3

Estuary Ecosystem Models

Irene Martins and Joao C. Marques

CONTENTS
3.1 Introduction ..................................................................................................63
3.2 An Estuarine-System Coastal Model: The Case Study of the Xiangshan Gang (East China Sea) ............................................................. 67
  3.2.1 Problematic ..........................................................................................67
  3.2.2 Aim .......................................................................................................67
  3.2.3 Study System .......................................................................................68
  3.2.4 Conceptual Diagram, Model Structure, and Main Equations ..................68
  3.2.5 Results .................................................................................................72
3.3 Brief Review of Some Recent Estuarine-Ecosystem Models .................77
3.4 Models of Primary Producers in Estuaries and Other Coastal Ecosystems .................................................................................................77
  3.4.1 Introduction .......................................................................................77
  3.4.2 Phytoplankton ...................................................................................84
  3.4.3 Macroalgae ......................................................................................95
  3.4.4 Microphytobenthos ........................................................................108
  3.4.5 Seagrasses .......................................................................................113
3.5 Conclusions ................................................................................................122
References .............................................................................................................124

3.1 Introduction

Estuaries worldwide are in severe decline, mainly as a result of pollution and the indirect impacts of climate change. This gives rise to an increasing awareness of the profound impact of humans on the functioning of estuarine ecosystems, and consequently to the need for approaches capable of sustaining those systems and where necessary, restoring them (Hughes et al. 2005). General environmental concern gave rise, approximately 2 decades ago, to the emergence of the idea of sustainable development (Pulselli et al. 2008), but researchers from different disciplines still attempt to understand and define more precisely the meaning of the term. Despite this, the most widely adopted definition has been “development that satisfies present
needs without compromising the possibility of future generations satisfying theirs” (Brundtland 1987). This is a rather vague nonoperational definition, which implies that the concept still requires a suitable quantification in socioeconomic, cultural, and scientific terms (Böhringer and Jochem 2007; Singh et al. 2009), taking into account (1) time, (2) relationships, and (3) biophysical limits (Pulselli et al. 2008).

Time is important as human society often does not evolve in accordance with the environment’s capacity to produce the resources required for our development. Different living and nonliving natural resources are needed by society, constituting what is called natural capital. Despite the fact that sustainable development has become a key challenge for the twenty-first century, the way human society interacts with that natural capital is still controversial. In fact, there are two clearly opposite positions regarding the practical meaning of sustainability: weak and strong sustainability. Weak sustainability implies that well-being must be maintained over intergenerational time scales, assuming that natural capital and man-made capital are substitutes within specific production processes (Brand 2009). As a consequence, weak sustainability accepts that the natural capital can be depleted, unless its requirement over time is declining (Brand 2009). Conversely, strong sustainability states that natural capital and man-made capital have to be viewed as complementary. As a consequence, human society must keep each type of capital intact over time, and the whole stock of natural capital has to be preserved for present and future generations in the long run (Brand 2009). In any case, the recognition that humans, with their cultural diversity, are an integral component of ecosystems, and the foreseeable threats represented by a serious worldwide environmental degradation have put ecological sustainability in international agendas.

Moreover, independently from the conceptual approach adopted, in cases in which uncertainties and change are key questions of environmental and social organization, critical factors for sustainability are resilience, the capacity to cope and adapt, and the conservation of sources of innovation and renewal (Lebel et al. 2006). The sustainable management of natural systems, in which estuaries are included, may then be described as achieving a balance between delivering the economic goods and services provided by the environment, which are required for societal health and functioning, while maintaining and protecting the ecological goods and services required for natural health and functioning.

Relationships therefore become crucial as the care of environment and natural resources might be not compatible with the present economical paradigm. In fact, economic instruments often appear to lack the criterion of efficient allocation of resources, since they tend to consider only things directly linked to the market (Pulselli et al. 2008). Such relationships imply interdependencies but it is necessary to determine at what scale (regional, national, etc.) different aspects are interdependent.
Finally, biophysical limits also need to be considered as each local human population can hardly meet its needs for materials, energy, land, waste sinks, and information from its own local resources. This is reflected in the concept of critical natural capital, which emerged between the “weak sustainability” and the “strong sustainability” positions, consisting of the part of the natural capital that performs important and irreplaceable environmental functions, that is, those ecosystem services that cannot be replaced by other types of capital (De Groot et al. 2003). In fact, it is widely accepted that the maintenance of such critical natural capital is essential to environmental sustainability and sustainable development (Ekins et al. 2003).

Sustainable management of estuaries can only be achieved if a multidisciplinary approach is undertaken; management actions within that approach are required to be environmentally and ecologically sustainable, economically viable, technologically feasible, socially desirable or at least socially tolerable, administratively achievable, legally permissible, and politically expedient (e.g., Elliott et al. 2006; Bunce et al. 2008; Mee et al. 2008; Ojeda-Martínez et al. 2009).

In estuaries, in particular, there is the need for environmental restoration involving dealing with problems such as: (1) losses of habitats and species diversity, as well as a decrease in habitats size and heterogeneity; (2) decrease in population size and changes in dynamics and distribution of many species; and (3) decrease in economically relevant services and goods naturally provided by the systems (e.g., Elliott et al. 2007). In this context, the search for estuaries ecologically sustainable management represents a great challenge, namely because if some ecological concepts are well understood, such as the nature of estuarine ecosystems structure and functioning, others such as resilience, carrying capacity, and estuarine ecosystem goods and services are in general still not well quantified (Marques et al. 2009).

The resilience concept, for instance, has suffered considerable changes in the past three decades (Walker et al. 2004). Recently, Elliott et al. (2007) attempted to remove the confusion regarding the term by taking the view that it referred the inherent ability of a system to return to a previous, or similar, state following disturbance. However, at least two other meanings for it can be distinguished. The first refers to dynamics close to equilibrium and is defined as the time required for a system to return to an equilibrium point following a disturbance event, or system’s recovery. It is termed engineering resilience (Holling 1996; Folke 2006) and is largely equivalent to the stability property elasticity (Grimm and Wissel 1997), which can be seen as resistance to change (Levin and Lubchenco 2008). A further meaning refers to dynamics far from any equilibrium steady state and is defined as the capacity to absorb stress and yet still maintain “function”—this has been termed ecological resilience (Gunderson and Holling 2002; Folke 2006), that is the capacity to maintain functioning despite multiple stressors that affect a developing system (Levin and Lubchenco 2008). This is more related to...
renewal, regeneration, or reorganization following disturbance than to the system's recovery (Folke 2006). In this case, disturbance events and spatial heterogeneity cause each system's behavior to be unique, and the complexity of the system combined with unanticipated compounded effects can make recovery trajectories difficult or impossible to predict. A recovered system may look similar but it is not the same system, because like any living system it is continuously developing (Folke 2006). Elliott et al. (2007) termed the differences in degradation and recovery trajectories as hysteresis in the system. Ecological resilience has to be estimated via resilience surrogates (Carpenter et al. 2005), based on a comprehensive resilience analysis, including the identification of specific disturbance regimes and societal choices of the desired ecosystem services (Brand 2009).

Estuarine ecosystems and their change due to human stressors require to be analyzed according to their carrying capacity and its loss following stress. The concept of carrying capacity was originally an ecological construct, defined as the number of individuals of a population an environment can support without significant negative impacts to the given population and its environment (Elliott et al. 2007). This definition does not fully capture the multilayered processes of human–environment relationships, which have a fluid and nonequilibrium nature, and it may disregard the role of external forces in influencing environmental change (Moore et al. 2009). Because of this, several authors (MacLeod and Cooper 2005; Elliott et al. 2007) emphasize that carrying capacity also should relate to social and economic aspects of ecosystems, that is, what human activities and anthropogenic change can an estuarine ecosystem withstand before adverse change is experienced.

The linking between these ecological concepts and the management framework is also relatively recent and the concepts are now being integrated to provide a holistic approach not only to understand, but also to manipulate and manage the environment. Of particular importance with regard to estuarine management are ideas relating to the dynamics of ecosystems and the relations between biodiversity and ecosystem function, which have led toward the view that estuaries are particularly complex adaptive systems, characterized by historical dependency, nonlinear dynamics, threshold effects, multiple basins of attraction, and limited predictability (Folke et al. 2004; Duit and Galaz 2008; Moore et al. 2009).

Estuarine environmental problems are therefore intrinsically complex, and there is a clear need for solutions in a multiuse/multiuser/multisectorial system. To achieve this goal, the use of models becomes indispensable.

In this chapter, we provide a brief overview of recent models used in understanding estuarine processes, as well as in dealing with estuarine management problems. First, we present a case study of a model operating at the system level: the multilayered model for Xiangshan Gang bay (East China Sea), which was developed for the sustainable management of coastal ecosystems and used to simulate management scenarios that account for changes in multiple uses and enable assessment of cumulative impacts of
coastal activities (Nobre et al. 2010). Then, we provide a summary, in the form of a table (Table 3.2), from other recent models developed for estuaries worldwide. Most of the presented models include a hydrodynamic submodel coupled to a biogeochemical one, whereas one of the presented models is an ECOPATH with ECOSIM model that analyzes the flows of energy and matter along estuarine food webs. Finally, because primary producers play quite relevant roles at estuaries and other coastal systems, we give particular insight into primary producer models from estuaries and coastal systems, contemplating all the four main different types of primary producers present at estuaries: phytoplankton, macroalgae or seaweeds, microphytobenthos, and seagrasses.

### 3.2 An Estuarine-System Coastal Model: The Case Study of the Xiangshan Gang (East China Sea)

#### 3.2.1 Problematic

Coastal zones provide considerable benefits to society while, at the same time, human activities exert significant pressure on coastal ecosystems, therefore threatening those same benefits (Nobre 2009).

To promote the sustainable use of coastal zone resources, an ecosystem approach is required because it will contribute to the understanding of the causal relationships between environmental and socioeconomic components, plus the cumulative impacts of the range of activities developed in coastal ecosystems (Nobre and Ferreira 2009) and to manage coastal resources and biodiversity (Murawski et al. 2008).

Ecosystem modeling is a powerful tool that can contribute the required scientific grounding for the adoption of an Ecosystem-Based Management approach (Hardman-Mountford et al. 2005; Murawski 2007). Some of the improvements generated by this approach are to allow the examination of different development scenarios by altering variables of both the catchment and coastal systems and to provide insights for managers (Nobre et al. 2010).

#### 3.2.2 Aim

The authors developed a multilayered catchment–coastal modeling approach to optimize the trade-offs presented above, through the use of a comprehensive set of models operating at different levels of complexity and geographical scales.

The specific objectives of the work were to (1) develop an integrated coastal management tool for decision-makers and (2) examine the outcomes of different development scenarios.
3.2.3 Study System

The Xiangshan Gang bay (volume of $3803 \times 10^6$ m$^3$; area of 365 km$^2$) located at the East China Sea (Figure 3.1).

3.2.4 Conceptual Diagram, Model Structure, and Main Equations

*Multilayered ecosystem model.* This work uses an integrated ecosystem modeling approach (Ferreira et al. 2008) to simulate the hydrodynamics, biogeochemistry, aquaculture production, and forcing functions, such as catchment loading within Xiangshan Gang (Figure 3.2).

The multilayered approach includes the coupling of several submodels, which were selected following the balance required in the choice of model complexity and structure (Jørgensen and Bendoricchio 2001). The considered key state variables and processes include: (1) production of multiple species in polyculture, (2) its effects on the coastal environment, and (3) impacts of other catchment–coastal system uses on the water quality and aquaculture resources.

*Catchment submodel.* The loading of substances into the Xiangshan Gang bay was simulated from the Soil and Water Assessment Tool (SWAT) model (Neitsch et al. 2002).

The main equations for catchment are the ones that describe the surface water balance and nutrient (for both N and P) export, respectively:

\[
\frac{dSW}{dt} = PP_t - Q_{St} - E_n_t - W_{St} - Q_{gw_t}
\]  

(3.1)

**FIGURE 3.1**

Location of Xiangshan Gang and some of its physical characteristics. (Modified from Nobre et al. *Estuarine, Coastal and Shelf Science*, 87, 43–62, 2010. With permission.)
where $SW$ is the soil water content ($mm^3 \ mm^{-2}$), $PP_t$ is rainfall, $Q_{St}$ is the surface water runoff, $Et$ is evapotranspiration, $W_{St}$ denotes the exchanges with the deep aquifer, $Q_{gw_t}$ is the subsurface water runoff, and:

$$\frac{dN}{dt} = F_{n_t} + R_{n_t} + A_{n_t} - P_{Un_t} - Q_{n_t} - L_{n_t} - V_{n_t} - D_{n_t}$$

(3.2)

where $N$ is the soil nutrient concentration ($kg \ ha^{-1}$), $F_{n_t}$ is fertilization, $R_{n_t}$ is residue decomposition, $A_{n_t}$ is atmospheric fixation of $N$, $P_{Un_t}$ is plant uptake, $Q_{n_t}$ is lateral export, $L_{n_t}$ is leaching, $V_{n_t}$ volatilization of $N$, and $D_{n_t}$ is denitrification.

The model was calibrated against annual average discharge estimates for the most important rivers in the catchment, using a 30-year model run based on the 1961–1990 climatic normal built with the model’s stochastic weather generator.

Model performance for water inputs was satisfactory as indicated by a significant correlation between simulated and observed values ($r^2 = 0.92$), low model bias (−5.3%) and high model efficiency (Nash–Sutcliffe efficiency...
Additionally, the simulated annual nitrogen inputs from diffuse agricultural sources (960 tons year\(^{-1}\)) compared well with estimates based on export coefficients (900 tons year\(^{-1}\); Huang et al. 2008a, 2008b).

The output from the catchment submodel was transformed into daily data series for offline coupling with the biogeochemical submodel.

The total nutrient load entering the bay was estimated to be about 11 tons day\(^{-1}\) of dissolved inorganic carbon (DIN) and 2 tons day\(^{-1}\) of phosphate. The point sources included untreated urban wastewater for ca. 600,000 inhabitants.

**Hydrodynamic submodel.** A three-dimensional hydrodynamic model (Delft3D-Flow-Delft Hydraulics 2006) was used to simulate the transport of substances among boxes and across the ocean boundary.

The calibration of the hydrodynamic model was achieved in two phases. First, the variations in tidal forcing were compared against measured water levels, followed by adjustment of bottom roughness to reproduce the water velocity characteristics (Huang et al. 2003). Overall, the model represented the amplitude of the main harmonic constituents well. In order to define the model boundary conditions, the salinity and temperature dataset was complemented with data from other authors (Hur et al. 1999; Isobe et al. 2004). In this second phase, the response of the system was gauged through existing knowledge of circulation as affected by tides and baroclinicity in tidal embayments (Fujiwara et al. 1997; Simpson 1997). Due to the lack of density and velocity data, the authors have used this procedure to tune the model within the theoretically acceptable boundaries for this type of system.

The model outputs provided a repeatable series of approximately 1 year of flows, which was used to force transport in the ecosystem model for calibration and validation years. The detailed flow fields were scaled up and converted into a data series of water fluxes between boxes and across the sea boundary with a 1-h time step and coupled offline with the biogeochemical submodel (see Ferreira et al. 2008).

**Aquatic resource submodel.** This submodel simulates the production of the Chinese oyster (*Ostrea plicatula*), the razor clam (*Sinonovacula constricta*), the Manila clam (*Tapes philippinarum*), and the muddy clam (*T. granosa*). The equations for shellfish aquaculture production were explicitly integrated into the ecosystem model with a four step approach: (1) use of a shellfish individual growth model (ShellSIM); (2) coupling of the individual growth model with a demographic model to simulate the population (Ferreira et al. 1997); (3) integration of the population growth model with an aquaculture practice model that implements the seeding of the population biomass and harvesting of the marketable cohorts for a given production cycle (Ferreira et al. 1997), and (4) use of a multiple-inheritance object-oriented approach (Nunes et al. 2003) to extend to multiple species in polyculture.

The individual growth model (ShellSIM) is driven by allometry, and it simulates feeding, metabolism, and individual growth of different shellfish
species, under different environmental conditions. Shellfish growth depends on several environmental drivers, including salinity, temperature, and suspended particulate matter (SPM):

$$\eta = f(B) \cdot f(POM) \cdot f(SPM) \cdot f(L) \cdot f(T)$$  (3.3)

where $\eta$ is the shellfish scope for growth, $f(B)$ is the function of phytoplankton, $f(POM)$ is the function of particulate organic detritus, $f(SPM)$ is the function of SPM, $f(L)$ is the function of salinity, and $f(T)$ is the function of water temperature.

For the Chinese oyster, razor clam, and muddy clam, the individual growth model was calibrated under local conditions (Ferreira et al. 2008). To simulate the growth of the Manila clam, the model used in Ferreira et al. (2007) was applied.

The population growth is simulated using a demographic model based on 10 weight classes, governed by the following equation:

$$\frac{dS(S,t)}{dt} = -d\left[S(s,t) \cdot \eta(s,t)\right]$$  (3.4)

where $S$ is the number of individuals in each shellfish weight class, $\eta$ is the shellfish scope for growth, and $\mu$ is the shellfish mortality rate.

The food resources (phytoplankton and detritus) removed by the population is scaled for each size class on the basis of the number of individuals in the class.

The aquaculture practice model (Ferreira et al. 1997) implements the seeding and harvesting strategies and interacts with the population model by respectively adding and subtracting individuals to the appropriate classes.

The model includes shrimp and fish production as forcing functions, contributing to dissolved and particulate waste (Ferreira et al. 2008).

**Biogeochemical submodel.** This submodel was developed to simulate the variation of salinity, dissolved nutrients, particulate matter, and phytoplankton. The main equations that describe the variations of these state variables are:

$$\frac{dB}{dt} = B \cdot \left(p_{\text{max}} \cdot f(I) \cdot f(NL) - r_b - \epsilon_b - m_b - S \cdot C_S\right)$$  (3.5)

where $B$ is the phytoplankton biomass, $p_{\text{max}}$ is the phytoplankton maximum gross photosynthetic rate, $f(I)$ is the Steele’s equation for productivity with photoinhibition, $f(NL)$ is the Michaelis–Menten function for nutrient limitation, $r_b$ is the respiration rate, $m_b$ is the natural mortality rate, and $C_S$ is shellfish grazing rate.
\[
\frac{dN}{dt} = B \left( e_b + m_b \right) \cdot \alpha + S \cdot e_S + \text{POM} \cdot m_{\text{pom}} \cdot \varepsilon - B \cdot \left( p_{\text{max}} \cdot f(I) \cdot f(NL) \right) \cdot \alpha
\]

where \( N \) denotes the dissolved inorganic nutrient, \( \alpha \) is the conversion from phytoplankton carbon to nitrogen units, \( \text{POM} \) denotes particulate organic matter, \( \varepsilon \) is the conversion from \( \text{POM} \) dry weight to nitrogen units, \( m_{\text{pom}} \) is the \( \text{POM} \) mineralization rate, and \( e_S \) is the shellfish excretion rate.

\[
\frac{d\text{POM}}{dt} = \text{POM} \cdot (e_{\text{pom}} - d_{\text{pom}}) + S \cdot f_S + B \cdot m_b \cdot \omega - \text{POM} \cdot (m_{\text{pom}} + p_{\text{pom}} \cdot S)
\]

where \( \text{POM} \) denotes particulate organic matter, \( e_{\text{pom}} \) is the \( \text{POM} \) resuspension rate, \( d_{\text{pom}} \) is the \( \text{POM} \) deposition rate, \( f_S \) is the shellfish feces production, \( \omega \) is the conversion from phytoplankton carbon to \( \text{POM} \) dry weight, and \( p_{\text{pom}} \) is the shellfish \( \text{POM} \) filtration rate.

\[
\frac{d\text{SPM}}{dt} = \text{SPM} \cdot (e_{\text{spm}} - d_{\text{spm}}) + S \cdot f_S - \text{SPM} \cdot p_{\text{spm}} \cdot S
\]

where \( \text{SPM} \) denotes suspended particulate matter, \( e_{\text{spm}} \) is the \( \text{SPM} \) resuspension rate, \( d_{\text{spm}} \) is the \( \text{SPM} \) deposition rate, and \( p_{\text{spm}} \) is the shellfish \( \text{SPM} \) uptake rate.

The parameterization of the model was in accordance with data obtained at the study site (Table 3.1).

The multilayered model was used to simulate coastal management options, which were based on scenario definition. The development scenarios were defined as a result of the participatory work among stakeholders, including modelers, local fishery and environmental managers, and aquaculture producers. The scenarios to be simulated by the multilayered ecosystem modeling framework were the following: (1) a reduction of fish cages corresponding to a 38% reduction in total fish production; (2) an extension of wastewater treatment to the entire population; and (3) a simultaneous reduction of fish cages and extended wastewater treatment.

The definition of scenarios is important for the evaluation of nutrient abatement strategies and to provide guidelines/grounding for future aquaculture policy and for eutrophication control.

### 3.2.5 Results

**Ecosystem simulation.** Simulations for the catchment submodel show two annual peaks for \( N \) input, in early spring and early summer, which can be related to both the fertilization of rice and the annual rainfall and runoff.
TABLE 3.1
Ecosystem Model Parameters for the Standard Simulation

<table>
<thead>
<tr>
<th>Shellfish Population</th>
<th>Number of Weight Classes</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality, ( \mu ) (% per day)</td>
<td>Oyster</td>
<td>0.40%</td>
</tr>
<tr>
<td></td>
<td>Clam</td>
<td>0.56%</td>
</tr>
<tr>
<td></td>
<td>Razor</td>
<td>0.20%</td>
</tr>
<tr>
<td></td>
<td>Muddy</td>
<td>0.15%</td>
</tr>
</tbody>
</table>

| Seed weight (gTWF ind\(^{-1}\)) | Oyster | 0.2 |
| | Clam | 0.5 |
| | Razor | 0.5 |
| | Muddy | 0.1 |

| Seeding period | Oyster | April–August |
| | Clam | May–June |
| | Razor | April–August |
| | Muddy | June–September |

| Harvestable weight (gTWF ind\(^{-1}\)) | Oyster | 8 |
| | Clam | 14 |
| | Razor | 11 |
| | Muddy | 15 |

| Harvesting period | Oyster | December–March |
| | Clam | January–February |
| | Razor | October–February |
| | Muddy | November–March |

| Aquaculture area (ha) and boxes cultivated | Oyster | 2286 (Boxes 1–5, 8, 9, 11, 12) |
| | Clam | 308 (Boxes 1–7, 10) |
| | Razor | 313 (Boxes 1–6) |
| | Muddy | 187 (Boxes 1–3, 5, 6) |

| Seedling density (tTWF ha\(^{-1}\)) | Oyster | 0.90 |
| | Clam | 0.45 |
| | Razor | 0.72 |
| | Muddy | 0.82 |

| Phytoplankton growth | \( P_{\text{max}} \) (h\(^{-1}\)) | 0.2 |
| | Lop (w m\(^{-2}\)) | 300 |
| | Death loss – \( m_b \) day\(^{-1}\) | 0.01 |
| | \( K_s \text{DIN} \) (\( \mu \) mol L\(^{-1}\)) | 1 |
| | \( K_s \text{Phosphate} \) (\( \mu \) mol L\(^{-1}\)) | 0.5 |

| Suspended matter | POM mineralization rate (day\(^{-1}\)) | 0.02 |
| | POM to nitrogen (DW to N) | 0.0519 |
| | POM to phosphorus (DW to P) | 0.0074 |

patterns. The same pattern was also found for particulate matter and P loads. Results indicate that the major sources of N are urban sewage discharges (56%), fertilization in rice crops (27%), and rangelands, mostly detritus decomposition from forests (17%). P followed a similar pattern, with 60% coming from urban sewage discharge and the rest from agricultural and natural sources.

Model outputs for DIN and phytoplankton fitted reasonably well with observed data (Figure 3.3), although in some points, the model overestimated DIN concentrations. Model outputs for SPM and POM in Box 10 (an outer box) did not represent the observed variability, but for an inner box (Box 3), there was a good agreement between predictions and observations. This may be related to the fact that the temporal resolution of SPM and POM being used to force the ocean boundary was not sufficient to represent the variability in the adjacent boxes. In the inner boxes, as the marine influence is lower and the catchment inputs of POM and SPM are more important, the daily inputs provided by the catchment model are realistic. Moreover, this limitation is not likely to significantly affect the simulation of aquaculture production, given that 83% of the bivalves are produced in the inner boxes (Boxes 1–5).

Simulations for total shellfish production were 2305 tons for an inner box (Box 3) and 741 tons (all oyster) for an outer box (Box 11). Overall, the outputs of harvested shellfish compared well with the landings data (Figure 3.4).

Development scenarios. In general, simulations indicate that the effects of changes implemented in the scenario simulations were mostly visible in the inner boxes. Variations of DIN, phosphate, phytoplankton, shellfish harvest, and productivity were less evident in the outer boxes, possibly due to exchanges with the ocean boundary.

In any of the scenarios, the reduction of nutrient loads resulted in very small changes in DIN concentration for any of the boxes, whereas phosphate concentrations were more sensitive to this. However, DIN and phosphate were still present in high concentrations for every scenario and in every box, which confirms the result of poor water quality in the Xiangshan Gang bay, even after scenario implementation.

For all scenarios, predictions indicate a decrease in shellfish productivity for all cultivated species, with more significant decreases in the inner boxes (e.g., less 286–864 tons year\(^{-1}\) in Box 3 compared to less 8–16 tons year\(^{-1}\) in Box 12).

Discussion. Model results indicate that the proposed scenarios will not achieve the management goals that they were designed to attain because (1) the modeled nutrient load reduction had no significant effect on the water quality of the Xiangshan Gang and (2) the decrease in phytoplankton biomass was limited to some areas of the bay.

Future work using this multilayered model includes the definition of further scenarios to assess how different land use and aquaculture practices may impact the bay.
FIGURE 3.3
Standard simulation outputs for an inner box (Box 3) and a middle box (Box 10) plotted against average daily data ± standard deviation. Dissolved inorganic carbon (DIN), phytoplankton biomass, phosphate, suspended particulate matter (SPM), and particulate organic matter (POM). (From Nobre et al. *Estuarine, Coastal and Shelf Science*, 87, 43–62, 2010. With permission.)

© 2011 by Taylor and Francis Group, LLC
The model outputs indicate that the nutrients and POM provided by fish cages and wastewater are sustaining shellfish growth in the inner boxes. In the scenarios that test a decrease of these substances, shellfish production also decreases, particularly in the inner boxes. The estimated total loss of harvested shellfish was between 4600 and 12,700 tons year\(^{-1}\), corresponding to a loss of annual revenue between €555,000 and €1,500,000. Thus, the authors recommend reallocating part of the shellfish culture toward the mouth of the embayment.

**Conclusions.** This work clearly indicates that multilayered ecosystems models can play a key role for the adoption of ecosystem-based approaches to coastal and marine resource management. Furthermore, the integration of ecosystem-based tools can be used to fill data gaps, improve the temporal/spatial detail of setup datasets, and provide guidance to monitoring programs.
3.3 Brief Review of Some Recent Estuarine-Ecosystem Models

In this section, we present a summary in the form of a table, of some other estuarine-ecosystem models developed within the past decade (2000–2010), for a variety of estuaries worldwide (see Table 3.2), covering estuarine systems from Northern and Southern Europe, America, Asia, and Australia.

Most of the described models are hydrodynamic—coupled to biogeochemical—models (Das et al. 2010; Fulton et al. 2004; Timmermann et al. 2010; Trancoso et al. 2005; Blauw et al. 2009; García et al. 2010; Sohma et al. 2008), while one is a food web flow model (Patrício and Marques 2006). Some of the models were developed to perform as generic system-level models (e.g., Integrated Generic Bay Ecosystem Model [IGBEM], Fulton et al. 2004; or Generic Ecological Model [GEM] for estuaries, Blauw et al. 2009), whereas others were developed with specific aims for a given estuary.

3.4 Models of Primary Producers in Estuaries and Other Coastal Ecosystems

3.4.1 Introduction

Net primary production is defined as the amount of photosynthetically fixed carbon available to the first heterotrophic level and, as such, is the relevant metric for addressing environmental questions ranging from trophic energy transfer to the influence of biological processes on carbon cycling (Lindeman 1942).

Essentially, there are four types of primary producers that may have significant impacts on estuaries and coastal areas: phytoplankton, macroalgae, microphytobenthos, and seagrasses.

The biomass ($B$) variation of any primary producer over time ($t$) can be generically described by:

$$\frac{dB}{dt} = GP - R - E - L - M$$

(3.9)

where $GP$ is the gross productivity, $R$ is respiration, $E$ is exudation, $L$ is loss, and $M$ is mortality.

Gross productivity is often described as a function of a maximum productivity rate ($\mu_{max}$) and some limiting factors, usually, light ($f_l$), temperature ($f_T$), and nutrients ($f_U$):

$$GP = \mu_{max} \cdot f_l \cdot f_T \cdot f_U$$

(3.10)
### Table 3.2
Summary of Some of the Estuarine Models Developed between 2000 and 2010

<table>
<thead>
<tr>
<th>Study System</th>
<th>Aims</th>
<th>Software, Integration Algorithm, Background Models</th>
<th>Main Equations/Characteristics</th>
<th>Main Results</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mondego estuary (Portugal)</td>
<td>To assess food web flows and interactions along an eutrophication gradient.</td>
<td>ECOPATH with ECOSIM</td>
<td>( B_i \times (P/B)<em>j \times EE_i - \sum</em>{j=1}^{n} B_j \times (Q/B)<em>j \times DC</em>{ji} ) - ( Y_i - BA_i - E_i = 0 )</td>
<td>Total sum of flows, total system throughput, annual rate of net primary production highest in Zostera meadows, followed by the strongly eutrophic area and the intermediate eutrophic area.</td>
<td>Patrício and Marques (2006)</td>
</tr>
<tr>
<td>Barataria estuary (Gulf of Mexico)</td>
<td>To calculate the fluxes of water, nitrogen and carbon through the estuary. To estimate the importance of estuarine derived N and C for the overall C-budget and development of hypoxia.</td>
<td>Fourth-order Runge–Kutta with an integration step of 0.1 h.</td>
<td>( \frac{\partial V_i}{\partial t} = F_i + P_i + R_i - E_i + Q_i )</td>
<td>Annual TOC export from the estuary = 57 g C m(^{-2}) yr(^{-1}), corresponding to 2.7% of the riverine TOC. Not significant for the development of the Gulf’s hypoxia.</td>
<td>Das et al. (2010)</td>
</tr>
</tbody>
</table>
Port Phillip bay (Australia)

System-level description of temperate embayment ecosystems—IGBEM (Integrated Generic Bay Ecosystem Model).

Based on two existing ecosystem models: the Port Phillip Bay Integrated Model (PPBIM) and the European Regional Seas Ecosystem Model II (ERSEM II).

IGBEM integrates the biological and physical modules of PPBIM (Murray and Parslow 1997, 1999) and the biological modules from ERSEM II (Baretta et al. 1995; Baretta-Bekker and Baretta 1997).

The model behaves according to Sheldon Spectrum (Sheldon et al. 1972) and Monbet's relationship between chl. a and DIN (Monbet 1992), and reproduces spatial zonation and long-term cycles.

It captures the system dynamics and allows exploration of the effects of ecological driving forces.

Horsens estuary (Denmark)

To assess the relative importance of nutrients supplied from freshwater outlets vs. nutrients entering the estuary from the adjacent sea.

To detect which improvements

3D hydrodynamic model (Gustafsson and Bendtsen 2007-estuarymodelB) based on the COHERENS model (Luyten et al. 1999). The ecological component uses a modified

Numerous equations to define the 3D coupled hydrodynamic–ecological model.

A numerical tracing technique (Menesguen et al. 2006) was used to assess the relative importance of nutrient discharges from streams, which requires a doubling of all equations dealing with state variables for nutrients. In this case, for simplicity, it was only applied to nitrogen tracking.

Results indicate that 40–90% of N in NO$_3$, NH$_4$, and detritus comes from streams, while only 15–50% of N in phytoplankton comes from streams; The impact of stream nitrogen reductions on NO$_3$, chl a and light attenuation was

Timmermann et al. (2010)

Fulton et al. (2004)
### TABLE 3.2 (Continued)

**Summary of Some of the Estuarine Models Developed between 2000 and 2010**

<table>
<thead>
<tr>
<th>Study System</th>
<th>Aims</th>
<th>Software, Integration Algorithm, Background Models</th>
<th>Main Equations/Characteristics</th>
<th>Main Results</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ria de Aveiro (Portugal)</td>
<td>can occur from different scenarios of nutrient load decrease.</td>
<td>version of the microplankton-detritus model (MPD model) (Tett 1998)</td>
<td>Primary production was described as $\frac{\partial \Phi_X}{\partial t} = \left( \mu_X - r_X - \omega_X - m_X - G_X \right) \Phi_X$</td>
<td>higher than the impact of open sea nitrogen reductions.</td>
<td>Trancoso et al. (2005)</td>
</tr>
<tr>
<td>Case 1—Veerse Meer (The Netherlands)</td>
<td>To study the influence of benthic macroalgae on phytoplankton and nutrient concentrations.</td>
<td>MOHID modelling system, which integrates hydrodynamic, sediment transport and water quality elements (e.g., Braunschweig et al. 2003)</td>
<td>$t$, time; $\Phi_X$, biomass (gC m$^{-3}$ for phytoplankton; kgC m$^{-2}$ for macroalgae); $\mu_X$, gross growth rate (day$^{-1}$); $r_X$, total respiration rate (day$^{-1}$); $\omega_X$, excretion rate (day$^{-1}$); $m_X$, natural mortality rate (day$^{-1}$); $G_X$, grazing rate (day$^{-1}$)</td>
<td>Macraolaegae significantly contribute to the system’s primary production and to the nutrient limitation of phytoplankton.</td>
<td></td>
</tr>
<tr>
<td>Case 2—North Sea</td>
<td>To integrate biological and physical processes in simulations of basic ecosystem dynamics for a generic application to</td>
<td>Generic Ecological Model (GEM) for estuaries, an integrated model including physical, chemical and ecological processes, within</td>
<td>Numerous equations to describe phytoplankton processes (production, respiration, and mortality), extinction of light, decomposition of POM in the water and sediments, nitrification and denitrification, reaeration, settling, burial, filter-feeder processes (grazing, excretion, and respiration).</td>
<td>In general, the model results are accurate in both the spatial (horizontal and vertical) and the temporal dimension (seasonal and annual) for a variety of water systems.</td>
<td>Blauw et al. (2009)</td>
</tr>
</tbody>
</table>
Case 4—Sea of Marmara (Turkey)

The “cost function” (OSPAR 1998; Radach and Moll 2006 in) was used to assess the “goodness-of-fit” between model outputs and measurements:

\[
C = \frac{1}{n} \sum_{i=1}^{n} \left( M_{x,t} - D_{x,t} \right)^2 / \left( s_{x,t}^2 \right) \times \left( 1 - c \right) + c \left( 1 - r_x \right)
\]

where \( C \) is the normalized deviation per station, annual value; \( M_{x,t} \) is the mean value of the model results per station per month; \( D_{x,t} \) is the mean value of the in situ data per station per month, and \( s_{x,t} \) is the standard deviation of the annual mean based on the monthly means of the in situ data (\( df = 11 \)), \( n \) is 12 months, \( c \) is 0.5, and \( r_x \) is the correlation over time between \( M_{x,t} \) and \( D_{x,t} \) (OSPAR 1998).

Model limitations are related to the application to shallow dynamic systems, with extensive tidal flats and periodic anoxia due to inappropriate formulations used in the sediment submodel.

Urdaibai estuary (Basque Country)

To assess the impacts from hydrological inputs and wastewater loading.

2D water quality model, including a hydrodynamic- and a water quality-submodel

For the water quality submodel, the following state variables were considered: ammonia-N, nitrate-N, phosphate-P, phytoplankton-C, dissolved BOD, suspended BOD, settled BOD and dissolved oxygen.

Pronounced decrease on phytoplankton concentration was obtained when decreased levels of nutrient discharge were coupled to highest river discharge.

García et al. (2010)

(continued)
**TABLE 3.2 (Continued)**

Summary of Some of the Estuarine Models Developed between 2000 and 2010

<table>
<thead>
<tr>
<th>Study System</th>
<th>Aims</th>
<th>Software, Integration Algorithm, Background Models</th>
<th>Main Equations/Characteristics</th>
<th>Main Results</th>
<th>Reference</th>
</tr>
</thead>
</table>
| Tokoy Bay (Japan) | To compare model outputs with the seasonal–daily dynamics of the benthic-pelagic compartments in the central bay and the tidal area. | Ecological Connectivity Hypoxia Model (ECOHYM)—a hydrodynamics–ecological model | General equation for the pelagic compartment: \[
\frac{\partial C_W}{\partial t} = -(V_W \cdot \nabla)C_W + \nabla \cdot (K \cdot \nabla C_W) + \sum R
\]

\[
= -u_w \frac{\partial C_W}{\partial x} - v_w \frac{\partial C_W}{\partial y} - w_w \frac{\partial C_W}{\partial z} + \frac{\partial}{\partial x} \left( K_x \frac{\partial C_W}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial C_W}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial C_W}{\partial z} \right) + \sum R
\]

where \( C_W \) is the concentration of pelagic substances (phytoplankton, zooplankton, detritus, DOM, NH\(_4\)-N, NO\(_3\)-N, PO\(_4\)-P, dissolved oxygen); \( V_W = (u_w, v_w, w_w) \) is the flow velocity; \( t \) is time; \( x, y, z \) are the spatial coordinates; \( \sum R \) are the biochemical reactions and fluxes from outside the system; \( K \) is the eddy diffusion tensor. | The seasonal dynamics is more noticeable in the central bay area. The daily/tidal dynamics is determinant in the tidal flat area. Results reproduce accurately DO profiles during hypoxic events. | Sohma et al. (2008) |
Macroalgal NPP can be estimated as (e.g., Duarte and Ferreira 1997):

\[
NPP = \sum_{k=1}^{n} (B_{k,t+\Delta t} - B_{k,t} + M + Q)/\Delta t
\]  

(3.11)

where \(B\) is biomass, \(M\) represents losses through mortality, \(Q\) is biomass removed by frond breakage, \(k\) is the algal size class, \(n\) is the total number of classes, and \(\Delta t\) is the number of days between two consecutive samples.

In many models, the respiration loss term of algae is defined as an Arrhenius relationship with a reference temperature of 20°C (EPA 1985):

\[
R = R_{\text{max}20} \cdot \theta^{(T-20)}
\]  

(3.12)

where \(R_{\text{max}20}\) is the maximum respiration rate at 20°C, \(\theta\) is the empirical coefficient, and \(T\) denotes temperature.

Some models account for dark respiration and photorespiration (Trancoso et al. 2005), which is stimulated at high light intensities and dissolved oxygen concentrations (Carr et al. 1997):

\[
R = k_{\text{re}}e^{0.069T} + k_{\text{rp}}\mu_A
\]  

(3.13)

where \(k_{\text{re}}\) is the endogenous respiration constant, \(k_{\text{rp}}\) is the fraction of actual photosynthesis rate oxidized by photorespiration, \(T\) is temperature, and \(\mu_A\) is the algal growth rate.

In a very similar formulation, Blackford (2002) combines microphytobenthos activity respiration \((r_{\text{act}})\) as a fixed proportion of actual assimilation \((\text{Assim})\) and basal metabolism \((r_{\text{rest}})\) related to ambient temperature \((f_i)\):

\[
R = (r_{\text{rest}}f_i) + (\text{Assim} \cdot r_{\text{act}})
\]  

(3.14)

Exudation \((\text{ex}_A)\) may be described as a dependency on light \((f_i)\) because of high photosynthate and photorespiratory compounds excretion at both low light levels and inhibitory high light levels (EPA 1985):

\[
\text{ex}_A = K_e A \mu_A (1 - f_i)
\]  

(3.15)

In some models, more complex formulations are used to describe algal excretion. Blackford (2002) describes three different processes of excretion. The excretion \((e_a)\) of a fixed proportion \((P_{ex})\) of production \((P)\):

\[
e_a = P \cdot p_{ex}
\]  

(3.16)
Nutrient stress lysis \((e_l)\) as a minimal rate \((r_{\text{lysis}})\) modified by the nutrient availability factor \((i_N)\):

\[
e_l = \frac{1.0}{i_N + 0.1} \cdot r_{\text{lysis}}
\]  

(3.17)

and nutrient stress excretion \((e_n)\) of the potential assimilate \((1 - p_{ex})\):

\[
e_n = P(1.0 - i_N) \cdot (1.0 - p_{ex})
\]  

(3.18)

Mortality can be divided into grazing and nonpredatory mortality. Grazing on algae can be defined by simple formulations, which use a maximum grazing rate \((Graz_{\text{max}})\) and a temperature limitation function, reflecting the dependency of grazer’s activity and abundance on temperature \((f_{T\text{Graz}})\) (Martins et al. 2007):

\[
Graz = Graz_{\text{max}} \cdot f_{T\text{Graz}}
\]  

(3.19)

Or, by more complex formulations, which take into account the proportion of algae (microphytobenthos) available to the prey and different types of prey (meiobenthos and macrobenthos) (Blackford 2002):

\[
Graz = \frac{r_{\text{prey}} \cdot p_A \cdot (p_A/(P_A + l))}{\sum_{\text{prey}} p_A + h}
\]  

(3.20)

where \(r_{\text{prey}}\) is the predator uptake rate, taking into account the uptake rate of microphytobenthos by deposit feeders, suspension feeders, and meiobenthos; \(p_A\) is the proportion of microphytobenthos available to each one of the predator groups; \(l\) is the feeding threshold for each one of the predator groups; and \(h\) is the half grazing rate constant for each one of the predator groups.

### 3.4.2 Phytoplankton

Phytoplankton constitutes the autotrophic component of the plankton with most species being microscopic unicellular organisms with a size range between 0.4 and 200 \(\mu\)m. Marine phytoplankton individuals live within the surface layers of the ocean, down to 200 m in the clearest waters (Simon et al. 2009). Although marine phytoplankters represent less than 1% of the Earth’s photosynthetic biomass, they are responsible for more than 45% of the planet’s annual net primary production (Field et al. 1998).

Estuarine phytoplankton is under strong temporal and spatial variations mostly due to tidal variations and seasonal freshwater runoff, which have significant effects on water column stability, residence time, light, and nutrient
availability (Gameiro et al. 2007). Vertical mixing of the water column is also greatly influenced by other factors, such as wind-driven water mixing.

Since phytoplankton is the basis of many coastal and oceanic trophic chains, quantifying its productivity and understanding the factors that control phytoplankton dynamics is essential both from the ecological and management point of view. Additionally, detailed studies on phytoplankton taxonomy and functional groups are also of interest, as ecosystem eutrophication indexes may be derived from it, for example, the shift from diatom-dominated communities to phytoflagellate-dominated ones (Cloern 1996).

One of the most commonly used types of phytoplankton model is a time-integrated NPP (net primary productivity) phytoplankton model (Behrenfeld and Falkowski 1997), which can be defined by:

\[
\sum_{z=0}^{z_{eu}} NPP = \int_{0}^{z_{eu}} P^b(z) \times PAR(z) \times DL \times Chl(z) \, dz
\]  

(3.21)

where \( z \) denotes depth, \( z_{eu} \) is the euphotic depth, \( P^b(z) \) is the photoadaptive variable at depth \( z \), \( PAR \) is the photosynthetic available radiation, \( DL \) denotes day length, and \( Chl(z) \) is the chlorophyll concentration at depth \( z \).

A common application of productivity models is the calculation of global annual phytoplankton primary production (PPannu) (Behrenfeld and Falkowski 1997) and values range from 27.1 (Eppley and Peterson 1979) and 50.2 pg C year\(^{-1} \) (Longhurst et al. 1995). According to Behrenfeld and Falkowski (1997), such differences are mainly attributed to changes in depth integrated biomass (i.e., \( C_{sat} \times Zeu \)) and to spatial (i.e., horizontal) variability in the photoadaptive variable (\( P^b \) opt), which is defined as the maximum chlorophyll-specific carbon fixation rate observed within a water column measured under conditions of variable irradiance during incubations typically spanning several hours (Behrenfeld and Falkowski 1997).

Primary productivity models can be either empirical formulations of the P–E relationships, capable of mathematically describing the observed results but not describing physiological processes (e.g., Webb et al. 1974; Franks and Marra 1994) or of a mechanistic type, derived from known sequences of metabolic transformations (e.g., Eilers and Peters 1988, 1993; Han 2001a, 2001b; Rubio et al. 2003). Some primary productivity models assume a maximum threshold (saturation models) (e.g., Jassby and Platt 1976; Franks and Marra 1994), whereas others include photoinhibition (e.g., Steele 1962; Parker 1974; Pahl-Wostl and Imboden 1990). Macedo and Duarte (2006) have investigated the differences between static and dynamic photoinhibition models in three marine systems (turbid estuary, coastal area, and an open ocean ecosystem), and their results indicate that when photoinhibition development time is considered (dynamic model), the primary production estimates are always higher than when calculated with the static model. The authors also suggest that the
quantitative importance of this underestimation appears to be more important in coastal areas and estuaries (21–72%) than in oceanic waters (10%).

3.4.2.1 Some Recent Phytoplankton Models

3.4.2.1.1 Nitrogen Isotope

3.4.2.1.1.1 Problematic In the past three decades, nitrogen transformations in the marine environment have been actively investigated using 15N techniques alone or in combination with other chemical techniques. Results from these studies, together with data on nutrients, particulate organic nitrogen, dissolved organic nitrogen, and biomass have improved the general understanding of nitrogen dynamics in marine ecosystems. Some models also describe the kinetics of nitrogen transformations and the factors that regulate such processes. However, the validation of transformation processes by only concentration data is difficult and limited. Furthermore, the incorporation of rates estimated by incubation experiments does not necessarily provide actual fluxes and concentrations. Since each approach has temporal and/or spatial limitations, combination studies provide a more comprehensive understanding of nitrogen dynamics in marine ecosystems (Sugimoto et al. 2010).

In recent years, ecosystem models incorporating δ15N have proven to be useful tools for elucidating nitrogen dynamics in both the past and modern ocean (Giraud et al. 2000, 2003).

3.4.2.1.1.2 Aim The aim of this model was to assess the quantitative contribution of different nitrogen sources (river, ocean, and regeneration) to primary production in Ise Bay (Japan) by using a combination of different approaches. For that, the authors have developed a three-dimensional physical-ecosystem model coupled to δ15N, which was used to understand the flow of nitrogen in the coastal system. The authors highlight the idea that a combination of methods (models, concentration data obtained in the field, incubation experiments) provides a more comprehensive understanding of nitrogen cycling in marine systems.

The ability to detect small differences in the 15N/14N ratio of different pools of nitrogen combined with knowledge of kinetic isotope discrimination during chemical and biological reactions may potentially provide new ways to monitor nitrogen fluxes in marine systems on various temporal and spatial scales (Sugimoto et al. 2010).

The 15N/14N signal of phytoplankton may be used to estimate the extent and/or source of nitrogen used by phytoplankton.

3.4.2.1.1.3 Study System The Ise Bay (Japan).

3.4.2.1.1.4 Model Structure and Main Equations Five N-based state variables were included: NO3−, NH4+, phytoplankton, zooplankton, and detritus
Estuary Ecosystem Models

(Figure 3.5). Besides photosynthesis, excretion, release, remineralization, sinking, mortality, grazing, egestion, and sedimentation, the processes of nitrification and denitrification are also included in the model.

Nitrification rates can be influenced by many factors, such as NH$_4^+$ concentration, oxygen, light, SPM, pH, and salinity (Herbert 1999). However, the seasonal rates of nitrification are more strongly correlated with temperature than with other factors (Berounsky and Nixon 1990), and the temperature coefficient of nitrification in the water column is higher than in the sediments (Sugimoto et al. 2008).

Thus, the authors described nitrification in the aphotic water column as:

\[
\text{Nitrification} = V_{\text{Nit}} \exp(k_{\text{Nit}} T)[\text{NH}_4^-] \tag{3.22}
\]

where $V_{\text{Nit}}$ is the nitrification rate at 0°C, $k_{\text{Nit}}$ is the temperature coefficient of nitrification, and $T$ is temperature.

Denitrification rate in the anoxic sediments was assumed to be dependent on temperature ($T$) and NO$_3^-$ concentration in the water overlying the sediments (Sugimoto et al. 2008):
Denitrification = $V_{\text{Denit}} \exp(k_{\text{Denit}} T)[\text{NO}_3]$ 

The fractionation of nitrogen isotopes in the model occurs in the processes of assimilation (photosynthesis) of NO$_3^-$ and NH$_4^+$ by phytoplankton, excretion, and egestion by zooplankton and nitrification and denitrification (dashed arrows in Figure 3.6). During photosynthesis, the lighter isotope ($^{14}\text{N}$) is more readily incorporated by phytoplankton and, thus, the $\delta^{15}\text{N}$ values of NO$_3^-$ and NH$_4^+$ increase as phytoplankton take up these nutrients (e.g., Waser et al. 1998a, 1998b).

The model includes $\delta$ values of nitrification in the water column and denitrification in the sediments obtained from field measurements (Sugimoto et al. 2008), and excretion and egestion by zooplankton were obtained from the literature (Yoshikawa et al. 2005), whereas the $\delta$ values of other assimilation processes were calibrated against measured values (Sugimoto et al. 2010).

The isotopic fractioning coefficient $\alpha_l$ was described by:
\[ \alpha_i = \exp\left(\frac{-\epsilon_i}{1000}\right) \]  
(3.24)

where \( \epsilon_i \) is the isotopic discrimination for the considered biogeochemical processes.

The prognostic variables for the \( ^{15}\text{N} \) cycle are calculated as:

\[
\frac{\partial}{\partial t} \left[ ^{15}\text{N}_{\text{NO}_3} \right] = -(\text{Photosynthesis}) \times F_{\text{new}} \times R_{\text{NO}_3} \times \alpha_1 + (\text{Nitrification}) \times R_{\text{NH}_4} \\
\times \alpha_5 - (\text{Denitrification}) \times R_{\text{NO}_3} \times \alpha_6
\]  
(3.25)

\[
\frac{\partial}{\partial t} \left[ ^{15}\text{N}_{\text{NH}_4} \right] = -(\text{Photosynthesis}) \times (1 - F_{\text{new}}) \times R_{\text{NH}_4} \times \alpha_2 + (\text{Excretion}) \\
\times R_{\text{Zoo}} \times \alpha_3 + (\text{Decomposition}) \times R_{\text{Det}} - (\text{Nitrification}) \\
\times R_{\text{NH}_4} \times \alpha_5 + (\text{Release}) \times R_{\text{Sediment}}
\]  
(3.26)

\[
\frac{\partial}{\partial t} \left[ ^{15}\text{N}_{\text{Phy}} \right] = (\text{Photosynthesis}) \times F_{\text{new}} \times R_{\text{NO}_3} \times \alpha_1 + (\text{Photosynthesis}) \\
\times (1 - F_{\text{new}}) \times R_{\text{NH}_4} \times \alpha_2 - (\text{Mortality}_{\text{Zoo}}) \times R_{\text{Phy}} - (\text{Grazing}) \\
\times R_{\text{Phy}} + (\text{Sinking}_{\text{Phy}}) \times R_{\text{Phy}}
\]  
(3.27)

\[
\frac{\partial}{\partial t} \left[ ^{15}\text{N}_{\text{Zoo}} \right] = (\text{Grazing}) \times R_{\text{Phy}} - (\text{Mortality}_{\text{Zoo}}) \times R_{\text{Zoo}} - (\text{Egestion}) \times R_{\text{Zoo}} \times \alpha_4 \\
- (\text{Excretion}) \times R_{\text{Zoo}} \times \alpha_3
\]  
(3.28)

\[
\frac{\partial}{\partial t} \left[ ^{15}\text{N}_{\text{DET}} \right] = (\text{Mortality}_{\text{Phy}}) \times R_{\text{Phy}} + (\text{Mortality}_{\text{Zoo}}) \times R_{\text{Zoo}} + (\text{Egestion}) \\
\times R_{\text{Zoo}} \times \alpha_4 - (\text{Decomposition}) \times R_{\text{Det}} + (\text{Sinking}_{\text{Det}}) \times R_{\text{Det}} \\
+ (\text{Sedimentation}) \times R_{\text{Det}}
\]  
(3.29)
where $R_C$ is the $^{15}\text{N}/^{14}\text{N}$ ratio for a specific compartment $C$. The $\delta^{15}\text{N}$ values for a specific compartment $C$ are calculated by:

$$
\delta^{15}\text{N} = \frac{\left( \frac{\left[ ^{15}\text{N} \right]}{\left[ ^{14}\text{N} \right]} \right)_C - \left( \frac{\left[ ^{15}\text{N} \right]}{\left[ ^{14}\text{N} \right]} \right)_{\text{Atmospheric}}}{1} \times 1000
$$

(3.30)

where Atmospheric $\text{N}_2$ is defined as the standard sample including $[^{15}\text{N}]$ and equals 0.365%.

3.4.2.1.5 Results and Discussion  Model results revealed that DIN (ammonium + nitrate) consumption by phytoplankton exceeds DIN supply from the rivers and ocean, indicating that a significant amount of phytoplankton production in Ise Bay depends on DIN regeneration within the bay. However, the ratio of consumption to external supply differs seasonally. The distribution of simulated $\delta^{15}\text{N}$ clearly showed the source of nitrogen incorporated by phytoplankton. The model reproduces well the decrease of $\delta^{15}\text{N}_{\text{NO}_3}$ by the isotope effect of nitrification in spring.

The authors claim that further observations of $\delta^{15}\text{N}$ values of $\text{NH}_4^+$ are required, as well as sensitivity analysis, in order to estimate more accurate values. Additionally, further monitoring of river discharges are needed, including flood periods, to assess more precisely the effects of river loadings on the coastal environment.

3.4.2.1.2 Deep Channels and Broad Shallow

3.4.2.1.2.1 Problematic  Many shallow estuaries around the world have one or more deep channels, laterally bounded by broad shallow regions (Lucas et al. 2009).

3.4.2.1.2.2 Aim  The authors developed a model to explore the potential significance of hydrodynamic connectivity between a channel and a shoal and whether lateral transport can allow physical or biological processes (e.g., stratification, benthic grazing, light attenuation) in one subregion to control phytoplankton biomass and bloom development in the adjacent subregion.

3.4.2.1.2.3 Study System  The South San Francisco Bay (USA) (SSFB).

3.4.2.1.2.4 Model Structure and Main Equations  The developed model consists of two one-dimensional, vertically resolved water columns (one deep, one shallow) that exchange mass horizontally. Each water column is assumed
to be laterally homogeneous. Lateral mass transport between the deep and shallow compartments is modeled as a diffusive process.

The two vertical subgrids are composed of several “boxes” or “control volumes” (Figure 3.6).

Within each compartment, the vertical transport, sources, and sinks of phytoplankton are represented by the advection–diffusion equation:

\[
\frac{\partial B}{\partial t} = (\mu_{\text{net}} - \text{ZP})B + \frac{\partial}{\partial z} \left( K_z \frac{\partial B}{\partial z} \right) - \frac{\partial}{\partial z} \left( W_z B \right) - \frac{\partial}{\partial z} \left( \text{BG} \cdot B \right)
\] (3.31)

where \( B \) is the phytoplankton biomass concentration as chlorophyll \( a \) (mg chl a m\(^{-3}\)), \( z \) is the vertical location (m), \( \mu_{\text{net}} \) is the phytoplankton net growth rate (day\(^{-1}\)), ZP is the zooplankton grazing rate (day\(^{-1}\)), \( K_z \) is the vertical turbulent diffusivity (m\(^2\) day\(^{-1}\)), and BG is the benthic grazing rate (m\(^3\) m\(^{-2}\) day\(^{-1}\)).

The lateral diffusion is given by:

\[
\frac{\partial B}{\partial t} = \frac{\partial}{\partial y} \left( k_y \frac{\partial B}{\partial y} \right)
\] (3.32)

where \( y \) is the transverse location (m) and \( k_y \) is the effective lateral diffusivity (m\(^2\) s\(^{-1}\)).

3.4.2.1.2.5 Results and Discussion Results indicated that (1) lateral transport from a productive shoal can result in phytoplankton biomass accumulation in an adjacent deep, unproductive channel; (2) turbidity and benthic grazing in the shoal can control the occurrence of a bloom system-wide; (3) turbidity, benthic grazing, and vertical density stratification in the channel are likely to only control local bloom occurrence or modify systemwide bloom magnitude.

The authors recommend that for other systems, which present a more gradual shallow–deep transition than SSFB, more compartments may be required to represent the range of functionalities present along the lateral bathymetric gradient. According to Lucas et al. (1999a, 1999b), transitional locations of moderate depth can be important ecologically, each offering a certain balance between light limitation and benthic grazing.

This study has a broader application for estuaries, in general, because it highlights the patchiness of process rates and the connectivity between subregions, indicating that kinetically distinct subenvironments can develop within an estuary and the hydrodynamic processes (e.g., tides, wind, river flow, density gradients) can drive the exchange of algal biomass between them.

3.4.2.1.3 Phytoplankton Motility 3.4.2.1.3.1 Problematic To understand plankton communities and dynamics it is important to know the interplay between different phytoplankton species
and the physical environment. Actually, the most successful approach in the prediction of harmful algal blooms focuses on the prediction of the physical environments in which blooms are known to occur, rather than an explicit prediction of the bloom itself (Ross and Sharple 2008).

It is known that about 90% of toxic phytoplankton species are dinoflagellates or flagellates (Smayda 1997) and that they seem to have significant physiological disadvantages compared to diatoms (e.g., lower photosynthetic rates and higher metabolic costs—Furnas 1990; Tang 1995; Smayda 1997), yet the two groups are often seen to coexist.

### 3.4.2.1.3.2 Aim

The focus is on a role for vertical migration in stratified coastal water, where the swimming speed is generally significantly less than the typical turbulent velocities in a tidally mixed bottom layer.

The specific aim is to address the question of whether motility is of any use in balancing resource requirements when a significant fraction of the water column is strongly turbulent.

### 3.4.2.1.3.3 Study System

Not applicable.

### 3.4.2.1.3.4 Model Structure and Main Equations

The model consists of three components: a $k$--$\varepsilon$ turbulence model to describe the physics, a Lagrangian particle tracking model to describe the vertical displacement of cells in response to turbulence and cell motility, and a biological submodel to account for the swimming behavior of phytoplankton in relation to light and nutrient requirements.

The turbulence model must be able to capture the temporal and spatial variability of the tidally driven mixing in the bottom layer, which was achieved through a two-equation model of the $k$--$\varepsilon$ variety (for details, refer to Canuto et al. 2001; Sharple et al. 2006).

The model accounts for tidal height variations through oscillating the sea surface slope at the period of the major lunar constituent of 12.42 h (M2). For the study area (Western English Channel), the current amplitudes are about 0.75 m s$^{-1}$, corresponding to a near-spring condition.

Vertical turbulence is controlled by the $k$--$\varepsilon$ turbulence closure scheme and a parameterization for internal wave mixing at the thermocline is included following Large et al. (1994) (for details, see Sharple et al. 2006).

The model accounts for a total water depth of 80 m. A homogeneous surface layer (20 m) is separated from a 50-m-thick bottom mixed layer (BML) by a linear thermocline between 50 and 60 m above seabed. A constant temperature difference of 3.5°C is kept across the thermocline to allow easier analysis of thermocline reaccess by particles.

Model simulation produces two diffusivity maxima in the BML corresponding to the ebb and flood flows, which produce turbulent diffusivities in excess of $10^{-2}$ m$^2$ s$^{-1}$. The turbulence decreases rapidly while approaching the thermocline and in the stratified region the diffusivity $K$ drops below $10^{-5}$ m$^2$ s$^{-1}$.
The following random walk equation is used to track a total of 10,000 individual particles through the eddy diffusivities produced by the $k$–$\varepsilon$ model:

$$z_{n+1} = z_n + w_p \Delta t + K'(z_n) \Delta t + R \left[ \frac{2K(z_n + \frac{1}{2}K'(z_n) \Delta t)}{r} \right]^{1/2}$$

(3.33)

The second term of the equation accounts for motility, the third is a deterministic term, and the fourth is a random term.

$Z_n$ is the vertical position of the particle after $n$ iterations, $w_p$ is the vertical swimming velocity, $K$ is the turbulent eddy diffusivity with the abbreviation $K' = dK/dz$, $\Delta t$ is the time step for the iteration and, $R$ is a random process (for details, see Ross and Sharples 2008).

The lower end of the observed range of phytoplankton swimming speeds was used ($w_p = 0.1 \text{ mm s}^{-1}$), to assess if even the lowest swimming velocities provide a measurable advantage to the cells.

The potential effectiveness of motility in a turbulent environment is the Péclet number, $Pe$, given by:

$$Pe = \frac{(\text{mixing time scale}/\text{swimming time scale})}{L/w_p} = \frac{w_p L}{K}$$

(3.34)

where $L$ is the mixed layer depth.

Model simulations indicate that only toward the base of the thermocline region should the swimming efforts of the cells be able to overcome the tidal turbulence.

3.4.2.1.4 The Phytoplankton Growth Model

The position and variation of the nutrient gradient within the thermocline is driven primarily by the uptake of nutrients by the cells within the subsurface chlorophyll maximum. In addition, the swimming strategies of motile cells also seem to depend on light and nutrient requirements (e.g., MacIntyre et al. 1997).

Phytoplankton production is described by a $P$–$I$ (production–irradiance) curve following Denman and Marra (1986):

$$P_{d/l} = P_{m_{d/l}} \left[ 1 - \exp \left( -I/I_{d/l} \right) \right]$$

(3.35)

$P_{m_{d/l}}$ is the maximum dark-/light-acclimated production, $I_{d/l}$ is saturation irradiance, and $I$ is irradiance in PAR at a certain depth.
PAR at a certain depth was calculated through a slightly modified Beer–Lambert equation:

\[
I(z) = I_0 \exp\left[-(k + k_s(z))(H - z)\right]
\]

(3.36)

where \(I_0\) is the irradiance level at the sea surface (45% of which is assumed to be PAR), \(H\) is the total depth of the water column, \(k\) is light absorption coefficient, and \(k_s(z)\) is the depth-dependent light absorption due to self-shading.

The model includes the limitation of dissolved inorganic nitrogen on phytoplankton growth. The uptake of DIN by phytoplankton was described through:

\[
U = U_m \left(1 - \frac{Q}{Q_{\text{max}}}\right) \frac{N}{k_N + N}
\]

(3.37)

\(Q\) is the cellular nitrogen/carbon ratio that needs to remain above a subsistence quota \(Q_{\text{min}}\) and below a maximum storage quota \(Q_{\text{max}}\). \(U_m\) is the maximum uptake rate, and \(k_N\) is the half-saturation constant for nitrogen.

A Droop-type function was used to calculate the cellular increase in carbon:

\[
\frac{dC}{dt} = \left[P \left(1 - \frac{Q_{\text{min}}}{Q}\right) - R - G - L_r\right]C
\]

(3.38)

where \(R\) is the respiration rate, \(G\) is the grazing rate, \(C\) is the cellular carbon, and \(P\) is the instantaneous production.

The model takes into account a lower carbon threshold \(C_{\text{starve}}\), at which cells begin to die, and an upper level \(C_{\text{fission}}\) at which cells begin to divide (and the number of cells per Lagrangian particle doubles) (Broekhuizen 1999). Losses due to grazing and mortality reduce the number of cells within a Lagrangian particle. \(L_r\) represents this carbon-dependent mortality rate and was defined as:

\[L_r = 0.1 \text{ day}^{-1} \text{ if } C < C_{\text{starve}} \text{ else } L_r = 0\]

The variation in the nitrogen concentration on a Eulerian grid was defined by:

\[
\frac{dN_i}{dt} = \frac{d}{dz} \left(K \frac{dN_i}{dz}\right) - UC_i + \left[r + \beta G\right]_i N_i + \beta L_r N_i^{\text{starve}}
\]

(3.39)

\(N_i\) denotes the total amount of cellular nitrogen in the \(i\)th element, \(N_i^{\text{starve}}\) is the cellular nitrogen content of cells that have \(C < C_{\text{starve}}\) and \(\beta\) is the fraction of the grazed and starved nitrogen that is released back into the water.
column. The reminder is assumed to sink to the seabed. A fixed value of \( \text{DIN}_{\text{bed}} = 70 \text{ mg N m}^{-3} \) is held in the model depth element at the seabed to include the resupply of DIN to the water column following remineralization processes in the sediments.

The light-nutrient driven swimming strategy of motile cells was expressed through (e.g., Broekhuizen et al. 2003):

\[
\begin{align*}
 w_p = \begin{cases} 
 -w_p, & \text{if } Q < f_1 Q_{\text{max}} \\
 +w_p, & \text{if } Q > f_2 Q_{\text{max}} \quad \text{and} \quad I_{(c)} > I_c \\
 0, & \text{if } Q > f_2 Q_{\text{max}} \quad \text{and} \quad I_{(c)} < I_c 
\end{cases}
\end{align*}
\tag{3.40}
\]

The cellular N/C ratio \( (Q) \) increases through uptake of N and decreases as a result of carbon assimilation. If \( Q \) falls below a certain fraction \( f_1 \) of \( Q_{\text{max}} \), the cell starts being nutrient limited and swims toward higher nutrient concentrations, that is, downward. As the cells encounter higher nutrient concentrations, \( Q \) starts to increase and when \( Q > f_2 Q_{\text{max}} \), the cell gets nutrient replete and begins to swim toward higher light intensities (upward) to minimize light limitation. If light is below a certain threshold \( (I_c) \), a nutrient-replete cell simply becomes neutrally buoyant.

3.4.2.1.5 Results and Discussion

Results from this model show that tidal turbulence in the BML helps both motile and neutrally buoyant cells by periodically pushing them into the base of the thermocline. Motile cells have the additional advantage that they can swim further into the thermocline toward higher light, which will reduce the chance of being remixed back into the BML.

3.4.3 Macroalgae

Macroalgae tend to proliferate in nutrient-enriched, shallow, photic costal areas (e.g., Brush and Nixon 2010). Macrophyte algae are not only important because of their productivity, but also because of their associated roles in the ecosystem nutrient dynamics and as a sink for conservative pollutants such as heavy metals (Ferreira and Ramos 1989).

Traditionally, models of macroalgal populations may be divided into two groups:

1. Demographic models, that simulate the numerical density of a population divided into size classes or different life history phases (Chapman 1993)

2. Models that simulate the biomass density dynamics (Duarte and Ferreira 1993)
Duarte and Ferreira (1997) have developed a third type of model, resulting from the combination of types (1) and (2) and simulating simultaneously biomass and numerical density of predefined size classes as a function of type. The population was divided in four size classes: <5, 5–10, 10–15, and >15 cm.

To preserve model stability, asymptotic biomass values were assumed for each class, which were chosen according to observed values. When the biomass of a class is greater than its asymptotic value, the excess biomass and corresponding individuals are transferred randomly to the next class. Model forcing functions were only temperature and radiation. Nutrients were not included as limiting factors.

Results indicated that biomass dynamics and productivity are more sensitive to the light extinction coefficient than to the initial biomass conditions, biomasses losses due to respiration and exudation are comparable to those resulting from mortality, and frond breakage and different parameters should be used in productivity–irradiance curves according to seasonal variations (Duarte and Ferreira 1997).

### 3.4.3.1 Recent Macroalgal Models and Processes Taken into Account

#### 3.4.3.1.1 Turbidity at the Intertidal Area

##### 3.4.3.1.1.1 Problematic
In shallow waters, primary productivity is strongly dependent on the regulation of underwater light climate by SPM (e.g., Schild and Prochnow 2001) and, in case of nutrient surplus, light availability will be the key limiting factor for primary production. In intertidal areas, the combination of shallow waters and strong tidal currents creates complex patterns of SPM transport, deposition, and resuspension dynamics. In addition, the formation of isolated water pools on tidal flats at low tide, where SPM deposits quite fast, increases the complexity of these systems (Alvera-Azcárate et al. 2003).

##### 3.4.3.1.1.2 Aim
The aim of the model was to develop a more mechanistic approach to model seaweed productivity, by improving the description of the underwater light climate in intertidal areas throughout the complete tidal cycle.

##### 3.4.3.1.1.3 Study System
The model was applied to Tagus estuary (Portugal), a large mesotidal system, by combining field and experimental data, small spatial scale modeling, and geographical information systems (GIS).

##### 3.4.3.1.1.4 Model Structure and Main Equations
Here, we will focus on the descriptions used by the authors for tide, velocity, and sediment dynamics. Details on the seaweed model can be found in the work of Alvera-Azcárate et al. (2003).

*Interpolation method versus erosion–deposition method.* Tidal variation was described from the basic harmonic constituents, considering a specific origin...
in time (January 1, 1980). The water velocity was simulated as a sinusoidal function:

\[ u = A \sin(\nu t + p) \]  

(3.41)

where \( A \) is the amplitude of the water current (m) and \( \nu \) is the wave velocity (m s\(^{-1}\)).

Velocity variation depends on the tide: the velocity was considered zero at high and low water, and reaches maximum values at mid-tide.

**Interpolation.** To describe the relationship between tidal range and the mass of suspended sediments in the water, the following equation was used:

\[ \text{SPM}_t = \frac{z_i - z_{\text{min}}}{z_{\text{max}} - z_{\text{min}}} \cdot \text{SPM}_{\text{hw}} + \frac{z_{\text{max}} - z_i}{z_{\text{max}} - z_{\text{min}}} \cdot \text{SPM}_{\text{lw}} \]  

(3.42)

SPM\(_t\) is the suspended particulate matter at time \( t \); SPM\(_{\text{hw}}\) and SPM\(_{\text{lw}}\) are the SPM concentrations for high and low water conditions, respectively; \( z_i \) is the tidal height at time \( t \); and \( z_{\text{max}} \) and \( z_{\text{min}} \) are high water and low water depths, respectively.

**Erosion–deposition.** The sediment modeling approach was improved by accounting for the sediment dynamics of tidal pools. The shear stress exerted over the bottom sediments depends mainly on water velocity and tidal height, and defines the rates of sediment erosion and deposition.

Deposition is given by Krone’s equation:

\[ D = \begin{cases} 
W_{\text{fall}} \cdot \text{SPM} \left( 1 - \left( \frac{\tau}{\tau_d} \right) \right) & \text{if } \tau \leq \tau_d \\
0 & \text{if } \tau > \tau_d 
\end{cases} \]  

(3.43)

where the fall velocity of particles was described through Stoke’s law:

\[ W_{\text{fall}} = \frac{2}{9} g \left( \frac{\rho_p - \rho_w}{\mu} \right) r^2 \]  

(3.44)

where \( \rho_w \) and \( \rho_p \) are the water and particle density, respectively; \( g \) is the acceleration gravity; \( \mu \) is the water viscosity, and \( r \) is the particle radius.

\( \tau_d \) is the critical shear stress and \( \tau \) is the bed-shear stress, expressed by:

\[ \tau = \rho_p c_b u^2 \]  

(3.45)

where \( u \) is the water velocity and \( c_b \) the bed-shear coefficient.
Ecological Models in Ecosystem and Environmental Management

\[ c_b = \frac{g n^2}{h^{1/3}} \]  

(3.46)

where \( n \) is the Manning roughness coefficient and \( h \) is the water column depth.

Erosion was calculated according to Partheniades (1965):

\[
E = \begin{cases} 
M \left( \frac{\tau}{\tau_e} - 1 \right) & \text{if } \tau \geq \tau_e \\
0 & \text{if } \tau < \tau_e 
\end{cases}
\]  

(3.47)

where \( M \) is the erosion rate coefficient and \( \tau_e \) is the critical shear stress for erosion. Erosion occurs when the bed shear stress is greater than the critical value.

During ebb, when tidal pools are formed, the deposition and erosion are different and must be treated separately from the rest of the tidal cycle (Alvera-Azcárate et al. 2003). In such circumstances, deposition is considered to be maximal, since there is no water turbulence; thus, the condition \( \tau \leq \tau_d \) is always true and deposition may be described by:

\[ D = w_{\text{fall}} \text{SPM} \]  

(3.48)

Bottom erosion is zero because there is no bed-shear stress, and the condition \( \tau > \tau_e \) is always true.

Erosion \((E)\) and deposition \((D)\) depend on the water velocity, and deposition rate also depends on the total SPM in the water column; therefore, at each time step SPM is recalculated as:

\[ \frac{d\text{SPM}}{dt} = E - D \]  

(3.49)

The seaweed species considered for the model occupy an area of 16.5 km\(^2\), with 36% coverage of \textit{Fucus vesiculosus}, 46% of \textit{Ulva lactuca}, and 18% of \textit{Gracilaria verrucosa}. It was assumed that 50% of this area is occupied by tidal pools.

The “interpolation” model was upscaled over the total area of 16.5 km\(^2\) and the “erosion–deposition” model was upscaled over 50% of this area, corresponding to tidal pools, and the remaining area was upscaled with the “interpolation” model. The two results were combined to determine the overall production.

Results upscaling were achieved through remote sensing and GIS (for details, see Alvera-Azcárate et al. 2003).
3.4.3.1.5 Results and Discussion  Results indicate that, in mesotidal or macrotidal turbid estuaries, the role of benthic autotrophs in cycling carbon and nutrients is quite significant. According to results, within the studied system (Tagus estuary), the annual carbon fixation by intertidal seaweeds corresponds to 21% of the total carbon fixed by all primary producers, and the nitrogen removal by seaweeds alone may be equivalent to the total loading of 490,000 people.

The authors argue that, in this type of estuary, where turbidity depends mainly on SPM resuspension rather than on phytoplankton, increased nutrient loading may not result in increased phytoplankton blooms, given the role of light as a limiting factor for pelagic production. Changes are more likely to occur as shifts in phytoplankton species composition and in alterations to benthic primary production.

The accurate description of the erosion–deposition processes used in this model has shown that estimates of carbon fixation and nutrient removal through uniform SPM dynamics may significantly underestimate the role of intertidal seaweeds and, thus, have important consequences to the understanding of carbon and nutrient cycles in mesotidal and macrotidal estuaries.

3.4.3.1.2 Macroalgal Life Stages (Adults and Spores) and Spatial Discrimination

3.4.3.1.2.1 Problematic  Macroalgal recruitment processes and factors affecting early life stages determine the development and dominance patterns of macroalgal blooms (Lotze and Worm 2000). Furthermore, the development of green macroalgal mats (frequently during spring) is either initiated by overwintering and regrowth of adult plants or by the formation of small propagules, such as vegetative fragments, zoospores, or zygotes (Schories et al. 2000). Thus, it is considered that macroalgal dynamics can only be fully understood if both adult individuals and early life stages are taken into account (Martins et al. 2007).

3.4.3.1.2.2 Aim  The aim of this work is to develop a model coupled to GIS, which is able to estimate algal productivity at the system-scale, taking into account the productivity of spores and adults, and predict the impacts of nutrient loading on the system and the adjacent coastal area (Figure 3.7).

For the sake of accuracy, productivity simulations take into account the spatial discrimination related to light and temperature conditions.

3.4.3.1.2.3 Study System  The Mondego estuary (Portugal).

3.4.3.1.2.4 Model Structure and Main Equations  Processes affecting macroalgal spores. Here, we will focus on the processes affecting the productivity of the initial life stages of macroalgae. A detailed description of the processes that control adult growth and productivity can be found in the work of Martins et al. (2007).
The biomass of spores was considered dependent on three basic processes: sporulation (Sp), germination assumed as germination and growth to the next life stage (G) and grazing by macroinvertebrates (Zs):

\[
\frac{dS}{dt} = Sp - (G + Zs)
\]  

(3.50)

Sporulation is the release of spores by adult macroalgae (Santelices 1990). In the present work, sporulation was defined as the concentration of spores...
present in the water column, able to attach to any hard substrate, and it was experimentally obtained (Sousa et al. 2007).

The germination and growth of spores was described as:

\[ G = G_{\text{max}} \cdot f(T) \cdot f(I) \cdot f(S) \cdot f(NP) \]  \hspace{1cm} (3.51)

where \( G_{\text{max}} \) is the maximum germination rate and the \( f \) functions are limiting factors for temperature, light, salinity, and nutrients, respectively (for details, refer to Martins et al. 2007).

According to experimental evidence, the maximum grazing rate on spores (\( Z_{\text{max}} \)) was set at 0.14 day\(^{-1}\) (Lotze and Worm 2000) and the grazing rate was considered temperature-dependent:

\[ Z_S = Z_{\text{max}} \cdot f(T_S) \]  \hspace{1cm} (3.52)

\[ f(T_S) = \exp \left[ -2.3 \left( \frac{T - T_{\text{opt}}}{T_{xZ} - T_{\text{opt}}} \right)^2 \right] \]  \hspace{1cm} (3.53)

where \( T_{xZ} = T_{\text{min}} \) for \( T \leq T_{\text{opt}} \) and \( T_{xZ} = T_{\text{max}} \) for \( T > T_{\text{opt}} \); \( T_{\text{opt}} \) is the optimum temperature for grazing activity, \( T_{\text{min}} \) is the lower temperature limit, below which grazing activity ceases, and \( T_{\text{max}} \) is the upper temperature limit, above which growth ceases.

Light climate and temperature: accounting for the effect of spatial discrimination on algal productivity. Light intensity at surface (\( I_0 \)) was estimated through the Brock model (1981), assuming a mean cloud cover of 0.41 (Martins et al. 2007). Photon flux density (PFD) was estimated from \( I_0 \), assuming that 42\% of the overall energy is available for photosynthesis (Ferreira and Ramos 1989). PFD at depth \( z \) was calculated according to the Lambert–Beer equation, which assumes an exponential decrease of light with depth within the water column. The light extinction coefficient assumes different values according to local hydrodynamics variation, which accounts for turbidity, and adult macroalgal biomass, which accounts for self-shading (Martins et al. 2001, 2007).

Tidal height was simulated using the basic harmonic constituents and the bathymetry of the system (Mondego estuary, Portugal) was taken into account. Thus, the depth of algae depends on time and space:

\[ \text{Algae depth} = \text{Tidal height} - \text{Bathymetry} \]  \hspace{1cm} (3.54)

Desiccation stress has been pointed out as a mechanism related to the summer decline of macroalgal populations (Rivers and Peckol 1995; Hernández et al. 1997), particularly of those, located at latitudes where spring and summer temperature and irradiance values may be very high, such as the Mondego.
estuary (Martins and Marques 2002). Therefore, the model accounts for the seasonal and daily effect of desiccation on algae by assuming that, from April to September and from 11 A.M. until 4 P.M., emerged algae will exceed the air temperature in 5°C. According to Bell (1995), desiccated thalli have no evaporative water and can exceed air temperature up to 20°C.

The model was run at 33 different bathymetries (from −0.9 m [below sea level] to 2.30 m [above sea level] with a discrimination of 0.1 m). Model results were obtained at a scale of 1 m² and subsequently upscaled to the system using a bathymetric map and GIS and, taking into account, the patchy distribution of adult macroalgae within the system (Lopes et al. 2006).

3.4.3.1.2.5 Results and Discussion Results indicate that there are significant spatial variations within the estuarine system regarding macroalgal growth. In this model, spatial variability is accounted for a dependency of light and temperature with depth, which determines that during winter and autumn, macroalgae growth is favored at lower depths (between +2.1 and +2.3 m above sea level) because it benefits from higher light availability, whereas in summer, macroalgae biomass is higher at deeper depths (between +1.8 and +2.2 m above sea level), where immersion periods are longer and desiccation stress is more limited.

Furthermore, the authors discuss that to account for a more accurate spatial variability of macroalgal standing stocks and growth at intertidal areas, other factors should be considered, such as the type of substrate (which affects the attachment conditions of algal spores and adults), the organic matter content of the underlying sediment, the presence or absence of rooted macrophytes, and the grazing pressure.

Calculations at the system level suggest that, in estuaries where hydrodynamics plays a major role, macroalgal biomass and, consequently, the amount of carbon, nitrogen, and phosphorus bounded to algal tissue, show enormous variations between years (240–21,205 tons macroalgal dry weight year⁻¹). Such variations will have significant impacts both in estuarine systems and on the adjacent coastal areas.

In years which do not favor macroalgal growth, there may be a potential nutrient surplus to the adjacent coastal areas because, in these circumstances, the role of macroalgae as nutrient sink is not significant. In years with intensive macroalgal growth, its internal requirements in nutrients may largely exceed the domestic loads of N and P to the Mondego estuary, indicating the significant role of opportunistic algae as a nutrient sink within this system. Nevertheless, in these years, up to 89 times more macroalgal tissue is likely to be exported to the adjacent coastal areas compared to years with limited algal growth. However, remineralization must occur before these nutrients are available to other primary producers, namely, coastal phytoplankton.

Regarding the impacts of spores on the dynamics of adult macroalgae, results suggest that in favorable years (mild winters and low rainfall) (Martins et al. 2001), the spring blooms occur at the expense of growth and
reproduction of overwintering adults. However, during years with adverse conditions (Martins et al. 2001), where high rainfall in winter and spring prevent the occurrence of significant biomass of overwintering adults, the onset of the spring bloom may depend on the biomass of viable dormant spores (Martins et al. 2008).

3.4.3.1.3 The Mechanistic Approach

3.4.3.1.3.1 Problematic The use of empirical approaches in data-poor estuaries requires extrapolation from estuaries with possibly different physical environments and biota. Alternatively, it is possible to replace some empirical descriptions of ecological processes with more mechanistic descriptions (Baird and Emsley 1999). Concerning ecological processes, mechanistic is used to refer to the method of equation development. For example, using the process of diffusion to the cell surface to describe nutrient uptake is considered mechanistic because it uses a well-understood physical law (Fick’s law of diffusion), and contains physically meaningful parameters such as the diffusion coefficient and the geometry of the cell (Pasciak and Gavis 1975). The use of mechanistic descriptions of ecological processes reduces the need for extrapolation of model to simulate ecological processes in data-poor estuaries (Baird et al. 2003).

3.4.3.1.3.2 Aim The aim was to develop a model of estuarine eutrophication built on mechanistic descriptions of a number of key ecological processes in estuaries.

3.4.3.1.3.3 Study Systems Several Australian estuaries.

3.4.3.1.3.4 Model Structure and Main Equations Photosynthetically available radiation (PAR) at the bottom of a layer of water \( I_{\text{bot}} \) (mol photon m\(^{-2}\) s\(^{-1}\)) is given by:

\[
I_{\text{bot}} = I_{\text{top}} e^{-K_d dz}
\]  

(3.55)

where \( I_{\text{top}} \) is the PAR at the top of the layer (mol photon m\(^{-2}\) s\(^{-1}\)), \( dz \) is the thickness of the layer (m), and \( K_d \) is the total light extinction coefficient (m\(^{-1}\)).

The equation that describes \( K_d \):

\[
K_d = k_w + n_{PS} a_{APS} + n_{PL} a_{APL} + n_{MPB} a_{A_{MPB}} + K_{other}
\]

(3.56)

where \( k_w \) is the background attenuation coefficient of water (m\(^{-1}\)); \( n_{PS}, a_{APS}, n_{PL}, a_{APL}, \) and \( n_{MPB} \) and \( a_{A_{MPB}} \) are the water concentration (cell m\(^{-3}\)) and absorption cross section (m\(^2\) cell\(^{-1}\)) of cells of small phytoplankton, large phytoplankton, and microphytobenthos, respectively. \( K_{other} \) is the attenuation coefficient due
to other components in the water column (e.g., dissolved organic matter or suspended organic matter, m\(^{-1}\)).

The average PAR in the layer, \(I_{av}\) (mol photon m\(^{-2}\) s\(^{-1}\)), is given by:

\[
I_{av} = \frac{I_{top} - I_{bot}}{K_d dz}
\]  

(3.57)

In the model, it is assumed that light reaching the benthos is first attenuated by macroalgae and then seagrasses, which is described, respectively, by:

\[
I_{below MA} = I_{bot} e^{-MAaA_{MA}}
\]  

(3.58)

and

\[
I_{below SG} = I_{below MA} e^{-SGaA_{SG}}
\]  

(3.59)

where \(MA\) and \(SG\) are the biomass values (mg N m\(^{-2}\)) and \(aA_{MA}\) and \(aA_{SG}\) are the biomass-specific absorption cross sections (mg N\(^{-1}\) m\(^{2}\)) of the macroalgae and seagrass, respectively.

The remaining light passes through a thin layer of microphytobenthos at the surface of the sediment:

\[
I_{below MPB} = I_{below SG} e^{-n_{MPB} aA_{MPB}dz}
\]  

(3.60)

where \(n_{MPB}\) is the concentration of microphytobenthos (cell m\(^{-3}\)) with an absorption cross section of \(aA_{MPB}\) (m\(^2\) cell\(^{-1}\)) in a sediment layer \(dz\) thick (m).

The average light flux available to microphytobenthos is given by:

\[
I_{av} = \frac{I_{below SG} - I_{below MPB}}{n_{MPB} aA_{MPB}dz}
\]  

(3.61)

Differently from other aquatic ecological models, autotroph absorption cross sections were used to parameterize both the dependence of autotroph growth rate on light availability and light attenuation in the water column.

In the Monod or Michaelis–Menten-type growth functions used in many ecological models, empirically determined half-saturation constants are required to determine the shape of the curve. In this model, the growth rate of autotrophs is determined from a functional form specifying the interaction of the maximum supply rates of nutrients and light, and the maximum growth rate.
Phytoplankton cells suspended in the water column obtain nutrients from the surrounding water, and light as a function of the average light in the considered layer. There is a physical limit to the rate at which a cell can absorb nutrients, which is given by the rate at which nutrient molecules can diffuse from the surrounding fluid to the cell surface and is known as the mass transfer limit (Pasciak and Gavis 1975). In this study, this parameter is used as the maximum rate of nutrient uptake (kN, mol cell⁻¹ s⁻¹) and is given by:

\[ k_N = \psi DN \]  

(3.62)

where \( \psi \) is the diffusion shape factor (m cell⁻¹), which for a sphere is \( 4\pi r \) and \( r \) is the cell radius (m); \( D \) is the molecular diffusivity of the nutrient (m² s⁻¹); and \( N \) is the concentration of the nutrient in the water column (mol m⁻³).

In the case of light, the maximum supply rate (\( k_1, \) mol photon cell⁻¹ s⁻¹) is given by:

\[ k_1 = I_{av} \overline{aA_{cell}} \]  

(3.63)

\( aA_{cell} \) is the absorption cross section of a cell (m² cell⁻¹) and \( I \) is the average PAR in the layer (mol photon m⁻² s⁻¹).

The absorption cross section of a spherical cell is given by (Kirk 1975):

\[ \overline{aA_{cell}} = \pi r^2 \left( 1 - \frac{2(1 - (1 + 2\gamma_C r)e^{-2\gamma_C r})}{(2\gamma_C r)^2} \right) \]  

(3.64)

\( \gamma_C \) is the absorption coefficient (m⁻¹), which gives the rate at which light is attenuated.

For benthic macroalgae, the maximum rate of nutrient uptake, \( k_N \) (mol m⁻² s⁻¹), can be calculated as a diffusion rate through an effective diffusive boundary layer thickness, \( \delta \) (m):

\[ k_N = \frac{D}{\delta} N \]  

(3.65)

where \( D \) is the molecular diffusivity of the nutrient (m² s⁻¹) and \( N \) is the concentration of the nutrient in the water column (mol m⁻³).

At typical hydrodynamic environments, the effective diffusive boundary layer thickness is of the order of 0.1 mm for typical benthic macrophytes. The effective thickness of the diffusive boundary layer is strongly influenced by shear stress at the water–benthos interface, which in turn is a function of surface roughness and water velocity (Hurd 2000).
Light capture by macroalgae, $k_1$ (mol photon m$^{-2}$ s$^{-1}$), is given by:

$$k_1 = I_{\text{bot}} \left( 1 - e^{-\frac{aA_{MA}}{MA}} \right)$$

(3.66)

where $I_{\text{bot}}$ is the incident radiation at the top of the macroalgae (mol photon m$^{-2}$ s$^{-1}$), $MA$ is the biomass of macroalgae (mg N m$^{-2}$), and $aA_{MA}$ is the nitrogen-specific absorption cross section of macroalgae (m$^2$ mg N$^{-1}$).

It is assumed that the projected area of the benthos is fully covered by macroalgae, but the macroalgae has varying thickness and, thus, absorbance depends on biomass.

The uptake rate of seagrasses is expressed as:

$$k_N = \frac{SG\mu_{\text{max}}}{K_{1/2}} N$$

(3.67)

where $SG$ is the biomass of seagrass (mol N m$^{-2}$), $\mu_{\text{max}}$ is the maximum growth rate (s$^{-1}$), $N$ is the sediment porewater nutrient concentration (mol m$^{-3}$), and $K_{1/2}$ is an experimentally determined half-saturation constant of nutrient-limited growth when fitted to the Monod growth equation (mol N m$^{-3}$).

The maximum uptake rate of benthic microalgae takes the same form as for suspended algal cells (Equation 3.62), although the diffusion coefficient is calculated from:

$$D_{\text{porewater}} = \frac{\vartheta D}{\theta}$$

(3.68)

where $\vartheta$ is the porosity and $\theta$ is the tortuosity (both dimensionless), which can be approximated by (Boudreau 1996):

$$\theta = 1 - \ln(\vartheta^2)$$

Light capture by microphytobenthos is modeled in the same manner as for algal cells suspended in the water column.

The authors have used a new empirical growth model scheme, which allows the logical use of mechanistically determined maximum uptake rates and maximum growth rates.

For planktonic autotrophs and assuming a light- and a single nutrient-limited system,

$$N = k_N \left( \frac{R_{N_{\text{max}}} - R_N}{R_{N_{\text{max}}}} \right) \text{mol N cell}^{-1} \text{ s}^{-1}$$

(3.69)
and

\[ I = k_I \left( \frac{R_l^{\text{max}} - R_l}{R_l^{\text{max}}} \right) \text{mol photon cell}^{-1} \text{s}^{-1} \]  

(3.70)

where \( R \) denotes the reserves of nutrient and light available for growth (energy from light is assumed to be stored as fixed carbon) and \( R_{\text{max}} \) is the maximum value of \( R \).

The growth rate, \( \mu \), is given by:

\[ \mu = \mu_{\text{max}} \frac{R_N}{R_N^{\text{max}}} \frac{R_l}{R_l^{\text{max}}} \]  

(3.71)

where \( \mu_{\text{max}} \) is the maximum growth rate (s\(^{-1}\)).

To determine growth at any combination of \( k_I, k_N \), and \( \mu_{\text{max}} \), a steady-state solution is obtained through:

\[ k_N \left( \frac{R_N^{\text{max}} - R_N}{R_N^{\text{max}}} \right) = \mu_{\text{max}} (m_N + R_N) \frac{R_N}{R_N^{\text{max}}} \frac{R_l}{R_l^{\text{max}}} \]  

(3.72)

\[ k_I \left( \frac{R_l^{\text{max}} - R_l}{R_l^{\text{max}}} \right) = \mu_{\text{max}} (m_I + R_l) \frac{R_N}{R_N^{\text{max}}} \frac{R_l}{R_l^{\text{max}}} \]  

(3.73)

where \( m_N \) and \( m_I \) are the stoichiometry coefficients specifying the number of moles of N and photons per cell.

3.4.3.1.3.5 Results and Discussion  The authors found significant differences for describing autotrophic growth between the mechanistic and empirical approaches. In many models, which follow empirical approaches (e.g., Madden and Kemp 1996), the growth rate of macroalgae is an exponential function of the biomass of the autotroph under all nutrient and light levels. In the mechanistic formulation, the rate of biomass increase varies from being an exponential function of biomass at nutrient and light-saturating conditions, to being independent of biomass at nutrient-limiting conditions, to having a complex exponential relationship with biomass at light-limiting conditions.

In the mechanistic approach, the half-saturation constants, which are often both poorly constrained and can impact significantly on model output, are
replaced by parameters with very specific physical interpretations. These parameters can often be measured accurately and, in many cases, will have similar values in all estuaries.

However, although empirical models are constrained by observations, mechanistic approaches have the underlying assumption that all important processes have been captured. Consequently, as long as the empirical model behavior does not deviate significantly from the calibration data set, the model should perform well. In contrast, the mechanistic approach relies on the modeler capturing the important processes.

The authors conclude that the use of mechanistic descriptions in models of estuarine eutrophication may provide predictive capabilities beyond those of models with empirical descriptions.

### 3.4.4 Microphytobenthos

Microphytobenthos are major primary producers in estuarine mudflats systems (MacIntyre et al. 1996; Underwood and Kromkamp 1999). They are composed of different microalgal groups (e.g., diatoms, euglenoids, green algae, cyanobacteria) that inhabit various types of intertidal systems, from fine silt and mud to sand (MacIntyre et al. 1996; Paterson and Hagerthey 2001; Jesus et al. 2006).

Although models of microphytobenthos are less abundant than models of phytoplankton or macroalgae, they can also be found in literature with a somehow more recent appearance. For instance, Guarini et al. (2008) have developed a “hybrid dynamic model” for microphytobenthos, where continuous dynamic processes (i.e., production and mortality) coexist with discrete events (i.e., resuspension of the biofilm at the surface of the mudflat). Their model takes into account specific microphytobenthos behavior. On intertidal mudflats, photosynthetic active radiations often saturate the production of microphytobenthos (Guarini et al. 2000). When saturation is reached, the production rate varies mainly with temperature (Guarini et al. 1998), salinity, and pH. A general thermo-inhibition can be observed in temperate intertidal mudflats during summer (Guarini et al. 1998), which may lead to an inversion of the production–loss balance, with a consequent decrease in microphytobenthos biomass (Guarini et al. 1998).

In another model of microphytobenthos (Guarini et al. 2002), the authors combine deterministic processes (water elevation, light–dark cycle) and stochastic processes (carbon assimilation of the microalgal community) to estimate the potential productivity of microphytobenthos at the system level. Results indicate that microphytobenthos productivity exhibits significant spatial heterogeneity, which was attributed to different photosynthetic competence of microphytobenthos in different subbasins and spatial differences in the phase shifts between the tidal and solar cycles controlling the exposure of intertidal areas to sunlight.
3.4.4.1 Some Recent Microphytobenthos Models

3.4.4.1.1 Microphytobenthos Productivity

3.4.4.1.1.1 Problematic  In the oceans, primary production is generally dominated by pelagic flora, but in shallow basins, primary production associated with the benthos may be locally significant (e.g., Barranguet et al. 1996). The annual production levels of intertidal benthic diatoms are reported to be significant and approaching the estimates of pelagic production in neighboring neritic habitats (e.g., McIntyre and Cullen 1995). In fact, several studies have shown that microphytobenthos contributes with a significant proportion of total microphytoplankton biomass and production, sometimes exceeding 50% (e.g., Cahoon and Cooke 1992). However, in many coastal systems worldwide, there is still a lack of studies that evaluate the contribution of microphytobenthos productivity to the system's dynamics and total production.

3.4.4.1.1.2 Aim  The aim of the study was to assess the potential influence of the unicellular forms of microphytobenthos, principally episammic and epipelic diatoms, within the context of a dynamic intertidal ecosystem and related to carbon fixation, aerobic layer activity, light versus nutrient limitation, and nutrient regeneration.

3.4.4.1.1.3 Study System  Northern Adriatic ecosystem.

3.4.4.1.1.4 Model Structure and Main Equations  The phytobenthic model (Figure 3.8) considers only diatoms, and their biomass variation is described by:

\[
\frac{\partial A}{\partial t} = \text{production} - \text{respiration} - \text{loss} - \text{predation} \tag{3.74}
\]

Gross production rate \(P\) is calculated as:

\[
P = r_{\text{max}} \cdot f_t \cdot f_i \cdot f_s \tag{3.75}
\]

where \(r_{\text{max}}\) is the maximum CO₂ uptake rate, and \(f_t, f_i,\) and \(f_s\) are the temperature-, light- and silicate limitation factors, respectively.

The temperature factor uses a standard Q10 formulation based on ambient temperature \(T\):

\[
f_t = q^{0.1(T-10)} \tag{3.76}
\]
And the light limiting factor is described by:

\[ f_l = \frac{I \cdot I_{opt}}{I_{opt}} \cdot e^{-\sigma D} \]  

(3.77)

where \( l \) is day length, \( \sigma \) is the extinction coefficient, \( D \) is depth, \( I \) is irradiance, \( P_{act} \) is the proportion of light that is photosynthetically active, and \( I_{opt} \) is the optimum irradiance.

The adaptation of the optimal light parameter is described by:

\[ \frac{d}{dt} I_{opt} = r_1 \cdot \left( I \cdot P_{act} - I_{opt} \right) \]  

(3.78)

where \( r_1 \) is the relaxation process time constant. \( I_{opt} \) is constrained by a minimum value \( I_{min} \).

The silicate limitation factor depends on the ambient silicate concentration and a constant:

**FIGURE 3.8**

Conceptual diagram of the microphytobenthic model and the ERSEM benthic model showing state variables and fluxes. (From Blackford, J. C., *Estuarine, Coastal and Shelf Science*, 55, 109–123, 2002. With permission.)
The nutrient limitation factor \( i_N \) employs Droop kinetics:

\[
  i_N = \lim_{0 \to 1} \left( \frac{p_{cell} - p_{min}}{p_{max} - p_{min}} \cdot \frac{n_{cell} - n_{min}}{n_{max} - n_{min}} \right)^{0.5}
\]

(3.80)

where \( n_{cell} \) and \( p_{cell} \) are the actual internal cell C/N and C/P ratios, the maximum ratios \( (n_{max}, p_{max}) \), and the structural content of the cell \( (n_{min}, p_{min}) \).

Nutrient uptake \((N\) and \(P)\) is defined by:

\[
  \text{uptake} = \min(P \cdot N_{\text{max}} + A \cdot N_{\text{max}} - A_N, N_{\text{aff}} \cdot [N] \cdot A)
\]

(3.81)

which depends on the shortfall in existing nutrient content \((A \cdot N_{\text{max}} - A_N)\), the uptake required to balance the calculated carbon production in the current time step \((P \cdot N_{\text{max}})\), and the cell’s physiological affinity to the nutrient and the available nutrient pool \((N_{\text{aff}} \cdot [N] \cdot A)\).

The phytobenthic model was coupled to ERSEM (Baretta et al. 1995), a biomass-based model, which determines the fluxes of carbon and nutrients between several functional groups.

The physical model used in this work is the vertical diffusion submodel of the Princeton Ocean Model (POM) (Blumberg and Mellor 1980) coupled to a turbulence closure scheme model (Mellor and Yamada 1982). This model was previously applied in the study area by Vichi et al. (1998) and Allen et al. (1998).

Model simulations were performed for several simulations, from 5 to 25 m, along an offshore transect.

3.4.4.1.1.5 Results and Discussion  Predictions indicate that mycrophytobenthos can contribute in excess of 50% of primary production in shallow depths (<5 m), where light availability is the key factor limiting mycrophytobenthos, with self-shading dominating this effect in established populations. Grazing is also shown to be a significant control on microphytobenthic populations. Nutrient stress is not a major limiting factor of microphytobenthos due to benthic nutrient pools. Although nutrient uptake and cycling through microphytobenthos are not significant compared with regional inputs, microphytobenthic populations have significant impacts on nutrient regeneration rates, aerobic layer processes, and benthic trophic dynamics. The effects on the pelagic ecosystem are minimal.
3.4.4.1.2 Hydrobia Ulvae, Microphytobenthos, and Mudflat’s Erosion

3.4.4.1.2.1 Problematic

Several studies have shown that the stability of intertidal mudflats is highly dependent on the biological activity and community structure (e.g., Herman et al. 2001). Benthic biology seems to influence the critical shear stress for erosion and the erosion rate significantly (Widdows et al. 2000; Amos et al. 2004).

Macroalgal mats, which occur more often during spring, summer, or early autumn, tend to stabilize the sediment bed, thus making mudflats more resistant to erosion (Paterson 1989). On the contrary, deposit-feeders such as Hydrobia ulvae may have a destabilizing action to the sediment bed, while moving and feeding on benthic algae (Andersen 2001).

Because it seems that there exists a strong positive feedback between mud deposition on mudflats and the functioning of the benthic food webs (Herman et al. 2001), it becomes important to estimate the overall net effect of biological processes on the sediment deposition rates at intertidal areas.

3.4.4.1.2.2 Aim

The authors have developed a numerical sediment transport model to describe how the presence of H. ulvae and microphytobenthos (mainly diatoms) affect the erosion and deposition patterns on the mudflat of a Danish estuary.

3.4.4.1.2.3 Study System

Lister Dyb tidal area at the Wadden Sea (between Germany and Denmark).

3.4.4.1.2.4 Model Structure and Main Equations

The authors have used an exponential erosion formulation (Parchure and Mehta 1985) appropriated to the dominant sediment type at the study area, that is, soft unconsolidated mud:

\[
S_E = E\left[\alpha \sqrt{\tau_b - \tau_{ce}}\right]
\]

(3.82)

where \(S_E\) is the erosion rate (kg m\(^{-2}\) s\(^{-1}\)), \(E\) is the floc erosion rate (kg m\(^{-2}\) s\(^{-1}\)), \(\alpha\) is a coefficient (m N\(^{-0.5}\)), \(\tau_b\) is the bed shear stress (N m\(^{-2}\)), and \(\tau_{ce}\) is the critical bed shear stress for erosion (N m\(^{-2}\)).

Deposition is calculated through the settling flux formulation (Krone 1962; Einstein and Krone 1962):

\[
S_D = w_s c_b p_d
\]

(3.83)

where \(S_D\) is the deposition rate (kg m\(^{-2}\) s\(^{-1}\)), \(w_s\) is the settling velocity (m s\(^{-1}\)), and \(c_b\) is the near bed concentration (kg m\(^{-3}\)):

\[
c_b = 1 + \frac{Pe}{1.25 + 4.75(p_d^{2.5})}
\]

(3.84)
where $Pe$ is the Peclet number, defined by:

$$Pe = \frac{w_s h}{D_z}$$  \hspace{1cm} (3.85)

where $D_z$ is the eddy diffusivity ($m^2 s^{-1}$) and $p_d$ is the probability of deposition:

$$p_d = 1 - \left( \frac{\tau_b}{\tau_{cd}} \right)$$  \hspace{1cm} (3.86)

where $\tau_{cd}$ is the critical bed shear stress for deposition ($N m^{-2}$).

The sediment settling velocity is calculated through the exponential relationship:

$$w_s = K c^m$$  \hspace{1cm} (3.87)

where $K$ and $m$ are time- and site-specific parameters.

The authors have run the model with four different sets of combinations covering the general range of erosion thresholds, erodibilities, and settling velocities observed in the study site. Only parameters related to the processes affected by the considered biological communities (microphytobenthos and $H. ulvae$) have been changed between different runs to predict and estimate the net effect of the varying biological parameters.

### 3.4.4.1.2.5 Results and Discussion

According to results, the net sedimentation on the intertidal mudflat is controlled by sediment characteristics, hydrography, meteorology, and also benthic biology. The presence of large numbers of destabilizing $H. ulvae$ results in higher net accumulation, particularly, if sediment aggregation comes in the form of fecal pellets from $H. ulvae$. These pellets cause settling velocities to be so high that, in spite of the destabilizing activity of the snail at the bed sediment, the increase in settling velocity compensates for this and the net result is enhanced deposition. However, the newly deposited sediment is loose and thus highly mobile and prone to subsequent resuspension. In contrast, the stability of the mudflats is increased by the presence of biofilms.

### 3.4.5 Seagrasses

Salt marshes are coastal systems from temperate zones, mainly occupied by halophytic vegetation, commonly designated as seagrasses or salt marshes plants. Ecologically, salt marshes are characterized by their high primary
productivity and species diversity, representing habitat for migratory waterfowl, transient fish species, and indigenous flora and fauna (Simas et al. 2001). These ecosystems also provide important commercial resources because they act as nursery grounds for several fish and crustacean fisheries (e.g. Van Dijkeman et al. 1990).

In addition, seagrasses help the stabilization of sediments and play an important role in the nutrient budget of coastal marine ecosystems, as they take up nutrients both through below- and aboveground biomass (Oshima et al. 1999; Elkalay et al. 2003). Seagrasses also provide a physical connection between the water column and sediments by transporting photosynthetic- and seawater-derived oxygen to their roots and rhizomes (e.g. Miller et al. 2007).

### 3.4.5.1 Recent Seagrass Models and Processes Taken into Account

#### 3.4.5.1.1 Effects of Sea-Level Rise in Salt-Marsh Areas

##### Problematic

The enhanced greenhouse effect results from human activities that have caused a recent increase in the atmospheric concentrations of the main greenhouse gases: carbon dioxide, methane, and nitrous oxide (e.g., IPCC 1990; Titus and Narayanan 1995; Houghton 1999). According to the reports from the IPCC (1990), the global average temperature of the planet will rise by about 2.5°C, with a range of 1.5–4.5°C, depending on the model used (Berner and Berner 1996; Houghton 1999; IPCC 1999). In spite of all uncertainties linked to these predictions, a rise in sea level is another expected consequence of the enhanced greenhouse effect, both because of oceanic thermal expansion and melting of Arctic and Antarctic glaciers (Titus et al. 1991). According to the estimates of the IPCC, the total average sea-level rise is predicted to be about 12 cm by 2030 and 50 cm by 2100 (IPCC 1999).

Salt marshes are important coastal ecosystems developed in temperate zones and, particularly, vulnerable to sea-level rise—as the sea rises, the outer salt marsh boundary will erode and new salt marsh will form inland (Simas et al. 2001). Salt marshes seem able to react by a negative feedback mechanism to the sea-level rise: a small increase in sea level leads to greater sediment deposition due to extended submersion time, and to reduced soil compaction due to reduced decomposition of organic matter (Nyman et al. 1994; Allen 1994). However, rapid sea-level rise may counteract this effect with a positive feedback one that increases salt-marsh loss, increased submersion times reduce salt marsh production and, consequently, organogenic sedimentation (Nyman et al. 1994).

##### Aim

The authors aimed at examining the consequences of sea-level rise in salt marsh areas, using an approach that combines ecological modeling, remote sensing, and geographical information analysis (Simas et al. 2001) (Figure 3.9).
3.4.5.1.1.3 Study System  The Tagus estuary (Portugal).

3.4.5.1.1.4 Model Structure and Main Equations  Salt marsh productivity was simulated by combining a biogeochemical model and a demographic model, which were developed for the aboveground vegetation. Because the biogeochemical model uses the same type of formulations previously described for other type of primary producers or described in the following section for another salt marsh plant (*Zostera noltii*), here we will focus in the demographic model. Details on biogeochemical models of seagrasses can be found in the work of Simas et al. (2001) and others (e.g. Simas and Ferreira 2007).

The demographic model. Seagrass population dynamics was simulated through a class transition model, between weight classes, in order to describe plant population density per unit area. Four weight classes were considered and class transition was described by:

\[
\frac{\partial n(s,t)}{\partial t} = - \frac{\partial}{\partial s} \left[ n(s,t) g(s,t) \right] - \mu(s) n(s,t) \tag{3.88}
\]

where \( t \) is time, \( s \) is weight class, \( n \) is the number of shoots, \( g \) is scope for growth, and \( \mu \) is the mortality rate.
The number of shoots in each weight class depends on the individual shoot scope for growth and on allometric natural mortality rate. The model also takes into account that the erosion losses in the number of individuals are higher for the lower weight classes. Recruitment to class 1 is explicitly modeled as a source of new recruits to the population, which is accounted for the reproduction in weight class 4.

**Sea-level rise scenarios.** To simulate the gradual water elevation, a simple model was developed and coupled with the production module. The simple module for the water elevation assumed that the relative elevation to tidal datum of the surface of a salt marsh at a place ($\eta$) changes annually with “natural” sea-level rise due to mineral and organic accretion, which includes natural subsidence, soil compaction and depletion of groundwater levels, and sea-level rise due to climate change (Allen 1990a, 1990b, 1995, 1997):

$$\frac{\partial \eta}{\partial t} = \partial S_{\text{min}} + \partial S_{\text{org}} - \partial M - \partial P$$  \hspace{1cm} (3.89)

where $t$ denotes time, $S_{\text{min}}$ is the thickness of added minerogenic sediment, $S_{\text{org}}$ is the thickness of added organogenic sediment, $M$ is the change in relative sea level (positive upward), and $P$ is change in the position of the marsh due to long-range compaction.

The water-level rise scenarios proposed by IPCC (1995) were chosen for the study. IPCC estimates a sea-level rise of 50 cm from 1999 to 2100, or 0.45 cm year$^{-1}$. The “high sea-level rise” scenario corresponds to a 95 cm rise, or 0.86 cm year$^{-1}$ (IPCC 1995, 1999). A linear increase in this variable was considered during the simulation period.

### 3.4.5.1.1.5 Results and Discussion

Biomass predictions for the lower and upper marshes fell within the range of observations (Catarino 1981; Catarino and Caçador 1981) (Figure 3.10).

Total plant production of the system was calculated by upscaling the ecological model using the GIS areas. Lower and upper marsh areas were simulated using the C$_4$ and C$_3$ models, respectively, because one C$_4$ species dominates the lower marsh (*Spartina maritima*), whereas two C$_3$ species dominate the upper marsh (*Halimione portucaloides* and *Arthrocnemum fruticosum*). According to the results, salt marsh production is responsible for the annual removal of about 1200 tons of nitrogen and 170 tons of phosphorus, which corresponds roughly to 270,000 and 170,000 inhabitants, respectively (Simas et al. 2001).

Further on, the model was used to simulate salt marsh production and biomass for both sea-level rise scenarios. In 2010, the model predicts losses in biomass and production of about 100% in the lower marsh, which suggests that by 2100, the current level of lower salt may potentially disappear. In the
same scenario, the upper marsh biomass will decrease by 35% and production losses will reach 50% (Figure 3.11).

Finally, the proposed methodology was also used to carry out risk assessment in order to determine the susceptibility to submersion of different salt marsh areas in the estuary. Results indicate that the eastern salt marsh area is the most resistant, because of its higher elevation, presenting a moderate to low risk of destruction. On the contrary, the lower salt marsh areas in the north and west of the estuary present high to very high risk.

3.4.5.1.2 Z. noltii and the Nitrogen Cycle

3.4.5.1.2.1 Problematic In some intertidal systems, rooted macrophytes show important standing stock values and cover significant areas (Gerbal and Verlaque 1995). The importance of their presence in those systems is related to their role in carbon fixation (e.g., Sfriso and Marcomini 1999), their impact on nutrient budgets (e.g., Touchette and Burkholder 2000) and their mitigation effect in eutrophication and anoxic episodes (e.g., Viaroli et al. 2001).

Z. noltii is an important macrophyte from the Thau lagoon system (Mediterranean coast of France), although few models of its growth or
productivity have been developed compared to its more subtidal counterpart Zostera marina (Plus et al. 2003).

3.4.5.1.2.2 Aim The authors aimed at developing a Z. noltii ecosystem model, able to simulate (1) the seasonal dynamics of biomass and nitrogen content of the rooted macrophyte and (2) the contributions of different primary producers (seagrass, phytoplankton, and epiphytes) to the nitrogen and oxygen cycle of the ecosystem.

3.4.5.1.2.3 Study System The Thau lagoon at the French Mediterranean coast.

3.4.5.1.2.4 Model Structure and Main Equations The model takes into account above- and belowground seagrass biomass, nitrogen quotas, and epiphytes. The forcing functions are light intensity, wind speed, rainfall, and water temperature (Figure 3.12).

Z. noltii is represented by five state variables: aboveground biomass, belowground biomass, density of shoots, aboveground- and belowground-nitrogen pools. In addition, the model includes a state variable representing epiphyte biomass, and two state variables for dissolved inorganic nitrogen, ammonia, and nitrate concentrations in the water column and in the sediment.

The model takes into account a vertical structure, with a water box on top (1.4 m depth), followed by three sediment boxes (0.5, 1.5, and 4.38 cm depth,
respectively). The vertical discrimination of the model allows describing the oxygen and nutrient fluxes at the water–sediment interface.

Seagrass photosynthesis is controlled by temperature and light according to the following equation:

\[
\text{Seagrass photosynthesis} = \text{Temperature} \times \text{Light} \times \left( \frac{\text{Temperature}}{\text{Light}} \right)^{\text{Temperature}}
\]
The effect of temperature on the physiology of *Z. noltii* is described directly through:

\[
P_{\text{max}} = \Theta_{\text{p}_{\text{max}}} \times t - P_{\text{max}}^{0^\circ C}
\]

where \( \Theta_{\text{p}_{\text{max}}} \) is the production increasing rate with temperature, \( t \) is temperature, and \( P_{\text{max}}^{0^\circ C} \) is the theoretical maximum production at \( 0^\circ C \).

The effect of light on seagrass productivity is described in a more complex manner because it depends on irradiance photosynthetic capacities and on shading effects caused by seagrass’s bed morphology and epiphytes.

Light at the top of the canopy is described via:

\[
Q_{\text{can}} = I \times f_1(E) e^{(-k_1 \times (D-0.3))}
\]

where \( I \) denotes the light at the sea surface, \( f_1(E) \) is the limitation due to epiphytes, \( D \) is the water column depth, and \( k_1 \) is the light extinction coefficient due to water.

\[
f_1(E) = e^{(-k_2 \times (EB/LB))}
\]

where \( k_2 \) is the light extinction coefficient due to epiphytes, \( EB \) is the epiphyte biomass, and \( LB \) is the aboveground biomass.

The dependency of seagrass growth on nitrogen was described taking into account the uptake by leaves and rhizomes/roots and the storing capacity of the plant (Plus et al. 2003). Additionally, the authors have also accounted for the nutrient redistribution and reclamation capacity of *Z. noltii*, which tends to occur in nutrient-poor conditions. For the leaves and the rhizomes/roots, the part of nitrogen reclaimed was generically described through:

\[
X_{\text{N}_{\text{rec}}} = \begin{cases} 
1 - \left( \frac{X_{\text{N}_{\text{sat}}}}{S_{\text{rec}}} \right)^2 & \text{if } X_{\text{N}_{\text{sat}}} < S_{\text{rec}} \\
0 & \text{if } X_{\text{N}_{\text{sat}}} > S_{\text{rec}}
\end{cases} \times \text{REC}_{\text{max}}
\]

where \( X_{\text{N}_{\text{sat}}} \) is the saturation level of leaf or rhizome/root nitrogen quota, \( S_{\text{rec}} \) is the internal reclamation threshold, and \( \text{REC}_{\text{max}} \) is the maximum reclamation rate.
Seagrass mortality includes two different processes, a temperature-dependent one \( f_5(t) \), which accounts for natural senescence and a physical stress-dependent mortality \( f_6(v) \), which describes the leaves or shoots sloughing due to wave motion:

\[
LM = LMR_{20^\circ C} \times f_5(t) + f_6(v) \tag{3.95}
\]

where \( LMR_{20^\circ C} \) is the maximum leaf mortality at \( 20^\circ C \)

\[
f_5(t) = \Theta_{LM}^{t-20} \tag{3.96}
\]

where \( \Theta \) is coefficient for leaf mortality

\[
f_6(v) = LMR_v \times \frac{1}{10} (V_{vent}) \times e^{-k_4 \times D} \tag{3.97}
\]

where \( LMR_v \) denotes leaf sloughing due to wind, \( V_{vent} \) is the wind speed, \( D \) is depth, and \( k_4 \) is the wind effect attenuation with depth.

For the macrophyte recruitment, the model only takes into account vegetative reproduction because the sexual reproduction of \( Z. noltii \) in areas where the species is dominant is almost null (Laugier 1998).

Recruitment is considered as a transfer of matter from the rhizomes to the aboveground biomass. The initial biomass of new shoots is fixed at a constant weight and its apparition is controlled by temperature.

Epiphyte dynamics was accounted for and described through dependencies on light, temperature, and nitrogen.

### 3.4.5.1.2.5 Results and Discussion

Simulations of the seasonal variations of \( Z. noltii \) biomass, shoot density, and nitrogen quotas followed the observed patterns. Although model validation was performed whenever possible, the authors point out the following weak points: (1) the model probably underestimates the seagrass rhizome and root biomass and (2) the absence of benthic detritus decomposition leads to an accumulation in the sediment.

Results also indicate that \( Z. noltii \) growth might suffer from nitrogen limitation during summer and that light competition with seagrasses is likely to take place. Epiphytes and phytoplankton also seem to compete for nitrogen.

Results from the coupling between the present model and another one developed for the same system (Chapelle et al. 2000) indicated that, within the Thau lagoon, seagrasses are more productive than phytoplankton and epiphytes and that such production increases oxygen concentrations in the water column. However, the impact of seagrasses on dissolved inorganic nitrogen in the water column is smaller than that of the phytoplankton’s. Results also indicate that the exportation of seagrass leaves contributes more than phytoplankton or epiphyte mortality to the detritus compartment.
3.5 Conclusions

In the past decade, models have been developed for estuaries worldwide aiming at answering and clarifying some of the questions that arise related to these peculiar areas: to predict management scenarios that encompass both the great natural and socioeconomic value of estuaries, to quantify flows of energy and matter along food webs within estuarine areas with different disturbance levels; to understand the relationships between nutrient cycles and hypoxia; to quantify the relative proportion of nutrient input from freshwater and the adjacent sea; to ascertain the impacts from hydrological changes on estuarine communities; to assess if different areas within the estuarine area (e.g., central bay versus tidal area, deep channels versus broad shallow shoals) promote different nutrient- and primary producers-dynamics; and to assess the impacts of estuarine primary producers on the nutrient budget of the system.

It becomes evident that one of the most striking needs of models for estuaries and other coastal areas is related to developing integrated coastal management tools for decision-makers and examining the outcomes of different scenarios, particularly, those related with different nutrient loads, fish farming, and sea-level rise.

As ecologists are increasingly challenged to anticipate ecosystem change and emerging vulnerabilities (e.g., Clark 2005), reliable forecasts of the ecosystem state and services, and the natural capital are urgently required (Clark et al. 2001). This can be achieved with the availability of new data sets, the progress in computation and statistics and an engagement of scientists and decision-makers (Clark et al. 2001).

Ecosystem modeling seems to be the most suitable methodology to achieve the urgently required Ecosystem-Based Management approach, as it will contribute to give insights about ecological interactions within the ecosystem, to estimate the cumulative impacts of multiple activities operating at a given coastal system and to evaluate the susceptibility of the system to several stressors by means of scenario simulation (Nobre et al. 2010).

In spite of all the advances achieved in ecological modeling during the past decades, which were mostly related to progress in computation coupled to acquisition of large data sets, models still entail the dilemma of simplicity versus complexity, where the tradeoffs are well known (Clark 2005). If simple models with high generalization of processes may fail to capture essential ecosystem features and engage situation-specific and scale-dependent effects (Levin 1992; Carpenter 1996; Skelly 2002), complicated models require large datasets for setup and validation (Nobre et al. 2005), frequently leading to overfitting (Clark 2005) and generating outputs that are difficult to synthesize and interpret. The model complexity and, consequently, its dimensional-ity are decided upon what will be treated deterministically, what is assumed to be stochastic, and what can be ignored (Clark 2005). Stochasticity is central...
Estuary Ecosystem Models

to the complexity dilemma, because it encompasses the elements that are uncertain and those that fluctuate due to factors that cannot be fully known or quantified (Clark 2005).

The ways or methodologies to overcome such dilemmas are still under discussion and few effective solutions have been presented. Among these options, there is the “Intermediate Approach,” which includes different models running at different scales integrated to optimize the trade-offs between simple and complex models (Ferreira et al. 2008; Nobre et al. 2010). Another approach to this issue is the new hierarchical Bayes structure, which is based on the Bayesian approach and describes sampling-based algorithms for analysis of complex systems (Clark 2005).

One aspect that also needs further attention in models of natural systems is the need to assess how uncertainties in each component of the models reflect uncertainty in the final predictions (Borsuk et al. 2004). Again, Bayesian parameter estimation seems to be a suitable methodology to quantify uncertainty in model predictions, besides expressing model outputs as probability distributions, which are suited for stakeholders and policy makers when making decisions for sustainable environmental management (Arhonditsis et al. 2007).

In general and not surprisingly, estuarine models give particular emphasis to nutrients and primary producers, especially, phytoplankton and opportunistic macroalgae. In contrast, seagrasses and particularly microphytobenthos have been somehow neglected when considering modeling approaches of estuaries. However, microphytobenthos can contribute significantly to the productivity of shallow mudflats (McIntyre and Cullen 1995), whereas salt marsh plants play important roles in stabilizing sediments (Elkalay et al. 2003) or acting as sinks of nutrients (Simas and Ferreira 2007). Thus, estuarine models could potentially improve and describe more accurately the whole-system dynamics, if they would include the processes affecting the different types of primary producers inhabiting estuaries. The idea is not original and has been presented in several papers that have modeled, for instance, the competition between opportunistic macroalgae (Ulva rigida) and rooted macrophytes (Z. marina) (Coffaro and Bocci 1997), several different functional groups of macroalgae (Biber et al. 2004) or C3 and C4 salt marsh plants (Simas et al. 2001). We suggest that models from estuaries should include, as state variables, all existing types of primary producers at a certain system and not just one or two, as is frequently the case.

Overall, it is possible to conclude that during the past decade, estuarine models have became increasingly more accurate, complete, and robust due to an increasing knowledge of the estuarine intervenients and the processes affecting them, the acquisition and handling of large datasets, and the progress on computational and statistical fields. From all of these, we can reliably affirm that ecosystem modeling of estuaries is already an indispensable tool for the present and the future management and preservation of these extremely important ecosystems.
References


Catarino, F. 1981. Papel das zonas húmidas do tipo sapal na descontaminação das água (in Portuguese). *Ciência* 1, 2 IV série.


Han, B. P. 2001b. A mechanistic model of algal photoinhibition induced by photodamage to photosystem-II. *Journal of Theoretical Biology* 214: 519–527.


Lumborg, U., T. J. Andersen, and M. Pejrup. 2006. The effect of *Hydrobia ulvae* and microphytobenthos on cohesive sediment dynamics on an intertidal mudflat
described by means of numerical modelling. *Estuarine, Coastal and Shelf Science* 68: 208–220.


