A SYSTEM DYNAMICS APPROACH TOWARDS ASSESSING *POSIDONIA OCEANICA* HABITAT

A dissertation presented in part fulfilment of the requirements for the Degree of Master of Science in Sustainable Environmental Resource Management/ Master of Science in Integrated Science and Technology

by

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ABSTRACT

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A System Dynamics Approach towards Assessing *Posidonia Oceanica* Habitat

Posidonia oceanica habitat is one of the most important coastal shallow water habitats in the Mediterranean region and provides highly valuable and varied ecological services such as supporting high species diversity, protecting against coastal erosion, and sequestering carbon. *Posidonia oceanica* habitat is declining as a result of a multitude of converging pressures, both natural and anthropogenic, in the coastal zone. The slow rate at which *Posidonia oceanica* meadows undergo recovery, in contrast to the rapid dynamics that bring about their decline, is consequently of great concern. The need to proactively manage this valuable resource must be met in order that the consequences of *Posidonia oceanica* habitat decline are not felt by social, economic and biological activities in the Mediterranean.

This work identifies system dynamics modelling as an appropriate means of integrating the various factors relevant to *Posidonia oceanica* habitat in the coastal zone. The dissertation aims to synthesise knowledge about *Posidonia oceanica* habitat into a working model for a generic, hypothetical *Posidonia oceanica* meadow. The model's purpose is to mimic the interactions of *Posidonia oceanica* growth with the algal epiphytes and algal grazers that occupy the meadow. These interactions are fundamental to the way in which *Posidonia oceanica* meadows contribute towards enhanced species diversity in the coastal zone.

The System for Assessing *Posidonia oceanica* Habitat developed and described in this work is a first step towards a model capable of revealing the natural properties of *P. oceanica* habitat. The System for Assessing *Posidonia oceanica* Habitat is also described and validated fit for purpose in this dissertation. The System for Assessing *Posidonia oceanica* Habitat fulfils important purposes such as synthesising various data types into a logically consistent and defendable structure, and simulating responses typical of natural *Posidonia oceanica* habitat. The System for Assessing *Posidonia oceanica* Habitat may be improved and adapted, by future research efforts, to a tool that may be used to complement coastal management and decision making. Among the main suggestions made to direct future research efforts are: altering the time scale from a yearly to monthly or even daily time unit; including nutrient, water movement and temperature variables and dynamics; and modelling below ground, as well as above ground biomass compartments for *Posidonia oceanica*. Furthermore, future research work should adapt this model to encompass broad-scale, human-related dynamics in order to confirm its use in informing coastal management decisions.

Keywords: *Posidonia oceanica*, System Dynamics modelling, SAPOH

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DECLARATION OF AUTHENTICITY

I, the undersigned declare that this dissertation is an original work done by myself as a result of my own research. Any conclusions, statements, suggestions or assumptions are mine unless otherwise stated.

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JUSTINE SCHEMBRI

TO MY SON,

JACK

"Twenty years from now you will be more disappointed
by the things you didn't do than by the ones you did do.
So throw off the bowlines. Sail away from the safe harbour.
Catch the trade winds in your sails. Explore. Dream. Discover."

MARK TWAIN

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To Jack, my son, for filling every day with laughter and happiness, for motivating me and inspiring me, and for loving me unconditionally.

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1 INTRODUCTION

1.1 BACKGROUND

1.1.1 PREAMBLE

This research study explores the use of system dynamics as a way of modelling and understanding changes in *Posidonia oceanica* habitat, the dominant seagrass habitat in the Mediterranean and, arguably, the most important coastal shallow water habitat in the region. The motivation behind this study is that while *P. oceanica* habitat offers varied and highly valuable services, it is undergoing decline in various areas of the Mediterranean. The decline is for the most part attributed to increased pressure derived from anthropogenic activities in the Mediterranean coastal zone, coupled with poor planning and management. To avoid unintended and undesirable consequences, a system dynamics approach was identified to help address and understand the complex dynamics between humans and natural systems in the coastal zone.

The present work provides a platform upon which further model development may be made, and constitutes an important first step towards creating a useful management tool for valuable *P. oceanica* resources in the Mediterranean. Furthermore, the system dynamics framework featured within this dissertation sets the work apart as unique.

In order to set the scene for the present work, a background to seagrasses and the seagrass species *Posidonia oceanica* is given in the next section. The stressors relevant to the habitat and the current management initiatives towards reducing and/or eliminating these stressors are also discussed.

1.1.2 SEAGRASS HABITAT

Seagrasses are marine flowering plants with terrestrial ancestors. The earliest fossils related to seagrasses can be traced to the Cretaceous, around 100 million years ago (Phillips & Menez, 1988; Beer & Koch, 1996). Seagrass species are the only terrestrial plants that have successfully colonised the marine environment (Hemminga & Duarte, 2000).

Despite their terrestrial origin, seagrasses are well adapted to life in the marine environment and grow close to the shore, in shallow water at water depths less than 50m (Duarte C. M., 1991). The some 60 species of seagrass comprise less than 0.02% of the total angiosperm flora (Green & Short, 2003) and constitute a relatively small group when compared to other marine groups (Hemminga & Duarte, 2000). All seagrass species are rhizomatous, clonal plants that occupy space via the repeated production of shoots, leaves and roots as a result of their rhizome extension (Marba & Duarte, 1998). Asexual propagation generally constitutes the main proliferation mechanism for seagrasses, although some species such as *Zostera marina* (Olesen, 1999) and *Enhalus acoroides* (Duarte, Uri, Agawin, Fortes, Vermaat, & Marba, 1997) have a high rate of sexual reproduction.

The small number of seagrass species is by no means proportional to their abundance or their ecological and economic importance. Seagrass input to primary productivity in coastal environments, having been much overlooked in the past, was first assessed during the 1970s (Mann, 1973). Their high growth and production rates were observed to compare to those that characterize tropical forests, and shown to exceed those of temperate forests (Ferguson et al., 1980; as in Pergent et al., 1997). In effect, seagrass meadows find their place amongst the world's most productive ecosystems and rival even crops of wheat, corn and sugar cane (Waycott, et al., 2009).

The importance of the ecological functions and services provided by underwater seagrass meadows is well recognized, as is their economic value. In their attempt to designate an economic value to the world's ecological systems and natural stocks, Costanza et al. (1997) determined an annual value of US$ 3.8 trillion for the services provided by seagrasses worldwide. While the services provided by such a habitat are various, the estimate by

Costanza et al. (1997) solely addresses nutrient cycling and raw material provision. It is therefore very likely that the value of seagrass systems exceeds the estimate quoted by these authors.

Seagrass material was traditionally valued by coastal communities for various purposes, including direct use. Eelgrass, *Zostera marina*, constituted an important part of traditional Seri diet and culture. The Seri Indians, who inhabited the Gulf of California, harvested carbohydrate-rich seeds of *Zostera marina* in the spring and used them to make flour, which was then used in a variety of dishes (Felger & Moser, 1973). Although primarily a food source, the Seri also used seagrass for other purposes such as thatching houses and roofs, treating diarrhoea and making children's toys. In the Philippines, the seeds of the tropical seagrass *Enhalus acoroides* were also a traditional staple food source and are still used nowadays as a source of food for coastal populations. The nutritional value of the flour derived from *Enhalus* seeds, while comparable to that of wheat and rice flour in carbohydrate and protein content, is superior in terms of calcium, iron and phosphorus content (Montano, Bonifacio, & Rumbaoa, 1999). There are further known uses of seagrass material; for example old sources refer to its widespread use as stuffing material for mattresses and pillows; packing material; soil conditioner, mulch, and compost; fodder; and insulation for sound and temperature (Fortes, 1990; Hemminga & Duarte, 2000).

The services that seagrass meadows provide to the functioning of coastal zone systems form the basis underlying the high ecological and economical values of this natural resource. Seagrasses modify the surrounding environment, a feat that commonly earns them the term of ecosystem engineer (Coleman & Williams, 2002; Duarte C. M., 2000; Jones, Lawton, & Shachak, 1997). With a leaf canopy that traps particles (Hendriks, Sintes, Bouma, & Duarte, 2008) and minimises the resuspension of sediment (Fonseca & Fisher, 1986), and a mesh of roots and rhizomes to bind it (Dauby, et al., 1995), seagrass meadows stabilise and consolidate mobile substrata, preventing the movement of sediments. Furthermore, as the hydrodynamics of seawater are modified by the seagrass canopy (Bouma, et al., 2005; Fonseca, Zieman, Thayer, & Fisher, 1983; Gambi, Nowell, & Jumars, 1990), currents are baffled, wave action is dampened and the shoreline is further

buffered against erosive elements (Orth, 1977). Once seagrass material has been beach-cast, it may also stabilise the shore by trapping sand and inducing dune formation (De Falco, Simeone, & Baroli, 2008; Hemminga & Duarte, 2000). The role of seagrasses in coastal protection is most apparent once a decline or loss is evident in a particular area (Christiansen, Christoffersen, Dalsgaard, & Nornberg, 1981; Orth, 1975; Wilson, 1949).

The sediment stability that results from seagrass colonisation is not only relevant to shoreline protection but has also been repeatedly identified as an important factor in determining the abundance and diversity of benthic fauna (Gray, 1974; Rhoads, 1974; Sanders, 1968; Snelgrove & Butman, 1994). The reduced particle loads within and around seagrass meadows create a favourable environment for associated suspension feeders, as well as nearby coral reefs, whose feeding apparatus would not function as efficiently in turbid conditions (Hinrichsen, 1997). By providing protection against the turbulent hydrodynamic regimes that characterise many nearshore environments, seagrass meadows increase the probability of successful recruitment for many benthic biota (Orth, 1977). As the seagrass canopy reduces the flow of water at its edges, larger particles settle out of the water column, while finer, lighter particles remain in suspension and are carried into the meadow. This makes for the accumulation of fine particles in the interior of the seagrass bed (Bologna & Heck Jr, 2002) and explains observations, such as those made by Orth (1977) of the presence of increasingly fine sediments in seagrass beds compared to nearby bare substrata. Many marine larvae also behave as passive particles because the scales of horizontal water motion are so much greater than their swimming capabilities (Butman, 1987; Eckman, 1990). Thus, just as seagrass beds act as sediment traps, they may also serve to 'trap' species whose larvae behave in this way. The success rate of settling larvae is further increased by the presence of a stable substratum for attachment, that is, the seagrass leaf canopy and its root-rhizome network; this is a scarce resource in unconsolidated bottoms.

Overall, seagrasses provide habitat for a variety of organisms unable to occupy unvegetated areas. In turn, the supplemental structures that associated organisms themselves create (e.g. macroalgae, colonial bryozoans, bivalves) further contribute toward the increased number

and complexity of distinct microhabitats within the meadow (Bell, Hall, & Robbins, 1995; Bologna & Heck Jr, 2002; Valentine & Heck Jr, 1993), enabling an even greater abundance and variety of species to settle and colonise.

A frequently cited measure of seagrass habitat value is its 'nursery function' (Heck Jr, Hays, & Orth, 2003); a concept derived for the most part from various studies reporting the presence of higher densities of juvenile animals in seagrass, in comparison to adjacent unvegetated areas (Beck, et al., 2001; Orth & van Montfrans, 1987). Heck Jr, Hays, & Orth (2003) evaluate the extent to which seagrass habitats fulfil the function of a nursery, not simply by having a higher density of juveniles present within, but also by bringing about their increased growth and survival. Indeed, juvenile survival may be promoted by the increased refuge potential that is imparted by the three-dimensional structure of the meadow, when compared to the often two-dimensional surface of nearby bare substrata (Borum, Duarte, Krause-Jensen, & Greve, 2004). The literature review conducted by Heck Jr, Hays, & Orth (2003) confirmed findings from studies which showed that juvenile growth was also significantly greater in seagrass habitat; again this was attributed to the meadow's structural complexity as opposed to the lack thereof in unvegetated habitat. By providing additional protection against predators, meadow structure may allow more time for feeding as well as more substrate for food resources to grow on. Food resources may also be trapped by the structure of the canopy by mechanisms similar to those for other particulate matter, as explained previously. In conclusion, there is substantial evidence to support the assertion that seagrass meadows serve as key nursery areas, as well key habitats in the life cycle of many organisms other than juveniles. Among the host of marine life present in seagrass meadows we find highly important commercial fish and shellfish species, migrating birds and others (Hinrichsen, 1997).

Seagrasses produce large quantities of organic carbon and have a significant role to play in the cycling of global carbon and other nutrients (Smith, 1981). Much of the biomass produced by seagrasses ends up as detritus that is buried in the sediment, making seagrass meadows hotspots for carbon sequestration in the ocean (Duarte, Middelburg, & Caraco, 2005). While seagrass primary production is a mere 1% of total primary production in the

oceans, seagrasses are responsible for about 12% of total carbon stored in ocean sediments (Duarte & Cebrian, 1996).

The high rate of biomass production by seagrasses implies an equally high rate of oxygen production, a photosynthetic by-product which, when released, becomes available for other marine life (Borum, Duarte, Krause-Jensen, & Greve, 2004). As the gross photosynthesis of seagrass leaves exceeds the respiratory demands of the plants by almost an order of magnitude (Touchette & Burkholder, 2000), oxygen is often released to the water column and sediment. The largest release of oxygen from seagrasses is from the leaves to the water column, during periods of high light intensity and photosynthesis. Oxygen is, on the other hand, continuously released from roots and rhizomes to the anoxic sediment, during both light and dark phases (Borum, Sand-Jensen, Binzer, Pedersen, & Greve, 2006). The enhanced mineralization of organic matter within sediments below a seagrass meadow, as a result of oxygen loss by seagrass roots and rhizomes, has been confirmed through research studies (Sand-Jensen, Prahl, & Stokholm, 1982). Other important implications of seagrass oxygen release to the sediments include enhanced redox processes such as sulfide reoxidation (Lee & Dunton, 2000), and nitrification and denitrification (Caffrey & Kemp, 1992). Seagrasses therefore do more than oxygenate surrounding waters; they constantly modify the sediments they inhabit, enhancing their own production and that of sediment dwelling organisms, which are also linked to nutrient cycling

Nitrogen is another nutrient that enters significantly into marine sediments via seagrasses. In contrast to terrestrial plants, seagrasses have the ability to take up inorganic nitrogen through both leaf and root tissues which means they are able to exploit the water column as well as the sediments for nitrogen (Lee & Dunton, 1999; Pedersen, Paling, & Walker, 1997; Terrados & Williams, 1997). Besides taking up dissolved inorganic ammonium and nitrate, seagrasses also support microbial nitrogen fixation, a process that occurs on the leaves and in the sediment of seagrasses (Bethoux & Copin-Montegut, 1986). Nitrogen-fixing bacteria in the leaf canopy and sediments of seagrass beds form a diverse community, including photoautotrophic heterocystous cyanobacteria and heterotrophic nitrogen-fixing bacteria (Pereg, Lipkin, & Sar, 1994). While studies balancing the losses and gains of nitrogen are

few, results obtained by Kenworthy, Zieman, & Thayer (1982) confirm a net increase in total sediment nitrogen for areas colonised by seagrasses *Zostera marina* and *Halodule wrightii*, while Risgaard-Petersen, et al., (1998) confirm this for a Danish *Zostera marina* meadow.   In summary, the various processes and dynamics that operate in seagrass meadows lead toward an accumulation of carbon and nitrogen in nearby sediments, making seagrasses central players in yet another important process, that of the biogeochemical cycling of essential elements.

1.1.3 *POSIDONIA OCEANICA*

Of the 60 or so seagrass species that exist worldwide, four are native to the Mediterranean (Borum, Duarte, Krause-Jensen, & Greve, 2004); these are *Zostera marina* (eelgrass), *Zostera noltii* (dwarf eelgrass), *Cymodocea nodosa* (seahorse grass) and *Posidonia oceanica* (Neptune grass). Classically considered one of the climax communities of the Mediterranean coast (Duarte, 1991), *P. oceanica's* distribution is completely restricted to the Mediterranean basin (Diaz Almela & Duarte, 2008), where it forms dense, extensive, monospecific meadows which extend to a maximum water depth of 45m (Procaccini, et al., 2003).

Posidonia oceanica belongs to the monogeneric family Posidoniaceae which, in turn, forms part of the monocot order Alismatales (Bremer, et al., 2003), and contains the single genus, *Posidonia*. The evolutionary history of the genus *Posidonia* can be traced back to the Cretaceous. The genus encompasses *P. oceanica,* as well as eight other species found off the temperate coasts of Southern Australia (den Hartog & Kuo, 2006). While 5% of the Mediterranean basin is considered inhabitable by *P. oceanica* (within the 0-50m depth range), its meadows are estimated to occupy a total area of around 1-2%, or 37,500 km^2 ± 12,500km^2 (Pergent, Rico-Raimondino, & Pergent-Martini, 1997).

Posidonia oceanica stands may occur in patches of various sizes or in continuous meadows (Borg, Attrill, Rowden, Schembri, & Jones, 2005; Colantoni, Gallignanii, Fresi, & Cinelli, 1982). Other growth patterns characteristic of this species of seagrass include 'collines'

(hillock-like stands generally surrounded by sand) and barrier reefs (Boudouresque, et al., 2006; Ribera, Coloreu, Rodriguez-Prieto, & Ballesteros, 1997). Long persistence, slow vegetative growth, infrequent sexual reproduction and low genetic variability are all typical characteristics of *P. oceanica* meadows (Mateo, Romero, Perez, Littler, & Littler, 1997; Procaccini & Mazzella, 1998). In their Mediterranean-wide study of *P. oceanica* population genetic structure, Procaccini, Ruggiero, & Orsini, (2002) analysed six polymorphic microsatellite loci and determined the possibility of encountering a different genotype of the seagrass to be a mere 11%. The limited number of genotypes in existence confirms that *P. oceanica* meadows in the Mediterranean form a mosaic of large and ancient clones (Procaccini, et al., 2003).

Posidonia oceanica habitat provides all of the previously discussed ecological services that are common to all seagrasses. *P. oceanica* meadows are central to the support of commercial fisheries (Francour, 1997), nutrient cycling (Herbert, 1999) and carbon sequestration (Duarte, Middelburg, & Caraco, 2004) in the Mediterranean region. The habitat's roles of sediment stabilization and protection against erosion (Gacia & Duarte, 2001) are equally important and valuable. There is much more to be said about the features and processes that concern this valuable habitat, which is the focus of the present work. For this reason, additional detail on the dynamics that concern *P. oceanica* habitat is provided in a later section. Figure 1.1 summarises the above discussion and illustrates the many ways in which *P. oceanica* habitat is linked to various other components in the surrounding coastal ecosystem.
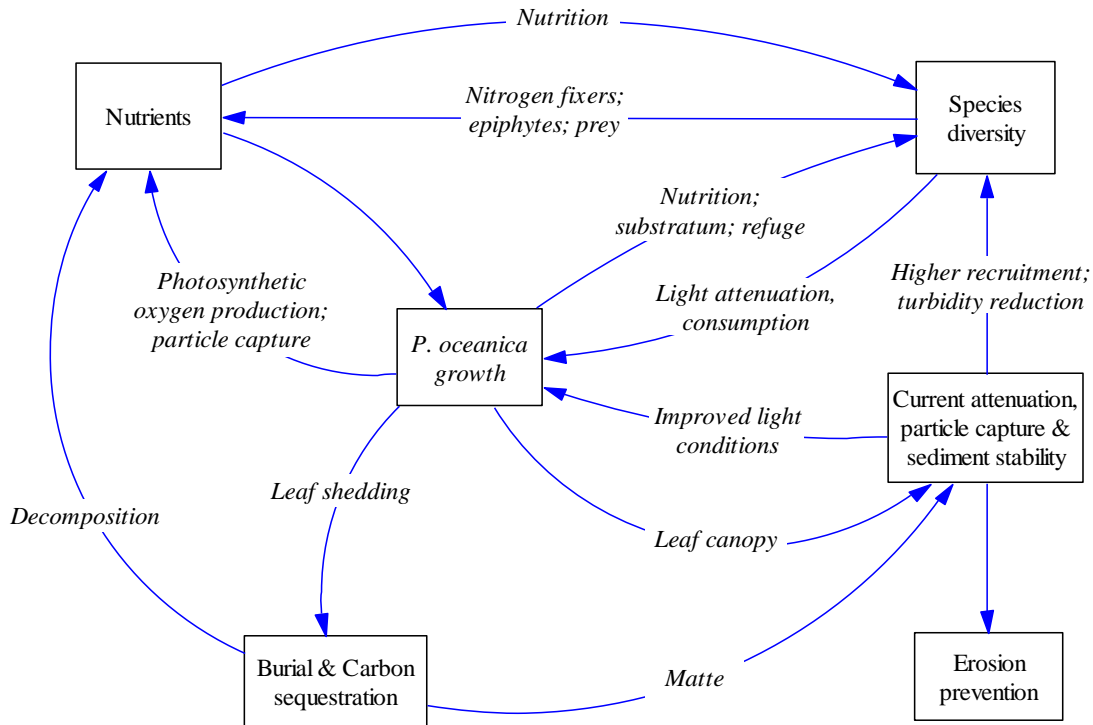
Figure 1.1 Some important links between *Posidonia oceanica* and the surrounding ecosystem.

1.2 TOPIC STATEMENT

1.2.1 SEAGRASS DECLINE

Coastal regions have been frequently identified as areas in which human activity is highly concentrated. According to the Millenium Ecosystem Assessment, 40% of the world's human population is concentrated on a mere 5% of inhabited land space, that is, in coastal regions. This implies that coastal areas support a disproportionate amount of infrastructure supporting industry, transportation and trade, energy generation, tourism and more (Olsen, 2009). The numerous human activities that are concentrated in the coastal zone impact the ecology of habitats located there, both directly and indirectly. The dilemma is adequately summarised by John Clark (1997) who identifies coastal areas as the place where storms hit, where boats make their landfall, where agency authority changes abruptly, where waterfronts are developed and where some of the richest habitats are situated. Moreover,

coastal zones are also where terrestrial-type planning and resource management programs are at their weakest (Clark J. R., 1997) Safeguarding the complex, interlinked ecosystems present at the coast while modulating human activity where it is most concentrated is very likely to be the world's most challenging management job!

Seagrass meadows worldwide are among the natural systems currently suffering decline as a result of converging pressures at the coast (Hall, Durako, & Fourqurean, 1999; Marba, Duarte, Cebrian, Gallegos, Olesen, & Sand-Jensen, 1996; Short & Wyllie-Echeverria, 1996; Stankelis, Naylor, & Boynton, 2003; Walker, Kendrick, & McComb, 2006; Waycott, et al., 2009). Up to the year 2000, large-scale declines were identified at a minimum of 40 locations and documented. At least 24 different species of seagrass have been identified to be in decline, and in more than 70% of the cases, human-induced disturbances were held responsible (Hemminga & Duarte, 2000).   While variability as a result of natural environmental factors does exist in such systems (Borg, Rowden, Attrill, Schembri, & Jones, 2009; Kendrick, Eckersley, & Walker, 1999), multiple human stressors, including dredging, fishing and anchoring on seagrass beds, eutrophication, coastal development, hypersalinisation, siltation and poor water clarity, habitat conversion, and climate change are becoming a major source of change to seagrass habitats worldwide (Duarte C. M., 2002).

Mechanical damage to seagrass habitat, such as that resulting from boat anchoring, directly leads to loss of vegetation, decreasing the meadow's physical integrity. In places where small boats are numerous, the cumulative effect of boat moorings and propeller scars may result in a considerable loss of vegetation as shoots and rhizomes are damaged, or even completely removed from the substratum (Walker, Lukatelich, Bastyan, & McComb, 1989). Fishing practices that disturb the bottom, such as trawling and dredging, similarly have direct, harmful effects. Use of dredge gear by mussel and cockle fisheries in the Dutch Wadden sea has earned them partial blame for the near extinction of eelgrass (*Zostera marina*) and its inability to re-establish in some areas (De Jonge & De Jong, 1992). Scallop harvest-related damage to eelgrass meadows in North Carolina was also documented by Fonseca, Thayer, & Chester (1984). Dredging to deepen and maintain

navigation routes and harbour entrances, as well as dredging for marine aggregates, have similar recognised effects (Erftmemeijer & Robin Lewis III, 2006). The consequences of such losses of seagrass habitat are known to be both serious and costly. As Thorhaug (1981) reveals, one dredge-and-fill operation for enlargement of a boat harbour destroyed a fifth of the seagrass bed present in Boca Ciega Bay, Florida. Furthermore, the unintended consequence of the intervention was that number of fish in the area was diminished by a total of four-fifths and cost almost $1.4 million in lost catches for local fishermen (Thorhaug, 1981)

Other than direct mechanical damage, activities disturbing bottom sediments may also affect seagrass meadow health by altering sedimentary regimes which may lead to seagrass burial, or erosion of the sediment under seagrass beds (MacInnis-Ng as in Erftmemeijer & Robin Lewis III, 2006; Pasqualini, Pergent-Martini, & Pergent, 1999). Seagrass burial may also derive from land-based erosion, a consequence of changes in land use leading to increased erosion rates and silt export from water sheds (Kirkman & Walker, 1989). Steep slopes coupled with high population and economic growth are fuelling deforestation in South-East Asia and making harmful siltation effects on seagrass habitats present there particularly severe (Fortes, 1990). Burial affects seagrasses negatively by reducing light availability to photosynthetic tissue, reducing oxygen diffusion to the roots and rhizomes, and preventing deeply buried meristems from producing new leaves (Vermaat, 1997). Sedimentation may indeed serve as a positive stimulus if it brings with it new nutrients (Marba, Gallegos, Merino, & Duarte, 1994), and its magnitude does not exceed the survival capacity of the seagrass species. Using *Cymodocea nodosa*, Marba and Duarte (1994) demonstrate that there most certainly are limits to the levels of sedimentation seagrasses can tolerate; in their experiments, no seedlings survive burial greater than 7cm. Vermaat (1997) reports a maximum sedimentation rate of up to 13 cm year^{-1} as a maximum threshold of what seagrasses of the genera *Cymodocea*, *Halodule*, *Posidonia*, *Syringodium*, *Thalassodendron*, and *Thalassia* can endure. Large inputs of silt and sediment material to coastal waters typically result in increased light attenuation and a deterioration of the underwater light climate for seagrasses (Hemminga & Duarte, 2000). Since seagrasses are photosynthetic organisms, one of the main requirements for their growth is adequate light,

usually an underwater irradiance of around 11% of that present at the water surface (Duarte C. M., 1991). Sedimentation events therefore, compromise seagrass ability to photosynthesise via reductions in light availability and water transparency (Vermaat, 1997). Suspended material derived from disturbed soft sediment bottoms has also been shown to have harmful effects on seagrasses via this mechanism of light reduction (Erftmemeijer & Robin Lewis III, 2006).

Light reduction features, once again, as the single most important mechanism leading to seagrass decline in waters subject to eutrophication (Hemminga & Duarte, 2000). Most eutrophication in coastal environments is caused by increased nitrogen and phosphorus input. The problem stems mainly from the intense use of fertilisers in agriculture, and sewage contamination, which lead to heightened nutrient loads in runoff to the coast (Nixon, 1995). The most common means by which light is reduced, as a result of nutrient over-enrichment, is the stimulation of high-biomass algal growth, specifically phytoplankton and more commonly epiphytes and macroalgae, that are considered superior competitors for light relative to seagrasses (Borum J., 1996; Burkholder, Tomasko, & Touchette, 2007; Dennison, et al., 1993). Light reduction due to attenuation in the water column and shadowing on seagrass blades limits seagrass ability to photosynthesize and in extreme cases may even lead to death of the plants that constitute the meadows altogether (Den Hartog, 1994; Short & Wyllie-Echeverria, 1996).

Explaining seagrass decline following eutrophication is not based on the sole response of marine alga, but also by the direct physiological response of seagrasses themselves. Evidence exists to show that highly elevated concentrations of nitrate and ammonium may be directly toxic to seagrasses (Burkholder, Mason, & Glasgow Jr, 1992; Van Katwijk, Schmitz, Gasseling, & Van Avesaath, 1999). Furthermore, once seagrass resilience has been conquered, a cascade of processes that accelerate further decline is evident (Duarte C. M., 1995). Other than the decreased availability of light, indirect effects that serve to aggravate the decline span from sediment resuspension due to loss of vegetation, sediment anoxia, and increased grazing pressures to increased system respiration and more. The response of *Thalassia testudinum* in Sarasota Bay, Florida to nutrient enriched waters,

before the deteriorated water quality was even detected by monitoring programmes at the site, demonstrates the sensitivity with which seagrasses respond to over-enriched waters (Tomasko, Dawes, & Hall, 1996). Other human-sourced pressures, such as increased temperatures and rising sea and CO_2 levels from global warming (Beer & Koch, 1996), exotic species introductions (Meinesz, De Vaugelas, Hesse, & Mari, 1993; Ruiz, Fofonoff, Carlton, Wonham, & Hines, 2000) and trophic imbalances leading to over- or under-grazing (Heck Jr. & Valentine, 2006), may all interact with the above mentioned threats to to make global seagrass decline a reality (Orth, et al., 2006). As seagrass habitat becomes increasingly fragmented under influence of the human dominated dynamics at the coast, decreasing population size and gene flow between meadows further compromises their resilience and adaptability (Procaccini, Ruggiero, & Orsini, 2002).

In conclusion, seagrass systems are being stretched thin, and predictions for the future of seagrass-dominated coastal systems are not hopeful as yet (Duarte C. M., 2002; Orth, et al., 2006). The handful of documented seagrass recoveries (Orth, Luckenbach, Marion, Moore, & Wilcox, 2006; Preen, Lee Long, & Coles, 1995) demonstrates the potential success of some management efforts. Given the importance of seagrasses to humans (Costanza, et al., 1997; Larkum, Orth, & Duarte, 2006), the preservation of seagrasses and their ecosystem services should be a worldwide priority, an effort that would provide benefits to all aspects of coastal ecosystems.

1.2.2 *POSIDONIA* OCEANIA DECLINE

The Mediterranean Sea is currently experiencing a "basin-wide urbanisation process", and more than two-thirds of the Mediterranean coastline is now urbanised (Benoit & Comeau, 2005). Associated with increasing coastal urbanisation is an escalating stress on *Posidonia oceanica* meadows present in the Mediterranean infralittoral; many meadows have already disappeared or been altered (Diaz Almela & Duarte, 2008). *P. oceanica* is under a great deal of pressure to survive in an almost enclosed sea, surrounded by countries that rely heavily on its services for fishing and tourism. In order to appreciate the magnitude of the risks associated with the decline of *P. oceanica*, one may consider a common method of

rating the severity of any impact on biodiversity. Using this measure involves evaluating the time that is needed for a decline to be reversed. While most pollution events, including oil spills, lie in the range of one to thirty years, and the near elimination of most long living species is in the range of ten years to one century, the destruction of *Posidonia oceanica* meadows in the Mediterranean sea would require one century to one millennium to be reversed (Boudouresque, Cadiou, & Le Direach, 2005). The only greater causes of concern are the irreversible impacts of species introductions and extinctions, and coastal development (Meinesz, Lefevre, & Astier, 1991).

An examination of 39 studies in 135 sites in the Mediterranean indicates that 46% of the *P. oceanica* meadows investigated have experienced some form of decline, while 20% have severely regressed since the 1970s (Diaz Almela & Duarte, 2008). Studies provide evidence of *P. oceanica* meadow regression in many areas of the Mediterranean. Dramatic losses of *P. oceanica* habitat have been documented in the Istrian Gulf (northern Adriactic Sea) by Zvodnik and Jaklin (1990). Most meadows previously present in the 1930s no longer exist nowadays (Krause-Jensen, Diaz Almela, Cunha, & Greve, 2004). Peirano et al (2005) record a state of regression for eight *P. oceanica* meadows in the shallow, coastal waters of Liguria, Italy. The authors attribute the deteriorating state of the habitat to local factors; in particular, the disorderly coastal development initiated in the Ligurian region during the 1960s. Among the local stressors that originated from the Ligurian coast are coastal construction, land reclamation, beach-replenishment projects, sewage outfalls and other disturbances (Peirano, Damasso, Montefalcone, Morri, & Bianchi, 2005). In Toulon, France, the construction of artificial beaches on top of 16 ha of reef-forming *P. oceanica* meadows took place in Rade de Vignettes. The destruction of a further 199 ha of the *P. oceanica* habitat followed as did the deterioration of an additional 37 ha by 1978 due to siltation (Nodot et al. 1978 as cited by Krause-Jensen, Diaz Almela, Cunha, & Greve, 2004). Regression is also evident in some of the coastal areas of the Maltese Islands, which Borg et al. (2009) allude to human-sourced pressures operating at the local scale (Borg, Rowden, Attrill, Schembri, & Jones, 2009).

Basin-wide factors are also held responsible for the deteriorating condition of *P. oceanica* habitat in the Mediterranean. Using long-term climate records, Marba & Duarte (1997) identify coupling between seagrass growth and climate variability in a total of 15 *P. oceanica* meadows in the Spanish Mediterranean. They attribute this regression to global factors such as climate change, rather than to local factors. Shoot mortality exceeds recruitment in 60% of the 25 Spanish Mediterranean meadows investigated by Marba et al. (2005), showing a prevalence of declining populations and a median annual exponential decline rate of 5% per year. To give some perspective, this annual decline rate, as well as that of seagrasses worldwide (2-5% according to Duarte, Dennison, Orth and Carruthers 2008), is a great deal more rapid than the global loss rate of tropical forests, estimated at 0.5% per year (Achard, et al., 2002).

Any losses of *P. oceanica* habitat are rendered even more consequential when one considers the slow growth rate of the plant, (1-6cm per year) (Mateo, Romero, Perez, Littler, & Littler, 1997). Meinesz and Lefevre (1984) illustrate this by describing a dense meadow in Rade de Villefranche, France, which suffered an exploded bomb in 1943 during the Second World War. The explosion removed a circular area, 80m in diameter, from the meadow, which was to remain perfectly distinguishable forty years later. As the crater is surrounded by dense and healthy meadows, these have migrated slightly inwards over the years, at an estimated linear growth of 3.4cm per year. Should rates of colonisation persevere, a period as long as 120 to 150 years should see this area completely recovered (Meinesz & Lefevre, 1984 as cited by Krause-Jensen, Diaz Almela, Cunha, & Greve, 2004). Low genetic diversity and small population sizes, identified at various sites in the Mediterranean by Procaccini, Ruggiero, & Orsini (2002), further compromise *P. oceanica*'s capacity for expansion and survival. The introduction of alien algae *Caulerpa* spp. (Meinesz, De Vaugelas, Hesse, & Mari, 1993) to the Mediterranean, is yet another complicating factor in the saga of *P. oceanica's* continued existence. While healthy *Posidonia oceanica* meadows have been shown to act as barriers against *Caulerpa* spp. (namely *C. racemosa* and *C. taxifolia*), dead or dying *P. oceanica* beds leave vacant niches open for colonisation, enabling *Caulerpa* species to invade successfully (Chisholm et al

1997). This may essentially mean that, once lost, an area of *P. oceanica* meadow may not be naturally recovered (Occhipinti-Ambrogi & Savini, 2003).

Recoveries of lost meadow area, while very few and far between, have been documented nonetheless. The two examples that follow both exhibit the good management practise in addressing local damaging pressures. Gonzalez-Correa et al. 2005 assess the recovery capacity of *P. oceanica* meadows in an area affected by illegal otter trawling, after intervention by means of artificial anti-trawling reefs. The authors identify positive growth rates in the affected meadows 8 years after protection, showing that *P. oceanica* recovery is indeed possible once the cause of impact is eliminated (Gonzalez-Correa, Bayle, Sanchez-Lizaso, Valle, Sanchez-Jerez, & Ruiz, 2005). The authors, however, draw attention to the very low rates of vegetative growth and estimate a total recuperation time of almost 100 years for the habitat. Recovery has also been documented in the city of Marseilles, France, following the establishment of a wastewater treatment plant in 1987. Reductions in urban wastewater effluent and improved water quality enabled Pergent-Martini et al. (2002) to register a net increase of 0.18ha of *P. oceanica* meadow in the area, over a 12 year period (Pergent-Martini, Pasqualini, Pergent, & Ferrat, 2002). Since recolonisation is not occurring on a completely bare area, and is therefore faster than usual, complete recolonisation is not projected to surpass 2023.

As *P. oceanica* habitat declines in the Mediterranean, fundamental consequences are to be felt in the social, economic and biological activities in the region. The considerable resources required for restoration, where possible, and the long time periods required for meadow recolonisation and recovery, in contrast to the rapid dynamics that bring about reduction, highlight the need for proactive management of this valuable habitat.

1.2.3 HABITAT MANAGEMENT

Ecosystem services, such as those provided by *P. oceanica* habitat in the Mediterranean, are often not given adequate weight in policy decisions. This is because it is particularly difficult to do so when such services are not marketable goods and their value is not

quantified as economic services and manufactured capital are (Costanza, et al., 1997). Furthermore, the impact of habitats such as *P. oceanica* meadows on human well-being is often "invisible" to policymakers partly because its effects are not immediate and also because they are figuratively buried under the surface of the ocean. Nevertheless, the ecological and economical importance of *P. oceanica* habitat is recognised and its regression is consequently of particular concern to policy makers and many governments in the Mediterranean. Efforts are being made for the protection (EEC, 1992) and restoration of valuable *P. oceanica* resources (Balestri, Piazzi, & Cinelli, 1998; Procaccini & Piazzi, 2001).

Protection for *P. oceanica* is specified in Appendix I of both the Bern and Barcelona international conventions. The species is also included in the Red List of threatened marine species of the Mediterranean (Boudouresque C. F., Bernard, Bonhomme, Charbonnel, Le Direach, & Ruitton, 2007). The Action Plan for the Conservation of Marine Vegetation in the Mediterranean Sea (United Nations Environment Programme) identifies the conservation of *P. oceanica* meadows as a main conservation priority (RAC/SPA, 1999). *P. oceanica* meadows are also listed in Annex 1 of the EC Habitats Directive as priority natural habitats of European Community interest. Their protection in this case stems from the designation of special areas of conservation (SACs) (EEC, 1992) that host the seagrass habitat. SACs are identified by EU member states and collectively form the ecological network titled Natura 2000. SACs must be maintained, or restored when necessary, at a status of favourable conservation. *P. oceanica* habitat additionally receives specific legal protection in some European countries such as Spain and France (Gravez & Boudouresque, 2003), while other states are bound by their obligations as signatories of the above mentioned international conventions or as EU member states.

The monitoring of *P. oceanica* meadows has been given much emphasis as an important management tool (Boudouresque C. F., Bernard, Bonhomme, Charbonnel, Le Direach, & Ruitton, 2007; (Lopez y Royo, Pergent, Pergent-Martini, & Casazza, 2009). Monitoring is useful in inventorying and detecting new seagrass habitat losses or gains, as well as evaluating the effects of policies and interventions. *P. oceanica* habitat may be monitored

at a variety of scales, three in particular: the system scale, in which areal cover is estimated; the meadow scale, where limits of the meadow and shoot density may be estimated; and finally the shoot scale, where sediment properties, leaf epiphyte biomass, and other fine scale details such as genetic structure may be obtained (Boudouresque C. F., et al., 2006). *P. oceanica* monitoring in the Mediterranean was initiated in 1984 with the establishment of the 'Resau de Surveillance Posidonies" in the French Riviera (Boudouresque C. F., Bernard, Bonhomme, Charbonnel, Le Direach, & Ruitton, 2007). Monitoring of this habitat has subsequently expanded to other regions in the Mediterranean including France, Italy, Spain, Algeria, Tunisia and Malta (Lopez y Royo, Pergent, Pergent-Martini, & Casazza, 2009). Increasing *P. oceanica* habitat monitoring was much encouraged by the EU Water Framework Directive (WFD), adopted in 2000. Linking the status of coastal waters to economic benefits such as coastal fish populations, the WFD made legally binding the duty to monitor water quality and biological quality elements, including aquatic macrophytes such as *P. oceanica* (EC, The EU Water Framework Directive, 2000). Recent adoption of an ecosystem-based approach towards the management of marine waters has further emphasised the importance of seagrass monitoring (EC, 2008).

The increasing loss of *P. oceanica* habitat and the species' slow rate of regeneration has prompted the development of methodologies for habitat restoration, rehabilitation and meadow creation. Restoration of *P. oceanica* meadows has focused on recruitment from seeds (Belzunce, Navarro, & Rapoport, 2008), laboratory seed germination and seedling development (Balestri, Piazzi, & Cinelli, 1998), and the transplantation of entire plants from donor beds to restoration sites (Genot, Caye, Meinesz, & Orlandi, 1994; Procaccini & Piazzi, 2001). The use of seeds and seedlings is advantageous as genetic diversity is sustained; a transplant would serve to simply propagate a clone. Furthermore, seagrass seed collection involves minimal damage to the donor bed, particularly if seeds are obtained from drifting fruit (Belzunce, Navarro, & Rapoport, 2008). Seagrass seed collection and plantlet management therefore constitute an additional and important route towards the conservation, propagation and restoration of *P. oceanica* habitat (Orth, et al., 2000).

Other active areas in managing *P. oceanica* habitat include the installation of anti-trawling reefs (Gonzalez-Correa, Bayle, Sanchez-Lizaso, Valle, Sanchez-Jerez, & Ruiz, 2005), the installation of seagrass friendly moorings (Francour, Magreau, Mannoni, Cottalorda, & Gratiot, 2006), and good practices in the management of beach cast *P. oceanica* material (Duarte, 2004). The heavy impact of bottom trawling on sensitive habitats like *P. oceanica* has led to restrictions on trawling over seagrass meadows in places like Spain, Italy and France (Diaz Almela & Duarte, 2008). In many cases, the deployment of protective artificial reefs has further reinforced such restrictions. Protective artificial reefs are heavy concrete constructions that are often armoured with protruding steel bars and cause any trawling gear passing over the structure to entangle and break. The low maintenance and high endurance of these structures has made them a popular solution to the discouragement of trawling in protected areas. Artificial reef initiatives have reported general success in curbing illegal trawling (Diaz Almela & Duarte, 2008). An early initiative is the installation of 358 anti-trawling reefs in 1992 at El Campello and Villajoyosa (Alicante, Spain) that effectively protected 540 ha of *P. oceanica* meadow. Furthermore, other protective reef projects such as those in the Marine Reserve of Cap Couronne, report positive effects on fish populations and yields in nearby areas (Bachet, 2006)

The provision of ecological moorings to boat users serves to decrease the erosive pressure of free anchoring and mooring in the shallow areas that typically host *P. oceanica* meadows. The availability of such moorings additionally benefits sailors as it ensures enhanced security over free anchoring. An example of such an initiative is the installation of 50 such moorings in the Cabrera National Park, Spain, in 1993, following the prohibition of free anchoring. The total cost of the installation was €200,000 including an additional yearly 15% of the initial installation cost for maintenance and management (Moreno, 2006). Free anchoring was also banned in the strictly protected area of the Medas Islands, Spain, in 1994. An installation of 54 ecological moorings formed part of the scheme for promoting and achieving sustainable tourism at the location (Medas, 2006). Other similar initiatives include the installation of ecological moorings in the Cerbere-Banyuls marine protected area in France which served to reduce free anchoring by 90% in just two years, even though free anchoring was not forbidden in the park (Licari, 2006).

Leaves that are shed from the *P. oceanica* leaf canopy are transported to the shore by currents and waves and are deposited along the coast. Material that is beach-cast in this way accumulates to form banks, termed 'banquettes' by the French, that range from a few centimetres to several metres in height (De Falco, Simeone, & Baroli, 2008). Removal of such banquettes may prove detrimental to beach stability as well as to nearby *P. oceanica* meadows (Duarte, 2004). For this reason, best management practises in this case involve the adoption of a no-removal policy. This may however prove difficult in beaches that are heavily used by bathers and tourists. In the latter case, a variety of policies are recommended, including the establishment of no-removal periods during off-peak seasons (Diaz Almela & Duarte, 2008).

Despite the above mentioned efforts towards the conservation of *P. oceanica* habitat in the Mediterranean, published studies continue to identify regressing meadow health and loss of habitat area (Arnaud-Haond, Marba, Diaz-Almela, Serrao, & Duarte, 2010; Marba & Duarte, 2010; Montefalcone, Albertelli, Morri, & Bianchi, 2010). Montefalcone et al. (2009) assess the health of fifteen *P. oceanica* meadows along the coast of Liguria, Italy, and identify a general deteriorating state for the habitat. Their results indicated that shallow water meadows within Marine Protected Areas (MPAs) did not show superior states of health to those subjected to moderate anthropogenic influence. Furthermore in deep waters this trend was even more marked, as the health of *P. oceanica* habitat located within MPAs did not surpass that of meadows located in moderate or highly anthropized areas. Montefalcone et al. (2009), as well as others (Peirano, Damasso, Montefalcone, Morri, & Bianchi, 2005), identify increased turbidity of Ligurian coastal waters as an explanation for the largely regressive condition present in deep meadows. Deterioration of water quality in the Ligurian Sea is said to stem from region wide activities that are leading to the deposition of large quantities of land-sourced material into the sea (Montefalcone, Albertelli, Morri, Parravicini, & Bianchi, 2009). Observations such as these point towards impacts that operate at large scales, and underline the ineffectiveness of relying solely on local protection regimes that have been the focus of most conservation efforts (EEC, 1992). In fact, other recent studies have also identified large scale factors at work (Marba &

Duarte, 2010), highlighting the need for increased large-scale management of the habitat, that extends beyond the boundaries of individual MPAs. In a six year monitoring study of seawater temperature and annual shoot demography, Marba & Duarte (2010) show that meadows at the Cabrera Archipelago National Park in the Balearic Islands experience an additional 2% annual mortality for every additional degree of annual maximum temperature, drawing attention to the threat posed by the warming action of climate change.

While marine protected areas are both necessary and important in the mitigation of local threats to *P. oceanica* habitat, they do not provide sufficient protection alone as they are not isolated from all critical impacts (Allison, Lubchenco, & Carr, 1998). The existence of global and regional, larger scale impacts on *P. oceanica* habitat implies that meadows within MPAs are still vulnerable to risks that originate outside their boundaries. Indeed, the premise that patterns and processes at a specific site can only be fully understood by scaling across landscapes and including broad-scale variables is one that is increasingly apparent (Bostrom, Jackson, & Simenstad, 2006). Bearing in mind the spatial and temporal scales over which coastal development and other anthropogenic impacts occur, broad scale evaluation is necessary for the management of *P. oceanica* meadows in the Mediterranean, in line with the ecosystem-based approach (Orth, et al., 2006). Furthermore, given that the timescale involved in mitigating climate change impacts and other worldwide processes is likely to exceed centuries, strategies to enhance the resistance and resilience of *P. oceanica* to inevitable change should feature as an additional part of an initiative towards habitat conservation. Efforts to alleviate harmful impacts that stem from climate change and other large scale dynamics, such as those operating in watersheds, should also be considered in the management of resources such as *P. oceanica* habitat.

Monitoring efforts for *P. oceanica* appear to be concentrated in the north western Mediterranean. The identification of processes operating at global / basin wide scales indicate how important it is to extend such efforts to other areas of the Mediterranean basin, where *P. oceanica* meadows are also present and hold similar value and importance. A basin-wide monitoring initiative would see an integration of the different data sets in existence and establish a Mediterranean-wide inventory of the habitat, allowing for a

comprehensive detection of changes. Furthermore, an improved understanding of the larger scale mechanisms that lead to habitat threats and losses is also likely to result. Problems with data integration have already been anticipated, due to the differences in monitoring strategy and design, methods and data management (Kirkman H. , 1996). Such obstacles of data comparability and quality assurance must be overcome if a Mediterranean wide initiative towards the conservation of the *P. oceanica* resource is to be realised.

Monitoring programmes contribute to optimal environmental management practices (Vos, Meelis, & Ter Keurs, 2000), but alone do not make for effective decision making. Conservation initiatives relying solely on monitoring programmes often detect habitat regression past the point at which corrective actions may prove fully effective (Delgado, Ruiz, Perez, Romero, & Ballesteros, 1999). Costanza et al. (1999) humorously liken the situation to that of the blind man and the elephant, where the subject is just too big and too complex to understand with one limited set of perceptual tools (Costanza, et al., 1999). For reasons such as these, developing a capacity for prediction as part of a comprehensive, integrated management programme is mandatory.

1.3 REVIEW OF RELEVANT MODELLING EFFORTS

The information needed by resource managers to exercise adequate environmental stewardship is not available through data monitoring alone. While ecosystem dynamics unfold into the future, they have been conventionally understood by examining past influences that shape present events. The capacity to anticipate is greatly advantageous to policy-makers dealing with complex systems. Qualitative forecasts, such as those by Duarte C. M. (2002) and Short & Neckles (1999) of future seagrass trends, identify with this critical need for predictive faculty. Planning and decision-making may be improved by adopting a "forward looking" frame of mind that comes with the ability to assess a broad range of possible future ecosystem states, and complements traditional, historical approaches to resource management (Carpenter, 2002). Quantitative forecasts may be used in determining the most cost-effective allocation of conservation resources and in anticipating collective, interacting effects of multiple stressors on natural resources, before they are made a reality. Risk analysis is also made possible and can be used to better

inform conservation and management strategies (Orth, et al., 2006). An increasing interest in using computer models for developing such predictive capacity and exploring future options for natural resource management is evident (Burd & Dunton, 2001).

Several seagrass models already exist; e.g. those addressing *Halodule wrightii* (Burd & Dunton, 2001; Fong & Harwell, 1994; Fong, Jacobson, Mescher, Lirman, & Harwell, 1997); *Zostera marina* (Bocci, Coffaro, & Bendoricchio, 1997; Wetzel & Neckles, 1986); *Zostera noltii* (Plus, Chapelle, Menesguen, Deslous-Paoli, & Auby, 2003); *Potamogeton perfoliatus* (Madden & Kemp, 1996) and polyspecific seagrass beds (Fourqurean, Boyer, Durako, Hefty, & Peterson, 2003; Kendrick, Eckersley, & Walker, 1999). Models focusing on *Posidonia oceanica* have also been formulated (Elkalay, et al., 2003; Zupo, Buia, & Mazzella, 1997), although most concentrate heavily on one aspect of the habitat's dynamics (Kendrick, Marba, & Duarte, 2005; Marba & Duarte, 1998; Molenaar, Barthelemy, de Reffye, Meinesz, & Mialet, 2000). Marba and Duarte (1998), use Monte Carlo simulation to model the spreading of the rhizome networks of three seagrass species; *P. oceanica* is one of these. Their developed model allows them to explore the differences in seagrass vegetative growth patterns for space occupation, and the consequent implications of these differences. *P. oceanica* rhizome growth is also simulated by Kendrick, Marba and Duarte (2005). This modelling initiative employs agent-based methods to investigate the role of rhizome growth in the formation of the topographically complex *P. oceanica* matte. Zupo, Buia and Mazzella (1997) direct their efforts towards the simulation of *P. oceanica's* above ground production and its relationship with spatial and temporal variation in temperature. The numerical model developed was specific to the Lacco Ameno meadows in the Gulf of Naples, but nonetheless produced satisfactory predictions for several other Mediterranean *P. oceanica* beds. *P. oceanica* seasonal growth and production is also investigated by Elkalay, et al. (2003); only this study is novel in its whole-plant approach, and changes in both above- and below-ground biomass are modelled. This latter initiative forms part of a larger model that attempts to describe the dynamics of the ecosystem present within the Bay of Calvi in Corsica.

The abovementioned studies employ a variety of methods to model and simulate seagrass communities. Individual component models are commonly linked together to produce more complex units that encompass a larger set of variables (Hutchings, Struve, Westen, Millard, & Fortune, 2002). The model simulating the ecosystem in the Lagoon of Venice, Italy (Bocci, Coffaro, & Bendoricchio, 1997; Canu, Solidoro, & Umgiesser, 2003) is one example of a coupled model. Baptised as VELFEEM (Venice Lagoon Finite Element Ecological Model), the model results from coupling a finite element hydrodynamic model, an energetic model and an ecological model. Baird et al. (2001), couple a physical circulation model to a complex biogeochemical / ecological model to produce the Simple Estuarine Response Model (SERM). The SERM model enables users to simulate the response of natural ecosystems, present in Australia's macrotidal estuaries, to physical and chemical perturbation (Baird M. , 2001). Seagrasses feature in both the VELFEEM and SERM models as one of the primary producers in the system, together with phytoplankton, zooplankton, benthic microalgae and macroalgae. Since seagrasses, like *P. oceanica,* are connected and influenced by other systems in the coastal zone, linking individual component models together enables the evaluation of a larger interacting set of dynamics, improving guidance for coastal management.

Modellers may also want to account for socio-economic factors or behavioural patterns at the coast given that humans are an integral component of coastal ecosystems. While coastal issues have been conventionally tackled by sectors on an individual basis, the advocation of a new integrated management of the coastal zone is evident (EEC, 2006). Integrated coastal zone management (ICZM) is a strategy for integrated planning and management, in which all policies, sectors and individual interests are to be taken into account. The strategy also gives appropriate consideration to temporal and spatial scales, and involves all coastal stakeholders in a participative way (Maes, Van Deursen, Timmermann, Fiandrino, & Engelen, 2007). A broad systems view such as this requires integrated assessment and modelling as a means of bringing all aspects into analysis (Costanza, et al., 1999).

While the coupling of component models is commonly employed in ecological sciences as a means of integrating knowledge, this often requires a common domain and medium due to the exchange of information between modules during runtime (Maes, Van Deursen, Timmermann, Fiandrino, & Engelen, 2007). For example, an integrated hydrological model of a river basin requires the coupling of precipitation, run off, water flow and water quality. Similarly predicting local air quality requires the coupling of meterological models with atmospheric chemistry models. In both examples, the medium (water, air) as well as the domain (a river basin, an urban airshed) provide a common basis on which the different modules may be linked. Extending model coupling to units from highly different disciplines however, is likely to result in models that are too complex. Compromised model visibility, calibration and validation may result, discouraging managers and users from actually using the model for guidance (Hutchings, Struve, Westen, Millard, & Fortune, 2002). Contrary to common thinking therefore, the broader and the more integrated a model is, the simpler it must be (Maes, Van Deursen, Timmermann, Fiandrino, & Engelen, 2007).

1.4 SYSTEM DYNAMICS

An alternative to conventional simulation techniques, system dynamics is an integrative modelling method for analysing complex feedback systems (Sterman, 2000). System dynamics makes available a unique framework for integrating highly contrasting disciplines that are pertinent to the system being modelled, and avoids the need to couple multiple models. System dynamics was developed in the 1950s, by Jay Forrester at the Massachusetts Institute of Technology (MIT) to improve the understanding of strategic management problems in complex, dynamic systems.

The often reactive nature of society in general means that a problem must often become obvious before interventions attempt to mitigate or correct the situation. With such an event-oriented mindframe, a problem is typically defined by the gap that is observed to lie between the current state of affairs and a desired situation. Human behaviour and policy interventions add complexity to an already complex system and when the effects of our interventions on a system are not recognised, yesterday's solution may become today's

problem (Sterman, 2000). While our interventions often alter our environment further, leading to new decisions and interventions, they may at the same time also trigger side effects, delayed reactions, and further changes in goals and interventions of other actors in the system, be they humans, or other species such as plants, animals and algae. These all interact and adapt to our actions to create unanticipated results rendering many policies ineffective or even further detrimental to the system. Trawler trajectories from the MPA Parc Marin de la Cote Bleue in France show that while the deployment of artificial reefs put a stop to trawling activities within protected *P. oceanica* meadows, activities have since moved elsewhere into unprotected seagrass meadows not previously exploited (Diaz Almela & Duarte, 2008). Accounting for the human element associated with seagrass systems is complex and responses to policy interventions may not be as predicted or desired. The need to decipher the complex and dynamic character inherent within seagrass and, more broadly, coastal areas, for the purpose of resource management beckons the application of an integrative modelling approach like system dynamics.

System dynamic models account for feedback in systems. A network of cause and effect relations between the elements within a given system is first constructed. These causal links constitute the feedback processes that generate a system's dynamics. Feedback processes feature a closed-loop structure, in which current actions precipitate system responses that "feed back" to influence later actions (Figures 1.1 & 1.2). Time delays represent another critical feature of dynamic systems and may prevent feedback from being immediately realised. The identification and simulation of the array of feed back dynamics and time delays relevant to the problem, in order to guide policy, is a primary goal of the system dynamics methodology.

Figures 1.2 and 1.3 below illustrate examples of the two types of feedback, positive and negative, both of which are found within *P. oceanica* habitat. Variables in the causal diagrams are related by causal links which are shown by arrows. Each link is assigned a polarity, either positive (+) or negative (-) to indicate the way in which the dependant variable changes with a change in the independent variable (Sterman, 2000). Positive links imply that an increase (or decrease) in the cause will result in the affected variable being

higher or lower than it would have been without that cause (all else being held constant). Negative causal links on the other hand imply that an increase (or decrease) in the cause results in the affected variable being lower (or higher) than it would have otherwise been. Feedback loops are highlighted by a loop identifier that indicates whether the loop brings about positive (reinforcing) or negative (balancing) feedback behaviour. Figure 1.2 illustrates positive feedback behaviour that serves to reinforce the growth of *P. oceanica*. As *P. oceanica* grows, the degree to which suspended particles are captured and light conditions are improved also increases. The increase in light availability positively feeds back to allow *P. oceanica* to photosynthesise more efficiently and be even more productive, promoting further particle capture and so on. This feedback dynamic has been described by de Boer (2007) as one of the most important positive feedback dynamics in seagrass systems. Note that the loop in Figure 1.2 rotates anticlockwise and therefore so does its loop identifier.
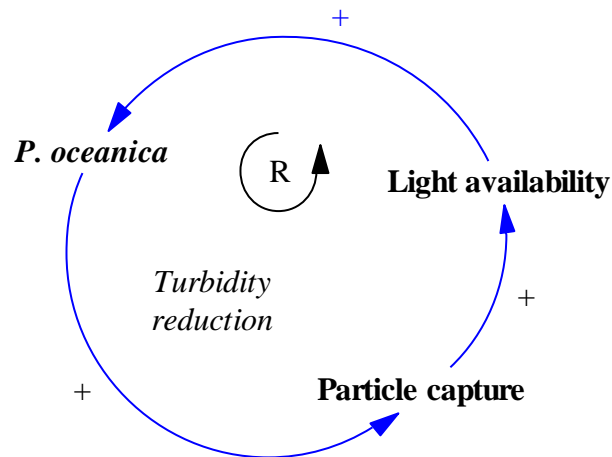
Figure 1.2 Reinforcing behaviour in *P. oceanica* habitat due to the improvement of light conditions via canopy particle capture.

Figure 1.3 identifies negative feedback behaviour, featured within *P. oceanica* habitat, which acts to balance out any reinforcing growth dynamics such as that illustrated in Figure 1.3. As *P. oceanica* grows, the growth of associated epiphytes is in turn promoted via the increased availability of substratum, or nutrition, or both. As epiphytes become more abundant however, so does the extent to which light is attenuated by their presence. A

decrease in light availability similarly brings about a decrease in the rate at which *P. oceanica* photosynthesises and grows, thus balancing out the initial increase at the start of the feedback loop.
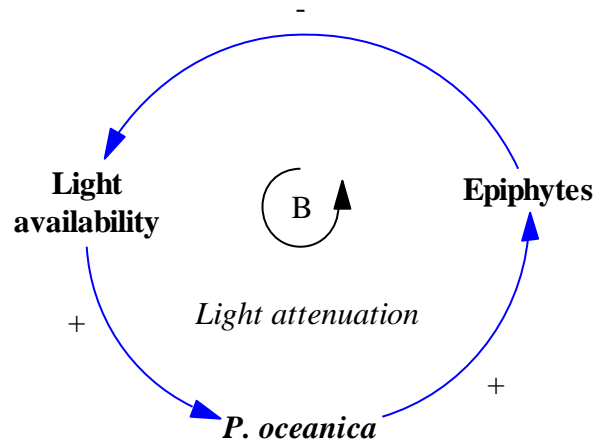
Figure 1.3 Light attenuation by epiphytes brings about balancing feedback in *P. oceanica* habitat.

In complex systems such as the *P. oceanica* ecosystem, feedback is often delayed in time. This means that the consequences of impacts on the habitat are not directly percieved. Such is the case of the effects of destructive fishing techniques illustrated in Figure 1.4. Destructive fishing techniques fragment and decrease *P. oceanica* meadows, bringing about an effective decrease in the nursery service provided by the habitat. Consequently, less fish are successfully recruited to the adult stage, an effect that is only perceived by fishermen after several years, due to the time it takes for juvenile individuals to mature into adults. Their undesired fishing practise therefore continues unabated for a number of years until the unintended consequence of their fishing practise is realised. Once fishing techniques are switched to less destructive methods, another step that may last a number of years due to economical and social complications, the abatement loop below may finally be completed. The time delays inherent within many of *P. oceanica*'s dynamics are a distinct reason underlying the lack of importance such valuable resources are given in policymaking.
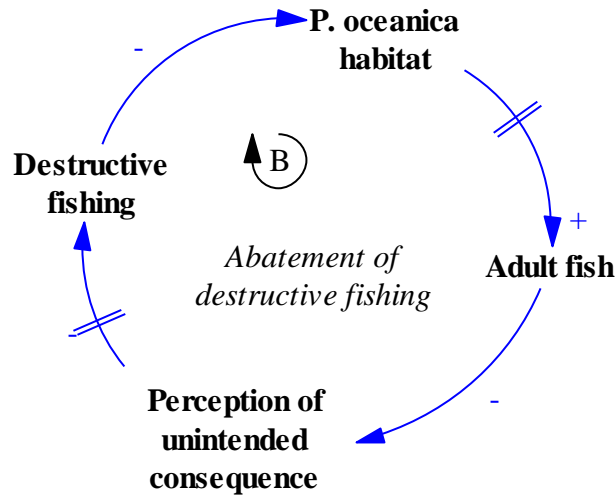
Figure 1.4 Feedback loop illustrating the contribution of time delays to the complexity of systems. Arrows featuring a delay hash mark connect variables that describe dynamics which take place on a longer time scale.

Complex dynamics have been identified in seagrass systems (Duarte C. M., 1995). Bostrom and colleagues (2004) evaluate a number of studies on seagrass landscapes and describe seagrass systems as complex and difficult to predict. The same authors also identify seagrass landscapes as areas in which various processes operate at various scales, with possible cascading effects (Bostrom, Jackson, & Simenstad, 2006). Time delays within systems lead to states of disequilibrium, causing oscillation in the presence of negative, goal seeking feedback loops (Sterman, 2000). Long term cyclic events in seagrass systems have been identified by ecologists (Den Hartog, 1979; Marba & Duarte, 1997) and such occurrences evidence the adaptive nature of seagrass systems to both natural and anthropogenic influences. The sudden shifts and step changes that characterise seagrass response to eutrophication are evidence of the presence of complex feedback and delayed dynamics within seagrass systems (Burkholder, Tomasko, & Touchette, 2007). Duarte (1995) describes the 'cascade of direct and indirect effects interacting in a self-accelerating manner" that leads towards seagrass decline under increased nutrient loading. Tight coupling and interdependancy of system elements is another feature that distinguishes complex systems (Sterman, 2000). Indeed, hydrodynamic and geological processes have shown to be strongly coupled to patterns and development within seagrass systems (Den Hartog, 1979; Koch, 1999; Fonseca & Fisher, 1986; Fonseca, Zieman, Thayer, & Fisher,

1983). Currents and porewater geochemistry act interdependently to affect seagrasses as evidenced by Koch (1999). Orth et al. (2006) acknowledge the complex ways in which multiple stressors affecting seagrasses operate simultaneously, at different temporal and spatial scales, with interacing effects.

Several advantages of adopting a system dynamics approach to complex systems' analysis have been asserted. Ahmad and Simonovic (2000) model reservoir operations at the Shellmouth reservoir on the Assiniboine River in Canada for the purpose of flood management. The authors experience faster prototyping than with conventional simulation methods and explain that effort recovered during the programming phase may be directed elsewhere. Other important tasks such as system conceptualisation, data collection, and the involvement of end users and stakeholders in model development all benefit from the ease of model construction and modification (Ahmad & Simonovic, 2000). The open and interactive environment in which model development takes place is one main strength of the system dynamics approach. By enabling end users to participate and be involved, model development may serve to increase confidence in the model, whether the users are members of the general public, stake-holders or policy makers. The model framework also makes possible the highly effective communication of system structure and model results (Tidwell, Passell, Conrad, & Thomas, 2004).

1.5 THESIS STATEMENT

The overall purpose of this study is to investigate the use of system dynamics modelling in describing and analysing the system characteristics of *Posidonia oceanica* habitat, a natural resource present in the Mediterranean coastal zone.

The main aims of this research study are:

1. to integrate knowledge about *P. oceanica* habitat and synthesise current data about seagrass community structure into a working model for a generic *P. oceanica* meadow;

2. to describe and test the preliminary model for the seagrass *P. oceanica* and to consider the influence of changes in exogenous variables such as light availability in scenario analysis.

Broad system-level modelling that features *P. oceanica* as part of a larger system containing other species, including humans, is lacking in published literature and is what prompted this modelling research effort. Furthermore, *P. oceanica* differs in growth and physiology from other seagrasses (Elkalay, et al., 2003), and therefore the application of a model that has been developed for other seagrass species in other areas is difficult. Most models that do address the species *P. oceanica* have been focused on one particular aspect of the habitat. Initiating an effort towards a broader, integrated model of *P. oceanica* habitat was therefore highly appealing.

The preliminary model developed through this research study can serve as a starting point for a more comprehensive model that would ultimately seek to integrate broad scale dynamics, including human behaviour, into the system. The involvement of multiple stakeholders such as fishermen, and decision makers would ultimately feature in model building at this later stage. During the development of the current prototype, input was sought from individuals that are experts on system dynamics modelling and the dynamics of *P. oceanica* habitat.

A modelling approach based on the principles of system dynamics (Forrester J. W., 1991; Sterman, 2000) was considered appropriate due to the following reasons:

i. The need for an integrated view of the seagrass habitat and its connections to other systems within the coastal zone was identified. System dynamics supports the integration of vastly different disciplines in the same framework.

ii. The need to anticipate future change was identified as being important to conservation efforts for *P. oceanica* habitat. System dynamics enables the simulation of future scenarios and conditions.

iii. The system dynamics framework provides an interactive interface and rapidly produces usable results. It may be easily tailored to the expectations of its end-users for involvement in the decision processes or be used for educational outreach.

1.6 SIGNIFICANCE OF THESIS QUESTION

This modelling effort is a direct contribution towards the need for an increasingly integrated understanding of what is happening in the entire coastal zone (EEC, 2006). The present study identifies *Posidonia oceanica* habitat as a complex ecosystem that forms part of an even more complex natural dynamic system at the coastal zone. The preliminary model described in this study addresses the complex dynamics that directly concern *P. oceanica* habitat and makes an important contribution towards modelling of this species and the habitat it forms.

System dynamics methodology has not yet been applied in modelling *P. oceanica* habitat and its role in coastal dynamics. Such an approach holds promise for developing a policy tool that may be understood and used by policymakers to evaluate options for conserving *P. oceanica* habitat. Once developed further, the simulation tool developed in this research study may furthermore complement other kinds of coastal policy discussion in the Mediterranean. Several important decisions are currently being taken without the benefit of an analytical tool that may better inform policymakers of the long-term impacts of their decisions on the health of *P. oceanica* habitat and the consequent effects of the state of this natural resource on the economy of the Mediterranean basin.

The system dynamics approach that is unique to the present study of *P. oceanica* habitat has several implications for educational purposes, and this particular prototype may be used to increase the awareness of policy makers as well as other stakeholders and the general public. The synthesis of data through this research study shall serve to identify further avenues of research needed to improve understanding and management relevant to *P. oceanica* habitat.

2 *POSIDONIA OCEANICA* HABITAT DYNAMICS

2.1 BASIC DYNAMICS

Several investigations have dealt with the primary production of *Posidonia oceanica* meadows (Dalla Via, et al., 1998; Ott, 1980; Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994; Pergent-Martini, Rico-Raimondino, & Pergent, 1994). The *P. oceanica* ecosystem plays a major role in benthic primary production in the Mediterranean Sea (Buia, Zupo, & Mazzella, 1992), with a contribution ranging between 0.4 and 2.5 kgDW/m^2/y (Boudouresque et al., 2006; Cebrian & Duarte, 2001). Environmental factors such as depth, light, water movement, and herbivore pressure play a large role in altering meadow primary production and the resulting flux of matter and nutrients (Pergent, Rico-Raimondino, & Pergent-Martini, 1997). Understanding the relationship between photosynthetic capacity, and the factors that regulate it is important for estimating the productivity of *P. oceanica* habitat (Alcoverro, Cerbian, & Ballesteros, 2001).

Similar to terrestrial angiosperms, light has often been identified as the primary environmental factor influencing photosynthesis of *P. oceanica* (Dennison, 1987). Morphological and physiological adaptations to photosynthesis in low light conditions allow seagrasses to colonise deep waters (Masini, Cary, Simpson, & McComb, 1995). By restricting seagrass ability to photosynthesise and grow, the depths to which light penetrates underwater consequently influences the vertical distribution of seagrass habitat (Dennison, 1987; Duarte, 1991). Light penetrates water around three orders of magnitude less than it does in air. In the clearest of waters, almost no photosynthetically active radiation (PAR) may penetrate beyond a depth of 200m (Hemminga & Duarte, 2000). Other than being absorbed by water molecules, other particulate or soluble substances present in the water also contribute to the total attenuation of light in the water column (Duarte, Agusti, & Satta, 1998). The higher load of particles and dissolved substances that characterise coastal waters means that seagrass distribution is restricted to a narrow depth range. While seagrasses are found down to depths of -90 m, the distribution of *P. oceanica* is usually limited to depths above -45 m (Duarte, 1991). Light also plays a key role in determining

other features such as the spatial structure and seasonal growth pattern of *P. oceanica* meadows (Alcoverro, Duarte, & Romero, 1995; Dennison, 1987). The relationship between the intensity of light and the rate of photosynthesis is one of critical importance to submerged plants like *P. oceanica,* as it determines the degree of impact that light reductions have on growth and survival (Vermaat, 1997). This relationship is species specific, and is often described using photosynthesis-irradiance, or P-I, curves (Figure 2.1) which indicate how efficiently light energy is used in the accumulation of plant biomass. Seagrass P-I curves are similar to those of terrestrial plants and show an initial linear increase in photosynthetic rate with increasing light. Once irradiance has become saturating, P-I curves level off towards a maximum rate of photosynthesis (P_{max}). The respiration term, R, must be included when deriving net photosynthetic rates as this corrects for the oxygen consumed in maintaining living plant tissue during respiration. The irradiance at which P_{max} is reached is termed the saturating irradiance, K_m in Figure 2.1, and at irradiances below this value, light is among those factors acting to limit plant growth. Other factors that play an important role in regulating photosynthetic capability in *P. oceanica* are temperature and nutrient availability such as nitrogen and phosphorus (Drew, 1978; Hemminga & Duarte, 2000; Nielsen & Sand-Jensen, 1990).
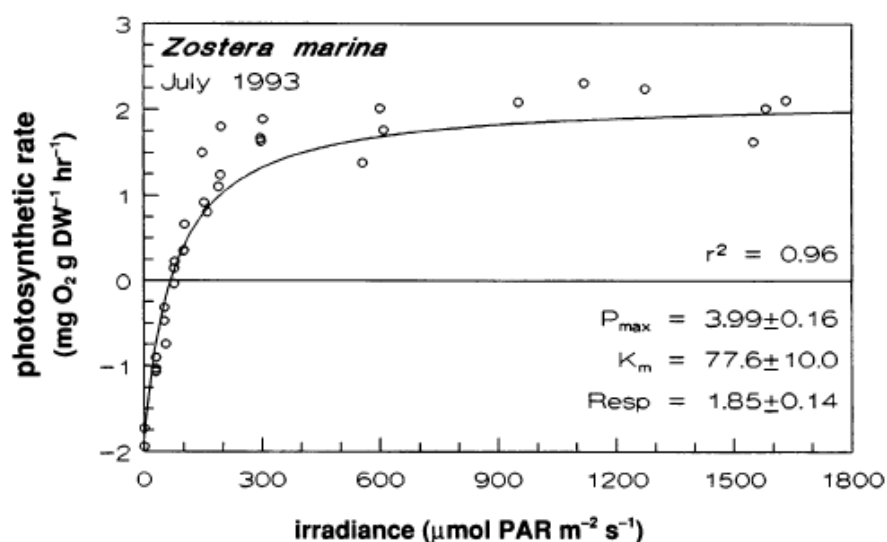
Figure 2.1 Exemplary photosynthesis-irradiance curve of a seagrass (specifically intertidal *Zostera marina* from the Zandreek, SW Netherlands). P_{max}, K_m and Resp are the maximum photosynthetic rate, saturating irradiance, and respiration terms respectively. Adapted from Vermaat (1997).

Matter that is produced as a result of *P. oceanica* photosynthesis (Figure 2.2) typically follows one of two main pathways: (1) as leaves age and fall, blades are detached and contribute to litter stock (Mateo & Romero, 1997; Pergent, Rico-Raimondino, & Pergent-Martini, 1997; (2) the leaf sheath base does not detach from the rhizome and continues to persist beneath the addition of new leaves (Pergent, 1990). In the former case, detached material may remain within the meadow to undergo decay (Romero, Pergent, Pergent-Martini, Mateo, & Regnier, 1992), or otherwise be exported to new areas by water movement. Exported litter may then decompose in the receiving systems and represent a trophic input of considerable importance (Cebrian & Duarte, 2001; Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994).
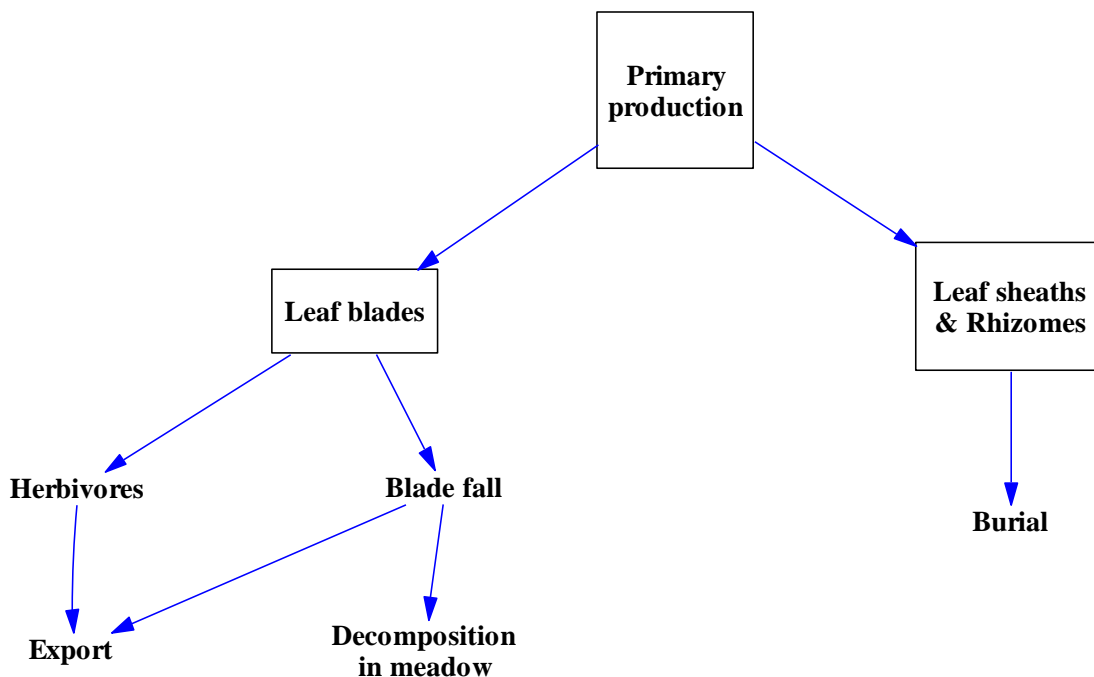
Figure 2.2 Fate of *P. oceanica* primary production. Adapted from Pergent et al. (1997).

The progressive burial of roots, rhizomes and leaf sheaths leads to the accumulation of large quantities of organic debris beneath *P. oceanica* meadows. The network of living and dead rhizomes with sediment filled interstices is commonly termed 'matte' (Figure 2.3) and is a characteristic unique to *P. oceanica* meadows (Pergent, 1990). The percentage of

seagrass production that is buried in the matte is rather noteworthy (25-35%) and, due to high resistance to decay, may furthermore persist for thousands of years (Mateo & Romero, 1997). Observation of the oldest materials by Mateo *et al.* (1997) indicates that plant parts that last the longest are the leaf sheaths (their external morphology is left intact after 3000 years) and roots, which are usually found in a fragmented state. Rhizomes are less resilient to decay, and no identifiable remains are found in the oldest (>1000 year) samples. Various studies identify this large reservoir of belowground detritus as an important and substantial sink for various biogenic elements (Cebrian & Duarte, 2001; Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994; Mateo, Romero, Perez, Littler, & Littler, 1997). Hundreds to thousands of grams of dry weight per square metre (gDW/m^2) have been discovered within the first 10-15cm from the sediment surface (Cebrian & Duarte, 2001; Mateo & Romero, 1997). At depths exceeding 1m in the sediment, carbon stocks reach up to $5000gC/m^2$ (Mateo, Romero, Perez, Littler, & Littler, 1997). Studies by Cebrian and Duarte (2001) have compared these values to those identified in populations of other seagrass species (Cebrian, Pedersen, Kroeger, & Valiela, 2000; Kenworthy, Zieman, & Thayer, 1982). The reservoir of belowground detritus accumulated beneath *P. oceanica* meadows was shown to greatly surpass that in other populations of seagrass (Cebrian & Duarte, 2001). In the course of time, *P. oceanica* matte rises to reach the water surface; a process that spans a time-scale of centuries (Duarte C. M., 1995) and may result in the formation of *P. oceanica* reefs (Romero, Perez, Mateo, & Sala, 1994). *P. oceanica* reefs have complex topographies and provide vertical relief, unlike the sedimentary banks formed by other seagrass species (Kendrick, Marba, & Duarte, 2005). Lagoon systems may also form in cases where temperature and salinity conditions between the coast and the reef exceed those tolerated by *P. oceanica* (Boudouresque C. F., et al., 2006).
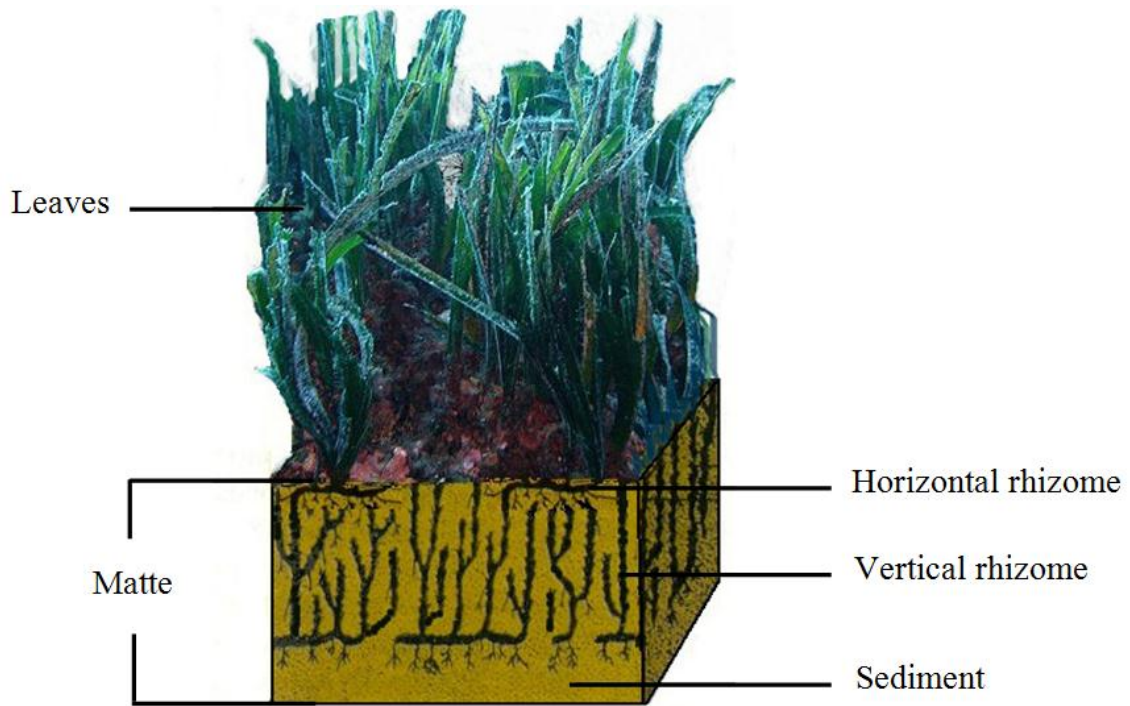
Figure 2.3 *Posidonia oceanica* **matte. Source: Academic, 2010.**

2.2 ASSOCIATED SPECIES

2.2.1 EPIPHYTES

The structure of *Posidonia oceanica* habitat makes available several resources that are vital to the survival of other organisms. *P. oceanica* leaves offer a substratum for attachment and growth of various organisms (Lepoint, Havelange, Gobert, & Bouquegneau, 1999). The epiphytic community (Figure 2.4) that makes use of this substratum consists mainly of crustose red algae *Fosliella* spp. and brown algae of the genera *Myrionema*, *Giraudia* and *Cladosiphon*. Some animals such as hydrozoans, bryozoans, serpulid polychaetes and foraminifera also attach to the plant, especially in deeper waters where light becomes limiting to epifloral species (Lepoint, Havelange, Gobert, & Bouquegneau, 1999). Novak (1984) also identifies a rich community of microorganisms on *P. oceanica,* and furthermore, on the epiphytes growing upon *P. oceanica* leaves (Novak, 1984).

Essentially, the epiphytic community on *P. oceanica* is itself dynamic, with numerous species growing over the first to settle. Consequently, a multi-layered stratum is present on *P. oceanica* leaves and rhizomes, where different species are mixed and whose composition varies with depth and other conditions that influence epiphytic dynamics such as the life cycle of the epiphyte species (Orth & van Montfrans, 1984) or grazing by fauna (Jernakoff, Brearley, & Nielsen, 1996). Photosynthesising epiphytes complement production by *P. oceanica* and may contribute up to 40% of the total biomass of *P. oceanica* canopies (Mazzella & Ott, 1984). While the average biomass of the autotrophic community growing on *P. oceanica* leaves and rhizomes ranges between 160 and 420 gDW/m^2 (Boudouresque, Mayot, & Pergent, 2006), its contribution towards primary production lies between 500-900 gDW/m^2/y (Boudouresque C. F., et al., 2006). It is the sum of seagrass and epiphyte stocks, in shallow waters, that enable the *P. oceanica* habitat to achieve the highest values of net primary production observed not only in the marine but also the terrestrial realm (Boudouresque, Mayot, & Pergent, 2006).
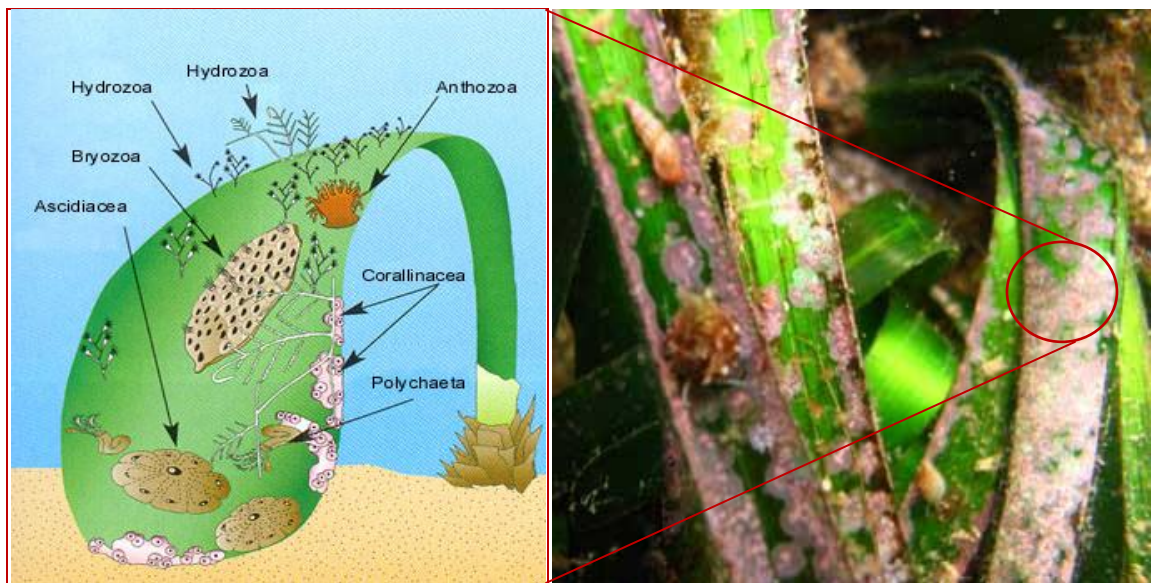
Figure 2.4 *P. oceanica* epiphytes. Source: Hofrichter R. (left) and KennaEcoDiving (right).

P. oceanica leaves may reach a maximum age of up to 300 days (Duarte, 1991) and consequently epiphyte loads may reach amounts that result in substantial effects on the growth of host leaves, such as gas and nutrient exchange and shading (Cebrian, Enriquez,

Fortes, Agawin, Vermaat, & Duarte, 1999). Indeed, the presence of nitrogen (N_2) fixing bacteria on *P. oceanica* leaves and/or within the rhizosphere has been inferred (Bethoux & Copin-Montegut, 1986). The exchange of fixed nitrogen between epiphytic bacteria and *P. oceanica* is thought to partly explain the paradoxically high biomass and productivity of *P. oceanica* systems; this is unexpected given the oligotrophic conditions that characterise Mediterranean waters (Boudouresque, Mayot, & Pergent, 2006). Shading by excessive epiphyte growth is, on the other hand, an effect that often proves detrimental to the host plant and has been commonly listed among the causes of seagrass decline around the world (Fitzpatrick & Kirkman, 1995; Neckles, Wetzel, & Orth, 1993; Valiela, Costa, Foreman, Teal, Howes, & Aubrey, 1990).

2.2.2 GRAZERS

P. oceanica and its epiphytes provide nutrition to organisms that consume them. Three species directly linked to *P. oceanica* habitat through their consumption of *P. oceanica* leaves are the fish *Sarpa salpa* (Harmelin-Vivien & Francour, 1992), the sea urchin *Paracentrotus lividus* (Pergent, Rico-Raimondino, & Pergent-Martini, 1997) and crustacean isopods *Idotea* spp. (Boudouresque C. F., et al., 2006) (Figure 2.5). When consuming seagrass leaves, these species additionally consume the epiphytic material growing on *P. oceanica*; *P. lividus* has in fact been shown to preferentially consume leaves covered with epiphytes over leaves that do not support epiphytes. Indeed, the epiphytic organisms that make *P. oceanica* their substratum provide nourishment for several other organisms that do not feed directly upon the seagrass (Orth & van Montfrans, 1984). As a result of their short generation times and rapid rates of growth, the algae attached to seagrass leaves are extraordinarily productive, despite the small biomass they represent. In some instances, the productivity of seagrass epiphytes equals that of the seagrass leaves to which they are attached (Williams & Heck Jr., 2001). Studies have revealed that a large number of seagrass-associated organisms feed heavily on epiphytic algae (Jernakoff, Brearley, & Nielsen, 1996) and that their mineralization is a short-term process (Williams & Heck Jr., 2001). The gastropods *Bittium reticulatum*, *Calliostoma langieri*, *Cerithium*

vulgatum, *Columbella rustica, Gibbula umbilicaris*, *Rissoa* spp. and *Jujubinus* spp. are frequent consumers of *P. oceanica* epiphytes (Boudouresque C. F., et al., 2006).

Figure 2.5 Left *Sarpa salpa*. Top right *Idotea baltica*. Bottom right *Paracentrotus lividus*. Source: Boyer M., Jonas P., and Maltagliati F., respectively.

Consumption by herbivores is not considered to be a major route for *P. oceanica* material on the other hand, and less than 10% of the leaves are directly consumed (Cebrian & Duarte, 2001). The majority of leaves are consumed after being shed, as detritus in the litter, through the action of crustaceans, gastropods and microorganisms (Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994). The low consumption of many seagrasses is often attributed to the poor nutritional quality of the plant material (Tomas, Turon, & Romero, 2005). *P. oceanica* has a high C/N ratio (Duarte C. M., 1990) and its high cellulose content often makes the digestion process difficult for most invertebrate grazers (Lawrence 1975). The presence of chemical deterrents is said to further contribute

to the unpalatabiliy of *P. oceanica* (Agostini et al 1998). Despite these observations, a number of studies have reported considerable impacts of grazers on seagrass biomass and production (see review by Valentine & Heck 1999) and herbivores have been known to defoliate vast areas of *P. oceanica* (Kirkman & Young, 1981). The gut of the sea-urchin *Paracentrotus lividus* in areas distant from *P. oceanica* meadows may contain as much as 31% of *P. oceanica* leaves (Verlaque & Nedelec, 1983 as in Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994). Furthermore, overgrazing of *P. oceanica* meadows by herbivorous fish (*S. salpa)* was observed in a number of MPAs (Tabarca in Spain, Port-Cros in France, El Kala in Algeria) (Boudouresque C. F., et al., 2006). Tomas et al. (2005) estimated that as much as 70% of the production of seagrasses (*Posidonia oceanica*) in the Medes Islands Marine Reserve in Spain was consumed by *S. salpa* (Tomas, Turon, & Romero, 2005). Occurrences such as these suggest that the modest grazing observed to be typical of *P. oceanica* is likely to be an artefact and a result of man's influence on marine systems. Hypotheses that link seagrass undergrazing to overfishing and loss of important herbivores such as sea urchins, green turtles, sirenians, fish and waterfowl are not uncommon (Valentine & Heck, 1999; Heck Jr. & Valentine, 2006). Indeed, trophic interactions are gaining recognition as critical structuring forces in seagrass systems (Cebrian & Duarte, 1998) and hypothesised overfishing is often put forward to account for seagrass decline, through a mechanism of epiphytic overgrowth, similar to that of eutrophication (Hughes, Bando, Rodriguez, & Williams, 2004; Williams & Heck Jr., 2001). Other than the loss of large herbivores, overfishing may also be responsible for a reduction in small invertebrate grazers of epiphytes (i.e. amphipods, isopods, gastropods and herbivorous crabs) via trophic cascade. Studies by Shurin et al. (2002) indicate that top-down control of plant biomass, as a result of indirect effects of predators on plants via shifts in herbivore abundance, is strongest in the marine environment (Shurin, et al., 2002). Furthermore, Borer et al. (2004) confirm that marine benthic species exhibit the strongest trophic cascades of any tested system, supporting assertions that grazers may be equally important in controlling the accumulation of algal biomass in seagrass habitats via top-down effects as are nutrient fluctuations via bottom-up effects (Heck Jr. & Valentine, 2006).

**Eutrophication
(Bottom Up)**

**Overfishing
(Top Down - Trophic Cascade)**
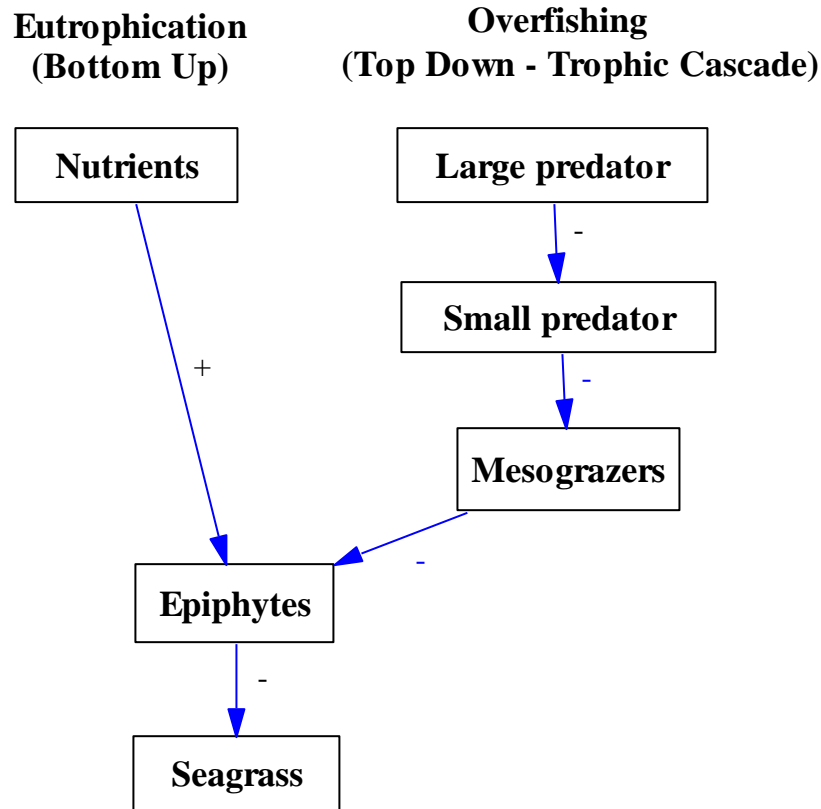
Figure 2.6 Two potential routes to seagrass decline, bottom up eutrophication and top down trophic cascades brought about by over harvesting of top predatory species. Source: Heck Jr. & Valentine, (2006).

2.2.3 OTHER ASSOCIATED SPECIES

Species other than direct grazers of leaf or epiphyte material are associated with *P. oceanica* meadows. Similar to the canopies of other seagrass species, those of *P. oceanica* function to trap particulate matter and make for a favourable feeding environment for filter feeders such as the endangered fan mussel, *Pinna nobilis,* another protected species in EU Member States (EEC, 1992). Several species feature in the detrital food chain, such as the sea urchins *Psammechinus microtuberculatus* and *Sphaerechinus granularis*, the amphipods *Atylus guttatus*, *Melita palmata* and *Gammarelli fucicola,* the isopod *Zenobiana prismatica* and the brachyuran *Sirpus zariquieyi,* all of which are supported by *P. oceanica* leaves shed in the meadow (Boudouresque C. F., et al., 2006; Gambi, Lorenti, Russo, Scipione, & Zupo, 1992). The sea cucumber *Holothuria tubulosa,* and brittle stars *Ophiura*

texturata and *Ophioderma longicauda,* also participate in the degradation of leaf litter, as do several species of bacteria and fungi such as *Corollospora maritima* (Boudouresque C. F., et al., 2006). This is the beginning of the detritus based food web, a main mechanism of energy transfer from *P. oceanica* leaves to higher trophic levels. The abundance of small invertebrates that are supported by *P. oceanica* leaves, leaf litter and matte are preyed upon by species such as the starfish *Asterina Panceri* and *Echinaster sepositus,* the crustacean *Palaemon xiphias,* the molluscs *Sepia officinalis* and *S. minima* and the fishes *Coris julis*, *Diplodus annularis*, *Hippocampus guttulatus*, and several species of *Symphodus*, amongst others (Harmelin-Vivien & Francour, 1992). The herbivorous sea urchin *Paracentrotus lividus* is consumed by the starfish *Marthasterias glacialis*, the spider crab *Maja squinado* and the fish *Coris julis*, *Diplodus vulgaris*, *D. sargus*, *Sparus aurata*, *Symphodus mediterraneus*, *S. roissali* and *S. tinca*, while the large bivalve *Pinna nobilis* is consumed by the octopus *Octopus vulgaris* (Boudouresque C. F., et al., 2006)*.* The diet of fish such as damselfish *Chromis chromis*, and spiracle *Spicara smaris* and *S. maena* consists of plankton that directs their day activity to exploiting the water column. During the night however, planktivorous fish seek refuge in *P. oceanica* meadows where they are preyed upon by scorpionfish *Scorpaena notata*, *S. porcus*, *S. scrofa*, combers *Serranus cabrilla* and *S. scriba,* and conger eel *Conger conger* (Francour, 1997). Of course*,* benefits other than nutrition are made available through *P. oceanica* habitat and interactions other than those of the predator-prey type operate to further boost the diversity of the meadows (Hughes, Williams, Duarte, Heck Jr, & Waycott, 2009). Important linkages are often established between species; the prawn *Pintonia pinnophylax* that inhabits the shell of its pinnid host *P. nobilis,* which in turn resides within the *P. oceanica* meadow, is one example. This particular guild, adequately described as a "Russian doll" kind of association by Richardson et al. (1997), is vulnerable at each of its three levels and is in actual fact a nested chain of endangered species (Richardson, Kennedy, Duarte, & Proud, 1997).

2.3 SEAGRASS COLONISATION

Given suitable conditions, seagrasses colonise new areas via the dispersion of seeds or via vegetative fragments, a process that is directly related to the availability of propagules (Di Carlo, Badalamenti, Jensen, Koch, & Riggio, 2005). As a member of the angiosperms, *P. oceanica* successfully produces flowers and fruits; such events have been observed in many areas of the Mediterranean (Diaz-Almela, Marba, & Duarte, 2007) despite extreme variation between years. Even so, flowering of *P. oceanica* is generally considered a rare occurrence (Hemminga & Duarte, 2000). Plant fragmentation may alternatively provide an asexual mechanism by which propagation may take place. Vegetative fragments have been observed to act as dispersal units, enhancing the recruiting ability of seagrass species (Campbell, 2003). Along with infrequent seed production, the actual establishment of *P. oceanica* seedlings in the natural environment is also an uncommon occurrence (Balestri, Piazzi, & Cinelli, 1998), although high germination rates have been achieved in laboratory and field studies. The asexual mode of propagation is therefore predominant for *P. oceanica.*

Clonal growth is the main mechanism by which *P. oceanica* occupies space, during the colonisation of new habitat for example, or in recovering from disturbance. Such means of vegetative propagation is common to all clonal plants, and is a key trait in understanding and modelling the dynamics of seagrass populations (Duarte & Sand-Jensen, 1990; Hemminga & Duarte, 2000). The growth of *P. oceanica* rhizomes regulates the rate at which shoots are formed within a meadow as well as their spatial distribution (Marba & Duarte, 1998). Rhizome growth is a tightly regulated process with rules that govern the rate at which rhizome internodes are added, the size of rhizome internodes, the frequency at which rhizomes branch, the angle at which branching takes place, and the rhizome length in between consecutive shoots (Cain, Dudle, & Evans, 1996). *P. oceanica* rhizomes elongate at a rate of 2.3 cm per year meaning that the production of a network with 5m of horizontal rhizome requires a time period of 55 years (Marba & Duarte, 1998). Nevertheless the structure of *P. oceanica* meadows is far from static. Variety and plasticity in *P. oceanica* architecture establishes a capacity to adapt to disturbance or resource heterogeneity (Hemminga & Duarte, 2000). Variability in the elongation rate of vertical rhizomes has

been shown to reflect fluctuations in sediment accretion, illustrating adaptive responses to sand burial (Vermaat, 1997). Adaptive responses to changes in other influencing factors such as light or temperature have also been documented (Marba & Duarte, 1995). Knowledge on the dynamics of *P. oceanica* rhizome growth makes it possible to predict and understand the extent and density of a population.

3 SYSTEM FOR ASSESSING *POSIDONIA OCEANICA* HABITAT

3.1 SYSTEM DYNAMIC CONCEPTS AND MODEL DEVELOPMENT
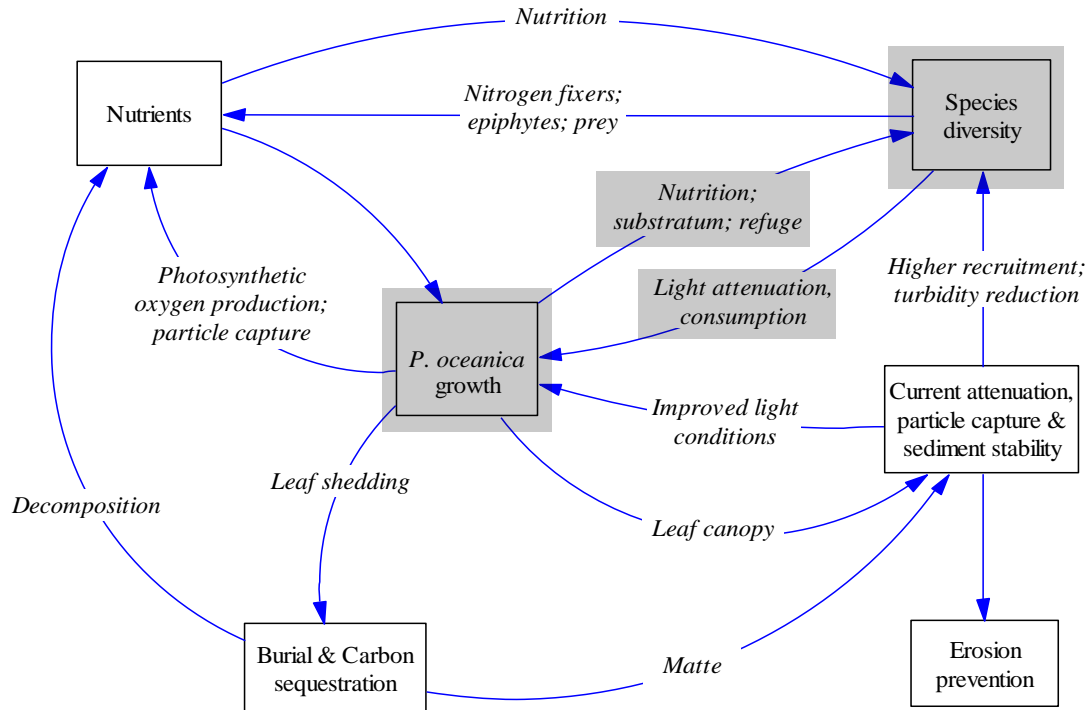
Figure 3.1 Links between *Posidonia oceanica* and the surrounding environment. Boxes represent dynamics that *P oceanica* meadows provide as ecological services to other species, including humans. Arrows are labelled to show the way in which variables in the diagram interact with one another. Shaded variables are the focus of this modelling effort.

Figure 3.1 brings together many of the previously discussed variables that characterise the complex *Posidonia oceanica* ecosystem, and some of the interactions between them. Boxed variables represent dynamics that *P oceanica* meadows provide as ecological services to other species, including humans. By impacting the growth of *P. oceanica* and other variables in the diagram, such as species diversity and nutrient levels in coastal waters, humans may compromise many of the services offered by this habitat. The model developed through this work, titled System for Assessing *Posidonia oceanica* Habitat (SAPOH), attempts to representaspects of the relationships between *P. oceanica* growth and species diversity within the habitat, shaded in Figure 3.1 below. Unshaded variables

are to eventually feature in an extended version of the protopype presented in this dissertation.

One of the main feedback loops that SAPOH features has already been presented in Figure 1.3, illustrating negative, balancing feedback, in which epiphytes present on the leaves of *P. oceanica* attenuate light to slow down or oppose any initial increase in seagrass growth via photosynthesis. The other main feedback loops in SAPOH involve epiphytic grazers (Figure 3.2) and their role in controlling the extent to which light is attenuated by epiphytes. As *P. oceanica* grows and its canopy becomes more dense, increased refuge from predators to organisms within is evident. Similarly, the number of larvae recruited as passive particles is also a function of canopy density, and it is assumed that the grazers in the SAPOH model benefit from both the refuge and recruitment services offered by *P. oceanica* habitat. As increased grazer survival and recruitment cause the number of adult grazers to increase, a larger amount of epiphyte biomass is consequently consumed, and the epiphyte population is thus kept under control. Therefore, as less light is attenuated, *P. oceanica* may photosynthesise more efficiently and its growth is thus reinforced via both loops in Figure 3.2.
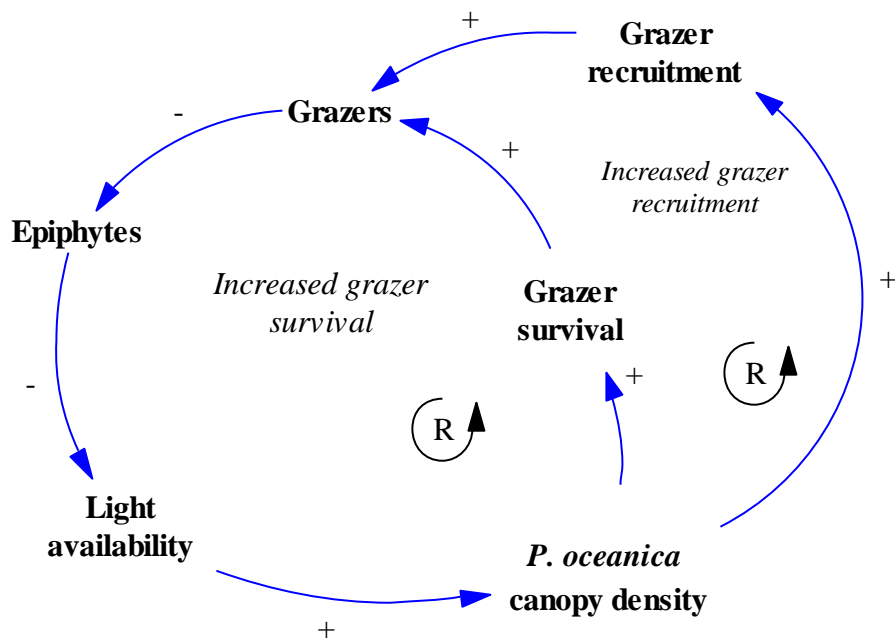
Figure 3.2 Reinforcing dynamics in the SAPOH model, the above diagram features two feedback loops.

Any attempt to simulate the above interactions must feature the following as part of the model:

 i. Light
 ii. *Posidonia oceanica*
 iii. Epiphytes
 iv. Grazers

System dynamics uses stocks and flows as the fundamental building blocks for modelling dynamic behaviour that emerges from complexity such as that displayed in Figure 3.2. Stocks and flows are familiar to every one of us. For example, the balance in our bank account is the accumulation, or stock, of the amount going in minus the amount going out. It increases as we deposit (flow in) and decreases as we spend (flow out). In other words, stocks represent sinks or reservoirs in a system and accumulate the difference between an inflow and an outflow to a process. Stocks serve to characterise the state of a system, they give systems memory and inertia, and are responsible for time delays. The inclusion of stocks and flows to a model of a system is what enables the dynamics of that system to be captured (Sterman, 2000). The populations of *Posidonia oceanica*, epiphytic and grazer organisms may all be represented by stocks in a model, as these accumulate or are depleted over time. Light on the other hand does not accumulate over time and therefore may not be modelled as a stock. This is highly evident in natural systems, where light is rather 'captured' and converted into stores of biomass by autotrophic organisms such as *P. oceanica* and several species of its epiphytes.

System dynamics uses a particular diagramming notation for stocks and flows (Figure 3.3):

 ▪ Stocks are represented by rectangles (similar to a container holding the contents of a stock);
 ▪ Inflows and outflows are represented by a pipe pointing into (adding to) and out of (subtracting from) the stock respectively;

- Valves control the flows and clouds represent the sources and sinks for the flows. A source represents a stock from which flows may arise while a sink represents the stock into which flows may drain into. Both sources and sinks originate outside the boundary of the model and are assumed to have infinite capacity, meaning they may never constrain any flow they support.

General Structure

Key
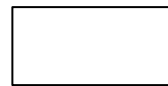
Stock
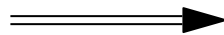
Flow

Valve (Flow Regulator)

Source or Sink
(Stocks outside model boundary)

Figure 3.3 Stock and flow diagramming details. Adapted from Sternman (2000).

If the biomass associated with a meadow of *P. oceanica*, the biomass of the epiphytes in the meadow, and the population of grazers that use the meadow are to be represented by stocks, we must also identify any flows that "grow" these stocks or "deplete" them. For example, the addition of *P. oceanica* biomass through photosynthesis is represented as an inflow into the *P. oceanica* biomass stock; senescence and shedding of leaf biomass in the stock is represented as an outflow. When modelling the stock of epiphyte biomass on the P.

oceanica canopy, the inflow corresponds to the production of biomass via the process of photosynthesis. The consumption of epiphyte biomass by grazers is an outflow from the epiphyte stock. An outflow from the epiphyte stock is biomass consumed by individuals that graze and consume the epiphytes. In the case of a stock of grazers, the recruitment of individuals to the habitat represents an inflow while the death of individuals is an outflow (Figure 3.4).
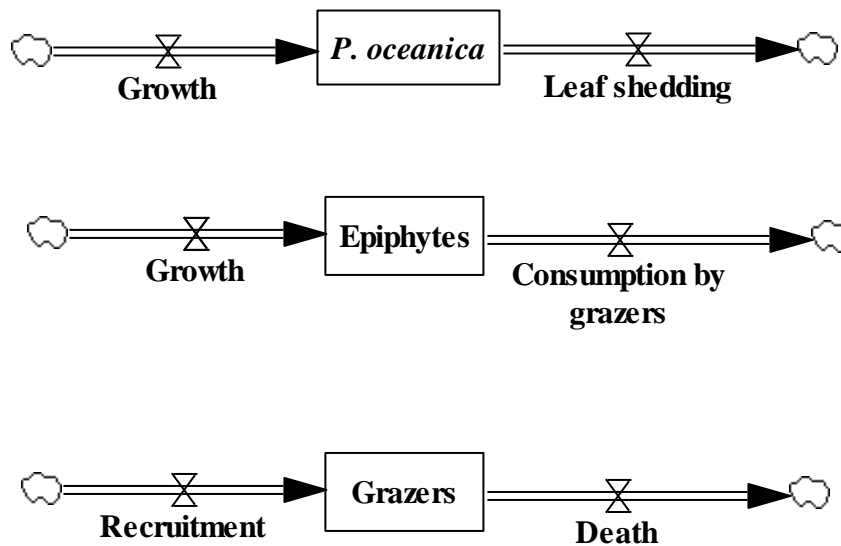
Figure 3.4 Example stocks and flows for *P. oceanica*, epiphytes and grazers in SAPOH.

The accumulation of material within a stock has a precise mathematical meaning, and is expressed as the integral of the flows of material into minus the flows of material out of the stock (Sterman, 2000). The structure presented in Figure 3.3 above therefore corresponds exactly to the integral equation below:

$$Stock\ (t) = \int_{t_0}^{t} [Inflow(t) - Outflow(t)]dt + Stock\ (t_0)$$

where Inflow(s) and Outflow(s) represent the value of the inflow and outflow at any time s between the initial time t_0 and the current time t. Expressing the accumulation of biomass or individuals in the stocks in Figure 3.4 similarly gives the following:

$$P.\,oceanica\,(t) = \int_{t_0}^{t} [growth(t) - leaf\,shedding(t)]dt + P.\,oceanica(t_0)$$

$$Epiphytes\,(t) = \int_{t_0}^{t} [growth(t) - consumption\,by\,grazers(t)]dt + epiphytes\,(t_0)$$

$$Grazers\,(t) = \int_{t_0}^{t} [recruitment(t) - death(t)]dt + grazers(t_0)$$

3.2 MODEL STRUCTURE AND FUNCTION

3.2.1 MODEL SETTINGS

While the focus of SAPOH is the 'system scale', it must also integrate important dynamics at the shoot- and meadow-scale that are central to the way in which this habitat provides its ecological services. Therefore, the functioning model described here restricts its boundaries to the ecological functioning of a hypothetical patch of *P. oceanica* habitat and does not address dynamics that span broad spatial scales beyond that meadow. The model structure could easily be adapted to a specific meadow by adjusting the starting values of several model parameters. Growth of *P. oceanica* and the way in which it interacts with epiphytes and their grazers is essentially what features in this developed SAPOH prototype. The model was programmed using Vensim® PLE Plus software of Ventana Systems Inc. and all model relationships were derived from published results.

The currencies used in the model are kg of dry biomass weight in the case of *P. oceanica* and epiphyte stocks, and individuals for the grazer stocks. This was considered suitable given that nutrient dynamics are not considered within the boundaries of this initial modelling attempt. Furthermore, data on matter fluxes in *P. oceanica* habitat were readily available in units of dry weight and this also influenced the choice of model currency.

The model makes use of Runge-Kutta (R-K) methods for numerical integration. Rather than assume that rates are constant over time intervals, i.e. that average rate from time t to time t + dt equals the rate at the start of the interval, R-K methods calculate the rate at time t + dt using temporary stock values at time t +dt which have been calculated by Euler's method. Stock values at time t + dt are then calculated by using a weighted average to approximate rates of change across the interval from time t to time t + dt. R-K integration methods require more computing power per time step over conventional methods of integration, but on the other hand provide a greater accuracy (Sterman, 2000). Using R-K integration enabled the avoidance of integration errors that were present when using the Euler method.

The SAPOH prototype uses years as the unit of time since the intended purpose of the model was to capture habitat dynamics that operate on time scales running across several years. Indeed, the goal of being able to simulate for a number of years is one common to many ecological models (Elkalay, et al., 2003). The smallest time constant in the model is the rate of photosynthesis for both *P. oceanica* and its epiphytes. The model is set to recalculate and update all system states 32 times per year in order to achieve an appropriate balance between numerical accuracy and computing speed.

3.2.2 MODEL STOCKS AND FLOWS

The current version of SAPOH does not model belowground biomass stocks, and draws its boundaries around the fluxes of material produced aboveground. The standing stock of *P. oceanica* is determined by the balance between the process of production that incorporates biomass, and processes that remove biomass such as leaf senescence. The burial and consumption of produced material also decrease the standing stock of *P. oceanica* biomass in the model. The *P. oceanica* stock is therefore expressed in biomass units of kg of dry weight (kgDW) and accumulates its inflows less its outflows. Figure 3.5 illustrates these flows while the integral equation below expresses the value of the *P. oceanica* stock, *P* (in kgDW), at a time *t*.

$$P(t) = \int_t^{t_0} [P\ growth - P\ leaf\ shedding - P\ consumption - P\ burial]dt + P(t_0)$$
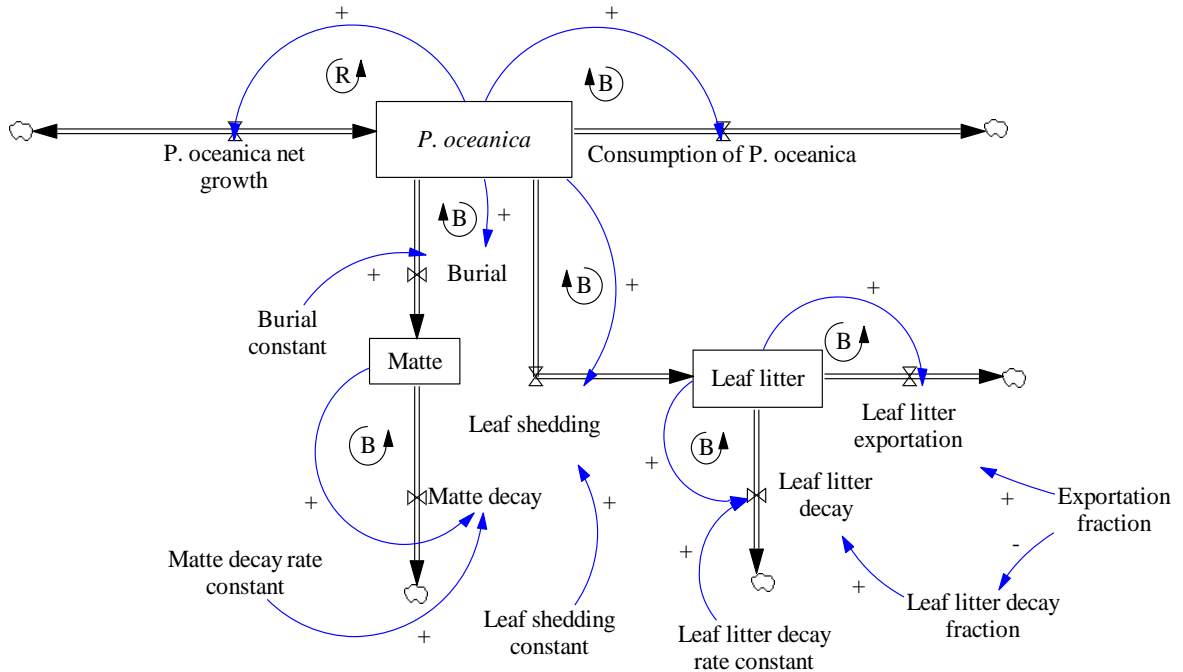
Figure 3.5 *P. oceanica* stocks and flows.

In the SAPOH model, *P. oceanica* epiphytes are represented by an autotrophic community that is dominated by microalgae in the SAPOH model. Similar to the stock of *P. oceanica* biomass, the modelled microalgal epiphyte community depends upon the presence of light for photosynthesis and growth. Loss of algal epiphyte biomass occurs once the leaf substratum to which it is attached is detached from the *P. oceanica* canopy, as a result of leaf senescence. Algal epiphytes are also consumed by herbivorous animals and this is the second loss of material accounted for in the model (Figure 3.6). The material (kgDW) in the algal epiphyte stock, *E*, at any point in time *t* may accordingly be described by the following integral:

$$E(t) = \int_t^{t_0} [E\ growth - E\ to\ litter - Consumption\ of\ E]dt + E(t_0)$$
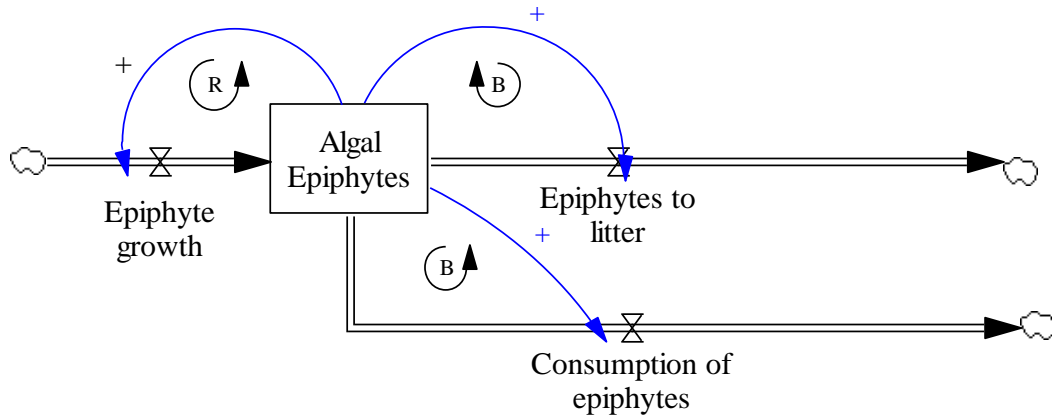
Figure 3.6 Algal epiphyte stock and flows.

Both *P. oceanica* and algal epiphyte stocks required the introduction of a mechanism to control their growth to not exceed the carrying capacity of the system. By incorporating balancing loops that seek to counteract the reinforcing growth pattern of *P. oceanica* and algal epiphytes, the required s-shaped, goal-seeking behaviour is created. The modelling equations correspond to the rate equations associated with the classic logistic model for bounded population growth. The value for *P. oceanica* maximum shoot density in the model (Table 3.1) is in accordance with maximum values quoted from several studies in the Mediterranean (Alcoverro, Cerbian, & Ballesteros, 2001; Zupo V. , Buia, Gambi, Lorenti, & Procaccini, 2006), while that adopted for maximum epiphyte loads is as identified in studies by Brush and Nixon (2002). The patch of *P. oceanica* habitat in SAPOH is set to an area of 100m². The dynamics by which the habitat patch may proliferate and increase in area are not considered in this model prototype. Nevertheless space acts to limit the density of the modelled patch of *P. oceanica* meadow. The balancing loop shown below counteracts the reinforcing growth pattern of *P. oceanica* and causes initial exponential growth to slow and seek equilibrium with a set maximum shoot density that has been assigned from published studies. A similar approach was used for modelling algal epiphyte growth.
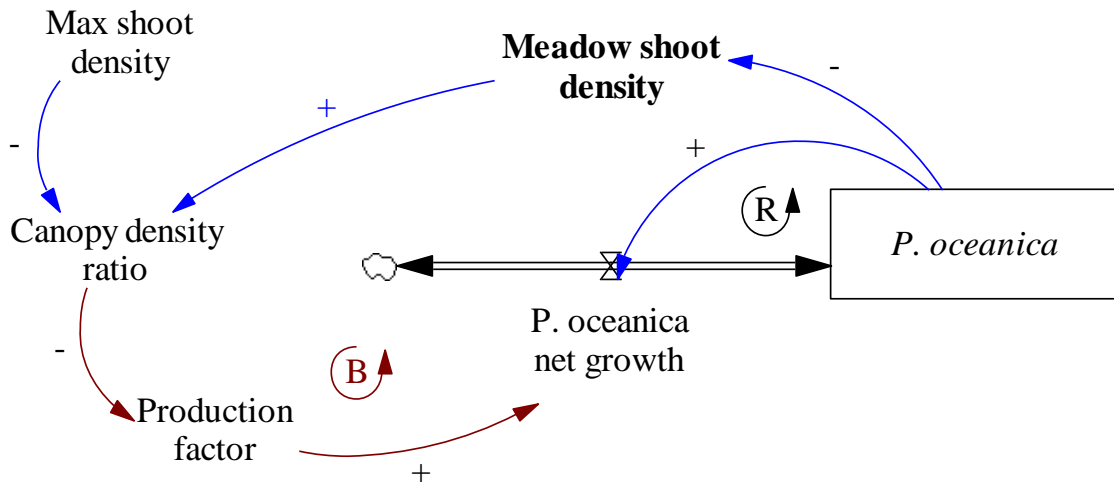
Figure 3.7 Counteracting reinforcing and balancing loops bring about S-shaped growth for *P. oceanica* biomass.

Individuals grazing on algal epiphytes comprise a third stock, 'Grazers', which has been based on epiphyte-consuming gastropods such as *Gibbula* and *Jujubinus* spp. Grazer larvae form another stock that increases as individuals are recruited into the meadow area (Figure 3.8). The process of recruitment in the model may represent births occurring within the meadow area or the immigration of individuals from areas outside of the meadow. The stock of grazers increases as larval individuals are recruited to the adult stage and decreases when adults die. While the stock unit for the *P. oceanica* and epiphyte stocks is kgDW, in this case the basic stock unit is an individual. The state of the grazer, *G*, and larval, *L*, stocks at any point in time may be therefore expressed by the following integrals, where the quantities L(t) and G(t) are expressed as the number of individuals:

$$L(t) = \int_t^{t_0} [L\ recruitment - L\ mortality\ - L\ maturity]dt + L(t_0)$$

$$G(t) = \int_t^{t_0} [L\ maturity - G\ mortality]dt + G(t_0)$$
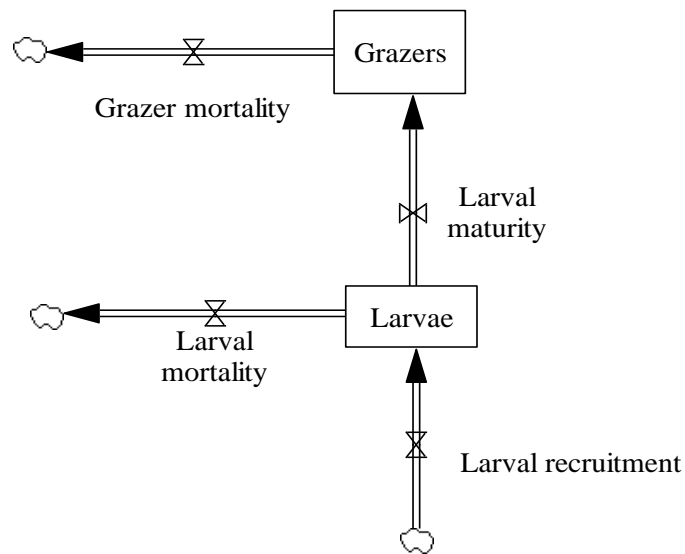
Figure 3.8 Grazer related stocks and flows in the SAPOH model.

Larval survival to the adult stage is based upon constants from published studies (Table 1). It is assumed that the density of the seagrass canopy affects the rate at which larvae are recruited to the meadow; a denser canopy captures more larvae as passive particles. The canopy density ratio, which is the meadow shoot density/shoot carrying capacity, therefore directly features as a factor in the equation accounting for larval recruitment (*LR*), which is expressed in larvae recruited per year.

$$LR = (annual\ recruits\ per\ m^2 * meadow\ area) * canopy\ density\ ratio$$

The *P. oceanica* canopy density ratio in the model is also set to affect the mortality of individuals at both the adult and larval stages as it is related to the shelter that is being offered from predators. In other words, as the canopy becomes less dense, the mortality of both adults and juveniles increases. The model assumes that all individuals that survive the larval stage mature into adult grazers. The canopy density ratio features directly in the equations describing larval maturity (*LM*) and grazer recruitment (*GR*), and indirectly, via the lack of shelter variable (1-canopy density ratio), in the equation describing the rate of grazer mortality (*GM*). All quantities on the left hand side below are expressed as individuals per year.

- 56 -

$$GR = \text{(annual recruits per m}^2\text{*meadow area)*canopy density ratio}$$

$$LM = \text{(larvae*average survival)*canopy density ratio}$$

$$GM = \text{((1/average lifetime)*grazers)*lack of shelter}$$

Table 3.1 Constants affecting stocks and flows

Parameter	Selected value	Units	Source
Maximum shoot density	1000	shoot m^{-2}	[1], [5]
Maximum epiphyte load	0.5	kgDW m^{-2} leaf area	[2]
Annual juvenile recruits per m^2	2000	individuals m^{-2}	[3]
Average adult grazer lifetime	2-4	year	[4]
Juvenile mortality	0.73	fraction/month	[3]

Sources: [1] Alcoverro, Cerbian, and Ballesteros, (2001); [2] Brush and Nixon (2002); [3] Sala and Zabala (1996); [4] Turon, Giribet, Lopez and Palacin, (1995); [5] Zupo, Buia, Gambi, Lorenti and Procaccini (2006).

3.2.3 *P. OCEANICA* OUTFLOWS (BURIAL, CONSUMPTION AND LEAF SHEDDING)

The rate at which matter from the *P. oceanica* biomass stock is lost to burial and leaf shedding was assumed to be constant in the SAPOH model and was set at a fraction of the plant biomass per annum as identified from published studies. The modelling constants determining annual burial and leaf shedding fluxes were assumed to be similar to those estimated for the *P. oceanica* habitat of Lacco Ameno within the Gulf of Naples (Pergent, Romero, Pergent-Martini, Mateo, & Boudouresque, 1994). While this prototype does not focus on the dynamics related to *P. oceanica* leaf senescence and burial, the magnitudes of these flows may nevertheless be adjusted to tailor SAPOH to the fluxes inherent within

meadows subject to different regimes. Flows of biomass, in kgDW, from the *P. oceanica* stock to the belowground matte stock or to the leaf litter stock are therefore described by the following equations respectively. Left-hand quantities are expressed in kgDW/year:

$$Burial \ = \ burial \ constant * P. oceanica$$

$$Leaf \ shedding \ = \ leaf \ shedding \ constant * P. oceanica$$

where the burial and leaf shedding constants are assigned values of 0.28 per year and 0.65 per year respectively, as identified in Pergent et al (1994). Once biomass is shed in the form of senescent leaves, the material enters the stock of leaf litter present within the meadow. From this stock of leaf litter, material may either decay within the meadow or be exported to areas outside the meadow. The leaf litter stock, *LL,* , in the meadow at any point in time *t* may therefore be expressed as the integral of the flow of material into the stock, in other words the shedding of leaves from the canopy, minus the outflows due to litter exportation or decay. *LL* is expressed in units of kgDW:

$$LL(t) = \int_{t}^{t_0} [leaf \ shedding - LL \ exportation - LL \ decay] dt + L(t_0)$$

The proportions of material that are exported from or remain within the meadow are also assumed to be constant for a particular habitat. This is because these fluxes are directly related to the hydrodynamics of the waters surrounding the *P. oceanica* habitat and are characteristic to a particular location or site. Once again, the fluxes identified for the Lacco Ameno meadow in Pergent et al (1994) are adopted for the purposes of this model and leaf litter exportation (*LLE*) and leaf litter decay (*LLD*) fluxes are therefore expressed in units of kgDW/year and defined as follows:

$$LLE = \ leaf \ litter \ * \ exportation \ fraction$$

$$LLD = \ leaf \ litter * leaf \ litter \ decay \ fraction * leaf \ litter \ decay \ rate \ constant$$

where the exportation fraction and leaf litter decay fraction are 0.62 per year and 0.38 per year respectively. The rate at which leaf litter material decays in the meadow must also be incorporated into the equation defining the outflow from the leaf litter stock due to decay. The decay kinetics of *P. oceanica* leaf blades were estimated on the basis of decay experiments by Pergent et al. (1994) and were shown to follow a simple negative exponential model. The average decay rate of k (exponent of the model) is therefore incorporated in the above equation and is assigned a value of 0.8421.

Any leaves that are shed and detached from the canopy of *P. oceanica* take with them any epiphytic organisms that are attached. This shedding of leaves therefore presents a route via which epiphytic material, as well as seagrass material is lost. The loss of epiphytic matter through this flux may be described by the following equation which is a function of the *P. oceanica* leaf shedding constant. Epiphytes to litter is a flow expressed in units of kgDW/year.

$$Epiphytes\ to\ litter\ =\ algal\ epiphytes\ *\ leaf\ shedding\ constant$$

In the case of material stored in the matte underground, decay is the only route via which it may be lost. The material in the matte, *M*, at any point in time *t* is therefore the integral of the rate at which biomass enters the stock via burial, minus the rate at which biomass decays. *M* is expressed in units of kgDW/year:

$$M(t) = \int_{t}^{t_0} [burial - M\ decay]dt + M(t_0)$$

The rate at which decay takes place within the matte is defined by a matte decay rate constant. The same value, 0.00036 per year, as that identified for the site at Ischia, Italy by Mateo, Romero, Perez, Littler M. and Littler D. (1997) is adopted for the purposes of the SAPOH prototype. Note that the value of this decay flow is much smaller than the decay of

material occurring in the leaf litter stock, indicating the vast difference in decay kinetics between these two stocks of material within *P. oceanica* meadows.

3.2.4 PRIMARY PRODUCTION

Photosynthesis is the only term in the model that is responsible for the growth of *P. oceanica* biomass. It is assumed that all other requirements, which may function to limit and modify the process of photosynthesis, such as temperature or nutrients, are satisfied and do not influence the growth process. As epiphyte growth is influenced by the same abiotic factors that influence the seagrass host (Alcoverro, Duarte, & Romero, 1997), light is similarly the main abiotic factor influencing this algal community in the developed model. The non linear model used to describe photosynthesis-irradiance (P-I) relationships for *P. oceanica* and the associated algal epiphytes, is based upon Michaelis-Menten kinetics, as presented in Vermaat (1997):

$$ P = \frac{P_{max} * I}{(K_m + I)} - R $$

where P is the net photosynthetic rate (mgO_2 gDW^{-1} hr^{-1}) at irradiance I (μmol PAR m^{-2} s^{-1}); P_{max} defines the gross maximal (or asymptotic) photosynthetic rate; K_m is the half saturation constant (μmol PAR m^{-2} s^{-1}); and R is the respiration rate. Light or irradiance is expressed as photosynthetically active radiation (PAR) which lies between wavelengths of 400 and 700nm. K_m is the parameter that represents the threshold for irradiance-saturated photosynthesis. Net photosynthesis is then determined by subtracting respiration from gross photosynthesis.

Photosynthetic parameters for *P. oceanica* were obtained directly from Vermaat (1997) (Table 3.2) while similar parameters for the epiphytic community growing on *P. oceanica* were not directly available from the literature search conducted. Consequently, assumptions had to be made and parameters for algal epiphyte photosynthesis were adapted from Enriquez, Duarte, Sand-Jensen, & Laurentius Nielsen (1996) (Table 3.2), who

document P-I relationships for a wide variety of unialgal cultures, marine and freshwater phytoplankton assemblages and terrestrial plants. Mean values derived from the 62 microalgal studies in Enriquez et al (1996) were adopted for algal epiphyte production in the model. Light saturating irradiances are derived in the model and are calculated from the initial slope of the P-I curve specific to *P. oceanica* and the 62 species of microalgae from Enriquez et al. (1996). The initial slope of P-I curves is from here onwards referred to as α as in Vermaat (1997). Light saturating irradiance values are calculated using the formula below. Photosynthetic values for the *P. oceanica* and the epiphyte stocks in the model are shown in Table 3.2 and their respective P-I curves shown in Figure 3.9.

$$\text{Light saturating irradiance} = \frac{\text{Maximum photosynthetic rate}}{\alpha}$$

Table 3.2 Parameters used to provide photosynthetic values for the model.

Parameter	Selected value	Units	Source
Max photosynthesis rate	7.1	mg O_2 gDW^{-1} h^{-1}	[9]
Max photosynthesis rate (epiphytes)	14	mgC gC^{-1} h^{-1}	[6]
A	0.05	mgO_2 gDW^{-1} h^{-1} / μmol PAR m^{-2} s^{-1}	[9]
α (epiphytes)	1	mgC gC^{-1} h^{-1} / μmol PAR m^{-2} s^{-1}	[6]
Respiration rate	1.3	mgO_2 gDW^{-1} h^{-1}	[9]
Respiration rate (epiphytes)	2	mgC gC^{-1} h^{-1}	[6]
Photoperiod	9	h	[7]
Background attenuation	0.035	m^{-1}	[5]
Attenuation coefficient A	95.7	%	[2]
Attenuation coefficient B	0.022	kgDW m^{-2}	[2]

O_2 to C factor	0.3	gC gO_2^{-1}	[8]
Photosynthetic quotient	1.25	/	[3]
C to DW factor	3.125	gDW gC^{-1}	[4]
C to DW (epiphytes) factor	6.67	gDW gC^{-1}	[1]

References quoted: [1] Alcoverro, Duarte, and Romero (1997); [2] Brush and Nixon (2002); [3] Dennison (1987); [4] Duarte (1990); [5] Duarte, Agusti, & Satta (1998); [6] Enriquez, Duarte, Sand-Jensen and Nielsen. (1996); [7] PVGIS European Commission (2008); [8] Ruiz & Romero (2001); [9] Vermaat (1997).
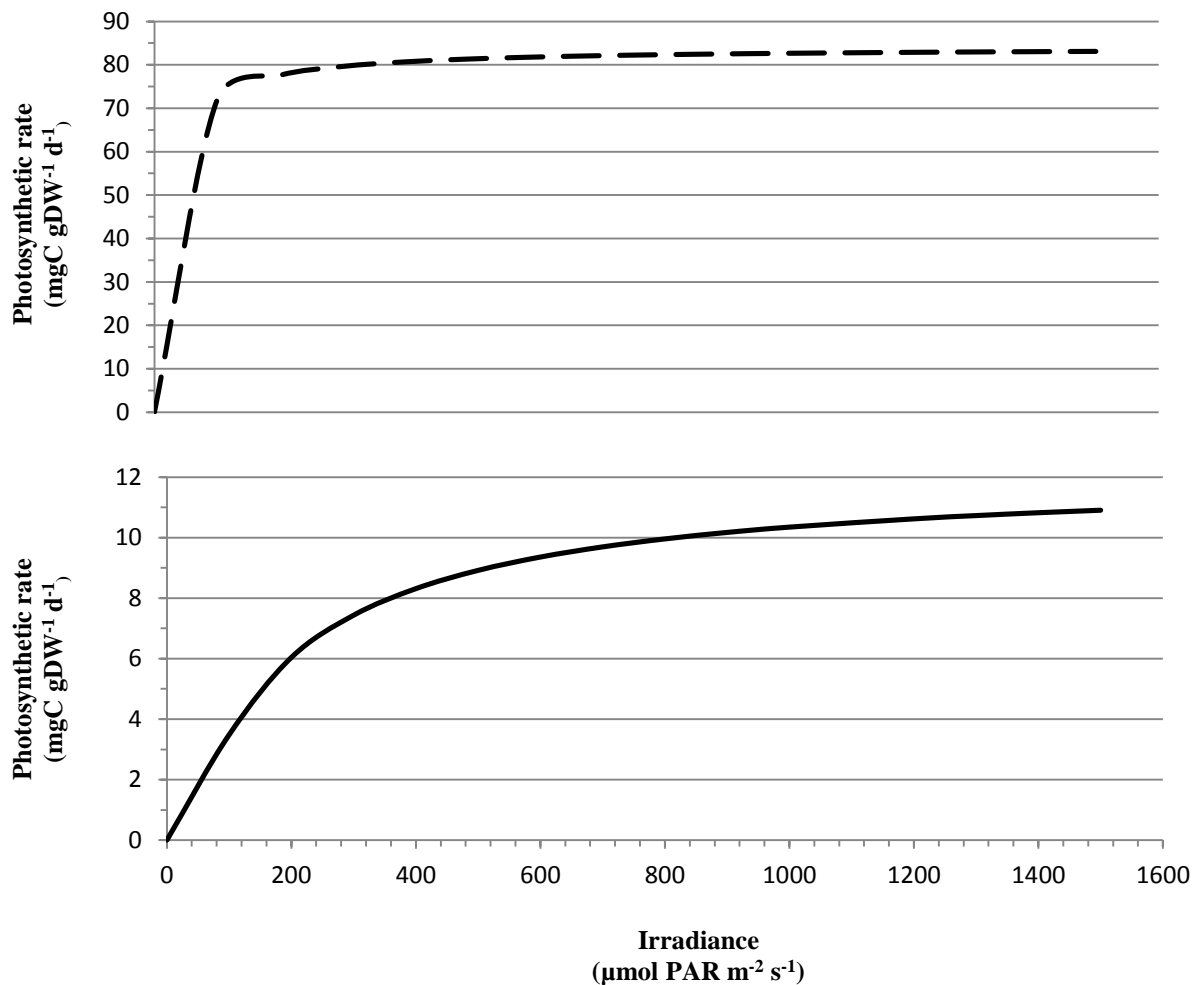
Figure 3.9   Photosythesis-Irradiance curves for the seagrass *P. oceanica* (solid) and its epiphytic community (dashed).

The approach utilised to calculate the annual amount of biomass fixed in the developed model involves the calculation of the daily carbon gain using a daily average photoperiod. The daily gain in carbon is then converted to a yearly gain in kg of dry biomass weight. The daily photoperiod and amount of irradiation present at the surface are both exogenously controlled. While these values may be varied to suit different environments, they are set to the values of 9 hours and 1150μmol PAR m^{-2} s^{-1} in most scenarios, reflecting average radiation conditions in the Mediterranean (PVGIS European Commission, 2008). Multiplying oxygen production values by a factor of 0.3 enabled conversion of daily oxygen production to net daily carbon gain. This is based on the assumption that a photosynthetic quotient (moles O_2 produced/moles C assimilated) of 1.25 is representative for seagrasses, including *P. oceanica* (Dennison, 1987; Ruiz & Romero, 2001). Since algal epiphyte photosynthetic parameters were already expressed in C units, conversion was necessary only for *P. oceanica* production values. The model also required a conversion of carbon photosynthesis values to DW production values. In this case a factor of 3.125gDW/gC was used for *P. oceanica* values, and a factor of 6.67gDW/gC for algal epiphytes. These factors were derived from Duarte (1990) and Alcoverro, Duarte, & Romero, (1997) which detail the nutrient content for *P. oceanica* and its algal epiphytes respectively. Alcoverro, Duarte & Romero (1997) perform their analysis in four different *P. oceanica* meadows and do not find any significant difference in epiphyte nutrient content. As the present model is concerned solely with C content, a content of 33% C was therefore assumed for *P. oceanica* and one of 15% C for its algal epiphytes.

Photosynthetic values and consequently growth may be negative as they are net rates, representative of a balance between photosynthesis and respiration. The model is set such that when meadow shoot density falls to below 0.01, growth ceases to be negative and just stops all together.

3.2.5 LIGHT ATTENUATION

Seagrasses depend on available light for photosynthesis. Irradiance typically decreases exponentially with increasing depth; this relationship is captured in the SAPOH model and is determined using the Beer-Lambert law as follows:

$$I_z = I_0 \, e^{-kz}$$

where I_z is the irradiance at depth z within the water column, I_0 is the surface irradiance, k is the water column light attenuation coefficient. Total light attenuation is often determined by summing the attenuation coefficients of the various particles in the water column. Background attenuation in the model was set to 0.035 m^{-1}, a value representative of relatively clear Mediterranean coastal waters (Duarte, Agusti, & Satta, 1998). The exponential decrease in light intensity through water with attenuation set at this value is displayed in Figure 3.10.
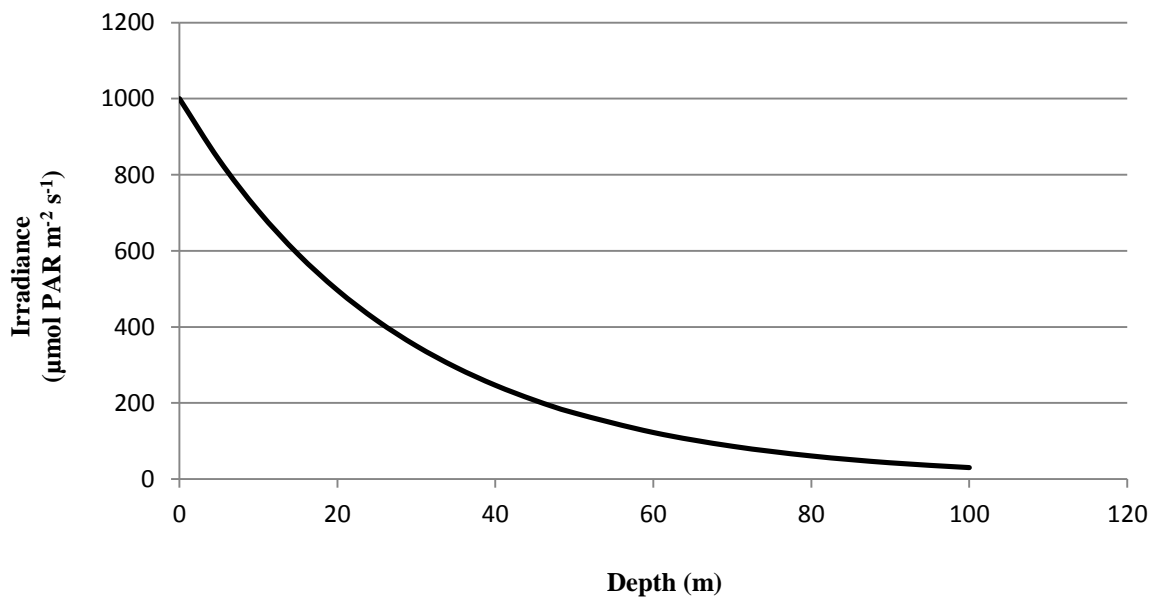
Figure 3.10 Irradiance extinction down the water column due to attenuation by particles.

Suspended sediment and turbidity in the water column act to add to the effect of depth in decreasing the amount of light available for photosynthesis. A turbidity coefficient was included in the model to explore the effects of low light regimes on *P. oceanica* habitat. This coefficient was varied between 0 and 0.75m^{-1} and added to the background attenuation coefficient to determine total light attenuation.

Due to the potential for shading when epiphytic load is high, the model also incorporates an important feedback between the abundance of epiphytes and the amount of light reaching seagrass blades, a critical link in the modelling of submersed plant growth (Fong, Jacobson, Mescher, Lirman, & Harwell, 1997; Madden & Kemp, 1996). Once light has made its way through the layer of water to the benthos, it is then attenuated by the algal epiphytes growing upon the seagrass. Epiphytes attenuate the amount of light reaching the blades of *P. oceanica* in a biomass or density dependent manner (Figure 3.11). Light attenuation due to the presence of epiphytes is frequently shown to be of hyperbolic in form, rarely reaching total attenuation at maximum epiphyte biomass (Best, et al., 2001). Experimental results from Brush and Nixon, (2002) suggest that the attenuation of PAR as a function of intact epiphyte dry weight is adequately described by a negative hyperbolic equation of the form:

$$y = 100 - A \left(\frac{x}{B + X} \right)$$

Given the lack of availability of attenuation data for *P. oceanica*'s epiphytic growth and that the majority of algae typical of *P. oceanica*'s epiphytic community are red or brown algae, it made sense to adopt values for A and B specific to a red algal species *Polysiphonia* sp. (Figure 3.12) from Brush and Nixon's (2002) results; values are 92.4% and 0.022 kgDW m^{-2} for coefficients A and B in the equation above, respectively (Table 3.2). The model therefore assumes that the layer of *P. oceanica* epiphytes attenuate light in a fashion similar to species of *Polysiphonia*; a reasonable assumption given that *Polysiphonia* is similar in colour to the red and brown algae that dominate *P. oceanica*'s epiphytic

community. This assumption is further supported by the fact that *Polysiphonia* spp. also grow epiphytically on *P. oceanica* (Novak, 1984).
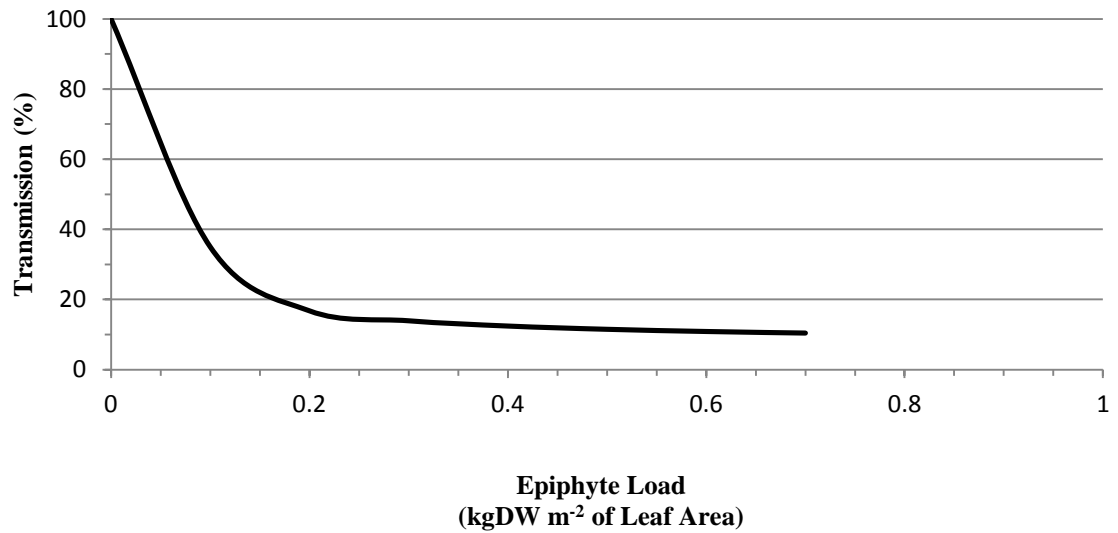
Figure 3.11 Transmission of PAR (%) as a function of epiphyte dry weight density on the seagrass leaves as described by a negative hyperbolic function of the form y = 100-A (x/B+x).
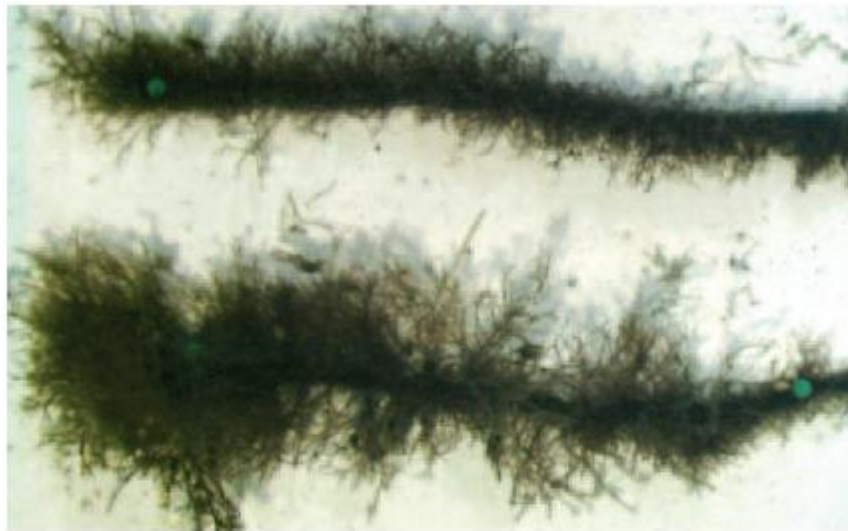
Figure 3.12 Photograph of *Polysiphonia* still intact on *Zostera marina*. Source: (Brush & Nixon, 2002)

3.2.6 CONSUMPTION

Posidonia oceanica and its attached algal epiphytes are both subject to consumption in the model. While for *P. oceanica* this is set as a constant flow out of the stock every year, in the case of the epiphyte stock, this outflow is a function of the size of the grazer stock, as well as other variables such as the annual amount consumed by an individual grazer. This SAPOH prototype does not take material consumed by larvae into account. The amount consumed per grazer is an exogenously controlled variable and its value, 0.043kgDW individual^{-1} day^{-1}, reflects consumption rates for *Gibbula umbilicalis* and *Jujubinus striatus* derived from published studies (Hily, Connan, Raffin, & Wyllie-Echeverria, 2004). Assumptions had to be made as the material consumed in the studies by Hily et al. (2004) does not consist of epiphytes found on *P. oceanica* but rather those found on a different species of seagrass, *Zostera marina*. The mortality of grazer individuals in the model is affected by the availability epiphyte material for consumption. As the latter decreases, the variable describing the average lifetime for an adult grazer, expressed in years, is modified as follows:

$$\text{Grazer lifetime} = (\text{max grazer lifetime*nutrition adequacy})$$

where the variable 'Nutrition adequacy' describes the difference between a value of 1 and the ratio of available food to that required by the grazer population.

Figure 3.13 summarises the ways in which the abovementioned stock and flow structures interact with one another in SAPOH. Circled variables represent dynamics that are described by a group of variables in the full SAPOH model. Although further detail and variables may be found within each of these circles, the purpose here is to present a summary and therefore one must note that not all model variables are illustrated hereunder. Variables that are not illustrated in the figure below may be found in Appendix III that details all variables as they appear in the complete SAPOH model. When looking at Figure 3.13, one can see that the stock of algal epiphytes exerts an influence on *P. oceanica* photosynthesis by attenuating irradiance present in the water column. The population of grazers, through their consumption of epiphytic material, directly exert an influence on the

stock of epiphyte biomass and indirectly so on *P. oceanica* photosynthesis. As previously explained, the growth of *P. oceanica* and algal epiphyte stocks is controlled by a set carrying capacity in the system, while that of the grazer population is a function of nutritional (epiphyte) availability and meadow canopy density – the latter represents the provision of shelter from predators and the extent to which larvae may be captured as particles. All model stocks, parameters and equations are detailed in Appendix I.
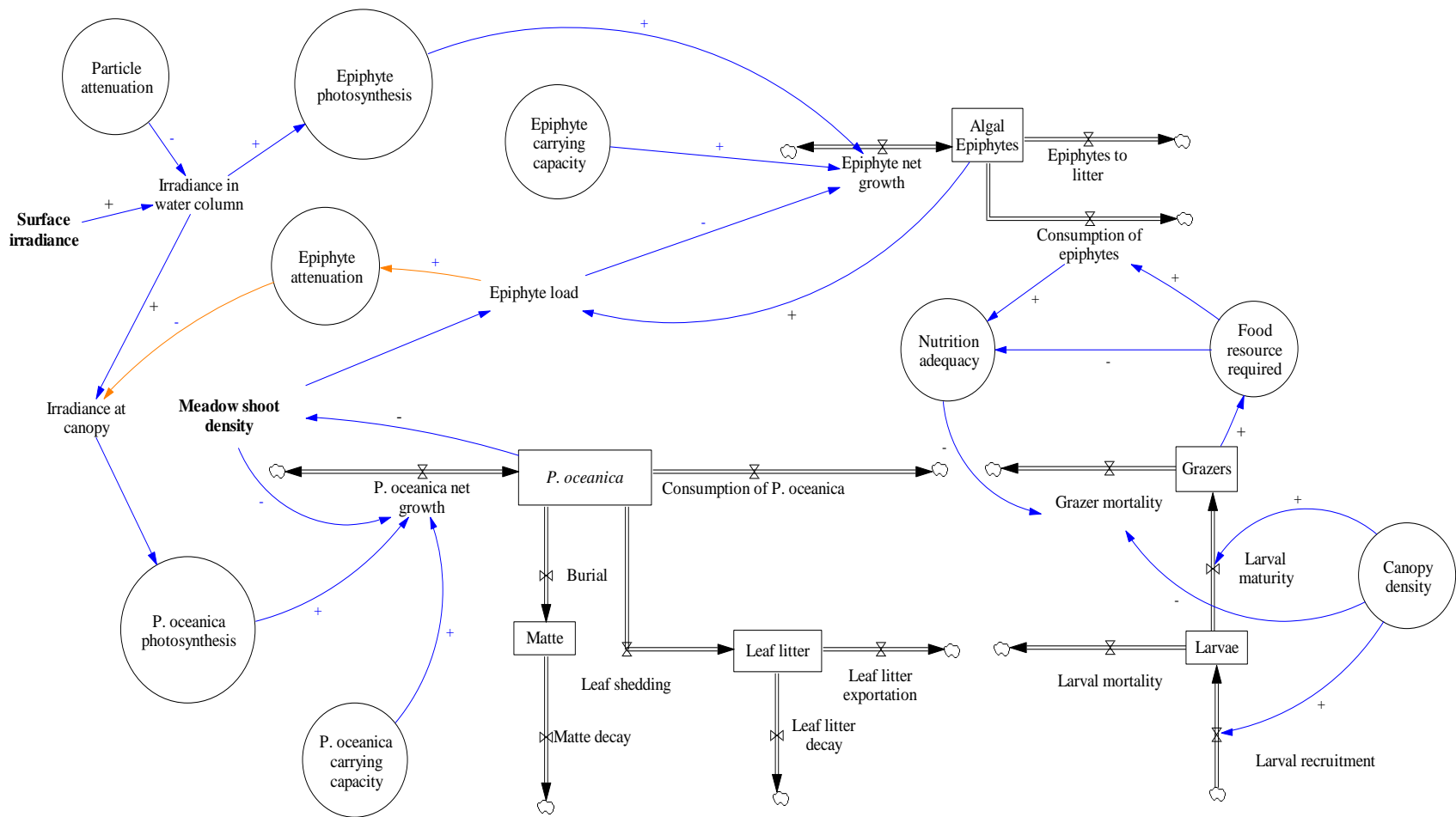
Figure 3.13 A summary of the SAPOH model. Circled variables represent relationships between stock and flow structures that are detailed by a number of variables in the full model.

4 MODEL VALIDATION

A model is considered as valid when it is fit to execute the purpose for which it has been designed. Model testing is often used to build confidence in a model's ability to perform its desired function. Recalling the shaded variables in Figure 3.1, shown again below, the intention behind this research work was to develop a working simulation model that would be able to mimic important dynamics found in *P. oceanica* habitat, apparent with time steps of the scale of one year. These were, in particular, *P. oceanica*'s growth pattern and its interactions with variables such as light, epiphytic algae and grazer organisms. In order to validate SAPOH, we must test the extent to which it is able to account for these relationships. This chapter therefore assesses whether SAPOH is successfully fit for its stated purpose.
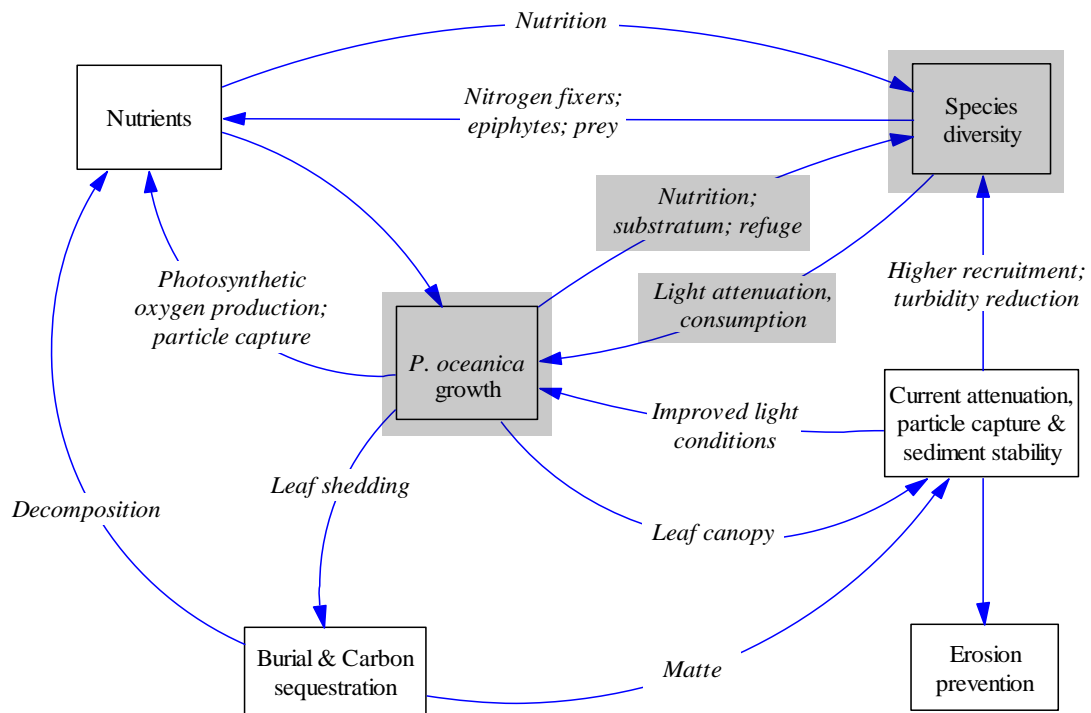
Figure 4.1 Links between *Posidonia oceanica* and the surrounding environment. Boxes represent dynamics that *P oceanica* meadows provide as ecological services to other species, including humans. Arrows are labelled to show the way in which variables in the diagram interact with one another. Shaded variables are the focus of this modelling effort.

Sterman describes a number of tests that may be used to uncover flaws in a model and contribute towards its improvement. Such tests form an important part of the modelling process and some have already been addressed in previous sections. Assessing the model's boundary adequacy is an example of a test that aims to ensure that concepts and variables central to addressing the model's purpose are endogenously included in its structure. Endogenous variables are ones that may receive feedback from other variables within the system. When important variables are treated exogenously, all relevant feedback is cut off; this prevents the model from properly simulating real system behaviour. Important variables and stocks have been identified in the previous chapter, as well as the main feedback loops involving these variables. An important decision that was made during the development of SAPOH particularly relates to boundary adequacy. This was the decision to change the epiphyte biomass consumed by the population of grazers from being an exogenously controlled flow from the epiphyte stock, to an endogenous stock of grazers within the system. This enabled the development model equations that describe the interactions between the grazer community and *P. oceanica* meadows via the provision of services such as larval capture and protection from predators. A second test that has already been presented in previous text is that for integration error. This test aims to assess the sensitivity of results to the choice of time step or the method used for numerical integration.

The following text aims to evaluate SAPOH with respect to Sterman's criteria for three tests that have not been addressed in the text presented so far. These are:

1. Robustness under extreme conditions
2. Response replication
3. Structural validation

4.1 ROBUSTNESS UNDER EXTREME CONDITIONS

An important way to test and validate a model's behaviour is to test for robustness under extreme conditions. In such a test, inputs to the model are assumed to take on extreme values. If the model is sound, then it should continue to behave appropriately (giving

behaviour you would expect), even if those values are of the kind never observed in reality. The question we want to answer is therefore, whether SAPOH behaves realistically when stressed by extreme conditions. This section describes three extreme conditions tests for evaluating the model. These are:

1. Extreme Depth
2. Extreme Irradiance
3. Absence of Epiphytes

4.1.1 EXTREME DEPTH TEST

Table 4.1 shows conditions corresponding to the extreme depths used in this test. At 0m, light has not yet passed through any medium and light availability in the water column is therefore expected to be equal to the irradiance present at the surface. At greater depths, light is attenuated as it passes through the water medium. Suspended particles additionally contribute by scattering or absorbing irradiance. As expected, the water column irradiance in Table 4.1 is identical to that present at the surface at 0m. Values for the epiphyte attenuation variable indicate the degree to which light has been scattered and absorbed by the layer of epiphytes growing upon *P. oceanica.* The presence of epiphytes at 0m causes a reduction in the amount of irradiance that passes through to the *P. oceanica* canopy. At 1000m, despite the absence of epiphytes, irradiance has fallen to a tiny fraction of that available at the water surface. This implies that the only cause of irradiance reduction at 1000m is its absorption and scattering by particles throughout the water column.

Table 4.1 Extreme conditions test 1. Conditions at extreme depth values at the end of a 5 year period.

Variable	Surface conditions	Extreme depth conditions
Depth (m)	0	1000
Surface irradiance (μmol PAR m^{-2} s^{-1})	1150	1150
Particle attenuation	0	0
Irradiance in water column (μmol PAR m^{-2} s^{-1})	1150	7.25×10^{-13}
Epiphyte attenuation	75	0
Irradiance at canopy level	287	7.25×10^{-13}

Figure 4.1 shows the decline in *P. oceanica* and algal epiphyte biomass at a depth of 1000m over a period of five years. As *P. oceanica* and algal epiphytes are absent at this depth, the grazer population cannot be sustained and also falls to 0. One may notice a delay in the time needed for the grazer population to decline to zero; in fact the population declines to one individual some time after the disappearance of both *P. oceanica* and algal epiphytes. This is unrealistic as grazer adults are unable to survive without the presence of a food source. This inaccuracy stems from the way in which the equation for grazer mortality combines the effect of lack of nutrition with that of lack of shelter from the meadow canopy. Future work dedicated towards fine-tuning SAPOH should address this inconsistency between simulated and real grazer population decline. Figure 4.2 displays *P. oceanica*, algal epiphyte and adult grazer stock behaviour at a depth of 0m. Note that the amount of biomass present in the epiphyte stock exceeds that in the *P. oceanica* stock at 0m. This is indicative of a meadow that is overloaded with algal growth and is an inaccuracy that stems from the fact that SAPOH does not account for nutrients and nutrient limitation to the process of photosynthesis. Without nutrient limitation, the algal epiphytes photosynthesise much more.

P. oceanica

Algal Epiphytes

Grazers
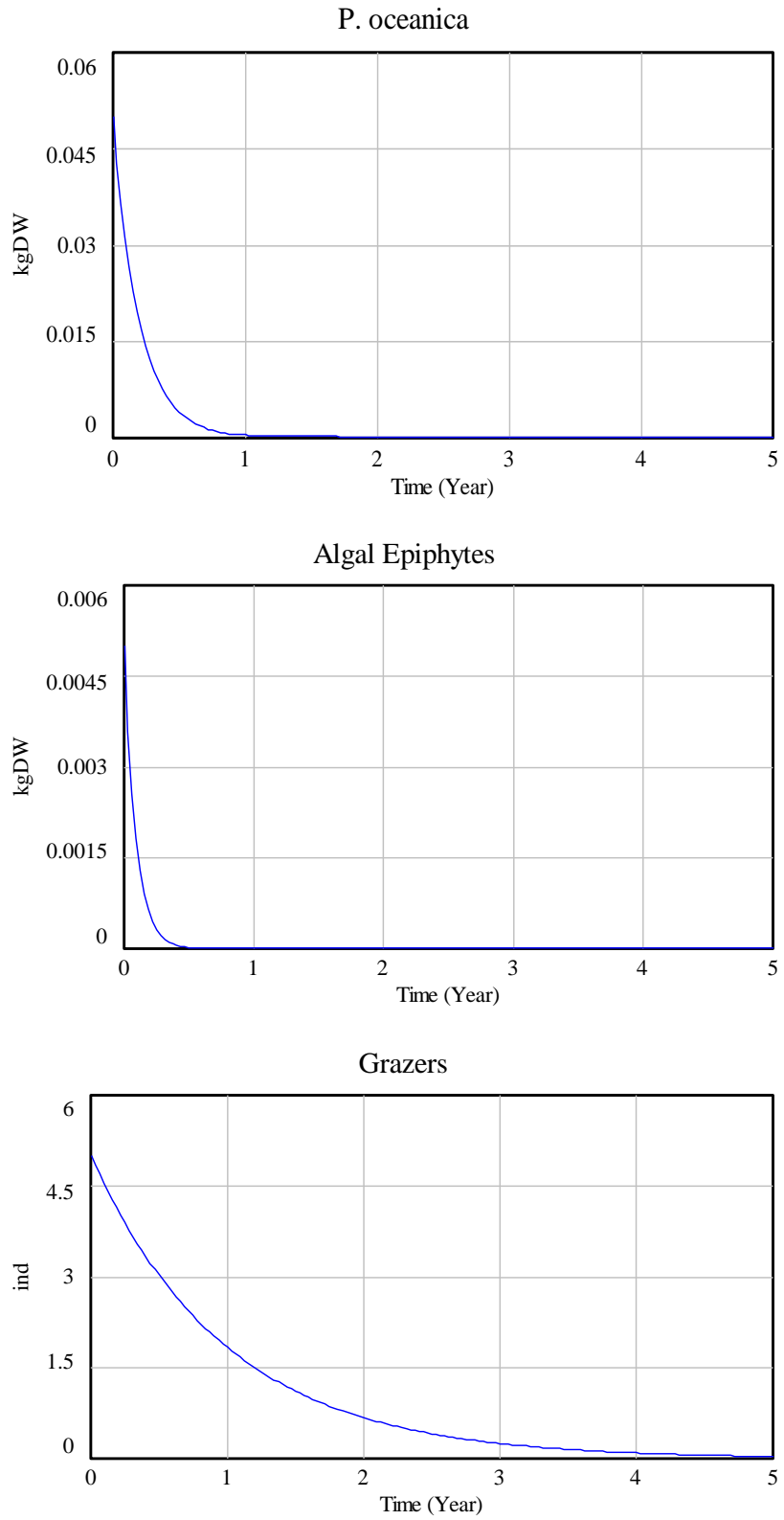
Figure 4.2 Major stock behaviour over a time period of five years, at a depth of 1000m

P. oceanica

Algal Epiphytes

Grazers
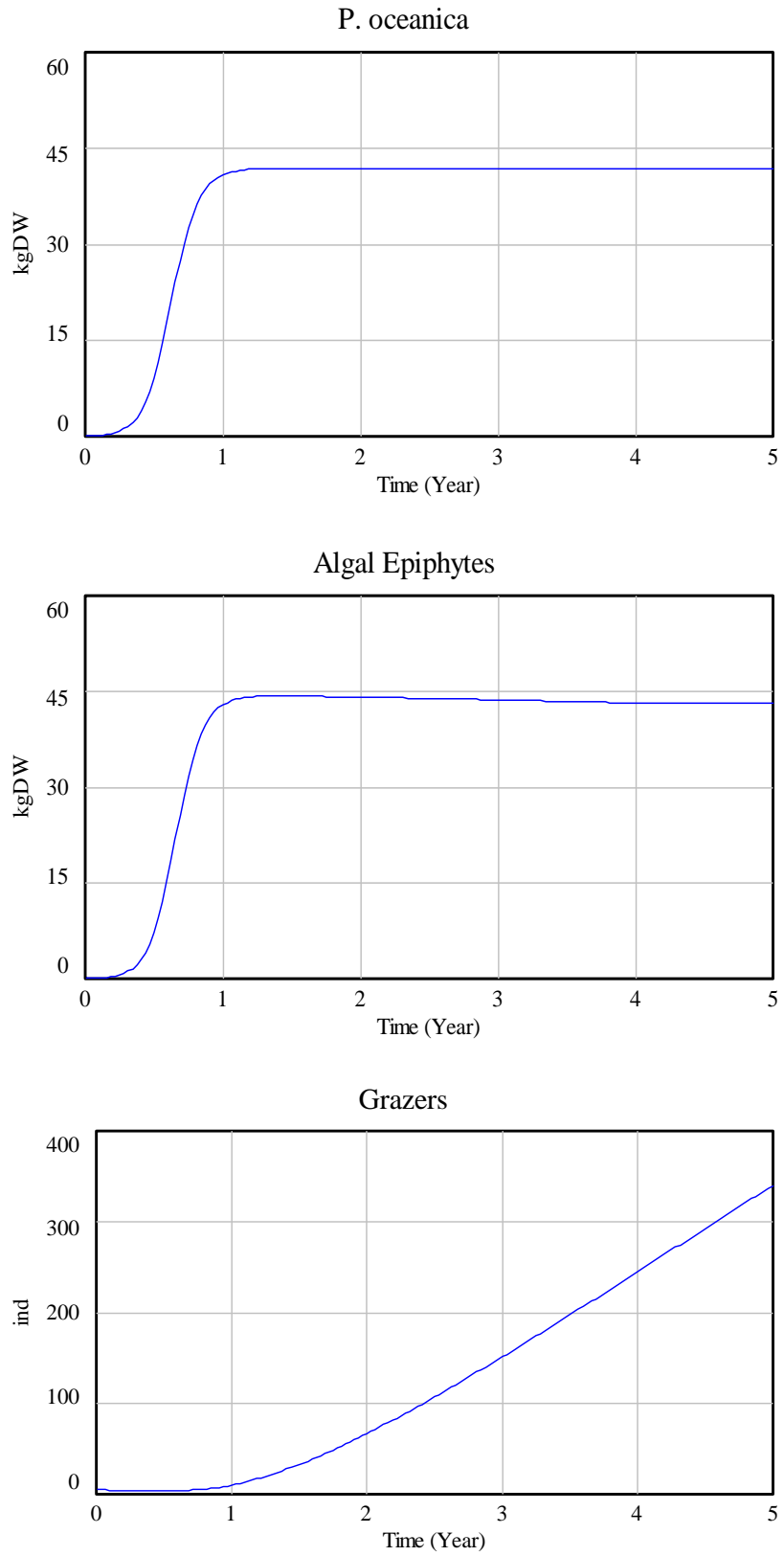
Figure 4.3 Major stock behaviour over a time period of five years, at a depth of 0m.

4.1.2 EXTREME IRRADIANCE TEST

Testing the way in which growth responds to variability in the light regime is a second test important to assessing the robustness of SAPOH. The model features a net growth rate for *P. oceanica* and its epiphytes which is essentially determined by the balance between the processes of photosynthesis and respiration.   While net production and growth can therefore be negative under highly deteriorated light conditions; *P. oceanica* and epiphyte stocks must never fall below zero, as this is impossible. On the other hand, when light is overabundant and no longer limiting, growth is always limited by other factors that are not as abundant. Space is one example of a factor that may act to limit growth in SAPOH (Figure 4.3). When recalling the P-I curves for *P. oceanica* and epiphytes (Figure 3.9) we should also expect both photosynthetic rates to reach a saturation point at a given irradiance.   This would essentially render any increase in irradiance past this point ineffective at enhancing growth. Setting the surface irradiance variable to zero simulates the absence of light in the environment while setting this variable up to a large value simulates a situation where light is not limiting.

Meadow shoot density
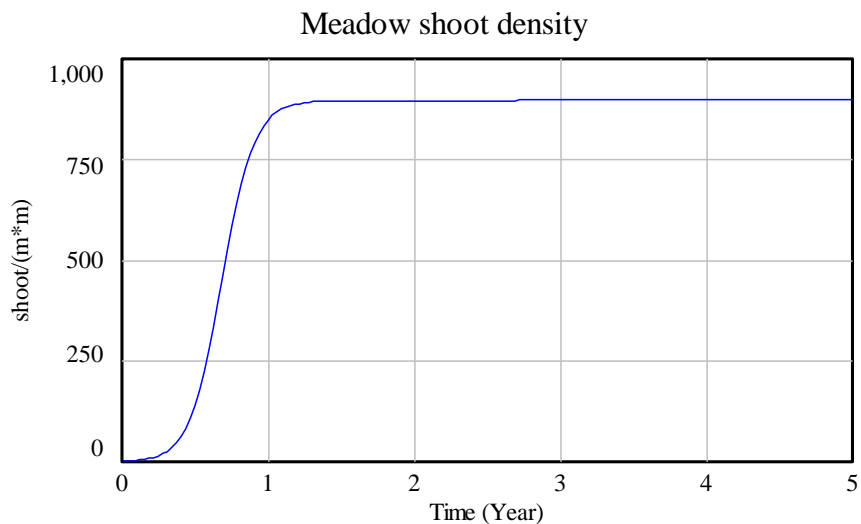
Figure 4.4 Space acts to limit growth in SAPOH causing meadow shoot density to level off at carrying capacity. The above simulation was run at a depth of 5m. .

Conditions during the extreme irradiance tests are presented in Table 4.2. Graphs showing behaviour over time for zero irradiance are identical to those presented in Figure 4.1. As expected, light-dependent growth quickly approaches and remains at 0 when no irradiance is present. Both *P. oceanica* and epiphyte stocks fall to very low values, but do not become negative. At the opposite extreme, doubling the available irradiance has no effect on either growth rate. This is because at 5000 µmol PAR m^{-2} s^{-1}, light in the water column has ceased to limit epiphytic photosynthesis. Similarly, even 88% of available light has been attenuated by epiphyte cover; *P. oceanica's* growth is not limited by insufficient irradiance. For this reason, at both 5000µmol PAR m^{-2} s^{-1} and 10000µmol PAR m^{-2} s^{-1} irradiances, *P. oceanica* and algal epiphyte stocks increase in an unrestricted manner until equilibrium is reached with their set carrying capacity in SAPOH. Graphs showing *P. oceanica*, and algal epiphyte stock behaviour over time for irradiances of 5000µmol PAR m^{-2} s^{-1} and 10000µmol PAR m^{-2} s^{-1} are identical to those presented in Figure 4.2. It is interesting to note the way in which the rate at which *P. oceanica* and epiphyte stocks grow behaves over time (Figure 4.4). Growth for both *P. oceanica* and its epiphytes increases exponentially until the balancing carrying capacity loop for each causes growth to seek equilibrium at a value that the system can sustain. In the case of algal epiphytes, growth falls below the equilibrium level before increasing again to stabilise at its equilibrium value. While this is not unrealistic, future adaptations to SAPOH may want to avoid the use of a set value for carrying capacity, and incorporate other variables, such as nutrients and temperature, which may function to limit photosynthetic growth.

Table 4.2 Extreme conditions test 2. Conditions at extreme irradiance values

Variable			
Irradiance in water column (µmol PAR m^{-2} s^{-1})	**0**	**5,000**	**10,000**
Epiphyte load (kgDW m^{-2} leaf area)	0	0.48	0.48
Epiphyte attenuation (%)	0	88	88
Irradiance at canopy (µmol PAR m^{-2} s^{-1})	0	583	1167
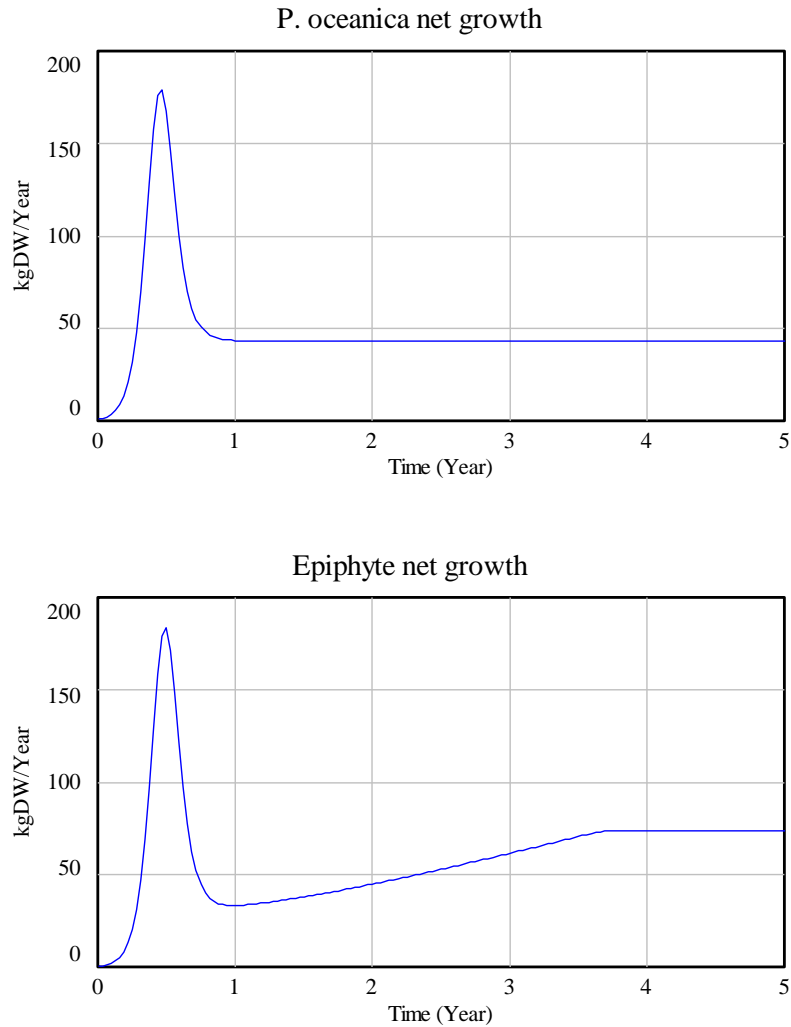
Figure 4.5   Behaviour over time for *P. oceanica* and epiphyte net growth at high irradiance values. System carrying capacity for *P. oceanica* and epiphyte biomass causes initial exponential growth to stabilise at a sustainable value.

The stock of grazers that is dependent on epiphytes for nutrition falls to zero when no nutrition is available at zero irradiance. The grazer population reaches its highest density of 15 individuals per m^2 when irradiance is saturating and does not limit the growth of its food source (Figure 4.5). There is no set carrying capacity value for the population of grazers in SAPOH.   The value at which this population reaches equilibrium in the simulated *P. oceanica* habitat is essentially a function of the amount of food and shelter offered by the meadow.
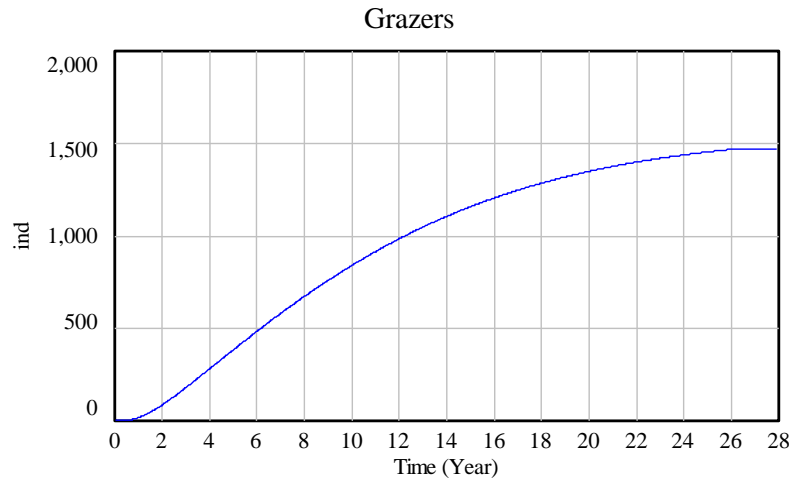
Figure 4.6   The grazer population levels off at around 1500 individuals per 100m^2 of meadow area when light does not limit its food source.

4.1.3 ABSENCE OF EPIPHYTES TEST

As a third test, system performance is assessed in the absence of epiphytes. This is simulated by changing the initial epiphyte stock value to 0. In the absence of epiphytes to attenuate light from the seagrass canopy, one would expect *P. oceanica* to photosynthesise and grow at higher rates due to the increased availability of irradiance. While larvae may benefit from the increased density of the *P. oceanica* canopy, grazer adults are not expected to survive for long in the absence of their only food source in SAPOH. Table 4.3 details system conditions in a zero epiphyte setting and compares these to a simulation in which epiphytes are present in normal amounts. As expected, irradiance at canopy level is equal to that in the water column in the absence of epiphytes. Figure 4.6 shows *P. oceanica* stock and meadow shoot density behaviour under both simulations and as expected, the biomass present in the *P. oceanica* stock and meadow shoot density are higher when epiphytes are absent from the system.

Table 4.3 Extreme conditions test 3. Conditions in the absence and presence of epiphytes

Variable	Epiphytes are absent	Epiphytes are present
Epiphyte attenuation (%)	0	88
Irradiance in water column (μmol PAR m^{-2} s^{-1})	965	965
Irradiance at canopy (μmol PAR m^{-2} s^{-1})	965	113
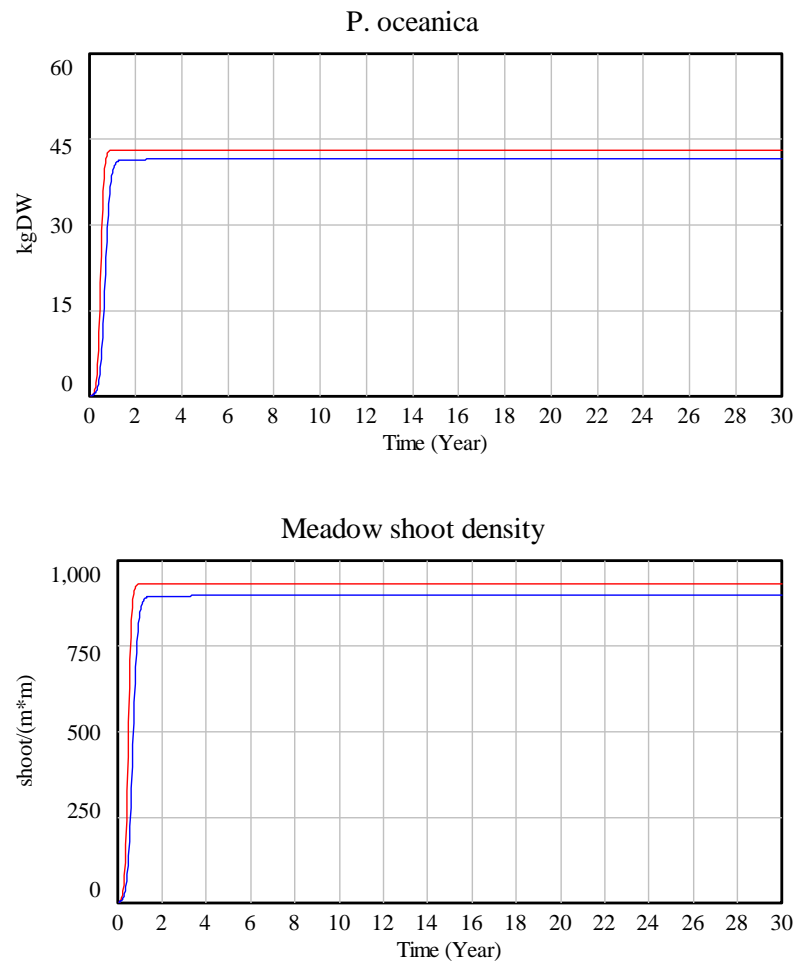
Figure 4.7 *P. oceanica* stock and meadow shoot density in the presence (blue) and absence (red) of epiphytes over a 30 year time period.

While larval maturity is higher in the absence of epiphytes, the adult grazer population is larger when epiphytes are present (Figure 4.7). Larval maturity is lower when epiphytes are present in the system as the meadow grows to a lower density and consequently has less shelter to offer (Figure 4.6). On the other hand, when left without any source of nutrition, adult grazer lifetime quickly drops, causing the grazer mortality rate to increase rapidly (Figure 4.7). When epiphytes are absent from SAPOH, the grazer population consists solely of those adults that have just matured from the larval stage. This is because larvae do not depend upon epiphytes as a food source in the simulated system and therefore the absence of epiphytes from the system does not affect larval mortality as it does for the adult grazer population.
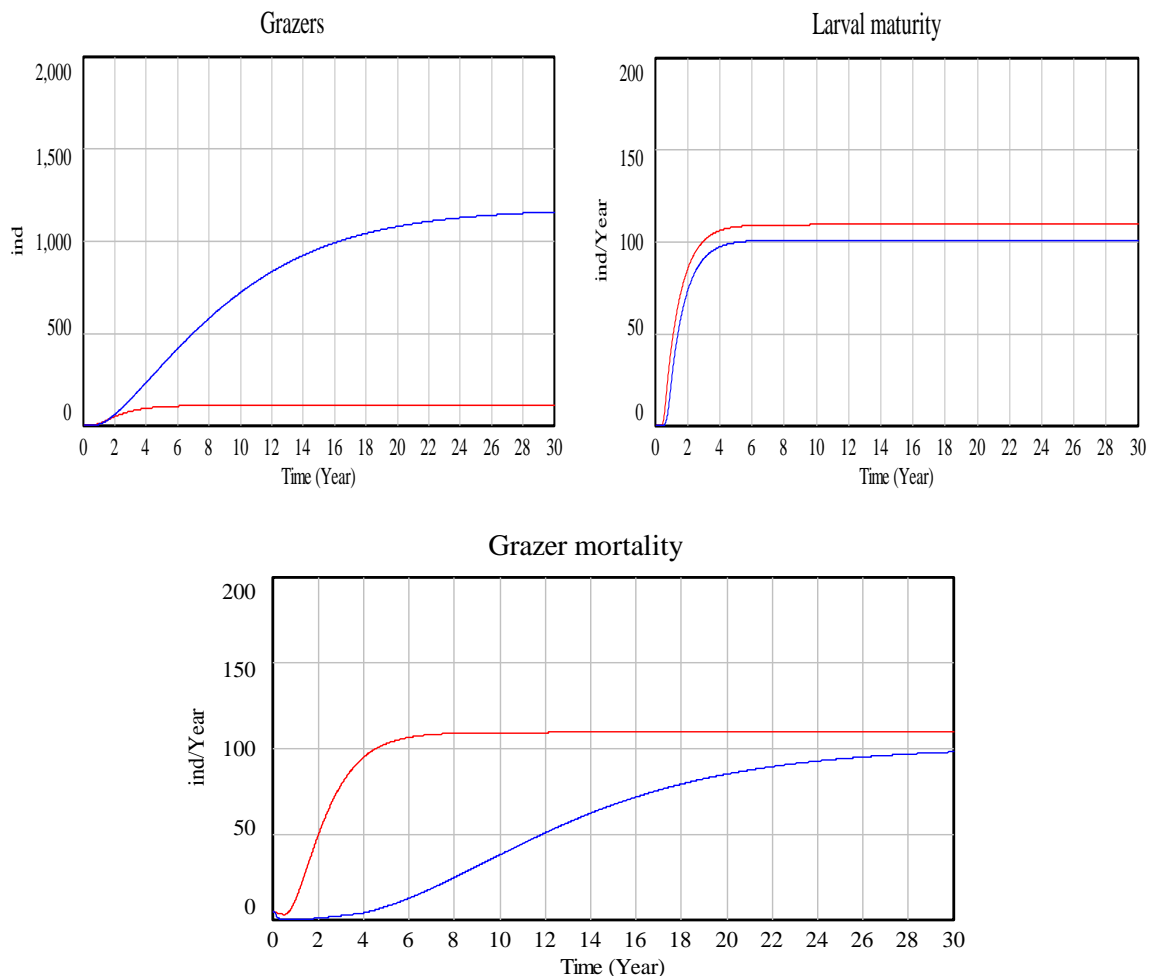
Figure 4.8 Grazer stock and the flows larval maturity and grazer mortality in the presence (blue) and absence (red) of epiphytes over a 30 year period.

4.2 RESPONSE REPRODUCTION

A second way of testing and validating a dynamic model is to see if it is able to generate the various system responses that are observed in the real system. Consistency between simulated and real responses helps to establish confidence in the model, and determines a range of conditions under which the model may be considered reliable.

The simulated depth limit for *P. oceanica* in SAPOH is well within the range that has been observed and published. Duarte (1991) determines an average depth limit of around 35m for *P. oceanica*, from a total of 29 different studies. At simulated depths greater than 55m, with a surface irradiance of 1150, the density of the *P. oceanica* meadow in SAPOH declines to 0 within a few years. Grazers are often observed in lower densities at greater depths (Turon, Giribet, Lopez, & Palacin, 1995). Simulating at increasing depths in SAPOH, while maintaining all other variables constant, also causes grazer density to decrease in accordance with field observations.

Authors have observed that light absorption by epiphytes is characterised by an initial rapid increase followed by a levelling off at some place below, and never reaching 100%. This pattern is consistent with the general parabolic law that governs light capture by photosynthetic organisms (Brush & Nixon, 2002; Cebrian, Enriquez, Fortes, Agawin, Vermaat, & Duarte, 1999). Light attenuation by epiphytes will not exceed 88% when simulating at high epiphyte loads in SAPOH, in accordance with observed system behaviour (Figure 4.9).
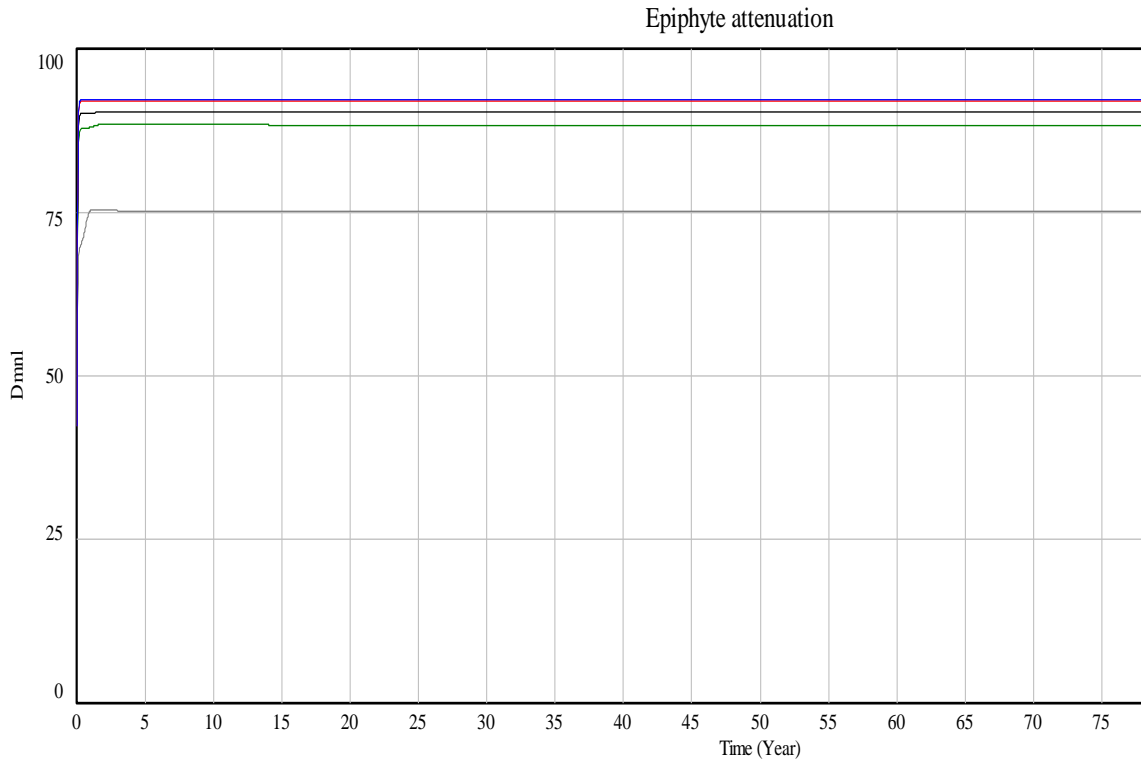
Figure 4.9 Simulating at increasing epiphytic loads. Coloured graphs represent epiphyte loads as follows: 0.1 (grey), 0.5 (green), 1 (black), 5 (red), 10 (blue). Epiphyte loads are expressed in units of kg/m² of *P. oceanica* leaf surface area. The extent to which light is attenuated initially increases until simulations at higher epiphytic loads are unable to attenuate further light.

The role of grazers in controlling the biomass of algae growing epiphytically on seagrasses (see Figure 3.2) has been identified as important and significant (Heck Jr. & Valentine, 2006). Although this feedback loop is present within SAPOH, it is particularly insensitive to fluctuations in the grazer population (Appendix II). While these results may stem from the simplification inherent within SAPOH, and it is also likely that the effect of grazing on epiphytes is only apparent when combined with other factors that have not been taken into account within the model.

4.3 STRUCTURAL VALIDATION

This section presents how SAPOH fares against tests for the structural assessment of a model. Sterman (2000) promotes the involvement of independent third parties in the model development process and encourages expert assessment and inspection of the model's structure. Specialist input to SAPOH was sought from two experts, one in the field of

system dynamic modelling, the other in the dynamics of *P. oceanica* habitat. Weekly interviews were held with these experts to review and evaluate SAPOH structure and design. Interviews essentially involved meeting in person or communicating over the phone. During every consultation, opinions were solicited and experts were helpful in pointing out important literature relevant to the research work. Furthermore, both experts participated by directly inspecting draft stock and flow structures, discussing system boundaries and reviewing model equations and system setup.

Sterman (2000) also asks the following questions with the purpose of assessing a model's structure; the questions have all been answered with respect to SAPOH's structure.

1. *Is the model structure consistent with relevant descriptive knowledge of the system?*

Every equation and stock and flow structure within SAPOH has been derived from published literature thus ensuring consistence between model structure and the descriptive knowledge of the system. The model equations and subsystem diagrams presented so far are consistent with the literature presented in earlier sections.

2. *Is the level of aggregation appropriate?*

Assumptions regarding aggregation in the model are present in the case of epiphytes and grazer organisms. SAPOH assumes that all algal epiphytes in the system photosynthesise uniformly according to a generalised equation for microalgae, and that all algal epiphytes attenuate light according to an equation specific to *Polysiphonia* spp. In fact, all epiphytes in SAPOH are aggregated within one stock. The same can be said for grazer organisms feeding upon the algal epiphytes; it is assumed that all organisms in the system that graze upon epiphytes are the same species and are placed together in a stock called grazers.

Although this is not the case in the real system, the implications of such assumptions do not modify the interactions between the mentioned stocks. The purpose behind the development of SAPOH has been to develop a model with the ability to replicate and simulate these interactions and for this reason, the level of aggregation within SAPOH is considered justified. The need to add further detail and expand these stocks to differentiate

between different algal and grazer species, each with their own specific characteristics, may never arise, even when designing a future prototype for policy analysis.

3. *Does the model conform to basic physical laws such as conservation laws?*

Physical laws, such as the conservation of matter, are not violated in SAPOH. The model's stock and flow structure has been derived from published literature, as have model equations. All stocks in SAPOH are stocks of biomass or, in the case of grazers and larvae, populations, and it has been already shown that these stocks do not fall to negative values. Furthermore, the outflows from these stocks approach zero as stocks approach zero. This is ensured by the presence of balancing feedback loops restricting stock outflows such that flows approach zero together with the stock itself.

Biomass is all fully accounted for in SAPOH. While the initiation for P. oceanica and algal epiphyte stocks is not accounted for by an influx of propagules, their biomass increases realistically via the process of photosynthesis, from a set initial value. In the case of the population of grazers, an exogenous influx of larval propagules represents the maximum potential number of adult grazers in the system. This number is then modified according to the ability of the patch of P. oceanica meadow to capture larvae as particles, provide shelter to both larvae and adults from predators and algal epiphytes for adults' nutrition.

In summary, SAPOH has the ability to generate responses that characterise the natural *P. oceanica* system and is structurally sound for its purpose. On the other hand, SAPOH's behaviour, when variables such as depth, surface irradiance and epiphytic loads take on extreme values, is not realistic due to the insensitivity of algal epiphyte growth to limiting factors within the system. It is recommended that future adaptations to SAPOH should address algal epiphyte growth dynamics by incorporating other limiting factors present in the real system, such as nutrients and temperature.

5 SCENARIO ANALYSIS

By considering a variety of possible futures that include important uncertainties in a system, scenario projection may serve to improve the level of understanding of a complex system and reveal how the system reacts to stresses and influencing factors. Ultimately, scenarios may be used to better inform decisions and provide greater resilience to unexpected and untended consequences (Peterson, Cumming, & Carpenter, 2003). *P. oceanica* habitat is one such complex system and this section is an effort to demonstrate the use of scenario analysis in revealing unexpected system characteristics and responses.

The scenario presented here causes the system to enter a turbidity related stress event. Reduced light availability in the marine environment is commonly brought about via turbid waters. In the natural environment, heightened and prolonged levels of turbidity may result from intense storms or rainfall. Various human-related activities may also lead to turbid waters. Coastal works and dredging both directly suspend solids and sediment in seawater, reducing the depths to which light may penetrate. Development on land may indirectly contribute towards suspended sediment in coastal waters, via reducing the permeability of the land's surface and increasing runoff. This scenario simulates a stress event on SAPOH, causing the system to go through a ten-year period of reduced light availability resulting from heightened water turbidity. The simulation is executed by setting the exogenous variable 'Turbidity factor' to values higher than zero. A STEP function is employed to "step" up the effect of turbidity from 0 to the specified value for 'Turbidity factor' value during the period of time that lies between t=20 years and t=30 years. Figure 5.1 shows irradiance available in the water column for the four turbidity simulations. Table 5.1 details the system's response to four different turbidity scenarios.
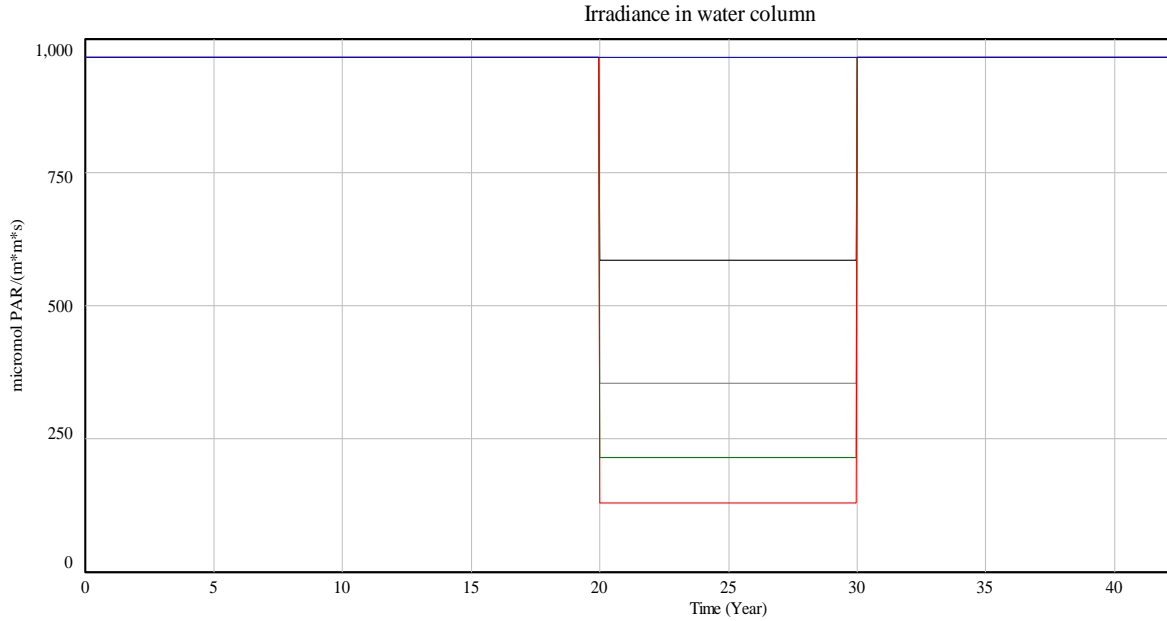
Figure 5.1 Available irradiance in the water column when simulating at turbidity values of 0 (blue), 0.1 (black), 0.2 (grey), 0.3 (green), and 0.4 (red) between t=20 and t=30 years.

Table 5.1 System response to turbidity between t=20 and t=30 years, at a depth of 5m.

Turbidity Conditions	0.1	0.2	0.3	0.4
Meadow shoot density (y 0) (shoot m^{-2})	860	860	860	860
Meadow shoot density (yr 30) (shoot m^{-2})	777	520	0.1	0
Time to return to pre-event levels (yr)	1	1	5	-
Epiphyte load (t_0) (kgDW m^{-2} leaf area)	0.24	0.24	0.24	0.24
Epiphyte load (t_{30}) (kgDW m^{-2} leaf area)	0.24	0.24	0.19	0
Time to return to pre-event levels (yr)	-	-	2	-
Grazer density (t_0) (ind m^{-2})	12	12	12	12
Grazer density (t_{30}) (ind m^{-2})	10	5	0	0
Time to return to pre-event levels (yr)	4	13	20	-

Results in Table 5.1 indicate that the epiphytes in SAPH are superior competitors to *P. oceanica* in conditions of deteriorated light. Values describing the density of the epiphytic community, 'Epiphyte load', are more resilient to changes in light availability than are values for 'Meadow shoot density' in the table above. This is explained by the fact that a given amount of radiation induces a higher rate of photosynthesis from algal epiphytes than *P. oceanica*. Furthermore, the irradiation at which the rate of photosynthesis is no longer limited by light is lower for algal epiphytes compared to that of *P. oceanica* (compare P-I curves in Figure 3.9). Decreased photosynthetic rates resulting from inadequate light resources are therefore more likely to be suffered by *P. oceanica* than by the epiphytic algal community. In addition to this, *P. oceanica* suffers further reductions in light due to shading by attached epiphytes. For these reasons, algal epiphytes endure light related stresses superiorly to *P. oceanica* in a system such as SAPOH, where light is the only factor that contributes towards growth.

The last simulation, in which the turbidity factor has a value of 0.4, features a sharp increase in the density of the epiphytic community (Figure 5.1) right before its decline. This spike ultimately results from the faster rate of decline suffered by *P. oceanica*, and therefore the epiphyte's substratum, compared to the rate at which epiphyte biomass is itself declining. This sudden increase in epiphytic density does not occur in a real life situation, and is only featured in SAPOH because of the way in which epiphyte density is calculated, ie. total epiphyte biomass / total substratum available. While this sharp increase in epiphytic density just before decline is unrealistic, it does signify a situation of stress for *P. oceanica*. As seagrass biomass is declining at a faster rate than epiphyte biomass, overloading by epiphytes may be an additional mechanism contributing to and spurring on seagrass decline in turbid conditions. Changes in the density of the seagrass meadow feed back to affect the epiphytic community in SAPOH, as a change in the substratum available for colonisation results. For this reason, once *P. oceanica* biomass in SAPOH declines to nothing then epiphytic organisms no longer have a substratum on which to grow. This attached algal community therefore disappears, along with the seagrass.
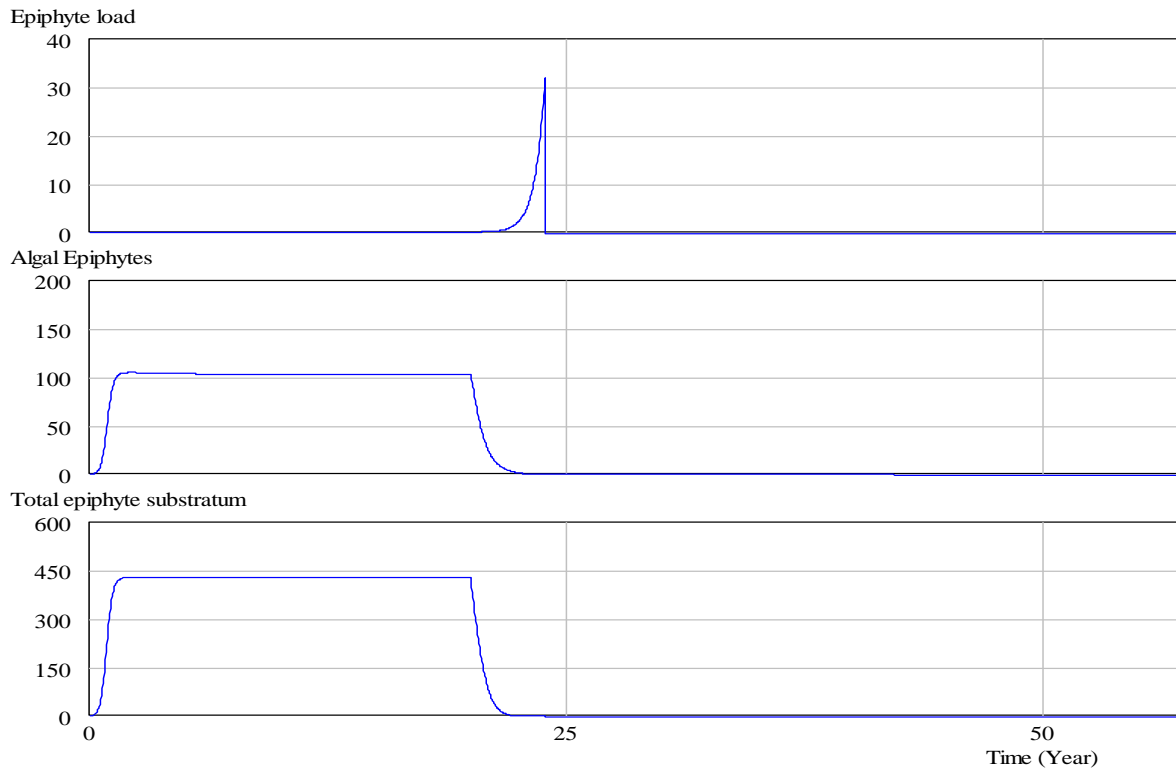
Figure 5.2 Epiphyte load spike and its causes when Turbidity factor = 0.4.

The population of grazers that is dependent on the presence of epiphytes for nutrition survives all simulations except the last, in which the turbidity factor is set at 0.4. The disappearance of *P. oceanica* and its attached epiphytic community during this simulation essentially means that the services of nutrition and shelter that once benefited the grazers is now gone. On the other hand, the grazers survive simulations in which the turbidity factor is given a value of 0.3 or less. The survival of their epiphytic food source enables the grazer population to rebuild itself from small numbers, although this occurs over a period of a number of years. It is important to note that the number of years that SAPOH takes to return to pre-stress event levels is not a matter of simple proportion. Recovery time for grazers more than doubles when turbidity levels are increased from 0.1 to 0.2, although when increased from 0.2 to 0.3 grazer recovery time is less than doubled. Similarly, when increasing the level of turbidity from 0.1 to 0.2, hardly any change in recovery time is observed for *P. oceanica*. On the other hand, a large change in observed on increasing the level of turbidity from 0.2 to 0.3. This highlights the importance of SAPOH in illustrating

the non linearity of the dynamics of a complex habitat and that system responses may not be predicted using simple proportion.

6 FURTHER RESEARCH

The insensitivity of the algal epiphyte stock to several variables in SAPOH (Appendix II) renders the simulation model somewhat unsuitable for reliable scenario testing. It is only in hindsight that the insensitive nature of some main feedback loops was perceived and it is for this reason that scenario projection has been limited. This section presents important modifications to the first SAPOH prototype with the aim of amending this problem and increasing model reliability.

The inclusion of nutrient dynamics is a must for any future adaptation of SAPOH. SAPOH assumes that nutrients are readily available to seagrass and epiphytes, an assumption that explains the highly insensitive nature of epiphyte growth in the model to changes in light. It is the interplay of light and nutrients that mainly function to limit primary production for both seagrass and epiphytic algae in the real system (Ruiz & Romero, 2001) and the inclusion of this important parameter is the first step towards unlocking important dynamics between epiphytes and grazers. This is because, when light and nutrients function to limit epiphyte growth together, the role of grazers in modifying the algal epiphyte stock becomes more prominent. Nutrients also have important implications for *P. oceanica* itself. While simulated results suggest a maximum of five years for *P. oceanica* shoot density to return to its pre-stress event level, this may in reality be even longer if nutrients function to limit seagrass growth. On the other hand, *P. oceanica*'s ability to tap into sediment nutrients may shorten the simulated recovery time, especially if coupled with increased light availability from reduced epiphyte cover under low nutrient conditions in the water column. Therefore, while SAPOH is able to make a first estimate of *P. oceanica* habitat response to stress events based on accurate information, this estimate may be further fine tuned in future work by including additional, important parameters such as nutrient levels. The inclusion of nutrient level parameters in turn extends the use of the simulating system as

system response to a greater variety of stress events may be forecasted. Physical water movement is fundamental to many of the dynamics concerning *P. oceanica* meadows. Leaf and shoot detachment, and the transport/recruitment of algal propagules or invertebrate larvae are examples in which water movement conditions are central. Including water movement in SAPOH would also capture the effect of *P. oceanica* meadows on water currents and enable the analysis of the habitat's role in protecting coasts (Fonseca, Zieman, Thayer, & Fisher, 1983). Adapting SAPOH to include the several interactions between the movement of water and *P. oceanica* meadows should be considered in a future extension to this work.

Converting SAPOH to a whole plant system, in which both above ground and below ground compartments are modelled, is central to capturing the way in which resources are translocated for improved survival during periods of stress as well as the value of *P. oceanica* habitat as a carbon and nutrient sink (Duarte & Chiscano, 1999; Elkalay, et al., 2003). Below-ground material is supported by photosynthetically produced carbon that is stored in rhizomes and used to maintain the plant during periods of low photosynthetic production (Burd & Dunton, 2001). Situations in which light is limited tends to result in increased biomass allocation to leaves while nutrient limitation tends to shift biomass allocation to roots (Hemminga & Duarte, 2000). This adaptation to SAPOH is central to capturing the resilience of *P. oceanica* habitat to stressful changes in light and nutrient levels.

It is now realised that a daily, or at least monthly, time unit is necessary for the proper representation of a *P. oceanica* system. The seasonality of many of the dynamics within *P. oceanica* habitat was much felt when constructing the present functioning model. Seasonality could not be captured in SAPOH due to its annual time unit. The *P. oceanica* canopy is longer during the summer, implying higher organism recruitment and survival in the canopy during these months. Changes in canopy length also have implications for epiphyte biomass and several other dynamics that have not been addressed in SAPOH, such as wave attenuation and the extent to which particle resuspension is reduced. Temperature is known to contribute much to seasonality as it affects the rate at which the plant respires

and consequently the overall rate of photosynthetic production (Hemminga & Duarte, 2000). The inclusion of a temperature parameter, and the way in which it affects respiration and photosynthesis, may be a further important alteration to SAPOH.

Oceanographic, meteorological and marine ecosystem models are making increasing use of data assimilation (Lawson et al. 1995, 1996, Anderson et al. 1996, Vallino 2000). Such techniques are useful in estimating the values of uncertain parameters in a model by adjusting such parameters until satisfactory agreement is achieved between simulated results and observations. Data assimilation is also useful in improving a model's short-term predictive capability (Burd & Dunton, 2001). The availability of datasets and time series of any parameters that have been included in SAPOH would improve the system's predictive faculty. SAPOH'S ability to predict responses to changes in parameters such as irradiance may then in turn be verified and tested against such datasets (Burd & Dunton, 2001; Zimmerman, Cabello-Pasini, & Alberte, 1994).

7 CONCLUSION

Posidonia oceanica habitat is one of the most important coastal shallow water habitats in the Mediterranean region due to its provision of highly valuable and varied ecological services. The decline of *P. oceanica* habitat in the Mediterranean is what identified a system dynamics approach to modelling the habitat as a worthy research aim and promoted the development of the System for Assessing *Posidonia oceanica* Habitat, SAPOH. The SAPOH prototype described in this work is a first step towards a model capable of revealing the natural properties of *P. oceanica* habitat. The SAPOH prototype presented here fulfils important purposes. It is a synthesis of various types of data into a defendable structure that is logically consistent and validated. SAPOH has been designed to describe the relationships between important actors in a hypothetical patch *P. oceanica* habitat, namely *P. oceanica* itself together with the algal epiphytes and epiphytic grazers that occupy the meadow. The SAPOH prototype presented in this work may be improved and adapted by future research efforts to a tool suitable for policy analysis. Among the main

suggestions made to direct future adaptations to SAPOH are: altering the time scale from a yearly to monthly or even daily time unit; including nutrient, water movement and temperature variables and dynamics; and modelling below ground, as well as above ground biomass compartments for *P. oceanica*. Furthermore, future research work should adapt this model to encompass broad-scale, human-related dynamics in order to confirm its use in coastal management and decision making.

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9 APPENDIX I

Terminology

Stocks: stocks (state variables) characterise the state of the system and accumulate the difference between their inflows and outflows, often creating delay. Many of the system's decisions and actions are based upon stocks. Stocks serve to create system memory and by decoupling rates of flow give the system inertia and disequilibrium. An example is the *P. oceanica* stock which is changed by the process of growth, or the process of senescence and grazer consumption.

Flows: flows are often functions of a stock, other stocks and parameters. Flows serve to change the value of stocks. For example, *P. oceanica* growth causes the *P. oceanica* stock to increase.

Parameters: parameters are variables whose values are often varied to investigate the effect of the variable on the particular system. It is common to modify parameters prior to running a simulation for comparative analysis. An example of a parameter in this system is the maximum photosynthetic rate of the algal epiphytic community.

Constants: constants are variables which, to a high degree of accuracy, do not vary between systems or in time. Examples include the number of days in a year and photosynthetic quotient for *P. oceanica.*

Model Equations: model equations mathematically represent the processes that link stocks. They are essentially a combination of stocks, parameters and constants. Equations should ensure that mass is conserved.

Stocks

Stock	Units
Posidonia oceanica	kgDW
Matte	kgDW
Leaf litter	kgDW
Algal epiphytes	kgDW
Grazers	individuals
Larvae	individuals

Flows

Flow	Description	Units
P. oceanica net growth	rate at which *P. oceanica* assimilates C into biomass	kgDW/Year
Epiphyte net growth	rate at which algal epiphytes assimilate C into biomass	kgDW/Year
Consumption of *P. oceanica*	rate at which *P. oceanica* is consumed by grazers	kgDW/Year
Consumption of epiphytes	rate at which algal epiphytes are consumed by grazers	kgDW/Year
Burial	rate at which above ground biomass is buried below ground	kgDW/Year
Leaf shedding	rate at which above ground biomass is shed as dead leaves	kgDW/Year
Epiphytes to litter	rate at which epiphyte biomass is lost due to loss of their substratum	kgDW/Year
Leaf litter exportation	rate at which hydrodynamic forces remove leaf litter from the meadow area	kgDW/Year
Leaf litter decay	rate at which leaf litter remaining in the meadow area is mineralised	kgDW/Year
Matte decay	rate at which matter stored in the matte is mineralised	kgDW/Year
Larval recruitment	rate at which grazer larvae are captured by the meadow canopy	ind/Year
Larval mortality	rate at which grazer larvae are lost from the meadow as a result of death	ind/Year
Larval maturity	rate at which grazer larvae mature to adults in the meadow	ind/Year
Grazer mortality	rate at which adult grazers are lost from the meadow as a result of death	ind/Year

Parameters

Parameter	Description	Value/Range and units
P P$_{max}$	*P. oceanica* maximum photosynthetic rate when light is no longer limiting	7.1 mgO$_2$ gDW^{-1} h^{-1}
E P$_{max}$	algal epiphytes maximum photosynthetic rate when light is no longer limiting	7-20 mgC gDW^{-1} h^{-1}
P R	*P. oceanica* respiratory rate	1.3 mgO$_2$ gDW^{-1} h^{-1}
E R	algal epiphytes respiratory rate	2.0 mgC gDW^{-1} h^{-1}
P α	*P. oceanica* initial rate of photosynthesis as	0.05 mgO$_2$ gDW^{-1} h^{-1} / µmol PAR m^{-2} s^{-1}

	irradiance increases from darkness	
E α	algal epiphyte initial rate of photosynthesis as irradiance increases from darkness	0.1-3 mgC gDW^{-1} h^{-1} / μmol PAR m^{-2} s^{-1}
Surface irradiance	amount of radiation present at surface of water column	μmol PAR m^{-2} s^{-1}
Depth	distance from the sea surface	0-50 m
Photoperiod	duration of irradiance period	9 hr
Background attenuation coefficient	background light extinction in typically clear coastal waters	0.035 m^{-1}
Annual recruits per m^2	number of grazer larvae recruited per 1 m^2 meadow area	4000 individual m^{-2}
Maximum grazer lifetime	maximum possible lifetime for adult grazers	6 years
Daily grazing rate	material consumed daily per grazer	0.0005 kgDW individual^{-1} d^{-1}
Leaf shedding constant	rate at which leaves mature, die and are shed	0.65 fraction y^{-1}
Exportation fraction	rate at which leaf litter is exported from the meadow	0.52 fraction y^{-1}
Burial constant	rate at which above ground biomass is buried underground	0.28 fraction y^{-1}
Leaf litter decay rate constant	rate at which leaf litter is mineralised in the meadow	0.8241 fraction y^{-1}
Matte decay rate constant	rate at which material in the matte is mineralised	0.00036 fraction y^{-1}

Constants

Constant	Description	Value and units
O$_2$ molar mass	weight of 1 mole of O$_2$	32g
C molar mass	weight of 1 mole of C	12g
P Photosynthetic quotient	moles of O$_2$ produced per mole of C assimilated	1.25
Days in year	Total number of days in the year	365 d
P C to DW factor	100/% C present in *P. oceanica* DW	3.125 gDW gC^{-1}
E C to DW factor	100/% C present in algal epiphytes DW	6.667 gDW gC^{-1}
kg to g factor	number of g in 1 kg	1000 g kg^{-1}

Model Equations

(01)   Algal Epiphytes= INTEG (Epiphyte net growth-Consumption of epiphytes-Epiphytes to litter,0.01)
        Units: kgDW
        0.01

(02)   Annual C fixed per gDW=Net photosynthetic rate in C*Days in year
        Units: kgC/gdw/Year

(03)   Annual DW fixed per gDW=Annual C fixed per gDW*P C to DW factor
        Units: kgDW/gdw/Year

(04)   Annual grazing rate=Daily grazing rate*Days in year
        Units: kgDW/ind/Year

(05)   Annual recruits per m^2=4000
        Units: ind/m/m/Year [0,10000,10]

(06)   Annual unit conversion=1
        Units: 1/Year

(07)   Attenuation effect=(Water column attenuation*Depth)
        Units: Dmnl

(08)   Average survival=0.000314
        Units: fraction/Year [0,0.1,0.0001]

(09)   Background attenuation coefficient=0.035
        Units: 1/m [0,1,0.05]

(10)   Burial=Burial constant*"P. oceanica"
        Units: kgDW/Year

(11)   Burial constant=0.28
        Units: fraction/Year

(12)   C molar mass=12000
        Units: mgC/molC

(13)   Canopy density ratio=IF THEN ELSE(Meadow shoot density/Max shoot density>1,1,Meadow shoot density/Max shoot density)
        Units: Dmnl

(14)   Coeff A=92.4
        Units: Dmnl

(15)   Coeff B=0.022
        Units: kgDW/m/m

(16)   Consumption constant=0.07
        Units: fraction/Year

(17)   Consumption of epiphytes=IF THEN ELSE(Algal Epiphytes*Annual unit conversion>Food resource required,Food resource required,IF THEN ELSE(Algal Epiphytes>0,Algal Epiphytes*Annual unit conversion,0))
        Units: kgDW/Year

(18)   "Consumption of P. oceanica"="P. oceanica"*Consumption constant
        Units: kgDW/Year

(19)   Daily grazing rate=0.0005
        Units: kgDW/ind/day [0,0.001,5e-006]

(20)   Days in year=365
        Units: day/Year

(21)   Depth=5
       Units: m [0,100,5]

(22)   E Alpha=1.5
       Units: (mgC/gC/h)/(micromol PAR/m/m/s) [0.1,3,0.1]

(23)   E annual C fixed per gDW=(E net photosynthetic rate in C*Days in year)/E C to DW factor in g
       Units: kgC/gdw/Year

(24)   E annual DW fixed per gDW=E C to DW factor in KG*E annual C fixed per gDW
       Units: kgDW/gdw/Year

(25)   E C to DW factor in g=100/15
       Units: gdw/gC

(26)   E C to DW factor in KG=100/15
       Units: kgDW/kgC

(27)   E Km=E Pmax/E Alpha
       Units: micromol PAR/m/m/s

(28)   E load ratio=IF THEN ELSE(Epiphyte load>0:AND:Max E load>0,Epiphyte load/Max E load,0)
       Units: Dmnl

(29)   E net photosynthetic rate in C=((E Pmax*Irradiance in water column/(E Km+Irradiance in water column))-E R)*Photoperiod*mgC to kgC factor
       Units: kgC/gC/day

(30)   E Pmax=14
       Units: mgC/gC/h [7,20,1]

(31)   E production factor=IF THEN ELSE(E load ratio<=1,1-E load ratio,0)
       Units: Dmnl

(32) E R=3

Units: mgC/gC/h [1,5,1]

(33) Epiphyte attenuation=Coeff A*(Epiphyte load/(Coeff B+Epiphyte load))

Units: Dmnl

(34) Epiphyte load=IF THEN ELSE(Algal Epiphytes>=0:AND:Total epiphyte substratum>0,Algal Epiphytes /Total epiphyte substratum,0)

Units: kgDW/m/m

(35) Epiphyte net growth=IF THEN ELSE(E production factor<1:AND:Algal Epiphytes>0,Algal Epiphytes* E production factor*kg to g factor*E annual DW fixed per gDW,0)

Units: kgDW/Year

(36) Epiphytes to litter=IF THEN ELSE(Algal Epiphytes*Annual unit conversion>Algal Epiphytes*Leaf shedding constant,Algal Epiphytes*Leaf shedding constant,Algal Epiphytes*Annual unit conversion)

Units: kgDW/Year

(37) Exportation fraction=0.52

Units: fraction/Year [0,1,0.1]

May be adjusted to suit the hydrodynamics at the particular location

(38) FINAL TIME = 50

Units: Year

The final time for the simulation.

(39) Food resource required=Annual grazing rate*Grazers

Units: kgDW/Year

(40) Grazer lifetime=IF THEN ELSE((Max grazer lifetime*Nutrition adequacy)>1,(Max grazer lifetime*Nutrition adequacy),1)

Units: Year

(41) Grazer mortality=IF THEN ELSE(Grazer lifetime>1,((1/Grazer lifetime)*Grazers)*Lack of Shelter ,(1/Grazer lifetime)*Grazers)

Units: ind/Year

(42) Grazers= INTEG (Larval maturity-Grazer mortality,5)

Units: ind

(43) INITIAL TIME = 0

(44) Irradiance at canopy =((100-Epiphyte attenuation)/100)*Irradiance in water column

Units: micromol PAR/m/m/s

(45) Irradiance in water column=Surface irradiance*(EXP(-1*Attenuation effect))

Units: micromol PAR/m/m/s

Expressed as Photosynthetically Active Radiation (PAR) which is irradiance of wavelength between 400 and 700 nm.

(46) kg to g factor=1000

Units: gdw/kgDW

(47) Km=P Pmax/P alpha

Units: micromol PAR/m/m/s

Half saturation constant: often referred to as Ik (37-40) and considered   to   describe   the   onset   of saturation. At irradiances below the half-saturation constant, Km, light is limiting.

(48) Lack of Shelter =1-Canopy density ratio

Units: Dmnl

(49) Larvae= INTEG (Larval recruitment-Larval mortality-Larval maturity,200)

Units: ind

(50)   Larval maturity=(Larvae*Average survival)*Canopy density ratio
         Units: ind/Year

(51)   Larval mortality=(Larvae*Annual unit conversion)-Larval maturity
         Units: ind/Year

(52)   Larval recruitment=(Annual recruits per m2*Meadow area)*Canopy density ratio
         Units: ind/Year

(53)   Leaf area index=IF THEN ELSE(Meadow shoot density>0.01,Meadow shoot density*Shoot surface area,0)
         Units: Dmnl

(54)   Leaf litter= INTEG (Leaf shedding-Leaf litter exportation-Leaf litter decay,0)
         Units: kgDW

(55)   Leaf litter decay=Leaf litter*Leaf litter decay fraction*Ll decay rate constant
         Units: kgDW/Year

(56)   Leaf litter decay fraction=1-Exportation fraction
         Units: fraction/Year

(57)   Leaf litter exportation=Leaf litter*Exportation fraction
         Units: kgDW/Year

(58)   Leaf shedding=Leaf shedding constant*"P. oceanica"
         Units: kgDW/Year

(59)   Leaf shedding constant=0.65
         Units: fraction/Year

(60)   Ll decay rate constant=0.8241
         Units: fraction

(61)   Matte= INTEG (Burial-Matte decay, 0)
         Units: kgDW

(62)   Matte decay=Matte*Matte decay rate constant
         Units: kgDW/Year

(63)   Matte decay rate constant=0.00036
         Units: fraction/Year

(64)   Max E load=0.1
         Units: kgDW/m/m [0,0.1,0.01]

(65)   Max grazer lifetime=6
         Units: Year [0,?]

(66)   Max shoot density=1000
         Units: shoot/m/m [0,1500,5]

(67)   Meadow area=100
         Units: m*m

(68)   Meadow shoot density=IF THEN ELSE("P. oceanica">0.0005,"P. oceanica"/Shoot biomass/Meadow
         area,0)
         Units: shoot/m/m

(69)   mgC to kgC factor=1/1000/1000
         Units: kgC/mgC

(70)   Net photosynthetic rate in C= Net photosynthetic rate in O_2*mgC to kgC factor*O_2 to C factor
         Units: kgC/gdw/day

(71)   Net photosynthetic rate in O_2=IF THEN ELSE(Meadow shoot density>0.01,(((P Pmax*Irradiance at
         canopy)/(Km +Irradiance at canopy)-R)*Photoperiod),0)
         Units: mgO_2/gdw/day

Michaelis-Menten equation for photosynthetic irradiance relationship

(72)   Nutrition adequacy=Consumption of epiphytes/Food resource required
        Units: Dmnl

(73) O_2 molar mass=32000
        Units: $mgO_2/molO_2$

(74) O_2 to C factor=C molar mass/(O_2 molar mass*P Photosynthetic quotient)
        Units: mgC/mgO_2

(75)   P alpha=0.05
        Units: $(mgO_2/gdw/h)/(micromol\ PAR/m/m/s)$

(76)   P C to DW factor=(100/32)
        Units: kgDW/kgC

(77)   P Photosynthetic quotient=1.25
        Units: $molO_2/molC$

(78)   P Pmax=7.1
        Units: $mgO_2/gdw/h$
        Gross maximal photosynthetic rate when light is not limiting

(79)   "P. oceanica net growth"=(Annual DW fixed per gDW*kg to g factor*"P. oceanica")*Production factor
        Units: kgDW/Year

(80)   "P. oceanica"= INTEG (("P. oceanica net growth"-Leaf shedding-"Consumption of P. oceanica"-Burial),0.05)
        Units: kgDW

(81)   Photoperiod=9
        Units: h/day

(82)   Production factor=1-Canopy density ratio
        Units: Dmnl

(83)   R=1.3
        Units: mgO$_2$/gdw/h
        The respiratory rate expresses the cost to maintain the living plant tissue and constrains the ability of
        plants to grow under low light supply.

(84)   SAVEPER = TIME STEP
        Units: Year [0,?]
        The frequency with which output is stored.

(85)   Shoot biomass=0.0004625
        Units: kgDW/shoot

(86)   Shoot surface area=0.005
        Units: m*m/shoot [0.005,0.01,0.0025]

(87)   Surface irradiance=1150
        Units: micromol PAR/m/m/s [0,5000,1]

(88)   TIME STEP = 0.03125
        Units: Year [0,?]
        The time step for the simulation.

(89)   Total epiphyte substratum=IF THEN ELSE(Leaf area index>0,Leaf area index*Meadow area,0)
        Units: m*m

(90)   Turbidity effect=STEP(Turbidity factor,20)-STEP(Turbidity factor,30)
        Units: 1/m

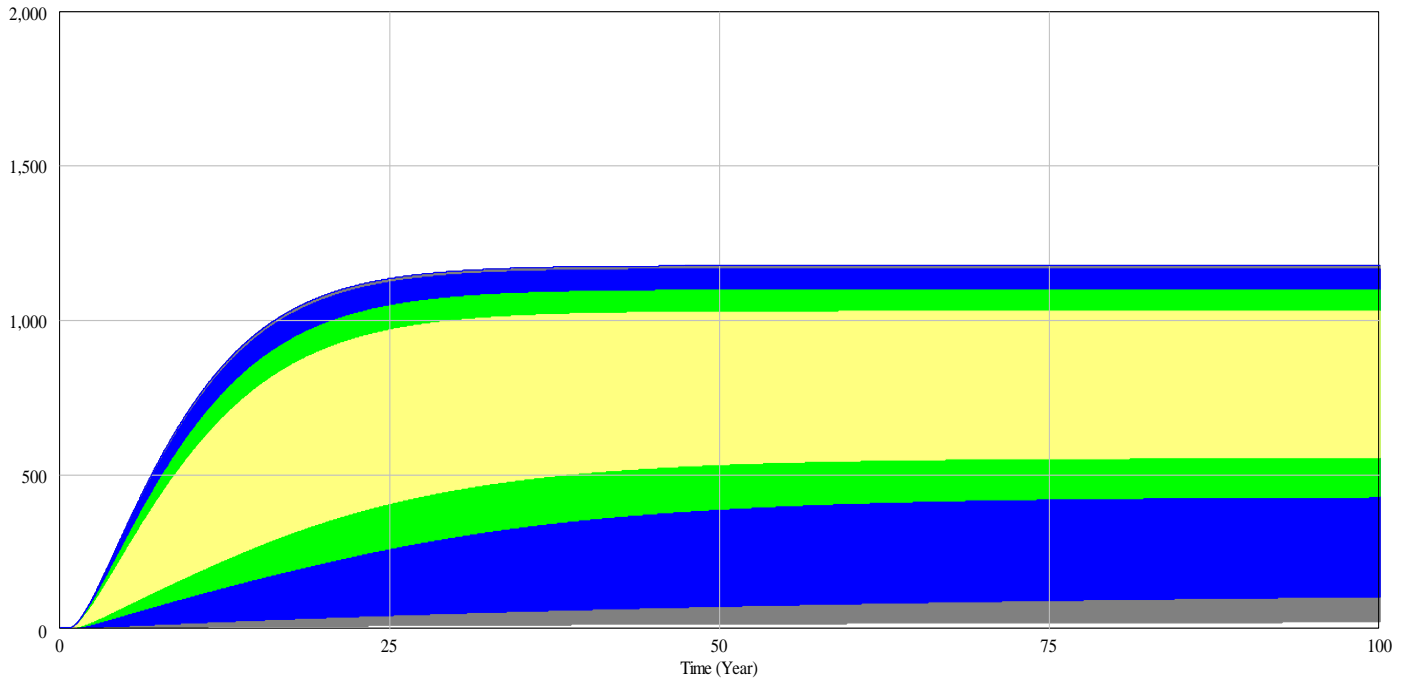(91)   Turbidity factor=0.1
        Units: 1/m [0,1,0.1]

(92)   Water column attenuation=IF THEN ELSE((Background attenuation coefficient+Turbidity effect)>1,1,Background attenuation coefficient+Turbidity effect)
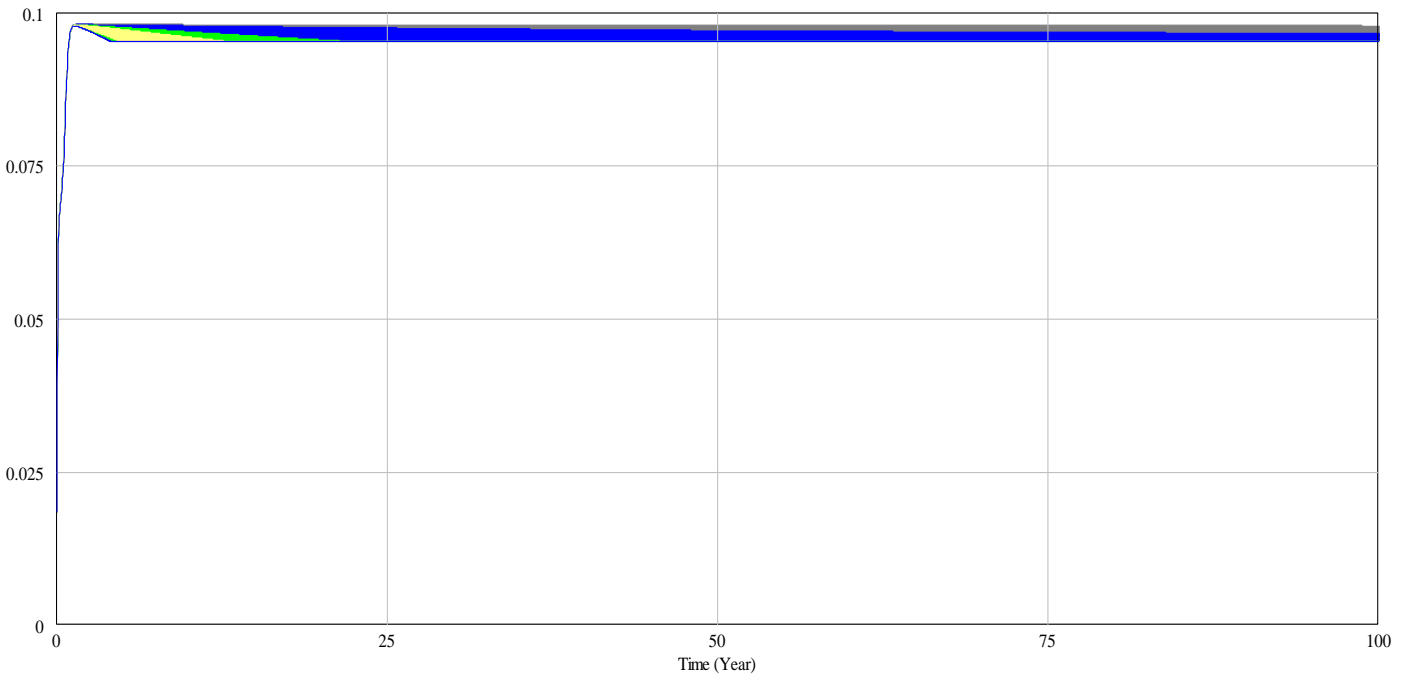
Units: 1/m [0,1,0.005]

10 APPENDIX II

Grazers

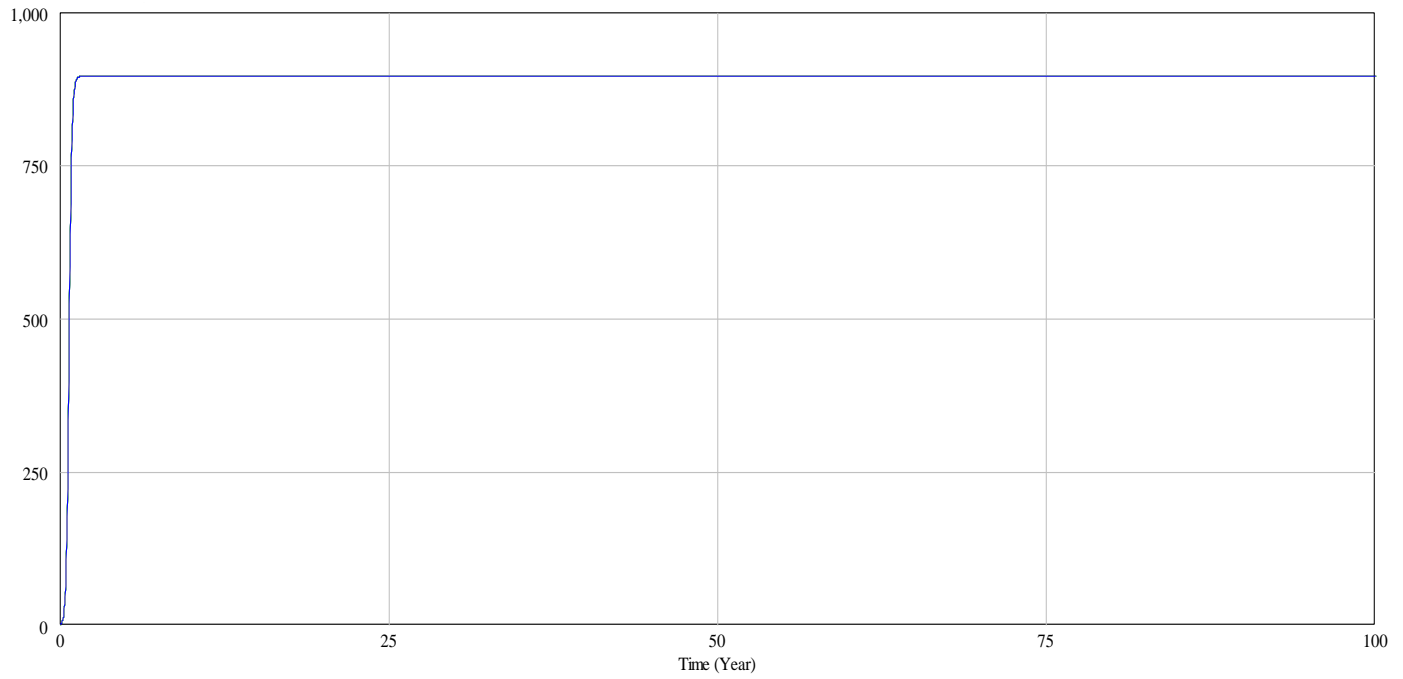## Epiphyte load

Meadow shoot density

Figure 10.1 Sensitivity analysis for grazer stock, epiphyte load and meadow shoot density variables over a 100 year period. Colours represent confidence bounds (grey 100%, blue 95%, green 75%, yellow 50%) for all output values of grazer stock, epiphyte load and meadow shoot density when the annual recruits parameter was randomly varied about its distribution.
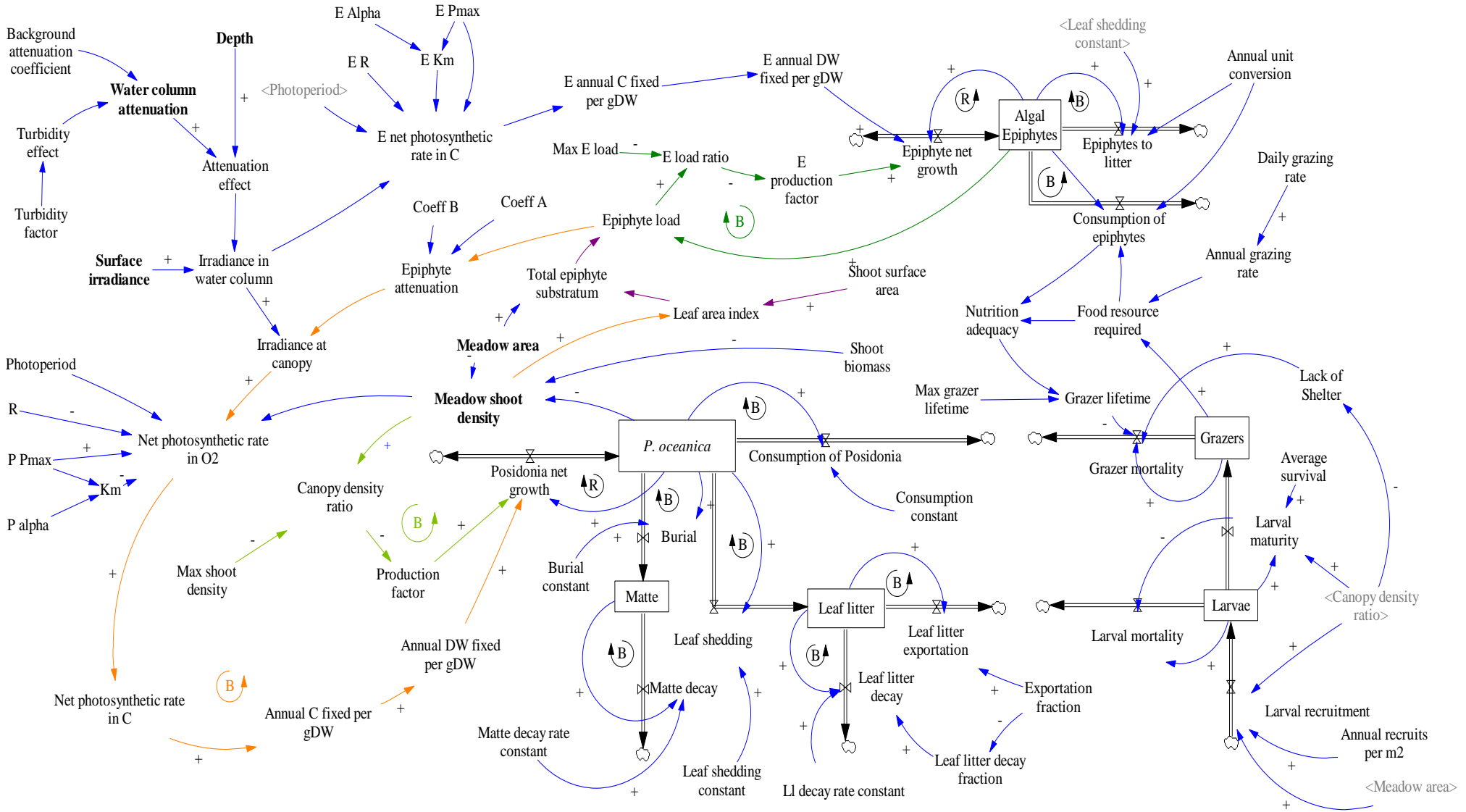
11 APPENDIX III

Figure 11.1 The complete, working SAPOH model.