CHAPTER TWO

LITERATURE REVIEW

2.0 LITERATURE REVIEW

2.1 Global phycogeographic distribution

For most groups of organisms, species richness seems to follow a pattern of latitudinal gradient: the tropics possess the greatest number of species, which then declines polewards. Phycological research, however, has shown that this common biogeographic pattern is not evident in global seaweed distribution. Worldwide, there are an estimated 6,500 - 8,000 species of macroalgae (Silva, 1992; Luning, 1990). Generally, coasts that are considered to be of high algal diversity are those possessing 600 - 800 species from 200 - 300 genera, and coasts such as these mostly lie within the temperate belt (Luning, 1990, p. 192).

Bolton (1994) gives an interesting overview on the patterns and anomalies observed in seaweed floras on a global scale, noting that on the basis of species diversity alone, three main phycogeographic regions may be identified:

i. **Species poor floral zone**: at latitudes higher than 60°, wherein the average species count is less than 200.

ii. **Fairly poor to rich floral zone**: encompasses a wide range of climatic zones, throughout cold and warm temperate, and tropical regions. Zones of fairly poor flora have been defined as those with an average species count of 200 - 400, represented in this study by Southwestern Africa, Chile-Peru, Northern Australia, Maldives, the Solomons, Carolina-Florida, West Indies, the Great Barrier Reef, and the Subantartic islands of New Zealand. The rich floral zone possesses an average of 600 - 700 species and is represented by Indonesia-Malaysia, New Zealand, Korea, the British Isles, California, Alaska-Oregon, the Caribbean, and the Agulhas province of South Africa.

iii. **Very rich floral zone**: encompasses four regions, namely southern Australia, the Mediterranean, and Japan, all of which lie within latitudes 30 – 50°; as well as tropical Philippines. Average species count is between 900 - 1,100.

The distribution above shows an apparent lack of a general pattern of greater species richness in the tropics, which is surprising considering that tropical regions, having maintained their warm-water temperature even in the Pleistocene, represent the world's oldest marine habitats. Amongst the reasons suggested are study bias (Huisman *et al.*, 1998; Bolton, 1994), outcompetition by massive hermatypic tropical corals (Luning, 1990, p. 192), and more intense fish herbivory (Gaines & Lubchenco, 1982).

Polewards, too, the red and green algae begin to lose dominance while the brown algae attain greater diversity (Luning, 1990). The R : P (Rhodophyta : Phaeophyta) index introduced by Feldmann in 1937 is a ratio of the number of red algal species to the number of brown algal species in a given flora. This index rises from 1.1 in the cold temperate regions to a maximum of 4.3 in tropical regions. From the accounts of Weber Van Bosse in 1928, the R : P index for Indo-Malaysian floras was 4.2 (Luning, 1990).

Whilst the worldwide distribution of seaweeds appears to be determined primarily by global temperature gradients, other factors such as light, nutrients, salinity, desiccation tolerance, grazing and competition appear to bear more importance for local patterns of distribution.

2.2 Seaweed diversity research in Malaysia

There have been relatively few reported studies on the diversity of Malaysian marine algae. Amongst these are the various published checklists of the marine algae of Malaysia and

Singapore (Phang, 1984, 1986; Teo and Wee, 1983; Phang & Wee, 1991), the latest being that of Phang's in 1998. There are, however, other publications that treat specific localities within Malaysian waters, namely Penang Island (Crane, 1981); Pulau Bidong Laut (Arumugam, 1981); Cape Rachado (Phang, 1989; 1995); Tioman Island (Ismail & Go, 1994); and the Straits of Malacca (Wong *et al.*, 2000). There is currently one published field-guide to the seaweeds of Malaysia (Ismail, 1995).

To date, 267 species have been recorded in Malaysian waters (from the combined records of Phang, 1998 and Wong *et al.*, 2000), of which the Rhodophyta constitute the majority. The breakdown of species is as follows: Rhodophyta 100 species, Chlorophyta 93 species, Phaeophyta 57 species and Cyanophyta 17 species. Calculating from these latest figures, the R : P index for seaweeds in Malaysian waters is 1.75.

2.3 Effects of Environmental Parameters

2.3.1 Light

Because of its effect on photosynthesis, reproduction, morphogenesis and germination, light is regarded as the most important abiotic factor affecting seaweed growth and development. The flora's light-harvesting pigments absorb across a broad region of wavelengths, often referred to as "photosynthetically active radiation" (PAR). PAR is defined as wavelengths of 350 nm to 700 nm (Clayton & King, 1990, p. 275). The most useful measurement of light is the "photon-flux density" (PFD), defined as the number of photons of PAR received by a unit of algal surface and expressed as microeinsteins per square meter per second ($\mu E\ m^{-2}\ s^{-1}$). However, light may also be measured in terms of the amount of energy falling on a flat surface, and when this is the case, the term "irradiance" is employed, expressed as watts per square meter (W m^{-2} = J m^{-2} s^{-1}). Lobban and Harrison (1994, p. 125), however, have used irradiance flexibly to refer to either quanta or energy at any one time (cf. Luning, 1990, p. 328).

Light requirements have long been thought to determine the vertical zonation of seaweeds. Beginning in 1883, Engelmann established a theory relating seaweed zonation to their pigment complements (Clayton & King, 1990; Lobban & Harrison, 1994). Engelmann, based on the assumption that underwater light becomes greener with depth, proposed that green seaweeds, because they carried only chlorophylls that absorb green light poorly, would be restricted to shallow water. Brown seaweeds, with their accessory fucoxanthins would enable them to live farther out (10-50 m), whilst the green light-absorbent phycobilins of the red seaweeds are an evolutionary feature designed to allow this group to extend into even deeper waters.

A series of rebuttals by various authors, such as Ramus (1983), Dring (1990) and Saffo (1987) led to a rethinking of Engelmann's hypothesis. Generally, their opposition to Engelmann's idea was based on the observation that in many parts of the world, green seaweeds grow as deep as red seaweeds, and that light is often not the sole factor in zonation. Moreover, evidence points to light intensity (light quantity) rather than light quality (spectral quality) as a stronger determinant of the vertical distribution of many algae (Larkum & Barrett, 1983).

Luning, from his work in Helgoland, the North Sea, has attempted to match annual irradiance to annual light requirements of specific sublittoral species found growing at different depths (Luning, 1990). The lower algal limit there was 15 m, receiving an annual light exposure of 6 E m^{-2}, and comprising crustose algae that have minimal light requirements, such as *Lithothamnion sonderi*. Towards the water surface where light increased, species of larger thallus size, such as the kelp *Laminaria hyperbora*, proliferated.

Light modelling in algal research has been performed with a certain degree of success. The research of Dring (1987) constituted a first attempt at assessing light climate changes in relation to the growth of intertidal macroalgae. The light climate in this zone is one of great complexity because of recurrent changes in water type[1] and tidal range, and the timing of high and low tides in relation to the diurnal changes in irradiation. Following up on the previous studies of optical oceanographers such as Jerlov and Kirk, Dring designed a model to predict the light available for photosynthesis by benthic algae at fixed depths. He found that his predictions of 1% and 0.05% depths for a series of sites in the Bristol Channel agreed well with observed lower limits for kelp forests and for foliose algae, respectively.

With light quantity strongly hypothesised as the determining factor of vertical distribution, it followed that in dim conditions, seaweeds respond by increasing all accessory pigments and making adaptations in thallus morphology and orientation. Observations such as these gradually led to a study of the relationship between species light requirements and functional form. The typical characteristics of shade-adapted species include minimal

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[1] In correspondence to Jerlov's optical water types (see also Jerlov, 1976), which has 9 categories of water types ranging from the clearest (oceanic type 1) to the murkiest (coastal type 9). In the latter, the maximum transmittance occurs at about 575 nm and is only 56% of the total irradiance at the surface.

respiration and therefore slow growth, and disproportionate storage of fixed carbon as reserve materials. In order to proliferate at slow rates of growth and development, these species must be able to physically withstand or deter grazing. This explains the dominance of crustose coralline algae in areas with low light condition and areas of depth (Luning, 1990; Paine, Slocum & Duggins, 1979).

It has been hypothesised that multilayered seaweeds are better equipped to absorb more light than monolayered ones in well-lighted habitats, whilst the opposite is true in dim light conditions where the flat structure of monolayered seaweeds reduces chances of self-shading (Hay, 1986; Norton, 1991). Intertidal algae have been reported to have large canopies, with a frond area index of 5 to 34 (Norton, 1991) although the study areas, whether temperate or tropical, were not stipulated, unfortunately, since latitudinal location may have a bearing on a species or population's external morphology.

Thallus thickness is also an important factor in light absorbance (Table 1). Filamentous plants and thin sheets allow a great deal of light into the innermost parts of the tuft, but the largest bushy plants have almost opaque branches that impede the passage of light (Norton, 1991).

Based on this type of thallus thickness classification, the vertical distribution for marine macroalgae has been observed to consist of three zones: an uppermost zone dominated by large brown algae; an intermediate zone with foliose and delicately-branched algae; and a deep community of mostly crustose algae (Vadas & Steneck, 1988, in Markager & Sand-Jensen, 1992). This zonation pattern was supported by the research of Markager & Sand-

Table 1 The characteristics associated with various growth forms of seaweeds (Norton, 1991)

Growth form	External morphology	Internal anatomy	Texture	Thallus capacity mean % absorption*	Examples of taxa
Thin sheets	Thin, tubular or laminate	Uncorticated, one to a few cells thick	Soft	30-40	*Ulva* *Dictyota* *Porphyra*
Filamentous	Delicately branched	Uniseriate, multiseriate or lightly corticated	Soft-bristly	70-76	*Cladophora* *Spongomorpha*
Thick sheets	Thick blades and branches	Corticated, many cell layers thick	Leathery-rubbery	81-91	*Fucus* *Dilsea* *Sargassum* *Padina*
Coarsely branched	Coarsely branched, upright	Corticated	Fleshy-wiry	98-99	*Chondrus* *Gymnogongrus* *Codium*
Jointed calcareous	Articulated, calcareous	Calcified except at the joints	Stony	99-100	*Corallina*
Crustose	Epilithic, prostrate, encrusting	Calcified or uncalcified parallel cell rows	Stony or tough	99-100	*Lithophyllum* *Ralfsia*

* Data from Kanwisher (1966), Ramus (1978), Hay (1986) and Norton (unpubl.).

Jensen (1996) who found that thin species are superior in growth rate to thick species at all irradiances, under otherwise optimal conditions. The presence of thick species in 'sun habitats' is, therefore more likely to be related to their competitive ability in exploiting variable nutrient concentrations, to overtop smaller neighbours and minimise loss rates due to grazing and mechanical exposure. In shaded habitats, thin species will be superior to thick species because of their higher absorbance per unit of carbon biomass. Therefore, thick species are likely to flourish in high light habitats whereas thin species can be distributed throughout all habitats.

Mismanaged land development projects are notorious for contributing high silt loads to their neighbouring intertidal flats and when this happens, the presence of high total suspended solids (TSS) further confounds the light climate in the intertidal zone. Phang (1988) noted a decrease in algal biomass as a result of increased TSS in water due to coastal land development. Diversity, however, seemed to remain without significant change, although microscopic species such as *Microdictyon* were not observed after the commencement of land development. Other parameters such as the total number of species, percent macroalgal cover and the number of unique species generally decrease with increasing silt load (Ganzon-Fortes, 1999; Walker & Kendrick, 1998). Apart from reducing water visibility, heavy siltation also leads to the development of muddy substrate, and this apparently diminishes the capacity of a site to support a diverse and abundant algal flora. However, sedimentation as a local stress may be necessary for the persistance of some components of an assemblage. For instance, the study of Airoldi & Cinelli (1997) on the subtidal macroalgal assemblages of a mediterranean, rocky shore revealed a decrease in diversity and evenness with lessened sediment supplies, primarily because the filamentous and seasonal distribution (Norton, Mathieson & Neushul, 1981) by affecting the well-being of seaweeds as well as producing heat-triggers that determine seasonality.

The optimal temperatures for growth range between 0 - 10°C for polar species, 10 - 20°C for warm temperate species, to 15 - 30°C in warm temperate to tropical species (Luning, 1990). However, stable environments tend to produce stenothermal responses, so the temperature optima of a species or community very much depend on fluctuations in seasonal temperature, as well. The tropical pelagic species *Sargassum natans* from the Sargasso Sea, for example, has a broad growth optimum of 18 - 20°C, but lacks the ability to grow at a temperature of 12°C, unlike the *Sargassum* species from Florida (Hanisak and Samuel, 1987). Often, physical changes in plant forms have been observed to coincide with thermal changes. Largo and Ohno (1992), for example, found that the tropical *Sargassum myriocystum* and *S. siliquosum* of the central Philippines developed longer primary lateral branches at a water temperature of 27°C. Likewise, De Wreede (1976) concluded that growth of *S. oligocystum, S. obtusifolium* and *S. polyphyllum* was best at or near 24°C and poorest at 32°C and these species, in fact, produced longer thalli at temperatures between 22 - 25°C. Intraspecies differences have also been recorded in high- and low-intertidal plants of *Enteromorpha linza* (Innes, 1988, in Lobban & Harrison, 1994).

Marine macroalgae also exhibit different photosynthetic responses to temperature in different parts of their respective life-history phases, and research on this has yielded interesting insights into the different ecological roles of life history phases (Zupan & West, 1990; Bacon & Vadas, 1991; Tseng, 1981). The reproduction processes of some species such as *Chorda tomentosa, Bostrychia radicans, Ectocarpus siliculosus,* *Urospora wormskioldii* and *Callithamnion byssoides* have been observed to be triggered and controlled by temperature that acts as an environmental signal for a season (reviewed in Luning, 1990).

The search to establish optimal temperatures has yielded only approximate data. Often, seaweeds are found to live in waters with temperatures above or below their respective temperature optima established in laboratory assays (Fong & Zedler, 1993; Fries, 1966; Yokoya & Oliveira, 1992). Such variations have been attributed to their adaptation to local conditions or laboratory procedures that do not duplicate the ecological complexities of an ecosystem (e.g. thermoperiodicity, interactions with other organisms).

The relationship between diversity, biomass and water temperature in the tropics remains yet unclear and conclusions have so far been tentative. In polar and temperate latitudes, biomass seasonality is strongly related to seasonal light and temperature changes, but this is less clearly seen in the tropics (Doty, 1971). In Doty's work on intertidal algae in Hawaii, temperature as a seasonal factor was thought to be less important an influence on the size of the harvestable frondose marine algal crop in comparison to the more random occurrence of storms in non-monsoonal areas (Doty, 1971). Rough waters produced by storms were observed to destroy the standing crop, and this was deemed a larger determining factor than water temperature.

However, the conclusion above was later revoked on account of sampling error, in a subsequent study at the same site (Glenn, Smith & Doty, 1990). Instead, both total crop and *Sargassum polyphyllum*, the dominant species of interest, exhibited a high correlation in standing crop size and antecedent water temperatures recorded 3 - 4 weeks prior to the estimate of standing crop. Considering that the temperature range was small, 22°C to 27°C, but accounted for 65% of the variation in the standing crop, shows it to be a remarkable force on the algal community there. Rising water temperatures were hypothesised to have stimulated the vegetative growth of new plants in spring and summer, leading to an increase in biomass through early fall. When temperatures fall in October, the plants are triggered to become fertile, and they respond by decreasing vegetative growth. Biomass then declines in later months (see also Josselyn & West, 1985). Various other researches on the *Sargassum* species, important in this case by virtue of its dominance in nearshore Malaysian waters, yielded different results pertaining to its seasonality (Wong, 1997). In the Philippines, for example, Ang's (1985) conclusion of greater growth rates of *S. siliquosum* in warmer months ran contrary to the reports of maximal growth and thallus length of the species in cooler months by Largo & Ohno (1992) and Largo *et al.* (1994).

Fong and Zedler (1993) reported the maximal growth of attached and floating macroalgae in spring and summer. They postulated that the combined effects of temperature and light in southern California coastal lagoons are the primary factors influencing the observed seasonal sequence: attached macroalgae dominate in early spring, floating macroalgae in summer, cyanobacterial mats in late summer and early fall, and phytoplankton in late fall.

The same biomass pattern was noted in other similar studies in the mid-latitudes, although the point was more on winter months as periods of greatest physical stress that inhibit growth, rather than water temperature *per se*[1] (Murray & Horn, 1989; Josselyn & West, 1985). This appears to be in contrast to tropical locales where summer appears to be the season of greatest environmental harshness and least macrophyte abundance (Murray & Horn, 1989; Hodgkiss, 1984). With specific reference to Cape Rachado, the period of greatest environmental stress via rainfall, strong waves and high turbidity would be the monsoon period between November and March. Here, the biomass and thallus length of *Sargassum baccularia* and *S. swartzii* between November and January have been reported to be minimal (Wong, 1997).

A rather more thorough study was conducted by McQuaid and Branch (1984) in the Cape of Good Hope, where factors such as shore exposure and substratum together with temperature were correlated to biomass and species richness and composition. In this particular research, species richness and composition were postulated to have been determined largely by water temperature, whilst the degree of shore exposure had an overriding effect on biomass. Similarly, by using seaweed community composition, temperature was again demonstrated to be the controlling factor in the changes around the Cape of Good Hope, by Bolton and Anderson (1990). It does appear that temperature has the ability to influence the population structure, since different species are triggered to grow or reproduce at different temperature levels. In Queensland, Australia, Ngan and Price (1980) reported that the majority of intertidal tropical species showed a tendency towards active growth in autumn, winter and spring. Some, however, grew actively only in the cooler periods of winter and spring, for example, *Caulerpa racemosa, C. taxifolia,*

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[1] Daylength, upwelling and air temperature increase in magnitude during summer months, whilst precipitation, daylight tidal emersion, surface seawater temperature and swell heights are factors that increase in magnitude during the winter months (Murray & Horn, 1989).

Ceramium sp., *Chaetomorpha antennina, Champia parvula* and *Dictyota dichotoma,* whilst others grew actively only in summer and autumn. Amongst these were *Gracilaria edulis, G. crassa, Lyngbya majuscula* and *Padina tetrastromatica* (Ngan & Price, 1980).

In terms of zonation patterns in the intertidal zone, however, limits of high or low temperature tolerances have not been found to correlate well with tidal elevation for particular groups of algae (Smith & Berry, 1986). It seems that although differential tolerance to temperature extremes may be an important influence for latitudinal ranges of species, that is, on a biogeographic level, temperature tolerance by intertidal algae does not appear to be an important influence on the distributional patterns of marine algae along intertidal gradients.

Since the recognition of the global warming phenomena, the question of how rising sea temperature could affect macroalgal distribution has been the focus of research attention. Beardall *et al.* (1998) gives a review of all related research and cites Barry *et al.* (1995), Breeman *et al.* (1996), and Raven and Johnston (1993).

In the study of Barry *et al.* (1995, in Beardall *et al.*, 1998), the 2.2°C rise in mean summer sea temperature on the Californian coast over a sixty year period was correlated with an increased dominance of low growing turf algae such as *Gelidium coulteri*, *Gigartina canalicuta, Endocladia muricata* and *Mastocarpus papillatus* at the expense of the larger, cold water species *Pelvetia fastigiata* and *Fucus distichus.*

Breeman (1990, in Beardall *et al.*, 1998) believes that for some species, even a small change of water temperature could bring about major changes in plant distribution.

Breeman predicts significant changes in community structure associated with the northward shift in the southern boundaries of the major canopy forming species *Laminaria hyperborea, L. saccharina* and *L. digitata*. The northward migration of warm to tropical species has been regarded to have less of an impact.

Raven and Johnston (1993, in Beardall *et al.*, 1998) have argued that the ones most likely to suffer are the austral polar flora, on account of being particularly susceptible to changing water temperatures. If these species cannot adapt their temperature responses as fast as lower latitude plants can adapt to changing photoperiod, the latter could become more dominant at high latitude and replace the Antarctic endemic species.

Despite growing studies such as these on temperature responses of macroalgae, Beardall *et al.* (1998) points out that none of these studies have considered the combined effects of global climate change in terms of both CO_2 and temperature. The observed relationship between the two factors is a positive one: elevated sea temperatures result in a decrease in CO_2 solubility and hence, availability to marine plants.

2.3.3 Salinity

"Salinity", often defined as grams of salts per kilogram of solution, bears biological significance in terms of ion concentrations, seawater density and osmotic pressure (Lobban & Harrison, 1994). In hypotonic solutions, seaweed cells experience plasmolysis when water flows rapidly out of cells and the plasmalemma tears away from the cell wall (Biebl, 1962). In hypertonic solutions, seaweed cells get swollen with water until rupture occurs, again, fatally. Some seaweeds, however, exhibit a greater tolerance of plasmolysis: *Enteromorpha* and *Ulva* can be repeatedly plasmolysed and deplasmolysed without injury to the membranes (Ritchie & Larkum, 1987). Species such as these tolerate salinity changes by altering their internal osmotic potentials, and maintaining elastic cells walls. The former is achieved by increasing or decreasing internal solute and metabolite concentrations. Whilst the plants work to achieve these counteracting potentials in response to salinity fluctuations, growth is minimal. Once these adjustments are made, they seem to "recover" and growth increases accordingly (Bäck *et al.*, 1992). These responses have been reported by Geesink and den Hartog for *Bangia fuscopurpurea* (Lobban & Harrison, 1994)

The salinity of standard seawater is approximately 35 ppt (Mosisch, 1993). Most seaweeds grow optimally at salinities around 30 ppt (Luning, 1990). Only three species have been documented to cross the salinity barrier: *Cladophora, Rhizoclonium* and *Bangia* (Lobban & Harrison, 1994). Others, such as *Fucus* and *Enteromorpha* (Raven, 1999), although found in waters of very high or low salinity for those species have not crossed the marine-freshwater divide, but are merely "especially euryhaline" species.

In general, intertidal seaweeds are better able to tolerate salinity fluctuations, and therefore their tolerance range of 10 - 100 ppt is much wider than that of subtidal seaweeds that generally withstand 18 - 52 ppt salinities and are especially sensitive to increased salinities (Russell, 1987). Salinity gradients have been noted to produce populations that have acclimated to their respective habitat's level of salinity. Acclimation, apart from occurring by way of phenotypic change that involves internal osmotic regulation or cell wall elasticity (as discussed above), may also result from the development of genetically diverse populations (ecotypes). Luning for one, discussed ecotypes of brown and red algae from brackish water that grew better in lower salinities even after years of culture, eventually leading him to suggest that independent salinity ecotypes may even be classified as separate species (Mosisch, 1999).

Reed and Russell (1979) studied salinity tolerances of *Enteromorpha intestinalis* populations in the intertidal zone, which they categorized accordingly: maritime pools 100 m from the top of the intertidal zone (almost zero salinity), high-intertidal pools, and open intertidal rock. Plants from high-intertidal pools and maritime pools had broader salinity gradients and tolerances to longer durations of exposure to various salinities. A study of these populations' progeny confirmed that these variations were genetic. Similarly, Mosisch (1999) observed that ecotypic differentiation had occurred in *Caloglossa leprieurii* var. *leprieurii* found along the Brisbane River from the estuary to upstream.

Gessner & Schramm (1971) noted that lowered salinity tends to stunt seaweed growth, resulting in reduced thallus size. Levring explains that diminished salinity most often results in a reduction in photosynthetic activity and an increase in respiration, hence the reduction in size (Levring, 1969). Norton *et al.* (1981) have reviewed the various research efforts conducted on salinity and morphological changes. The most obvious changes are those of branching, blade width, vesicle size and reproductive potential. Often, cell size also changes, with smaller cell sizes encountered in waters of fluctuating salinity. Mosisch (1999) hypothesised that macroalgae respond to fluctuating conditions by developing greater turgor compensation and this is done by reducing cell size, thereby improving their surface area: volume ratio to the prevailing salinity.

Special mention should be made of the Baltic region where the distinct salinity gradient from the Kattegat to the Baltic sea provides an avenue for the study of species distribution and composition (Middelboe *et al.*, 1997), ecotypic variation (Bäck *et al.*, 1992) and reproduction (Serrão *et al.*, 1999) in response to salinity.

Middelboe *et al.* (1997) found salinity strongly correlated with species numbers and composition of benthic macroalgae for the inner part of the Kattegat-Baltic region. Here, the species richness of benthic macroalgae varied from up to 318 species in the most saline waters (23 ppt) to less than 100 species in low salinity waters (5 - 6 ppt). The Bangiophyceae, in agreement with other studies (Gessner & Schramm, 1971), were greatly reduced where salinity was low, leading to the postulation that this taxa have greater salinity requirements than others observed (Chlorophyceae, Tribophyceae, Fucophyceae). In a separate study on Baltic estuaries, Middelboe's assertion that "Salinity influences species richness by defining the proportion of the regional species pool that can potentially grow within the estuary while other factors influence the realized species richness" (Middelboe, 1998) gives us an idea of how great an influence salinity is hypothesised to be on macroalgal distribution.

Bäck *et al.* (1992) researched the possibility of ecotypic differentiation occurring in *Fucus vesiculosus* in the Baltic region, one population coming from Atlantic waters and the other from Baltic waters, where the former live in water of greater salinity. The factor of comparison was growth, on a length and fresh weight basis. The Atlantic population grew best in salinities of 12 - 34 ppt, whilst their Baltic counterparts experienced optimal growth at 6 - 12 ppt, indicating to the authors a great possibility of ecotypic variation. The upper salinity tolerance limit for both was 45 - 68 ppt.

Low salinities have been found to reduce the success of fertilization by decreasing the motility and longevity of gametes and increasing polyspermy in *Fucus vesiculosus* (Serrao, 1999). The former happens when the oogonia take a longer time to release their eggs in low salinity, resulting in the release of over-mature and therefore, less viable eggs. Polyspermy increases because the fast electrical block that impedes the attachment of sperms to an already-fertilised egg becomes less efficient when the concentration of external Na^+ is reduced. In terms of distribution, the populations of *F. vesiculosus* in the northern Baltic were found to live at the limits of their gametes' salinity tolerance.

Salinity also appears to influence reproductive seasonality in environments of fluctuating salinities. Adult *Fucus ceranoides* in an estuarine environment release gametes at the time of the tidal cycle when salinity is highest, resulting in most eggs being fertilised near slack high tide (Brawley, 1992, in Raven, 1999).

2.3.4 Desiccation

Desiccation imposes four possible stresses on intertidal seaweeds: dehydration, salinity, heat, and nutrient stress. The extent of stress is of course contingent on factors such as the duration of emergence, the time of day at which emergence occurs, air humidity, and temperature, and thallus surface area. It is now widely believed that desiccation plays an important role in the horizontal banding pattern in the intertidal zone. This view began with Connell who, in 1961, suggested that whilst biotic factors such as predation and competition govern the lower limits of intertidal species, upper limits are usually determined by physical constraints (Dring & Brown, 1982), in particular physiological stresses associated with emersion (Brown, 1987).

In 1937, Zaneveld established the early view that species from the upper shore lose water at a slower rate than those lower down and are, therefore, better able to survive long periods of emersion (Brown, 1987). This was later reexamined by a series of researchers who proceeded to study the relationship between intertidal zonation and biochemical features (Haas & Hill on fat content, 1933; Berard-Therriault & Cardinal on alginic acid content, 1973, both in Dromgoole, 1980), morphology (Dromgoole, 1979; Jones & Norton, 1979; Brown, 1987), photosynthesis (Quadir *et al.*, 1979), and nutrient uptake (Thomas *et al.*, 1987; Dring & Brown, 1991).

Currently, the strongest view pertaining to desiccation tolerance is that of the morphology school. Dromgoole (1980) states that "there exists no clear relationship between the rate of dehydration of different species under standard conditions and their bathymetric position". Instead, Dromgoole postulates that the rate of water loss is mainly determined by the surface area to volume ratio of the thallus, of which the relationship is a positive one. When algal thalli dry, they shrink, causing a reduction in surface area by 40% for species such as *Fucus* and *Laminaria* (Jones & Norton, 1979) and more than 50% in sheet-like red algae (Kain & Norton, 1990, in Norton, 1991); this shrinkage impedes the further loss of water. Similarly, species that are filamentous (especially those lacking cortication), less finely branched and less bushy exhibit a significantly lower rate of water loss. In terms of shape, Norton (1991) recorded how the near-cylindrical axes of *Ascophyllum* and the stipes of *Fucus* species dry almost three times faster than flattened blades. Dromgoole notes, however, that plants of high surface to volume ratio rehydrate faster upon reimmersion, thus calling for further studies on algal recovery from desiccation.

Dromgoole's call was heeded by researchers (Dring & Brown, 1982; Brown, 1987) who turned their attention to photosynthetic recovery, and who found a significant correlation between the extent of photosynthetic recovery from severe desiccation and vertical position: high intertidal species recovered more completely from desiccation than low intertidal ones. These researchers rejected the (Zaneveld) view that the photosynthetic apparatus of species growing high on the shore is more resistant to water loss than those of species lower down, and subsequently drew the conclusion that the most important correlation with species position is the extent of photosynthetic recovery after desiccation. What remains to be resolved is the exact mechanism by which desiccation tolerant species are able to protect their photosynthetic apparatus during long hours of exposure.

Quadir *et al.* (1979), as a result of their work on the effects of emergence and submergence on the rates of net photosynthesis for three intertidal algae, *Fucus distichus* (high intertidal), *Ulva fenestrata* (mid-intertidal) and *Iridaea cordata* (low intertidal), concluded that relative net photosynthetic activity during emersion could be yet another important factor contributing to intertidal algal zonation. The responses of these species to emergence and submergence, in terms of net photosynthesis, were found to correlate to their positions on the shore. *F. distichus* in the high intertidal zone, for instance, displayed greater maximum gross and net photosynthesis for emerged than submerged thalli, while it was vice versa for *I. cordata*.

Although desiccation also constitutes a nutrient stress by removing intertidal seaweeds from their main source of nutrients, nitrate, ammonium (Thomas *et al.*, 1987) and phosphate (Hurd & Dring, 1991) uptake rates have been observed to increase upon resubmergence, with this recovery rate correlated to the position of a species on the shore:

high intertidal species exhibit a greater enhancement and recovery of nutrient uptake following desiccation then mid- and low-intertidal species (discussed in greater detail in section 2.3.5.3 Effects of nutrient supply at the community level).

2.3.5 Nutrients

2.3.5.1 Nutrient requirements

DeBoer (1981) lists 17 essential elements in seaweeds, but because nitrogen and phosphorus occur at such low concentrations in seawater, they often become limiting nutrients. Recent studies have shown nitrogen to be the element most frequently limiting algal growth, followed by phosphorus (Lobban & Harrison, 1991). The nitrogen ions most easily used by seaweeds are ammonium and nitrate. Although nitrate is usually the most abundant form of organic nitrogen in seawater, many seaweed species show uptake preferences for ammonium (Jones *et al.*, 1996; Naldi & Wheeler, 1999). Some observations have shown ammonium to be responsible in inhibiting the uptake of nitrate in certain species (DeBoer, 1981).

Phosphate is most often taken up by seaweeds as orthophosphate. High concentrations of nitrate (>100 μM) have been shown to inhibit orthophosphate uptake in *Ulva* (Lundberg *et al.*, 1989, reviewed in Lobban & Harrison, 1994). There has been less research on requirements for vitamins. Vitamin B_{12} is regarded as the one most needed by seaweeds; others are thiamine and biotin (reviewed in Lobban & Harrison, 1994).

2.3.5.2 Nutrient availability in seawater

The availability of nutrients is probably the limiting factor in the primary production of most marine systems, except in turbid and eutrophicated coastal waters and estuaries where solar radiation, and not nutrients, often limits production (Nienhuis, 1981). Both nitrogen and phosphorus may be limiting in some areas but in coastal waters, nitrogen may exert primary control (Bunt, 1975).

Nutrients are not uniformly distributed in seawater, but vary both spatially and temporally. These patches of higher nutrient concentrations are caused by local effects such as run-off, up-welling and excretion (Turpin & Harrison, 1979), rock weathering (Newman, 1995), and the decomposition of drifting and beach-cast vegetation (Kirkman & Kendrick, 1997). A number of studies have investigated the relationship between seasonal variations in ambient nutrient concentration, nutrient allocation patterns and physiology in macroalgae. *Fucus serratus* and *Himanthalia elongata* were found to utilise temporal variations in resource availability to satisfy reproductive requirements through two contrasting strategies (Brenchley *et al.*, 1998). The onset of reproduction in *F. serratus* coincided with low nitrogen availability, but peak levels of tissue nitrogen in spring. In *H. elongata*, receptacle initiation coincides with increasing ambient nitrogen in autumn. The receptacle tissue assimilates nitrogen during this phase to sustain growth and development during the spring, when nitrogen levels drop.

The ability of some species of seaweeds to increase their nutrient utilisation during patches of abnormally high nutrient concentrations appears to determine how they fare seasonally, that is, as ruderal or persistent species. Ramus & Venable (1987) found *Ulva curvata* to be capable of utilizing transiently high ammonium concentrations and capable of high growth rates, contributing to its role as a ruderal species (that blooms during these patches but may experience die-back/local extinction at other times).

In contrast, *Codium fragile* is not able to do the same in transiently high ammonium concentrations, thereby contributing to its role as a persistent species with low but uniform growth rate despite seasonal nutrient enrichment. These differences were explained by Ramus & Venable using the form function hypothesis: the ammonium uptake rate for *Ulva* is 20 times greater than that for *Codium*, coincident with the difference in surface area to volume ratio. Likewise, *Chordaria flagelliformis* is able to scavenge efficiently low ambient ammonium concentrations and to sequester rapidly transient ammonium pulses, in comparison to *Fucus distichus*, making it better adapted to short-term fluctuations in nutrient availability (Rosenberg *et al.*, 1984).

The presence of a nutrient gradient has been thought to influence the swimming behaviour and therefore, settlement rates of spores. Spores either swim towards nutrients at concentrations that stimulate their growth or reproduction, or swim away from nutrients at concentrations that inhibit growth or reproduction. This has been verified for *Macrocystis pyrifera* and *Pterygophora californica* (Amsler & Neushul, 1989). The nutrient gradient, however, had no effect on the swimming behaviour and settlement rate of *Ectocarpus siliculosus* spores (Amsler *et al.*, 1999).

Wallentinus (1984) compared the uptake abilities of algae in relation to their morphology and found that in general, short-lived, filamentous, delicately branched or monostromatic forms (e.g. *Cladophora glomerata, Enteromorpha ahlneriana, Ceramium tenuicorne*) had higher uptake rates than long-lived, coarse species with low surface to volume ratios (*Fucus vesiculosus, Furcellaria lumbricalis, Phyllophora truncata*). The hyaline hairs of *Fucus spiralis* and *F. vesiculosus*, function to enhance uptake, and exhibited significantly higher uptake rates than the smooth-surfaced *Pelvetia canaliculata* and *Ascophyllum nodosum* (Hurd & Dring, 1990).

However, ecophysiological traits have not been found to be the single factor of influence on species distribution in all cases. Lotze & Schramm (2000) found that the larger surface area to volume ratio of *Pilayella littoralis* did not translate into greater physiological capacity (uptake kinetics, growth rates and nutrient assimilation) when compared to the sheet-like *Enteromorpha intestinalis*. The authors postulated on the influence of ecological traits such as susceptibility to herbivory as possible factors of significance in determining species distribution in the field.

2.3.5.3 Effects of nutrient supply at the community level

Since nitrate and phosphate concentrations in the sea vary according to season and location, it is important to establish how different nutrient conditions affect seaweeds at the community level. Previous investigations have given us a general picture of how marine primary producers respond to increasing levels of nutrient enrichment, which is summarised as follows (Schramm, 1999):

a) **'Un-eutrophicated' marine or brackish shallow coastal waters**: the dominant primary producers are usually perennial benthic macrophytes, such as seagrasses and other phanerogams on soft bottoms, or long-lived seaweeds on hard substrata, which successfully compete with the faster growing ephemeral benthic or planktonic algae because of their specific nutrient partitioning.

b) **Slight to medium eutrophication**: blooms of opportunistic species occur, in particular fast-growing epiphytic macroalgae and bloom-forming phytoplankton. Phanerogams and perennial macroalgal communities gradually decline. This decline is also associated with changes in community structure and function.

c) **Further eutrophication, towards hypertrophic conditions**: free-floating macroalgae, in particular 'green-tide' forming taxa such as *Ulva* and *Enteromorpha* species alternate with heavy phytoplankton blooms. These dominate and replace the perennial and slow-growing benthic macrophytes.

d) **Hypertrophic conditions**: phytoplankton constitute the dominant primary producers, and benthic macrophytes completely disappear.

The EU-ENVIRONMENT Project entitled Marine Eutrophication and Benthic Macrophytes (EUMAC) was launched in 1993 to study the responses of seaweeds to eutrophication at eight different sites along the European coasts from the Baltic to the Mediterranean. The results of this project show that the changes occurring in eutrophication-stressed seaweed communities may also be attributed to complex interactions of primary and secondary effects during the eutrophication process, and not just eutrophication *per se*. Amongst these are changes in the light climate, oxygen depletion, hydrological and hydrodynamic conditions, and the role of grazers (Schramm, 1999).

Rivers and Peckol (1995) review the conflicting literature concerning the success of *Ulva* species in areas undergoing eutrophication: *Ulva fasciata* showed higher growth rates under sewage-seawater medium than under control conditions (Dhalgalkar, 1986); green algae, including *U. lactuca,* increased in abundance associated with sewage-polluted estuaries (Hardy *et al.*, 1993); *Ulva* species bloomed around a sewer outfall along the coastline of Sydney, South Wales (Borowitzka, 1972). In contrast, Sreeramulu *et al.* (1977) and Subbamariah & Parekh (1966) documented the negative effect of untreated town sewage and nitrogen enrichment on *Ulva* species, respectively.

The ability of a species to store nutrients for use in periods of low nutrient concentration may determine its seasonal abundance and dominance. The summer replacement of *Ulva lactuca* by *Gracilaria tikvahiae* as the dominant species in a shallow, eutrophic embayment, for example, was partly attributed to the latter's capability of higher nitrogen storage, a characteristic that enabled *G. tikvahiae* to continue growing during periods of low ambient nitrogen (Rivers & Peckol, 1995). Similarly, the perennial habit and relatively slow biomass turnover rate of *Fucus distichus* favour an important role for storage of reserve ammonium that are mobilised when conditions for growth become more favourable (Rosenberg & Probyn, 1984). In laboratory culture experiments, Creed *et al.* (1997) found *Fucus serratus* germling growth to be greatly stimulated under high nutrient levels, resulting in a more variable distribution of plant sizes in the population, which tended to be positively skewed. Those grown under low nutrient conditions presented a near-normal size distribution.

Seaweed zonation along the intertidal gradient has also been studied in relation to nutrient uptake. In the study of Thomas *et al.* (1987), the ratio of nitrogen uptake rates in desiccated plants to rates in hydrated plants (controls) was correlated with the position of the species in the intertidal zone. High intertidal species showed up to a two-fold enhancement of nitrate and ammonium uptake following 30% - 50% desiccation, indicating that these macrophytes are adapted to higher levels of desiccation and shorter periods of immersion in seawater containing nutrients. Low intertidal species showed no enhancement of nitrogen uptake following desiccation.

Likewise, Hurd & Dring (1991) found the rate and extent of recovery of phosphate uptake after resubmersion increased with the height on the shore at which each species is typically found, leading to the suggestion of how the recovery of phosphate uptake after periods of desiccation may also be critical in determining the zonation of fucoid algae on the shore.

2.3.6 Biotic Factors

2.3.6.1 Competition

Competition is an important process that often determines patterns of abundance of macroalgal species in shallow coastal environments (Paine, 1990). Two kinds of competition have been recognised: "Exploitative competition" and "interference competition".

"Exploitative competition" involves the race for a limiting resource without direct antagonism between competitors. In an early laboratory study of exploitative interspecific competition, *Ectocarpus siliculosus* appeared to be the one most involved in the competitive interactions between *Ectocarpus siliculosus, Erythrotrichia carnea* and

Ulothrix flacca, meaning that growths of the others were lower in its presence (Russell & Fielding, 1974). Irradiance, salinity and temperature were manipulated to check for each species' competitive optima. What emerged was an indication that competition heightens the sensitivity of a species to its environmental conditions, and reduces the amplitude of those conditions in which the species would normally be vigorous. All three species, for example, suffered a loss of competitive ability in reduced salinity, more so than that observed in monocultures.

More recently, Peckol & Rivers (1995) attempted to explain macroalgal patterns of abundance in relation to interspecific competition of this kind. Their microcosm study was of the competition between the dominant *Cladophora vagabunda* and *Gracilaria tikvahiae* for photon flux density (PFD) during the summer period of peak growth rates and under conditions of nitrogen sufficiency in the eutrophic Waquoit Bay in Massachusetts. PFD becomes a limiting resource during this period because of the increasing phytoplankton abundances that attenuate down-welling PFD. *C. vagabunda* and *G. tikvahiae* had significantly higher growth rates under saturating PFD and consistently showed greater performance when grown in single-species rather than in mixed-species stands. Under limiting conditions, however, the growth rate for *C. vagabunda* was greater in mixed-species stands, whilst the growth rate of *G. tikvahiae* was four times greater than that of *C. vagabunda* in mixed-species stands but at high PFD. It appears that *G. tikvahiae* is better able to compete in high PFD conditions particularly since it possesses greater nutrient uptake abilities, whilst the opposite is true for *C. vagabunda*. In reflection of the results of this study, *G. tikvahiae* was dominant in shallow (< 1 m), well-lit areas whilst *C. vagabunda* displayed dominance in deeper (2 m) regions of the eutrophic bay. Peckols and Rivers cite higher photosynthetic efficiency, tolerance of long-term burial and perennating abilities as the mitigating features of *C. vagabunda* in reduced PFD conditions.

In unialgal stands, plant size and survival appear to be density-dependent, with self-thinning occurring as a population matures. Part of this decline in individual numbers and size is due to intraspecific exploitative competition. Creed *et al.* (1997) studied the link between intraspecific competition at the germling stage with nutrient and light availability. The outcome of intraspecific competition appears to be dependent on the environment the population inhabits and its own developmental stage. With regards to the latter, Creed *et al.* (1997) found nutrient competition between *Fucus serratus* propagules far more intense than competition for light since, at this stage, shading effects are minimal. They found that under low nutrient conditions (filtered seawater medium changed every 15 days), there was no difference in mean plant size between population densities. At high nutrient levels (F/2 enriched seawater medium changed weekly), plants in low-density populations were larger than in high-density ones. Survivorship, however, was not only dependent on nutrients but also on density and light levels. Fewer plants survived in high-density populations in high nutrient conditions, but high-density populations grown under low nutrient conditions seemed to be more susceptible to the harmful effects of strong irradiance, maybe because they were already most nutrient stressed. Creed *et al.* are of the opinion that once beyond the germling stage, the population develops a hierarchy of sizes and this might be when competition for light becomes more significant.

"Interference competition" results from the interactions between organisms that may not relate directly to any limiting resource, for example, the whiplash effect, allelopathy, and epiphytism.

The whiplash effect is most effective in wave-exposed areas where the thalli of large canopy species show continuous wave-induced movement which may clean the adjacent rock surface and their own surface. Kiirikki (1996) offers the whiplash effect of *Fucus vesiculosus* as an explanation for differences in the decline of *Fucus* observed between exposed and sheltered sites in the northern Baltic. Two observations were made: filamentous algal volume increased where the *Fucus* canopy (and thus the whiplash effect) was removed, with up to a five fold increase in the most exposed sites; and where the potential whiplash effect of *F. vesiculosus* was present, the filamentous algae decreased with increasing exposure, most conspicuously for the epilithic algae. Epiphytes also decreased, but only at the most exposed end of the gradient. This indicates that the whiplash effect may provide *F. vesiculosus* with a competitive advantage in areas where wave action keeps the algal vegetation in continuous movement. Likewise, clear space was maintained around *Lessonia* plants on wave-swept shores in Chile by the whiplash effect of the laminae (Santelices & Ojeda, 1984).

In the race for space and light, a species may establish itself on the surface of another, thus forming an epiphyte-basiphyte relationship. Epiphytes may be detrimental to the health of their anchor species by impeding gas and nutrient exchange, reducing the receipt of light, and increasing drag on the fronds. Its cover of dense epiphytes, especially on sunny intertidal shores (Lobban & Harrison, 1994) may however, alleviate desiccation stress on the host species.

Allelopathy is the process of production and release of compounds that inhibit other algae. The characteristic phenolics of the brown *Sargassum*, for example, appear to serve as anti-fouling compounds (Conover & Sieburth, 1964).

Figueiredo *et al.* (1997) studied the effects of the microtopography of the surface and the antifouling ability of crustose coralline alga on the recruitment of epiphytes under different shading conditions. The rough-surfaced *Phymalithon lenormandii* provided a better refuge of *Enteromorpha* and *Ulva* zoospores than for the larger *Fucus* zygotes. However, *Fucus* density was greater on the crusts of the rough (nearly 100 µm protuberances) than on those of the smooth *P. purpureum*. Dead crusts and epoxy replicas of crusts were more infested with epiphytes. Live crusts apparently discourage epiphytes via shedding and allelopathy. There seemed to be an interaction of living crusts with shading, where *Fucus* density was depressed by living crusts but only in shaded areas, for reasons yet unknown.

2.3.6.2 Grazing

Herbivores may be categorised into three groups: fish (large foraging ranges, low densities), urchins (intermediate ranges and densities) and mesograzers (small foraging ranges, but high densities (Lobban & Harrison, 1994).

Evidence suggests that grazing may be the major determinant of the upper limits of vertical distribution of many species of macroalgae. This was found to be true of foliose macroalgae on New South Wales coasts (Underwood & Jernakoff, 1984). These authors also observed that where grazers were active, there were fewer species of algae present. As previously explained by Lubchenco (1978, in Lobban & Harrison, 1994), grazers eliminate the sporeling stages of most foliose and ephemeral algae, leaving perennial, encrusting species.

Fish herbivory appears to explain the geographic gradient of *Sargassum* abundance across the central Great Barrier Reef (McCook, 1996). These fleshy macroalgae are abundant on nearshore reefs and virtually absent from mid-shelf reefs. This gradient correlates well with differences in abundance of herbivorous fish. *Sargassum siliquosum* plants transplanted to the mid-shelf survived and thrived only if protected in herbivore exclusion cages.

Worm and Chapman (1998) demonstrated that growth of established germlings (2 mm size) and juveniles (6 cm size) of *Fucus evanescens* in Nova Scotia is depressed independently by the presence of grazers and by the presence of *Chondrus* canopy. Grazing, however, had a greater relative effect than competition at the low shore site. Still, the mean net growth rate of *F. evanescens* was depressed by more than one order of magnitude when *Chondrus* canopy was present, presumably by low light intensity in the understorey and the removal of *Fucus* germlings from *Chondrus* crust by surface sloughing. However, neither *Chondrus* presence nor grazing alone excluded established *Fucus* germlings. Only when both factors were combined was there a significant loss in

Fucus weight, implying that *Fucus* is unable to compensate for losses to grazing only when shaded by *Chondrus*. The results of this study contradict those of Lubchenco (1980) who found that *Chondrus* crust alone can completely inhibit *Fucus* colonisation regardless of the presence of grazers. Worm and Chapman attribute this difference to Lubchenco's non-replicated experimental design that did not allow a sampling of the range of natural variability in *Fucus* recruitment. However, in a later study, Lubchenco (1982) concluded that the absence of fucoids from mid-littoral, protected pools in New England was due to the joint action of herbivores (*Littorina littorea, L. obtusata* and *Acmaea testudinalis*) and algal competitors (*Chondrus crispus, Ulva lactuca, Rhizoclonium tortuosum, Polysiphonia* species and *Dumontia incrassata*).

Knowledge of the diet preferences of mesoherbivores may be applied in mariculture. Brawley & Fei (1987) identified the amphipod *Pontogeneia rostrata* as the best choice amongst the studied species as a control for epiphytes on *Gracilaria asiatica* in an unbarricaded mariculture farm. This amphipod eats up established epiphytes such as *Enteromorpha linza*. The other amphipods, *Caprella irregularis* and *Jassa falcata*, are second-best choices because they prevent epiphytism by removing spores and young sporelings from the surfaces of macrophytes but are of little use in elimination of established epiphytes. *C. irregularis* moreover, ate small pieces of *G. asiatica* in its epiphyte-grazing process, although it allowed net growth in most cases. Other amphipod species that display preferences for epiphytes are *Ampithoe valida* for *Porphyra* > *Ulva* > *Gracilaria* (Nicotri, 1980) and *Ampithoe mea* for diatom-covered *Sargassum muticum* (Norton & Benson, 1983).