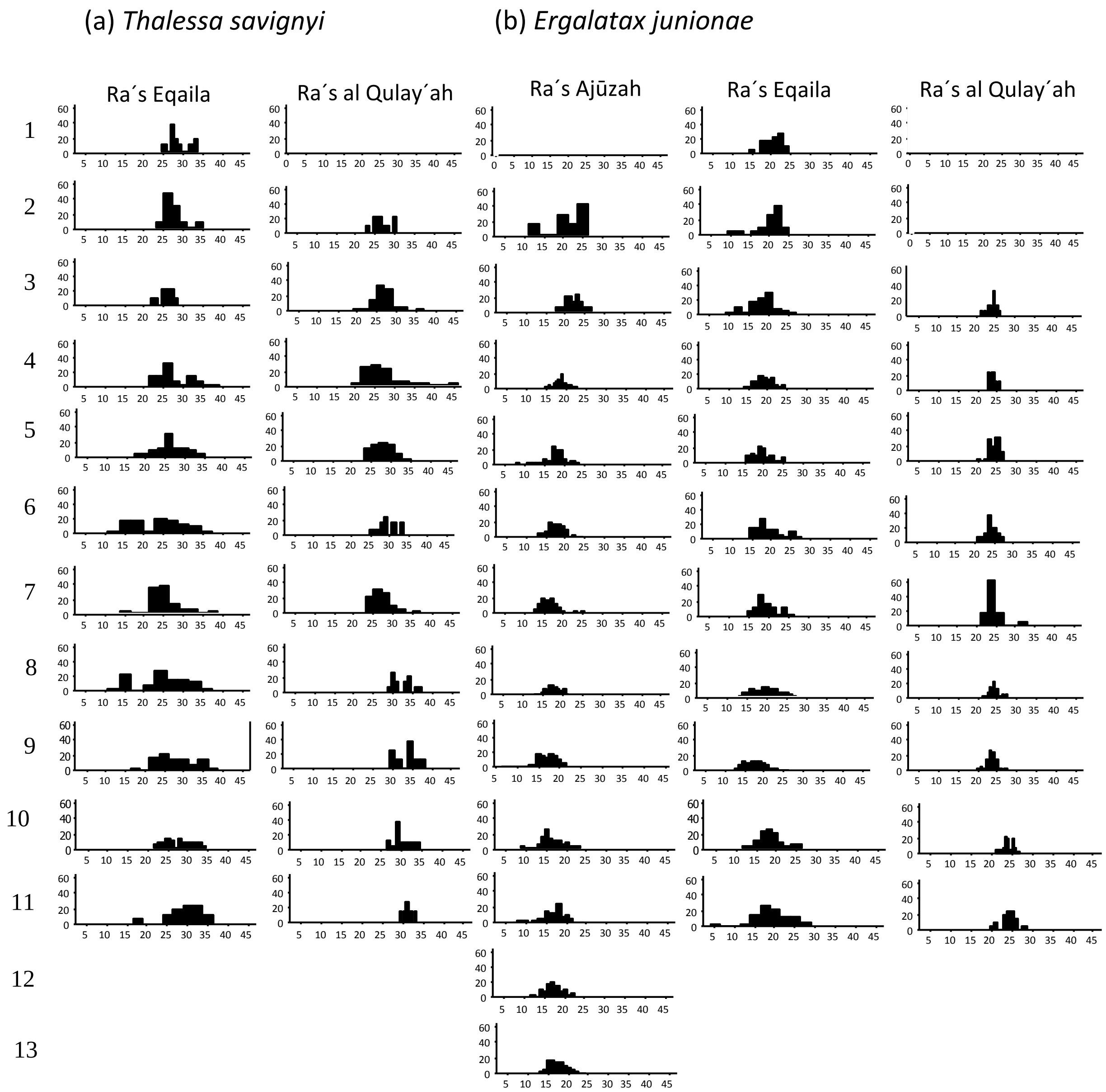


Figure 4.5 Spatial patterns in the population length-frequency distributions of (a) *Ergalatax junionae* and (b) *Thalessa savignyi* collected from each station along the three shores. The data from all the seasons are combined to evaluate differences in structure between high and low water mark. Y axis represents Percentage Frequency of individuals at the different shore positions (1-13). X axis is shell length (mm).

Table 4.1 Summary of the estimated mean modal size classes of *Thalessa savingyi* and *Ergalatax junionae* determined using Bhattacharya’s method.

species	site	Estimated shell length of modal classes ± SD. (mm)				
		1	2	3	4	5
Thalessa savignyi	Ra’s Eqaila	15.2 ± 2.2	23.1 ± 1.0	26.0 ± 1.0	29.2 ± 0.9	33.0 ± 1.9
	Ra’s al Qulay’ah	26.0 ± 2.4	31.0 ± 2.2	35.5 ± 2.1		
Ergalatax junionae	Ra’s Ajūzah	9.3 ± 1.9	16.4 ± 1.9	20.1 ± 1.8	26.1 ± 1.4	
	Ra’s Eqaila	11.8 ± 1.7	15.7 ± 1.2	18.3 ± 1.0	20.8 ± 1.0	23.4 ± 1.5
	Ra’s al Qulay’ah	23.4 ± 1.4				

The maximum size of *E. junionae* from the three sites is smaller than *T. savignyi* and the population from Ra´s Ajūzah has 2 modal size classes, the population from Ra´s Eqaila has 5 modal classes, whilst the population from Ra´s al Qulay´ah could be resolved into only one modal class size (see table 4.1). When the juveniles from the boulders at Ra´s Eqaila were included in the length frequency data and were re-analysed using Bhattacharya's method a similar number of size classes were identified but of different modal length (see table 4.1 and figure 4.7). The analysis of the population structure of the two species using the method of Bhattacharya is useful in highlighting possible length (age) classes in the populations, however it remains to be determined whether these modal size classes are representative of the age of animals in the population. Later in chapter 5 I will attempt to verify whether the modal classes are indicative of age classes using the analysis of growth rings in the statoliths (Chatzinikolaou and Richardson, 2007).

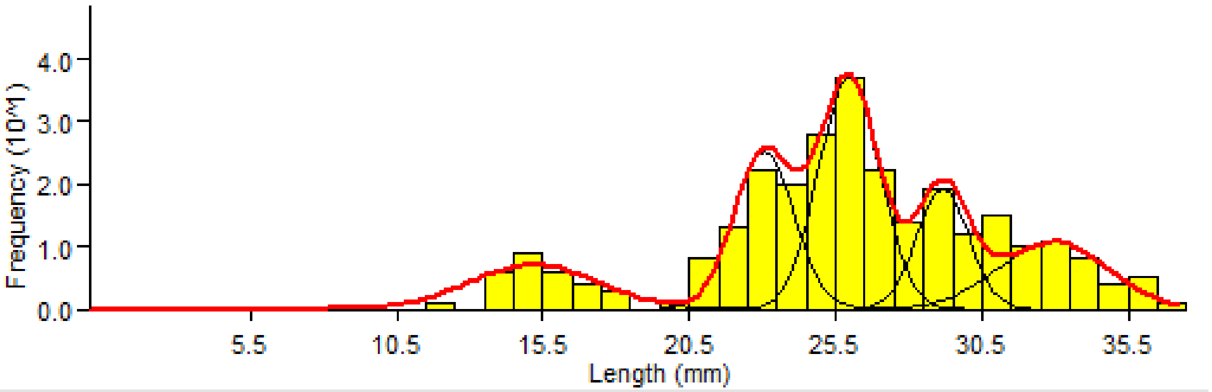
4.2.2 Age and growth estimation

The marking experiments and deployment of the two species onto the shore at Ra´s Eqaila resulted in no returns – none of the marked specimens were ever seen again during the quarterly sampling programme. Similarly, the deployed cages and marked gastropods disappeared after only one spring neap tidal cycle i.e. 2 weeks. The cages were either washed away during rough weather or they were stolen by local shellfish collectors. In view of the disappointing results following considerable investment of my time this area of research was abandoned.

Examination of the outer surfaces of the shells from both species did not reveal any lines or rings that might represent a growth cessation that could be used to determine the age of the animals. The operculum of *T. savingyi* is thick (Figure 4.8a) and when mounted on a glass slide and observed in transmitted light did not allow light

(a) *Thalessa savignyi*

Ra´s Eqaila



Ra´s al Qulay´ah

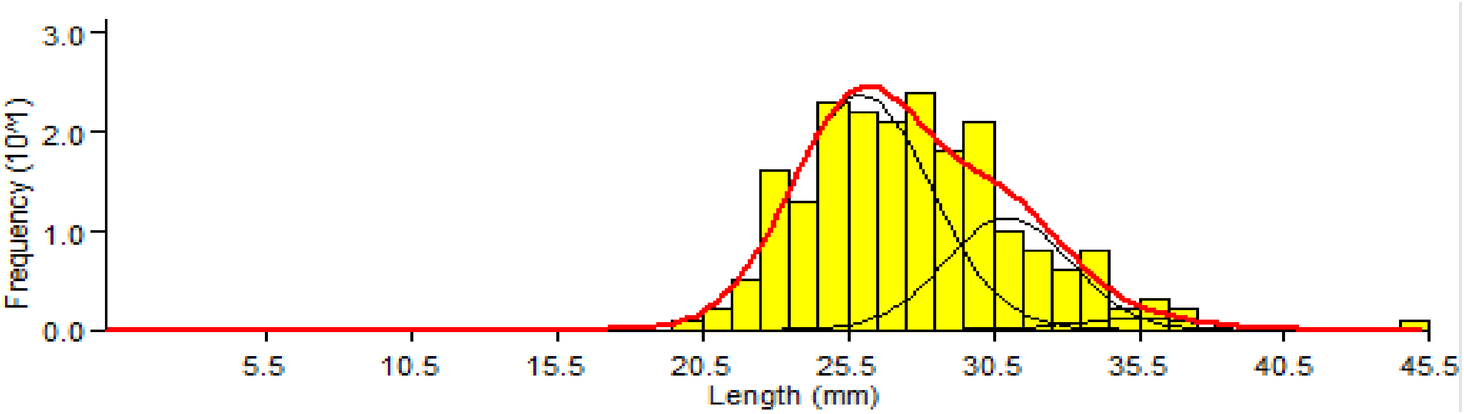
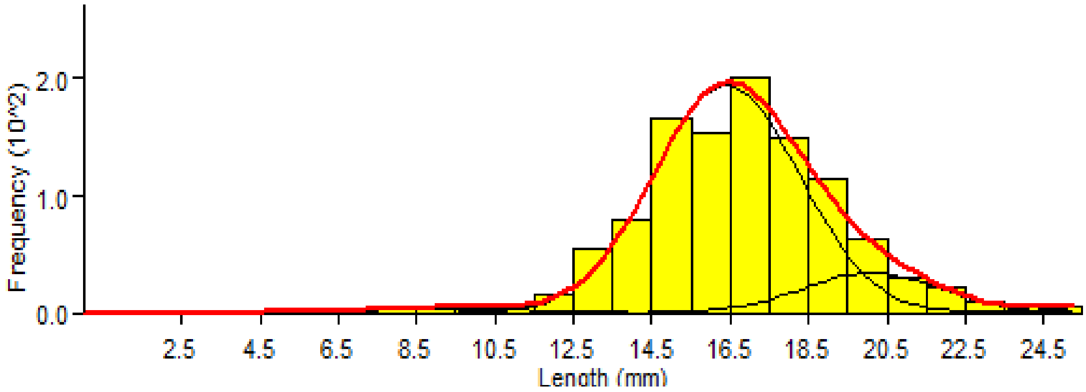
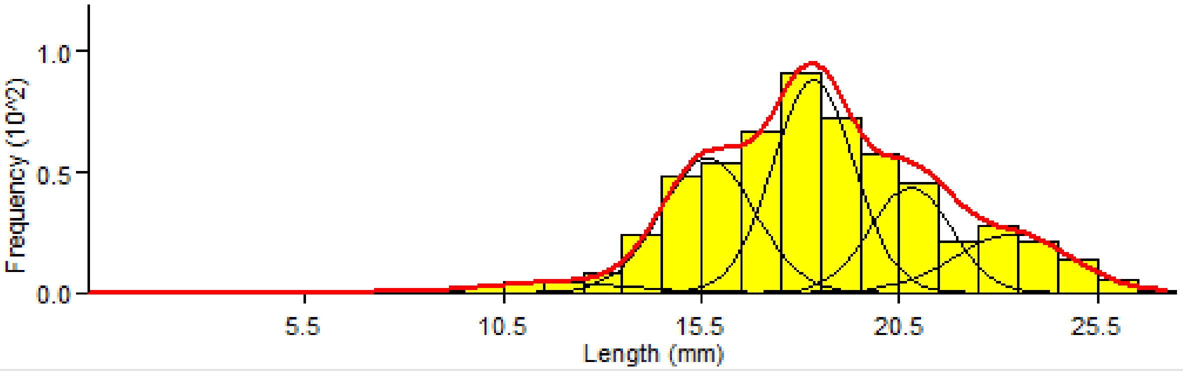
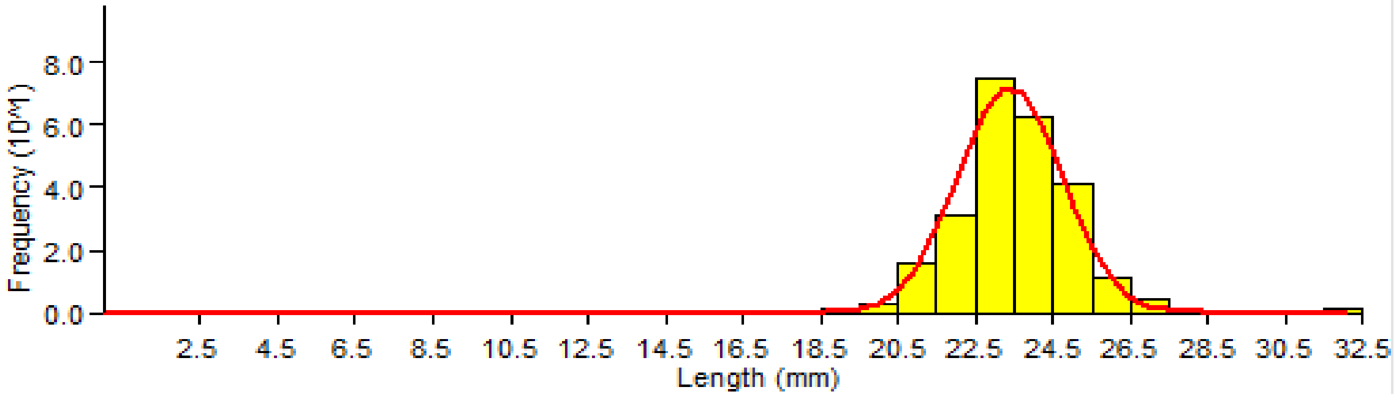


Figure 4.6 Graphical estimation of the modal size classes from (a) *Thalessa savignyi* and (b) *Ergalatax junionae* (next page) population length-frequency distributions separated using the method of Bhattachyra. The figures are screen prints of the original outputs and so the axes could not be adjusted post-analysis of the data.

(b) *Ergalatax junionae*


Ra’s Ajūzah


Ra´s Eqaila


Ra´s al Qulay´ah

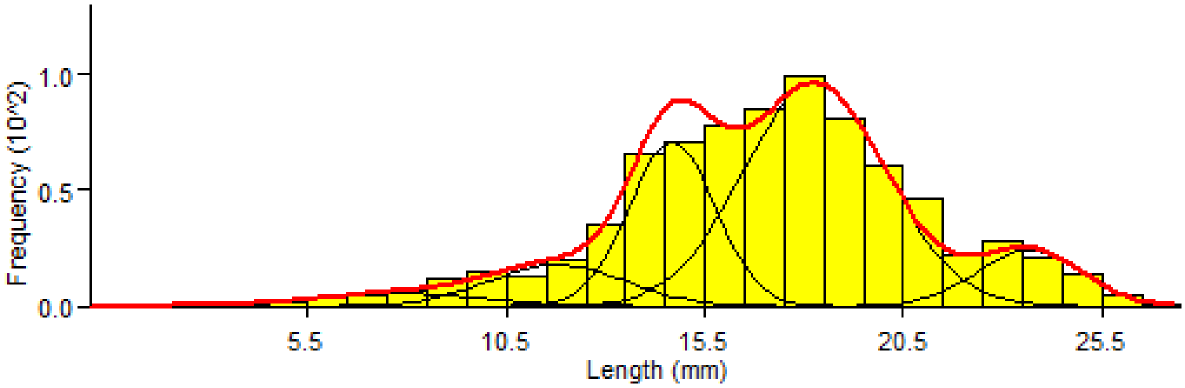


Figure 4.7 Graphical estimation of the modal classes in a length-frequency distribution separated using the method of Bhattacharya for the *Ergalatax junionae* population from Ra´s Eqaila shore, with the inclusion of small individuals collected from boulders.

passage through it and prevented the identification of any rings or lines that have been used previously to estimate the age of species such as *Buccinum undatum* (Kideys, 1996). The validation of operculae growth rings has not been properly undertaken for other gastropod species and many researchers have found the method to provide highly variable results (Kideys, 1996; Ilano *et. al.*, 2004; Richardson *et. al.*, 2005). However the thinner whole operculum from *E. junionae* did reveal a series of alternating dark and light rings (figure 4.8c) that could be counted. This technique was not, however, followed further as there did not appear to be any relationship between the operculum growth rings and statolith growth rings (see Chapter 5). Sectioned operculae from both species (figure 4.8b & d) did not however reveal any clear patterns or lines that could consistently be used as an independent estimate of age. Often the sectioned peels from the operculae had air bubbles and the lines were not clearly obvious.

Figure 4.9 to 4.13 shows Von Bertalanffy growth (VBG) curves, fitted to the modal size class data generated from the length frequency distributions determined using the method of Bhattacharya, using the programme Fishparm. Figure 4.9 a & b show the growth curves for *T. savignyi* and Figures 4.10 a, b & c for *E. junionae*. Figure 4.11 compares the VBG curves between of *E. junionae* from the three sites and figure 4.12 a compares the VBG curves of *T. savignyi* and figure 4.13 the growth curves of the two species. *Ergalatax junionae* grows faster at Ra´s al Qulay´ah than at the other two sites. *Thalessa savignyi* similarly grows faster at this site than at Ra´s Eqaila (figure 4.11 and 4.12). Figure 4.13 determines that *T. savignyi* grows faster than *E. junionae*. Despite the small size of *E.junionae* it is older than *T. savingnyi* of similar size. The differences in growth rate and final size maybe the result of the availability of potential prey items and therefore slower growth rates in *E. junionae*. More likely it is differences in the genetic make up of the two species, as *Ergalatax junionae*'s habit of residing and feeding in crevice on tube worms has, through evolution selected for individuals of a smaller size and hence slower growth than *T. savignyi*.

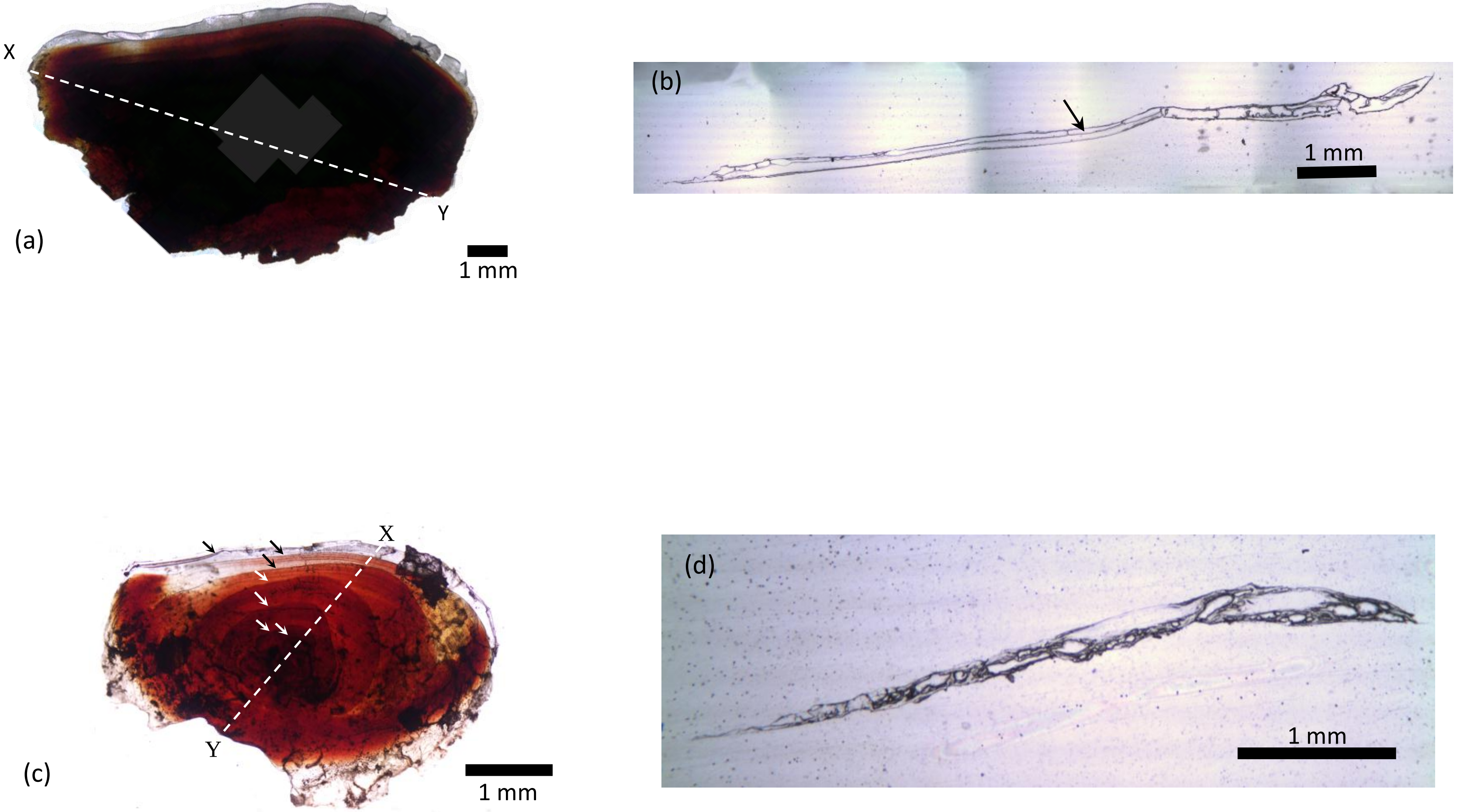


Figure 4.8 An operculum from a) *Thalessa savignyi* viewed under bright transmitted illumination that did not reveal any growth rings and X-Y the position of the section, b) section of a resin embedded *T. savignyi* operculum showing a growth lines (arrow), c) an operculum from *Ergalatax junionae* observed under bright transmitted illumination showing clear rings (arrows) and d) a section of a resin embedded of the same operculum in which no lines can be seen.

4.3 DISCUSSION

Thalessa savignyi was absent from the northern most site (Ra´s Ajūzah) and the reasons for this are unclear. In this chapter I have shown that the size frequency histogram of *Thalessa savignyi* from Ra´s Eqaila has a polymodal form unlike the distribution from Ra´s al Qulay´ah where the population has a unimodal form. Cerrato (1980) claimed because recruitment is seasonal a size frequency histogram will usually be polymodal, with each peak representing one or more spawning events and the subsequent recruitment of individuals arising from that spawning into the population. In the case of *Ergalatax junionae*, a unimodal shape was apparent in the populations from all three locations with the shape of the size frequency histogram either being influenced by continuous recruitment into the population throughout the year so that there are no apparent separate cohorts in the population, or that they represent one recruited age class, or highly variable ontogenetic growth rates of the juveniles, thus blurring the lines between each cohort. *Thalessa savignyi* and *E. junionae* appeared to recruit into the populations in October 2012 and January 2013. Although at Ra´s al Qulay´ah no seasonal recruitment into the *T. savignyi* population was obvious. Newly recruited individuals may have been missed in rock crevices and or they may have recruited into the subtidal zone before migrating uo shore when they had reached a size of ~20mm.

The size frequency distributions for both *T. savignyi* and *E. junionae* populations at Ra´s al Qulay´ah were different from the rest of the studied sites in that the populations of the two species lacked any small sized individuals and probably a missing recruitment of juveniles. The obvious increase in size of *T. savignyi* down shore at Ra’s Eqaila and Ra´s al Qulay´ah (Figure 4.5) reflects the effects of physical stress (i.e. desiccation, extreme temperature and salinity) on individuals on the middle and upper shore levels and the increased availability of prey species e.g. mussels and tube worms on the lower shore (see chapter 6 table 6.4 and 6.5 and discussion in chapter 7).

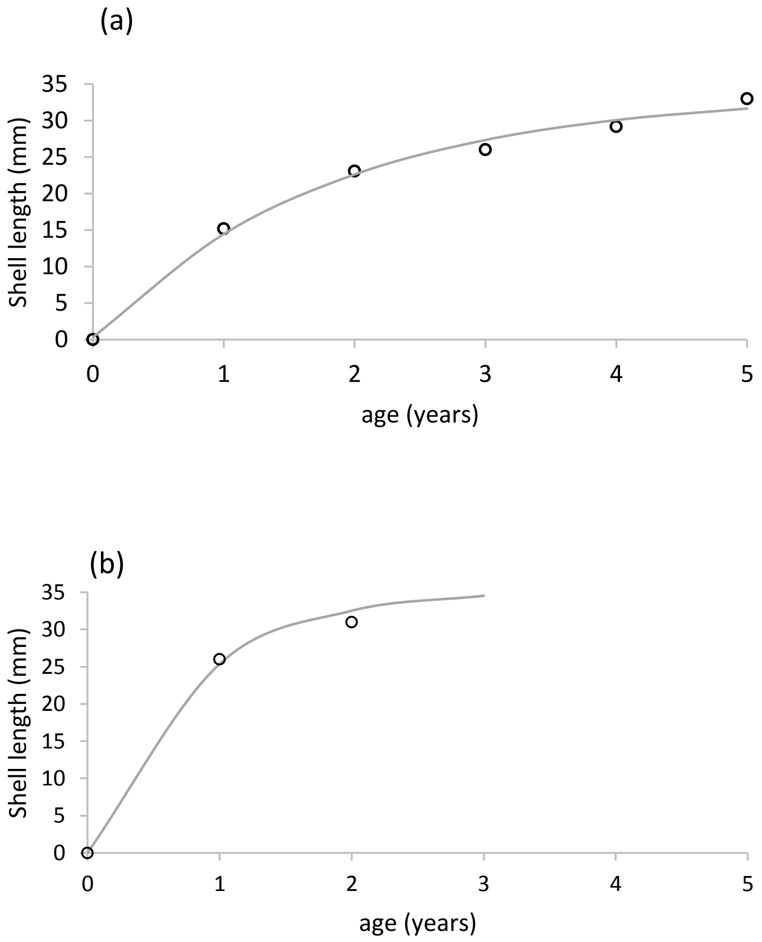


Figure 4.9 Population growth curve for *Thalessa savignyi* from a) Ra's Eqaila based on the modal sizes determined using the method of Bhattacharya. Von Bertalanffy growth curve fitted to the data ($Lt = 38.83(1\text{-}exp^{-0.321(t-0.5986)})$ and b) from Ra's al Qulay'ah Von Bertalanffy growth curve fitted to the data ($Lt = 35.32(1\text{-}exp^{-1.267(t-0.00057)})$.

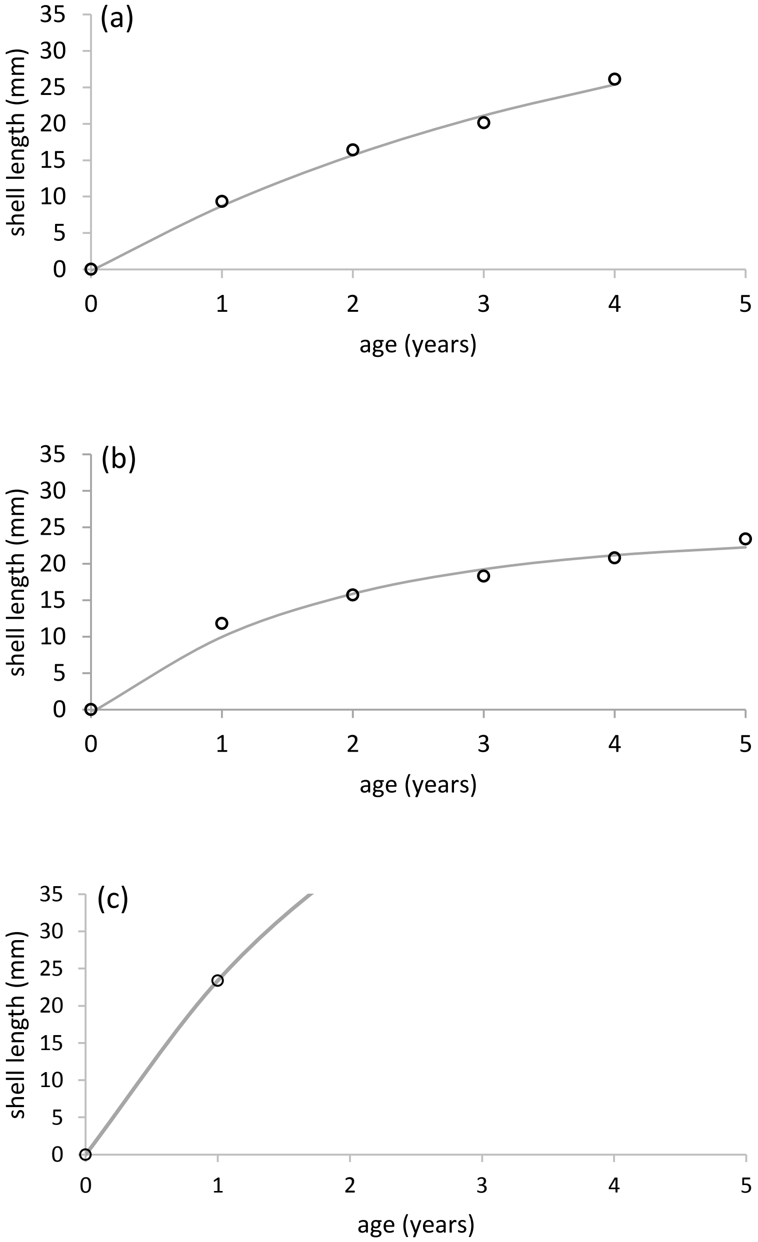


Figure 4.10 (a) Population growth curve for *Ergalatax junionae* from Ra´s Ajūzah based on the modal sizes determined using the method of Bhattacharya. Von Bertalanffy growth curve fitted to the data (Lt = 40.67(1-exp $^{-0.2457(t-0.01845)}$), (b) Population growth curve for *Ergalatax junionae* from Ra's Eqaila based on the modal sizes determined using the method of Bhattacharya. Von Bertalanffy growth curve fitted to the data (Lt = 23.70(1-exp $^{-0.5632(t-0.03287)}$) and (c) Population growth curve for *Ergalatax junionae* from Ra's al Qulay'ah ah based on the modal sizes determined using the method of Bhattacharya. Von Bertalanffy growth curve fitted to the data (Lt = 71.23 (1-exp $^{-0.398(t-0.000000000016)}$)

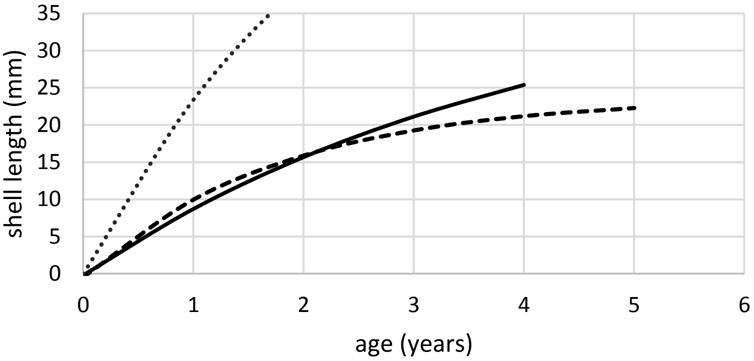


Figure 4.11 Comparison of Von Bertalanffy growth curves for *Ergalatax junionae* from Ra´s Ajūzah (solid line) and Ra´s Eqaila (dashed line) and Ra’s al Qulay’ah (dotted line).

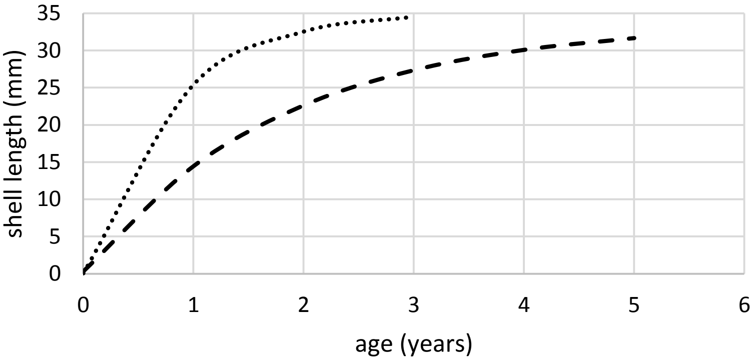


Figure 4.12 Comparison of Von Bertalanffy growth curves for *Thalessa savignyi* from Ra´s Eqaila (dashed line) and Ra’s al Qulay’ah (dotted line).

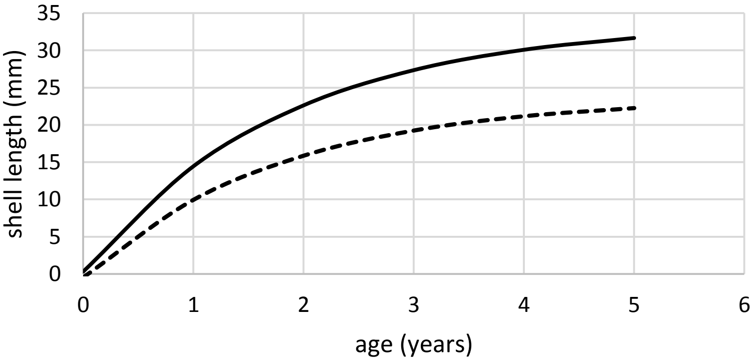


Figure 4.13 Von Bertalanffy growth curves for *Thalessa savignyi* (solid line) and *Ergalatax junionae* from Ra´s Eqaila (dashed line).

The maximum length of *E. junionae* declined down shore at Ra´s Ajūzah compared with the other 2 sites. The reasons for this are likely the presence of appropriate habitat in the form of small boulders (chapter 2, figure 2.8 and chapter 6, table 6.2) and more food availability (i.e. barnacles and mussels) on the upper shore than elsewhere on the shore at this site (see chapter table 6.3). Vermeij (1972) has earlier suggested that some gastropod species (e.g *Littorina saxatilis rudis*, *Nodilittorina helenae* etc.) may be larger on the upper shore and decline in size down shore than other species (e.g. *Neritidae sanguinolenta*, *L. littorea* etc.) and that these kinds of distribution patterns may reflect the ability of a species to withstand the harshness and physical stresses encountered on the upper shore that are associated with the transition from the terrestrial to the marine environment. Coupled with the availability of food this may control the patterns of size distributions with decreasing tidal level such that within a population, individual organisms of the same age will not be the same size.

Using growth marks (known as striae or rings) on the surface of operculae to estimate the age of some gastropods, including whelks, is a widely accepted method and has been used by many researches (*i.e.* Kideys, 1996; Ilano *et. al.*, 2004; Richardson *et. al.*, 2005). For instance, the operculum was successfully used to determine the age of *Buccinum isaotakii* through counting the number of striae (Ilano *et.al.*, 2004). Ilano *et.al.* (2004) found that almost all operculae had clear striae when they were stained with methylene blue and tetracycline hydrochloride. They found that there was a significant correlation between the number of striae on the operculum and the shell length and body weight. Whereas in the current study the operculae of *Thalessa savignyi* were not easy to read either with transmitted illumination or in section. This was associated to a great extent with the thickness of the operculum layers. On the other hand, *Ergalatax junionae* operculae were thin showing clear rings on their surface but no clear growth lines in polished sections. Although the result of this study was not very helpful in estimating the age of the two muricids, this does not mean that the technique could not be further developed. I do not dismiss the use of operculae growth rings as a potential method for estimating the age of these gastropods however for the technique to be reliable the periodicity of the rings would need to be established experimentally using marked individuals in field and laboratory experiments and this was beyond the scope of this thesis work.

Using the method of Bhattacharya it was possible to separate the size frequency distributions into their modal size (age) classes and then to plot growth curves using the modal size class length and age data. *Thalessa savignyi* grows faster than *E. junionae* and both grew faster at Ra´s al Qulay´ah than at the other sites. I will discuss this further in chapter 5 when I compare a range of methods for estimating the age of the two gastropods.

4.4 CONCLUSION

1) In this chapter I investigated the seasonal and spatial distribution of the lengths of *Thalessa savignyi* and *Ergalatax junionae* on three different shores along a latitudinal gradient from northern to southern Kuwait.
2) There was little evidence of recruitment into the populations although small juveniles appeared into the populations between October and January. Newly recruiting juveniles favoured rock boulders with small crevices and it was shown that when boulders and stones were transferred to the laboratory and left overnight, many small juveniles crawled out of the rocks. It is therefore recommended in future that during shore surveys for these and other gastropod species that boulders are collected overnight to ensure that all of the smallest size classes are measured.

3) Size frequency distributions of both species were successfully separated into their component modal size classes using the method of Bhattachyra and growth curves constructed for some of the populations where there were polymodal size classes.
4) *Thalessa savignyi* grows faster than *E. junionae* and both grew faster at Ra´s al Qulay´ah than at the other sites sampled.

4.5 REFRENCES

Bertness, M.D. (1977). Behavioural and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology*, Vol. **58,** pp. 87–97.

Cerrato, R. M. (1980). Demographic analysis of bivalve populations, pp. 417-465 *in* Rhoads, D. C. & Lutz, R. A. editors. Skeletal growth of aquatic animals. Biological records of environmental change. Plenum Press, New York, New York, USA.

Chatzinkolaou, E. & and Richardson, C. A. (2007). Evaluating the growth and age of the netted whelk *Nassarius reticulatus* (Gastropoda: Nassaridae) from statolith growth rings. *Marine Ecology Progress Series*, Vol. **342**, pp. 163-176.

Delany, J.; Myers, A.A. and McGrath, D. (1998). Recruitment, immigration and population structure of two coexisting limpet species in mid-shore tide pools, on the West Coast of Ireland. *Journal of Experimental Marine Biology and Ecology*, Vol. **221**, pp. 221–230.

Feare, C. J. (1970). Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). *Oecologia*, Vol. **5**, pp. 1-18.

Garrity, SD. (1984). Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology*, Vol. **65**, pp. 559-574.

Gedan, K. B., Bernhardt, J., Bertness, M. D., & Leslie, H. M. (2011). Substrate size mediates thermal stress in the rocky intertidal. *Ecology*, Vol. **92**, pp. 576-582.

Gendron, R.P. (1977). Habitat selection and migratory behaviour of the intertidal gastropod *Littorina littorea* (L.). Journal of Animal Ecology, Vol. **46**, pp. 79–92.

Ilano, A. S., Ito, A., Fujinaga, K., & Nakao, S. (2004). Age determination of *Buccinum isaotakii* (Gastropoda: Buccinidae) from the growth striae on operculum and growth under laboratory conditions. *Aquaculture*, Vol. **242**, pp. 181-195.

Kendall, M. A., & Lewis, J. R. (1986). Temporal and spatial patterns in the recruitment of Gibbula umbilicalis. *Hydrobiologia*, Vol. **142**, pp. 15-22.

Kendall, M. A. (1987). The age and size structure of some northern populations of the trochid gastropod Monodonta lineata. *Journal of Molluscan Studies*, Vol. **53**, pp. 213-222.

McGrath, D. (1992). Recruitment and growth of the blue-rayed limpet, *Helcion pellucidum* (L.), in southeast Ireland, *Molluscan Studies*, Vol. **58**, pp. 425-31.

Kideys, A. E. (1996). Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgol Meersunter*, Vol. **50**, pp. 353-368.

McQuaid, D. (1981). Population dynamics of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. *Journal of Experimental Marine Biology and Ecology*, Vol. **54,** pp. 65-76.

M.J. Moran, P.G. Fairweather, A.J. Underwood. (1984). Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology*, Vol. **75**, pp. 1–17.

Murray, S. N.; Ambrose, R.; Dethier, M. N. (2006). Monitoring Rocky Shores. University of California Press, Berkley.

Pardo, L. M. and Johnson, L. E. (2006). Influence of water motion and reproductive attributes on movement and shelter use in the marine snail *Littorina saxatilis*. *Marine Ecology Progress Series*, Vol. 315, pp. 177–186.

Richardson, C.A., Crisp, D.J. and Runham, N.W. (1979). Tidally deposited growth bands in the shell of the common cockle *Cerastoderma edule* (L). *Malacologia*, Vol. **18**, pp. 277-290.

Richardson, C. A., Saurel, C., Barroso, C. M., & Thain, J. (2005). Evaluation of the age of the red whelk *Neptunea antiqua* using statoliths, opercula and element ratios in the shell. *Journal of experimental marine biology and ecology*, Vol. **325**, pp. 55-64.

Roach, A. C. & Lim, R. P. (2000). Variation in the population dynamics of the intertidal pulmonate gastropod Salinator solida Martens (Gastropoda: Amphibolidae) at Towra Point, NSW, Australia. *Wetlands Ecology and Management*, Vol. **8**, pp. 53-69.

Saier, B. (2000). Age-dependent zonation of the periwinkle *Littorina littorea* (L.) in the Wadden Sea. Helgoland Marine Research, Vol. **54**, pp. 224–229.

Takada Y (1996).Vertical migration during the life history of the intertidal gastropod *Monodonta labio* on a boulder shore. *Marine Ecology Progress Series*, Vol. **130**, pp. 117–130.

Vermeij, G. (1972). Intraspecific shore-level size gradients in intertidal molluscs, *Ecology*, Vol. **53**, pp. 693-700.

CHAPTER FIVE

Determination of Age and Growth Using Statolith Growth Rings

5 Determination of Age and Growth Using Statolith Growth Rings

5.1 INTRODUCTION

Many molluscs, particularly bivalves have clear external annual growth rings (checks) and internal annual growth lines that can be used to determine their age (see Richardson, 2001). Early investigations demonstrated that bivalves contained tidally induced growth bands in the shells of intertidal bivalve species e.g. *Clinocardium nuttalli* (Evans, 1975) and the common cockle *Cerastoderma edule* (Richardson *et al.* (1979; Richardson 2001 and refernces therein). Richardson *et al.* (1979, 1980 a & b and 1981) showed, using marked cockles held under laboratory and field conditions that a growth band was deposited in the shell during emersion and that the growth increment, between adjacent growth bands, was formed at high tide when the cockles were feeding and accreting their shells. At the same time Jones (1980) built upon the findings of Ropes (1971) and demonstrated that Quahog clams *Arctica islandica* formed annual growth lines in the shell that were thought to be laid down annually during the winter. Schone et al (2003) demonstrated using oxygen isotopes, as a proxy for seawater temperature, that in fact the annual growth lines were deposited between late August and September. The reasons for the cause of these lines has been speculated to range from spawning to changes in the abundance of phytodetritus on the seabed (Schöne et al., 2003)

The use of annually resolved growth lines in the shells of a wide range of bivalve species but particularly focusing on *A. islandica* (see Schöne et al., 2003; Butler 2009, Butler et al. 2010a &b 2011) has expanded over the last 25 years and this area of research investigating periodic lines in shells is termed “sclerochronology”. A similar line of research on tree growth rings i.e. dendrochronology studies the spacings of the annully deposited tree rings in sections of the tree trunk. This approach has been used successfully to investigate seasonal changes in growth rates in both trees (dendrochronology) and shells (sclerochronology) to construct growth chronologies. Such chronologies have been used to reconstruct the environmental conditions that were present many hundrreds or even thousands of years ago before environmental records e.g. air temperatures were recorded (see Baillie & Pilcher, 1973; Leavitt & Long,1983).

Unlike bivalve shells the whorled shells of gastropods do not readily display growth marks on the shell surface or in shell section and thus cannot be easily used to determine their age. Some studies have successfully used mark and recapture methods to follow growth in some gastropods. For example, Clarke *et. al.* (2004) used mark/recapture to obtain length increment data for the limpet *Nacella concinna* from two contrasting sites in Antartica. They used a non-toxic calcium marker Calcein, a dye that is incorporated into the mineralising shell and produces a fluorescent mark to internally mark the shell and date the release of the limpets back into the field. Individual limpets were measured before release and after recapture several months later and the growth of their shells in the natural environment was estimated from sectioned shells that revealed the fluorescent Calcein mark. The distance between the mark and the shell margin was measured to give an estimate of shell growth between marking and release and final recapture. Their results revealed that this method was a suitable approach to determine growth rate in this species that lives in the severe environment of Antarctica and where shell growth is very slow and as a consequence difficult to determine with other methods i.e. bands on the shell (Clarke *et. al*., 2004). Bownes and McQuaid (2006) found that incorporated Calcein dye was only viable for 6 months in brown mussels *Perna perna* on South African shores. Earlier Murray *et.*

al. (2006) commented that using marking methods e.g. filing the shell edge or incorporating dyes was impractical as these marks could not be found later in the life of the animal and therefore could not be used to follow a mollusc's entire growth history from recruitment to death.

In the absence of any identifiable annual rings (checks) on or in the shell for determining growth rates other methods have been used to identify age classes of animals in a population. A key method that has been widely used to estimate demographic parameters in invertebrates (such as age) is by using the method of Bhattacharya and this graphical method of analysis, where age classes are separated statistically from size frequency distributions in a large population (e.g. Kideys, 1996), was used successfully in chapter 4 to resolve the modal classes in the populations of *Thalessa savingyi* and *Ergalatax junionae*. Although it is a useful tool in the study of population dynamics of marine invertebrates, it is recommended to use this method when no other reliable option is available to estimate age (see Cerrato, 1980).

There are other ways to successfully determine age in molluscs including gastropods using their hard parts e.g. the shell, opercula, and statoliths which have been extensively studied. Williamson and Kendall (1981) studied the gastropod *Monodonata lineata* using growth checks on the external shell surface and compared the age estimates with those obtained using Bhattacharya's method to separate length frequency distributions into their component modal size classes. They found that checks were formed annually between successive growing seasons and were also confirmed by size frequency analysis. Richardson *et. al.* (2005) evaluated the age of *Neptunea antiqua* using growth rings in statoliths, opercula growth layers, and element ratios cycles in the shell. Their study revealed that sectioned opercula exhibited distinct patterns of growth lines or adventitious layers that were clear to count. Statoliths are small microscopic calcified structures enclosed in the statocyst and are located in the foot and involved with balance and orientation. While statolith rings were often difficult to observe under transmitted light in resin mounted whole statoliths, due to refraction of the transmitted light, acetate peel replicas of sectioned statoliths (Kingley-Smith, 2002 and Chatzinikolaou, 2006) allowed more details to be seen and the rings to be more clearly seen. The results indicated an equivalence between the number of operculae adventitious layers and the number of statolith rings. Validation of the annual periodicity of the statolith rings was determined from an exact correspondence between the number of Mg: Ca ratio cycles taken from between the growth rings on the outer shell whorls and the number of statolith growth rings (Richardson *et. al.*, 2005).

In this chapter I will use the statoliths from adult *Thalessa savignyi* and *Ergalatax junionae* to illustrate the relationship between the statolith size (diameter) and shell size. I will also investigate the structure of the statoliths to understand and validate the annual deposition of the growth rings and to use these rings to estimate the age of both gastropod populations. This will allow an estimation of the population growth rate of both species to determine and compare any differences in the latitudinal growth rate of each species.

5.2 MATERIALS AND METHODS

5.2.1 Statolith extraction

Following collection of the seasonal samples of *Thalessa savignyi* and *Ergalatax junionae*, the shell length of each individual was measured (see chapter 3) and each one placed in an individual labelled plastic bag and frozen until further study. Using the seasonal length frequency distributions (chapter 4) gastropods covering the full size range sampled were selected from each population at each site regardless of the season when they were collected to study their statoliths. Sixty three *T. savignyi* from Ra´s Eqaila (12.2-40mm), thirty five from Ra´s al Qulay´ah (20.6-45.0mm), and thirty five *E. junionae* from Ra´s Ajūzah (6.7-28.6mm), fifty five from Ra´s Eqaila (4.9-24.9mm), and twenty five from Ra´s al Qulay´ah (20.2-27.2mm) were separated from the stored populations' samples. The frozen material was kept at room temperature (20^{o}C) and defrosted (~30 minutes) before crushing the shell using a vice, the sex of each species of gastropod was determined (presence or absence of a male penis) and dissection of the flesh undertaken to remove the operculae (see chapter 4) and the statoliths removed. A proportion of the animals were recorded as juveniles as no sexual characters were displayed.

A pair of microscopic statoliths (<1mm diameter) lie in the foot region of each gastropod each enclosed individually in a sac, the statocyst (see figure 5.1a). The walls of the statocyst were carefully teased apart under a transmitted dissecting microscope using fine forceps (Inox 5) and each tiny statolith carefully picked up, transferred to a watch glass containing distilled water for cleaning and then placed in 70% alcohol before storing in a labelled Eppendorf tube. To assist in picking up the statolith the water or alcohol were first removed from the watch glass using a pipette so all that remained in the watch glass were the statoliths.

Periodically statoliths were removed from the alcohol in their Eppendorf tube and processed in batches. One of the pair of statoliths was transferred and placed in a small (~3mm diameter) drop of thermoplastic resin on a glass slide which was made molten by warming over an alcohol burner. The statolith was manipulated and orientated in the molten resin under a dissecting microscope and the resin allowed to cool (~5 minutes) (see Richardson *et. al*., 2005). If the orientation of the statolith was not correct (see figure 5.1b) then the slide and resin were re-warmed and the statolith re-orientated. The slides and statoliths were viewed under a transmitted light microscope. Each statolith from an animal of known shell length was photographed and its total diameter measured using calibrated image analysis software (Image Pro Premier 9.1). A few statoliths were sectioned by grinding them very carefully on damp wet and dry paper (400-1000 grit) and finally polishing them on a soft cloth impregnated with diamond paste to try and improve the clarity of the internal structure of the statoliths.

Each statolith contains a series of rings. Sometimes the rings were clear (figure 5.1c & d) and unambiguous and easy to count but in some individuals they were weakly defined. The clarity of the rings was improved by taking a series of different focus photographs of the same statolith and then combining all the images to produce a multifocus image of the statolith (“focus staking”); a feature available in “Adobe Photoshop CS6”. This technique improved the clarity of the rings which were then counted to estimate the age of every individual of each species to construct a population growth curve. In addition ten of the largest individuals of each species from one site, Ra´s Eqaila, were selected and the diameter of the statolith at each annual ring was measured using the image analysis software. These data were then used to reconstruct the change in statolith diameter with age for these selected individuals in order to produce individual growth curves for *T. savignyi* and *E. junionae*.

5.2.2 Timing of growth ring formation

Between ten and fifteen statoliths from both species were selected from samples collected from the different sites collected in January, May, July and November to investigate the season of growth ring formation. Figure 5.2a & b show a series of photographs of statoliths collected throughout the year to illustrate the position of the growth ring in relation to the edge of the statolith in both gastropod species; the growth

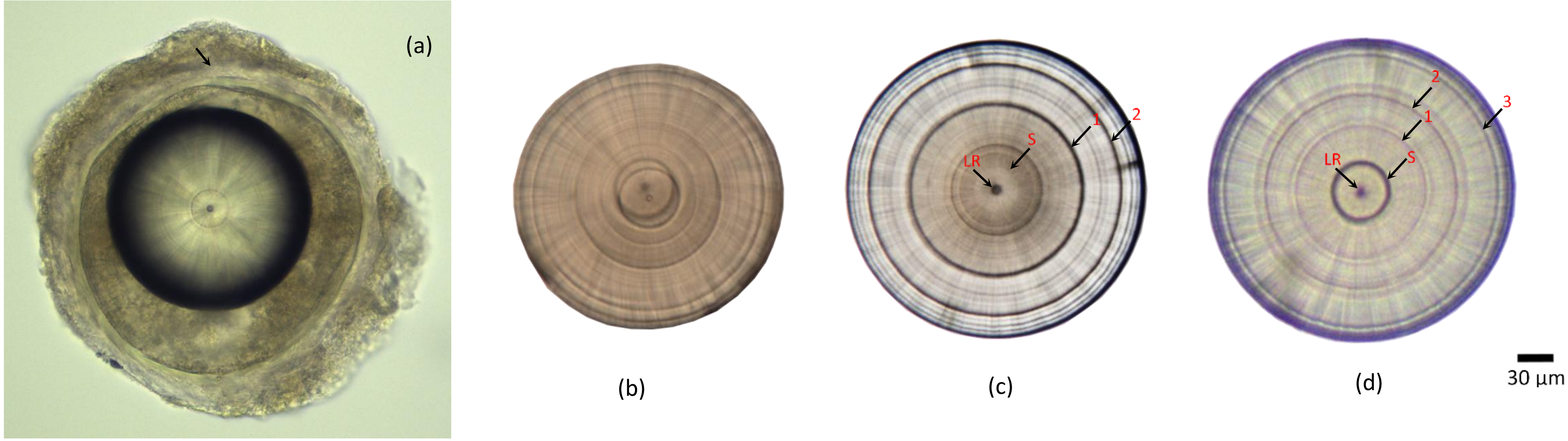


Figure 5.1. a) Appearance of a 171.63 µm statolith inside the statocyst (arrow) taken from *Ergalatax junionae* to show that the statocyst has to be teased apart before the statolith can be removed and examined. Photomicrographs of statoliths (b, c & d). b) showing the "double ring" appearance of a ring when a statolith from *Thalessa savignyi* is incorrectly aligned in resin, c) from an adult *Thalessa savignyi* (shell length 28.7mm and statolith diameter 154µm) and d) an adult *Ergalatax junionae* (shell length 20.5mm and statolith diameter 157µm). LR: Larval egg case statolith ring; S: larval metamorphosis ring; Annual rings labelled 1, 2 etc. The larval metamorphosis ring in (c) is weak in definition and not as clear as in (d).

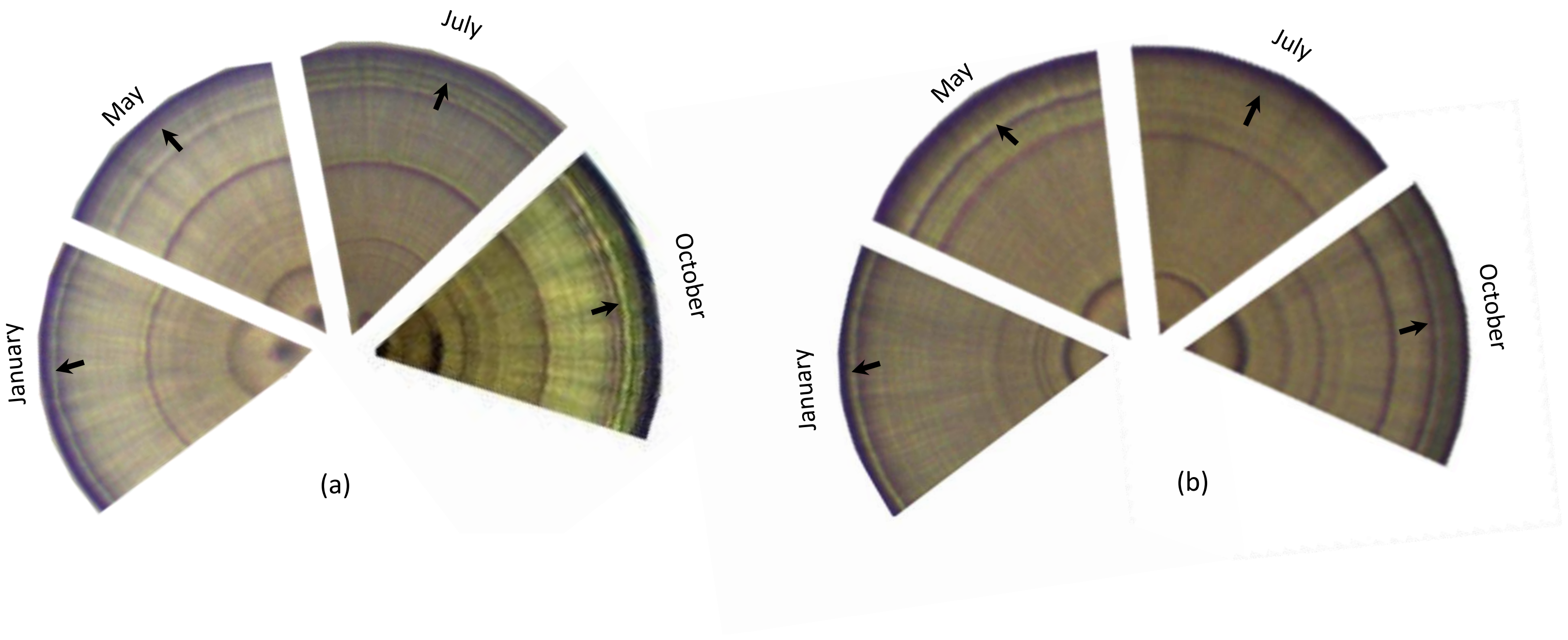


Figure 5.2. Photomicrographs of segments of statoliths from a) *Thalessa savignyi* and b) *Ergalatax junionae* collected in January, May, July and October to illustrate the seasonal formation of the annual growth ring (arrow).

ring likely forms between October and January, because in statoliths from the January collection the ring had just appeared at the statolith margin.

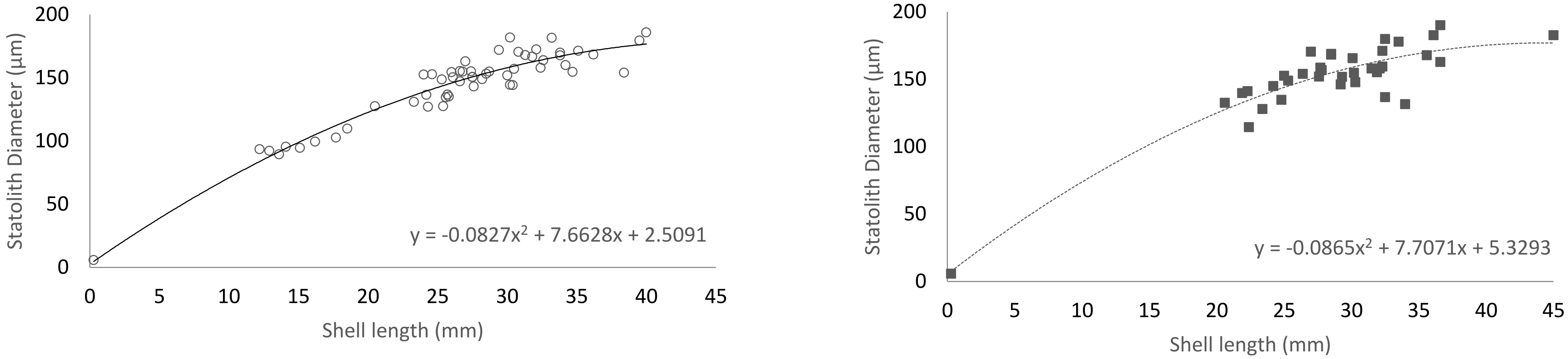
5.2.3 Comparison of the growth curves obtained from statoliths and analysis using Bhatacharrya's method

Statolith diameter against shell length was plotted for each species at each site (*T. savignyi*: figure 5.3a & b; *E. junionae*: figure 5.4a, b & c) and then the data combined together for each species (figure 5.3c & figure 5.4d respectively). The quadratic equations describing the relationships between these two dimensions are given on the appropriate figures. Using the equations from the combined data (*T. savignyi*: figure 5.3c and *E. junionae*: figure 5.4d) the predicted shell length at each statolith growth ring diameter was reconstructed to construct individual growth curves for the ten largest *T. savignyi* and *E. junionae* from only one site, Ra´s Eqaila. These predicted shell lengths against age (ring) data were then plotted and a growth curve fitted using Fishparm (see chapter 4) to estimate the Von Bertalanffy growth constants. The VBG curves generated from 1) the size frequency determinations, previously in chapter 4, 2) the population growth curves using the statolith rings and 3) the individual reconstructed growth curves were visually compared. Finally the estimates of the VB growth constants (K, Linf & t_0), determined using methods 1, 2 and 3, were tabulated and compared.

5.3 RESULTS

5.3.1 The Statoliths

The growth rings in the statoliths taken from *Thalessa savignyi* and *Ergalatax junionae* were generally clear when they were embedded in thermoplastic resin and viewed in transmitted light using a compound microscope. Grinding and polishing the surface to section the statolith was not successful in improving the details within the


(a) Ra´s Eqaila

(b) Ra´s al Qualay´ah

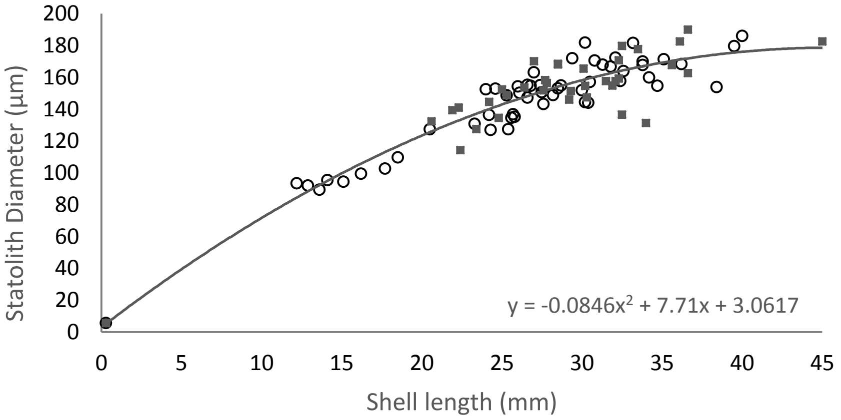

(c) *Thalessa savignyi*

Figure 5.3. *Thalessa savignyi* statolith diameter against shell length of individuals collected from a) Ra´s Eqaila and b) Ra’s al Qualay’ah and the data from both sites combined in c). The quadratic equations that describes the relationships between these two dimensions are indicated on each figure.

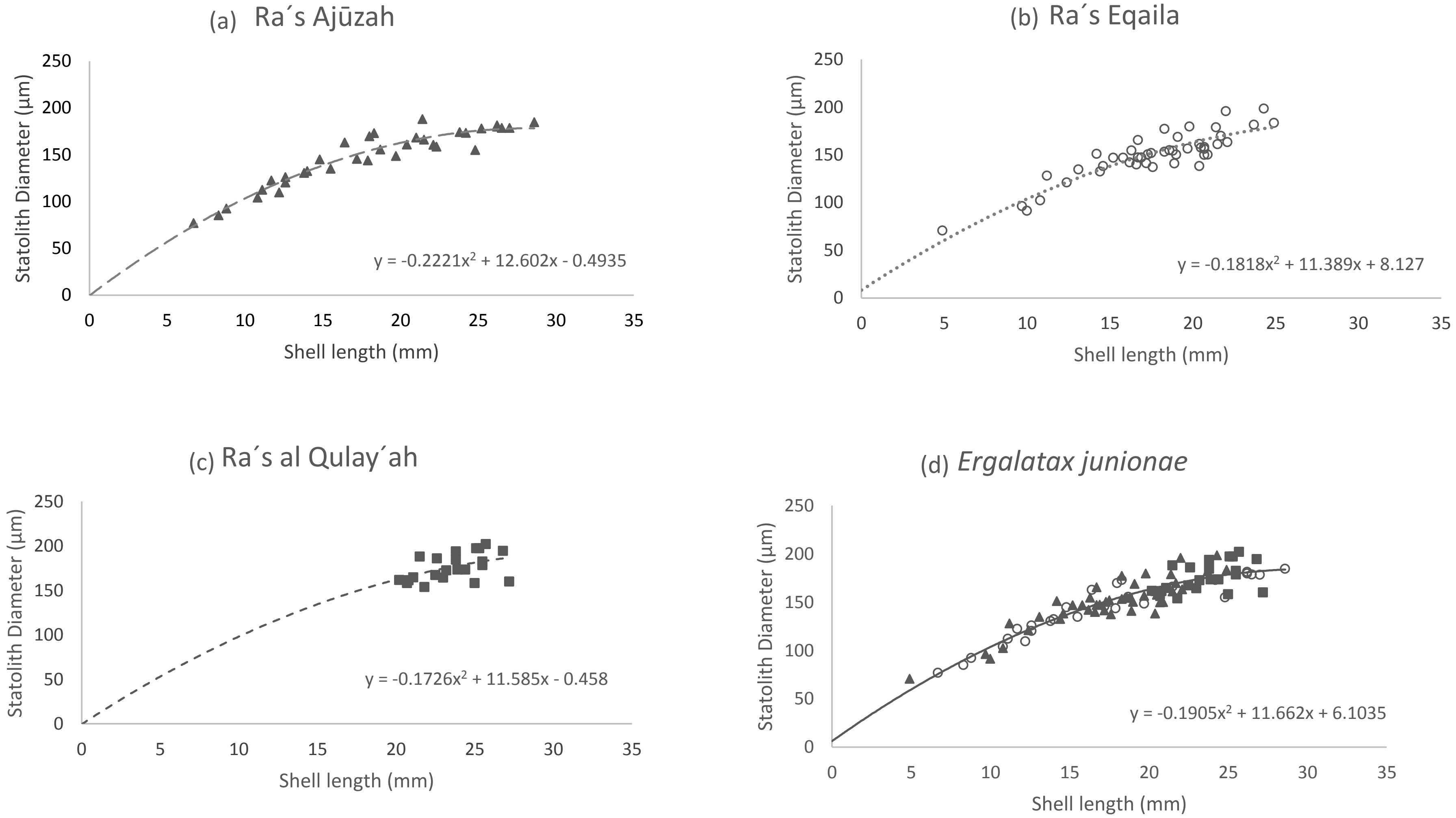
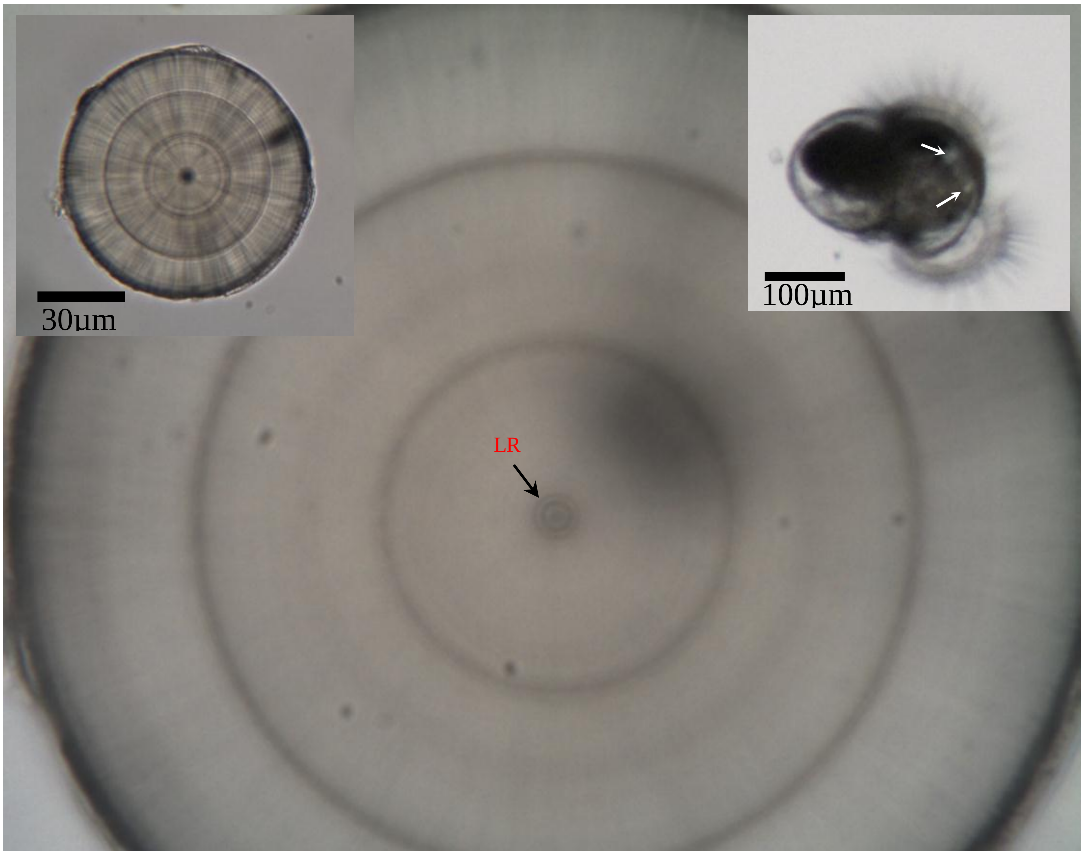


Figure 5.4. *Ergalatax junionae* statolith diameter against shell length of individuals collected from a) Ra´s Ajūzah, b) Ra´s Eqaila and c) Ra’s al Qualay’ah. d) is the combined data from individuals from all three sites. The quadratic equations that describe the relationships between these two dimensions are shown on each figure.



Figuer 5.5. Photomicrograph of a statolith from *Thalessa savignyi* (22.4mm shell length 114µm statolith diameter) collected from Ra's al Qualay'ah and observed under oil immersion (x100) to illustrate that the larval statolith is composed of several rings (LR). Inset (left) the same statolith observed under low power magnification. Inset (right) a larval *Thalessa savignyi* (=280µm) to show the position and size of the larval statoliths (white arrows).

statoliths and was quite time-consuming. Viewing the whole embedded statolith was satisfactory although a few minor problems occurred. On a few occasions a ‘double image’ of the first ring was observed (see figure 5.1b). This arose because the statolith was not orientated exactly on a vertical axis through the centre of the statolith. However its position was easily changed by warming the resin and re-orientating the statolith in the correct plane. Sometimes photographs of a statolith did not always reveal clearly focused growth rings, however using the multi-layer “focus stacking” feature in Photoshop it was possible, through the amalgamation of a series of photographs taken through the statolith, to increase the definition and appearance of the growth rings. The appearance of a statolith from *T. savignyi* and one from *E. junionae* is shown in figure 5.1c & d. A statolith contains a series of concentric rings of varying definition, clarity and spacing.

All the statoliths examined revealed the presence of a small diameter central core (figures 5.1c & d and 5.5). The diameter of this central core was 5.27± 0.06µm (n=74) and equates to the diameter of the larval statolith (see inset figure 5.5). On one occasion right at the start of my study an egg mass was laid by *T. savignyi* in the laboratory and larval development observed inside the egg capsules (see Chapter 6). The mobile larvae were observed, the egg capsule cut open and the released developing larvae photographed immediately. In only one image could the larval statolith be seen clearly and its diameter measured 5.6µm, which is very similar to the measured diameter of the central core of the adult statolith (i.e. 5.27± 0.06µm). These data demonstrate that the central core is laid down during embryonic life in the egg capsule and will now be referred to as the ‘larval egg case’ statolith ring (LR).

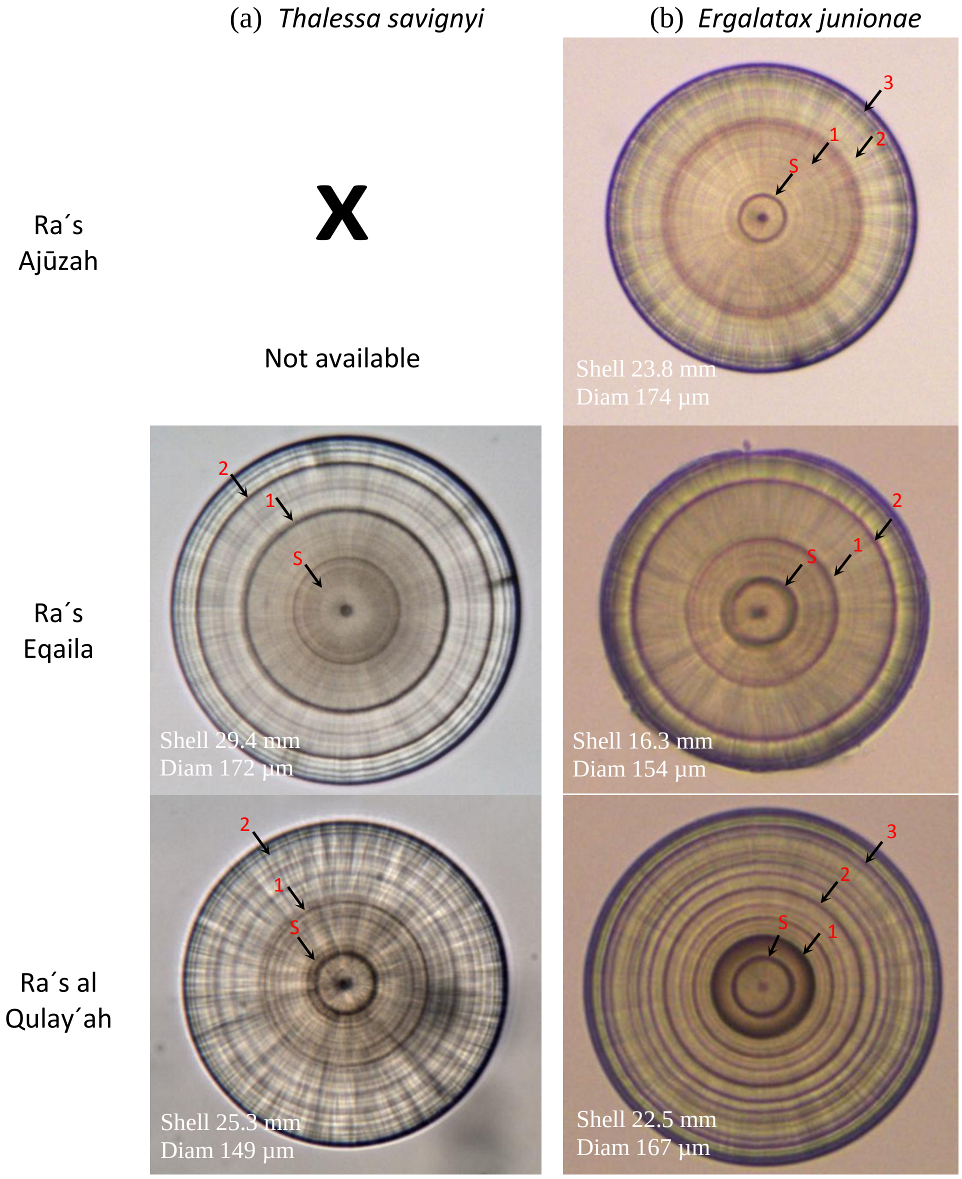


Figure 5.6. Statolith photomicrographs to show latitudinal variations and differences in the clarity and definition of the growth rings in (a) *Thalessa savignyi* and (b) *Ergalatax junionae*. The shell length (mm) and statolith diameter for each statolith are shown. S: larval metamorphosis ring; Annual rings labelled 1, 2 etc.

The obvious and strongly defined ‘first ring’ in the statoliths of both species of gastropod studied (see figure 5.1) are similar in appearance to those measured by Chatzinikolaou (2006) in *Hinnia (=Nassarius) reticulatus.* In studies by Chatzinikolaou (2006) and Chatzinikolaou & Richardson (2007) larvae of *H. reticulatus* were reared through to metamorphosis and the diameter of the last ring laid down in the larval statolith measured. The diameter of this ring (33.19 ± 0.13 µm) confirmed the existence of a ‘larval metamorphosis ring’. In *T. savignyi* and *E. junionae* the diameter of a similar positioned ring was measured in their statoliths. There was no significant difference in the diameter of the ring in *T. savignyi* from Ra´s Eqaila (30.15 ±0.34 µm) and Ra´s al Qulay´ah (29.30 ± 0.26 µm) (F value= 1.529, P= 0.221 and d.f. = 66). Similarly the diameter of this ring in *E. junionae* was not significantly different amongst the 3 populations at Ra´s Ajūzah (28.85 ± 0.37 µm), Ra´s Eqaila (28.72 ± 0.25 µm) and Ra’s al Qualay’ah (27.72 ± 0.42 µm) (F= 0.768, P= 0.467 and d.f. = 81) but there was a significant difference in the diameter of the ring between the two species (F=5.005, P= 0.001 and d.f. =150).

During my observations of the statoliths it soon became clear that there were differences in the definition of the growth lines, some were very darkly defined whilst others were weak in appearance. Also the definition of the rings and the number of weakly defined rings in the statoliths varied in statoliths taken from *E. junionae* and *T. savignyi* in the north and south of Kuwait. This was investigated further. Figure 5.6a shows a photomicrograph of a representative statolith taken from *T. savignyi* collected from Ra´s Eqaila and Ra´s al Qulay´ah. The rings in the statolith from Ra´s Eqaila are distinct and clear in definition with almost no fine rings present, unlike the statoliths from Ra´s al Qulay´ah in the south of Kuwait where it was often difficult to distinguish any prominent rings from the weakly defined rings. Similarly statoliths from *E.*

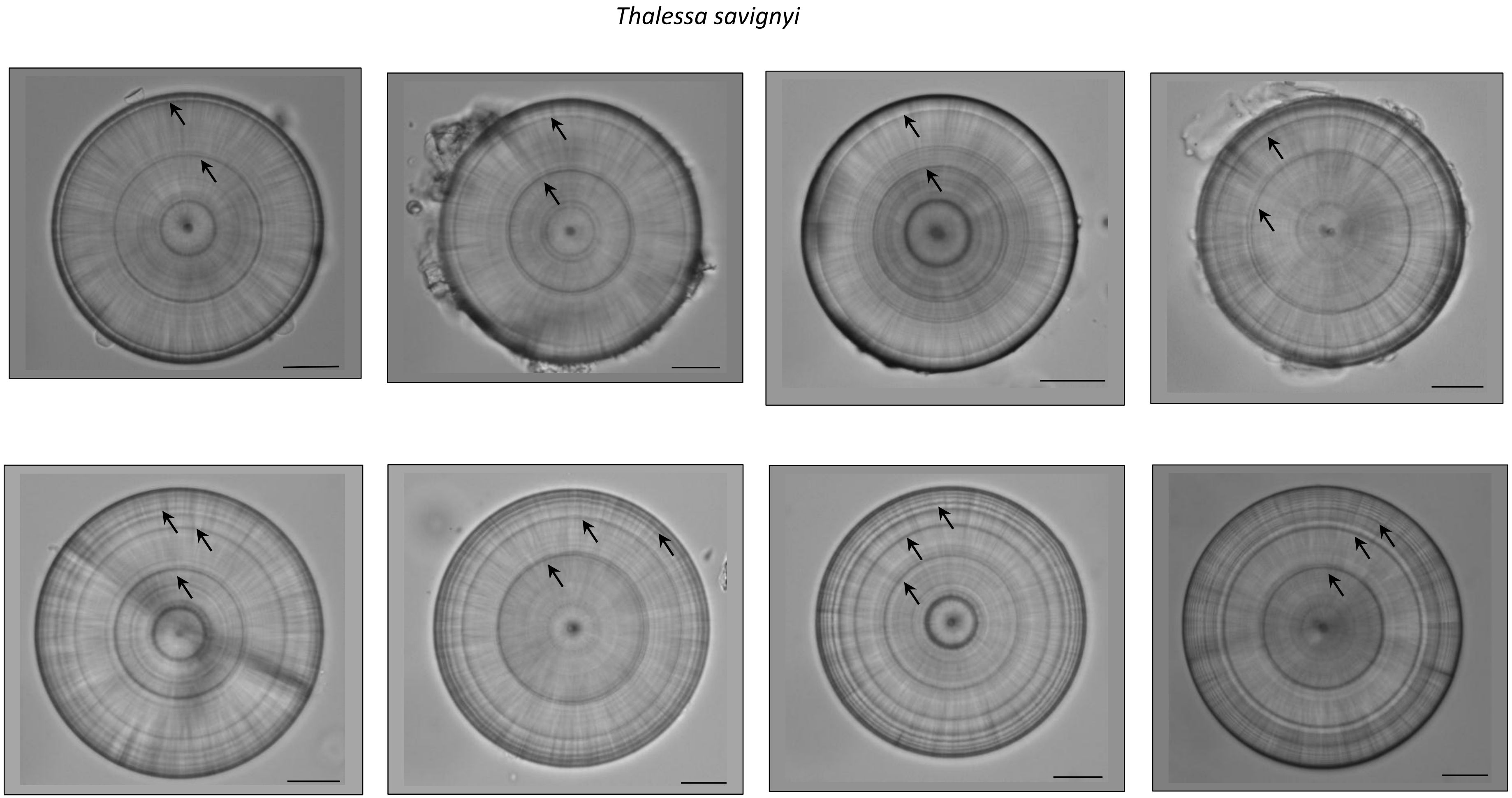


Figure 5.7. Photomicrographs of the statoliths of *Thalessa savignyi* to show the similarity of the width of the annual growth rings from animals of two and three years of age. Arrow indicate the position of the rings. (Scale bar = 30μm)

junionae at Ra´s Ajūzah contained more clearly defined rings than statoliths from Ra´s al Qulay´ah (see figure 5.6b).

Within any group of statoliths from one site there was variability in the definition of the growth rings and the presence of weak rings. Figure 5.7 from *T. savignyi* and figure 5.8 from *E. junionae* illustrates the variability in ring definition amongst animals of the same age and between animals of different ages. Counting of the number of rings was made difficult because of the variability in ring definition and the presence of weaker rings. Nevertheless when groups of statolith images from different individuals were viewed together apparent patterns of strongly defined rings appeared in the sequences of images (see figure 5.7 & 5.8) thus allowing the ages of the two species to be determined. Using this approach reliable estimates of the number of rings (ages) of between 30 to 50 *T. savignyi* and *E. junionae* of a range of shell lengths were obtained. These length at ring (age) data were plotted (see figures 5.9 & 5.10) for each species at each site, except Ra´s Ajūzah where no *T. savignyi* were collected, and VBG growth curves constructed (see chapter 4 for details of the VBG equation). Figure 5.12 shows a comparison between the growth curves generated using the population length at age data to compliment these population growth curves, growth curves from approximately ten individual *T. savignyi* and *E. junionae* were reconstructed using the established relationships between statolith diameter and shell length for each species from Ra´s Eqaila (*T. savignyi:* see figure 5.3 and *E. junionae* see figure 5.4) The individual length/age data for each species are shown in figures 5.12 with their fitted VBG curves.

In Chapter 4, I investigated the possibility of using the growth rings in the operculae of *T. savignyi* and *E. junionae* to estimate the age of these two species. Only

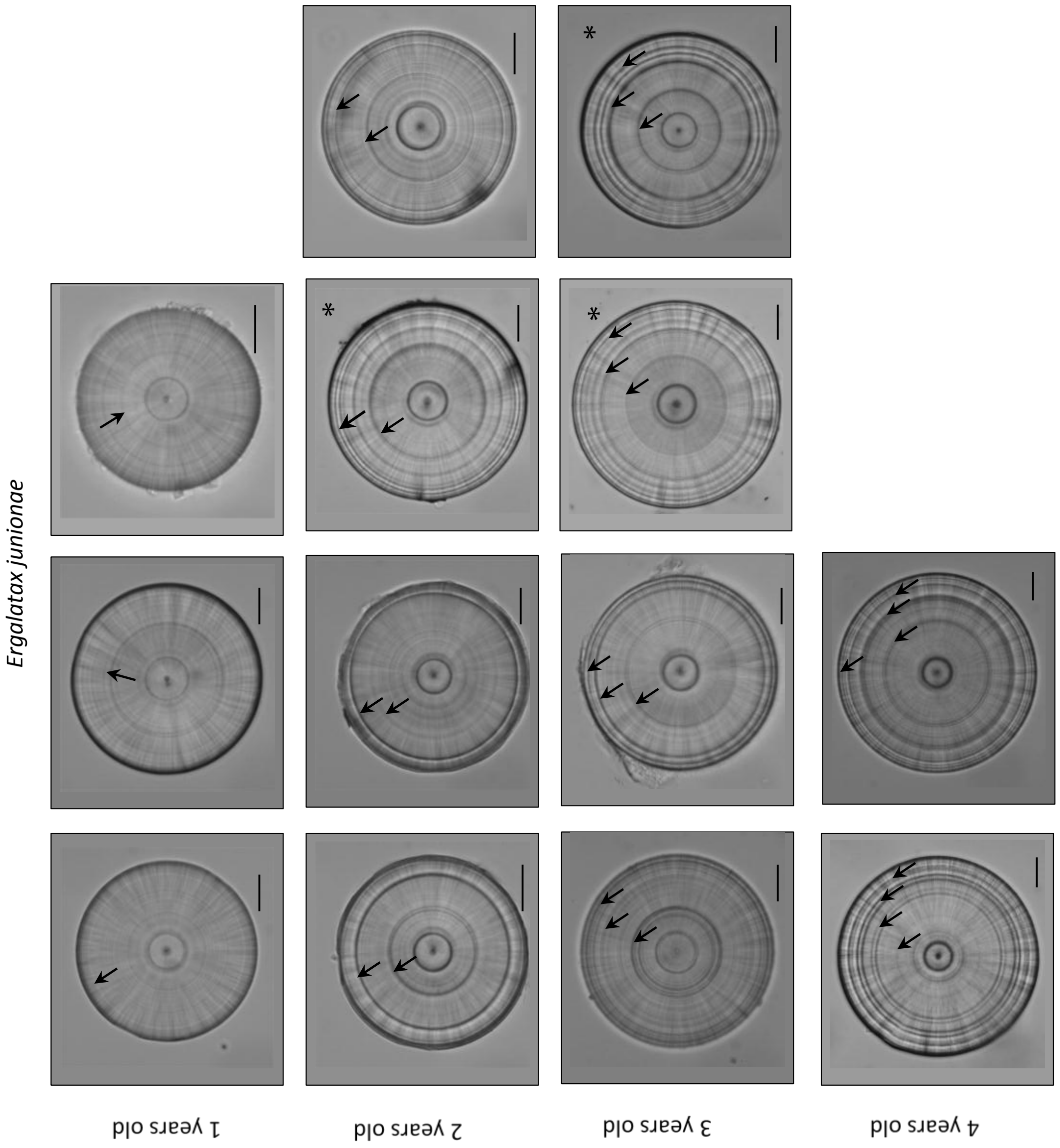
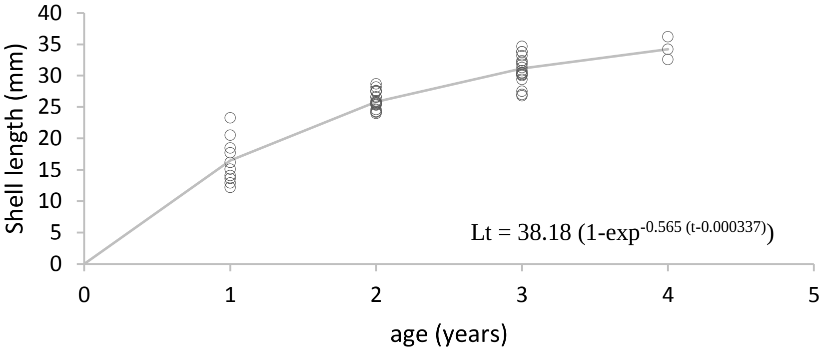


Figure 5.8. Photomicrographs of the statoliths of *Ergalatax junionae* to show the similarity of the width of the annual growth rings from animals of one, two, three and four years of age. Arrows indicate the positions of the annual rings. In some cases (asterisk) although the rings appeared clear during observation these rings did not extend throughout the entire statolith and were therefore not considered to be annual rings and not counted. (Scale bar = 30µm).

(a) Ra´s Eqaila



(b) Ra´s al Qualay´ah

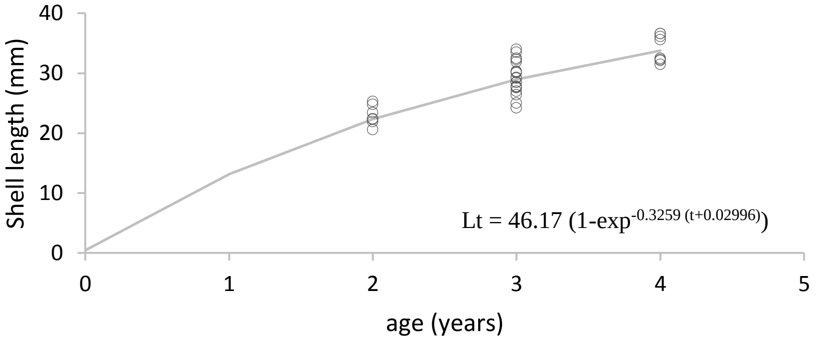
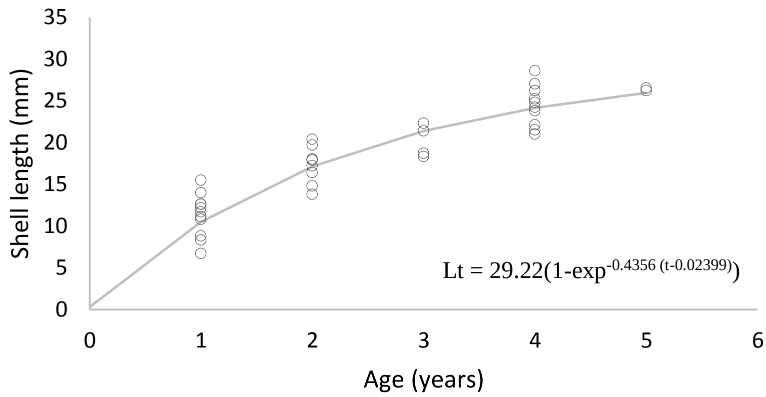
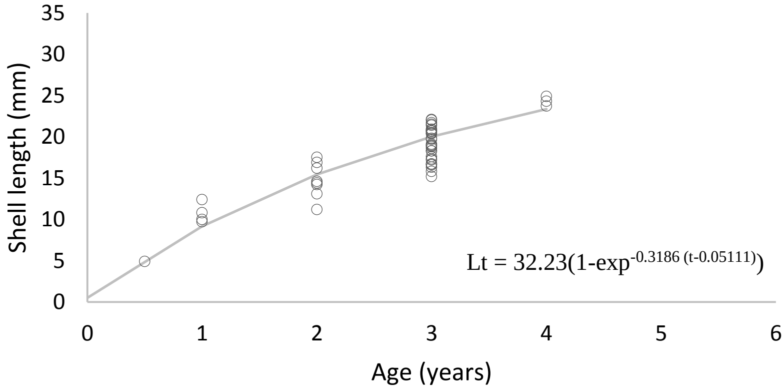


Figure 5.9. Population growth curves for *Thalessa savignyi* from a) Ra’s Eqaila and b) Ra’s al Qualay’ah based on estimates of the number of annual rings in the statoliths of animals of known shell length. Von Bertallanfy growth curves fitted to the data. No data were available for Ra´s Ajūzah.


(a) Ra´s Ajūzah


(b) Ra´s Eqaila

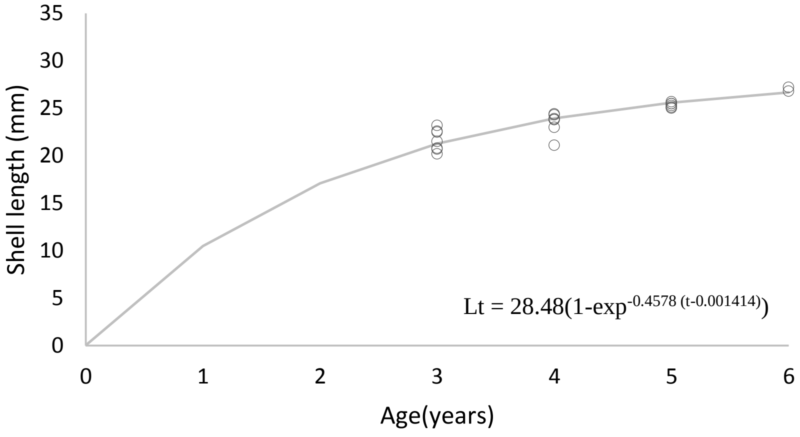

(c) Ra´s al Qulay´ah

Figure 5.10. Population growth curves for *Ergalatax junionae* from a) Ra's Ajuzah, b) Ra's Eqaila and c) Ra's al Qualay'ah based on estimates of the number of annual rings in the statoliths of animals of known shell length. Von Bertallanfy growth curves fitted to the data.

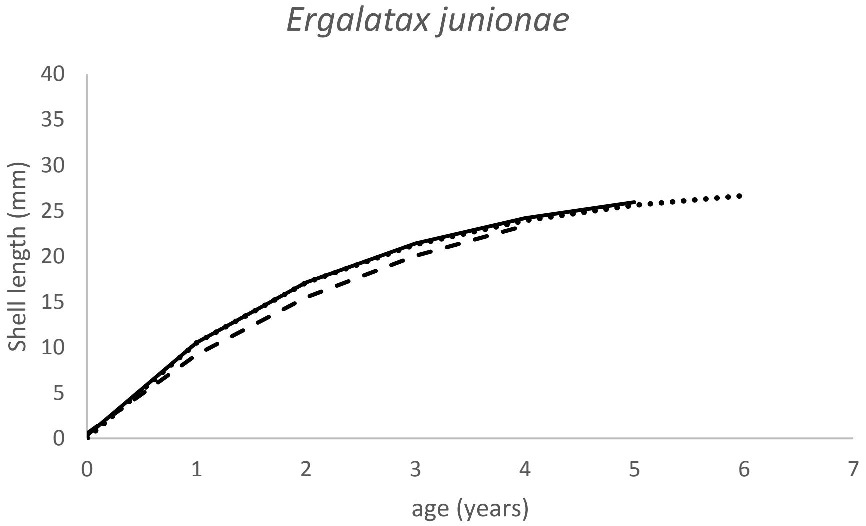


Fig. 5.11. Comparison of the population VBG growth curves of a) *Thalassa savignyi* Ra´s Eqaila (dashed line) and Ra´s al Qulay´ah (dotted line) and b) *Ergalatax junionae* from Ra´s Ajūzah (solid line) and Ra´s Eqaila (dashed line) and Ra´s al Qulay´ah (dotted line).

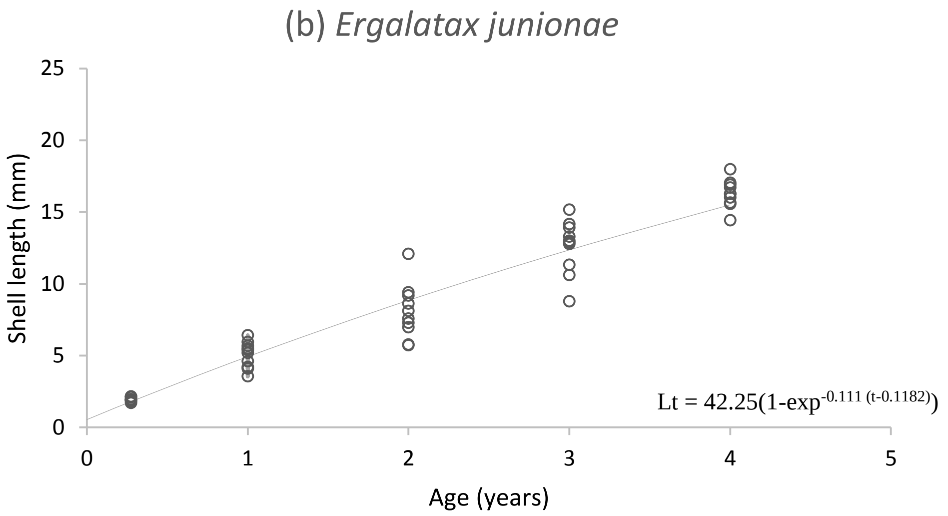


Figure 5.12. Reconstructions of the size at age determined from the statolith rings taken from the 10 largest individuals. a) the curvilinear relationship between shell length and age (statolith rings) for *Thalessa savignyi* from Ra’s Eqaila and b) *Ergalatax junionae* from Ra’s Eqaila.

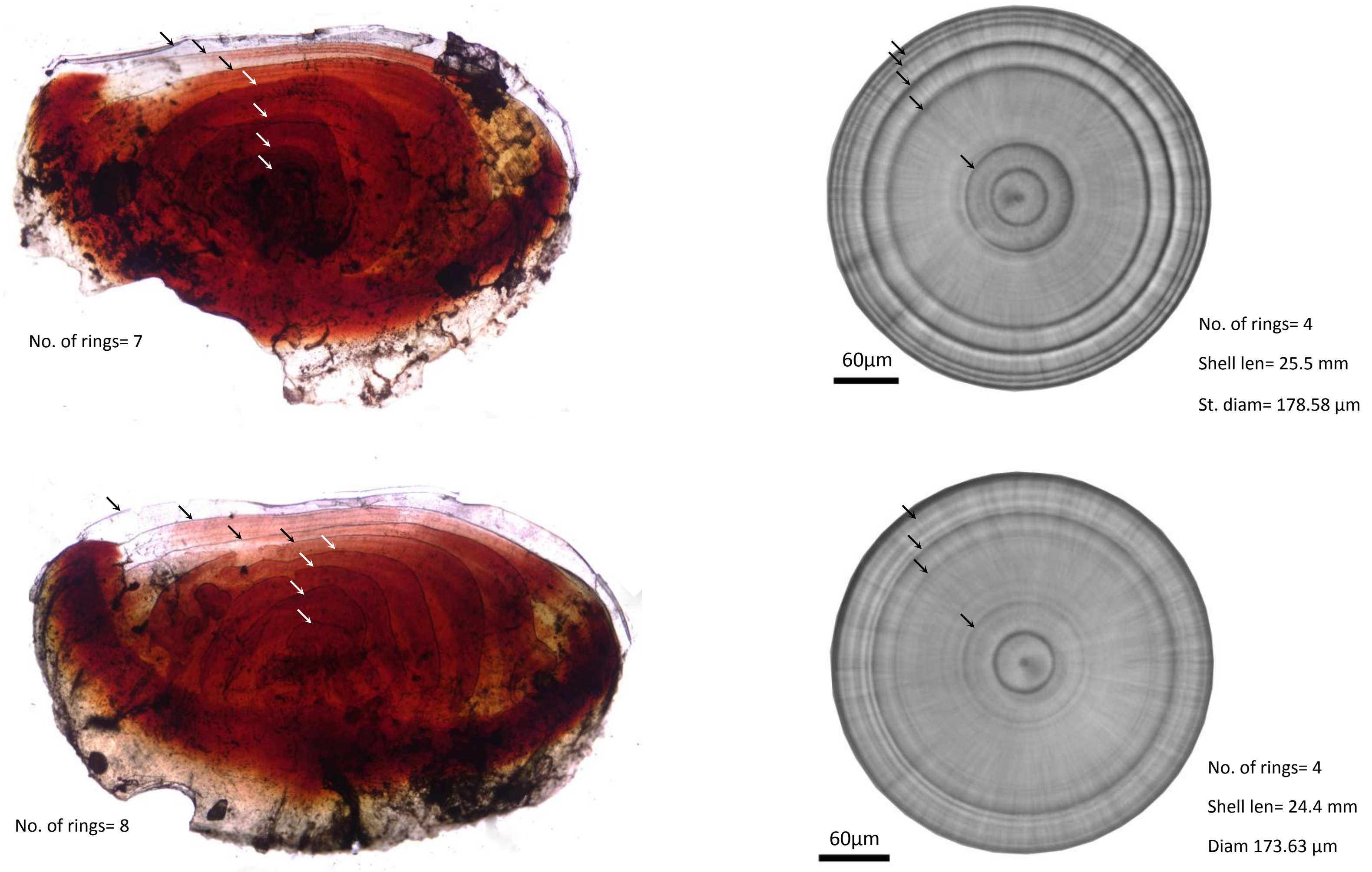


Figure 5.13. a) Appearance of growth rings in the operculum of *Ergalatax junionae* and for comparison and b) growth rings in a statolith taken from the same individual.

the operculum of *E. junionae* was transparent enough to view any growth rings (see Chapter 4). Figure 5.13 shows the appearance of the growth rings in an operculum from *E. junionae* and for comparison the rings in the statolith from the same individual. Many more growth rings (3 or 4 more) can be observed in the operculum compared to the statolith (4 or 5 rings). Since an annual periodicity of growth ring formation in the statolith has been validated in this chapter it is concluded that the operculum rings are not deposited annually and therefore these rings were not used to estimate age and to construct growth curves for the species.

Table 5.1 summarises the Von Bertalanffy growth constants determined using the length at age data from the length frequency distributions (Bhattachary's method – Chapter 4)and from this chapter, the population growth curves using age estimates from the statoliths and the reconstructed growth curves determined using the statolith growth rings. Comparison between the estimates of L∞ and K for *T. savignyi* using the length frequency distribution data and the population growth curves using the statoliths showed similarity in the L∞ values between animals from Ra´s Eqaila although a K value of 0.565 day^{-1} was higher using the statolith data. L∞ estimated for length frequency distribution from Ra's al Qulay'ah were misfit with a much higher value of K (1.267 day^{-1}). Comparison of the VBG constants for *E. junionae* shows that the values of L∞ determined using the length frequency distributions are either greater (Ra´s Ajūzah) or smaller (Ra's Eqaila) (*vice versa* for the K values) than the values determined using the statolith estimates; all 3 sites had similar estimates of the K and L∞ values using data from the statolith age estimates (see table 5.1). Construction of growth curves using the statolith ring width reconstructions from Ra's Eqaila was difficult because the size at age data for *T. savignyi* and *E. junionae* over-estimated L∞ and underestimated the K values using the other two methods (table 5.1). From these

Table 5.1. Summary table showing the Von Bertalanffy growth constants K, L_∞, and t_0 determined using three methods based on the separation of age classes using Bhattacharya's method, population growth curves determined using the population age estimates from the statolith growth rings and from reconstructions of the growth curves using the width of the statolith growth rings.

Method based on:	Location	*Thalessa savignyi*			*Ergalatax junionae*		
		K (day^{-1})	L_∞ (mm)	t_0 (years)	K(day^{-1})	L_∞ (mm)	t_0 (years)
Length Frequency distributions (Bhattacharya's method)	Ra´s Ajūzah	NA	NA	NA	0.246	40.67	0.01845
	Ra´s Eqaila	0.321	38.83	0.5986	0.563	23.70	0.03287
	Ra´s al Qulay´ah	1.267	35.32	-0.00057	0.398	71.23	1.6E-10
Population age (statoliths)	Ra´s Ajūzah	NA	NA	NA	0.436	29.22	-0.02399
	Ra´s Eqaila	0.565	38.18	0.00037	0.319	32.23	-0.05111
	Ra´s al Qulay´ah	0.326	46.17	-0.02996	0.458	28.48	-0.00141
Statolith reconstructions	Ra´s Ajūzah	NA	NA	NA	ND	ND	ND
	Ra´s Eqaila	0.157	58.87	-0.0768	0.111	42.25	-0.1182
	Ra´s al Qulay´ah	ND	ND	ND	ND	ND	ND

NA: Not applicable as *Thalessa Savignyi* was not present at this site. ND: No data as measurements were not undertaken.

comparisons it appears that the best estimates of K and L∞ were obtained from the population growth curves determined from the statoliths.

5.4 DISCUSSION

There were less fine rings present in the statoliths of *Thalessa savingnyi* from Ra´s Eqaila and the annual rings were feinter in appearance than in the statoliths collected from individuals from Ra´s al Qulay´ah in the south of Kuwait. In these statoliths there were numerous fine rings and the annual rings were more strongly defined. This same pattern was apparent in the statoliths of *E. junionae*; statoliths obtained from individuals in northern Kuwait had very few minor rings and the annual rings were clearer and weakly defined compared with the statolith rings from individuals in southern Kuwait where there were numerous feint rings and strongly defined annual rings. This is the first documented evidence of latitudinal differences in the definition of statolith rings and the frequency of fine rings. Previous work on *Polinices pulchellus* (Richardson *et al.*, 2005) and *Hinnia reticulatus* (Barroso *et al.*, 2005; Chatizinikolaou & Richardson, 2007) concentrated on investigating the use of statolith rings in estimating the age of these species from one locality i.e the coastal waters of the Rio de Formosa, Portugal or Anglesey, North Wales. Of the environmental factors, seasonal seawater temperature variations may affect the formation of the growth lines in the statoliths. Richardson *et al.* (1993), for example, observed that the annual lines in the shells of the European flat oyster *Ostrea edulis*, from northern Scotland, where winter seawater temperatures are colder, were more clear and distinct than growth lines in the shells of oysters from the River Fal in Cornwall where there is less of a seasonal (summer-winter) change in seawater temperatures. In Kuwait, however, the seasonal difference in seawater temperatures is not noticeably different in northern Kuwait compared with southern Kuwait so it is unlikely that seawater temperature alone is controlling the definition of the growth rings. Wind, waves and swell may suspend sediment and this can disturb the shell growth of molluscs (see Richardson, 2001). This is however unlikely in Kuwait as the wind direction is predominately on-shore in northern Kuwait compared with offshore in southern Kuwait as evidenced by the wind roses for the area (see chapter 2). One possible factor that might be influencing the formation of the weak statolith growth rings in both species from the southern latitudes is that the food supply might be more variable in abundance than in the north and this causes interruptions in body growth and less energy is available for deposition of the statolith and gives rise to weak rings. Without an abundance of prey items both species will be searching for food more frequently and therefore there will be interruptions in growth, seen as weak growth rings, in statolith deposition. In Chapter 6 I document the biodiversity of the fauna on the shores at the three locations and there is evidence that the northern site has a greater diversity of organisms and potential prey species. At Ra´s Ajūzah ten of the identified prey items were present whilst at Ra's Eqaila only 3 prey items were seen (see chapter 6).

The statoliths contained rings of different width. The first ring formed in *Thalessa savignyi* was a small one in the centre of the statolith. It is concluded that this ring is formed during larval development as a larva, where the statolith could be observed, was 5.6 µm in diameter. Statoliths of juvenile and adult *T. savignyi* contained a central small diameter ring (average 5.25µm) that was similar in diameter to the larval statolith. No larvae of *Ergalatax junionae* were reared (chapter 6) and therefore there was no evidence to support the idea that the first ring was the larval ring in this species, although the visual similarity of diameters in both species is strong evidence to suggest that the ring was also formed during larval development in *E. junionae.* The second ring that was clearly seen in all the statoliths was a ring of ~27-30µm diameter that was identified as a settlement ring. Although I have no direct evidence for this, its diameter is similar to the ring that was formed in *Hinnia reticulatus* following larval development and settlement (Chatzinikolaou & Richardson, 2007). Therefore it is assumed that this ring observed in the statolith of *E. junionae* and *T. savignyi* is also formed at metamorphosis from a larval to a post-metamorphic lifestyle. The wider growth rings are assumed to be formed annually.

In the 3 monthly samples of both species, growth ring formation appeared to start in May and by July the statolith ring had formed in most individuals. The warmest seawater temperatures and warmest air temperatures occur between May and July (26-33^{o}C) and (35-40^{o}C) respectively and this presumably causes a cessation in growth, either through increased metabolic rate and/or reduced shell and statolith growth. Also timing of growth ring formation appears to occur at the end of the egg laying season. Both *E. junionae* and *T. savignyi* laid egg masses in the laboratory at the end of June/beginning of July and in the field egg laying by *T. savignyni* was interrupted during the July collections (see Chapter 6). Egg laying by *Ergalatax junionae* was not observed in the field. It is suggested that annual ring formation is a combination of high summer water temperatures and breeding (egg laying in females) that causes the formation of the growth ring in females and high seawater temperatures and breeding in males. Thus the rings reflect a change in the rate of statolith deposition and are interpreted as being formed annually. Evidence from the work of Chatiznokolaou & Richardson (2007) on the statolith of *Hinnia retiuculatius* showed, using netted whelks grown over several annual cycles in the laboratory, that the rings were formed annually during the winter when seawater temperatures were coldest. It is therefore concluded that the rings in the statoliths of *T. savignyi* and *E. junionae* are similarly annual and are formed when seawater temperatures are highest and egg laying takes place.

Initially there was difficulty in deciding when a ring was an annual growth ring, however with time I became more experienced in the interpretation of the growth ring patterns. I also found it easier to distinguish between weak non-annual rings and annual rings when a series of images of the statoliths were prepared and the images quickly scanned. It soon became apparent that some rings were occurring in every statolith and these were usually the most strongly defined. The rings were difficult to resolve at the edges of the statoliths as they were often crowded together. However it was possible to estimate the age of the two species and to construct population growth curves. These data were supplemented with reconstructions of the shell length at each of the growth rings using the largest (oldest) shells.

The longevity of *Ergalatax junionae* is greater than *T. savignyi* with a maximum age of 6 years, whereas in *T. savignyi* the maximum age is exceptionally 5 years, but *T. savignyi* grows more quickly and is much larger in shell length (47mm) compared with *E. junionae* (27mm). The reconstruction of the growth of both species using the widths of the statolith growth increments between the growth rings provided some data but the growth curves were weakly curvilinear so that estimates of $L\infty$ were greater and K were lower than using the other methods. The likely reason is that the conversion of statolith widths to shell length was undertaken using a quadratic equation relating statolith diameter to shell length. Within these data there was considerable variability so that when statolith width was converted to shell length there was also uncertainty about the estimated shell length.

The operculum from both species was not used to determine their age. In *T. savignyi* the operculum rings were obscured because the operculum was thick and light could not penetrate. However in *E. junionae*, although rings were observed, they did not correlate with the number of rings in the statolith. The use of operculum rings as a reliable method has not been proved and in some studies e.g. Kideys (1996) a very large proportion (52%) of operculae could not be used to estimate the age of *Buccinum undatum*. Given the difficulties encountered in the literature and the clear validation of the annual periodicity of the statolith rings, it is not recommended that the operculae rings are used in age estimates or in the construction of growth curves for *E. junionae.* Despite the draw backs with the different methods the data that have been presented provide the first information about the difference in growth and longevity of two species of intertidal gastropods from the shores of Kuwait.

5.5 CONCLUSION

1) A method has been developed to estimate the age of *Thalessa savignyi* and *Ergalatax junionae* using statoliths removed from the foot of these gastropods.
2) An annual periodicity of the statolith growth rings has been validated using seasonally collected samples and it has been shown that the rings are deposited between November and January.
3) Other rings deposited during larval life, the “larval egg case” statolith ring (LR) and at the time of settlement, the larval metamorphosis ring ‘S’, from the plankton have been validated. There was no difference in the ‘S’ ring within species but a significant large diameter ring between species
4) A difference in the definition of the statolith growth rings and the number of weak growth rings has been shown to vary latitudinally with statoliths in the two species from northern Kuwait being more clearly defined and having less weak rings than individuals from southern Kuwait.
5) The difference in the number of weak rings maybe related to the availability of

prey items; the southern Kuwait sites have less potential prey species than those in North Kuwait.

6) *Thalessa savignyi* is a faster growing species and has a shorter longevity than the longer-lived and slower growing *E. junionae*.

5.6 REFRENCES

Baillie, M. G. L. & Pilcher, J. R. (1973). A simple cross-dating program for tree-ring research. *Tree-Ring Bullitten.Vol.* **33**, pp. 7–14.

Barroso, C. M., Nunes, M., Richardson, C. A., and Moreira, M. H. (2005). The gastropod statolith: a tool for determining the age of *Nassarius reticulatus*. *Marine Biology*, Vol. **146**, pp. 1139-1144.

Bownes S, & McQuaid, C.D. (2006). Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa? *Journal of Experimental Marine Biology and Ecology,* Vol. **338**, pp. 140–151.

Butler, P. (2009). Establishing the *Arctica Islandica* archive: Development of the definitive shell-based proxy for the North Atlantic shelf seas. Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Butler, P. G., Wanamaker Jr, A. D., Scourse, J. D., & Richardson, C. A. (2010 a). Reconstructions of summer seawater temperatures and water mass variability on the North Icelandic shelf using the shell of the bivalve clam *Arctica islandica*. In *EGU General Assembly Conference Abstracts*.Vol. 12, pp. 4133.

Butler, P. G., Richardson, C. A., Scourse, J. D., Wanamaker, A. D., Shammon, T. M., & Bennell, J. D. (2010). Marine climate in the Irish Sea: analysis of a 489-year marine master chronology derived from growth increments in the shell of the clam *Arctica islandica. Quaternary Science Reviews*, Vol. 29, pp. 1614-1632.

Cerrato, R. M. (1980). Demographic analysis of bivalve populations, pp. 417-465 *in* D. Rhoads, C. & Lutz, R. A. editors. Skeletal growth of aquatic animals. Biological records of environmental change. Plenum Press, New York, New York, USA.

Chatzinikolaou, E. (2006). The ecology and growth of the netted dogwhelk *Nassarius reticulatus* (Gastropoda: Nassariidae). Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Chatzinkolaou, E. & Richardson, C. A. (2007). Evaluating the growth and age of the netted whelk *Nassarius reticulatus* (gastropoda: nassaridae) from statolith growth rings. *Marine Ecology Progress Series*, Vol. **342**, pp. 163-176.

Clarke, A., Prothero-Thomas, E., Beaumont, J. C., Chapman, A. L. & Brey, T. (2004b) Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. *Polar Biology*, Vol. **28**, pp. 62–71.

Evans, J. W. (1975). Growth and micromorphology of two bivalves exhibiting non-daily growth lines. *Growth Rythms and the History of the Earth's Rotation. Wiley, New York*, pp. 119-134.

Jones, D. S. (1980). Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. *Paleobiology*, Vol.57, pp. 331-340.

Kideys, A E. (1996) Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgol Meersunter*, Vol. **50**, pp. 353-368.

Kingsley-Smith, Peter. (2002). The ecology of *Euspira pulchellus* (Gastropoda: Naticidae). Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Leavitt, S. W., & Long, A. (1983). An atmospheric 13C/12C reconstruction generated through removal of climate effects from tree-ring 13C/12C measurements. *Tellus B, 35*(2), 92-102.

Murray, S. N.; Ambrose, R.; Dethier, M. N. (2006). Monitoring Rocky Shores. University of California Press, Berkley.

Richardson, C. A., Crisp, D. J., & Runham, N. W. (1979). Tidally deposited growth bands in the shell of the common cockle, *Cerastoderma edule* (L). *Malacologia*, Vol. 18, pp. 277-290.

Richardson, C. A., Crisp, D. J., & Runham, N. W. (1980 a). Factors influencing shell growth in *Cerastoderma edule*. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, Vol. 210, pp. 513-531.

Richardson, C. A., Crisp, D. J., Runham, N. W., & Gruffydd, L. I. (1980 b). The use of tidal growth bands in the shell of *Cerastoderma edule* to measure seasonal growth rates under cool temperate and sub-arctic conditions. *Journal of the Marine Biological Association of the United Kingdom*, *60*(04), 977-989.

Richardson, C. A., Crisp, D. J., & Runham, N. W. (1981). Factors influencing shell deposition during a tidal cycle in the intertidal bivalve *Cerastoderma edule*.*Journal of the Marine Biological Association of the United Kingdom*, Vol. 61, pp. 465-476.

Richardson, C. A., Collis, S. A, Ekaratne, K., Dare, P., and Key, D. (1993). The age determination and growth rate of the European flat oyster, *Ostrea edulis*, in British waters determined from acetate peels of umbo growth lines. *ICES Journal of Marine Science*, Vol. **50**, pp. 493-500.

Richardson, C. A. (2001). Molluscs as archives of environmental change. *in* Gibson, R. N., Barnes, M., & Atkinson, R. *Oceanogrphy and Marine Biology: an Annual Review*, Vol. **39**, pp.103-164.

Richardson, C.A.; Kingley-Smith, P.; Seed, R. & Chatzinikolaou, E. (2005). Age and growth of the naticid gastropod *Polinices pulchellus* (Gastropoda: Naticidae) based on length frequency analysis and statolith growth rings. *Marine Biology*, Vol. **148**, pp. 319-326.

Ridgway, I. D., & Richardson, C. A. (2011). *Arctica islandica*: the longest lived non colonial animal known to science. *Reviews in Fish Biology and Fisheries*, Vol. 21, pp. 297-310.

Ropes, J. W. 1971. Surf clams and ocean quahogs. Annual Report American Malacological Union Bulletin.Vol. 37, pp.22-23.

Schöne, B. R., Oschmann, W., Rössler, J., Castro, A. D. F., Houk, S. D., Kröncke, I., Dreyer, W. , Janssen, R., Rumohr, H. & Dunca, E. (2003). North Atlantic Oscillation dynamics recorded in shells of a long-lived bivalve mollusk. *Geology*, Vol. 31, pp. 1037-1040.

Williamson, P., & Kendall, M. A. (1981). Population Age Structure and Growth of the Trochid *Monodonta Lineata* determined From Shell Ring. *Journal of the Marine Biological Association of the United Kingdom*, Vol. **61**, pp. 1011-1026.

CHAPTER SIX

Shore Biodiversity and Notes on Feeding and Reproduction in Two Muricacean Gastropods

6 Shore Biodiversity and Notes on Feeding and Reproduction in Two Muricacean Gastropods

6.1 INTRODUCTION

Several large taxonomic expeditions have been undertaken to the Gulf regions (e.g. the SIBOGA expedition (1889-1900) and John Murray Expedition (1933-34), etc.) which produced lists of marine species that were collected. The first attempt to gather this information into one identification guide to help scientists was accomplished by Jones (1986) who illustrated and described the common intertidal marine fauna and flora of Kuwait and the Arabian Gulf. Although Jones's (1986) guide is helpful in identifying many intertidal organisms, he did not specify where these intertidal species were found on the shores of Kuwait or whether they were from other areas of the Gulf region. In 2012 another guide was published (Al-Yamani, *et. al.*, 2012) that illustrated the wide diversity of the common macro-benthos from 19 subtidal and 19 intertidal stations across the breadth of the intertidal and coastal waters of Kuwait. This guide has similarly provided useful general information on the benthic species present along the coastline of Kuwait. The surveys were qualitative and were designed to elucidate the diversity of the organisms with a consideration of their spatial distribution. Neither of these publications provide any information on seasonal patterns of occurrence or the zonal distribution of the macro-algae and fauna. Therefore, there is a large gap in the understanding of the distribution of the fauna, what area they occupy and what physical and biological factors influence their distribution. Information on the zonal distribution of the fauna and flora is necessary in order to appreciate the distribution of the gastropods in my study, *Thalessa savignyi* and *Ergalatax junionae*, and their interactions with other intertidal species. In this final chapter I will document the seasonal occurrence and zonal distribution and discuss the dominance of the most common macro-organisms that were found on the three shores.

Prosobranch gastropods display three developmental strategies – oviparity, semioviviparity and oviviparity (see Fretter & Graham, 1994). Members of the Neogastropoda are oviparous gastropods that deposit spawn (egg masses) on a substratum and the larvae develop within egg capsule within the egg mass. This gives rise to crawl away larvae e.g. in the dog whelk *Nucella lapillus* and the common whelk *Buccinum undatum* or veliger larvae are released directly into the plankton e.g. in the netted whelk *Hinnia* (=*Nassarius*) *reticulatus* (Chatzinikolaou, 2006; Chatzinikolaou and Richardson, 2007) or the necklace shell *Polinices pulchellus* (Kingsley-Smith, 2002 and Kingsley-Smith *et. al*., 2005). Encapsulated eggs protect the developing larvae from physical damage and predation. In the only publication that I could find on the reproductive biology of *Thalessa* this species like other neogastropods lays encapsulated egg masses. Eisawy & Sorial (1974) found that the breeding season of *Thais* (=*Thalessa) savinignyi* in the Egyptian Red Sea occurred annually between August and November. The size of the egg capsules that were laid in laboratory aquaria was related to the size of the adult *T. savignyi* (Eisawy & Sorial, 1974) and *H. reticulatus* (Chatzinikolaou, 2006). Eisawy & Sorial 1974 found that the embryos development inside the egg capsules was variable between 30 and 60 days.

Members of the family Muricidae and Naticidae are the dominant groups of marine organisms that predate animals that possess thin calcified shells and tubes and employ a method of drilling a hole using their radula and acidic secretions (see Morton & Chan, 1997) to obtain access to the flesh inside. Naticids and muricids leave a permanent record of their predation in the valves of their prey in the form of characteristic drill holes (Carriker, 1981). Populations of drilling gastropods occur in every coastal water around the world (Carriker, 1981), although a wider variety of species are found in tropical waters. The greatest abundance of muricid and naticid drilling gastropods occur in shallow waters. Muricid gastropods are common members of intertidal rocky shore communities and are specialist predators of shelled prey particularly bivalve species. Muricids also commonly predate barnacles, small crabs, encrusting bryozoans and fish carrion (see Kabat, 1990). The Muricid *Nucella lapillus* for example feeds mainly on mussels (Hughes & Dunkin, 1984) and limpets by drilling through their shells. However barnacles are sometimes drilled through their tergal plates or sometimes they are predated by prising apart the plates (Dunkin & Hughes, 1984; Hughes, 1986).

In this chapter I survey the distribution of the fauna and flora along transects across the three shores in an attempt to understand the distribution of *Thalessa savignyi* and *Ergalatex junionae*. During the course of my surveys and laboratory studies I gathered some opportunistic data on the feeding, egg laying and larval development of the two muricacean gastropods. This information is intended to assist in understanding the distribution of the two predatory gastropods on the shores of Kuwait.

6.2 MATERIALS AND METHODS

6.2.1 Estimates of species composition of the shores

At each station and for each of the four seasons, the organisms within a $1m^2$ quadrat (subdivided into $10cm^2$ areas), were identified by collecting one representative individual of every species from within the quadrat and then identified later. The area within the quadrat was photographed to record the substratum type and size (e.g. bare rock, small or large boulders, pools, sand etc.) and the images were later viewed to determine the percentage cover of the substratum, algal cover and abundant organisms. The organismal distribution data were then used to establish the limits of the biological zones on the shore at the three sites. A table of the presence and absence of each species at each sampling station, including a relevant photograph taken by myself, was contructed for each of the three locations. These data were further analysed to investigate the contribution of the numbers of each species in each phyla of organsims expressed as a percentage of the total number of species counted at each location. These data are presented as pie charts to visually demonstrate the contribution of each phylum of organisms to the total diversity of organisms at each location.

6.2.2 Observations of reproduction

In the spring (May) approximately 20 large adult *Thalessa savignyi* were collected from mid shore at Ra's Eqila and together with some large stones, (20-30cm) in length and covered with tube worms (*Spirobranchus kraussii*) and mussels (*Brachidontes variabilis*), were placed in seawater in a bucket and transferred to the aquarium at KISR (Kuwait Institute for Scientific Research). A few large individuals of *Ergalatax junionae* were also collected and placed in a separate aquarium. Over the following weeks both species were observed to lay vasiform shaped egg capsules during the middle of June (~20th June); *T. savignyi* laid egg capsules (~ 4.5 mm) (figure 6.1 and 6.2) on the rocks in the tank whilst *E. junionae* crawled up the glass sides of the aquarium and laid small (~ 3 mm) egg capsules close to the bubbles from the aeration pumps (figure 6.3). The egg capsules of *E. junionae* degenerated after a few days and did not mature. Every 10 days an egg capsule from *T. savignyi* was removed from the egg mass and examined in a dissecting microscope. Around the end of July the developing larvae in the egg capsule became more active and could be observed trying to hatch from the egg capsule. The capsule was then opened gently and the released larvae observed (figure 6.1 c) and photographed.

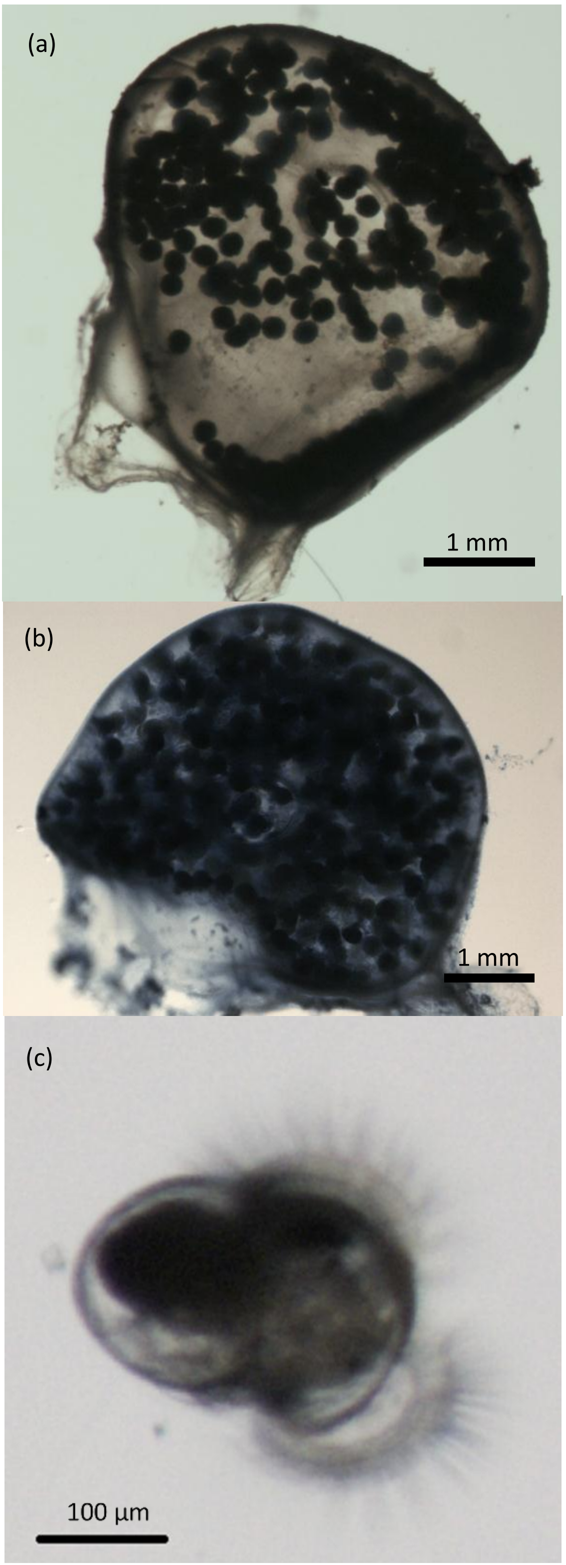


Figure 6.1. Photographs of the vasiform-shaped capsules of *Thalessa savignyi*. a) during the early stages of development (1 week following laying), b) after about 30 days and close to hatching and c) a newly hatched larva.

6.2.3 Observations of feeding

During the field surveys for *T. savignyi* and *E. junionae* feeding individuals were observed on a variety of organisms including *Spirobranchus kraussii, Brachidontes variabilis, Amphibalanus Amphitrite, Clypeomorus bifasciata, Striostrea margaritacea, Cerithium scabridum.*

6.3 RESULTS

6.3.1 Biological patterns of zonation

The seasonal presence (P) or absence (A) of each genus and species at the three sites is summarized in Table 6.1 and the P/A of individuals at each station surveyed throughout the year documented in Tables 6.2 to 4. In the following section I will discuss the P/A of groups of organisms and of each of the common organisms both in terms of their latitudinal occurrence and tidal distribution (high, mid and low shore).

Algae: *Ulva flexuosa* was only found at Ra´s Ajūzah on the high to mid shore (stations 1-6) and was not present on the other two shores. It was present on these shores during the winter season (January). *Colpomenia sinuosa* was absent at the north site Ra´s Ajūzah, as well as not being present at Ra´s Eqaila, but the species was found in numbers in the lower eulittoral fringe (below M.H.H.W.N. level) in January at Ra´s al Qulay´ah. Like *Colpomenia*, the species *Sargassum oligocystum* was only found at Ra´s al Qulay´ah but at only one station on the lower part of the shore (station 7). *Padina gymnospora* was present at all of the three sites investigated during May, however, it was more abundant at Ra´s Ajūzah and Ra´s al Qulay´ah than at Ra´s Eqaila. Also, according to my observations, I found this species was almost entirely absent from high water level at Ra´s Ajūzah whilst at Ra´s al Qulay´ah it was present at almost all of the stations (except stations 2 & 5). Different species of the genus *Padina* were also present at the southern site, Ra´s al Qulay´ah, and this was identified as *P. tetrastromatica*. It was more common in July and was never seen at the other two sites. *Iyengaria stellata* only occurred at Ra´s Eqaila, specifically at the middle (stations 2 & 3) and the lower parts of this shore (stations 4, 6-9). This species was recorded in winter season (January) and was absent the rest of the year. *Feldmannia mitchelliae* was present in January at all three shores but it is variable in its distribution at each locality. For example, at Ra´s Ajūzah it occurred in good (>10 individuals) numbers on the upper-mid shore (station 2), as well as in the upper- low shore (station 7-10). While at Ra´s Eqaila it was only found at two stations on the lowest part of the low-shore (station 8-9). Likewise, at Ra´s al Qulay´ah *F. mitchelliae* was more abundant on the low shore. The turf-forming alga *Gelidium crinale* was clearly seen only at the lowest stations of the low-shore at all three studied sites during the winter season (January).

Porifera: It was obvious that individuals belonging to this group only occurred at extreme low level on the shores, a level where it is usually continually immersed throughout the year but on rare occasions was seen during extreme low waters. Several species in this phylum were recorded during the current investigation, at Ra´s Ajūzah (7 species) and at Ra´s al Qulay´ah (2 species). No sponges were seen at Ra´s Eqaila. The genus *Haliclona (*or *Gellius)* and *Terpios* were the most common at both sites. As well, an unidentified sponge (sponge number 1) was common at Ra´s Ajūzah (see table 6.2). Information on the taxonomy of sponges at Kuwait and the Gulf Region are very limited or not available which make it difficult to identify each species properly.

Cnidaria: like members of the phylum Porifera, Cnidarians were confined to the extreme low level of the three shores. The most common genus was *Zoanthus* (number 1) which was present at all three shores (see table 6.2). Another species of this genus was also recorded but only at Ra´s Ajūzah *Zoanthus* (number 2). Coral colonies of *Dipsastraea pallida* were present at Ra´s Ajūzah and Ra´s al Qulay´ah, coral colonies of *Platygyra daedalea* and of the genus *Porites* existed at Ra´s al Qulay´ah. No coral was recorded at Ra´s Eqaila.

Annelida: The most representative species of this group that was found at all of the investigated sites was the tube worm *Spirobranchus kraussii*. This species was common at Ra´s Ajūzah and Ra´s Eqaila where it occupied nearly all transect stations while it was almost absent (occupies only one station (3)) at Ra´s al Qulay´ah throughout the year. One individual of *Onuphis eremita* was recorded at station 7 at Ra´s Eqaila.

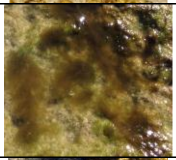
Mollusca: **Gastropoda:** Three species of *Clypeomorus* were more abundant during the spring time (May) with *C. persica* much more abundant at Ra´s Ajūzah than at the other two sites, particularly at Ra´s al Qulay´ah were it was only found at station 3. During the summer season (July) the odd boulder and the surrounding sand were covered with *Cerithideopsilla cingulata*, but only in the north at Ra´s Ajūzah. *Cerithium caeruleum* was present at all the investigated sites but was more dominant at Ra´s Ajūzah, specifically at stations 7 and 9 (below low shore level), while it was distributed along the transect from high to low shore at Ra´s Eqaila (stations 1-4, and 6-10) and Ra´s al Qulay´ah (stations 1-4,6, 8-10). *Cerithium scabridum* was common on the low shore of Ra´s Ajūzah while it appeared to inhabit only the middle shore level of Ra´s Eqaila. This species was completely absent in the southern shore Ra´s al Qulay´ah. The Mauritian Conch *Conomurex decorus*, was restricted to extreme low tide levels at Ra´s Eqaila and Ra´s al Qulay´ah. Likewise, *Hexaplex kusterianus* which occupies station 9 only at Ra´s Eqaila was completely absent on the other two shores. *Indothais lacera* was only present at Ra´s Ajūzah, where it was found at the first station on the high shore then appeared again at station 8 where it gradually increased in number below this station. *Lunella coronata* was present at all three examined shores but it seems to be zoned differently. For example, at Ra´s al Qulay´ah it was common at high shore level (stations 1-3), while at Ra´s Ajūzah it was found at station 4 and 9, and has shown a different distribution at Ra´s Eqaila where it appears to be dispersed from high to low shore (all stations except station 4). *Monodonta nebulosi* occupies much the same zone along the shore stretch of Ra´s Ajūzah and Ra´s Eqaila where it extends from high to upper-low tide level. *Mitrella blanda* was present on the three surveyed shores but with low numbers that did not exceed 10 ind.m^{-2} occupying sand patches in pools or areas close to pools. Scavengers *Nassarius persicus* were scarce and only present where suitable sediment was present along the transects at Ra´s Ajūzah and Ra´s al Qulay´ah. *Planaxis sulcatus* was only recorded at Ra´s Eqaila and did not extend as far as the upper-middle part of the shore. *Priotrochus obscurus* was present at all investigated sites and seems to occupy the upper levels of the shores. *Semiricinula tissoti* was present on the high shore at Ra´s al Qulay´ah beach while at Ra´s Eqaila it was present both on the high shore and low shore but was absent from the middle shore stations. *Trochus erithreus* occupies the highest station of Ra´s Ajūzah shore and was not recorded on the other two shores. *Umbonium vestiarium* was only found at Ra´s Eqaila where it seems to be limited to stations above station 7. One individual of the sea slug *Peronia peronii* was recorded at station 9 at Ra´s Eqaila and at station 3 at Ra´s al Qulay´ah and was absent from the Ra´s Ajūzah shoreline. The limpet *Siphonaria belcheri* was only present at the highest station of Ra´s al Qulay´ah shore.

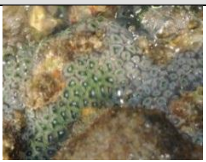
Bivalvia: Bivalve species were found during examination of the three shores, four species were recorded at Ra´s Ajūzah, five species at Ra´s Eqaila and two species at Ra´s al Qulay´ah. *Brachidontes variabilis* was present at the high shore of Ra´s Ajūzah where it was found to occupy the low shore (station 5 & 6) at Ra´s Eqaila and was absent from Ra´s al Qulay´ah beach. *Striostrea margaritacea* seems to prefer attaching itself to rock platforms at Ra´s Ajūzah and Ra´s Eqaila. It was found colonising bed rock on the low shore at Ra´s Eqaila. On the other hand, at Ra´s Ajūzah *S. margaritacea* individuals were attached to boulders on the high shore and to rock platforms on the low to middle shore and at extreme low water of spring tides. *Malleus anatinus* was found at station 8 at Ra´s Ajūzah and was absent from the other sites. *Pinctada imbricata radiata* was present on all three shores but more frequently (1.m^2) at Ra´s Eqaila were small individuals (10-20mm) occupied station 1 at high shore and larger individuals (30-40mm) stations 9 and 10. At Ra´s Ajūzah and Ra´s al Qulay´ah one solitary individual was found on the lowest part of the low shore. *Saccostrea cucullata*, *Pinna bicolor,* and *Circe intermedia* were all only found at Ra´s Eqaila. *Saccostrea cucullata* was restricted to the high shore level, while *Pinna bicolor*, and *Circe intermedia* were found embedded in patches of sand on the low shore. *Acar abdita* was only found at Ra´s al Qulay´ah where it was common in the upper-middle shore.

Arthropoda: **Crustacea:** Two barnacle species were identified on rocks from the three stations. *Amphibalanus amphitrite* was found at all three sites and was commonest at Ra´s Ajūzah where it occupied the upper shore (stations 1-6). At Ra´s Eqaila its distribution was patchy with barnacles present at stations 2 and 6. However at Ra´s al Qulay´ah it was only present at station 2. The only other barnacle species identified was *Microeuraphia withersi* and this species was only present at high water station 1 at Ra´s Ajūzah. The pistol shrimp *Alpheus lobidens* was only present at station 9 at Ra´s Ajūzah whilst the porcelain crab *Petrolithes rufescens* was not recorded at Ra´s Ajūzah, but was present on the upper shore at Ra´s Eqaila (stations 1 & 5). This species was present on the low shore (station 9) at Ra´s al Qulay´ah.

Two species of hermit crabs were recorded – *Diogenes* sp. & *Paguristes* sp. At 2 sites hermit crabs had a wide distribution across all tidal levels; stations Ra´s Ajūzah (stations 3-11) and Ra´s al Qulay´ah (stations 2-9). However, at Ra´s Eqaila this species was only found at station 3. Four crab genera were found on some of the shores. Two genera, *Portunus pelagicus* and *Leptodius exartus* were found at all three sites.

Table 6.1. Summary of the presence or absence (P/A) and photograph of each organisim recorded throughout the year at the three studied shores. (Image taken by: *[1] David Roberts, and *[2] Zainab Al-Wazzan).

Classification and Scientific Name	Presence			Photograph
	Ra´s Ajūzah	Ra´s Eqaila	Ra´s al Qulay´ah	
Kingdom: Chromista				
Phylum: Ochrophyta				
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier, 1851	A	A	P	
Feldmannia mitchelliae (Harvey) H.-S.Kim, 2010	P	P	P	
Iyengaria stellata (Børgesen) Børgesen, 1939	A	P	A	
Padina gymnospora (Kützing) Sonder, 1871	P	P	P	
Padina tetrastromatica Hauck, 1887	A	A	P	
Sargassum oligocystum Montagne, 1845	A	A	P	
Kingdom: Plantae				
Phylum: Chlorophyta				
Ulva flexuosa Wulfen, 1803	P	A	A	
Phylum: Rhodophyta				
Gelidium crinale (Hare ex Turner) Gaillon, 1828	P	P	P	
Kingdom: Animalia				
Phylum: Porifera				
Class: Demospongiae				

Halichondria (Halichondria) glabrata Keller, 1891	P	A	A	
Haliclona (Gellius) Gray, 1867	P	A	P	
Haliclona Grant, 1836	P	A	A	
Tedania (Tedania) anhelans Vio in Olivi, 1792	P	A	A	
Terpios Duchassaing & Michelotti, 1864	P	A	P	
Sponge sp. 1	P	A	A	
Sponge sp. 2	P	A	A	
Phylum: Cnideria				
Class: Anthozoa				
Zoanthus (1) Lamarck, 1801	P	P	P	
Zoanthus (2) Lamarck, 1801	P	A	A	

Dipsastraea pallida Dana, 1846	P	A	P	
Porites Link, 1807	A	A	P	
Platygyra daedalea Ellis & Solander, 1786	A	A	P	
Phylum: Annelida				
Class: Polychaeta				
Spirobranchus kraussii Baird, 1865	P	P	P	
Onuphis eremita Audouin & Milne Edwards, 1833	A	P	A	
Phylum: Mollusca				
Class: Gastropoda				
Cerithideopsilla cingulata Gmelin, 1791 *[1]	P	A	A	
Cerithium caeruleum G. B. Sowerby II, 1855*[1]	P	P	P	
Cerithium scabridum Philippi, 1848 *[1]	P	P	A	
Clypeomorus bifasciata G. B. Sowerby II, 1855*[1]	P	P	A	

Clypeomorus persica Houbrick, 1985*[1]	P	P	P	
Clypeomorus sp. Jousseaume, 1888 *[1]	P	P	P	
Conomurex decorus Röding, 1798	P	P	A	
Hexaplex kusterianus Tapparone Canefri, 1875*[2]	A	P	A	
Indothais lacera Born, 1778	P	A	A	
Lunella coronata Gmelin, 1791	P	P	P	
Monodonta nebulosa Forsskål in Niebuhr, 1775*[2]	P	P	A	
Mitrella blanda G. B. Sowerby I, 1844 *[1]	P	P	P	
Nassarius persicus Martens, 1874*[1]	P	A	P	

Nassarius sp. Duméril, 1805*[1]	P	A	A	
Planaxis sulcatus Born, 1778 *[1]	A	P	A	
Priotrochus obscurus W. Wood, 1828*[2]	P	P	P	
Peronia peronii Cuvier, 1804	A	P	P	
Siphonaria belcheri Hanley, 1858*[1]	A	A	P	
Semiricinula tissoti Petit de la Saussaye, 1852*[1]	A	P	P	
Trochus erithreus Brocchi, 1821*[1]	P	A	A	
Umbonium vestiarium Linnaeus, 1758*[2]	A	P	A	
Class: Bivalvia				
Acar abdita Oliver & Chesney, 1994 *[1]	A	A	P	
Brachidontes variabilis Krauss, 1848	P	P	A	
Circe intermedia Reeve, 1863	A	P	A	

Malleus anatinus Gmelin, 1791 *[1]	P	A	A	
Pinna bicolor Gmelin, 1791	A	P	A	
Pinctada imbricata radiata Leach, 1814*[1]	P	P	P	
Saccostrea cucullata Born, 1778	A	P	A	
Striostrea margaritacea Lamarck, 1819	P	P	A	
Phylum: Arthropoda				
Class: Maxillopoda				
Amphibalanus amphitrite Darwin, 1854	P	P	P	
Microeuraphia withersi Pilsbry, 1916	P	A	A	
Class: Malacostraca				
Atergatis integerrimus Lamarck, 1818	A	A	P	

Alpheus lobidens De Haan, 1849 [in De Haan, 1833-1850]	P	A	A	
Diogenes sp. Dana, 1851*[1]	P	P	P	
Leptodius exaratus H. Milne Edwards, 1834	P	P	P	
Metopograpsus messor Forskål, 1775*[2]	A	P	A	
Paguristes sp. Dana, 1851	P	A	P	No photograph
Petrolisthes rufescens Heller, 1861	A	P	P	No photograph
Portunus (Portunus) pelagicus Linnaeus, 1758*[2]	P	P	P	
Phylum: Bryozoa				
Class: Gymnolaemata				
Schizoporella errata Waters, 1878	P	A	A	
Phylum: Echinodermata				
Class: Asteroidea				
Aquilonastra burtoni Gray, 1840	P	P	P	
Class: Echinoidea				
Echinometra mathaei Blainville, 1825	A	P	P	
Class: Holothuroidea				

Holothuria (Thymiosycia) arenicola Semper, 1868	A	A	P	
Phylum: Chordata				
Class: Actinopterygii				
Pseudosynanceia melanostigma Day, 1875	P	A	P	
Class: Ascidiacea				
Phallusia nigra Savigny, 1816	P	P	P	

Table 6.2. The occurrence of different species along the transect from high (1) to low shore (13) at Ra´s Ajūzah. Three shading colours are used to differentiate between the shore levels upper (light grey), middle (15% darker grey) and lower (35% darker grey). Details of each species's general abundance are presented X= 1 individual.m^2; XX= 2-10 individuals.m^2; and XXX= 11-100 individuals.m^2. Details about the physical characteristics and algal coverage are also presented. B: Boulder; Bed: rock platform; C: cobles; P: Pool; S: sand; Sh: shingle.

Classification and Scientific Name	**station**												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Kingdom: Chromista													
Phylum: Ochrophyta													
Padina gymnospora (Kützing) Sonder, 1871						XX	X	XXX	XXX	X	XXX	XXX	
Feldmannia mitchelliae (Harvey) H.-S.Kim, 2010)		XX					XXX	XX	XX	XX			
Kingdom: Plantae													
Phylum: Chlorophyta													
Ulva flexuosa (Wulfen, 1803)	XXX	XXX	XX	XX	XX	XX				X			
Phylum: Rhodophyta													
Gelidium crinale (Hare ex Turner) Gaillon, 1828												XXX	XXX
Kingdom: Animalia													
Phylum: Porifera													
Class: Demospongiae													
*Halichondria (Halichondria) glabrata (*Keller, 1891)									X			X	XXX
Haliclona (Gellius) (Gray, 1867)												X	XX
Haliclona (Grant, 1836)												X	X
Tedania (Tedania) anhelans (Vio in Olivi, 1792)									X			XX	XX
*Terpios (*Duchassaing & Michelotti, 1864)												XX	XXX
Unidentified sponge sp. 1												XX	
Unidentified sponge sp. 2													X
Phylum: Cnideria													
Class: Anthozoa													
Zoanthus sp. 1 (Lamarck, 1801)												XXX	XXX
Zoanthus sp. 2 (Lamarck, 1801)											XXX		
Dipsastraea pallida (Dana, 1846)													X
Phylum: Annelida													
Class: Polychaeta													
Spirobranchus kraussii (Baird, 1865)		XX	XX	X	XXX	XXX	XXX	XX	X			XXX	
Phylum: Mollusca													
Class: Gastropoda													
Cerithideopsilla cingulata (Gmelin, 1791)	XXX	XXX	XX	XX	XX	X							

Classification and Scientific Name	Station												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Cerithium caeruleum G. B. Sowerby II, 1855							XX		XX				
Cerithium scabridum (Philippi, 1848)							XX	XXX	XX	XX	XXX		
Clypeomorus bifasciata (G. B. Sowerby II, 1855)	XXX	XXX	XXX	XXX	XXX	XX							
Clypeomorus persica (Houbrick, 1985)	XXX	XXX	XXX	XXX	XXX								
Clypeomorus sp. (Jousseaume, 1888)	XX	XXX	XX	XXX	XX								
Conomurex decorus (Röding, 1798)												X	
Indothais lacera (Born, 1778)	XX							X		XX	XX		XX
Lunella coronata (Gmelin, 1791)				XX					XX				
Monodonta nebulosa (Forsskål in Niebuhr, 1775)	XX				XX	XX							
Mitrella blanda (G. B. Sowerby I, 1844)	XX	XX							XX	XX			
Nassarius persicus (Martens, 1874)	XX								XX				
Nassarius sp.(Duméril, 1805)		X											
Priotrochus obscurus (W. Wood, 1828)	XX	X			X		XX		XX				
Trochus erithreus (Brocchi, 1821	XX												
Class: Bivalvia													
Brachidontes variabilis (Krauss, 1848)	X	XX											
Malleus anatinus (Gmelin, 1791)								XX					
Pinctada imbricata radiata (Leach, 1814)													X
Striostrea margaritacea (Lamarck, 1819)	XX				XX						XX		
Phylum: Arthropoda													
Class: Maxillopoda													
Amphibalanus amphitrite (Darwin, 1854)	XX	XX	X	XX		XX							
Microeuraphia withersi (Pilsbry, 1916)	XX												
Class: Malacostraca													
Leptodius exaratus (H. Milne Edwards, 1834)						XX		X		XX			
Portunus (Portunus) pelagicus (Linnaeus, 1758)								X					
Alpheus lobidens De Haan, 1849 [in De Haan, 1833-1850]									XX				
Paguristes sp. Dana, 1851			XX			XXX			XXX	XXX	XXX		
Diogenes sp. Dana, 1851			XX			XXX			XXX	XXX	XXX		
Phylum: Bryozoa													

Class: Gymnolaemata													
Schizoporella errata (Waters, 1878)												XX	XX
Phylum: Echinodermata													
Class: Asteroidea													
Aquilonastra burtoni (Gray, 1840)						XX			X		X		
Phylum: Chordata													
Class: Actinopterygii													
Pseudosynanceia melanostigma (Day, 1875)									X	XX			
Class: Ascidiacea													
Phallusia nigra (Savigny, 1816)									X				
Physical characteristics	S/C	S/C/B/P	S/C/B/P	S/B	S/Bed	Bed	Bed/S/Sh	S/P/B	S/P/B	Bed/S	Bed/S	Bed/B	Bed
Algal cover %	62	27	18	11	7	11	51	54	17	3	14	84	24

Table 6.3. The occurrence of different species along the transect from high (1) to low shore (11) at Ra´s Eqaila. Three shading colours are used to differentiate between the shore levels upper (light grey), middle (15% darker grey) and lower (35% darker grey). Details on their general abundance are presented X= 1 individual.m^2; XX= 2-10 individuals.m^2; and XXX= 11-100 individuals.m^2. Details about the physical characteristics and algal coverage are also presented. B: Boulder; Bed: rock platform; C: cobles; P: Pool; S: sand; Sh: shingle.

Classification and Scientific Name	**station**										
	1	2	3	4	5	6	7	8	9	10	11
Kingdom: Chromista											
Phylum: Ochrophyta											
Feldmannia mitchelliae (Harvey) H.-S.Kim, 2010)								XXX	XX		
Iyengaria stellata (Børgesen) Børgesen, 1939)		XX	XX	XX		XX	XXX	X	XX		
Padina gymnospora (Kützing) Sonder, 1871			X					XX			
Kingdom: Plantae											
Phylum: Rhodophyta											
Gelidium crinale (Hare ex Turner) Gaillon, 1828							XX	XX	XXX	XXX	
Kingdom: Animalia											
Phylum: Cnideria											
Class: Anthozoa											
Zoanthus sp. 1 (Lamarck, 1801)									XXX		
Phylum: Annelida											
Class: Polychaeta											
Spirobranchus kraussii (Baird, 1865)	XX	XXX	XX	X	XX	XXX	XX	XX	XX		
Onuphis eremita (Audouin & Milne Edwards, 1833)							X				
Phylum: Mollusca											
Class: Gastropoda											
Cerithium caeruleum (G. B. Sowerby II, 1855)	XX	XX	XXX	XX		XX	XXX	XXX	XXX	XX	
Cerithium scabridum (Philippi, 1848)		XX	XXX	X							
Clypeomorus bifasciata (G. B. Sowerby II, 1855)	X				X						
Clypeomorus persica (Houbrick, 1985)	XX	XX		X	X	X					
Clypeomorus sp. (Jousseaume, 1888)	XXX	XXX	XXX	XX		XX	XXX	XXX			
Conomurex decorus (Röding, 1798)										X	
Hexaplex kusterianus (Tapparone Canefri, 1875)									X		
Lunella coronata (Gmelin, 1791)	XX	XXX	XX		XXX	XXX	XX	XX	XX	X	
Mitrella blanda (G. B. Sowerby I, 1844)			XX								
Monodonta nebulosa (Forsskål in Niebuhr, 1775)	XX	XXX	XX	XX		X					
Planaxis sulcatus (Born, 1778)	XX	XX									
Priotrochus obscurus (W. Wood, 1828)	XXX	XX		X		XX	XX				

Classification and Scientific Name	**station**										
	1	2	3	4	5	6	7	8	9	10	11
Peronia peronii (Cuvier, 1804)									X		
Semiricinula tissoti (Petit de la Saussaye, 1852)	X			X		X					
Umbonium vestiarium (Linnaeus, 1758)	XX		XX	XXX	XX	XX	XX				
Class: Bivalvia											
Brachidontes variabilis (Krauss, 1848)					XX	XX					
*Circe intermedia (*Reeve, 1863)					XX						
*Pinna bicolor (*Gmelin, 1791)								X			
Pinctada imbricata radiata (Leach, 1814)	X								X	X	
Saccostrea cucullata (Born, 1778)	XXX	XX									
Striostrea margaritacea (Lamarck, 1819)						XX	XX	XX	XX		
Phylum: Arthropoda											
Class: Maxillopoda											
Amphibalanus amphitrite (Darwin, 1854)		XX				XXX					
Class: Malacostraca											
Diogenes sp. Dana, 1851				XX							
Leptodius exaratus (H. Milne Edwards, 1834)	X										
*Metopograpsus messor (*Forskål, 1775)		XX									
Petrolisthes rufescens (Heller, 1861)	XX				XX						
Portunus (Portunus) pelagicus (Linnaeus, 1758)					X						
Phylum: Echinodermata											
Class: Asteroidea											
Aquilonastra burtoni (Gray, 1840)									X	X	
Class: Echinoidea											
Echinometra mathaei (Blainville, 1825)									XX	XXX	
Phylum: Chordata											
Class: Ascidiacea											
Phallusia nigra (Savigny, 1816)									X		
Physical characteristics	B/C/S	B/C/S/p	B/C/S/p	S/C /p	B/C/S	Bed/S/B	Bed/B	Bed	Bed/B	Bed/B	
Algal cover %	0	1	9	15	0	3	43	39	33	28	

Table 6.4. The occurrence of different species along the transect from high (1) to low shore (11) at Ra´s al Qulay´ah. Three shading colours are used to differentiate between the shore levels upper (light grey), middle (15% darker grey) and lower (35% darker grey). Details on their general abundance are presented X= 1 individual.m^2; XX= 2-10 individuals.m^2; and XXX= 11-100 individuals.m^2. Details about the physical characteristics and algal coverage are also presented. B: Boulder; Bed: rock

Classification and Scientific Name	station										
	1	2	3	4	5	6	7	8	9	10	11
Kingdom: Chromista											
Phylum: Ochrophyta											
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier, 1851)								XX	XX	XXX	XXX
Feldmannia mitchelliae (Harvey) H.-S.Kim, 2010)			XX				XXX	XX	XX	XX	XXX
Padina gymnospora (Kützing) Sonder, 1871	XX		XX	XX		XXX	XXX	XXX	XXX	XXX	
Padina tetrastromatica Hauck, 1887							XXX	XX	XX		
Sargassum angustifolium (C.Agardh, 1820)								XX			
Kingdom: Plantae											
Phylum: Rhodophyta											
Gelidium crinale (Hare ex Turner) Gaillon, 1828										XX	
Kingdom: Animalia											
Phylum: Porifera											
Class: Demospongiae											
Haliclona (Gellius) (Gray, 1867)											X
Terpios (Duchassaing & Michelotti, 1864)											XX
Phylum: Cnideria											
Class: Anthozoa											
Zoanthus sp. 1 (Lamarck, 1801)										XXX	XX
Dipsastraea pallida (Dana, 1846)											X
Porites (Link, 1807)											X
Phylum: Annelida											
Class: Polychaeta											
Spirobranchus kraussii (Baird, 1865)			XX								
Phylum: Mollusca											
Class: Gastropoda											
Cerithium caeruleum (G. B. Sowerby II, 1855)	X	XX	XXX	XX		XX		XXX	XXX	XX	
Clypeomorus persica (Houbrick, 1985)			XX								
Clypeomorus sp. (Jousseaume, 1888)	XXX	XX	XXX	XX	XX	XX					

Classification and Scientific Name	station										
	1	2	3	4	5	6	7	8	9	10	11
Lunella coronata (Gmelin, 1791)	X	XX	XXX			X					
Mitrella blanda (G. B. Sowerby I, 1844)	XX			XX	XX						
Nassarius persicus (Martens, 1874)				X							
Priotrochus obscurus (W. Wood, 1828)	XX	XX	XX	XX							
Peronia peronii (Cuvier, 1804)			X								
Siphonaria belcheri Hanley, 1858	XX										
Semiricinula tissoti (Petit de la Saussaye, 1852)	XX										
Class: Bivalvia											
Acar abdita (Oliver & Chesney, 1994)		XXX									
Pinctada imbricata radiata (Leach, 1814)									X		
Phylum: Arthropoda											
Class: Maxillopoda											
Amphibalanus amphitrite (Darwin, 1854)			XXX								
Class: Malacostraca											
Atergatis integerrimus (Lamarck, 1818)											X
Diogenes sp. Dana, 1851		XXX			XXX	XX			X		
Leptodius exaratus (H. Milne Edwards, 1834)	XX							XX			
Paguristes sp. Dana, 1851	X							XX			
Petrolisthes rufescens (Heller, 1861)									X		
Portunus (Portunus) pelagicus (Linnaeus, 1758)					X			X			
Phylum: Echinodermata											
Class: Asteroidea											
Aquilonastra burtoni (Gray, 1840)								X		X	
Class: Echinoidea											
Echinometra mathaei (Blainville, 1825)							XX	XX			
Class: Holothuroidea											
*Holothuria (Thymiosycia) arenicola (*Semper, 1868)								X			
Phylum: Chordata											
Class: Actinopterygii											

Pseudosynanceia melanostigma (Day, 1875)									X		
Class: Ascidiacea											
Phallusia nigra (Savigny, 1816)										X	
Physical characteristics	Bed/S	Bed/S	S/C/Bed/B/P	S/Bed	S/Bed	S/P /B	S/Bed	S/Bed	S/Bed	S/Bed	Bed
Algal cover %	16	17	14	8	50	29	63	53	45	20	30

Portunus pelagicus occupied the mid shore stations 5-7, whilst *L. exartus* had a widely variable distribution at the 3 sites; at Ra´s Ajūzah it was recorded between stations 6-9, at Ra´s Eqaila at the highest shore station 1 and at Ra´s al Qulay´ah similarly at high shore station 1 but also lower down the shore at station 8. *Metopograpsus messor* was only recorded at Ra´s Eqaila under rock boulders in the upper-middle part of the shore. One individual of *Atergatis integerrimus* was found near to the waters edge of extreme low water only at Ra´s al Qulay´ah.

Bryozoa: *Schizoporella errata* was only observed at Ra´s Ajūzah and at a similar level to where members of the Porifera and Cnideria were found.

Echinodermata: the number of species belonging to this group appears to increase from northern to southern Kuwait. One species was recorded at Ra´s Ajūzah, two at Ra´s Eqaila, and a total of the three were found at Ra´s al Qulay´ah. All individuals were present below mean low tide level. *Aquilonastra burtoni* a common starfish was more abundant at the northern site Ra´s Ajūzah whilst it was present in lower numbers at Ra´s Eqaila and Ra´s al Qulay´ah. The sea urchin *Echinometra mathaei* was absent in the north at Ra´s Ajūzah and was observed on the lower low-shore level at Ra´s Eqaila and Ra´s al Qulay´ah. *Holothuria (Thymiosycia) arenicola* was only recorded at Ra´s al Qulay´ah at one station (station 8).

Chordata: The tunicate *Phallusia nigra* was common at extreme low shore levels at all three studied shores. Similarly, the stone fish *Pseudosynanceia melanostigma* which was present at Ra´s Ajūzah and Ra´s al Qulay´ah was not recorded at Ra´s Eqaila.

Figure 6.2 summarises, using three pie charts, the data presented in the previous tables. This was undertaken to highlight the contribution that some of the major faunal and floral groups make to the diversity of organisms on the shores at the three locations. Molluscs were the predominant group (upto 50%) with the arthropoda representing the next largest group. Poriferan species were abundant at the northen site.

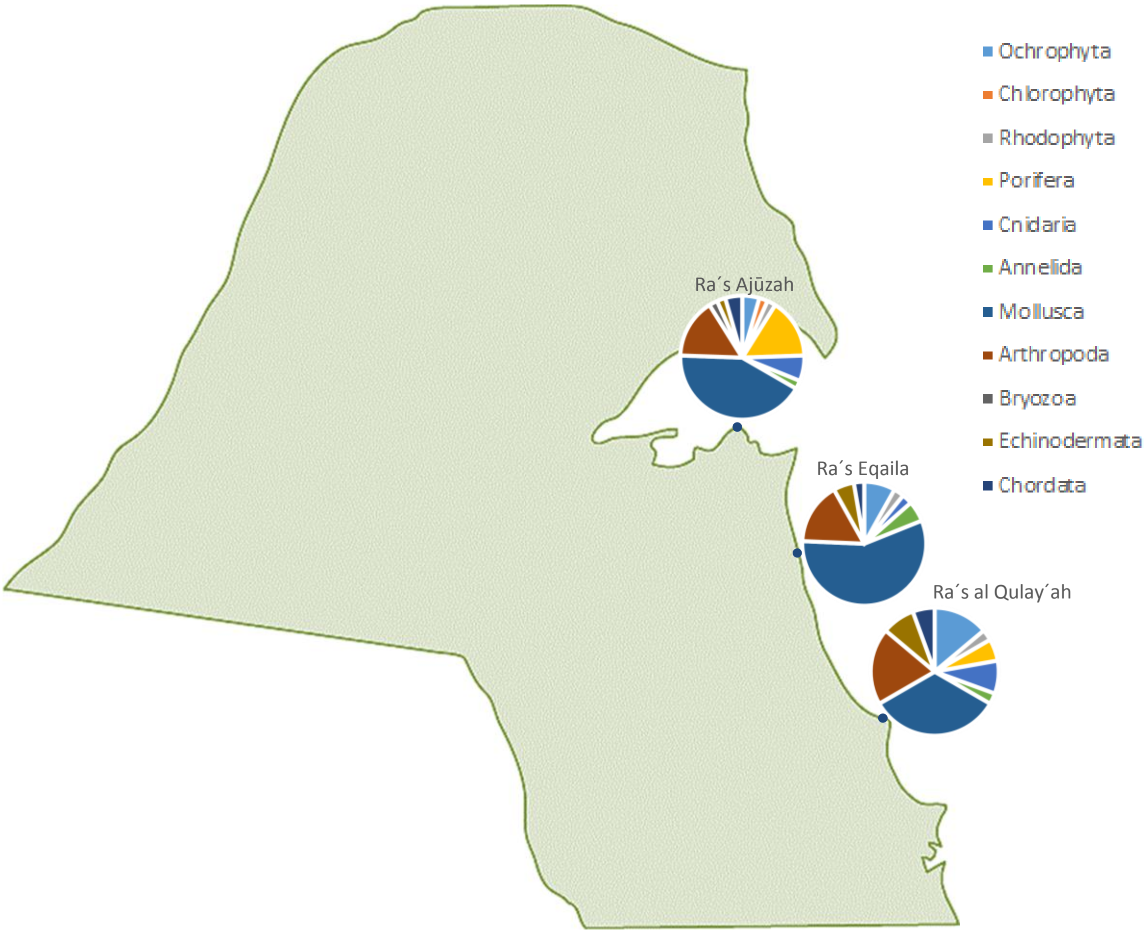


Figure 6.2. A summary of the relative proportions of the different algal groups and the major taxonomic animal groups observed on the rocky shores at the three locations in Kuwait, Ra's Ajuzah, Ra's Egaila and Ra's al Qulay'ah.

Figure 6.3. a) *Thalessa savignyi* in the process of egg laying when collected in the field during late July at Ra's Eqaila b) four days before laying eggs 26th June c) female *Thalessa savignyi* depositing egg capsules on the 1st July d) egg capsules 10 days after laying showing different colouration and some had degenerated(Arrows).

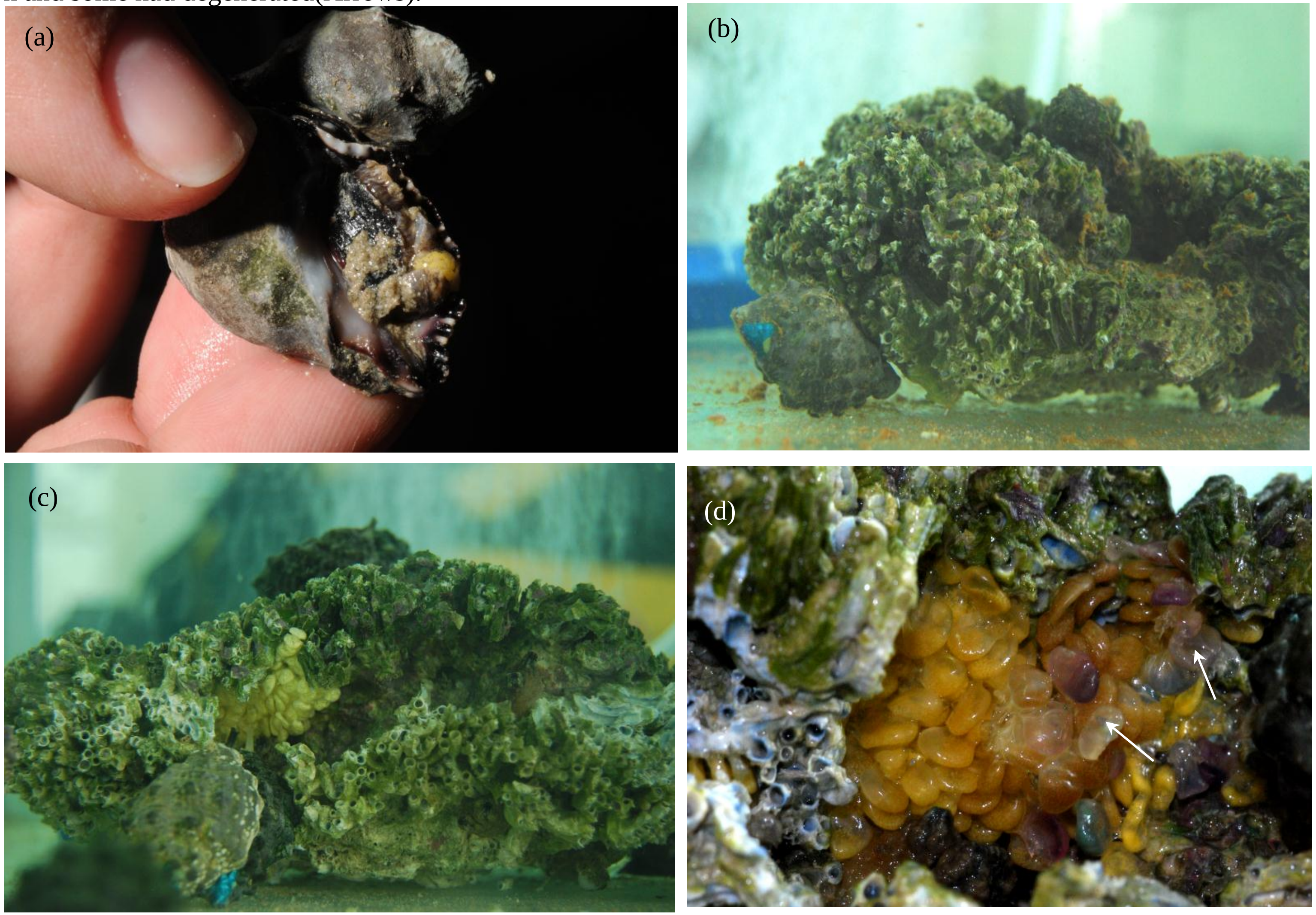


Figure 6.4. Laboratory observations of *Ergalatax junionae* laying (~3mm) egg capsules above the water line (a) and out of water on the glass sides of an aquarium (b & c).

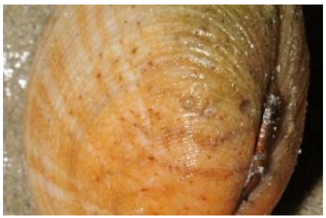
6.3.2 Reproduction

During the course of larval development the colour of the egg capsules of *T. savignyi* turned from yellow (just after laying) through orange and then a violet colour just prior to hatching. *Ergalatax junionae* capsules were transparent immediately following laying, turned white during the first few days of development and then changed a violet colour. These capsules did not develop further but began to degenerate. Maturation of the *T. savignyi* capsules took approximately 36 days at 26±1.4°C. The larvae can be those laid in the laboratory were seen in the field and individuals of *T. savignyi* were observed in the process of egg capsule laying in late July in the field.

6.3.3 Feeding

Several food items observed to be consumed by *Thalessa savignyi* and *Ergalatax junionae* during the field and laboratory were listed in table 6.5. Feeding gastropods were observed on the surfaces and in the crevices of the stones that had been brought into the laboratory. Amongst the animals consumed were mussels *Brachidontes variabilis* whose empty shells and those of the bivalve *Circe intermedia* with their characteristic countersunk drill holes were found on the base of the aquarium. In addition tube worms *Spirobranchus kraussii*, were probably eaten because both *T. savignyi* and *E. junionae* were seen for long periods on stones covered with the tubeworms and the remains of the tubes were seen on the base of the aquarium. The barnacle *Amphibalanus amphitrite* was also eaten by *T. savignyi* and *E. junionae* as they were observed amongst this barnacle species.

Table 6.5. Photographs of food items consumed by *Thalessa savignyi* and *Ergalatax junionae* during the field survey and laboratory observations. The predatory gastropods are shown with their prey items (arrows).

Thalessa savignyi	**Photograph**	***Ergalatax junionae***	**Photograph**
Spirobranchus kraussii		*Spirobranchus kraussii*	
Amphibalanus amphitrite		*Amphibalanus amphitrite*	
Clypeomorus sp.		*Cerithium scabridum*	
Striostrea margaritacea		*Platygyra daedalea*	
Brachidontes variabilis	No Photograph	*Brachidontes variabilis*	No Photograph
Circe intermedia			

6.4 DISCUSSION

The distribution of macroalgae on the shores of Kuwait was patchy and sparse on the upper shore levels and this is a consequence of the hostile environmental conditions (exposure to the sun and air temperatures) during the summer season when air temperatures can exceed 50°C. *Ulva flexuosa*, for example, was only found at Ra´s Ajūzah and on the upper part of the shore where I observed considerable freshwater runoff from Kuwait City behind and onto the shore. Areas of freshwater runoff are a typical habitat of this algal species. The majority of the brown algae recorded during the current investigation were distributed in the eulittoral region. While the single Rhodophyte species found only occurred at the edge of the sublittoral fringe at all 3 sites. This pattern of macro-algae distribution was expected since previous research in the Arabian Gulf e.g. Al-Hassan and Jones (1989) and Al-Muzaini and Jacob (1996) have documented the spatial and seasonal variations in macro-algae on shores of the Gulf.

The distribution of the barnacle *Amphibalanus amphitrite* was mainly in the upper shore stations at Ra´s Ajūzah and Ra´s Eqaila where there was suitable habitat i.e. small boulders and rocks for settlement and colonization. At Ra´s al Qulay´ah the only suitable settlement areas were in the upper stations (station 2). Hermit crabs *Diogenes* sp. and *Paguristes* sp. commonly inhabited *Ergalatax junionae* shells, as well as those of the scavenging snail *Mitrella blanda* and the grazer *Clypeomorus* sp. Hermit crabs were widely distributed across the shores at Ra´s Ajūzah and Ra´s al Qulay´ah where there is a mixed shore of pools, sand and small rocks. However, this hermit crab was only found at station 3 at Ra´s Eqaila where there were patches of sand (see chapter 2, figure 2.10). Hermit crabs commonly occupied the shells of *E. junionae* but very rarely those of *T. savignyi*. Crab species are common predators of gastropods and

Figure 6.4. A range of different intertidal species collected predominantly by foreign workers for food or fishing use or for selling on the black market. (a) *Leptodius exaratus*, (b) *Indothais lacera*, (c) *Conomurex decorus*, (d) *Portunus (Portunus) pelagicus*, (e) *Circe intermedia* and a few *Meretrix meretrix* , (f) *Lunella coronata* and (g) young men searching for fishing bait *Leptodius exaratus*. (6.5)


(a)
(b)
(c)
(d)
(e)
(f)
(g)

bivalves (e.g. Hughes, 1989; Seed & Hughes, 1995; Yamada & Boulding, 1996) The crab *Leptodius exartus* is frequently collected for use as a fishing bait (Alwazzan, 2012) and its absence from the shores at Ra´s Eqaila and Ra´s al Qulay´ah, both areas frequented by holiday makers and anglers may indicate a depletion of these crabs because they are used by Anglers as a fishing bait for recreational fishing during their holidays. The presence of crabs at upper shore station 1 and low station 9 likely indicates that they are overlooked in the upper shore and not reached at low shore except on the lowest tides. Ra´s Ajūzah is not a popular holiday shore and is more extensive than the shores at the other two sites so here the crabs are present in the mid to lower shore. On occasions I observed large numbers of individuals collecting crabs at Ra´s Ajūzah (see figure 6.4) but because of the area of the shore their activities likely do not affect crab presence and distribution in the same way as on the other two shores. Whether hermit crabs predate *E. junionae* is unclear but they do occupy the deserted shells. One possible predator of *T. savignyi* and *E. junionae* is the crab *Leptodius exartus* although there I am unaware of any published data on the feeding habitats of this crab species. In the laboratory when *L. exartus* was placed together with *E. junionae* in the same tanks the crabs showed no interest in the gastropod. The highest densities of *E. junionae* were observed at Ra´s Ajūzah where *L. exartus* was also at its most abundant. These observations taken together suggest, although it is not conclusive, that this crab species is unlikely to be a predator of *E. junionae.* Another possible predator of both muricacean gastropods is the starfish *Aquilonastra burtoni* although the starfish was only found on the low shore in low numbers and nothing is known about its feeding biology.

One potential prey item of the two gastropod species is *Brachidontes variabilis* a small (~40mm) bivalve that lives attached to hard substrata and small crevices by its tuft of short byssus thread. Bivalves are known to form part of the diet of predatory gastropods (e.g. Dye, 1991; Hughes *et. al.*, 1992; Wieters and Navarrete, 1998). *Brachidontes variabilis* was absent from Ra´s al Qulay´ah and occurred on the upper shore at Ra´s Ajūzah, whilst it was present in the mid shore at Ra´s Eqaila. Although not widely distributed across the shores of Kuwait this bivalve was consumed by both gastropods when boulders containing *B. variabilis* were placed in laboratory aquaria with the predators. After 24 hours the shells of *B. variabilis* were found on the bottom of the aquaria with small countersunk shaped drill holes through their shell valves indicating that they had been recently consumed by the muricacean gastropods. Another potential bivalve prey species is *Circe intermedia.* This species was only found alive in sediment under small boulders at Ra´s Eqaila , although the single shell valves with drill holes were seen on the other two shores. When 1-2cm *C. intermedia* were placed in tanks with *T. savignyi* and *E. junionae* only the former species was observed to attack and drill the shell valves of *C. intermedia.* Taylor (1976) demonstrated in experimental studies that muricacean and thaidid gastropods consume polychaete tube worms. In my experimental aquaria when boulders with attached tube worms *Spirobranchus kraussii* were offered to *E. junionae* and *T. savignyi* both species were observed to be feeding on this tube worm indicating that it is an important component of the diet of these predatory gastropods. *Spirobranchus krausii* is commonly distributed across the entire shores of Ra´s Eqaila and Ra´s Ajūzah but was present only at station 3 at Ra´s al Qulay´ah . At this latter site *E. junionae* was at its lowest densities. The presence of *S. kraussi* did not appear to influence the presence or absence of *T savignyi* or *E. junionae* since *T. savignyi* was completely absent from the northern site Ra´s Ajūzah, yet there was an abundant supply of *S. krausii* there. *Ergalatax junionae* was present on the mid to lower shore at Ra´s Ajūzah and would have access to a supply of tube worms. At Ra´s Eqaila *S. krausii* was abundant and both gastropod species were abundant across the shore. Only at Ra´s al Qulay´ah in the south was *S. krausii* patchy in distribution but *T. savignyi* was at its highest abundance and mostly on the lower part of the shore. These observations of predator and prey distribution from high to low shore at the 3 sites suggest that they are likely correlated in some instances, but it is probable that the two muricacean gastropods are opportunistic predators and consume a wide variety of prey species, some of which currently remain unknown.

When placed in laboratory aquaria *T. savignyi* and *E. junionae* laid egg masses in July on small stones and on the sides of the glass aquaria respectively. This coincided with the arrival of *T. savignyi* capsules being laid in the field at stations in the mid-shore. Eisawy & Sorial (1974) similarly observed that egg masses of *T. savignyi* were deposited on hard substrata in laboratory aquaria and in the field egg laying took place between August and November. In their study they found egg masses were laid on the shells of the oyster *Ostrea forskali* (now known as *Saccostrea cucullata*) and when shells were not present egg masses were laid on the walls of the aquaria close to the water level. In my study *E. junionae* laid egg capsules on the walls of the glass aquaria whilst *T. savingyi* deposited egg capsules on stones on the base of the aquaria. My laboratory studies were insufficient to study whether there was a relationship between capsule size and adult female as was observed in the Egyptian Red Sea *T. savingnyi* (Eisawy & Sorial 1974). However on the shores in Kuwait there were obvious differences in the size of the laid egg capsules in *T. savignyi.* The summer months saw larger numbers of both gastropod species at mid shore, thus perhaps indicating that they had migrated further up the shore to mate and lay egg masses. In subsequent months the lower and mid shore levels remained continuously immersed by the tide and it is interesting to speculate that the timing of the laying of egg masses might be related to the maximum chances of survival of the larvae in the egg capsules during these months when they were continuously immersed. Also the newly hatched larvae may then be retained in the mid low shore areas and then metamorphose and settle and recruit into the existing populations. Eisawy & Sorial (1974) observed that *T. savignyi* deposited egg masses on the shells of *Ostrea forskali* (now known as *Saccostrea cucullata*). In my survey this oyster species occurred on the upper shore in Ra´s Eqaila and in the summer months *T. savignyi* were seen to be congregated around them, perhaps preparing to deposit egg masses on the shells and thus indicating an up shore movement during the summer.

6.5 CONCLUSIONS

1) This is the first study to attempt to describe the latitudinal and zonal distribution of organisms on the rocky shores of Kuwait.
2) The hermit crabs *Diogenes* sp. and *Paguristes* sp. were found to only inhabit the empty shells of *Ergalatax junionae* but they are not considered to be likely predators of *E. junionae*.
3) In laboratory tank aquaria the hermit crabs *Diogenes* sp. and *Paguristes* sp. and the crab *Leptodius exartus* showed no interest in consuming both species of muricacean gastropods. However the mussel *Brachidontes variablis* was found in laboratory aquaria to have been drilled by both gastropod species whilst the bivalve *Circe intermedia* was only drilled and consumed by *T. savignyi.*
4) Tube worms *Septibranchia krausii* attached to rocks placed in experimental aquaria were readily consumed by both muricacean gastropods.
5) The relationship between the abundance of potential prey items on the shore and the distribution of *Thalessa savignyi* and *Ergalatax junionae* is weak. The presence of the bivalve *Brachidontes variablis* and presence of predatory crabs did not appear to control the distribution of the two muricacean gastropods. Both *T. savignyi* and *E. junionae* were associated with the tube worm *Septibranchia krausii* on the lower stations at the three sites.

6) Held in captivity, *T. savignyi* and *E. junionae* were observed to lay egg masses on stones and the glass sides of aquaria respectively. The egg masses laid by *E. junionae* did not develop and no larvae were produced. By contrast ~40 days after laying egg masses the larvae of *T. savignyi* were released from egg capsules.

6.6 REFRENCES

Al-Muzaini, S., and Jacob, P.G. (1996). Marine plants of the Arabian Gulf. *Environment International* Vol. **22**, pp. 369-376.

Al-Wazzan, Z. A. (2012) Distribution, population structure, and Intertidal bait fishery of the xanthid crab *Leptodius exaratus* (Brachyura: Xanthidae) in Kuwait’s rocky shores. MSC thesis. Bangor University, UK.

Al-Yamani, F. Y., & Saburova, M. A. (2011). Illustrated Guide on the Benthic Diatoms of Kuwait’s Marine Environments. Kuwait Institute for Scientific Research, Lucky Press, Kuwait.

Carriker, M. R. (1981). Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, Vol. **20**, pp. 403-422.

Chatzinikolaou, E. (2006). The ecology and growth of the netted dogwhelk *Nassarius reticulatus* (Gastropoda: Nassariidae). Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Chatzinkolaou, E. & and Richardson, C. A. (2007). Evaluating the growth and age of the netted whelk *Nassarius reticulatus* (Gastropoda: Nassaridae) from statolith growth rings. *Marine Ecology Progress Series*, Vol. **342**, pp. 163-176.

Dye, A. H. (1991). Feed preferences of *Nucella crassilabrum* and juvenile *Concholepas Concholepas* (Gastropoda: Muricidae) from a rocky shore in southern Chile. *Journal of Molluscan Studies.* Vol. **57**, pp. 301-307.

Eisawy, A.M. & Sorial, A.E. (1974). Egg Capsules and Development of *Thais-Savignyi*, *Bulletin of the Institute of Oceanography and Fisheries,* Vol. **4**, pp. 237-258.

Fretter, V. and Graham, A. (1994). British Prosobranch Molluscs: Their functional anatomy and ecology, Ray Society, London.

Hughes, R. N., & Dunkin, S. D. B. (1984). Behavioural components of prey selection by dogwhelks, Nucella lapillus (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology*, Vol. **77**, pp. 45-68.

Hughes, R. N. (1986). A functional biology of marine gastropods. Croom Helm, London.

Hughes, R. N. (1989). Foraging behaviour of a tropical crab: Ozius verreauxii.*Proceedings of the Royal Society of London. B. Biological Sciences*, Vol. 237, pp. 201-212.

Jones, D. A. (1989). Field Guide to the Sea Shores of Kuwait and the Arabian Gulf, University of Kuwait. Blandford Press, Kuwait, pp. 123-129.

Kabat, A. R. (1990). Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia: International Journal of Malacology*, Vol. 32, pp. 155-193.

Kingsley-Smith, Peter. (2002). The ecology of *Euspira pulchellus* (Gastropoda: Naticidae). Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Kingsley-Smith, P. R., A Richardson, C., & Seed, R. (2005). Growth and development of the veliger larvae and juveniles of Polinices pulchellus (Gastropoda: Naticidae). *Journal of the Marine Biological Association of the United Kingdom*, Vol. **85**, pp. 171-174.

Morton, B., & Chan, K. (1997). First report of shell boring predation by a member of the Nassariidae (Gastropoda). *Journal of Molluscan Studies*, *63*(3), 476-478.

Rittschof, D., Williams, L. G., Brown, B., & Carriker, M. R. (1983). Chemical attraction of newly hatched oyster drills. *The Biological Bulletin*, Vol. **164**, pp.493-505.

Taylor, J.D. (1976). Habitats, abundance and diets of Muricaecean gastropods at Aldabra Atoll. *Zoological Journal of the Linnean Society*, Vol. **59**, pp. 155–193.

Wietersa, E. A.; Navarrete, S. A. (1998). Spatial variability in prey preferences of the intertidal whelks *Nucella canaliculata* and *Nucella emarginata. Journal of Experimental Marine Biology and Ecology*, Vol. **222**, pp. 133–148.

Kingsley-Smith, Peter. (2002). The ecology of *Euspira pulchellus* (Gastropoda: Naticidae). Thesis (Ph. D.), University of Wales, Bangor (Ocean Sciences).

Seed, R., & Hughes, R. N. (1995). Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology*, Vol. 193, pp. 177-195.

Yamada, S. B., & Boulding, E. G. (1996). The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology*, Vol. 204, pp. 59-83.

CHAPTER SEVEN

General Discussion

7 General Discussion

Muricid gastropods are predators that generally feed on economically important molluscs as well as barnacles (Carpenter and Niem, 1998). *Thalessa savignyi* and *Ergalatax junionae* are two common predatory snails, belonging to the family Muricidae that inhabit the intertidal rocky shores of Kuwait. My investigation in chapter 3 into the distribution of these two gastropods showed that *T. savignyi* (maximum size 42mm) was absent at Ra’s Ajūzah in the north of Kuwait, but increased in abundance towards the south of Kuwait. By contrast the smaller gastropod *E. junionae* (maximum size 27mm) was present at all of the three studied shores but decreased in number towards the southernmost site, Ra’s al Qulay’ah. The geographical distribution and the seasonal pattern in abundance and migration in the intertidal zone of both species have been identified and related to different physical and biological factors on the studied shores.

On rocky shores in the south of Kuwait *T. savignyi* attained low densities, so for example during the summer (June to September) the average density on the lower shore was 1.0 ± 0.5 individual.m^2). By contrast *E. junionae* was more abundant in the North of Kuwait and altogether more common than *T. savignyi* where the average density in the summer on the lower shore was 47.0 ± 16.7 individual.m^2). Within each species there was little difference in the intertidal distribution or densities although there was a wide variation in their seasonal abundance. Both species were more abundant during the summer months than in the winter (November to January). The presence of large rocky platforms and associated fissures on the southern shore sites were related to an increased abundance of *T. savignyi*. Whilst small boulders and crevices on the shores of the northern sites were preferred by *E. junionae*.

The demographic study of *T. savignyi* and *E. junionae* populations showed that all of the populations, except the population of *E. junionae* at Ra´s al Qulay´ah had polymodal size distributions composed of several year classes; the population at Ra´s al Qulay´ah was unimodal in distribution. In chapter 4 I showed that there was very little annual recruitment into the populations and when a few juveniles did appear in the populations this occurred in the mid and lower shores between October and January. Egg laying by both species occurred in the laboratory in late June and these egg masses hatched in late July, although the larvae did not survive in the laboratory. At the same time of year *T. savignyi* were observed egg laying on the upper shore at Ra´s Eqaila, although *E. junionae* was never observed laying egg masses on the shore. From the known development time of the eggs in the capsules in the laboratory it is likely that newly settled juveniles began recruiting into the populations around late July and inhabiting the tiny holes and crevices in boulders and stones on the shore. However they were not observed entering the populations until between October and January when they were captured and measured.

The size frequency distributions in some of the populations were separated into their component size (age) classes using the method of Bhattacharya. However where populations were resolved into three or more size (age) classes it was possible to construct growth curves using estimates of the modal size and age of the animals and to compare the growth of both species. It was found that *T. savignyi* grows faster than *E. junionae* and both grew faster at Ra´s al Qulay´ah than at the other sites sampled. Whilst the use of Bhattacharya’s method can be useful in separating size frequency distributions into their component size (age) classes (Grant, 1989) this can only be done when a population contains multiple year (age) classes and for some of the populations this kind of data were not available.

In chapter 5 I explored a number of different methods for obtaining independent age estimates of *T. savignyi* and *E. junionae*. Traditionally rings on the gastropod operculum have been used to estimate age. However Kideys (1996) found only a small fraction of the operculae from the whelk *Buccinnum undatum* that he examined could be reliably used to estimate the whelks' age. I similarly found difficulty in estimating the age of both the muricid species in my study. The operculum of *T. savignyi* was thick and rings on the operculum could not be viewed easily under transmitted light. The operculae of *E. junionae* by contrast were thin and transparent to transmitted light and revealed a series of growth lines. Sections of the operculae did not reveal any useful information on the growth lines. An analysis of the growth rings in statoliths (Richardson, 2001) was undertaken as this method has been shown to be highly successful when applied in estimating the age of other gastropod species e.g. *Nassarius* (=*Hinnia*) *reticulatus* (Barosso *et. al.*, 2005; Chatzinikolaou & Richardson, 2007) and *Neptunea antiquata* (Richardson *et al.*, 2005). When the statoliths of *T. savignyi* and *E. junionae* were viewed beneath a light microscope at 40x or 100x magnification they revealed a series of growth rings that I demonstrated, using seasonal collected samples, were deposited annually in the winter months between November and January. The statoliths also contained rings that were shown to be deposited during the larval stage in the egg capsule and at the time of settlement. It is likely that the effort of the larva as it hatches from the egg mass and a change from a diet of nurse eggs in the capsules to one of a planktonic existence and dependence on life in pelagic waters, causes an interruption in statolith growth and the formation of a ring.

This is the first study to validate the use of statolith growth rings in gastropod species from the Gulf and to use the rings successfully to estimate the age of two muricacean gastropod species. *Thalessa savignyi* was found to be a faster growing species with a shorter longevity (4 years) than the smaller, longer-lived (5 years) and slower growing *E. junionae*. When the age estimates from the *E. junionae* statoliths and those obtained from the operculae were compared the operculae routinely over-estimated the age of this muricid by as many as three years. However the statolith ring technique is not without its difficulties as differences in the definition of the statolith growth rings and the number of weak growth rings was soon apparent. I was able to show in Chapter 5 that the definition and the number of weak growth rings varied latitudinally. Statoliths in the two species from northern Kuwait had more clearly defined rings and less weak rings than individuals from southern Kuwait. It is suggested that the difference in the number of weak rings maybe related to the availability of prey items since in chapter 6 I was able to show that the southern Kuwait sites had less prey species than those in North Kuwait.

A survey of the intertidal shores was undertaken (chapter 6) to investigate if the distribution of *T. savignyi* and *E. junionae* might be related to the distribution of their prey species. Surprisingly my study is the first to attempt to describe the latitudinal and zonal distribution of organisms on the rocky shores of Kuwait even though there have been several guides to the organisms of the shores of Kuwait published (e.g. Jones, 1986; Al-Yamani *et. al*., 2012). In the laboratory the tube worm *Septibranchia krausii* attached to rocks was readily consumed by both muricacean gastropods. Both *T savignyi* and *E. junionae* were associated with the tube worm *Septibranchia krausii* on the lower shore stations at the three sites. However, the relationship between the abundance of this potential prey species and the distribution of both *T. savigni* and *E. junionae* was a weak one. In the laboratory the bivalve *Brachidontes variablis* was observed to be drilled and consumed by both species suggesting that this species together with *S. krausii* are prominent items in their diets. The presence of predatory crabs on the shore did not appear to control the distribution of the two muricacean gastropods. Molluscs in the Gulf region are frequently overlooked as a group for study so this thesis provides some interesting and potentially useful data on the distribution, growth and age of two species, *T. savingnyi* and *E. junionae* along the coastline of Kuwait.

REFRENCES:

Al-Yamani, F. Y., Skryabin, V., Boltachova, N., Revkov, N., Makarov, M., Grinstov, V., & Kolesnikova, E. (2012). Illustrated Atlas on the Zoobenthos of Kuwait. Kuwait Institute for Scientific Research.

Barroso, C. M., Nunes, M., Richardson, C. A., and Moreira, M. H. (2005). The gastropod statolith: a tool for determining the age of *Nassarius reticulatus*. *Marine Biology*, Vol. **146**, pp. 1139-1144.

Chatzinkolaou, E. & Richardson, C. A. (2007). Evaluating the growth and age of the netted whelk *Nassarius reticulatus* (gastropoda: nassaridae) from statolith growth rings. *Marine Ecology Progress Series*, Vol. **342**, pp. 163-176.

Grant, A., 1989. The use of graphical methods to estimate demographic parameters. *Journal of the Marine Biological Association of the United Kingdom*, Vol. **69**, pp. 367-371.

Jones, D. A. (1986). Field Guide to the Sea Shores of Kuwait and the Arabian Gulf, University of Kuwait. Blandford Press, Kuwait, pp. 123-129.

Kideys, A E. (1996) Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgol Meersunter*, Vol. **50**, pp. 353-368.

Richardson, C.A. (2001). Molluscs as archives of environmental change, *Oceanography and Marine Biology Annual Review*, Vol. **39**, pp. 103–64.

Richardson, C.A.; Kingley-Smith, P.; Seed, R. & Chatzinikolaou, E. (2005). Age and growth of the naticid gastropod *Polinices pulchellus* (Gastropoda: Naticidae) based on length frequency analysis and statolith growth rings. *Marine Biology*, Vol. **148**, pp. 319-326.