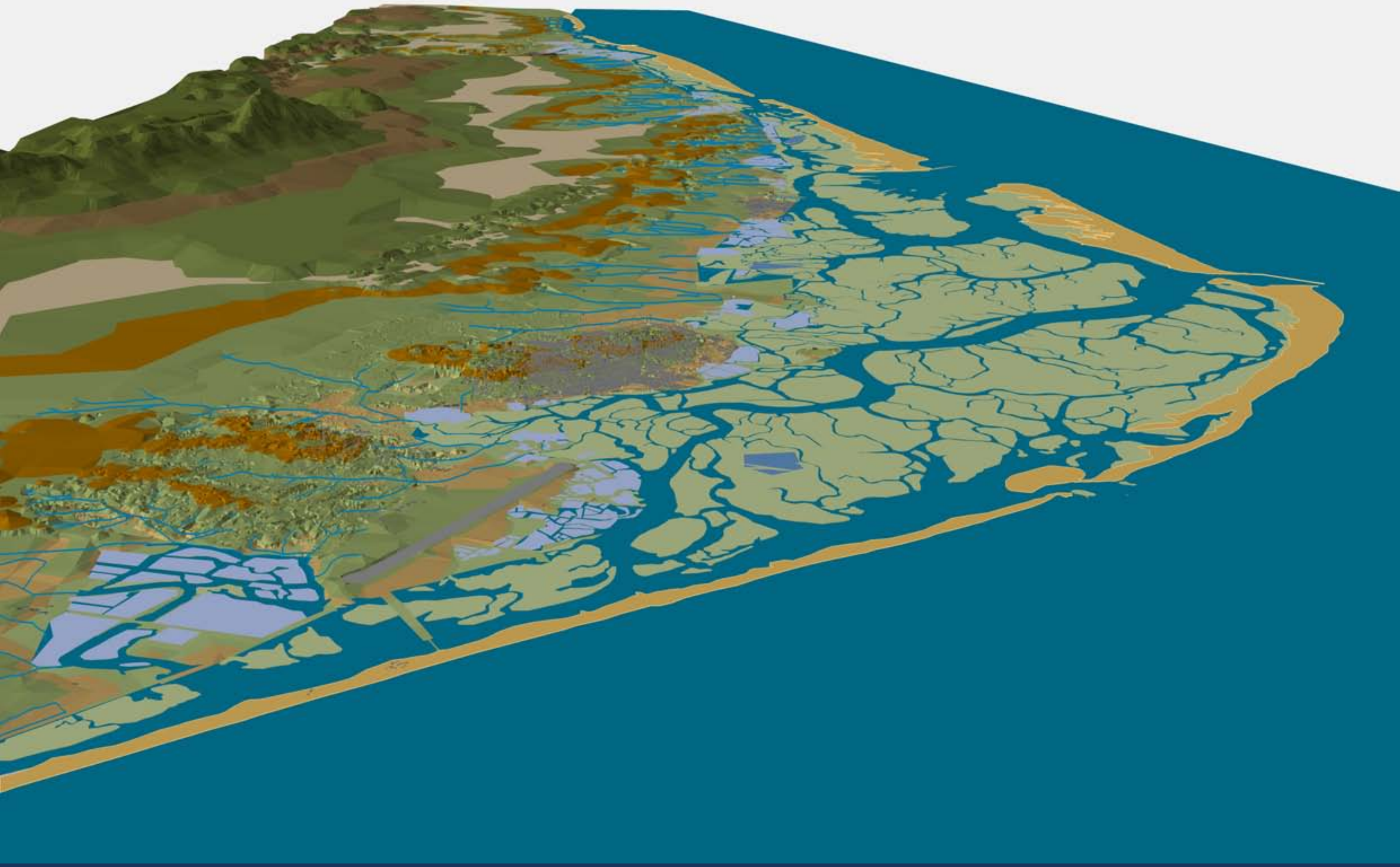

RIA FORMOSA

Challenges of a coastal lagoon in a changing environment

Edited by
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CENTRO DE INVESTIGAÇÃO MARINHA E AMBIENTAL

6. Ecological dynamics of green macroalgae Ulvales in Ria Formosa: a tale of blooms and shapes

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6.1. Starting with a click...

The History of Science is the sum of the stories of men and women that produced it. They spent their lives gathering information, that once treated becomes knowledge and it is compiled in articles and books. Many stories in Science start with a bang, but this tale started with a humble click, back in 1988. In a cold winter morning, a very tall man stood alone in a windy road, near a Ria Formosa's mudflat taking photographs in low tide, apparently to nowhere. That same man, called Martin Sprung, repeated this monthly ritual, in the same spot, for the next years. Martin was a German zoologist, that came to the Algarve in the eighties to implement a German-Portuguese project to study the biology of Ria Formosa, which was very important in the development of the Marine Biology and Fisheries graduation course, in the recently created University of Algarve.

After two years of monthly photographs, a striking and unexpected pattern began to emerge: there was an intense bloom of green macroalgae mats (see Box 6.1) that started after the first Autumn rains, peaked during Winter and disappeared gradually during the following Spring, being almost non-existent during the Summer months (Sprung, 1994). These annual dynamics have been observed ever since, and their repetitive occurrences were studied in several surveys (Figure 6.1).

Box 6.1. Macroalgae bloom

Macroalgae is a name used for seaweeds and other benthic (attached to the bottom) marine algae that are visible to the naked eye. Macroalgae can be considered marine plants because they are photosynthetic organisms (produce sugar molecules using sunlight energy) and have similar ecological roles to other plants. However, macroalgae are distinct from other marine plants (e.g. seagrasses and mangroves) because they lack roots, leaves, flowers, and vascular tissues. Therefore, they normally live attached to hard surfaces (e.g. shells from dead animals, rocks or debris), and have quite complex life cycles and a wide variety of reproduction modes, that allow them to be considered opportunistic species. When environmental conditions are adequate to their development, macroalgae tend to growth very rapidly, covering wide intertidal surface areas. This phenomenon is called a macroalgae bloom (Lobban & Harrison, 1997; Barsanti & Gualtieri, 2006; Lee, 2008).

Traditionally, macroalgae are divided in three groups according to their colour and photosynthetic pigments: red, brown and green. This chapter focus only on some species of the green macroalgae.

Figure 6.1.
Macroalgae coverage in January (left) and September (right) 2001. The green macroalgae bloom had previously started in November 2000 and occurred again in October 2001 (Photographs by Jaime Aníbal, 2001).

Unfortunately, all the original photographs that were taken between 1988 and 1994 were lost after the tragic accident that took Martin Sprung's life in 2003. This chapter describes the research that was done thereafter in order to add lost pieces and try to solve the puzzle of the unusual annual pattern of Ria Formosa green macroalgae. As an Opera, this manuscript is also divided in three acts: the first will look over *What* is the green macroalgae annual dynamics in Ria Formosa; the second chapter will focus on *Where* are the algae blooms happening; and the third one will be dedicated to *Why* are all these phenomena occurring.

6.2. *What* is the green macroalgae annual dynamics in Ria Formosa?

In order to understand what are the issues related to this unusual green macroalgae winter bloom in the western area of Ria Formosa (along the Faro beach), several scientific studies were performed during a period of more than 20 years, from 1996 to 2018 (Figure 6.2).

In a study executed between February 1996 and February 1997, the macroalgae dynamics empirically observed in 1990 was for the first time quantitatively registered.

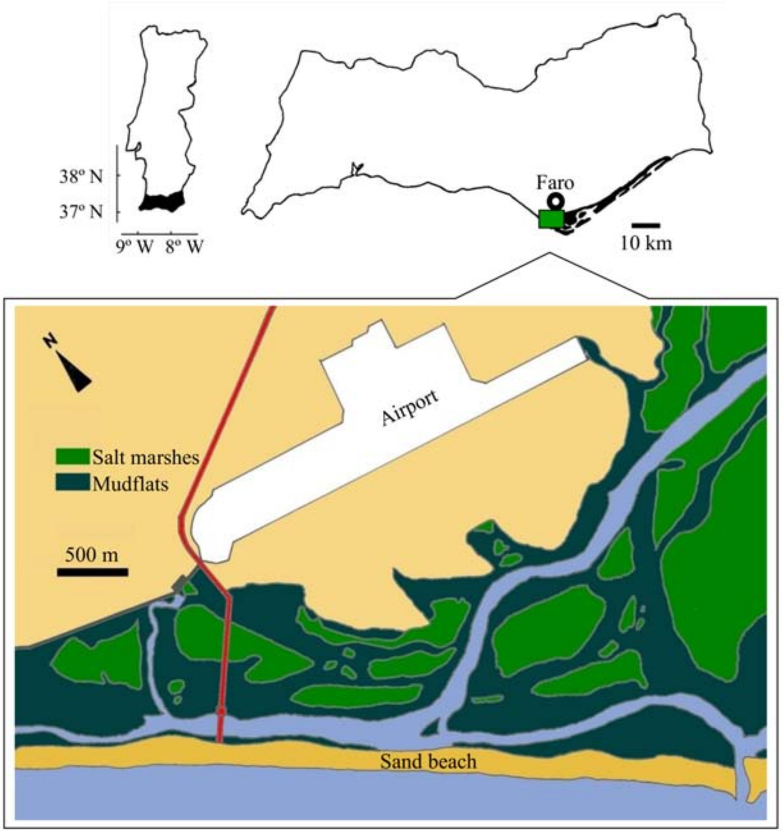

Figure 6.2.
Ria Formosa area adjacent to Faro beach.

The green macroalgae coverage peaked in the Winter months, decrease during Spring, almost disappeared in Summer, and bloomed again in Autumn (Figure 6.3).

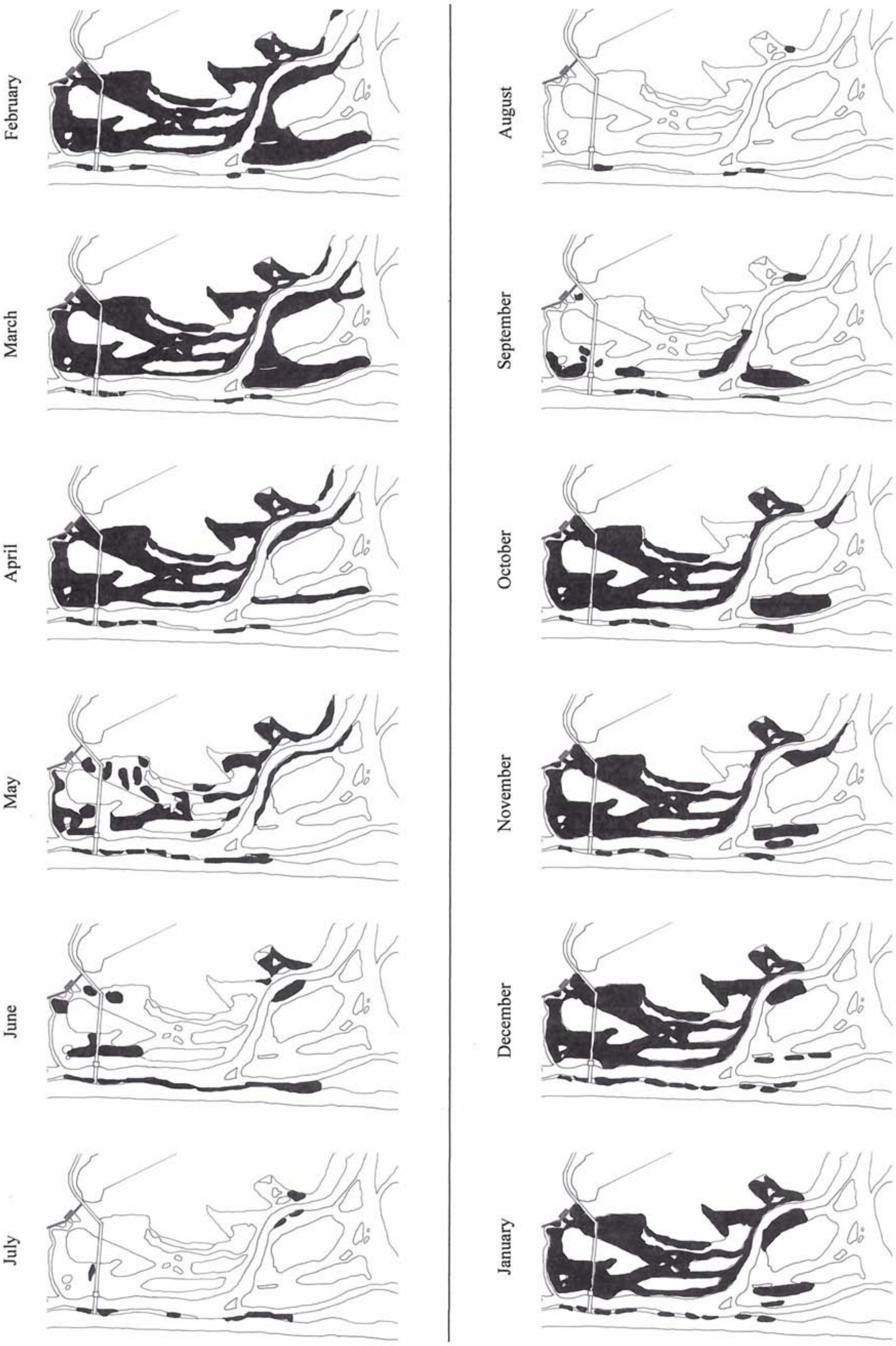

Figure 6.3.
Monthly variation of green macroalgae coverage (in black) between February 1996 and January 1997.

In the same study, the green macroalgae were identified as belonging to the order Ulvales, and to genera *Ulva* and *Enteromorpha*. Although morphologically distinct, both *taxa* coexisted in the same habitats. *Ulva* has a fan form appearance, and *Enteromorpha* presents a filamentous, hair-like, shape (Figure 6.4 and Box 6.2).

Figure 6.4.
Green macroalgae from the genera *Ulva* and *Enteromorpha* (Photographs by Jaime Aníbal, 2018).

The macroalgal biomass, measured as ash-free dry weight (AFDW), accompanied the sediments' coverage dynamics, with higher values in the Winter and Autumn months, and lower values in the end of Spring and beginning of Summer (Figure 6.5). After minima values of biomass during the Summer months, the new Ulvales bloom occurred in the end of September, after the first heavy rains of Autumn. Ulvales presented an annual average biomass of 25.9 g AFDW m^{-2}, with an annual production of 72,6 g m^{-2} y^{-1}. The annual average biomass of *Enteromorpha* (22.3 g AFDW m^{-2}) exhibited a clear dominance over *Ulva*'s (3.5 g AFDW m^{-2}), with annual production values of 74.6 g m^{-2} y^{-1} and 10.5 g m^{-2} y^{-1} respectively. Nevertheless, both genera followed the same dynamics of the Ulvales as a whole (Aníbal, 1998).

Box 6.2. Are *Ulva* and *Enteromorpha* distinct genera?

Although some phylogenetic research has been providing indications that *Ulva* and *Enteromorpha* are not distinct evolutionary entities and should not be considered as separate genera (Hayden et al., 2003), the morphological differences between species of the genus *Ulva* and species of the genus *Enteromorpha* can be responsible for distinct adaptive strategies to stress factors such as current induced shear stress. These differences might be important as to whether the species settle on more exposed convex areas or in more sheltered concave zones of the tidal flats. Therefore, in this chapter, the two *taxa* will be presented as separate genera.

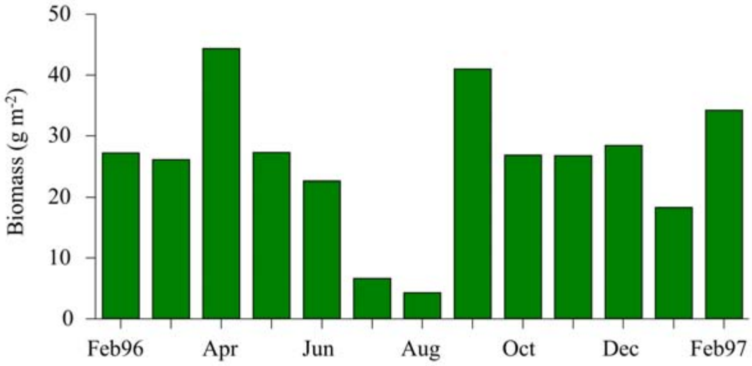

Figure 6.5.
Monthly variation of Ulvales biomass between February 1996 and February 1997.

In another field study done between 1999 and 2001 (Aníbal, 2004), the same Ulvales dynamics was observed (Figure 6.6 and Box 6.3).

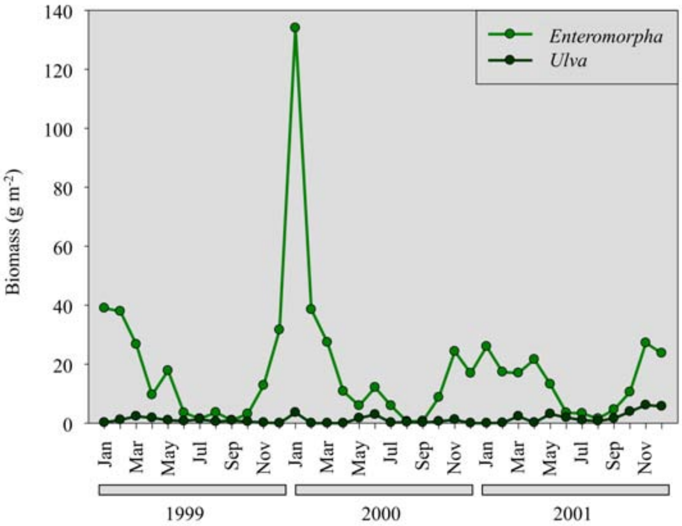

Figure 6.6.
Monthly variation of *Enteromorpha* and *Ulva* biomass between January 1999 and December 2001.

Box 6.3. Economic impact of macroalgae production in the world

According to the annual report on the state of the world fisheries and aquaculture of the Food and Agriculture Organization of the United Nations (FAO, 2018), aquaculture was the source of 96.5 percent by volume of the total 31.2 million tonnes of wild-collected and cultivated aquatic plants combined. Global production of farmed aquatic plants, overwhelmingly dominated by seaweeds (also known as macroalgae), grew in output volume from 13.5 million tonnes in 1995 to 30.1 million tonnes in 2016, with the first-sale value estimated at USD 11.7 billion.

Seaweeds and other algae are used as food (traditionally in China, Japan and the Republic of Korea), in animal feed, fertilizers, pharmaceuticals and cosmetics and for other purposes. Seaweeds are industrially processed to extract thickening agents such as alginate, agar and carrageenan or used, generally in dried powder form, as an animal feed additive. Increasing attention is also focusing on the nutritional value of several seaweed species, because of their high content of vitamins (particularly A, C and B-12), minerals (e.g. iron, calcium, iodine, potassium, selenium) and plant-based protein. Seaweed is also one of the only non-fish sources of natural omega-3 long-chain fatty acids. Several cosmetics have been commercialized from the seaweeds. Research is also exploring the use of seaweed as a salt substitute and in the industrial preparation of biofuel.

For more information about these issues consult http://www.fao.org/home/en/

6.3. *Where* are the green macroalgae blooms happening?

When using a bird's eye view to observe the muds and sands adjacent to Faro beach, they all seem flat plains, although a closer look reveals another geomorphologic reality. The flat plains are a succession of concave and convex section, especially in the mudflats (Figure 6.7).

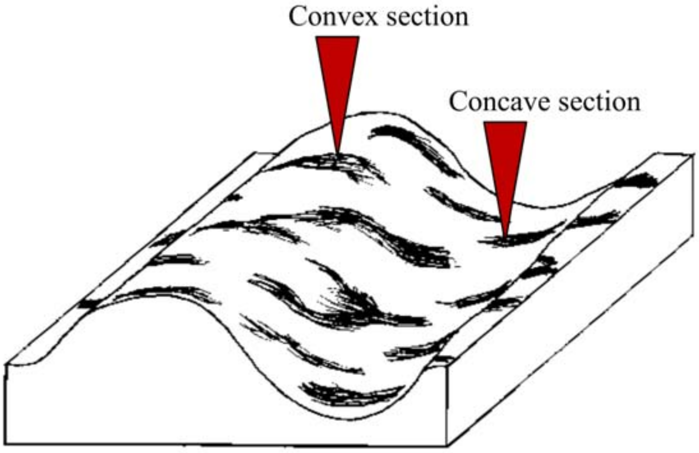

Figure 6.7.
Tidal flats' convex and concave sections.

A survey done in the study area in 2001 showed a clear distinction between convex and concave sections regarding sedimentological parameters (Aníbal et al., 2007). The concave sections presented a higher percentage of silt sediments, water content and organic matter. On the other hand, the convex sections had a higher composition in clay sediments. These results supported all the experimental design of the studies implemented to solve the following "*Why…*" question.

6.4. *Why* are all these phenomena occurring?

Once this green macroalgae phenomenon was characterized, the foundations for more detailed and specific research studies were created.

Photosynthetic organisms, such as green macroalgae live in the surface of sediments. Their lifecycle and dynamics can be constrained by two types of controls (Figure 6.8 and Box 6.4): "top-down control" done by herbivores, versus "bottom-up control" performed by nutrients availability and other abiotic factors (Valiela, 1995; Lynam et al., 2017).

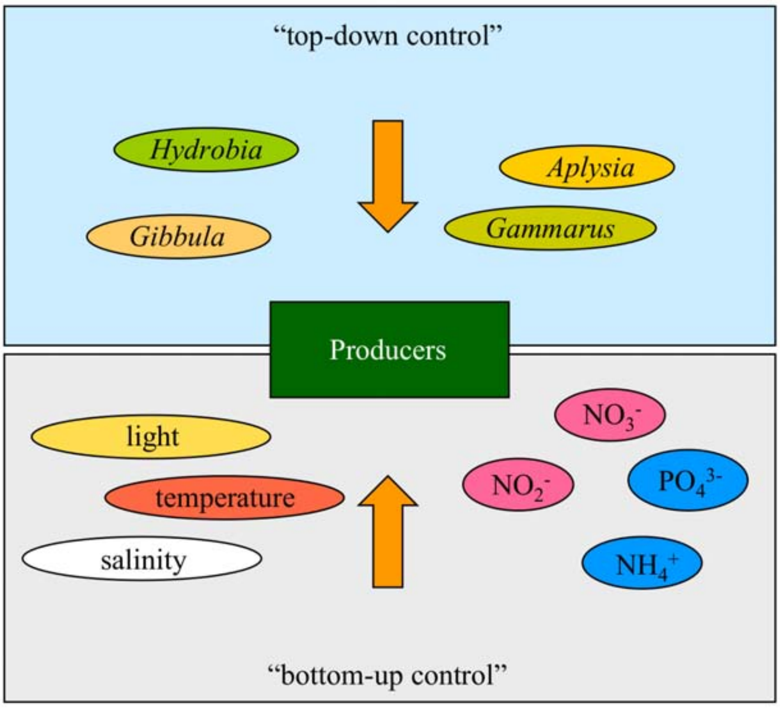

Figure 6.8.
"top-down control" versus "bottom-up control".

Box 6.4. Top-down control & bottom-up control

In an ecosystem, there are two types of controls on a population: bottom-up control, which is the limitation placed by resources allowing growth such as food source, habitat, or space, and top-down control, which is the limitation placed by factors controlling death such as predation, disease, or natural disasters.

In a world of limitless food resources, a population should be able to reproduce and expand their population exponentially. But in the real word, there will be years with abundant food resources, and years with scarcity. Thus, food resources can set the maximum limit of a population at any given time (bottom-up control).

Conversely, when the population gets too large, the predators drive it back down (top-down control). But the resulting decrease in their prey reduces the predator population, by reducing their food supply, allowing the prey to bounce back. Consequently, the bottom-up and top-down controls tend to regulate the stability of a population in an ecosystem. The bottom-up resources set the limit for the maximum healthy population, and the top-down forces kill off individuals from a large population, preventing overexploitation. The idea that populations interact and regulate one another is the fundamentals for wildlife conservation policies.

Because Martin Sprung was a Zoologist, the obvious starting hypothesis focused on the potential herbivory (top-down control) performed on the green macroalgae by the macroepifauna (Box 6.5).
The study of the potential top-down control done by the macroepifauna on the Ulvales was based on the following hypothesis: normally the animals' lifecycle is related to the seasons; the animals species begin to increase in numbers during the Spring, peaks their abundance and biomass during the Summer and start to decrease during Autumn; if these animals feed on the macroalgae, the only period of the year when the macroalgae can bloom is during the Winter period, because it corresponds to the macroepifauna minima for abundance and biomass.

Box 6.5. Macroepifauna

Organisms that are visible to the naked eye, bigger than 0.5 mm (macro), living at the sediment surface (epi) and belonging to the animal kingdom (fauna). The animals may originate from very diverse taxonomic groups, such as gastropods, crustaceans, insects, echinoderms or fishes.

The aim of the herbivory study was to access the impact of the herbivory performed by the macroepifauna over the green macroalgae present in the intertidal zones in the western area of Ria Formosa. The annual survey made in 1996-1997 allowed to identify and quantify, besides Ulvales' genera, 44 *taxa* of macroepifauna (Table 6.1).

In the mudflats, there was a clear distinction between the convex and the concave sections (Figure 6.9). The convex sections were characterized by higher Ulvales biomass, but fewer macroepifauna species and lower faunistic biomass, with a clear dominance in abundance of *Hydrobia ulvae* (Mesogastropoda). Concave sections of the sediment presented lower Ulvales biomass, but a more diverse macroepifauna, dominated by the higher biomass of *Gibbula umbilicalis* (Archaeogastropoda), *Cerithium vulgatum* (Mesogastropoda), *Nassarius pfeifferi* (Neogastropoda), *Haminaea navicular* (Cephalaspidea), *Melita palmata* (Amphipoda) and *Carcinus maenas* (Decapoda).

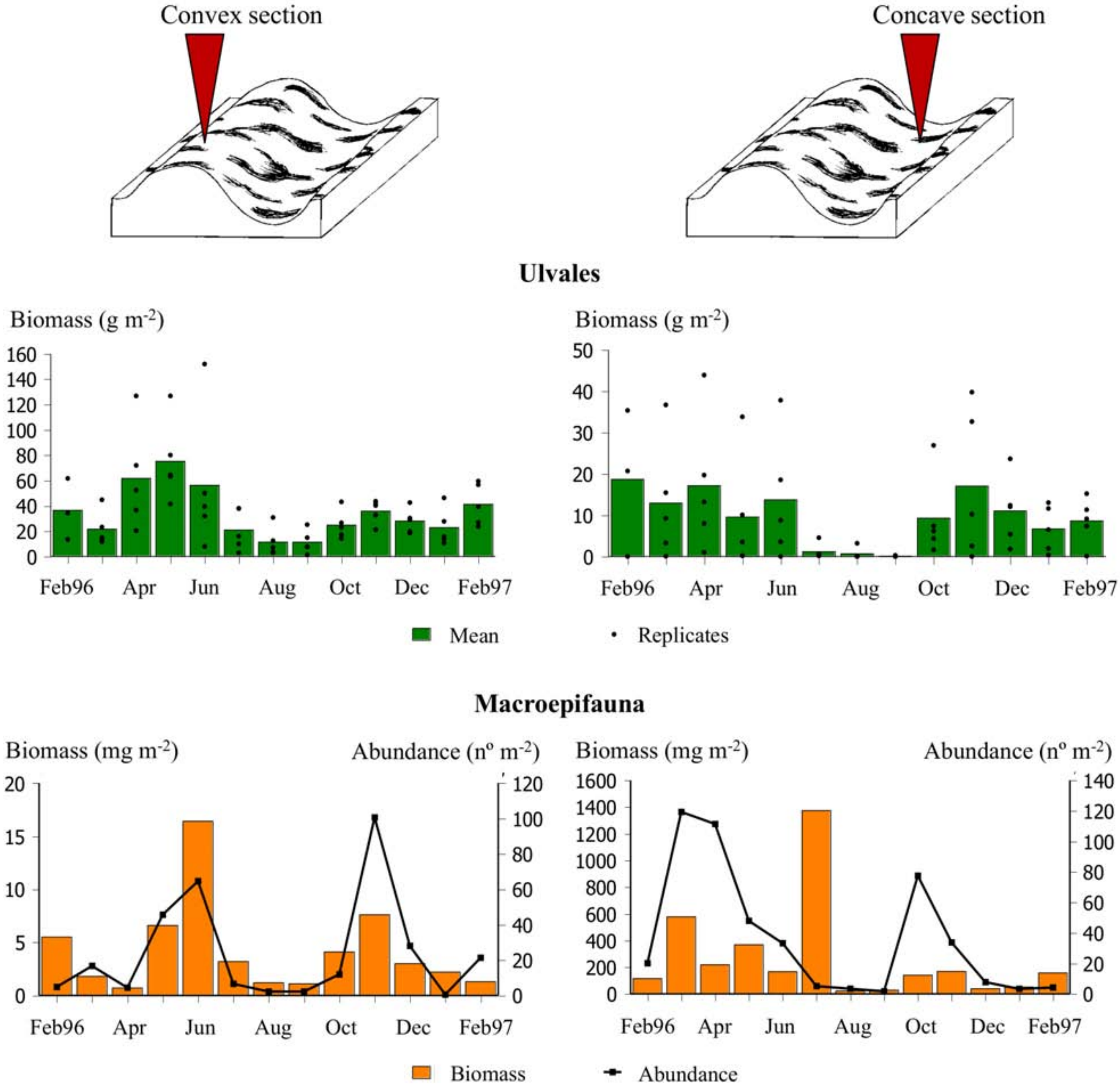

Figure 6.9.

Comparison of the green macroalgae and the macroepifauna dynamics between convex and concave sections of the sediment.

Table 6.1.
Macroepifauna identified during the field survey dedicated to the impact of herbivory over the green macroalgae. Abundance (n.º individuals m^{-2}) and biomass (mg AFDW m^{-2}) are average values for the western region of Ria Formosa.

Phylum	**Class**	**Species**	**Abundance (nº m^{-2})**	**Biomass (mg m^{-2})**
Cnidaria	Anthozoa	*Actinia equina*	0.02	1.22
		Anemonia sulcata	0.48	10.08
Mollusca	Amphineura	*Acanthochiton crinita*	0.03	0.60
		Chiton olivaceus	0.15	0.31
	Gastropoda	*Monodonta lineata*	0.92	83.48
		Gibbula umbilicalis	9.30	297.31
		Gibbula varia	2.28	158.15
		Gibbula pennanti	0.14	5.80
		Hydrobia ulvae	536.53	76.48
		Hydrobia ventrosa	8.22	0.67
		Rissoa membranacea	0.19	0.54
		Cerithium vulgatum	0.43	66.02
		Bittium reticulatum	1.43	1.97
		Calyptraea chinensis	0.01	0.03
		Ocenebra erinacea	0.01	1.68
		Ocinebrina aciculata	0.10	0.13
		Columbella rustica	0.01	0.93
		Amyclina cornicula	1.00	23.62
		Nassarius pfeifferi	9.34	236.93
		Haminaea navicula	8.64	104.53
		Aplysia depilans	0.02	11.47
		Aplysia fasciata	0.11	345.27
Arthropoda	Crustacea	*Balanus perforatus*	0.02	0.13
		Nebalia sp.	0.46	0.16
		Tanais dulongii	36.85	8.75
		Cyathura carinata	13.38	8.24
		Sphaeroma spp.	0.31	0.54
		Idotea chelipes	0.64	0.88
		Gammarus sp.	3.39	2.67
		Melita palmata	135.45	35.28
		Elasmopus rapaz	0.07	0.03
		Microdeutopus sp.	5.19	0.98
		Palaemon elegans	0.55	9.35
		Palaemonetes varians	0.17	6.06
		Crangon crangon	0.01	0.05
		Upogebia pusilla	0.03	3.08
		Carcinus maenas	3.60	728.23
		Pachygrapsus marmoratus	0.36	179.15
	Insecta	Chiromidae (larvae)	4.44	0.41
		Tipulidae (larvae)	7.67	6.84
Echinodermata	Holothurioidea	*Holothuria* sp.	0.09	0.41
	Ophiuroidea	*Amphipholis* sp.	0.01	0.03
Vertebrata	Osteichthyes	*Anguilla anguilla*	0.21	5.13
		Pomatoschistus minutus	0.17	7.90

An interesting fact was that the dynamics of the macroalgae and the macroepifauna were not complementary, as expected in our original hypothesis, but almost concordant in peak seasonality, and biomass and abundance dynamics. Almost all macroepifauna species had similar trends to those of the Ulvales, but for different reasons. From the species that are associated to the algae, almost all of them are detritivorous, possibly because the algae detritus is more easily assimilated by the individual gastric system, since it is already conditioned by microorganisms. There were some species that feed on the epiphytes on the algae (e.g. *Hydrobia*) and others just sought for refuge from its predators (e.g. juvenile fishes) or adverse abiotic conditions (Valiela, 1995; Schories et al., 2000).

To confirm these evidences, an herbivory laboratory study was done in 1999. The top potential herbivores (the previous mentioned seven species that dominated the macroepifauna) were chosen between the 44 identified species, taking into account their high values of biomass or abundance. Interestingly, none of these species exhibited a significant consumption of green macroalgae.

In conclusion, the intertidal areas of Ria Formosa are systems with low Ulvales herbivory, meaning that they are not top-down controlled. As other similar systems in the World, like the Mondego Estuary (Martins & Marques, 2002) or the Lagoon of Venice (Sfriso, 1995), the green macroalgae primary production is controlled by nutrients availability and favourable climatic conditions, which correspond to the bottom-up control paradigm (Valiela et al., 1997).

Between 1999 and 2001, another survey done in the same Ria Formosa area (Aníbal, 2004) allowed to assess which abiotic factors were dominant in controlling the Ulvales dynamics (bottom-up control). This study focused on the effects of the following abiotic factors on the Ulvales dynamics: temperature (water, sediment and air), rainfall, solar radiation, sediment characteristics (organic matter, water content and porosity) and pore water nutrients (nitrates, ammonia and phosphates).

After gathering and analysing all field and laboratory data, the Ulvales dynamics seemed to be controlled by two key moments: 1) the bloom beginning and 2) the bloom decay. The starting point of the Ulvales bloom appears to be originated by the conjunction of temperature decrease, photoperiod reduction, heavy rainfalls and high nutrient reserve concentrations in the sediment. On the other hand, the bloom decay seems to be related to temperature increase (leads to desiccation), photoperiod and solar radiation increase (provokes photoinhibition) and air relative humidity decrease (aggravates desiccation). It is important to note that phosphorus was the limiting element when compared with nitrogen, making sediment's pore water phosphate concentration a paramount nutrient resource for the primary producers (Schlesinger, 1997). Another striking observation was the fact that nitrates seemed to have higher concentrations in the deeper sediments layers, which might indicate the presence of submarine groundwater discharges (Rocha et al., 2016).

In this type of intertidal environment, macroalgae are not the only photosynthetic organisms with opportunistic life strategies. Along with Ulvales, microphytobenthos (Box 6.6) are competing for the same abiotic and nutrient resources (Figure 6.10).

Box 6.6. Microphytobenthos

Organisms smaller than 0.5 mm (micro), that are photosynthetic (phyto) and live in the sediment (benthos). In this work, chlorophyll a determinations were used as a proxy for microphytobenthos quantification. The taxonomic composition of microphytobenthos was mainly constituted by diatoms from the genera *Navicula*, *Pleurosigma* and *Tabellaria*.

The two previous mentioned key moments in the annual Ulvales dynamics may happen in two phases: 1) high primary production, from October to May, where nutrient competition between macroalgae and microphytobenthos controls the nutrient availability to Ulvales and 2) low primary production, from May to September, where photoinhibition, desiccation, organic matter increase and higher remineralisation impairs the development of photosynthetic organisms.

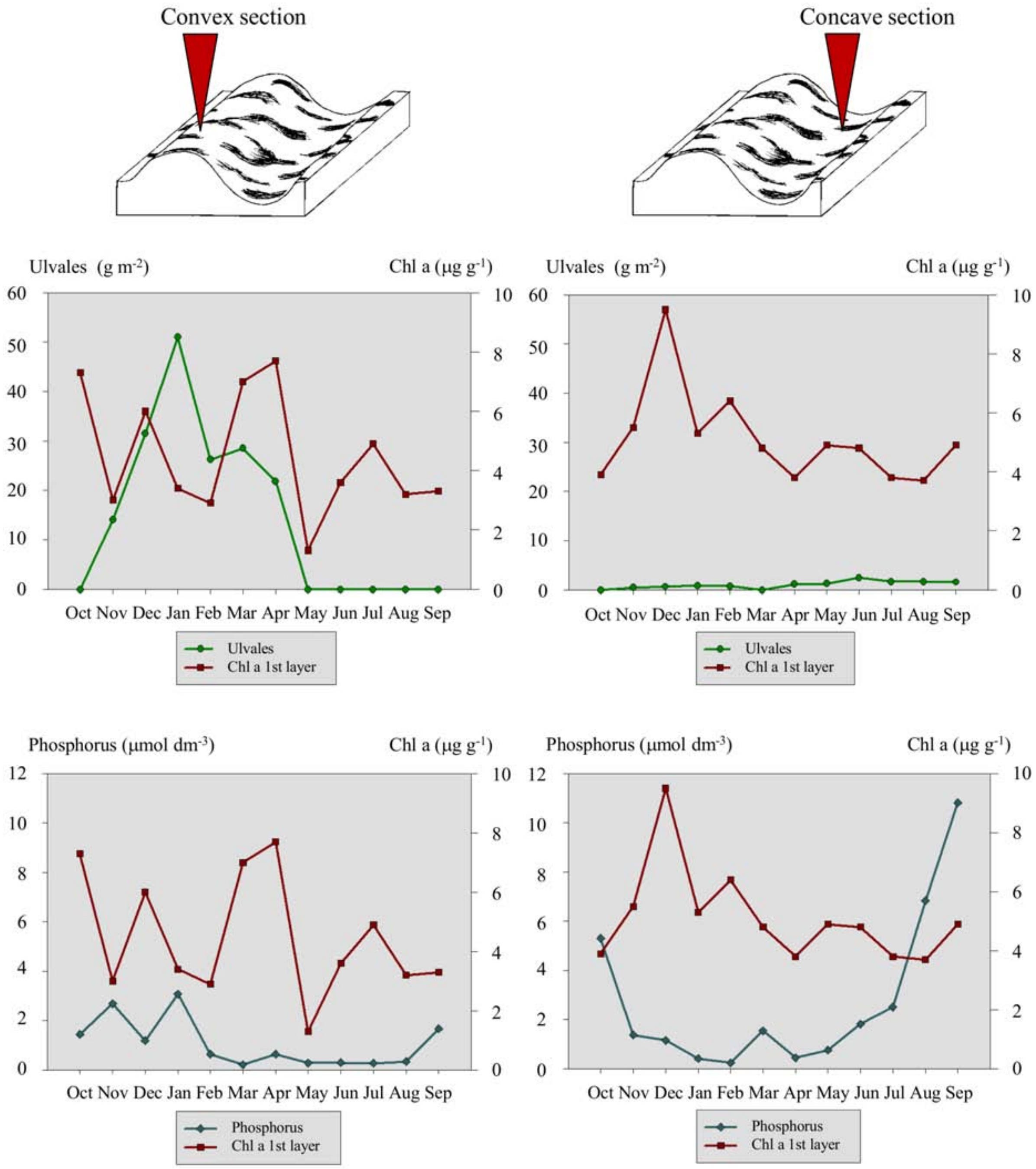

Figure 6.10.
Monthly dynamics of Ulvales biomass, chlorophyll a content in the first layer (1 cm) of sediment and phosphorus concentration in convex and concave sections of the sediments.

In Ria Formosa, the main source of nutrients for the benthonic primary producers is sedimentary remineralization, meaning that nutrients come from below and not from the water above. Since microphytobenthos lives in the first millimetres of the sediment, they are in a position that allows them to be able to uptake nutrients prior to other photosynthetic organisms (e.g. macroalgae), that only live in the sediment surface.

From the two previous described surveys, a conceptual diagram arose, linking the green macroalgae dynamics with the microphytobenthos competition and the nutrients availability (Figure 6.11).

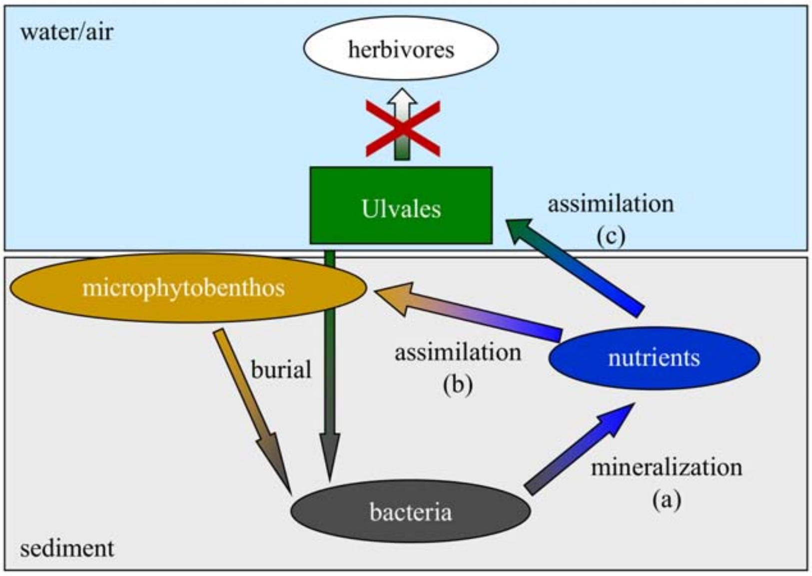

Figure 6.11.
Conceptual diagram of the forcing factors controlling the Ulvales dynamics in Ria Formosa.

From the conclusions of the field survey done in 1996-1997, it was possible to withdraw the herbivory as a significant forcing function in the Ulvales dynamics. The 1999-2001 survey allowed to acknowledge that when the increase in bacterial mineralization (a > 0) leads to a swift nutrients assimilation by diatoms (b > 0), creating conditions to a microphytobenthos bloom (b = a), the Ulvales are hindered to assimilate nutrients (c = 0) and increase their biomass. As the microphytobenthos increases, it also increases its demand for nutrients, until the point where they will begin to decrease (b > a), leading to the microphytobenthos collapse and posterior burial. This new source of organic matter to be remineralized will rapidly increase the nutrients pools in the sediment (a > b), creating conditions for the assimilation by the Ulvales (c > 0) and consequent green macroalgae bloom.
This conceptual diagram allowed to create a dynamic model using STELLA visual programming language (Figure 6.12), where the Ulvales biomass dynamics was simulated based on its intrinsic characteristics, temperature, light, nutrients and meteorological data (Jørgensen & Bendoricchio, 2001).

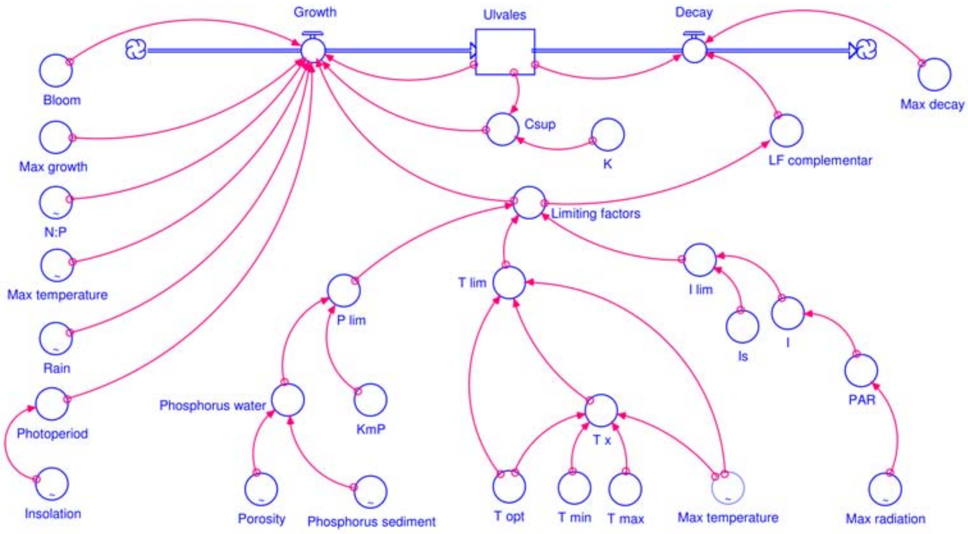

Figure 6.12.
Dynamic model of Ulvales using STELLA visual programming language.

The biomass results obtained from the model were compared with the observed values using statistical methods, that allowed to attain the following outcomes:

Model II regression

Simulated biomass = 0.586 Observed biomass – 1.075; $p < 0.005$; $n = 11$; $r^2 = 0.604$

Spearman correlation

$r = 0.863$; $p < 0.001$; $n = 11$

In conclusion, the model's output produced a simulation of the Ulvales's biomass dynamics that could explain more than 60% of the observed biomass variation (Figure 6.13).

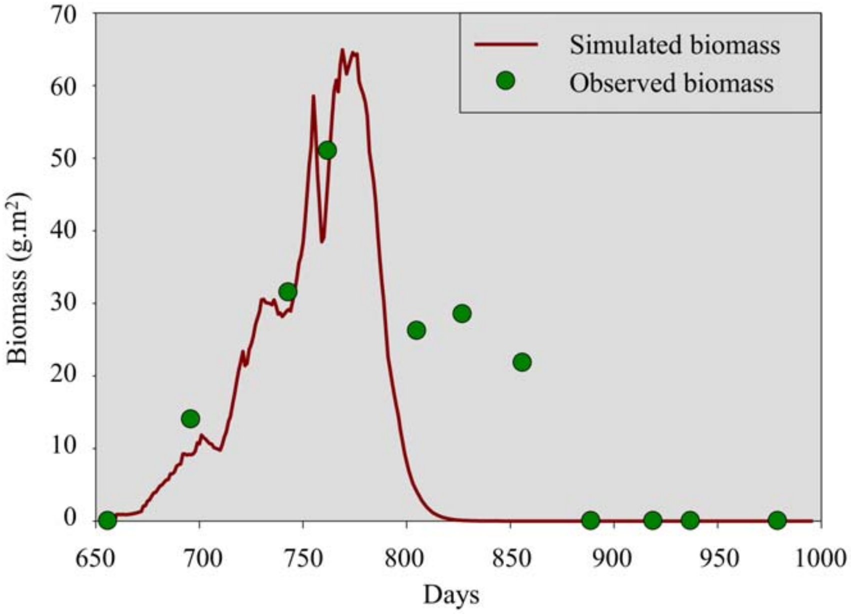

Figure 6.13.
Comparison between the Ulvales observed biomass and the simulated values obtained though the STELLA model output.

Ecological systems are very complex, and include many external variables. In this case, it can be considered that the 60.4% adjustment corresponds to the variables temperature, solar radiation and phosphorus concentration; the remaining 39.6% would explain the effect distributed by many other system variables, which were not considered in the model.

6.5. Ending with a click...

This tale of blooms and shapes started with a click and should also end with a click. In order to achieve this objective, monthly photographs were taken from December 2016 to June 2018, near the bridge that allows access to the Faro beach (Figure 6.14).

Figure 6.14.
Green macroalgae sediments coverage from December 2016 to June 2018. Photos were taken in the west (left) and east (right) sides of the road leading to Faro beach bridge (Photographs by Jaime Aníbal, 2018).

As expected, the Ulvales dynamics followed a very pronounced seasonal variation, with Winter blooms and Summer months without any macroalgal biomass. Once again, the beginning of Ulvales blooms followed the first Autumn or Winter heavy rains. This issue was especially evident in the last green macroalgae bloom. The Autumn of 2017 was particularly dry and the first rains only occurred during the month of January 2018; a couple of weeks following this phenomenon, the Ulvales bloom materialised. In the following March, the rainfalls were very heavy, and a week later the bloom was further increased.
The visual observation of the Ulvales dynamics shown in the photographs clearly indicates that the green macroalgae dynamics observed for the first time in 1988, still happens presently, and probably will continue to happen in the future.
With a starting click, an interesting puzzle was unexpectedly revealed, and with a finishing click, a few more pieces were added to an almost solved puzzle. Usually in science, the questions that arise after a concluded work are always more numerous than those that have been objectively answered.
Notwithstanding, this chapter might be the basis for a series of future work, which could unveil explanations to the questions that were still unanswered.

Acknowledgements

I would like to thank Martin Sprung and Carlos Rocha for their truly inspiring supervision during my MSc and PhD thesis, without whom I would have never reach the end of the tunnel.
Unfortunately, Martin Sprung left us before he could see the conclusion of the field work and all the interesting hypothesis raised by the results. To him, I dedicate this chapter!

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