The Linkage Between Environmental Heterogeneity And Biodiversity In Algal Assemblages On The Rocky Shore

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The Linkage Between Environmental Heterogeneity And Biodiversity In Algal Assemblages On The Rocky Shore

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Abstract

This study inspected the complex relationship between algae species diversity and the environmental heterogeneity, attempting to reveal the ecological processes that shape algal intertidal community on abrasion platforms. The structure of the platforms, seasonal fluctuations, constant water flushing, and possibly rising temperatures, all affect community structure and the distribution of algae on the platforms. According to habitat heterogeneity hypothesis, a cornerstone in ecological theory, a more heterogenic environment will support higher species diversity. This theory was examined comparing species diversity and an index of structural heterogeneity on six abrasion platforms at Akhziv rocky shore. I also studied the effects of individual environmental parameters, temporal and spatial variability on species diversity and composition at the small to medium spatial scales. Field sampling was carried out in four seasons over one year. Seasonality had the strongest effect on species diversity and on community composition. Winter was the richest and most diverse season, and summer was the least diverse. The second most important factor was the different sub-habitats on each platform. Tide pools were the most diverse, and harbored some sub-tidal species. The following factors were significantly correlated to algal diversity: surface verticality and roughness, sand and water cover, presence of biogenic rim and limpets. Water flux was significantly greater at the edge of the platforms than at the center. Height above sea level played a major role in community structure and affected species distribution collaterally through other parameters as flux, water cover and grazer distribution. Lower platforms exhibited weaker differences between sub-habitats, and community structure was significantly different from higher platforms. This finding has critical implications for the intertidal habitat in case of acceleration in sea level rise. Correlation between the structural heterogeneity index and species diversity was insignificant. Nevertheless, individual heterogeneity components had high correlation to algal diversity. It seems that most community-forming processes operate at small spatial scales, suggesting that high environmental heterogeneity as recorded here, with high species densities on such a small area, might have a negative effect on diversity, contrary to the classic theory.

List of abbreviations

Cm	Centimetres
M	Meters
Gr	Grams
MLWL	Mean low water level
ANOVA	Analysis of variance
PERMANOVA	Permutational multivariate analysis of variance
MDS	Multidimensional scaling
nMDS	Non metric multidimensional scaling
CCA	Canonical correspondence analysis
Aca	*Acanthophora najadiformis*
Chondri	*Chondria dasyphylla*
Chondra	*Chondracanthus spp.*
Cor	*Corrallina elongata*
Das	*Dasya spp.*
Gel	*Gelidium spp.*
Gra	*Gracilaria spp.*
Hyp	*Hypnea spp.*
Jan	*Jania rubens*
Lau	*Laurencia spp.*
Nem	*Nemalion helminthoides*
Poly	*Polysiphonia/Neosiphonia complex*
Pter	*Pterocladiella capillacea*
Ryt	*Rytiphlaea tinctoria*
Sol	*Solieria filiformis*
Spy	*Spyridia spp.*
Cer	*Ceramiaceae*
Bry	*Bryopsis spp.*
Cau	*Caulerpa mexicana*
Cla	*Cladophore spp.*

Cod	*Codium elongatum*
Ulv	*Ulva spp.*
Val	*Valonia utricularis*
Col	*Colpomenia sinuosa*
Dic	*Dictyota spp.*
Ect	*Ectocarpus siliculosus*
Hal	*Halopteris scoparia*
Pad	*Padina spp.*
Sty	*Stypopodium schimperi*
Sar	*Sargassum spp.*
Scy	*Scytosiphon lomentaria*
Taon	*Taonia atomaria*
Bot	*Botryocladia spp.*
Gal	*Galaxaura spp.*

1. Introduction

In this study I address several fundamental ecological concepts and regional and habitat specific issues that are relevant to the question leading this work. These include, biodiversity, biodiversity in the marine environment, biodiversity issues in the Mediterranean Sea, the link between biodiversity and habitat heterogeneity, and the specific habitat and taxonomic group of focus: macroalgae on rocky shore vermetid reefs. I will now address these concepts and issues as a lead for the objectives of my thesis.

1.1 Biodiversity

In an ever-changing world, undergoing continuous anthropogenic stress and recently intensified climate changes, ecological systems are changing. Our ability to explain or to predict these changes is still arguable since it has become clear that it is a multi-scale process which involves many contributing factors, maybe too many to account for all at once. Some of the threats that effect ecosystems are direct, such as habitat loss and pollution, while other threats are indirect, such as increased atmospheric and dissolved CO_2 levels, sea level and temperature rise. Besides the obvious result of species loss and therefore a change in community structure, there have been also many cases of species invasions, attributed to human activity. The change in species composition ultimately leads to modifications of interspecific relationships such as competition, predator-prey, host-parasite or mutualism (Bellard et al., 2012).

The motivation for maintaining high and intact biodiversity includes aesthetic, cultural, and economic factors. Furthermore, from a strictly ecological functionality point of view, species matter so far as their individual traits and interactions contributed to maintain the functioning and stability of ecosystems and the biogeochemical cycles. As Yachi and Loreau (1999) proposed in their “insurance hypothesis”- biodiversity provides ecosystems with an “insurance” or a buffer, against environmental fluctuations. Different species respond differently to these fluctuations, leading to more predictable aggregate community or ecosystem properties. Recent studies showed that multiple

species interactions maximize a community's ability to resist invasion and increase recovery after disturbance, or in other words, greater diversity of functional groups may increase the likelihood that functional groups can individually or interactively reduce the spread of an invasive species (Kimbro et al., 2013) as are likely to fulfill more ecosystem functioning (Stachowicz et al., 2008). As stated above, biodiversity functionality works differently at different scales. The direct effects of individual species and species richness on ecosystem processes is expected to be greatest at small-to-intermediate spatial exposes, but this link may be weakened at regional scales, where environmental heterogeneity is greater and other parameters become more important (Loreau et al., 2001). Thus, exploring smaller scale environmental heterogeneity may be more informative for our understanding of ecosystem processes. There is evidence that biodiversity enhances habitat productivity, although the form of the relationship is still debatable (Gessner et al., 2004). It has been also suggested that biodiversity links directly to ecosystem services. Some argue that ecosystems are so complex that we cannot really understand their workings mechanistically, so that maintenance of biodiversity may serve as a useful proxy for the state of the system and provide multiple ecosystem services. Thus, managing to maximize biological diversity (however defined) may be a workable way to ensure long-term maintenance of an acceptable balance among the competing demands for various ecosystem services (Duffy, 2008).

1.1.1 Marine Biodiversity

The marine habitat is by far the largest on the planet, yet our knowledge of marine biodiversity patterns is very small and fragmented (Hooper et al., 2005). According to Hendriks et al. (2006), marine biodiversity research remained grounded, as only approximately 10% of the research published or presented at international biodiversity conferences concerns marine biomes. This may be largely due to the fact that many marine habitats are difficult to sample and that the real diversity lies in rare and hard to identify species—up to a third of which are too small to be retained in standard sampling gear (Webb, 2009).

All of the aforementioned threats apply greatly to marine ecosystems, especially since coastal development and resource exploitation is rapidly increasing (Coll et al.,

2012; Worm et al., 2006). Generally, ecological principles apply equally in terrestrial or marine ecosystems. However the special conditions prevailing in a watery 3D medium that channeled evolution and adaptation of marine organisms, have led to differences in the organization of marine communities compared with terrestrial communities (Nybakken, 2001) and therefore for several inconsistencies in ecological theory. For example, there is a stronger top-down control in the sea relative to terrestrial habitats (Shurin et al. 2002 as stated in Stachowicz et al. 2007), suggesting that in marine systems, traditional measures of ecosystem functioning such as production or biomass may be influenced more by herbivores or predators than by plant diversity as in terrestrial habitats (Stachowicz et al., 2007). The oceans, as open systems, tend not to comply with some theories often built by terrestrial ecologists. For example the concept of succession as a deterministic process of distinct stages in the community structure moving towards a given climax is largely irrelevant in the ocean (Palmer et al., 1997). Marine ecologists have developed marine-specific ecological concepts. A notable example is supply-side ecology, which suggests that in benthic marine systems we are unable to correctly predict the course of change in the community structure after a disturbance, since it is not dependent only on competition and predation but also on the stochastic recruitment of propagules and larvae (Palmer et al., 1997; Underwood and Fairweather, 1989).

1.1.2 Current Biodiversity Issues in the Mediterranean

The Mediterranean Sea is presently undergoing a rapid alteration. There is an increased occurrence of warm-water biota, and it has been said that the Mediterranean is under a process of 'tropicalization'. While species composition in Mediterranean Sea communities is constantly changing, the coastal marine ecosystems in the Mediterranean are still dominated by algae and not by corals as is typical in tropical seas (Bianchi, 2007).

A recent assessment of Mediterranean marine biodiversity described the Mediterranean Sea as a biodiversity hot spot, hosting approximately 17,000 marine species, of which one quarter is endemic and about 3.3% are alien (Zenetos et al. 2010, Bianchi and Morri 2000). The occurrence and spread of warm-water species in the Mediterranean Sea results from the action of four distinct causes, namely: Atlantic influx,

Lessepsian migration, introductions by humans and recent sea warming. While the first factor is a natural cause, the three other factors are clearly anthropogenic. Lessepsian migration indicates the penetration of Red Sea species into the Mediterranean that started soon after opening of the Suez Canal in 1869 and is still ongoing. For a long period, the vast majority of these Lessepsian migrants remained confined to the Levant Sea, however many of them have now penetrated also into the western Mediterranean (Bianchi, 2007). Species are being intentionally or accidentally introduced via ship fouling, ballast waters, aquaculture, trade in live bait, wrapping of fresh seafood with living algae, aquariology, and even scientific research (Bianchi and Morri, 2000). Finally, an increase trend in Mediterranean temperatures is clearly seen from the mid-1980s and up to 2006 (Bianchi, 2007; Nykjaer, 2009). Although with a large spatial variability, sea level rise in the Mediterranean has been estimated at 10 cm in the last two decades (Klein et al., 2004) . However uncertain the expected rate is, several studies have suggested that a rise larger than 1 meter per century cannot be ruled out (Milne et al., 2009). These ongoing and future changes may endanger and change marine habitats, particularly the intertidal habitats. This is especially true for the Israeli Mediterranean where most of the rocky shore is found at mid sea level due to the unique formation of the coast (see below).

1.2 Heterogeneity

The ‘habitat heterogeneity hypothesis’ is one of the cornerstones of ecology (e.g. Simpson, 1949; MacArthur & Wilson, 1967; Lack, 1969). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity. In most terrestrial habitats, plant communities determine the physical structure of the environment, and therefore, have a considerable influence on the distributions and interactions of animal species. For example, for bird species diversity in forests, MacArthur & MacArthur (1961) showed that the physical structure of a plant community, or how the foliage is distributed vertically, may be more important than the actual composition of plant species. Although most studies show a positive relationship between habitat heterogeneity and species diversity, there are also some contradictory results. The nature of this correlation is greatly affected by the taxonomic group in question and what is perceived as a habitat by

the organism, the structural parameters that are defined as habitat heterogeneity and how they are measured, the measurement of species diversity and the temporal and spatial scale of the study. It is important to select biologically meaningful variables in studies of habitat heterogeneity effects. We must take into account that what is considered as an important structural variable may vary between studies, dependent on, e.g., habitat requirements of the species group, home range, or the scientific perspective (Tews et al., 2004). Therefore species diversity may also decrease with increasing habitat heterogeneity, whether the original theory really does apply on the system in question or not.

As reviewed in Tews et al. (2004), one third of the terrestrial habitats studies still deal with the research of vegetation-shaped habitat heterogeneity and species diversity, mostly avian fauna. In these cases, habitat heterogeneity is composed of physical structure of vegetation. In other cases exploring the environmental heterogeneity and plant species diversity relationship, the habitat heterogeneity is defined as soil properties and surface microenvironment (Ricklefs, 1977), rainfall, aspect, evapotranspiration, soil depth, temperature and area (Pausas et al., 2003) or simply the number and types of habitats available (Kadmon, 1993).

In marine habitats, particularly in intertidal rocky shores, environmental heterogeneity is usually perceived as topographic heterogeneity and its relation to a certain process or component in the community structure, e.g., substrate microtopography and its effect on fucoid establishment (Lubchenco, 1983) and species diversity (Menge et al., 1985), the effect of boulder size (as part of the habitat's structure) on flow velocity (Guichard and Bourget, 1998) and effect of sand deposition on algae species abundance patterns (Littler et al., 1983) or species richness (Mcquaid and Dower, 1990). Increasing evidence indicates that spatial and temporal patterns in ecological systems are not independent of the scale of measurement and that these scales must be taken into account when trying to explain community structure in the context of environmental heterogeneity.

Indeed, the role of topographical heterogeneity may change with scale. It is known to alter predator-prey relationships at small scale, while at larger scales, topographical heterogeneity probably does not modify this interaction, and usually

factors affecting recruitment or mortality may be increasingly important (Archambault and Bourget, 1996; Chapman and Underwood, 2008; Fraschetti et al., 2005).

Many recent studies in marine ecology are trying to determine and predict scale patterns that can be generalized across species and habitats (Archambault and Bourget, 1996; Benedetti-Cecchi et al., 2003; Chapman and Underwood, 2008; Denny et al., 2004; Díaz et al., 2011; Fraschetti et al., 2005; Russell et al., 2006; Terlizzi et al., 2007). It can be concluded that small-scale variability substantially emerges as a general property of benthic assemblages in marine coastal habitats. In all intertidal or subtidal aforementioned studies, increase in environmental heterogeneity correlated to species diversity increase at small scales (10ths of cm). As for larger scales, patterns differ between habitats and regions and species diversity is weakly related to heterogeneity. Therefore, at large scales (10ths of km), each coastal habitat should be approached individually.

As can be seen from the few examples presented, the definition of 'environmental heterogeneity' varies amongst researchers (even for the same habitat), and derived mostly from their unique point of view on the same question and from their ability, or perhaps lack of ability to measure certain parameters. This fact creates a confusing reality when approaching the question under discussion in a specific habitat. Since in each research the definition and measurement of heterogeneity is different and usually limited to several species or a single genus, there is no way of to synthesize the results to a comprehensive conclusion. Furthermore, most studies that examine a number of environmental parameters relate to the individual effect each of them has on species diversity, without attempting to combine them into a single measure or index of environmental heterogeneity. Since different aspects of heterogeneity are used, a general fit-for-all index will not be suitable. However, the conclusions from previous results combined with general ecological logic concerning the relative effect of the fundamental environmental parameters on species diversity and community structure can be applied for general types of habitats in order to develop a uniform heterogeneity index. This study roughly attempts to do so for the Israeli Mediterranean rocky shore.

1.3 Intertidal Rocky Shores

Although the intertidal zone constitutes the smallest area of all marine ecosystems, because of its accessibility, this ecosystem has been the subject of many classic community ecology studies. Of all the intertidal shores, the rocky shores are the most densely inhabited and have the greatest diversity of autotroph and animal species. This is attributed to the great variation in environmental factors in this habitat, which occur among other things, because of the air exposure for a certain amount of time during a day and due to the high structural complexity of the habitat (Nybakken, 2001).

One of the ways to describe community structure on rocky shores is patterns. The best-known pattern in rocky intertidal communities is zonation. Zonation describes the pattern of distribution and abundance of organisms as one moves from the low shore to the high shore. As Stephenson and Stephenson (1949) proposed it in the classic zonation scheme, it occurs universally in all rocky intertidal regions, even where tidal range is only a few centimeters. According to the scheme, the intertidal area has three main zones:
1) The supralittoral fringe, or the upper zone, that is never covered completely with water, but often flushed or sprayed by waves. This zone supports only a few species, and the dominant species is usually littorine snails. 2) The midlittoral zone, which extends from the highest high tide down to the lowest low tide, is the broadest in extent and often subdivided. It is sometimes covered by tides and frequently washed by waves. It is dominated mostly by sessile organisms: barnacles in the upper section and mix of barnacles and macroalgae in the lower part. In the Israeli shore it is also inhabited by vermetid gastropods and rapidly-moving arthropods, crustaceans and other invertebrates. 3) The lower part is the infralittoral fringe, which is really an intertidal extension of the sublittoral area, and as such it is only rarely exposed. This is a species rich area that is densely populated only by organisms that can tolerate limited exposure to air (Lipkin and Safriel, 1971; Menge and Branch, 2001; Nybakken, 2001; Stephenson and Stephenson, 1949). The unique structure of the intertidal rocky shore under inspection on the Israeli shore makes the zonation pattern less distinctive, especially for the midlittoral zone because it is very flat nature.

The vertical distribution of organisms along the shore is confounded by the specific conditions in each zone. It is believed that physical factors limit the upper limits of species distribution, through the extreme conditions of desiccation, high temperatures and sometimes wave action, and high salinity. At lower shore levels, where physical stress is less harsh, biological interactions (predation, herbivory, competition) become more important (Connell, 1972). These zones however, are also modified by biogeographic changes that impose larger-scale patterns. Gradients in wave exposure produce a horizontal distribution of organisms along the shore, respectively to their suitability to resist wave force and proximity to the breaking of the waves (Connell, 1972). Species composition can shift dramatically from wave-exposed to sheltered sites while still maintaining vertical zonation. The combination of these two environmental gradients can produce a complex range of conditions in rocky intertidal habitats (Connell, 1972; Menge and Branch, 2001).

The intertidal rocky habitat is also characterized by small scale patchiness. Species who live in the same habitat at a large scale (for instance all midlittoral rocky platforms in Akhziv), on a smaller scale (at each platform) may have partitioned to microhabitats according to their physical demands or adjustments to the habitat, hence creating patches of species, or groups of species that do not comply with the zonation scheme (Connell, 1972). The most common example for this is tide pools, which are often found on rocky shores, especially in the mid zone. Tide pools imitate subtidal conditions where there is no harsh effect of wave action or air exposure and therefore they commonly inhabit sublittoral species alongside the middlitoral ones. Nevertheless, if low tides last for several days, the conditions in them may become extreme for some of the species as a result of large fluctuations over short time in physico-chemical parameters such as temperature, salinity, oxygen, carbon dioxide and pH inside the pools (Martins et al., 2007).

Incompatibility of succession as a deterministic process in marine habitats has been previously discussed here. In the intertidal habitat there is evidence of an orderly sequence of establishment of species colonizing newly vacated spaces and different species replacing them in time. The order is primarily a result of differences in length of breeding seasons, motility of planktonic stages, rates of growth after settlement, and

ultimate size reached by the organisms themselves (Connell, 1972). The latter two are of course influenced also by the habitats' constraints such as predation, space competition and physical stressors. So the organisms comprising the community certainly do modify the environment in such a way that others are enabled to live there, but these modifications do not necessarily produce a predictable succession.

Intertidal assemblages on rocky shores are particularly vulnerable to changes in climate variables. Thermal fluctuations and desiccation due to aerial exposure can drastically affect spatial and temporal patterns in assemblages. Underlying mechanisms include photoinhibition and thermal and osmotic stresses. These effects can be exacerbated by climate events such as global warming and storminess which in turn can affect biological interactions (Bertocci et al., 2007).

Many hypotheses were proposed to explain species diversity patterns in the intertidal (e.g., Menge and Sutherland 1976; Connell 1978; Huston 1979; Lubchenco and Gaines 1981). These can be divided into two general groups: those concerning environmental characteristics (e.g., evolutionary or ecological time, climatic variability, habitat heterogeneity, habitat area, levels and patterns of productivity) and those concerning regulating mechanisms (e.g., physical and biotic disturbances, consumer-prey and competitive interactions, rates of reductions and recovery of populations) (Menge et al., 1985). As addressing all of these factors and processes at once is impossible, this work also focused on one in particular, i.e. the environmental characteristics.

1.4 Macroalgae

Macroalgae are dominant if not the most dominant space occupiers on many rocky shores. They are usually divided into three major divisions: Chlorophyta (green), Phaeophyta (brown) and Rhodophyta (red). All three types are found on rocky shores, attached to the substrate by a holdfast and usually referred to as seaweed. When all algal genera are considered, temperate regions consistently have higher algal richness than tropical areas. The peak in algal genus richness at mid-latitudes on a global scale makes benthic marine algae an exceptional group, in that there are very few taxa that have diversity peaks outside of the tropics (Kerswell, 2006).

Algae are the first link in most food chains at the intertidal habitat. Their main herbivores are certain fish species and mainly mobile gastropods and crustaceans. Just like terrestrial plants, macroalgae receive their energetic demands through photosynthesis, using assistant pigments in the process in addition to chlorophyll-*a*, from which they receive their coloring. When exposed to air, there is still photosynthetic ability, but it decreases with time of exposure and depends on the amount of water lost. Evaporation rates differ among algae and some have counter mechanisms, such as coating resembling the plant cuticle (e.g. *Saragassum spp.*). Some algae have the ability to recover even after severe dehydration (90% water loss) when submerged again, for example *Ulva spp.*. It is clear that such adaptations make the algae compatible for the intertidal habitat (2004 ,עינב).

Several types of reproduction exist in algae. Alternation of generations is the most common, but many species reproduce sexually or have the ability for vegetative reproduction too. The different reproductive stages usually correspond to specific seasons and change between perennial and annual algae. The propagules (gametes) are usually free-living in the water until the settlement on the substratum, with the exception of a few species (Fletcher and Callow, 1992; 2004 ,עינב). Algae species distribution mainly depends on their dispersal range, and it ranges from a few meters up to 5km (Kinlan and Gaines, 2003). In some species, the propagules settle very close to the mother plant (Fletcher and Callow, 1992). It has been suggested that the initial settlement of macroalgae is facilitated by biofilm, formed on the substratum by organic material and microorganisms such as diatoms and bacteria (Park et al., 2011).

The differences in reproductive strategies of algae affect their ability to reoccupy cleared space after a disturbance. Algae that occupy space by vegetative propagation usually rehabilitate more successfully than those who occupy space mostly by dispersal of sexual propagules. This is because vegetative propagation can be achieved at all times of the year, while sexual dispersal is dependent on the timing of the disturbance and the availability of propagules (Airoldi, 2000). Therefore, a more diverse community that consists of a mixture of different reproductive strategies will have high prospects of recovery after a disturbance.

Intertidal macroalgae communities respond to changes in nutrient levels, problems of eutrophication, toxic substances and most importantly to habitat modification and general stress. As such, the Water Framework Directive (WFD) states that macroalgae are a biological quality element to be used in defining the ecological status of a transitional or coastal water body (Pinedo et al., 2007; Wells et al., 2007). Both the use of single key species (as *Cystoseira*) or opportunists/late successionals or Rhodophyta/Chlorophyta ratios has been tested and implemented.

The environmental heterogeneity effect on algal community was tested in previous studies and compared rocky shores substratum heterogeneity to heterogeneity of soils for plants in terrestrial systems, in the manner that it can influence algal species composition and performance (Stachowicz et al., 2008). For example, Lubchenco found that the presence of cracks, small crevices, depressions and pits all provide spatial refuges for young *Fucus* germlings, allowing them to become established and grow to a less vulnerable size (Lubchenco, 1983). Moreover, the scale of the substratum heterogeneity was found important. If cervices were small they allowed the algae to grow while protecting it from grazers. Larger cervices weren't as effective protection and less grown algae was found in them. Along with the roughness of the substratum, its verticality as a stress factor for algal assemblages has been investigated. So far, there is evidence that vertical habitat on a rocky shore is more favorable for algae than a horizontal one. Although vertical surfaces can experience long periods of aerial exposure and increased stress due to fast drainage of sea water, it seems to be compensated by diminishing solar radiation and thus the rate of evaporation (Benedetti-Cecchi et al., 2000).

Some algal species require modification in the physical environment by other algae before they can establish on the shore. Young *Fucus* plants were shown to be establishing more quickly under larger individuals than in the open (Connell, 1972). The canopy-forming *Cystoseira* has been shown to be a habitat-forming species, as the assemblage living under its canopy is distinct, in terms of composition and structure, from that found on open space, without the algae cover (Bulleri et al., 2002). Nevertheless, it's important to remember that algae also function as competitors for settlement space with other algae and sessile invertebrates on the shore surface.

Intertidal rock surfaces are rarely perfectly flat; therefore sand is deposited unevenly across the shore causing greater habitat heterogeneity. Sediment accumulation and inundation often excludes some species from specific areas through the mechanisms of physical injury due to scouring, smothering due to reduced light and nutrients and by making it difficult for algal propagules to attach to the surface in early life stages (Littler et al., 1983; Mcquaid and Dower, 1990).

Unlike nearshore sessile animals, algae do not have a stiff armor to protect them from the great power of breaking waves, which are often accompanied by water velocities of $2ms^{-1}$. Algae can withstand these forces mainly due to a flexible structure that allows them to sway along with the waves (Denny and Gaylord, 2002). There are striking differences in community structure between sites exposed to and protected from wave action. Some algae were shown to be more dense at exposed than at protected areas (Lubchenco and Menge, 1978). The morphology of these species probably makes them more resistant to wave action and therefore can escape the grazers that are usually more abundant at protected areas. A study carried out on a detached platform around the small Hayonim Island (c.a. 35 km south of Haifa) compared algal communities and showed that the sides more exposed to the effect of waves had higher algal species richness than less exposed areas (Einav and Israel, 2007).

As Foster et al. nicely summarized, understanding the influence of species diversity and composition of algae cover is important for understanding overall community structure because algae cover (1) regulates the space available for colonization by sessile invertebrates, microalgae, and other macroalgae species; (2) is an important determinant of the structural complexity of the habitat and microenvironmental conditions; and (3) represents the primary food resource for the local food web (Stachowicz et al., 2008). Algae therefore comprise a major factor in determining the composition and abundance of intertidal communities.

1.5 Rocky Shore on the Israeli Coast

Most of the rocky shores (excluding beachrock) on the coast of Israel appear in the form of flat platforms known as vermetid reefs or abrasion platforms (עינב, 2004) which are part of the shore cliffs eroded to the sea level and protected from further erosion by a

crust of sedentary, aggregative vermetid gastropods and calcareous algae. They are usually formed by eolianite rock, but in some cases also formed by white limestone. The edges are usually higher than the rest of the platform surface, forming rims which enclose some parts of the platforms. This potentially provides some protection from waves and hold water on the platform during low tides and calm seas. These edges are the result of biological accretion of the marine snails *Vermetus triquetrus* and *Dendropoma petraeum* (Safriel, 1974). There is evidence that the *Dendropoma petraeum* populations have been deteriorating and are all but extinct today along the Israeli coast for reasons that are still unknown (Rilov et al., 2004). This can potentially affect the habitat topography and its community, making the entire ecosystem more vulnerable to change.

Tidal range along the Israeli coast is relatively narrow and limited to a range of about 30-40 cm (Einav et al., 1996). There is a strong tidal seasonality with a range of 20 cm among seasons, highest sea levels occur at the summer and lowest sea levels occur at the end of winter (Goldsmith and Gilboa, 1986). Because the tide is small, wave force is more influential than tidal amplitudes in this region. The Israeli Mediterranean shore is straight in most parts, and facing the prevailing southwesterly to northwesterly winds. Therefore, the platforms along the shore are most of the time subjected to intensive flushing during both high and low tides and to strong wave action during storms. Conversely, they are exposed entirely to air and desiccation during periods of calm seas and prolonged high barometric pressure, which occur on special synoptic conditions characterized by winds blowing from land and usually associated with heat waves. Such extreme conditions can push the sea level below the Mean Low Water Level (MLWL), exposing sessile organisms to air for long periods. This phenomenon is typical to the region mostly during spring and autumn but can also occur during winter. The size, width and shape of the platforms vary greatly; this probably affects the diversity and the abundance of species of algae present (Lundberg, 1996).

In general, very little ecological research has been performed on the unique ecosystem of vermetid reefs in their entire Mediterranean range. This is true also for the rocky shores of Israel, although these reefs constitute about 10% of the Israeli Mediterranean shore. Most of the pioneer work on intertidal community on abrasion platforms was done by Lipkin and Safriel at Mikhmoret (Lipkin and Safriel, 1971),

describing the algal and faunal species by classic zonation patterns and comparing them to the more explored western Mediterranean. From the algal standpoint a few works had followed (Einav and Israel, 2008; Hoffman, 2004; Lundberg, 1996; 2004 ,עינב ;1999 ,כץ), but the main focus remained on generally describing the algal community per site, zonation and season distribution with very little quantitative analysis. Gil et al. examined the effect of wave action on the distribution of marine macroalgae species at the small detached platform of the Newe-Yam Island (Gil et al., 2008). They concluded that three systems of environmental factors influence the distribution of algae: orientation, platform parameters that affect water mixing on the platform and microhabitat conditions. These results were taken into account in the present study. So far, a comprehensive, multi-scale multi-season study on the relationship of environmental heterogeneity and the communities on abrasion platforms have not been conducted in Israel, and to that effect, anywhere in the Mediterranean. In fact, a multifaceted study as described below testing the fundamental relationship between habitat heterogeneity and algal biodiversity has not been performed on the rocky intertidal worldwide.

1.6 Research objectives

This study attempts to explore the possible relationship between environmental heterogeneity of the intertidal habitat and its algal community. My working hypothesis is that with increased heterogeneity diversity will increase as well. Using field sampling and statistical methods I wish to examine how certain environmental parameters affect the algal diversity and composition, separately and conjoint. Patterns of species distribution are not independent of geographical context. No attempt to explain algal species diversity in the Levant area of the Mediterranean has been done. I attempt to find out whether previously proven factors in other parts of the world influence the intertidal community here. Understanding the factors affecting the algal biodiversity could help resolve the role this group plays in ecosystem functioning, ultimately leading to increased predictive ability. It is especially relevant in the context of the evident changes this ecosystem is undergoing.

The study included the following objectives:

1.6.1 To describe the spatio-temporal variability of species diversity and composition at the small to medium spatial scales.

1.6.2 To identify the physical components of the habitat that affect community composition and algal diversity.

1.6.3 To test the hypothesis that high environmental heterogeneity positively affects algal biodiversity on abrasion platforms.

2. Materials and methods

2.1 Study site

The study was performed on the eastern Mediterranean coast at the northern rocky shore of Akhziv, Israel, where vermetid reefs are abundant (Figure 1). Due to focus on a relatively small spatial scale, the study was held only in one location. A local scale of less than a km of highly exposed shore allows the assumption that all examined platforms are exposed to the same species pool and with similar larval supply.

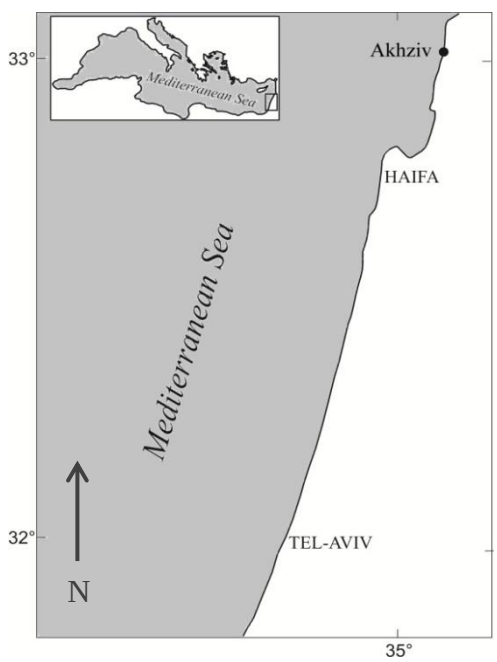

Figure 1. The location of the study site, Akhziv, on the eastern coast of Mediterranean Sea

In this site, along a stretch of coast several hundreds of meters long there are a number of broad abrasion platforms (vermetid reefs) situated at the midlittoral zone of the intertidal and separated from each other by several meters. Field sampling and measures were held on six of the platforms (between 33° 03'51.36"N 35° 06'14.55"E and 33° 03'46.61"N 35° 06'13.60"E) (Figure 2), that differ in many parameters including shape, size, height above sea level and number and distribution of micro-habitats.

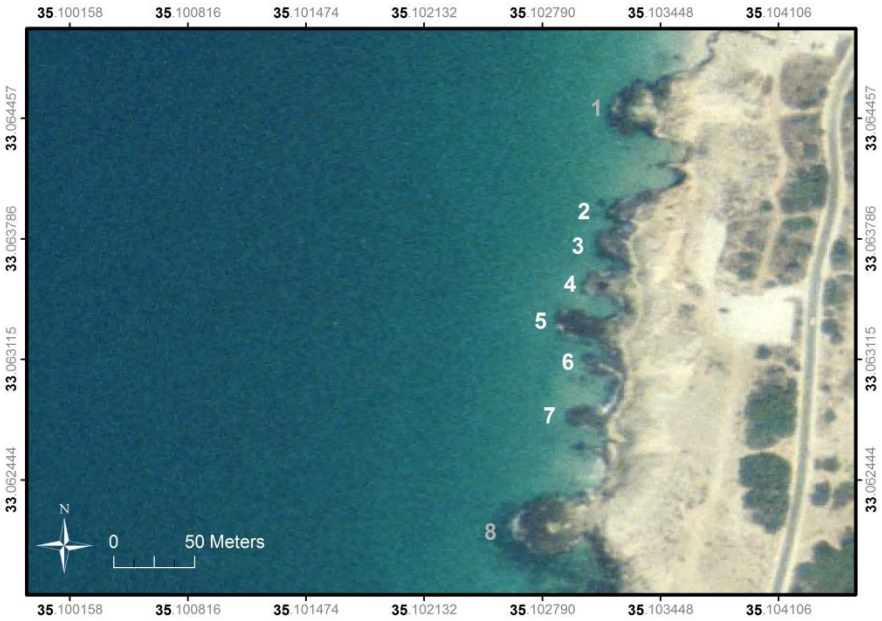

Figure 2. Satellite image of the study site. Platforms 2-7 were selected for the present study.

All platforms have at least two major habitats, the center of the platform and its edge. Platforms 2, 3 and 7 have an additional habitat of tide pools, a different number on each (Figure 3). The platforms are dominated mostly by a dense coverage of macroalgae. Patches and individuals of the mollusks as the vermetid gastropod *Vermetus triquetrus*, the invasive mussel *Brachidontes Pharaonis*, as well as the snails *Patella caerulea*, *Fissurella nubecula*, *Chitons* and the barnacle *Chthamalus stellatus*, occur at the edge and the center habitats on all platforms. The rocky shore at this site is a part of the Rosh ha Nikra Beach nature reserve, where fishing is prohibited using nets and speargun, while angling is allowed. Yet the site is concidered as "overfished" (אנגרט ויהל, 2011) as it is frequently visited by fishermen, who use some of the algae as bait and stand on the platforms for long periods of time, trampling the algae.

2.2 Field Sampling

2.2.1 Sampling Scheme

Field sampling efforts took place in four consecutive seasons during one year, starting in the spring of 2010. The sampling was conducted using a 0.5x0.5 m quadrat, divided to 100 equal squares (sub-quadrats) for ease of evaluation of percentage cover. Sampling locations at the edge and the center habitats were selected at random. In order to re-sample the same locations in the following seasons, a map of the sampling locations was drawn for each platform. Tide pools were sparse; therefore all tide pools were included in the sampling.

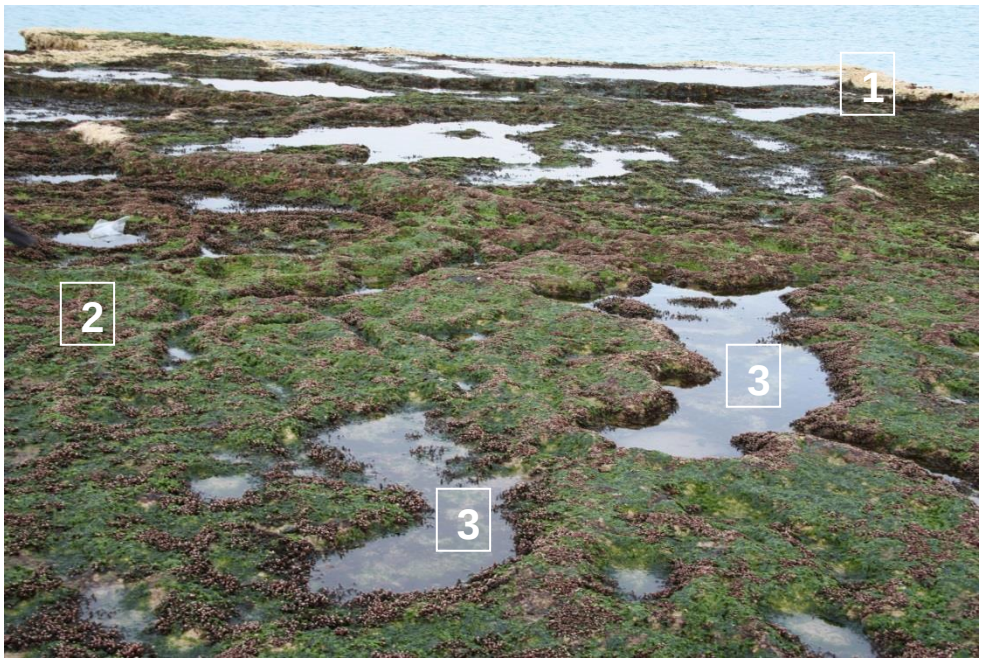

Figure 3. Platform number 3 on February 2012 during extreme low-tide. The three habitats are indicated: 1-Edge, 2-Center, 3-Tide Pools

In order to determine the required sample size for each platform, a preliminary sampling session was conducted on April 2010. Random locations were sampled on the largest and on the smallest platforms, 5 and 6 respectively. A species accumulation curve was generated for each of the platforms. Number of required quadrats for sampling was determined as the minimum number of sampling units required to obtain the maximum number of sampled species. According to the results, both the center and the edge habitats required five quadrats for the smallest platform and eight quadrats for the largest platform. The number of sample units for the other platforms was decided based on their

relative size and the relative size of each habitat within them (Table 1). In total, in each season 36 and 38 quadrats were sampled at the center and edge habitats, respectively in every season .Sampling the tide pools using a quadrat was not possible because of pool shape and sizes, and the need to sample the vertical dimension of the pools. Therefore, a categorical index of abundance was used instead of estimation of percentage cover (see below).

Table 1. Number of Sample units for each platform, divided by habitats. Area of each platform is indicated

Platform	***Area (m^2)***	***Number of sample units***	
		Center	*Edge*
2	*281.8*	*6*	*6*
3	*299.7*	*6*	*5*
4	*322.7*	*6*	*7*
5	*401.2*	*8*	*8*
6	*167.9*	*5*	*6*
7	*225.1*	*5*	*6*

2.2.2 Species

In each quadrat, the percent cover of macroalgae and macrofauna were evaluated. If limpets occurred, they were counted. In the pool habitat, the cover of algae was evaluated according to three categories: Abundant, Frequent and Rare, These categories were converted to percentage cover according to Burrows et al. (2002) (Table 2). Sessile fauna in the tide pools were cryptic and therefore were not recorded there. During the cover evaluation, algae were shifted around in order to include overlapping algae in the count (Dethier and Graham, 1993). All macroalgae covering more than 0.5% were recorded. A number of species were difficult to identify to species level in the field, therefore for 16 species, identification has been limited to the genus level only, although sometimes microscopic identification in the lab was still required. 17 algae were identified to the species level, and one group of species could be recorded at the family level. Hence, the biodiversity under discussion is actually taxon diversity, but will be referred as biodiversity throughout this paper. In case it was not possible to identify an alga during the field work, a sample of it was taken to the lab for identification using a binocular or a microscope, assisted by field guides (Littler et al. 1989 , Huisman et al. 2007, Guiry and

Guiry 2010, 2004 עינב) and consulting with experts at the Israel Oceanographic and Limnological Research (IOLR) institution.

Table 2. Abundance categories for sampling in the pool habitat and their respective percentage cover

Cover Category	Percentage cover range
Rare	0.5 - 2.4 %
Frequent	2.5 – 44 %
Abundant	45 – 100 %

2.2.3 Environmental Parameters

2.2.3.1 Structural parameters

2.2.3.1.1 Quadrate Scale

In each quadrat, the percentage cover of sand, bare rock and water during low tide were estimated. Surface roughness (as proxy for complexity) was assessed using a relative rank between 1-4, when 1 = smooth rocky surface with no pits or bulges and 4 = rocky surface with many textural transitions, grooves or holes. Surface verticality was also assessed with a relative rank between 1-4, when 1 = absolutely horizontal surface, 4 = the rocky surface is vertical. When sampling quadrats at the edge habitat, presence of elevated rim was recorded. Presence of large depressions in a quadrate was also recorded.

2.2.3.1.2 Platform scale

The area of each platform was calculated using ArcGis 10 (ESRI, 2011). The height of each platform was measured at 7-10 points at the center and the edge habitats using a laser level (Spectra Precision® Laser LL100) and a laser rod receiver (Agatec SmartRod®). Measurement points were determined using the sampling locations map, thus each height measurement related to a single seasonal sampling quadrat. Height of each platform was calculated as an average of all its measurement points. Orientation was found using the sampling locations map.

2.2.3.2Water flux assessment

Because not only static environmental parameters can describe heterogeneity and because flow is critical for rocky intertidal organisms, we decided to measure relative water flux

at the two major habitats as another measure of heterogeneity. For flux comparison between habitats and platforms, gypsum buttons were prepared to serve as dissolution blocks (Figure 4). Bolts were screwed into plastic caps collected from empty standard water bottles of the same brand. The edges were extended with strips of stiff paper glued

Figure 4. A gypsum button for evaluation of water flow on the platforms, using the gypsum dissolution

to the caps; that way they can be removed before use. After stabilizing the molds, the gypsum mixture prepared according to (Boyd, 2006) was poured into the caps and left to dry for 24 hours. After air-drying, the buttons were also dried in 60ºC for additional 24 hours. Since gypsum dissolution was found to vary with its shape (Boizard and Dewreede, 2006), a finishing polish with sandpaper was performed for shape unity.

In the field, 38 buttons were screwed into drilled holes on three of the platforms at the study site (3, 5 and 6) at the center and edge, during low tide. The placing was determined in accordance with quadrate sampling locations, using the sampling location map. It was impossible to drill inside the tide pools; therefore this habitat was excluded from this experiment. The buttons were left on the platforms for 24 hours (Figure 5). At the same time, a control button was left in standing water (taken from the study site), for subtraction of the gypsum dissolved in standing water from the rest of the buttons that were at sea according to Boyd. After 24 hours, the buttons were removed from the platforms and left to air-dry for 24 hours. After air-drying, the buttons were also dried in 60ºC for additional 24 hours. After drying completely of water, the buttons were weighed and the amount of dissolved gypsum in 24 hours was calculated. Relative weight loss is related to the relative water flux over the surface.

Figure 5. Gypsum buttons at (a) center and (b) edge habitats during 24 stay on the platforms

2.3 Data processing and analysis

Species richness was calculated as the number of all species sampled in a quadrat, or in a habitat or platform on larger scales. When comparing between habitats and platforms, total species richness and average species per quadrat were used. Shannon ($\log_e$) index was also calculated at the quadrat level. It was decided as the most relevant diversity measure, since it emphasizes rare species (Bakus, 2007). It would be preferable to use percentage cover abundance for most analyses, yet in the pool habitat it was not possible to estimate exact percentage cover. Instead, I estimated the cover using three categories (Table 2). Therefore, in order to compare between habitats, I transformed the percentage cover in the center and edge habitats into the respective categories using the ranges in Table 2. For the multivariate analyses, I used the median of each range to represent the cover category.

Coefficients were regarded as significant at $p \leq 0.05$. At all places where averages were recorded, standard errors were indicated. Levene's test was used for assessing the equality of variances in different samples. Shapiro-Wilk test was used to test normality – if p-value was greater than 0.05 it was concluded that the data distribution is normal.

Univariate statistical analysis was performed using SPSS 16.0 (SPSS Inc., 2007). To test the effect of season and habitat on species diversity, one–way ANOVA with Bonferonni Post Hoc was used. Kruskal-Wallis test was applied for non-parametric data to test the effect of platform on species diversity. Mann-Whitney Test for non-parametric independent data was applied to test differences between habitats in sand cover, the effect of rim presence on species diversity and differences in gypsum dissolution between habitats. In order to test differences in gypsum dissolution between habitats divided by platforms, Independent T-Test was applied.

Correlations between species and environmental factors were tested by Spearman rank (marked as r_s) as a non-parametric measure of statistical dependence between two variables, or Pearson rank in case the data distribution was normal.

To test season, habitat and platform effects on species abundance and composition, multivariate analyses were performed using PRIMER 6.1.12 (Clarke, 1993) and PERMANOVA 1.0.2 (Anderson, 2001). All multivariate analyses were performed on percentage cover data, grouped by season, habitat and platform following a log(X+1) transformation, for a down-weighting of the abundant species, allowing the mid-range and rare species to exert more influence on the similarity calculation (Clarke and Warwick, 2001). First, the non-metric Bray-Curtis similarity index (Bray and Curtis, 1957) was used for building multivariate resemblance matrices from the transformed quadrat data. This measure calculates the similarity between any pair of samples (quadrates), in terms of the algal community they contain. For example, two samples are considered perfectly similar only if they contain the same species in exactly the same abundance. In order to visualize data similarities, non-metric multidimensional scaling (nMDS) ordinations were plotted. The purpose of MDS is to construct a configuration of the samples, in this case in two dimensions, while preserving the similarity ranking calculated using Bray-Curtis, as Euclidean distances in the plot. Since we cannot assume linear relationships between the species, the regression used to fit the samples in the distances of the ordination plot is non-parametric, hence a non-metric MDS (Clarke and Warwick, 2001). The degree of correspondence between the distances among points implied by the MDS map and the matrix input of similarity ranking is measured (inversely) by a stress function. Thus, the smaller the stress, the better the

representation. Stress values were always less or equal to 0.2, which is considered the threshold value for interpretable nMDS (Clarke, 1993). PERMANOVA (permutational multivariate ANOVA) was performed on the basis of the resemblance matrix of all abundance data with season, habitat and platform as factors, based on 9999 permutations. Pair-wise tests were also performed.

Gradient analysis and constrained ordinations were performed using Canoco 4.56 (Braak, 2009). Assuming unimodal model of species response to environmental gradients, Canonical Correspondence Analyses (CCA) were done with all species abundance data. In each analysis, different sets of environmental variables were used to examine the variability in species composition explained by seasons, habitats and environmental parameters along with the relationship of these variables to species axes. To assess deviation from a randomly generated distribution and significance of the variables and the ordinations, I performed Monte Carlo test (499 unrestricted permutations). Results were visualized using biplots created from the CCA algorithm. The ordination axes represent weighted linear combinations of the environmental variables, with arrows indicating the variables relationship to the species and length of the arrow indicating the size of that effect across the environmental variables. The angle among the arrows of the environmental variables can be also used to approximate correlation among those variables. The species are represented by points. The species point distribution in the biplot represents both the chi-square distance between the species distributions along with an approximate ordering of those species correlation in respect to the environmental variables (Lepš and Šmilauer, 1999). . For environmental parameters, the combined analysis was based mainly on edge samples, in order to include parameters that were only present in this habitat, as Rim.

In order to test for possible correlation between environmental heterogeneity and algal diversity, a simple index of heterogeneity was developed, and estimated for each platform. The six platforms were ranked for each structural parameter according to its contribution to the spatial heterogeneity of each platform (see Table 3). In scoring the platforms, I made the following assumptions: higher substrate roughness contributes to surface heterogeneity; hence the platform with the highest average roughness, platform two, scored six on this category and the platform with the lowest average roughness,

platform six, scored one. Additional habitat of tide pools increases platform heterogeneity. Presence of elevated biogenic rim adds to the heterogeneity through the added dimension of the substrate, added height variation and water holding capability. Depressions in the substrate add to its complexity, water holding, sand aggregation and lower height, thus increasing heterogeneity. Water cover affects different algae differently, and thus the platforms scored according to the variability of water cover: the platform with the highest standard error in water cover during low tide received the highest scores and so on. The score for sand cover was calculated in the same way. Similarly, a height heterogeneity index was calculated for each platform as the standard error of height measurements in that platform. The scores for all parameters were added to a cumulative heterogeneity score that represents each platform's structural heterogeneity. The main assumption of this index is that each parameter contributes equally to heterogeneity. Spearman rank was used as a measure of statistical dependence between the heterogeneity score and algal diversity. For each platform, Shannon diversity index was used to estimate its algal diversity.

Table 3. Heterogeneity score calculation. Ranking of the platforms for each parameter is shown. The sum of the scoring adds to the Heterogeneity Score. High number represents high Heterogeneity Score.

Platform	Roughness	Pools	Rim	Depression	SE Water	SE Height	SE Sand	Heterogeneity Score
2	6	4	3	2	6	2	6	**29**
3	3	5	2	4	4	6	3	**27**
4	5	0	1	5	3	5	5	**24**
5	2	0	6	6	1	4	4	**23**
6	1	0	4	3	2	1	1	**12**
7	4	6	5	1	5	3	2	**26**

3. Results

3.1 Species diversity and composition

Within one year of sampling at the study site of Akhziv, 34 species of macroalgae were found (Figure 6). This species richness is according to taxon identification that was used for the algae during the field sampling. When including all species that were seen on the platforms during the sampling but were outside of sampling range, a total of 44 algal species were found at the study site during that year (Appendix 1).

The algal community is dominated by five species that occurred consistently in all habitats and at all seasons: *Jania rubens*, *Laurencia spp*., *Acanthophora najadiformis*, *Chondria dasyphylla* and *Hypnea spp*.. Six species appeared only once – *Gracilaria spp*., *Rytiphlaea tinctoria* and *Halopteris scoparia* were found at the center, *Caulerpa mexicana* was found at the edge and *Botryocladia spp*. and the invasive Indo-Pacific species *Galaxaura rugosa* were found in the tide pools. No relation was found between these rare species and a specific season.

3.1.1 Temporal analysis

Algal community composition varied greatly among seasons, hence the importance of sampling throughout the year. Temperature, salinity and wave periodicity, which change seasonally, affect the algal diversity on the abrasion platforms. A significant difference in number of species per quadrat was found among seasons (1-way ANOVA: $F_{3,333}$ =46.951, $P<0.001$, R^2= 0.291) as shown in Figure 7. Highest richness was in the winter (average of 9 species per quadrat and 26 species total), while the lowest was in the summer (5 species per quadrat and 17 species total). Differences between spring and autumn were insignificant (Bonferonni Post hoc analysis, p=0.05). Overall, a similar trend was also recorded for total species richness and for Shannon index.

Community structure in the summer seems to be the most distinct compared to the other seasons (Figure 8), probably due to the low diversity. However, there is no total separation for any of the seasons. The winter, which reflected the highest diversity was also tightly grouped together in the MDS ordination, yet some points show high resemblance to the autumn and the spring. The spring and the autumn values are much

more scattered in the ordination, which indicates greater spatial variability in community structure among platforms and habitats during those seasons. Out of the three explored habitats, pools algal community seems to be the most season-independent, as seen by the distinct differentiation from the rest of the plot.

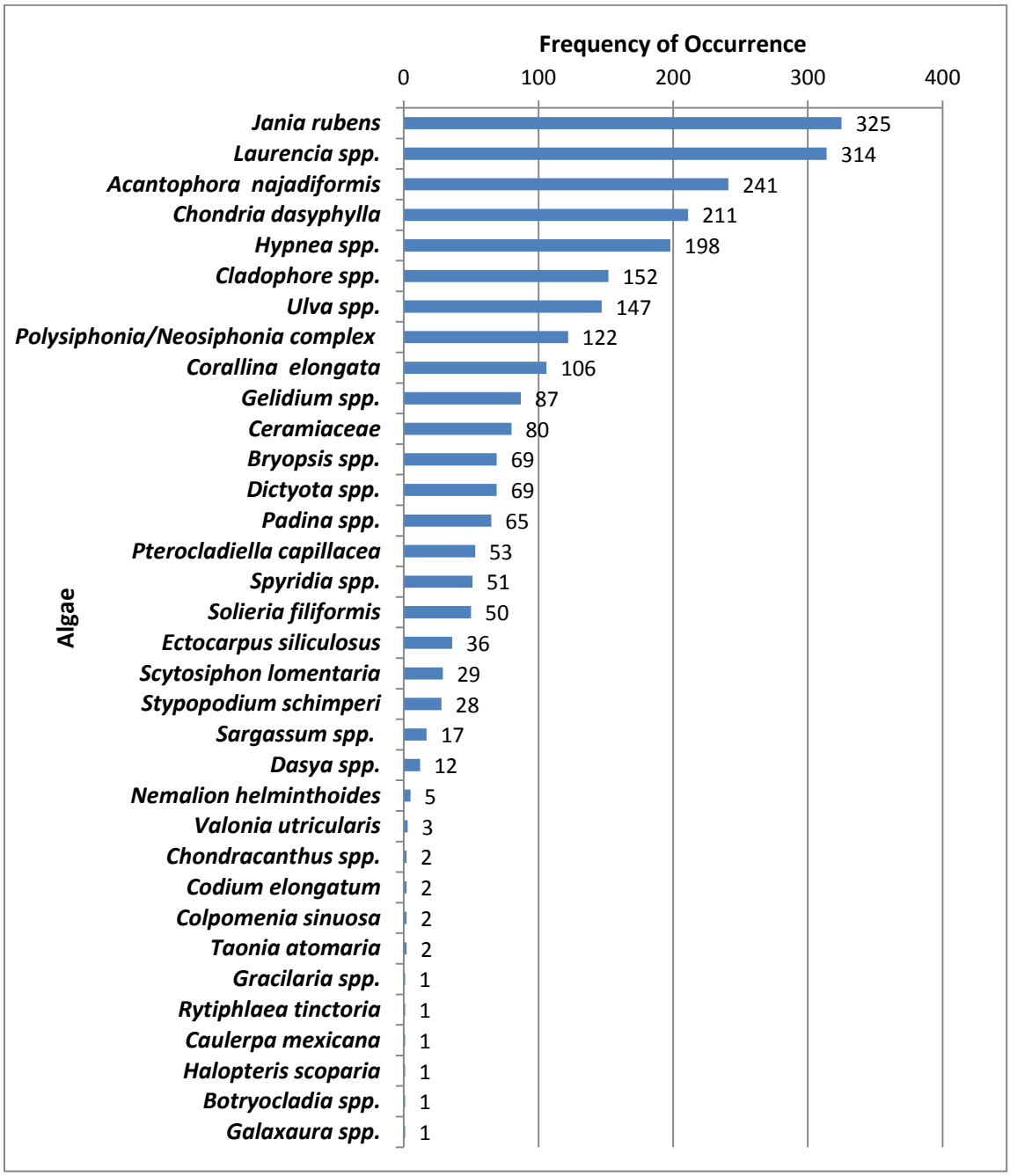

Figure 6. Presence distribution of all algae sampled during the one-year sampling of the study based on frequency of occurrence in all quadrats sampled during the study.

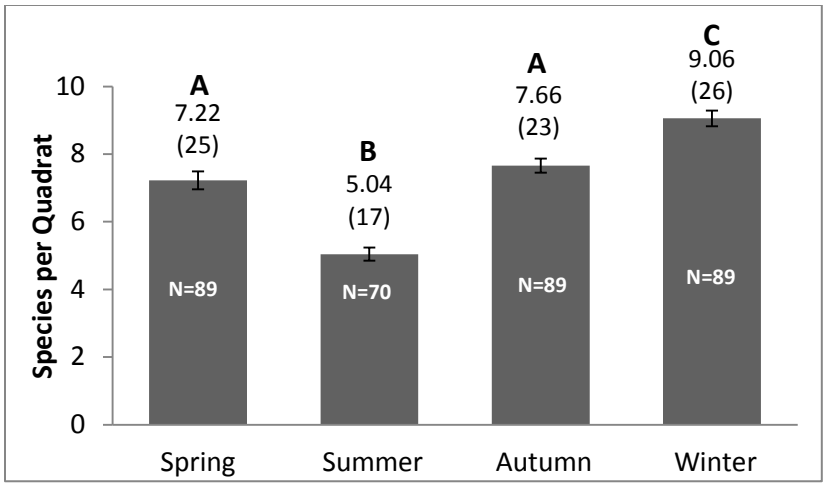

Figure 7. Average species per quadrat (and total species richness) for each of the seasons during the sampling year. Error bars represent standard errors. Different letters indicate means that differed significantly in Bonferroni Post hoc.

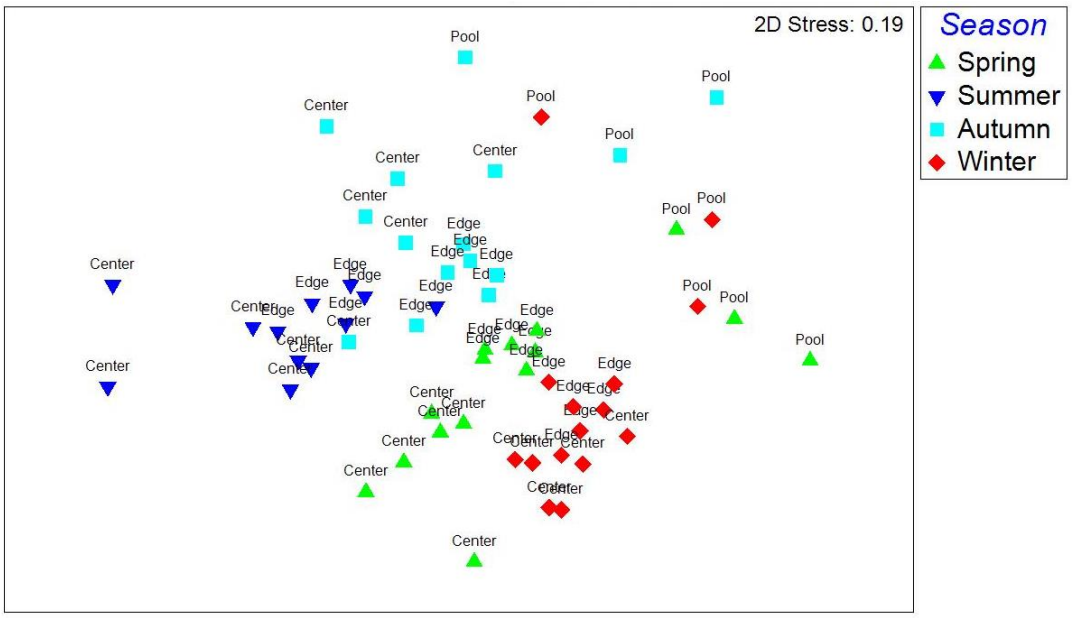

Figure 8. 2D MDS ordination (stress level 0.19) of the surveyed algal community by seasons. Each symbol on the ordination represents an average assemblage of a habitat in one of the platforms at a specific season. Habitats are indicated.

The affinity of algal species to seasons was explored using CCA Biplot (Figure 9). Axes I and II accounted for 82.1% of variance (57.8% and 24.3%, respectively).The winter and the spring contribute the most to algal diversity. The summer is less important in determining diversity. Species located at the edge of a season's arrow show high affinity to the specific season. Species grouped around the center are not associated with a specific season, amongst them *Padina spp.* which seems to be the most generalistic

concerning seasons. The summer season is associated with a single species; *Caulerpa mexicana*. *Botryocladia spp*. and *Galaxaura rugosa* show high correlation to autumn. Winter shows the largest number of associated species (six). This result agrees with the fact that winter is the richest season in species. Three species show high association with spring. All the species that show the highest associations with different seasons, are those who appeared only at that particular season. More interesting are the species that appeared in several seasons during the sampling and yet show, a specific association, even if moderate: *Stypopodium schimperi* and *Saragassum spp.* for spring, *Spyridia spp.* for autumn and *Cladophore spp.* and *Bryopsis spp.* for winter.

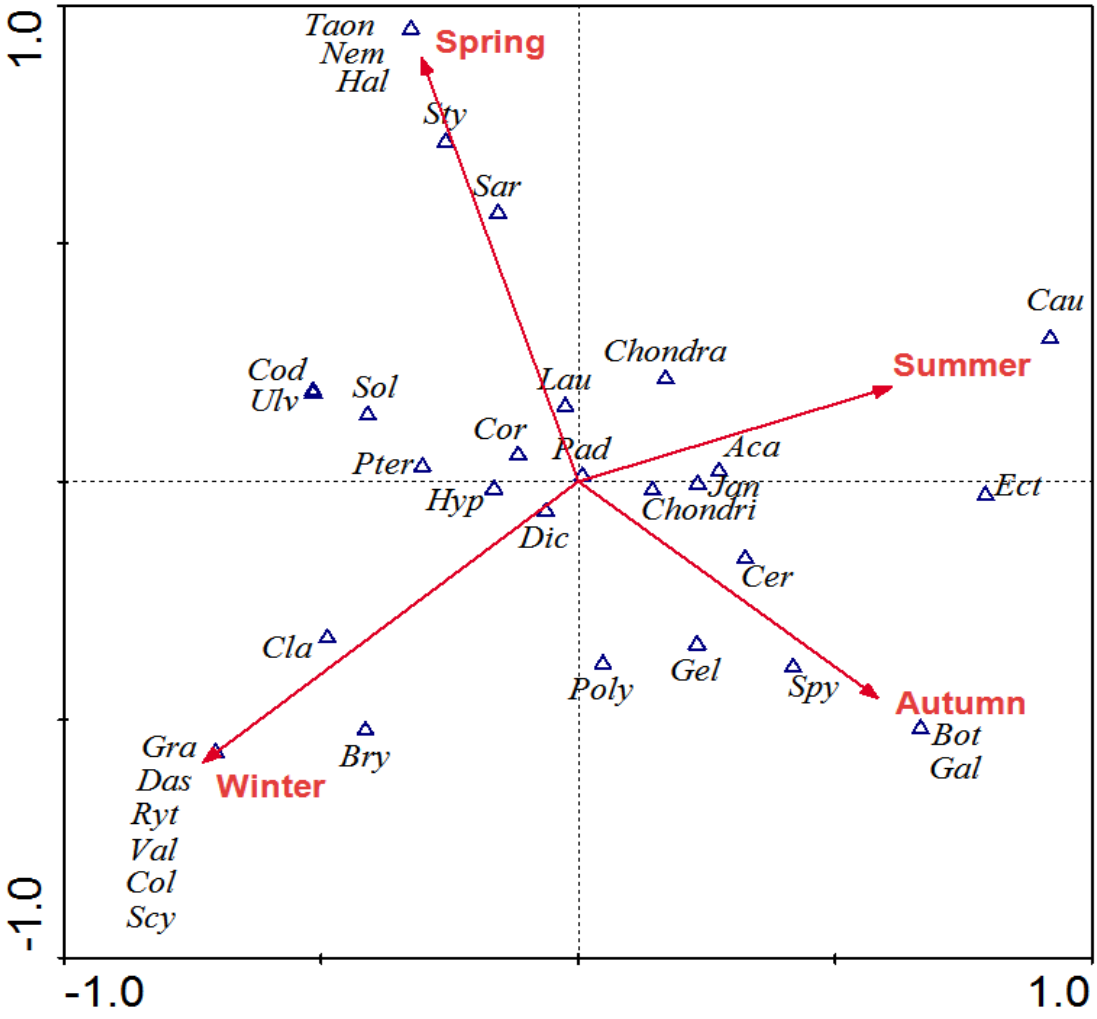

Figure 9. CCA (F=12.494, p= 0.002) of algae species distribution as a function of season. Length of the season arrow indicates a larger contribution of that season in the regression. Triangles mark the different species.

3.1.2 Spatial analysis

3.1.2.1 Platforms

In order to test whether each platform is a unique habitat, I compared species diversity richness and composition between platforms (Figures. 9, 10). Differences in the number of species per quadrat between the platforms were small but significant (Kruskal Wallis: χ_5^2=13.083, P=0.023). Platforms 3 and 7 were the richest, with 7.9 and 7.96 species per quadrat, respectively. Total species richness on platform 7 (22) was lower than on platform 3 (31). Platform 3 was the richest in algal species, a fact that most probably can be attributed to the presence of tide pools on this platform. Platform 2, which also had a tide pool, had the second highest species richness (24) but the lowest number of species per quadrat. Platform 5, the largest platform, had the lowest total species richness and a low number of species per quadrat. There was little difference in species composition between the platforms. The MDS in Figure 11 shows almost no separation between assemblages from different platforms and no visible aggregation of samples of the same platforms. Hence, there is no consistent difference in species abundance and composition between the platforms across seasons and habitats.

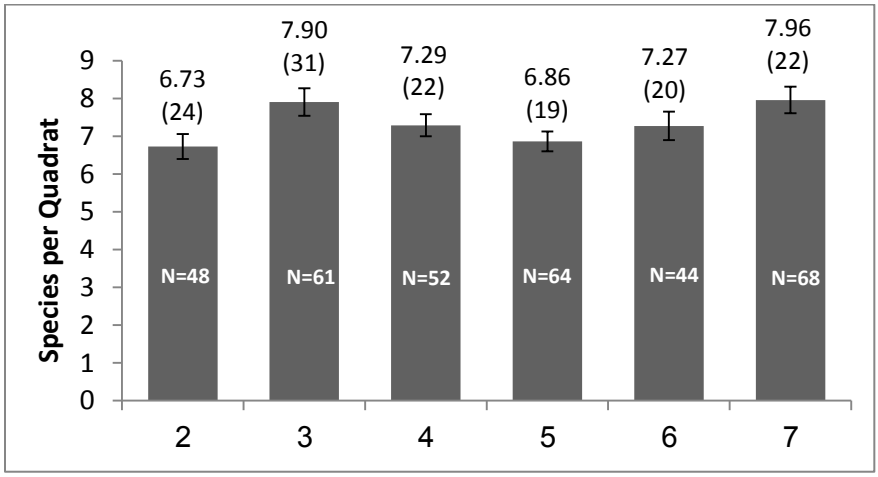

Figure 10. Average species per quadrat (and total species richness) for the 6 platforms sampled throughout the year at edge, center and pool habitats. Error bars represent standard errors.

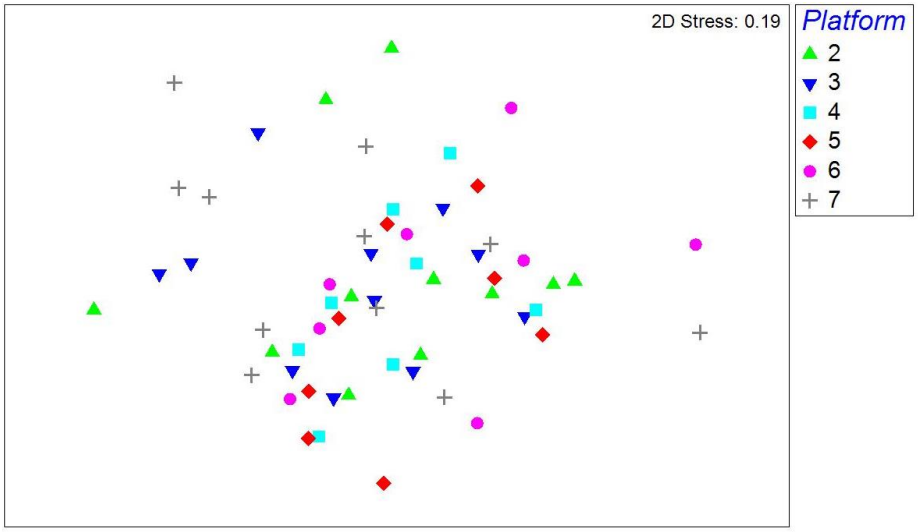

Figure 11. 2D MDS ordination (stress level 0.19) of the surveyed algal community by platforms. Each symbol on the ordination represents an average assemblage of a habitat at a specific season.

3.1.2.2 Habitats

During the field work, I observed a clear visible difference in species composition and richness between the three habitats on the abrasion platforms. I tested this observation using one-way ANOVA, and found a significant difference in the number of species per quadrat between all three habitats ($F_{2,334}$ =53.381, P<0.001, R^2= 0.238) (Figure 12). The highest richness was at the tide pool habitat, with an average of 10.13 species per quadrat. In contrast, the center and the edge had an average of 6.28 and 7.59 species per quadrat, respectively.

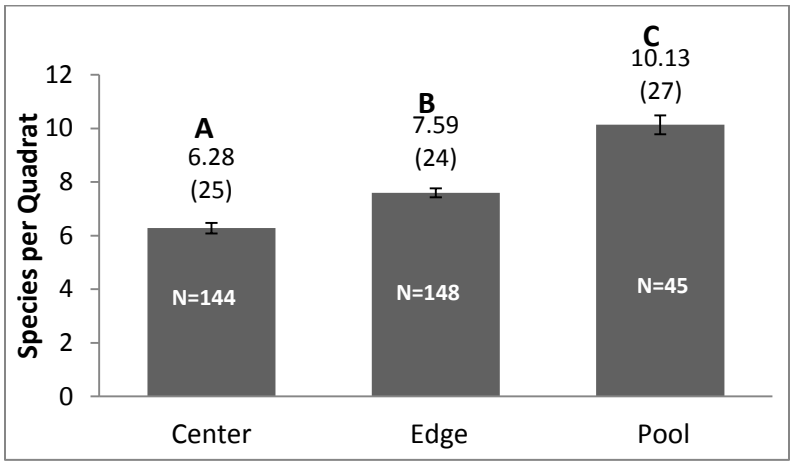

Figure 12. Average species per quadrat (and total species richness) in each habitat during the one year sampling. Error bars represent standard errors. Different letters indicate means that differed significantly in Bonferroni Post hoc.

The MDS results (Figure 13) showed a strong grouping of all habitats. The pool habitat was distinctly separated from the center and edge, the edge was tightly aggregated (therefore representing a more homogenous habitat), while the center samples were more dispersed. However, the center assemblages clearly separate into two distinct groups that differ by seasons (spring and winter at the bottom of the ordination and summer and autumn at the top). In fact, in the center habitat season separation is clearly seen, much more than in the edge. This suggests that season most strongly influence the center habitat. The two symbols on the right that are separated from the rest of the cluster are of platforms 6 and 7 assemblages in the summer. In order to find the species that were responsible for the high diversity and the composition differences in the pools habitat, a biplot on the basis of CCA was prepared (Figure 14).

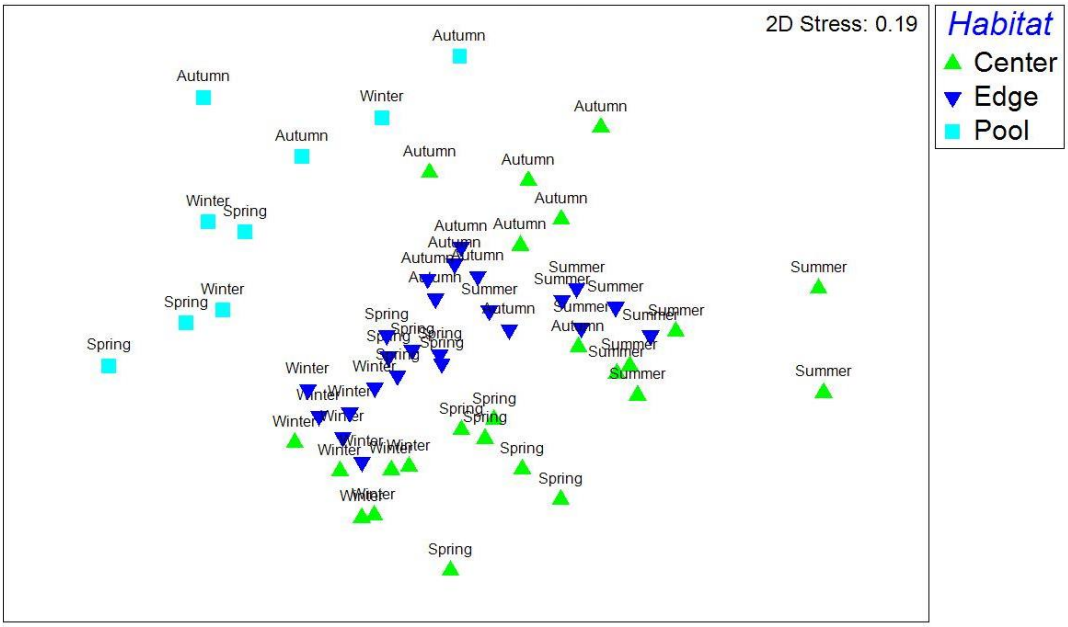

Figure 13. 2D MDS ordination (stress level 0.19) of the surveyed algal community by habitats. Each symbol on the ordination represents an average assemblage in a season on a specific platform. Seasons are indicated.

Axes I and II explained 100% of variance (67.6% and 32.4%, respectively). Seven species showed high affinity to the pools habitat. Field observations showed that five of these seven species were seen only in tide pools. *Dictoyota spp.* and *Padina spp.* showed a moderate affinity to pools habitat too. Three species showed high affinity to the center habitat. *Caulerpa mexicana* showed high affinity to the edge habitat, probably since it

was sighted only once in the sampling at that habitat. *Corallina elongata*, *Pterocladiella capillacea*, *Hypnea spp.*, *Scytosiphon lomentaria* and *Acanthophora najadiformis* all showed a mild affinity to edge habitat.

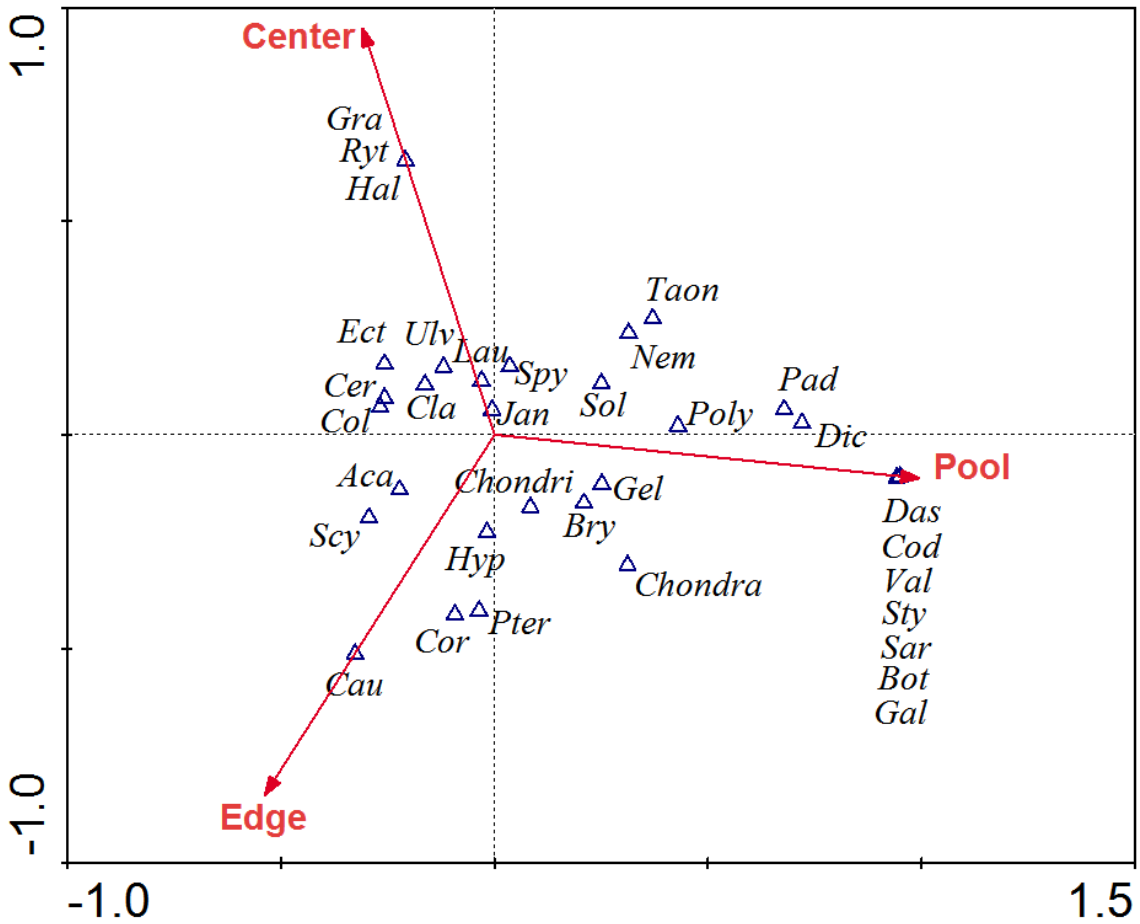

Figure 14. CCA (F=14.706, p= 0.002) of algae species distribution as a function of habitats. Length of the habitat arrow indicates a larger contribution of that habitat in the regression. Each species marked in a triangle.

3.2 The relative importance of the major factors

In order to understand the combined effect of seasonality and the spatial aspects of platform and habitat on algal diversity, a PERMANOVA analysis was performed (Table 4). The results indicated that all three factors had a significant effect, and season contributed the most to the explained variability (greatest estimates of variation) while platform contributed much less than season or habitat. According to Underwood and Petraitis (1993) as stated in (Anderson et al., 2008), the correct basis for comparing the

relative importance of different terms in the PERMANOVA model should be components of variation. All two-factor interactions were significant. The unexplained variability is low (14%), suggesting that these tested factors account for most of the variability in the algae community in this ecosystem.

Since season turned out to have a large effect, a set of MDS ordinations divided by season, was prepared (Figure 15). Separating the habitats by season increased the stress of the ordinations for all seasons except autumn, suggesting that differences among habitats are much greater when explored per season.

Table 4: Results of Permutation Multivariate Analysis of Variance (PERMANOVA) using three factors: season, habitat and platform.

Source	*df*	*MS*	*psuedo-F*	*p-value*	*Variation estimates*	*Square root*
Season	3	5425.4	28.826	0.0001	436.43	20.891
Habitat	2	5900.3	31.349	0.0001	346.19	18.606
Platform	5	1026.8	5.455	0.0001	94.071	9.699
Season x Habitat	5	672.68	3.574	0.0001	100.93	10.046
Season x Platform	15	355.06	1.886	0.0008	73.611	8.579
Habitat x Platform	7	410.64	2.181	0.0012	59.884	7.738
Residual	19	188.21			188.21	13.719

A separation of the pools habitat demonstrates the composition difference and the higher diversity in this habitat, especially in the spring and winter. The pools habitat is missing from the summer ordination, since it was not possible to sample it due to constant high sea level during that season. In all seasons except winter, the edge samples are more tightly grouped than those of the center and the pools. This finding further supports the observation from Figure 13, that algae composition and abundance at the edge habitat is more homogenous than at the center and the tidepools. In the winter plot, the edge and center habitats are clumped together, indicating that these algal communities are very similar during this season. The algal community on the platforms during autumn and summer are the least grouped, indicating that during these seasons spatial variability is greatest and differences among habitats are more obscured. As for the platforms, grouping is not evident even within season probably because habitats have a much stronger effect.

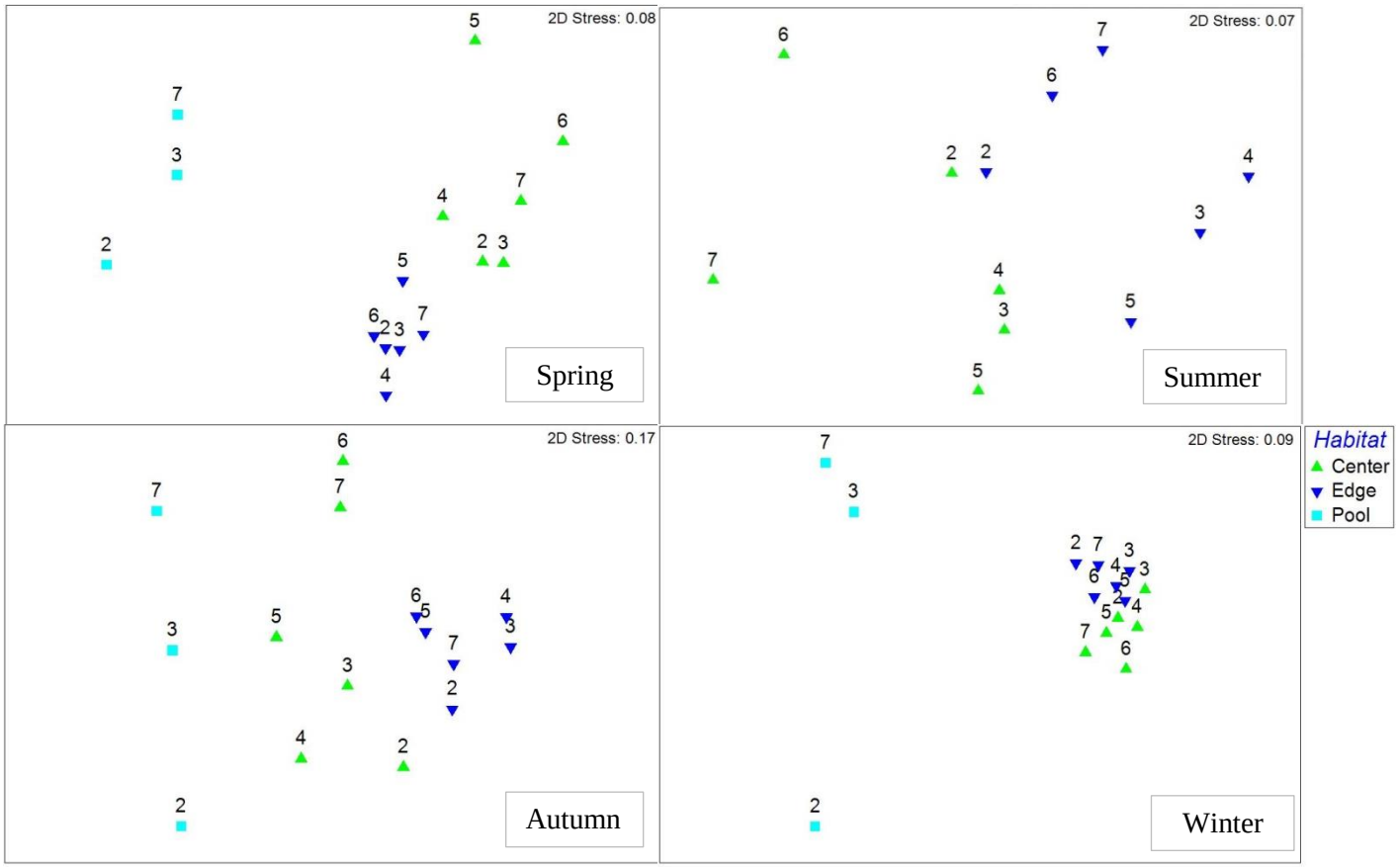

Figure 15. 2D MDS ordinations of the surveyed algal community divided by seasons (stress: spring-0.08, summer- 0.07, autumn-0.17, winter-0.09). Each symbol on the ordination stands for an average abundance on a specific platform. Numbers above the symbols indicate platforms. Resemblance on log(x+1) transformed data was measured by Bray-Curtis similarity method.

3.3 Environmental Parameters

One of the major questions of this work is which environmental parameters that contribute to habitat heterogeneity, affect algal biodiversity the most and to what extent. Unfortunately it is not possible within this framework to test all possible effects of the environment on the algal community; therefore it is important to note that the parameters considered here may account for only a part of the environmental effects on the algae, if at all.

3.3.1 Structural Parameters

The parameters of bare rock and platform height did not have a significant correlation to algae richness or diversity measures. Surface verticality and roughness showed a low but significant positive correlation to species diversity as Shannon Index (For verticality: r_s=0.198, p=0.001, N=292. For roughness: r_s=0.149, p=0.011, N=292). Sand cover showed a small but significant negative correlation to species richness (r_s= -0.157, p=0.007, N=291) and a similar but weaker trend was found for species diversity (r_s= -0.120, p=0.041, N=291). Following field observations on differences in sand cover among habitats during sampling, habitat differences were tested and showed that the center habitat had much significantly more sand cover (45.4%) than in the edge habitat (8.55%) (Figure 16).

Contrary to my expectations, a significant negative correlation was found between water cover and species diversity (Figure 17), i.e. species diversity is lower in places on the platform where water cover is high. A similar result was found also for species per quadrat.

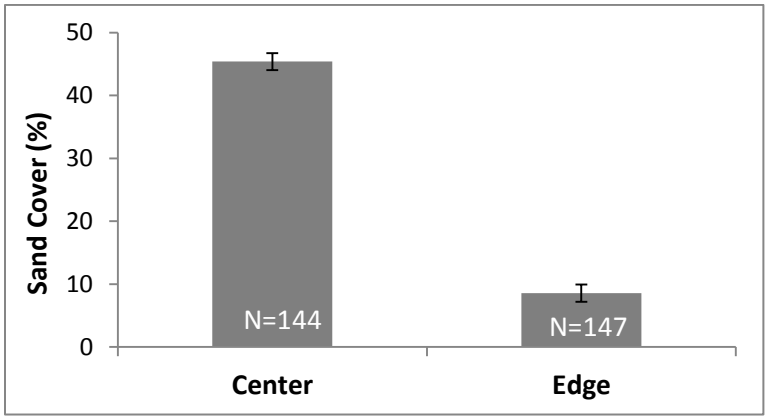

Figure 16. Average Sand cover in center and edge habitats. Error bars represent standard errors. Mann Whitney: U= 4546, p<0.001, N=291.

3.3.1.1 Rim presence

Presence of elevated rim at the edge of platforms is an important factor which contributes to the extent of water cover of the platforms during low tides. This capability prevents most algae species from drying during low tide and calm sea when desiccation conditions

can develop, thus I expected to find higher algal diversity on platforms with more intact rim and specifically higher diversity in quadrats where rim was present, especially due to adding more three dimensionality to the substrate.

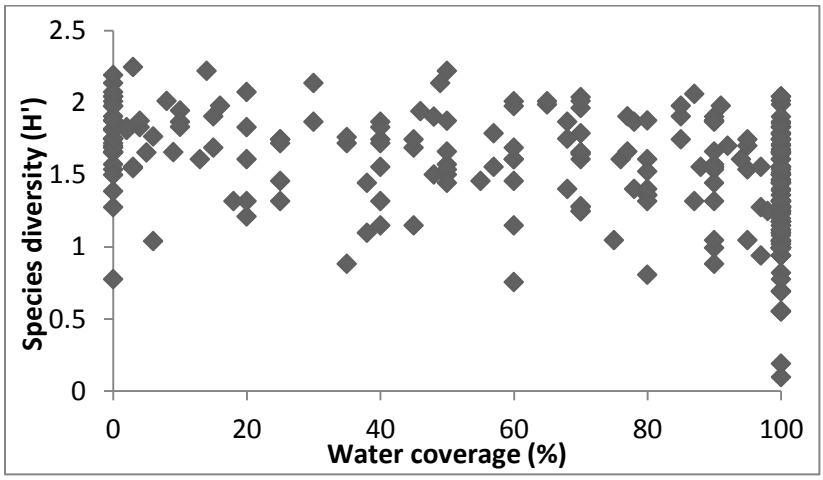

Figure 17. A significant negative correlation between water coverage and species diversity, expressed as Shannon index (H'), r_s= -0.492, p<0.001, N=292.

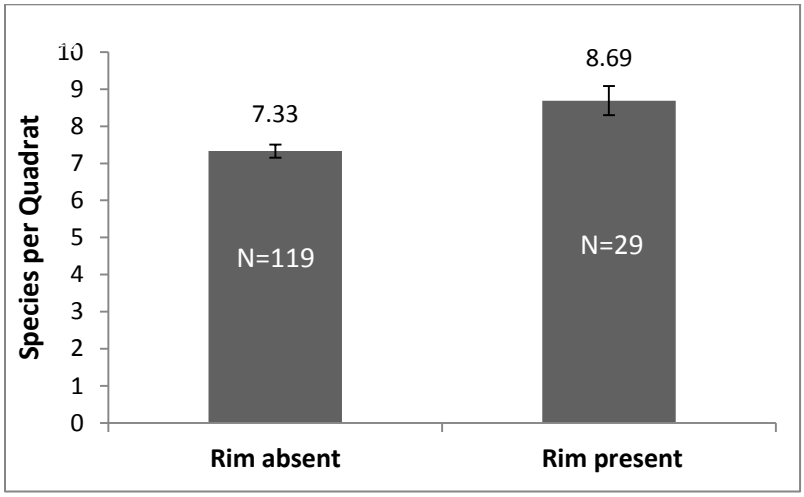

Figure 18. Average species per quadrat for sampling units with and without rim. Error bars represent standard errors.

A significant difference was found for species diversity between sampling units with and without rim (Mann Whitney: U=1113, p=0.003) (Figure18). Average species richness was higher in quadrats where rim was present (8.69), compared with no-rim quadrats (7.33). Additionally, a positive significant correlation was found between rim presence and species per quadrat (r_s= 0.247, p=0.002, N=148). The platform in which the rim was best conserved is platform 5, where 40% of edge quadrats included a relatively intact rim.

This platform also demonstrated a strong and significant positive correlation between rim presence and species per quadrat (r_s= 0.541, p=0.001, N=32). A similar trend was observed for diversity (using Shannon index).

According to my initial expectation regarding the importance of rim on the platforms, a test for a relation between rim presence and water coverage on the platform was performed. No significant correlation was found between water coverage and rim presence (r_s= 0.047, p=0.574, N=143).

3.3.2 Limpet abundance

Limpet snails are assumed to be important main herbivores of most algae on abrasion platforms. I found a significant correlation between number of limpets and percent cover of bare rock (Figure 19).

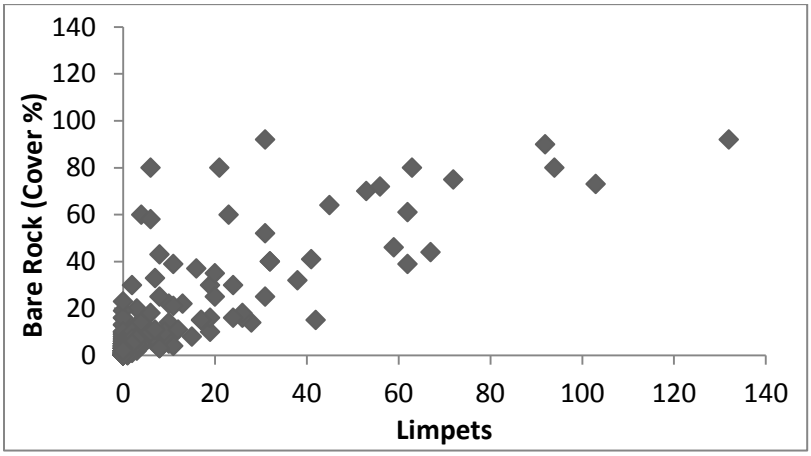

Figure 19. A significant positive correlation between bare rock cover and limpets number, r_s= 0.758, p<0.001, N=291.

Correlation coefficient for this relation is relatively high, r_s= 0.758, supporting the assumption that limpets are the main factor removing macroalgae from the platforms' rock surface. This is evident also due to the negative relation between algae cover and number of limpets (Figure 20). Limpets had a low but significant positive correlation to height above sea level (Figure 21). Moreover, here we find that the largest density of limpets (and bare rock) was on platform 4, which is the second highest platform of the six studied.

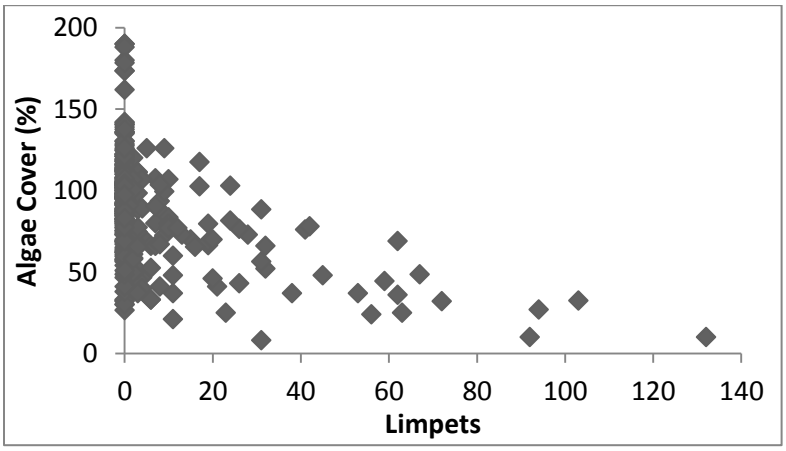

Figure 20. A significant negative correlation between algae cover and limpets number, r_s= -0.469, p<0.001, N=292.

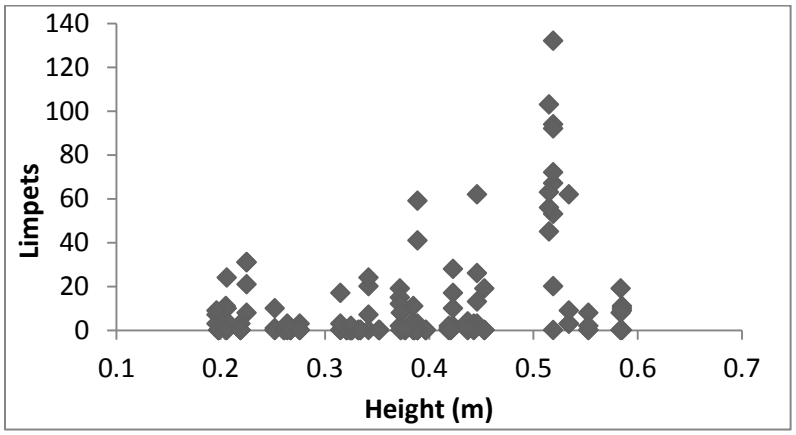

Figure 21. A significant positive correlation between height above sea level and limpet number, r_s= 0.273, p<0.001, N=163.

3.3.3 Water Flux

Assessment of water flux was carried out in a 24 hour in-vivo experiment (see methods). Water flux was significantly different between the edge and center habitats (Mann Whitney: U=111, p=0.042) as seen in Figure 22. Gypsum dissolution serves as a direct but relative measure for flux intensity; hence water flux was greater at the platform edge. There was a significant difference in water flux between the three platforms where I performed that measurement (1-way ANOVA: $F_{2,35}$ =18.261, P<0.001, R^2= 0.483).

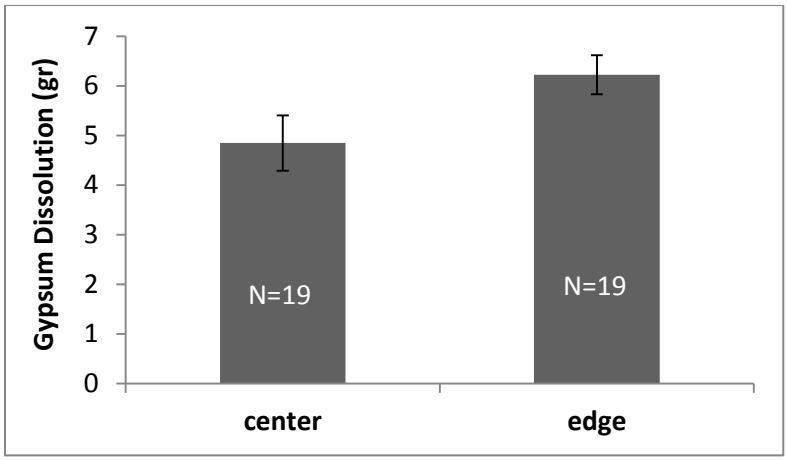

Figure 22. Average gypsum dissolution in 24 hours on the platforms for center and edge habitats. Error bars represent standard errors.

Figure 23 illustrates the flux in different habitats for three platforms. Water flux was significantly greater at the edge habitat on platforms 3 and 5 (T-Test$_{platform3}$: t_9=-2.448, P=0.036, , T-Test$_{platform5}$: t_{14}=-5.16, P<0.001). On platform 6 there was no significant difference between water flux at the center and edge habitats (T-Test: t_9= 1.085, P=0.305).

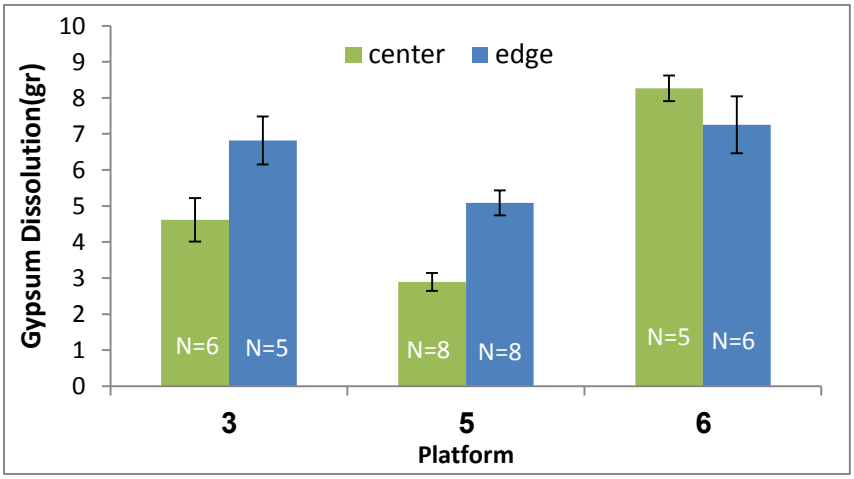

Figure 23. Average gypsum dissolution in 24 hours, on the three platforms of the experiment, divided by habitats. Error bars represent standard errors.

Platform 6 had the largest gypsum dissolution on average, and therefore the most intense water flux amongst the three platforms. Gypsum dissolution decreased with platform height (Figure 24). Platform 6 is also the lowest of explored platforms, while platform 5 is the highest. Examining the algal community by platforms (Figure 25) reveals that

species diversity at the center of platform 6 was different from the other platforms. No significant correlation was found between water flux and orientation on the platform.

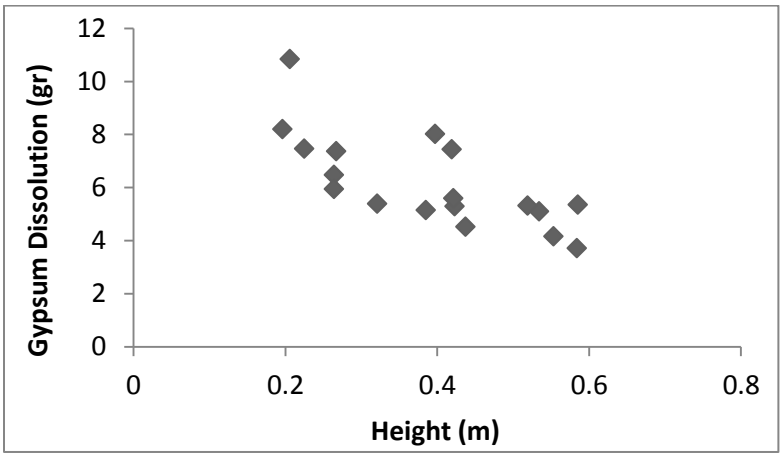

Figure 24. A significant negative correlation between gypsum dissolution in 24 hours and height above sea level, r_s= -0.797, p<0.001, N=18.

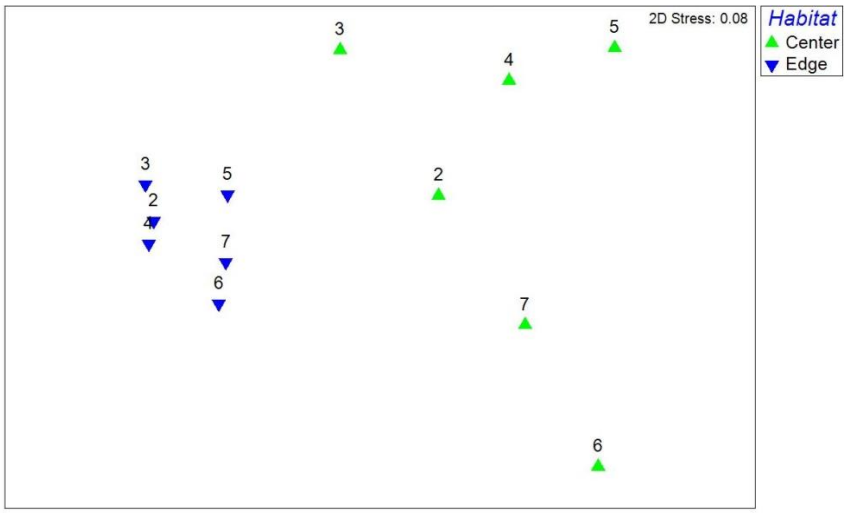

Figure 25. 2D MDS ordination (stress level 0.08) of the surveyed algal community by habitats. Each symbol on the ordination stands for an average abundance in all seasons on a specific platform. Numbers indicate the platform number.

3.3.4 Combined analysis

One of the main questions of this work is which environmental parameters are the most important in terms of their influence on algae distribution and composition. The combined examination of environmental parameters and their effect on species diversity was performed for abiotic parameters only. Due to mismatch of sampling points for

height and water flux measurement, it was based mostly on edge habitat samples (Figure 26). Axes I and II accounted for 62.7% of variance (49.3% and 13.4%, respectively). Water cover, sand and verticality had the strongest effect on algae distribution and composition. Water has the longest arrow, indicating it as the most influential. Roughness ranking, which represents habitat complexity at the small scale of centimeters to tens of centimeters, was the least important parameter.

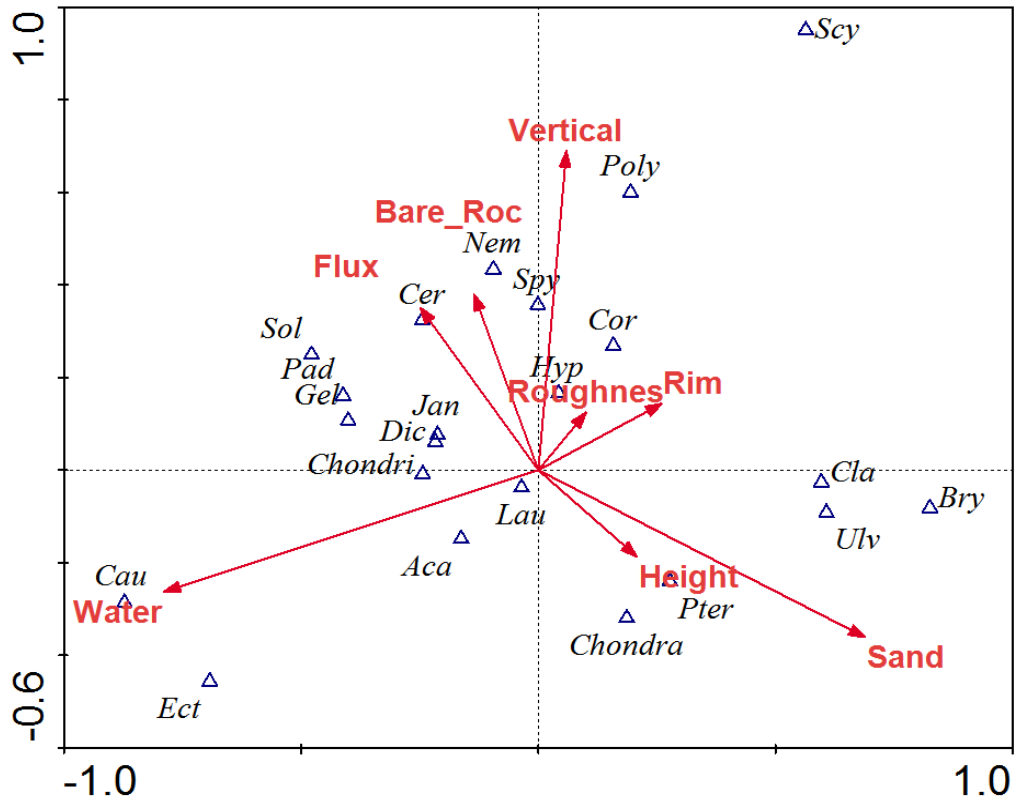

Figure 26. CCA (F=2.204, p= 0.002) of algae species distribution as a function of environmental parameters. Length of the environmental parameter arrow indicates a larger contribution of that variable in the regression. Species are marked with triangles.

Most species did not show a particular affinity to one of the parameters, yet there was a clear affinity on the biplot of *Caulerpa mexicana* to water coverage, *Nemalion helminthoides* to bare rock (indeed they were mostly observed on rims and other elevated areas that were mostly bare), *Ceramiaceae* to water flux and *Pterocladiella capillacea* to height above sea level. Sand had a negative effect on algae; therefore there are no algae that show any affinity to this parameter. Moreover, most species are on the opposite

direction from the sand arrow on the biplot, meaning that most of the community is affected negatively by sand cover on the platforms.

Water cover and platform height are expected to be negatively correlated to one another, yet the angle between them is not small (correlated parameters have a small angle between their arrows on CCA). Flux and height are as expected positioned in a 180º angle between them; hence they relate to each other and the species in opposite ways, as also shown in Figure 24. Bare rock also shows an opposite relation to height, a result which can be attributed to limpets activity. Roughness, rim presence and height had little importance in this analysis.

3.3.5. Heterogeneity index

The structural heterogeneity of each platform, as indicated by different structural parameters, is described in Appendixes 3, 5, 6 and 8. It became clear in this work that a single component of heterogeneity cannot explain strongly the diversity because the links of habitat heterogeneity and diversity are complex. Therefore, searching the combined affect using an integrated heterogeneity index seemed more appropriate. Linking the structural parameters together in order to test their integrated effect on species diversity was done using the *Heterogeneity score* described in the methods. According to this index (Table 3), there seems to be a strong relation between heterogeneity score and species diversity, with the single exception of platform 2, which was the most heterogeneous, yet had the lowest species diversity (Figure 27). The correlation between the heterogeneity index and species diversity was insignificant.

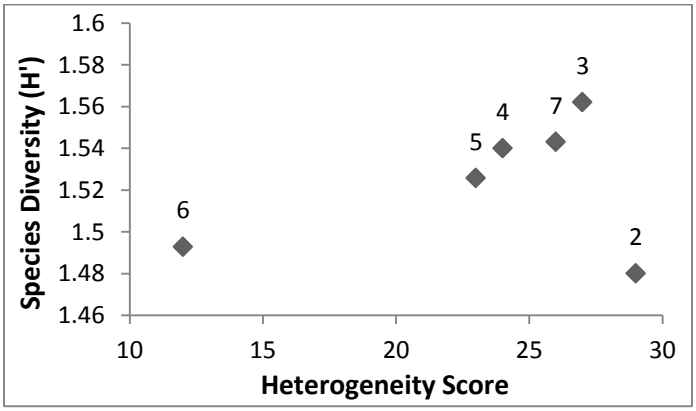

Figure 27. Correlation between the heterogeneity score (Table 3) and algal species diversity, expressed as Shannon index (H'), r_s= 0.143, p=0.787, N=6. Data labels indicate platform number.

4. Discussion and Conclusions

This study examined the influence of seasonality, spatial differentiation and physical parameters on the algal community diversity, composition and distribution on abrasion platforms at Akhziv, focusing ultimately on the contribution of environmental heterogeneity to biodiversity. The most interesting and perhaps surprising result was that individually each environmental parameter could explain very little of the diversity but in combination there was a strong correlation between heterogeneity and diversity. This discussion focuses on the ecological processes that led to the observed results and their significance in shaping the algal community.

4.1 Akhziv community characteristics

The 34 species recorded during this study are generally representative of the known algal community at the Israeli coast. The dominant species that occurred in all seasons and habitats can be referred to as generalists, since the results indicate that their distribution in space and time is not severely restricted by any of the common environmental constraints such as weather shifts, air exposure and extreme wave action. *Jania rubens*, the most abundant algae in this system is a good example (also evident in surveys all along the coast, Rilov unpublished data). This is a coralline species, which is described mostly as an opportunistic species and highly competitive, known to be among the first ones to recruit to cleared algal assemblages (Coleman, 2003; Einav and Israel, 2007; עינב, 2004). It is also referred to as an epiphytic algae by Lipkin & Safriel (1971), that grows mainly on the base of *Laurencia Spp.*, which was the second most dominant algae (Figure 6). My results are consistent with these previous observations, yet in some cases during the sampling of *J. rubens* it was not epiphytic. Moreover, in many cases it seemed as the substrate for other epiphytes, such as *Polysiphonia/Neosiphonia* and species from the *ceramiaceae* family. The dominance of this species in all habitats, suggests its importance as a habitat-forming species, that may promote the settlement of other algae and most definitely gives shelter to many invertebrates and other young algae under its

canopy. The question to what extent the non-epiphytic young settlers succeed in the competition for space against *J. rubens* in later stages requires further investigation.

The rare species observed in this study are mostly subtidal ones, which were found only once or twice in tide pools or shallow depressions. This is coherent with tide pools being the rarest habitat on the platforms and thus also the species inhabiting them.

After reviewing the relevant published research and surveys that were carried out to date on the Akhziv coast (Einav and Israel, 2008; Lipkin and Safriel, 1971; Lundberg, 1996; Rilov et al., 2004; Ukabi et al., 2012; 2004 ,עינב ;1999 ,כץ), a few new observations were discovered. This is the first recorded sightings of *Ectocarpus siliculosus, Stypopodium schimperi* and *Galaxaura spp.* at an intertidal habitat in Akhziv. *E. siliculosus* is a common alga in the Mediterranean that appears in most of the rocky shore zones but was not recorded in the thorough surveys of Lundberg (1996) all along the Israeli coast during the 1980-90s. It is unclear if it was not present then or not correctly identified in her surveys. *S. schimperi* is a relatively new species to the Mediterranean that appeared only in the last decade and is attributed to the Lessepsian migration (Zenetos et al., 2010). *S. schimperi* has been recorded at the north shores of Israel in 1999, but not at Akhziv (Einav and Israel, 2008). *Galaxaura spp.* occurred only once, in a tide pool, but it is now frequently observed subtidally along the Israeli coast. Hence, there is no certainty whether it was attached to the surface in the pool or swept in there by waves.

In the rest of the Discussion, I will examine the individual and combined environmental parameters that influence macroalgal community structure and diversity. These include both temporal and spatial parameters and patterns.

4.2 Seasonality

Seasonality greatly affects species composition on the platforms. Multivariate analysis revealed that it has the strongest effect on the community, more than the spatial distribution to platforms or habitats (Table 4). This complies with similar studies around the world (Menconi et al., 1999; Pinto, 2011) and confirms the need to include all seasons when planning a sampling scheme designed to examine ecological process in this system,

and to isolate the seasonality effect when trying to assess other parameters affecting community structure.

Winter conditions seem to facilitate the highest diversity. Moderate temperature on the platforms during this period (mean temperature measured by data loggers on the flat was 18.6°C, Rilov, unpublished data); frequent wetting by waves and many sunny days that characterize the Israeli winter, might make it the best growing season for many macroalgae. Some species that are not well adapted to lower temperatures clear their way to opportunist species who thrive in the winter (עינב, 2004). In most research on seasonal variations, algae cover or abundance have been shown to be the highest usually in the winter (Cubit, 1984; Noda et al., 2003; Underwood and Jernakoff, 1984; Williams, 1993), mainly due to increased rates of primary production that exceed rates of consumption by herbivores and general reduction in physical constraints. Surprisingly though, there are very few studies that document and describe seasonal variation in biodiversity measures on rocky shores to allow a comparison of my results with others in the Mediterranean or in fact, the world. There are a few exceptions. On Orchid Island off the southeastern Taiwan coast, the highest species richness also occurred in winter (Su et al., 2009). Several studies on tropical rocky shores that investigated the seasonality effect on algal diversity measures (García and Díaz-pulido, 2006; Prathep, 2005), found the highest diversity and species richness during the dry season (December to April). Because there is no information from the Mediterranean on seasonality in macroalgal diversity in the intertidal and there doesn't seem to be a conclusive paradigm regarding this question in algal communities it is hard to make any conclusive statements on the reasons for the pattern that I found. In a longer dataset (2009-2012) in four sites along the coast higher diversity was also detected in the winter and spring than in summer and fall (Rilov, unpublished data). It seems that many species disappear during late spring and reappear in winter. These population declines may be a result of prolonged desiccation stress events naturally caused by "Sharav" conditions (characterized by hot dry easterly winds that dry the platforms sometimes for days) followed by very hot summer sea surface temperatures. Indeed, during the end of spring and autumn I sighted several algal bleaching events, following extremely hot weather and low tides (Figure 28).

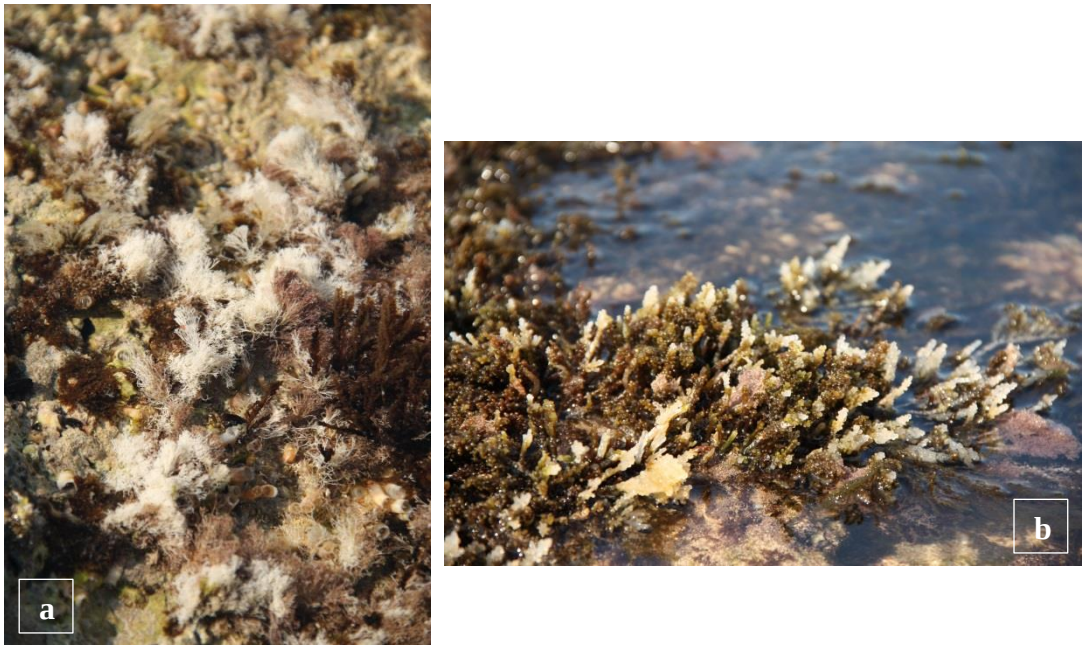

Figure 28. Bleaching on *Jania rubens* (a) and *Laurencia Spp.*(b) on November 2011 at Akhziv

Autumn and spring displayed larger spatial variability in community composition (Figure 8) that may be interpreted as multiple transitional phases, when "old" end-of-season species occur in some patches and "young" start-of-season species occur in others thus not yet clearing space for the opportunist species of the winter. Autumn was the most heterogeneous season, with lowest distinctiveness between habitats (Figure 15). Perhaps while the conditions are still mild in autumn, species settlement and growth is equal among the different habitats, until temperatures drop in the winter and incompatible species are phased out of the community.

Naturally, extreme physical stress and herbivory could also take part in the seasonal variation, but the natural seasonal fluctuations in algal cover are generally explained by variations in rates of algal production, rather than in rates of herbivory (Cubit, 1984).

Winter and spring were the seasons with the highest species richness (Figure 7), what makes them the most contributing to community diversity (Figure 9).

There are indications of shifts in the distributional boundaries of species due to global ocean warming in the intertidal, which is characterized by changes in abundance of key taxa, abundance decrease of temperature-sensitive algae and increase of invertebrate grazers (Schiel et al., 2004). *Padina spp.* is the most generalistic species

concerning seasons, although in the literature (Littler et al., 1989; 2004 ,עינב) it is described as a summer species. This may indicate a shift in the species' seasonal boundary and distribution due to warmer winters in the past years. If this is the case, this could affect the interplay between species and influence the community structure in the winter.

Additional unexpected seasonal affinities were observed, such as *Stypopodium schimperi* and *Spyridia spp.* that were expected to appear all year long (2004 ,עינב), although their absence from the sampling does not necessarily indicates they were totally missing.

4.3 Platform Scale

In the PERMANOVA, platform effect on community structure was the less significant. The multiple interaction effects indicated that the influence of "platform" is highly context-dependent. The analysis shows clearly that it strongly depends on season and the habitat on the platform (edge, center or pools). Although individual attributes of the platforms (size, height, different complexity attributes) could not explain diversity, the combination of all showed very strong influence on it (see below).

After seasonal cues, primary settlement of spores and the survival rate during growth are dependent mostly on the local heterogeneity (substrate, height, water flow) and the grazing stress that occur at the scale of the few centimeters around each individual algae (Fletcher and Callow, 1992). This micro-world is highly influential on the settlement, survival and growth of individual algae and can vary a lot within one platform to the point that small scale variability is more important in explaining community structure than the larger scale (Fraschetti et al., 2005). Despite there are obvious community differences at the platform scale, we cannot explain them with a single parameter, but with a combined score.

Platforms with additional habitat of tide pools displayed miscellaneous results. Species diversity was highest on platforms 3 and 7, while platform 2 and 7 had the highest total species richness with no evident correlation to the number of pools (Figure 10). Platform 3, which had substantially more species than all other platforms and no

other meaningful characteristics, probably displays this higher richness as a result of greater niche diversity which could not be captured by a single parameter. Although platform 3 species richness represented 91% of the total sampled species, it did not represent the entire species pool in the area. These conclusions suggest that habitat richness increases species richness on the platform, according to habitat heterogeneity theory.

According to species-area relationship theory, it is expected to find higher species richness in larger areas because of their ability to include more different niches that should support more species (Macartur and Wilson, 1967). Examining this theory in this study showed no such relation; the largest platform (5) actually displayed the lowest species richness (Appendix 4). Perhaps one of the reasons is that the variability in size of the platforms was not large enough for this pattern to emerge. Alternatively, we do not know if in intertidal habitats, the number of available niches correlates to platform size. Because most intertidal organisms are small, platform size may only matter when you examine diversity among scales (moving from cm to 10s of m and to 10 km) and not within a scale because of the relatively open nature of marine systems. As reviewed in the Introduction, continuous supply of new species through larval settlement from the open sea leaves some basic ecological relationships irrelevant. It may be the case here, especially at the platform scale. This interesting issue requires further examination.
Although there aren't decisive conclusions that can indicate the uniqueness of each platform as an autonomic sub-habitat, it is clear that none of them is expendable.

4.4 Habitats

Three main habitats were sampled in this study. The main difference between them is in the degree of water emersion and flush, air exposure and sand aggregation. Tide pools were the richest in species (Figure 12) and the most diverse with the highest number of species per pool. Organisms within rock pools are continually submerged, and hence are not subject to the same emersion-related stresses as on freely draining rock. As a consequence, rock pools provide a favorable habitat even during low tide and a suitable habitat for sub-tidal algae too. Nevertheless, the pools can be a stressful environment

during the low-water period with large fluctuations over short temporal scales in physico-chemical parameters such as temperature, salinity, oxygen, carbon dioxide and pH (Martins et al., 2007). When such conditions last too long, this favorable habitat may turn into a trap. Besides being the richest, the pools is also the most unique habitat on the platforms, since it inhabits 6 species that were not seen in the other two habitats (Appendix 2), some of them are more characteristic to deeper water, such as *Valonia utricularis*, *Codium elongatum* and *Saragassum spp.*. In fact, the presence of this habitat in the intertidal broadens the boundaries of this zone by giving suitable niches to species that may not be present in it otherwise and thus increasing species richness at the whole site.

It was previously shown that more wave-exposed areas on abrasion platforms have richer algal assemblages than on less exposed ones (Einav and Israel, 2007; Prathep, 2005). The more exposed edge habitat had higher species richness than the center at the sampling unit scale, and less so at the platform scale (Figure 12). As previously discussed (see Introduction), species richness differences are the most visible at the smaller spatial scale. These scale-dependent results emphasizes the importance of multiple-scale analyses of the interactive effects of physical or biological factors and the necessity in defining the relevant scale of importance to the organism in question in order to understand the organization of natural assemblages (Benedetti-Cecchi et al., 2000).

At the edge, the physical conditions are much harsher, especially concerning wave action and air exposure in places where the rim is still elevated. Harsher environment is suitable for more durable algae that can withstand higher water turbidity and velocity. The harsh conditions could explain why the edge community is more homogeneous (Figures 12, 14). Edge species have several different adjustments for survival in high water flux. For example, *Corallina elongate*, a relatively small branching calcareous alga has numerous uncalcified ‘joints’ (geniculae) in their fronds that allow it to flex back and forth under high velocity flow (Denny and Gaylord, 2002). *Pterocladiella capillacea* of the Gelidiaceae family is a rigid alga with a very strong thallus attachment to the substrate that keeps it in place even under strong water movement (2004 ,עינב).

Acanthophora najadiformis is mentioned as having a very limited distribution (עינב, 2004), generally attributed to the edge habitat. It has been shown that this species is very sensitive to high temperatures and has low photosynthetic rate underwater compared to when it is exposed to air when its growth and photosynthetic rate is 5 times higher (Einav and Beer, 1993). This should make the edge the most suitable habitat for it. Nevertheless, *A. najadiformis* (Figure 14) does not show any particular significant affiliation to one of the habitats on the platforms. This raises a conflict between the known literature and this finding. Especially after noting additional species who demonstrated the same distribution mismatch pattern, as *C. dasyphylla* and *Ceramiaceae* (עינב, 2004). We know that the configuration of the edge habitat have been changing for the past years, since the decline of *Dendropoma petraeum* populations and disappearance of elevated rims at the edges of the platforms. Perhaps the reduction in rim presence facilitates *A.najadiformis* and other edge-affiliated species to spread to less favorable habitats and by reducing the amount of water held on the platform center during low tide that allows more exposure to air, thus opening more space of these species to thrive on.

The center habitat had the lowest species richness per area, although it is the largest in area on the platforms and functions as the "intermediate" habitat. At the center, there is a chance for less competition for space and no extreme wave action or prolonged air exposure during low tide in routine conditions. This habitat however has much higher accumulation of sand, due to lower water movement rate and the many depressions on it. Species that showed high affinity to this habitat are those that have weaker substrate attachment and have sand deposition resistance.

4.5 Environmental Parameters

In the framework of analyzing which environmental components of the intertidal habitat most affect algal community composition and diversity, I examined physical parameters at the quadrate scale. These included surface height, verticality, roughness, bare rock, sand cover and rim presence as well as water flux and density of limpets as a proxy for grazing pressure. Some of the investigated parameters did not show any statistical significance for community structure or distribution in individual analyses, but did turn out as prominent in the combined analysis (Figure 26). This is probably due to crossed

and combined correlations among individual parameters. Therefore, the environmental parameters biplot should be referred as a manner of scaling the importance of each parameter, as opposed to concluding which of them is important and which is not.

4.5.1 Structural Parameters

4.5.1.1 Bare Rock

Bare rock did not turn out as influential on community structure, though it is a necessary preliminary condition for algal existence in early successional stages or after a disturbance. It serves as new space for settlement or occupation by a fast growing species in a near patch and once it is occupied, the seasonal changes and local herbivore density will determine to what extent it will continue to be a bare rock space or not. The exposure of newly free space is a dynamic process which occurs at all times and in the context of the explored research questions it is a transitional phase that's influenced by the rest of the processes ongoing on the platforms. Since the dynamics of these processes are not included in the framework of this research, this result settles with the nature of the analysis. *Nemalion helminthoides*, that show high affinity to bare rock, is a vigorous species that has been shown to endure harsh nutrient insufficiencies and high temperatures. Its main limiting requirement is a high light dose to sustain growth and reproduction (Pato et al., 2011). Possibly, this affiliation with bare rock demonstrates a life strategy for the loose and long algae, to grow in such places on the platform where there is no competition for light.

4.5.1.2 Roughness

Surface roughness was assessed using an ordinal scale that ranged from smooth rocky surface with no pits or bulges to a surface with many textural transitions, grooves or holes. According to the habitat heterogeneity hypothesis, structurally complex habitats may increase species diversity and previous work on the intertidal showed this theory to apply on small and large spatial scales (Johnson et al., 2003; Kostylev et al., 2005; Lubchenco, 1983; Menge et al., 1985). In this intertidal site, the roughness of the substrate was measured at the small scale and indeed exhibited a small but significant

correlation with species diversity which indicated that higher surface complexity contributes moderately.

4.5.1.3 Verticality

Vertical surface in the intertidal is seldom referred to as physical stress due to fast drainage of sea water and higher air exposure. Nevertheless it has been suggested that this stress is compensated by diminished solar radiation on vertical substrata. It has been shown that the temperature of the substratum and the rate of evaporation are higher on horizontal than vertical rocky intertidal surfaces, and these differences can explain variability in patterns of distribution and abundance of organisms in relation to the inclination of the shore, and substrates with increased verticality have higher algal abundance (Benedetti-Cecchi, 2000). In contrast, a smaller depression can offer a more favorable refuge against hydrodynamic forces (Granhag et al., 2004).

Individually, there was a weak correlation between verticality and species diversity, but in the combined bi-plot, verticality was one of the three most influential parameters on the community structure. In the field, very few of the quadrates were completely vertical and the differences among them were relatively small. The analysis therefore suggests that even minor changes in verticality at the small scale can affect species composition (the relative abundance of species) but not necessarily diversity. Also, since the combined analysis was based mainly on edge samples, this conclusion valid mainly for this habitat.

4.5.1.4 Sand

Sand cover and aggregation are one of the stressors algae need to cope with on the platforms, especially in the center habitat where sand cover it highest (Figure 16). Sand causes scouring and in large amounts could smother algae (Littler et al., 1983). Sand deposits also have been considered to be temporary and unstable, especially for early stages of propagule attachment to the surface, resulting in lower richness communities (e.g. Stephen 1929). Indeed this study showed a negative correlation between sand cover and species richness (Figure 26). Because intertidal rock surfaces are rarely flat, sand is deposited unevenly across the shore causing greater habitat heterogeneity and thus

maintaining a balance between sand tolerant and sand intolerant competitors for space. Species are often excluded from specific areas by the presence of sand, but the patchiness of deposit results in very few species being eliminated from the shore as a whole (Littler et al., 1983; Mcquaid and Dower, 1990). Sand may affect algae negatively on a small scale, by limiting most species distribution to patches without sand aggregation, but on larger scales it creates a mosaic in space competition and habitat differentiation potentially leading to higher species diversity.

Species that are reported to be highly sensitive to sand stress, such as *Cladophore spp.* and *Ulva spp.* (Littler et al., 1983) are actually seen in the combined biplot in proximity of the sand arrow. Since this particular analysis was driven mostly from edge data where sand was not that abundant it might explain how this opposite correlation has occurred.

4.5.1.5 Surface height and air exposure

As mentioned above, platform height above sea level did not show a direct relationship to species diversity or richness. This was surprising given the fact that it is clear that this parameter directly influences other features as water cover and flux, air exposure, wave force etc.. However, most of these parameters were shown in my study to be highly influential on the smaller (quadrate) scale. This discrepancy suggests that the high variability in all these parameters within platforms mask the overall effect at the platform scale. Increasing aerial exposure had been shown to reduce temporal variance in abundance of encrusting coralline and filamentous algae, and increased fluctuations in aerial exposure generated opportunities for colonization and persistence to a wider range of taxa than more regular environmental conditions, thus promoting larger temporal variances in abundance (Bertocci et al., 2007). This implies that variations in aerial exposure, caused by height variations on the platforms, could generate a more diverse community. This is of course context-specific to the local species pool, since some species have greater rates of photosynthesis in water than air, whereas others show opposite patterns (Einav and Beer, 1993; Stachowicz et al., 2008). This is consistent with the negative correlation found between water cover and species diversity (Figure 17). It seems that air exposure is significant to some of the intertidal species, such as *Pterocladiella capillacea*, previously discussed as an edge species. *P. capillacea* indeed

showed high affinity to surface height in the biplot, which agrees with previously discussed species distribution (Figure 26).

Platform 6 and 7, which were the lowest platforms (Appendix 3), consistently displayed different community structure from the other platforms, specifically at the center habitat (Figures 12, 24). Water flux on platform 6 did not differ between the edge and center habitats (Figure 23). This suggests that at a lower tidal position, the different hydrodynamic regime greatly reduces differences between the center and edge habitat, in terms of species composition. This effect was visible especially in the summer, when desiccation effects are most extreme and strongly contribute to differential species distribution between the habitats, according to their abilities to withstand air exposure. Greater similarity between the edge and center, independent of season, may become dominant in the future, if extreme sea level rise forecasts are realized (Pe'er and Safriel, 2000; Rosen, 2004).

4.5.1.6 Rim Elevation

Accentuated marginal rims, made of a continuous crust 10-30 cm thick, which is composed of *Dendropoma petraeum* shells, are a known characterization of abrasion platforms on rocky shores in the eastern and western Mediterranean (Lipkin and Safriel, 1971). The rims are mostly developed on the exposed sides of the formation. Vermetid reefs have been used as biological indicators of historic sea-level fluctuations (using ^{14}C date) in different regions of the world (Antonioli et al., 1999; Morhange et al., 2006). In the past few years there are almost no findings of living *Dendropoma petraeum*, which may be associated with changes in sea temperature (Rilov, Unpublished data). This has important implication on the formation of the platforms in the intertidal rocky shore, since loss of elevated rim reduces the "water holding" capacity of the platform and makes it much dryer during low tides. Reduction in rim formations is already seen and there are very few locations on the Akhziv intertidal where it is still present. Clear correlation was found between edge sample units with rim present and species richness (Figure 18). The magnitude of the differences was not large, but indicates that rim presence allows the distribution of more algal species at the edge habitat. This is evident for quadrat scale but

not in the scale of the whole platform, since platform 5 which had the most intact rim had the lowest species richness.

4.5.2 Grazers

Limpets are important herbivores in the mid-littoral zone (Keasar and Safriel, 1994). They feed mostly on microalgae, diatoms and opportunist and temporal macroalgae especially in early life stages , such as *Ulva spp*. and *Cladophore* spp (Díaz et al., 2011). Limpet feeding time is usually restricted to high tide periods and night time, in order to avoid predators and desiccation (Connell, 1972; Nybakken, 2001).

Total algae cover was lower where limpets were abundant (Figure 20) and limpet abundance displayed a very strong relation to bare rock, supporting it as the main factor clearing macroalgae from the platforms. The most common limpet in the site, *Patella caerulea* has a territorial foraging trait and usually individuals avoid foreign mucus trails while seeking food. But in high-patella-density and low food availability they increase their territorial foraging to maximize potential finding of food (Keasar and Safriel, 1994). This leads to a situation where when the grazer population grows, it reduces algal cover much quicker and the platform becomes vacant for newcomers. It has been shown that there are only few species of algae on limpet-dominant shores, those that are big enough not to be eaten when mean limpets size is very large and with small variation (Connell, 1972). Menge et al. (1985) showed that at a small spatial scale, such as a sampling unit, high grazer density sustains low diversity by keeping algae scarce and causing local extinctions. At larger spatial scales, they may maintain and even produce high diversity through their interaction with and contribution to substratum heterogeneity and possibly low dispersal rates of other sessile species. Indeed, during my observations, the limpets were variant in size, and as the results show, there are more than a few algal species in areas adjacent to limpet activity. Therefore, I conclude that this is not a grazer-dominant rocky shore. Limpets did show a low but significant correlation to height above sea level (Figure 21), as they are usually more abundant in mid and high zones of the littoral (Lipkin and Safriel, 1971; Nybakken, 2001).

4.5.4 Water flux

Algae must contend sometimes with the hydrodynamic forces imposed by extreme water velocities without the strong, stiff armor that is typical of nearshore sessile animals (Denny and Gaylord, 2002). On the other hand, waves reduce drying out of intertidal organisms during low tides and can have positive effects on larval supply and transport of nutrient particles to filter-feeders, who are space competitors with algae (Bertocci et al., 2007). There are many contradicting pieces of evidences regarding the effect of high water flux on intertidal communities. As water flow has been shown to mediate productivity, competition, community structure and larval supply and settlement, the expected influence of increased flow on local species richness and species density is still not clear, although there are more and more indications that enhanced water flow results in higher levels of species richness (Burrows, 2012; Palardy and Witman, 2011). In this study there were no conclusive results that support this tendency. The platform with the highest flux was not the one with high species richness. This is attributed to its lower height and probably longer submergence underwater, possibly limiting strictly intertidal species that need high exposure to air. In this context, the results indicate higher gypsum dissolution due to submergence, rather than high wave action. The edge habitat, which showed higher water movement than the center habitat, is a more reliable anchor to this theory since it did show higher species diversity compared to the center.

The irregular topography and steep slopes of rocky shores produce exceptionally complicated flows that have proven difficult to describe (Gaylord, 1999). Therefore, I focused on relatively measuring water flux intensity on different locations on the platforms. As a direct consequence of the habitat formation, water flux is greater at the edge habitat than at the center (Figure 22). As already discussed, lower platforms display a different flow pattern because of higher submergence while increase in height above sea level characterized in weaker water flux (Figure 24). It's important to note that although the results are statistically conclusive and are not ambiguous, more repetitions are required to deduce more specific conclusions on water flux influence on algal community structure.

4.6 Heterogeneity index

All the parameters examined thus far suggest a general pattern where algal community is affected and shaped mostly through processes that vary at small-scales and are driven by high variability at these scales. Here, I attempt to test the habitat heterogeneity theory using a single score incorporating all aforementioned structural parameters. Each platform scored in each parameter based on its expected contribution to environmental heterogeneity at a small scale (based on the literature and my findings). I tested the overall score against macroalgal diversity. No significant correlation was found between this index of environmental heterogeneity and species diversity on abrasion platforms (Figure 27). This index is a rather simplified way to examine a very complex question. Its obvious constrain is that each parameter was given an equal weight in the calculation and no consideration was given to the mixed effects of the parameters, some of which were previously discussed.

Although the correlation was insignificant, a closer examination raises some interesting points. Firstly, platform 6 which displayed very different community characteristics throughout the analyses received the lowest heterogeneity ranking and according to the habitat heterogeneity theory, had the lowest species diversity. Platforms 5, 4, 7 and 3 display a positive trend between heterogeneity and diversity. The only outlier in this analysis is platform 2, which scored the highest heterogeneity and the lowest diversity. A recent study have reexamined the heterogeneity- diversity relationship and showed that the relations between environmental heterogeneity and species richness are unimodal rather than a positively linear (Allouche et al., 2012). This result was explained by a tradeoff between environmental heterogeneity and the amount of suitable area available for individual species: as heterogeneity increases within a fixed space, it leads to a reduction in the average amount of effective area available for individual species thereby reducing population sizes and increasing the likelihood of stochastic extinctions, leading to a decrease in diversity when heterogeneity is very high. Although it's hard to conclude from such small sample size (6 platforms) if this theory describes well the results, it may be suitable, especially due to the observed small scale significance in the intertidal. If indeed most of the community-forming processes operate through small spatial scales, it

is expected that high environmental heterogeneity as recorded here, with high species densities on such a small area, will have a negative effect on diversity.

To develop this idea further, the index needs to be applied on more abrasion platforms. Also, specific modeling of each parameter and the most probable courses of its affect along with proper scaling of each contribution to the total score will be needed. I am unaware of such attempt to develop a simple and general environmental heterogeneity index, but perhaps simplifying a complex problem instead of attempting to accurately model it can be a good way forward.

4.6 Summary and future implications

This work demonstrated that regardless of each environmental parameter effect on specific species or their distribution in sub habitats on the platforms, when collated they are all contributing to intertidal heterogeneity, which leads to higher species diversity. Temporal effects explain the largest part of community variability, among other things because seasonality greatly affects some of the studied parameters, and it will be interesting to try and combine the two aspects in future community studies. The most significant physical parameters were dependent on the spatial distribution to habitats, and surface height seems the most influential on community composition and diversity, mainly because it indirectly affects other parameters such as water cover, air exposure, sand cover, density of grazers etc..

Some of the species on the platforms showed specific habitat demands or preferences which require further study. Regardless of the initial individual approach to each parameter examined here, it is clear from the results and the reviewed literature that the physical and biological processes in the intertidal habitat interact in complex ways, what makes it as equally difficult to refer to each of them individually as to combine all of them in a single package. The small scale relationships described in this study are important for basic biological understanding, but larger scale processes that integrate them, are crucial for understanding the patterns and dynamics of the ecological community at the regional scale.

It is important to maintain the heterogeneity of the vermetid reefs to maintain the high diversity of the community of this habitat. With increased population and development

pressure on the coastal area, along with future global changes; competition for space along the shore between people and nature will increase, which will increase stress on the system. Less than a year ago it was publicized that there are authorized recreational development plans for Akhziv beach, just 4 kilometers south of the study site, which can serve also as a precedent to additional development in the area. It is therefore urgent to maintain the efforts to protect the marine environment with its existing algal population, particularly the unique intertidal habitat. I hope this work will be able to contribute vital information for these efforts in the future.

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Appendix

Appendix 1. List of all species found at the study site during the sampling year (44), but were not necessarily included in the framework of the sampling. Numbers indicate cases in which more than one species was identified but exact name is uncertain:

Acanthophora najadiformis

Chondria dasyphylla

Chondracanthus spp.

Corrallina elongata

Dasya spp.

Gelidium spp.

Gracilaria spp.

Hypnea cornnuta

Hypnea musciformis

Jania rubens

Laurencia obtusa

Laurencia papillosa

Nemalion helminthoides

Polysiphonia/Neosiphonia complex

Pterocladiella capillacea

Rytiphlaea tinctoria

Solieria filiformis

Spyridia filamentosa

Spyridia hypnoides

Centroceras clavulatum

Ceramium Roth (2)

Bryopsis spp.

Caulerpa mexicana

Cladophore Kutzing

Cladophora pseudopellucid

Cladophoropsis membranacea

Codium elongatum

Ulva Linnaeus (2)

Valonia utricularis

Colpomenia sinuosa

Dictyota spp.

Ectocarpus siliculosus

Halopteris scoparia

Padina spp.

Stypopodium schimperi

Sargassum spp.

Scytosiphon lomentaria

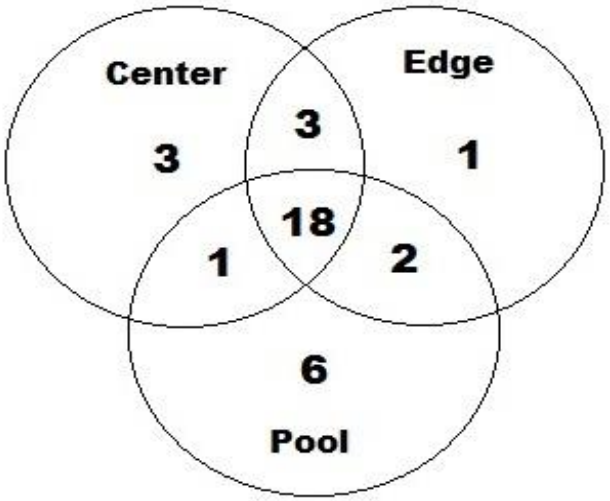
Taonia atomaria

Botryocladia spp.

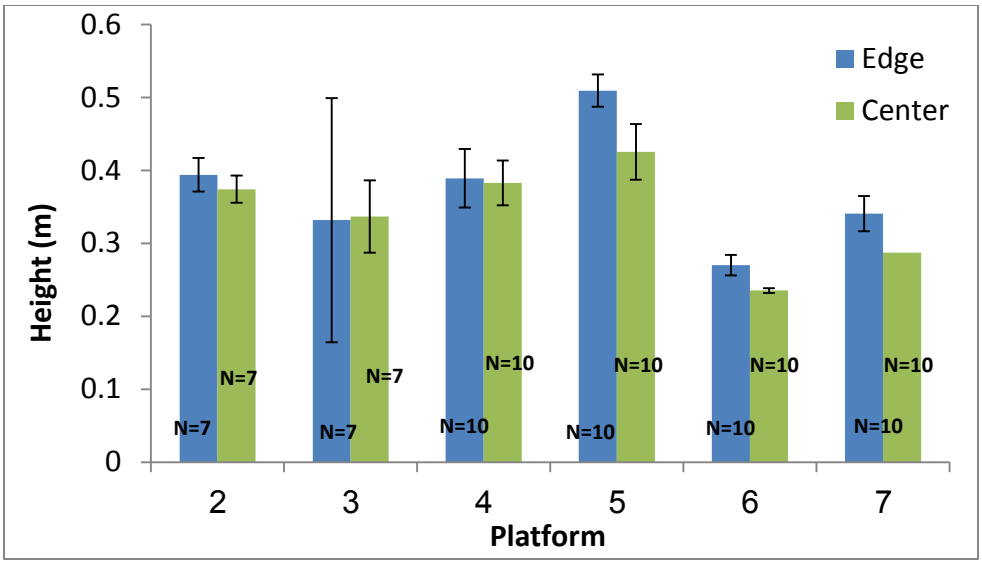
Galaxaura spp.

Halopithus spp.

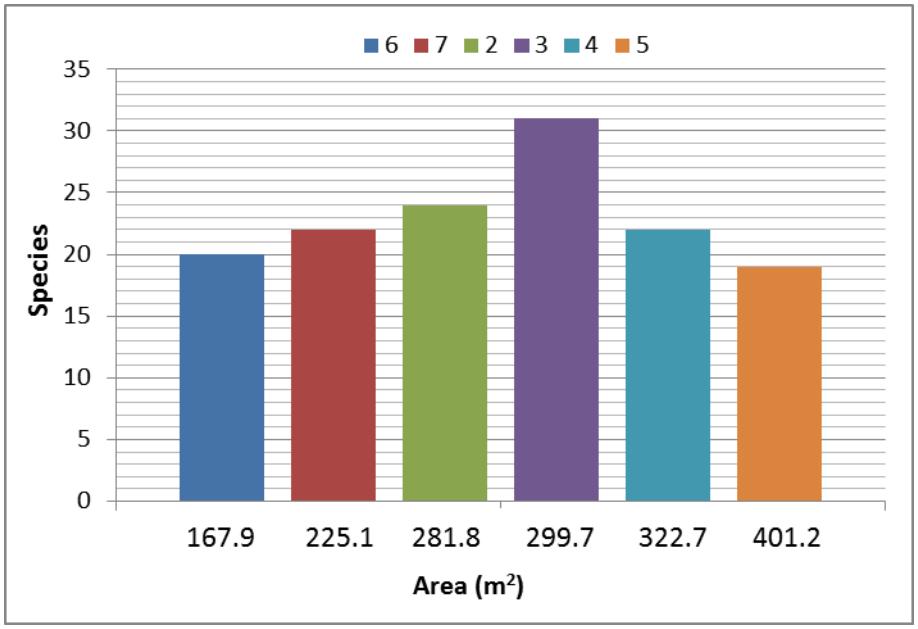
Porphyra leucosticta



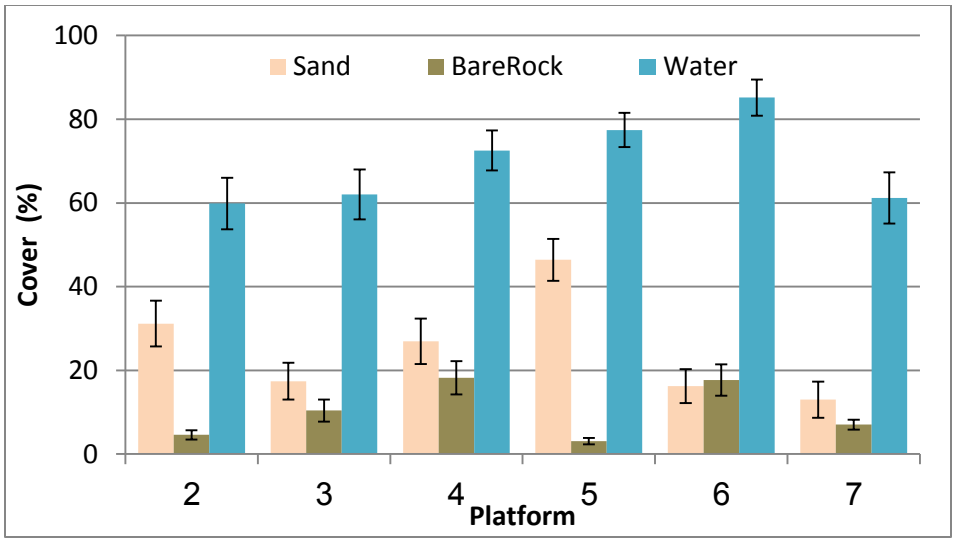
Appendix 2. Diagram of number of the common and unique algae species for each of the three habitats. There are 18 generalistic species that are common to all habitats and 10 habitat-specific species. Pools habitat has the largest number of unique species.



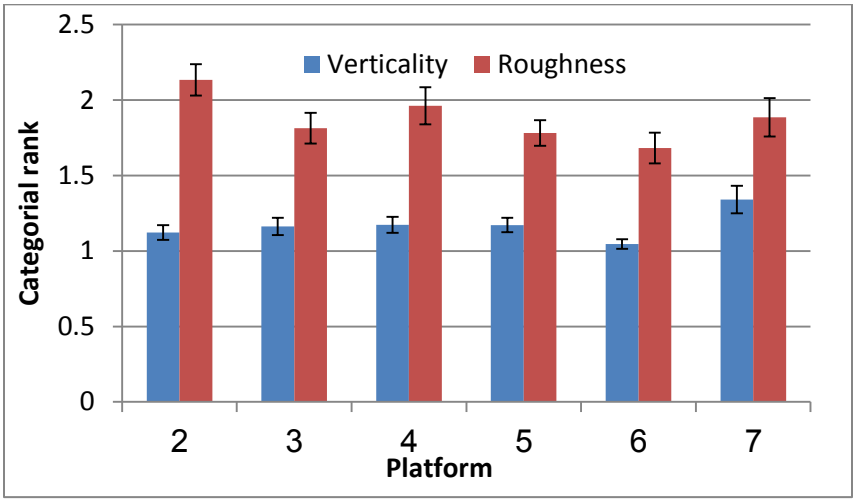
Appendix 3. Mean platform height, with standard errors divided by habitats.



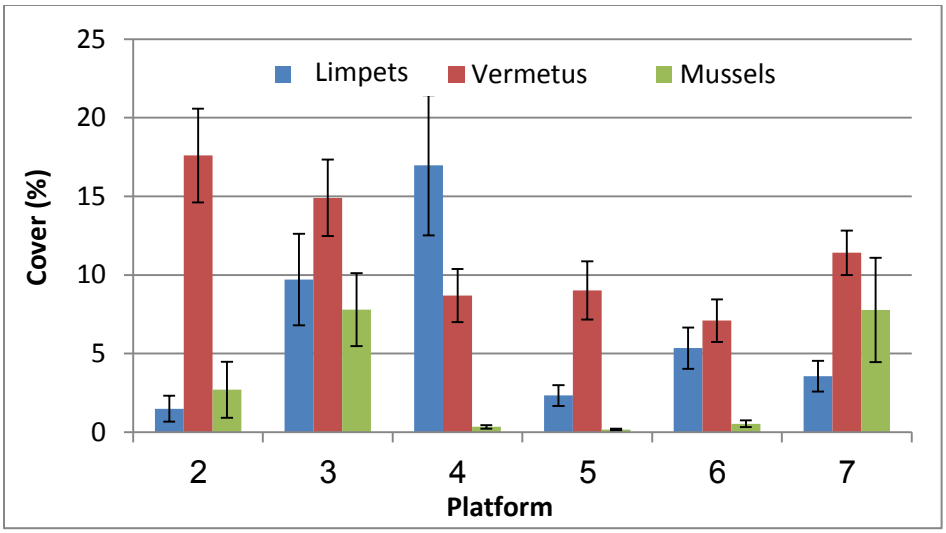
Appendix 4. Species area curve for the six platforms sampled. Number of platforms indicated in the legend.



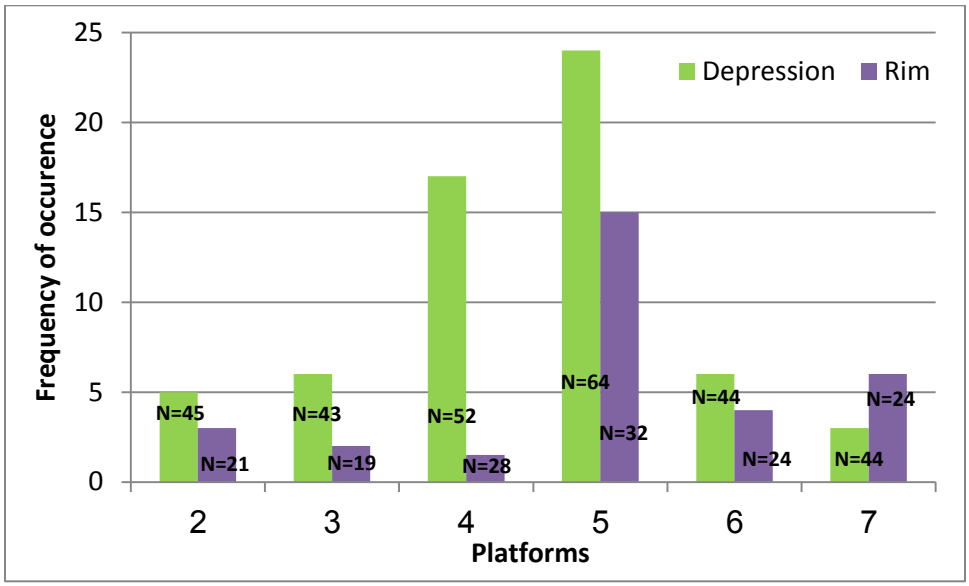
Appendix 5. Mean Cover percent with standard errors of sand, bare rock and water on the sampled platforms. N_{p2}=45, N_{p3}=43, N_{p4}=52, N_{p5}=64, N_{p6}=43, N_{p7}=44.



Appendix 6. Mean surface verticality and roughness with standard errors on the sampled platforms. Both variables measured in categorical rank of 1-4. N_{p2}=45, N_{p3}=43, N_{p4}=52, N_{p5}=64, N_{p6}=44, N_{p7}=44.



Appendix 7. Mean Cover percent with standard errors of Limpets (mainly *Patella caerulea)*, *Vermetus triquetrus* and *Brachidontes Pharaonis* mussels on the sampled platforms. N_{p2}=45, N_{p3}=43, N_{p4}=52, N_{p5}=64, N_{p6}=43, N_{p7}=44.



Appendix 8. Frequency of occurrence for depressions and biogenic elevated rim on the sampled platforms. Both variables measured in presence/absence.

צלחיות, כיסוי מים ושטף. הצלחיות הראו נטייה להתרכז במקומות גבוהים יותר על פני הטבלאות. הצלחיות הן הרביבור חשוב על פני הטבלאות ומהוות גורם עיקרי בחישוף הסלע מאצות. שטף המים היה משמעותית חזק יותר בשולי הטבלאות מאשר במרכזן. עם זאת טבלאות נמוכות יותר הראו הבדלים קטנים בהרבה בין שני בתי הגידול, ולא נמצא הבדל בשטף בין שוליים ומרכז בטבלה הנמוכה ביותר. מבנה החברה בטבלה זו היה שונה באופן מובהק משאר הטבלאות ועושר ומגוון מיני האצות בטבלה זו היו הנמוכים ביותר. ממצא זה בעל משמעות רבה במקרה של האצה בקצב עליית פני הים, העלול להוריד את מגוון המינים בטבלאות הגידוד.

הקשר בין אינדקס ההטרוגניות למגוון המינים לא היה מובהק בעוד שנראה קשר במרבית הטבלאות, הטבלה עם המורכבות הגבוהה ביותר הייתה בעלת המגוון הנמוך ביותר. עם זאת, מרכיבים בודדים של ההטרוגניות הראו קשרים חיוביים חזקים למגוון האצות. נראה שמרבית התהליכים הבונים את החברה פועלים בסקאלות מרחביות קטנות ולכן ייתכן כי ההטרוגניות הסביבתית הגבוהה שנצפתה במחקר זה, ביחד עם צפיפות המינים הגבוהה הקיימת בשטח קטן מאוד של עשרות ס"מ, היא דווקא בעלת השפעה שלילית על מגוון מינים, בניגוד לתיאוריה האקולוגית הקלאסית.

גידוד שונות זו מזו בצורתן ובגודלן אשר נדגמו עונתית במשך שנה. דיגום אקראי התבצע על שש הטבלאות באמצעות קוודרט דיגום בגודל 0.5 מ' X 0.5 מ', בשלושת תת בתי הגידול העיקריים בהן- שולי טבלה הפונים לים, מרכז הטבלה ובורות שפל. הדיגום כלל את כל מיני האצות המאקרופיטיות שהופיעו ביחידת הדיגום וכן פרמטרים סביבתיים הכוללים את אחוז הסלע החשוף, מספר הצלחיות, אחוז כיסוי על ידי מים ועל ידי חול, קיום שוליים ביוגניים ומידת המורכבות והאנכיות של המסלע. בנוסף נמדדו וחושבו עבור כל טבלה שטחה, גובהה מעל פני הים וכן התבצע ניסוי בשלוש טבלאות לאפיון משטר הזרימה והשוואת מידת השטף בין בתי הגידול של שוליים ומרכז הטבלה. הערכת עוצמת השטף נעשתה באמצעות התמוססות של תבניות גבס, שהוכנו במיוחד והוצבו במקומות שונים על הטבלאות למשך 24 שעות. על מנת לברר האם הטרוגניות סביבתית גבוהה מובילה למגוון מינים גבוה יותר בבית הגידול, יצרתי אינדקס הטרוגניות באמצעות דירוג כל הטבלאות עבור כל אחד מהפרמטרים המבניים, המהווים חלק מההטרוגניות הסביבתית וסכימתם יחד. כך התקבל דירוג הטרוגניות כולל של כל טבלה ודירוג זה נבחן מול מגוון המינים המחושב בכל טבלה.

במהלך שנה אחת נדגמו 34 סוגי אצות, 3 מינים מתועדים כאן לראשונה בחוף הסלעי באכזיב. לעונות השנה הייתה ההשפעה הגדולה ביותר על מבנה החברה ומגוון המינים. החורף היה העונה המגוונת והעשירה ביותר באצות ואילו בקיץ נמצא המגוון הנמוך ביותר. בשל החוסר במידע על ההשפעה העונתית על אצות בים התיכון קשה לקבוע את הסיבות למגוון הגבוה שנמצא בחורף. ניתן לשער שהחורף החם יחסית בארצינו מקנה תנאים טובים למגוון רב של אצות ואילו תנאי חום קיצוניים וימי שרב ארוכים בקיץ גורמים למגוון נמוך של אצות. בין שתי הסקאלות המרחביות שנבדקו, בתי הגידול היו חשובים יותר למבנה החברה מאשר הטבלאות השונות. ממצא זה תומך בידע הקיים אודות השפעת סקאלות מרחביות קטנות יותר על החברה בחוף הסלעי במקומות נוספים. בית הגידול של הבורות היה המגוון ביותר ונמצא קשר בין בית גידול זה למספר מינים אופיניים לתת-הכרית. זאת כיוון שהוא מספק תנאי מחייה ללא עקת יובש (כמו בשאר בתי הגידול על הטבלאות) המתאימים למינים רבים, שאינם דורשים חשיפה מוגברת לאוויר. בבדיקה פרטנית, המשתנים הבאים הראו קשר מובהק למגוון אצות: מורכבות המסלע, אנכיות המסלע, כיסוי של מים בעת שפל, כיסוי חול, שוליים ביוגניים ונוכחות צלחיות. באנליזה משולבת של כל המשתנים יחד, התקבל כי אנכיות, כיסוי מים וחול חשובים יותר במבנה החברה משאר המשתנים. השפעת כיסוי מים על מגוון המינים הייתה שלילית באופן מובהק. קשר זה מבטא את הדרישה של מיני אצות מסויימים על הטבלה לחשיפה זמנית לאוויר המגבירה את קצב הפוטוסינתזה. נמצא קשר שלילי בין כיסוי חול ומגוון מיני האצות. אנו יודעים כי כיסוי חול יכול להיות גורם מעכב להתיישבות וגדילת אצות. לשיפוע המסלע יש משמעות רבה לאצות והשפעות לכאן ולכאן נמצאו בעבר. ככל שהמסלע אנכי יותר, ניקוז המים ממנו רב יותר, אך עם זאת הוא מקנה גם צל והגנה מפני קרינה חזקה בשעות היום. ככל שהמסלע היה משופע יותר, כך מגוון המינים היה גבוה יותר. כיוון שהשיפועים שנצפו במהלך הדיגום היו קטנים יחסית, ניתן לומר שהשיפועים במסלע מהווים חלק מהמורכבות המבנית של הטבלאות המגבירים את ההטרוגניות הסביבתית. גובה הטבלאות מעל פני הים הראה תפקיד עיקרי בהשפעתו על מבנה החברה ומגוון המינים. השפעתו על האצות עקיפה, דרך משתנים סביבתיים אחרים שהראו קשר חזק לגובה:

תקציר

בעולם משתנה העומד בפני לחצים אנתרופוגניים מתמשכים יחד עם התעצמות שינויי האקלים, המערכות האקולוגיות כפי שאנו מכירים אותן משתנות גם הן. שינויים בקני מידה מרחביים גדולים (ברמת המערכות) לרוב ניתנים להסבר על ידי שינויים בתפוצות מינים בודדים ואף העלמותם בשל אובדן בתי גידול או דחיקה תחרותית וכן שינויי אקלים. הצורך לשמור על מגוון מינים גבוה במערכות השונות מתבטא בהנחה שכל מין תורם לתפקוד ויציבות של האקוסיסטמה בה הוא חי במאפייניו הייחודיים והאינטראקציות שלו עם שאר המינים בחברה. מחקרים קודמים הראו כי מערכות בעלות מגוון מינים גבוה עמידות יותר לפלישות מינים ובעלות יכולת שיקום מהירה יותר לאחר הפרעה לעומת מערכות דומות עם מגוון נמוך. למרות שטחן הגדול של המערכות הימיות בעולם, מחקרים ימיים על מגוון מינים עדיין מועטים יחסית למערכות יבשתיות. החוף הסלעי הינו בית גידול ייחודי הקיים במקומות רבים בעולם ובחופי ישראל. המופע העיקרי של בית גידול זה בארץ הינו בצורת טבלאות גידוד הנמצאות בתחום הכרית. תחום זה מאופיין בתנאי מחייה קשים ודינמיים, שכן פני הטבלה נחשפים לאוויר בזמן שפל ומצויים מתחת לפני הים בזמן הגאות, זאת כמובן כתלות בגובה פני הטבלה מעל פני הים ובמצב הים המשתנה עונתית. מבנה המסלע בטבלאות יוצר נקיקים, בלטים, שקעים ובורות היוצרים תת בתי גידול בעלי תנאי מחייה שונים המשפיעים על מבנה החברה ותפוצת המינים על פני הטבלאות ובכך נוצרת הטרגוניות מרחבית מאוד מגוונת המשתנה בין טבלה לטבלה. על פי תיאוריית ההטרוגניות הסביבתית, אחת התיאוריות הבסיסיות באקולוגיה, ככל שבית גידול הוא בעל הטרוגניות סביבתית גבוהה יותר, הוא יתמוך במגוון מינים גבוה יותר בגלל מגוון הנישות האקולוגיות הרב יותר ולכן מציע דרכים רבות יותר לניצול משאבי הסביבה שביכולתו של בית הגידול לספק. עבודות שנעשו בחופים סלעיים ברחבי העולם, התייחסו להטרוגניות סביבתית בעיקר כהטרוגניות טופוגרפית וברוב המקרים היא הראתה השפעה חיובית על מגוון המינים. בבית גידול זה, הקשר נמצא משמעותי בעיקר בסקאלות מרחביות קטנות של כמה עשרות ס"מ, כנראה בשל גודלם הקטן יחסית של האורגניזמים בחופים סלעיים. האצות הינן המרכיב הדומיננטי ביותר במגוון המינים בטבלאות הגידוד וכוללות עשרות מינים. מלבד זאת, הן משפיעות על מבנה כל החברה והתהליכים המתרחשים בה בהיותן 1) גורם מרכזי בוויסות השטח הפנוי להתיישבות של חסרי חוליות ומיני אצות אחרים, 2) בעלות תפקיד עיקרי במורכבות המבנית של בית הגידול על ידי תוספת תנאים מיקרו-סביבתיים המקנים הגנה או מקום התיישבות עבור מינים אחרים הדורשים זאת, 3) הן מהוות מקור מזון חשוב בשרשרת המזון המקומית ושינויים בחברת האצות ישפיעו על מבנה החברה כולה.

מחקר זה בחן את הקשר בין המגוון הביולוגי של האצות המאקרופיטיות על טבלאות הגידוד לבין מאפיינים שונים בהטרוגניות הסביבתית של בית הגידול. מטרתו הייתה לבדוק האם בית גידול זה מתנהג בהתאם לתיאוריית ההטרוגניות הסביבתית, לבחון את מידת ההשפעה של סקאלות הזמן והמרחב על מגוון המינים והרכב החברה ולזהות מהם המשתנים הסביבתיים המשפיעים ביותר על הרכב החברה ומגוון מיני האצות. לצורך בחינת קשרים אלו, נבחר החוף הסלעי באכזיב, בצפון הארץ. באתר נבחרו שש טבלאות

תודות

מחקר זה בוצע בהנחייתם של פרופסור יוחאי כרמל מהפקולטה להנדסה אזרחית וסביבתית וד"ר גיל רילוב במכון לחקר ימים ואגמים לישראל, חיפה.
אני מודה מקרב לב לשניהם על הייעוץ, התמיכה והזמן שאינו מובן מאליו, שהקדישו לעבודה זו.

ברצוני להודות גם לוועדת הבוחנים שלי, על הבדיקה המסורה וההערות המועילות.

אני מודה לטכניון על התמיכה הכספית הנדיבה בהשתלמותי.

ברצוני להודות לחבריי ועמיתיי מהמעבדה בחקר ימים ואגמים על עזרתם בים ובמעבדה, כמו גם אחרי שעות העבודה.

תודה לד"ר אלוורו ישראל על ששיתף עמי את הידע שלו בעולם האצות. לא ניתן היה לעשות את הגדרת המינים בלעדיו.

אני מודה לחבריי למעבדת ממ"ג באקולוגיה וסביבה בטכניון על הייעוץ והעזרה.

תודה מיוחדת להורים שלי, שכל זאת אפשרי בזכותם. על שתמיד גרמו לי להאמין שאין שום דבר בלתי אפשרי.

אחרון אחרון חביב, אני רוצה להודות לבן זוגי, ברק, על האוזן הקשבת והסבלנות הבלתי נדלית בבית ועל הסיוע האדיר בים.

הקשר בין הטרוגניות סביבתית ומגוון ביולוגי בחברת האצות של החוף הסלעי

חיבור על מחקר

לשם מילוי חלקי של הדרישות לקבלת התואר

מגיסטר למדעים במדעי איכות הסביבה

אולגה ודוב

הוגש לסנט הטכניון- מכון טכנולוגי לישראל

כסלו תשע"ד חיפה נובמבר 2013

הקשר בין הטרוגניות סביבתית ומגוון ביולוגי בחברת האצות של החוף הסלעי

אולגה ודוב