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10.02 Hydrology and Biota Interactions as Driving Forces for Ecosystem Functioning

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Abstract

This chapter examines the interactions between biologic and hydrologic processes in estuarine and nearshore coastal ecosystems, and their relevance to ecosystem functioning. The role of specific hydrologic variables and processes upon key functional groups of organisms (phytoplankton, heterotrophic bacteria, holozooplankton, merozooplankton, benthos, and nekton) is addressed considering both bottom-up and top-down effects. The impact of biologic processes on relevant hydrologic features, including dissolved gases, inorganic nutrients, organic matter, chemical and biological contaminants, turbidity, and water flow, is then evaluated. Biologic and hydrologic-driven changes are integrated, specifying how they reverberate into ecosystem functioning over different spatial and temporal scales.

10.02.1 Introduction

Aquatic ecosystems represent functional units embracing two basic components that interact within specific water bodies, biotic and abiotic components. The biotic component includes all organisms (biota) living in the water column or in association with the bottom, whereas the abiotic component comprises their nonliving environment and related geological, physical, chemical, and hydrodynamic dimensions. As most of these environmental dimensions are included under different fields of limnology or oceanography, interactions between

biota and hydrology (*sensu lato*) are evidently implicit in our definition of aquatic ecosystems. However, the strength and relevance of hydrology and biota interactions to ecosystem dynamics vary across and within ecosystems (Zalewski and Naiman, 1985; Levin et al., 2001; Kaiser et al., 2005; Mann and Lazier, 2006).

Estuaries, wetlands, and nearshore coasts are relatively small and shallow aquatic ecosystems, located at the interface between land and the ocean. They are, therefore, effectively controlled by multiple natural processes occurring on terrestrial, freshwater, oceanic, and atmospheric systems, at different

spatial and temporal scales (Mann, 2000; Wolanski et al., 2004; Gonenc and Wolfin, 2005; Bianchi, 2007; Wolanski, 2007). As approximately 60% of world's human population lives around coastal areas and connected watersheds, these ecosystems are also strongly affected by different anthropogenic influences (Alongi, 1998; see Chapter 8.01). Estuarine and coastal ecosystems are critical transition zones, which provide valuable goods and services, such as seafood, recreation opportunities, transformation and storage of organic matter and inorganic nutrients, and protection of the coast line (Levin et al., 2001). Despite their low aerial coverage (~2% of the ocean's volume), estuaries and coasts are among the most productive natural ecosystems on the Earth, being responsible for nearly 30% of total net aquatic production and 90% of the global fish catch (see Alongi, 1998; Wolanski, 2007).

Climate change and increased human pressures are eroding biodiversity and leading to a severe degradation of essential ecological functions and services provided by estuarine and coastal ecosystems. These growing problems have accelerated our efforts to manage and restore these critical transition zones (Levin et al., 2001; Lotze et al., 2006; Duarte et al., 2008; Waycott et al., 2009). Effective coastal management warrants a holistic, ecosystem-based approach. This approach undoubtedly requires a comprehensive understanding of ecosystem functioning and its driving forces, considering different temporal and spatial scales, different levels of ecosystem complexity (e.g., individual, population, and community levels), and all adjoining ecosystems (e.g., oceanic, freshwater, and terrestrial) and catchment basins (Wolanski et al., 2004; Cloern, 2007; Wolanski, 2007; Levin and Lubchenco, 2008).

Ecosystem dynamics, properties (e.g., resilience, robustness, and carrying capacity), ecological functions, and services depend on the structure and diversity of biological communities, and the fluxes of energy and materials occurring within and across nonliving and living ecosystem reservoirs (Levin et al., 2001; Bianchi, 2007; Levin and Lubchenco, 2008). All organisms require external sources of energy, chemical nutrient elements (e.g., C, N, P, and Fe), and electron acceptors (e.g., O_2 , NO_3^- , and SO_4^{2-}) for maintenance, growth, and reproduction. Primary producers use inorganic compounds (chemoautotrophs) or radiation (photoautotrophs) as energy sources, whereas consumers (heterotrophs) use organic compounds and are, therefore, stringently dependent on the activity of primary producers. Energy flow within aquatic ecosystems is continuous, unidirectional (from primary producers to consumers), and highly inefficient. Yet, this inefficiency, a consequence of thermodynamic constraints and physiological requirements, is rather crucial as it allows the recycling of chemical elements, namely essential nutrients and organic matter that usually are in short supply (Kaiser et al., 2005).

Primary producers in estuaries and coasts mostly use visible radiation as an energy source and include phytoplankton, microphytobenthos, macroalgae, and floating, emergent (e.g., marsh grasses and mangroves), and submerged (e.g., seagrasses) aquatic vegetation. The photosynthetic fixation of inorganic carbon and nutrients into their biomass constitutes the primary source of organic matter within these ecosystems. While a fraction of this fixed carbon enters the grazing pathways, being directly or indirectly grazed by benthic and pelagic herbivores and their predators, a significant proportion of fixed carbon enters the detrital pathways, in the form

of either dissolved or nonliving particulate matter (Duarte and Cebrián, 1996; Alongi, 1998; Mann, 2000; Kaiser et al., 2005). Autochthonous dissolved and particulate organic detritus are continuously produced *in situ* by biological processes associated with all living organisms, and physical-chemical processes. Autochthonous dissolved and particulate organic detritus, as well as allochthonous detritus derived from adjacent ecosystems, are converted into living biomass mostly by heterotrophic bacteria. Subsequently, heterotrophic bacteria are grazed by bacterivorous protists, and then channeled into larger protists or multicellular consumers (Mann, 2000; Kaiser et al., 2005; Bianchi, 2007; Wolanski, 2007; Sherr and Sherr, 2008). All functional groups referred (primary producers and microbial and metazoan consumers) have representatives in pelagic and benthic domains, and both domains are strongly coupled within estuaries and nearshore coastal areas. Aquatic microbes, embedded in an overall microbial food web, are specifically considered central players in ecosystem respiration, primary production, organic matter decomposition, and nutrient regeneration (Miller, 2004; Kaiser et al., 2005; Ducklow, 2008).

It is increasingly evident that biological processes in estuarine and nearshore ecosystems are strongly influenced by hydrological properties and processes occurring within the ecosystem and adjacent ecosystems and their catchment basins. Relevant determinants of biologic activity and ecosystem dynamics, namely temperature, light, and inorganic nutrients, are clearly under climatic and hydrologic control (Levin et al., 2001; Zalewski, 2002; Bianchi, 2007). Conversely, fundamental hydrological properties and processes, such as water quality and flow, are clearly under biologic control. Consequently, our efforts to understand ecosystem functioning and establish effective management practices should evidently consider the multiple feedbacks between hydrology and biota within estuarine, coastal ecosystems and connected watersheds. Ecohydrology assumes such holistic integrated approach, and uses physical and biological interventions, in tandem, to manage, remediate, and control the health of freshwater (Zalewski et al., 1997; Zalewski, 2000), as well as estuarine and coastal ecosystems (Chícharo et al., 2001; Wolanski et al., 2004; Wolanski, 2007).

The aims of this chapter are to examine the interactions between biologic and hydrologic processes in estuarine and nearshore coastal ecosystems, and to assess their relevance to ecosystem functioning. Our approach is mostly based on information derived from natural surface ecosystems, neglecting natural groundwaters, hyporheic zones, and modified or created ecosystems. We will first address the role of specific hydrologic variables and processes upon key functional groups of organisms, considering both bottom-up and top-down effects. Due to differences imposed by organism size, mobility, and ecological function, free-living microbes and metazoans will be presented separately, and planktonic life forms will be strongly highlighted. We will then examine the impacts exerted by biota on specific hydrologic features, emphasizing aspects related to water quality, turbidity, and water flow. To provide an integrated view of biota and hydrology interactions, we will explore how changes in specific biological and hydrological processes interact, and how they reverberate into ecosystem functioning over different spatial and temporal scales. This information will enable a comprehensive understanding of

the controls and functioning modes of estuarine and coastal ecosystem under natural conditions. It will also constitute a framework for ecohydrology studies aiming to actively shape biota–hydrology interactions for environmental management and restoration purposes.

10.02.2 Hydrologic Regulation of Microbes in Estuarine and Nearshore Coastal Ecosystems

Aquatic microbes include viruses and a wide diversity of unicellular organisms (e.g., archaea, bacteria, fungi, and auto-, mixo-, and heterotrophic protists), usually within the size range of 0.02–200 μm (Sherr and Sherr, 2008), which inhabit pelagic and benthic domains. Due to their small size, elevated growth rates, and restricted mobility, aquatic microbes are highly sensitive to environmental perturbations, namely hydrologic alterations, and are often used as sentinels for ecological condition and change (Paerl et al., 2005; Smetacek and Cloern, 2008). Aquatic microbes also play pivotal roles in a wide range of ecosystem functions (Ducklow, 2008); thus, any hydrologically induced alteration of microbial standing stocks or activity will probably reverberate into global ecosystem functioning. Aquatic microbes include two quite different functional groups, primary producers (e.g., phytoplankton, microphytobenthos, and photoheterotrophic and chemoautotrophic bacteria) and consumers (e.g., viruses, heterotrophic bacteria, and photoheterotrophic and phagotrophic protists), which rely on different external resources (Ducklow, 2008). This section will examine the hydrologic regulation of key representatives of each of these functional groups, taking into consideration both bottom-up and top-down influences. The former involve direct regulation of microbial growth rates by hydrologic properties (e.g., resources, temperature, and contaminants), whereas the latter embrace processes directly controlling microbial biomass (e.g., grazing, viral lyses, wash-out by advection, and sinking). Due to their fundamental

ecological roles, phytoplankton and heterotrophic bacterioplankton (Ducklow, 2008; Sherr and Sherr, 2008) will be specifically addressed.

10.02.2.1 Phytoplankton

Phytoplankton comprise a diverse assemblage of photosynthetic organisms (e.g., cyanobacteria, diatoms, chlorophytes, and dinoflagellates), which are quite variable in terms of cell size, morphology, motility, physiology, palatability, and toxic potential (Smayda, 1997; Miller, 2004) (see Chapter 6.03). Phytoplankton represent the dominant primary producers in most aquatic ecosystems. Their variability patterns and underlying driving forces in estuarine and coastal ecosystems have been extensively analyzed (see reviews by Boynton et al., 1982; Knox, 1986; Knoppers, 1994; Cloern, 1996; Underwood and Kromkamp, 1999; Knox, 2001; Cloern and Dufford, 2005). Overall, phytoplankton distribution patterns reflect the interplay between phytoplankton growth rates and loss rates (see Figure 1), and can therefore be associated to multiple natural and anthropogenic processes (Cloern, 1996, 2001). However, to simplify the analysis of the hydrologic regulation of phytoplankton, we will consider, in turn, how specific hydrologic variables or processes affect phytoplankton growth rates (bottom-up control) and loss rates (top-down control).

10.02.2.1.1 Hydrologic control of phytoplankton resources and growth rates

Phytoplankton growth rates are modulated by a wide diversity of physical–chemical variables (Figure 1), including resources (e.g., nutrients, light, and carbon dioxide) and nonresources (e.g., temperature, bioactive compounds, and turbulence). Yet, two hydrological variables, dissolved inorganic macronutrients and underwater radiation, are currently considered central drivers of phytoplankton growth rates in estuarine and nearshore coastal ecosystems (see Cloern, 1996). The relationship between phytoplankton growth rate and the concentration of

Figure 1 Schematic representation of the environmental variables and processes influencing phytoplankton growth rates and loss rates in estuarine and nearshore coastal ecosystems. Black box outlines or arrows indicate growth determinants, and blue box outlines or arrows represent loss determinants. Phytoplankton growth and loss determinants affected by hydrologic features are underlined.

specific resources is usually described as a hyperbolic function, with clear saturation kinetics. In case of light, however, a photoinhibition phase occurs at high light intensities. These functional responses are obviously taxa specific; diatoms, for instance, are clearly adapted to higher resource levels than picoplanktonic cyanobacteria (see review Barbosa, 2009).

A comprehensive understanding of linkages between hydrology and phytoplankton growth rates in coastal ecosystems requires a previous evaluation of interactions between hydrology and phytoplankton resources. In estuaries and coastal areas, nutrient concentrations typically increase from lower to upper estuarine reaches, and from surface to deeper water levels (see Wolanski et al., 2004; Wolanski, 2007). Hence, climatic and hydrodynamic processes enhancing horizontal advection of freshwater (e.g., river discharge, runoff, and submarine groundwater discharge) and vertical mixing and advection of deeper water masses, including sediment pore water (e.g., tidal forcing, wind-driven mixing, convective mixing, internal waves, and coastal upwelling), are typically associated to nutrient enrichment (Wolanski, 2007; see Chapter 4.01).

Climate and hydrodynamics are relevant drivers of underwater photosynthetic available radiation (PAR), as well. As phytoplankton cells are being continuously mixed throughout the mixed layer, mean PAR intensity in the mixed layer (I_m) is generally used as a proxy for light availability. I_m is directly proportional to surface incident irradiance, and inversely proportional to mixed-layer depth and underwater light attenuation (Kirk, 1986). Incident irradiance is regulated by climate and latitude. Mixed-layer depth depends on the balance between buoyancy forces (solar heating and freshwater runoff) and mechanical energy inputs (wind, tidal forcing, and also freshwater runoff), and is further constrained by basin morphology, namely by depth (Cloern, 1987; Underwood and Kromkamp, 1999; May et al., 2003). Underwater light attenuation depends on the absorbance and scattering of light by water, photosynthetic organisms, nonliving particulate matter, and colored dissolved organic matter. Contrary to open ocean waters, light attenuation in estuarine and nearshore coastal ecosystems is primarily a function of suspended sediment concentration (Cloern, 1987). Then, climatic and hydrodynamic processes leading to increased import of terrestrial-derived suspended matter (river discharge and runoff), vertical mixing, and sediment resuspension (e.g., tidal forcing and wind speed and fetch) usually result in decreases in light availability (May et al., 2003).

Generally, both nutrients and light are clearly under strong climatic and hydrodynamic control. As a result, interactions between phytoplankton growth, nutrients, and light inherently imply linkages between phytoplankton, hydrodynamics, and climate. It is worth noting that climate changes can easily impact on estuaries and nearshore coastal areas due to their relatively small size and shallowness (Cloern et al., 2005; Paerl et al., 2006; Lloret et al., 2008; Smetacek and Cloern, 2008). The relevance of interactions between phytoplankton growth, nutrients, and light in estuarine and coastal ecosystems is unequivocal, and may be studied using phytoplankton distribution patterns over different spatial and temporal scales.

Cross-system comparisons of estuarine and coastal ecosystems usually reveal positive relationships between phytoplankton biomass or production and nutrient concentration or loading

Figure 2 Cross-system comparisons of phytoplankton and their key resources, dissolved inorganic nutrients and light, in estuarine and near-shore coastal ecosystems: (a) relationship between annual phytoplankton primary production and annual nitrogen loading for shallow coastal ecosystems and (b) relationship between annual phytoplankton primary production and mean photic depth in selected estuarine ecosystems. Note that close associations between phytoplankton, nutrients, and light generally imply strong interactions between phytoplankton, climate, and hydrologic processes (see text). From Figure 1, Cloern, J.E., 1999. The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment. *Aquatic Ecology* 33, 3–16.

(see Figure 2(a) see reviews by Boynton et al., 1982; Nixon, 1982; Monbet, 1992; Cloern, 2001). These relationships are usually interpreted as evidence for bottom-up control of phytoplankton by nutrient availability. However, large deviations around these empirical functions do occur, namely for nutrient-rich coastal ecosystems (Figure 2(a)). Phytoplankton growth rates within these systems are largely light limited. Hence, light availability appears to be an equally good predictor of phytoplankton production as nutrient loading in turbid estuarine ecosystems (see Figure 2(b); Cloern, 1987, 1999, 2001).

Strong linkages between phytoplankton growth, inorganic nutrients, light, and hydrology are also referred for specific ecosystems, over different spatial and temporal scales. Episodic phytoplankton blooms after major climatologic and hydrologic perturbations (river floods, storms, heat waves, rainfall, and upwelling events) have been associated to the enhancement of phytoplankton growth by intermittent injections of nutrients, transient increases in light availability, and direct atmospheric inputs (Rudek et al., 1991; Mallin, 1994; Cloern, 1996; Cloern et al., 2005; Paerl et al., 2005; Wetz and Paerl, 2008a; Guadayol et al., 2009; Barbosa, 2010). In meso- and macrotidal ecosystems, periodic (diurnal and fortnightly)

changes in phytoplankton biomass, growth, and production are usually coupled to tidal forcing (Demers et al., 1986). This phenomenon does not directly control phytoplankton but, instead, modulates key limiting proximal agents (e.g., light and nutrients). Thus, its effects vary across and within ecosystems, namely in the case of fortnightly neap–spring tidal cycle (Ragueneau et al., 1996). During neap tides, the relaxation in tidal energy leads to enhanced stratification, whereas during spring tides higher tidal stirring leads to increased vertical mixing and resuspension of sediments. Phytoplankton biomass in nutrient-limited ecosystems is usually enhanced during spring tide periods due to increased nutrient availability. Conversely, in turbid coastal ecosystems, phytoplankton growth rates are frequently light limited, and neap tides usually lead to increased phytoplankton growth and biomass (Cloern, 1996; Ragueneau et al., 1996; but see next section).

Phytoplankton annual variability patterns in estuaries and coastal areas also provide opportunities to examine the interactions between hydrology and phytoplankton growth rates. Seasonally varying solar heating and thermal stratification of the water column are considered key drivers of phytoplankton annual cycles in temperate exposed ecosystems, typically leading to bimodal cycles with spring and autumn blooms. During late autumn–winter, intense vertical mixing is usually associated to light-limited phytoplankton growth, whereas increased stratification during summer blocks the injection of nutrients from deep waters, leading to nutrient-limited growth. Phytoplankton spring blooms are related to the shallowing of the mixed layer and concurrent increase in light availability, and autumn blooms are related to the effect of thermocline erosion on nutrient availability (Cebrián and Valiela, 1999; Miller, 2004). Increased phytoplankton grazing and sinking losses, namely in case of dense and nonmotile taxa (e.g., diatoms), may further explain phytoplankton collapse during summer (Cloern, 1996; Miller, 2004; see next section).

This classic bimodal annual cycle is not necessarily the norm for estuarine and nearshore ecosystems. Recent reviews by Cloern and Jassby (2008, 2010) revealed a wide spectrum of phytoplankton seasonal patterns across and within estuaries and nearshore waters, reflecting the complexity of terrestrial, atmospheric, and oceanic influences acting at the land–sea interface. Phytoplankton seasonality within these ecosystems is impacted by periodic and aperiodic oceanic processes (e.g., coastal upwelling and tidal forcing), and the effects of river discharge (e.g., water turbidity, nutrient concentrations, water-column stratification, and water residence times; Cloern and Jassby, 2008). Freshwater runoff, for instance, can have quite contrasting effects on phytoplankton annual patterns. At low to medium river discharge rates, increased buoyancy and saline stratification may lead to an earlier onset of phytoplankton productive season. Yet, high river discharge rates may effectively delay the timing of phytoplankton blooms, due to increased flushing of phytoplankton vegetative cells and resting stages into adjacent coastal waters, and displace the location of peak phytoplankton biomass into lower estuarine regions (Therriault and Levasseur, 1985; Cloern, 1996; Sin et al., 1999; Borsuk et al., 2004).

Shallow coastal ecosystems usually receive high nutrient inputs from anthropogenic sources, particularly in intensively urbanized water basins. Additionally, the strong benthic–pelagic coupling also implies significant nutrient fluxes from

the sediments into the water column. High nutrient loading frequently minimizes the occurrence and intensity of nutrient-limited growth, namely during summer. As a result, shallow nutrient-rich ecosystems, such as mixed estuaries and coastal lagoons, usually exhibit a unimodal annual cycle with summer maxima. This pattern is usually interpreted as evidence for light and/or temperature growth regulation (Valiela, 1995; Cebrián and Valiela, 1999; Barbosa, 2010). Indeed, both specific phytoplankton production, a proxy for phytoplankton growth, and phytoplankton blooms are controlled primarily by light availability in turbid, nutrient-rich, temperate ecosystems (Cloern, 1987; May et al., 2003).

Due to strong spatial heterogeneity, phytoplankton seasonal patterns and hydrologic driving forces frequently vary within specific ecosystems. Phytoplankton annual patterns in the partially stratified York River Estuary (NE USA), for example, show unimodal cycles in upper estuarine reaches (sustained light limitation), and bimodal cycles (alternation between light and nutrient limitation) at lower estuarine locations (Sin et al., 1999). Likewise, phytoplankton in the mesotidal Ria Formosa coastal lagoon (SE Portugal) consistently depict unimodal cycles at inner and shallower locations, indicating a more persistent light or temperature control. Yet, at lagoon inlets, phytoplankton present less regular bimodal annual cycles, reflecting increased nutrient limitation during summer and the effects of irregular nutrient enrichment by upwelling events occurring at the adjacent coastal area (see Figure 3; Barbosa, 2010).

Further evidence for the hydrologic regulation of phytoplankton growth in estuarine and coastal ecosystems is provided by phytoplankton interannual trends. Long-term trends in phytoplankton biomass, composition, and phenology have been recently connected to climate-driven hydrologic changes, and anthropogenically induced alterations of hydrological variables (Borkman et al., 2009; Barbosa, 2010). In estuaries, phytoplankton interannual patterns are frequently related to river flow variability. Due to direct relationships between annual river flow and nutrient concentrations, phytoplankton biomass in stratified nutrient-limited estuaries is usually positively related to annual river flow (Malone et al., 1988; Mallin et al., 1993; Harding, 1994; Adolf et al., 2006; Lohrenz et al., 2008). Conversely, phytoplankton in mixed, turbid estuaries typically is inversely related to river flow, due to increased turbidity or higher phytoplankton flushing at higher river discharge rates (Mallin et al., 1999; Howarth et al., 2000; Jassby et al., 2002; Borsuk et al., 2004; Paerl et al., 2006; Valdes-Weaver et al., 2006; Murrell et al., 2007). These interannual patterns clearly reveal the relevance of hydrologic variables (nutrients and light) and processes (river flow) as natural drivers of phytoplankton growth in estuarine ecosystems.

In some ecosystems, light was also reported as a prevalent driver of phytoplankton interannual trends though its variability was not strictly related to river flow, but instead, to climate-driven changes in coastal circulation and water transparency (McQuatters-Gollop et al., 2007), and anthropogenic activities. Anthropogenic-driven light changes are related to different activities, including dredging (Facca et al., 2002) and hydraulic manipulations, which increase the retention of suspended sediments behind dams (Wetsteyn and Kromkamp, 1994; Jassby et al., 2002; Jiao et al., 2007). In the Guadiana Estuary, the Alqueva dam construction period, with

Figure 3 (a) Aerial view of the Ria Formosa, a mesotidal coastal lagoon (SE Portugal), with location of sampling stations. Blue circles comprise stations located at lagoon inlets, and red circles represent stations located in navigational channels. (b) Box and whisker plot showing the annual distribution of chlorophyll *a* concentration, a proxy for phytoplankton biomass, within different water bodies of the Ria Formosa, binned into months, for the period 1967–2008. Blue boxes represent lagoon inlets ($n=299$), and red boxes depict lagoon channels ($n=915$). Median value is represented by the line within the box, 25–75th percentiles are denoted by box edges, and 5–90th percentiles are depicted by the error bars. See Table I in [Barbosa \(2010\)](#) for data sources.

intense land excavation and soil reworking, was associated to increased turbidity (even at low river discharge rates). This alteration was connected to a marked decline in phytoplankton biomass, particularly at the start and end of the phytoplankton growing period. However, further phytoplankton decreases after dam filling, with parallel reductions in turbidity and nutrient concentrations, suggest that phytoplankton regulation may shift from light limitation to a more nutrient-limited mode in the near future (see [Figure 4](#); see [Barbosa, 2010](#)).

Phytoplankton interannual trends in coastal ecosystems undergoing anthropogenic eutrophication or its reversal also illustrate the relevance of hydrologic variables and processes. The general increase in human population densities within catchment basins leads to increases in nutrient loads, and concurrent reductions in relative silica availability. These changes, sometimes exacerbated by artificial hydraulic retention by dams ([Humborg et al., 1997, 2008](#)), have been associated to increases in phytoplankton biomass and production, and relative reductions of siliceous phytoplankton in favor of flagellates ([Cloern, 2001](#); [Paerl et al., 2006](#); [Danielsson et al., 2008](#)). In some cases, the implementation of nutrient reduction practices already alleviated, or even reversed, the

Figure 4 Time series of mean monthly values of physical, chemical, and biological variables at the Guadiana upper estuary (SE Portugal), a mesotidal system under Mediterranean climate, for the period 1996–2005; (a) mean monthly Guadiana River flow ($\text{m}^3 \text{s}^{-1}$), and concentration of dissolved inorganic nitrate, NO_3^- (μM) and (b) light intensity in the mixed layer, I_m ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), and chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), a proxy for phytoplankton biomass. Horizontal boxes mark two phases of the Alqueva dam construction, the building period with extensive land excavation, and the filling period. Data derived from [Barbosa, A.B., Domingues, R.B., Galvão, H.M., 2010. Environmental forcing of phytoplankton in a Mediterranean estuary \(Guadiana Estuary, southwestern Iberia\): a decadal of anthropogenic and climatic influences. Estuaries and Coasts 33, 324–341.](#)

symptoms of anthropogenic eutrophication ([Cloern, 2001](#); [Paerl et al., 2006](#); [Carstensen et al., 2007](#)). These ecosystem responses clearly show the relevance of nutrients as drivers of phytoplankton long-term variability, namely on ecosystems sensitive to nutrient enrichment. Yet, some estuarine and coastal ecosystems are quite resistant to nutrient enrichment due to a series of system-specific properties, which include biological and hydrodynamic attributes (e.g., tidal forcing and river flow advection). Turbid coastal ecosystems with low water residence times are particularly resistant to anthropogenic eutrophication ([Cloern, 2001](#)).

In addition to light and nutrients, phytoplankton growth rates are also regulated by other hydrologic variables (e.g., temperature, turbulence, salinity, oxygen, dissolved inorganic carbon, toxic compounds, and ultraviolet radiation) that are, in turn, controlled by climatic and hydrodynamic processes. Different phytoplankton species usually exhibit different tolerance ranges ([Underwood and Kromkamp, 1999](#); [Miller, 2006](#)). With regard to salinity, for example, filamentous cyanobacteria, euglenids, and green algae are particularly well adapted to low salinity, whereas dinoflagellates and coccolithophorids are more adapted to high salinities. Concerning turbulence, dinoflagellates are noticeably more sensitive to

turbulent shear stress than diatoms, but mixing-drift-adapted dinoflagellates clearly tolerate pronounced vertical mixing and shear stress (Smayda, 2002). For toxic compounds, namely cadmium and copper, cyanobacteria are noticeably more sensitive than eukaryotic phytoplankton (e.g., Sherr et al., 2005).

Temperature regulates most physical and biological processes and is, therefore, a key hydrologic variable. In the Urdaibai estuary (NW Spain), for example, interannual changes in temperature were recently related to increased phytoplankton biomass, probably due to a direct stimulation of phytoplankton growth (Villate et al., 2008). However, beyond its direct effect, temperature has also indirect impacts on phytoplankton, mostly through its effects on nutrient regeneration rates, water-column stratification, and grazers' activity (Cloern, 1996; Sin et al., 1999). Thus, any particular change in temperature may be associated to different, eventually contrasting, phytoplankton responses (see next section).

10.02.2.1.2 Hydrologic control of phytoplankton loss rates

Phytoplankton dynamics was traditionally viewed as a result of resource-driven, bottom-up regulation, factored by light and nutrient availability. However, the discovery of small-sized phytoplankton cells, phagotrophic protists, and planktonic viruses visibly raised our awareness of the importance of phytoplankton loss in aquatic ecosystems (see Barbosa, 2009). It is well known, although frequently overlooked, that a phytoplankton bloom can arise from either an increase in phytoplankton growth rates or a decrease in loss rates, or both (Cloern, 1996; Smayda, 2008). Phytoplankton loss rates comprise biological processes (grazing, viral- and eukaryotic-mediated lyses, programmed cell death, and cell aggregation) as well physically driven processes (sinking, wash-out by advection, and aggregation into near-bed fluff layers; Bidle and Falkowski, 2004; Cloern and Dufford, 2005; Jones et al., 2009). Loss processes are key determinants of phytoplankton dynamics, but they are also fundamental for global ecosystem functioning (Kirchman, 2000a; Cloern and Dufford, 2005). In order to explore the relevance of hydrologic features to phytoplankton loss rates, it is convenient to separate biologically and physically controlled phytoplankton loss processes.

Hydrodynamic processes (e.g., tidal forcing, wind mixing, and river discharge) and circulation patterns regulate vertical and horizontal advection of water masses and associated planktonic organisms, namely those with reduced mobility such as phytoplankton. In estuaries, phytoplankton cells are longitudinally advected, by river-driven transport, from upper- to lower estuarine locations, being eventually exported into adjacent coastal ecosystems. Advective phytoplankton washout losses are more pronounced within ecosystems (Knoppers, 1994) or periods (events, seasons, and years) of low hydraulic residence times (high flushing times). This fact is well illustrated by phytoplankton changes associated to events of increased (e.g., river floods and hurricanes) or decreased residence time (closure of bar-built estuaries; see review Cloern and Jassby, 2008). On a longer timescale, years of increased river flow are usually related to delays in the seasonal development of estuarine phytoplankton (Pinckney et al., 1998; Mallin et al., 1999; Sin et al., 1999; Lionard et al., 2008), and reductions in phytoplankton biomass due to increased phytoplankton advection (but see Sin et al., 1999; Jassby, 2008).

Tidal forcing induces substantial horizontal and vertical mixing, as well as the upstream and downstream displacement of phytoplankton along estuarine axis. Tidally induced mixing and advection contribute to phytoplankton washout losses, but exchanges across interconnected habitats or ecosystems should evidently be taken into consideration. Lateral transport of phytoplankton from shallow-water, donor habitats (e.g., lateral shoals) commonly subsidizes deeper, recipient habitats (Lucas et al., 1999; Lopez et al., 2006; Cloern, 2007), and may be used to explain high phytoplankton production under stringent light conditions (Cole et al., 1992; Stoetaert et al., 1994). Overall, high flushing rates are used as an explanation for ecosystem resistance to eutrophication (Cloern, 2001; Barbosa, 2010), and weak flushing has been referred to as a condition favoring harmful algal blooms (HABs) (Cloern, 2001; Yamamoto et al., 2002). However, the relationship between phytoplankton biomass and flushing time varies within and across ecosystems because it reflects the global phytoplankton growth–loss balance (see Lucas et al., 2009).

Oceanic waters are also a source of phytoplankton biomass to estuaries and nearshore coastal ecosystems, under specific oceanographic conditions. Upwelling events may provide coastal-produced phytoplankton biomass to adjacent estuaries and coastal lagoons (Cermeno et al., 2006; Banas et al., 2007), and dinoflagellates within offshore frontal zones (pelagic seed banks) may be advected onshore, seeding nearshore blooms (Smayda, 2002). Furthermore, oceanic processes can also affect adjacent estuarine ecosystems, indirectly. Alterations in the water circulation and flushing inside the Rias Baixas (NW Spain) over the last decades, caused by a reduction in coastal upwelling intensity, were recently considered responsible for increased recurrence of harmful dinoflagellate blooms, and dramatic effects on mussel raft cultivation (Álvarez-Salgado et al., 2008).

Phytoplankton sinking away from the euphotic zone constitutes a relevant loss mostly for nonmotile, nonbuoyant, large, and mineralized phytoplankton cells or life-stages (but see Kahl et al., 2008). Water-column stability, dependent on tidal- and wind-driven mixing and thermal and saline stratification, is a key modulator of phytoplankton sinking rates. Phytoplankton sinking losses are usually considered negligible in shallow, mixed estuaries, and more pronounced in stratified estuarine and coastal ecosystems. Under stratified conditions, increased deposition of phytoplankton biomass sometimes leads to bottom hypoxia or anoxia events (Cloern, 2001). Turbulence and hydrodynamic conditions also regulate phytoplankton aggregation into near-bed fluff layers (Jones et al., 2009), the resuspension of microphytobenthos (see Underwood and Kromkamp, 1999), and the recruitment of phytoplankton resting stages from sediments into the water column (Rengefors et al., 2004).

As physically driven loss processes, biological processes leading to phytoplankton mortality (e.g., grazing, lyses, programmed cell death, and aggregation) are also affected by hydrologic features. Programmed cell death and aggregation are usually induced by environmental stresses (e.g., nutrient and light deprivation, and ultraviolet radiation; Bidle and Falkowski, 2004; Kahl et al., 2008), which are visibly linked to climatic and hydrologic processes (see previous section). Viruses, by far the most abundant biological entities in aquatic ecosystems, are sensitive to ultraviolet radiation, temperature,

and organic and inorganic suspended particles (see reviews Wilhelm and Matteson, 2008; Weinbauer et al., 2009). Hence, both climatic (surface heating and irradiance) and hydrodynamic processes (vertical mixing, light attenuation, sediment resuspension, and river flow) should be considered potential determinants of phytoplankton viral lyses. Moreover, environmental conditions promoting high density of host cells and intensified turbulence will increase the contact rates between viruses and specific host cells, enhancing viral-induced lyses (see Wilhelm and Matteson, 2008).

Grazing by pelagic and benthic herbivores is currently considered a major mortality source for phytoplankton. Phytoplankton grazing was classically attributable to multicellular organisms, such as copepods (Underwood and Kromkamp, 1999; Knox, 2001). Yet, we now recognize that microzooplankton are the main herbivores consuming, on average, 60% of phytoplankton daily production in estuarine and coastal ecosystems (see Calbet and Landry, 2004). Microzooplankton are dominated by phagotrophic protists, such as aplastidic nanoflagellates, ciliates, and heterotrophic dinoflagellates, and impact a wide range of phytoplankton cell sizes (Sherr and Sherr, 2007; Calbet, 2008; Montagnes et al., 2008a). Due to their shallowness, estuarine and nearshore coastal ecosystems are often characterized by intense benthic–pelagic coupling. Consequently, phytoplankton grazing by benthic suspension feeders is also a relevant driver of phytoplankton annual and interannual variability (Cloern, 1996; Petersen, 2004; Caraco et al., 2006; Mohlenberg et al., 2007; Strayer et al., 2008).

Grazing rates of metazoan herbivores (see Section 10.02.3) and phagotrophic protists are regulated by their internal environment (e.g., feeding ultrastructures, mechanoreception and chemoreception capacities, physiological state, and feeding history), and the external environment. The external environment includes variables dependent on the availability and characteristics of prey (e.g., abundance, size, mobility, biochemical composition, physiological state, surface characteristics, and grazing resistance properties) and variables independent of prey. Among the latter, temperature, salinity, light, ultraviolet radiation, nutrient concentrations, turbulence, suspended nongrazable particles, and toxic compounds can regulate feeding activity (see Montagnes et al., 2008a and references therein). Most of these external variables are clearly under strong climate and hydrologic control (see previous section).

Phytoplankton interannual trends in estuarine and coastal ecosystems can be used to illustrate the effects of local- and global-hydrologic processes on phytoplankton grazing. Long-term temperature increases were recently hypothesized to cause reductions in phytoplankton biomass and bloom intensity in estuarine and coastal ecosystems through an indirect temperature-mediated stimulation of their metazoan grazers (Oviatt, 2004; Wiltshire et al., 2008; Borkman and Smayda, 2009; van Beusekom et al., 2009; Barbosa, 2010). River flow changes have been shown to influence phytoplankton grazing rates indirectly through their propagation along trophic cascades. In tributaries of the Chesapeake Bay (NE USA), during high-river-flow years, increased grazing control of microzooplankton (grazers) by copepods alleviated top-down control of phytoplankton. Thus, reduced microzooplankton grazing on phytoplankton, and not only increased nutrient availability, can potentially explain increases in

phytoplankton biomass during high-river-flow periods (Reaugh et al., 2007).

Far-field global climatic and oceanic processes may also affect phytoplankton grazing rates in estuarine ecosystems. Indeed, interdecadal upwelling regime changes were recently linked to increased phytoplankton biomass in San Francisco Bay (SW USA), through trophic cascades. In this case, increased upwelling intensity promoted the transport of bivalve predators into the bay, subsequently leading to the suppression of their control on phytoplankton (see Cloern et al., 2007).

Phytoplankton annual and interannual variability in San Francisco Bay clearly illustrates the relevance of benthic predators as phytoplankton mortality sources (see Cloern, 1996). The grazing impact of benthic suspension feeders on phytoplankton is jointly controlled by ecosystem bathymetry, predator's filtration rates, and overlying hydrodynamics (e.g., wind- and tidally driven vertical mixing; Jones et al., 2009). Benthic grazing on phytoplankton is usually enhanced during periods of increased vertical mixing, such as summer- and spring-tide periods (Cloern, 1996; Lucas et al., 1999; Thompson et al., 2008a). Increased benthic grazing (and tidal advective losses) may explain, to some extent, why spring tides usually promote low net phytoplankton growth rates (Cloern, 1996; Barbosa, 2006), and why macrotidal estuaries usually have lower mean annual phytoplankton biomass than microtidal estuaries for a given mean nutrient input (Monbet, 1992).

10.02.2.1.3 Hydrologic control of phytoplankton composition

On the whole, species-specific physiological tolerances, resource uptake strategies, key ecophysiological attributes (e.g., mobility, intracellular nutrient storage, nitrogen fixation, mixotrophy, grazing resistance, resting stages, and allelopathic compounds), and loss processes determine where and when particular phytoplankton groups flourish or fail (see review Barbosa, 2009). Therefore, climate- and hydrodynamic-driven environmental changes in estuaries and coastal systems affect not only phytoplankton biomass, growth, production, and loss, but also phytoplankton composition.

Spatial changes in phytoplankton composition along the longitudinal axis of estuaries, and across frontal systems (upwelling, tidal, river-, and estuarine plume fronts) clearly illustrate how changes in hydrodynamic forcing affect phytoplankton composition (Rocha et al., 2002; Mann and Lazier, 2006). Moreover, short-term changes in phytoplankton composition associated to upwelling/downwelling cycles (Nogueira and Figueiras, 2005; Sherr et al., 2005; Mann and Lazier, 2006) or river-driven nutrient pulses (Spatharis et al., 2007), annual changes associated to phytoplankton succession (Levasseur et al., 1984; Harris, 1986; Barbosa, 2010), and interannual changes associated to river-flow variability (Pinckney et al., 1998; Paerl et al., 2005, 2006; Barbosa, 2010) further demonstrate the relevance of climatic and hydrodynamic processes as drivers of phytoplankton composition in estuarine and coastal ecosystems. In general, environmental conditions (episodes, seasons, or years) of reduced river discharge rates, low nutrient loading (e.g., N and Si) and N:P and Si:N molar ratios, increased stratification and water temperature, and long residence times usually favor buoyant or motile species, such as cyanobacteria and dinoflagellates, in contrast to fast-growing diatoms and

green algae (Paerl et al., 2005; Barbosa, 2010). Forecasted climate warming may eventually promote specific phytoplankton groups, such as cyanobacteria and dinoflagellates (Johnk et al., 2008; Thompson et al., 2008b).

Climatically and hydrologically induced alterations in phytoplankton growth, biomass, and composition, occurring at different timescales, are propagated to higher trophic levels, affecting trophodynamics, nutrient cycling processes, and global ecosystem functioning (Mallin, 1994; Cloern, 1996; Edwards and Richardson, 2004; Cloern and Dufford, 2005; Paerl et al., 2005; Álvarez-Salgado et al., 2008; Nixon et al., 2009).

10.02.2.2 Heterotrophic Bacterioplankton

Heterotrophic bacteria (*sensu lato*) comprise a wide diversity of representatives of archaea and bacteria, inhabiting aerobic and anaerobic, and pelagic and benthic domains (Kirchman, 2008). Heterotrophic bacterioplankton are the most abundant organisms in aquatic ecosystems, and play key roles in biogeochemical cycles of aquatic ecosystems including the assimilation of dissolved organic matter (DOM) and its transformation into bacterial biomass and inorganic nutrients, and the solubilization of particulate organic detritus (Fenchel et al., 1998; Kaiser et al., 2005; Sherr and Sherr, 2008). Heterotrophic bacteria are a relevant biomass source to phagotrophic protists (Jurgens and Massana, 2008), and may constitute a relevant energy link to metazoans under conditions of depressed primary production (Legendre and Rassoulzadegan, 1995; David et al., 2006) or when dominant primary producers are not directly consumed by herbivores (e.g., macrophyte dominated ecosystems, Duarte and Cebrián, 1996; Alongi, 1998; Kaiser et al., 2005; Wolanski, 2007).

Distribution patterns of heterotrophic bacterioplankton and underlying environmental drivers were assessed by a series of reviews, which emphasized oceanic (see Church, 2008) and estuarine and nearshore coastal ecosystems (Ducklow and Shiah, 1993). Dynamics of heterotrophic bacteria mostly reflect the interactions between bacteria growth rates and loss rates and, for the sake of simplicity, we will consider, in turn, how specific hydrologic variables or processes affect bacterial growth rates (bottom-up control) and loss rates (top-down control).

10.02.2.2.1 Hydrologic control of bacterial resources and growth rates

Growth rates of heterotrophic bacterioplankton are modulated by a wide diversity of physical-chemical variables, including resources (e.g., dissolved, colloidal, and particulate organic matter, and dissolved inorganic nutrients) and nonresources (e.g., temperature, salinity, non-nutrient bioactive compounds, turbulence, and ultraviolet radiation). Yet, the availability of organic substrates, namely DOM, and temperature are currently considered key drivers of bacterial growth rates and single-cell activity in a wide variety of aquatic ecosystems (see del Giorgio and Gasol, 2008; Hitchcock et al., 2010). When the quality and stoichiometry of organic matter are not suitable to the elemental and biochemical composition of bacterial cells, dissolved inorganic macro- and micronutrients (e.g., Fe and Zn) also exert control on bacterial growth rates (Kirchman, 2000b; Church, 2008). In benthic habitats, the availability of

oxygen acceptors further controls the activity, efficiency, and metabolic pathways (e.g., aerobic respiration, fermentation, and anaerobic respiration) of the assemblages of heterotrophic bacteria (Fenchel et al., 1998; Bianchi, 2007).

In order to explore the linkages between hydrology and bacterial growth rates in estuarine and coastal ecosystems, we will first address the interactions between hydrology and bacterial resources. Dissolved and particulate organic substrates (detritus) are continuously being produced *in situ*, by all benthic and pelagic organisms, through a variety of biological processes, such as extracellular release by primary producers, grazer-mediated processes (excretion, egestion, and sloppy feeding), molting, abandoned larvacean mucous houses, programmed cell death, parasite-induced cell lyses, production of mucous polymers, and particle solubilization via exoenzymatic activity. Physically and chemically mediated processes, such as fragmentation of aquatic macrophytes, photochemical transformation, flocculation, and sinking of phytoplankton away from the euphotic zone, are also autochthonous sources of organic substrates for heterotrophic bacteria (Nagata, 2000; Carlson, 2002; Bertilsson and Jones, 2003). Estuarine and nearshore coastal ecosystems also receive allochthonous DOM and particulate organic matter through terrestrial runoff, riverine inputs, lateral transfer, groundwater inputs, and atmospheric deposition. Allochthonous inputs of organic matter are produced within adjacent ecosystems and watersheds, and include terrestrial plant detritus, freshwater plankton, and industrial and agricultural anthropogenic inputs (Cawet, 2002; Aitkenhead-Petersen et al., 2003; Bianchi, 2007). Shallow and intertidal coastal ecosystems, where primary producers are dominated by macrophytes, may constitute relevant organic matter subsidies to adjacent coastal ecosystems (Duarte and Cebrián, 1996; Alongi, 1998; Mann, 2000; Duarte et al., 2005).

Overall, DOM in estuarine and coastal ecosystems consists of a diverse collection of autochthonous and allochthonous molecules, with variable reactivity and biological availability (Carlson, 2002). Terrestrial allochthonous sources of organic matter (e.g., humic compounds) are commonly classified as highly refractory, some autochthonous sources are considered refractory (e.g., halophytic vascular plants), and DOM produced autochthonously through plankton production is usually considered the most bioavailable fraction of the DOM pool (Alongi, 1998; Mann, 2000; Kaiser et al., 2005; Bianchi, 2007). Primary production represents the direct source of autochthonously produced organic matter in any ecosystem; hence, the availability of organic substrates for heterotrophic bacteria is ultimately constrained, directly or indirectly, by the magnitude of primary production rates (Nagata, 2000). Indeed, the concentration of DOM in coastal and open ocean waters is generally positively correlated to phytoplankton biomass. However, this coupling is not always apparent in estuarine systems due to the existence of multiple primary producers, including microphytobenthos and macrophytes, and to allochthonous inputs of organic matter from hydrologically connected ecosystems (see Bianchi, 2007).

Vertical distribution of organic matter in aquatic ecosystems usually parallels biological activity, decreasing from surface to deeper layers (e.g., Barbosa et al., 2001). In estuaries, DOM and particulate organic matter typically increase from lower to upper estuarine reaches (Cawet, 2002; Mulholland, 2003; Jaffé et al., 2004), but estuarine turbidity maximum zones clearly

show increased detrital concentrations due to enhanced flocculation and retention processes (Wolanski et al., 2004; Wolanski, 2007). Sediments may represent a relevant source of organic matter to the water column, namely cohesive sediments associated to highly productive communities of benthic primary producers (e.g., mudflats, saltmarsh- and mangrove-fringed estuaries, seagrass meadows, and macroalgae beds; Fenchel et al., 1998; Burdige, 2002; Bianchi, 2007).

For these reasons, climatic and hydrodynamic processes enhancing horizontal advection of freshwater (e.g., rainfall, river discharge, runoff, and submarine groundwater discharge) and promoting fluxes of sediment porewater into overlying water (e.g., tidal forcing, wind-driven mixing, and convective mixing) are typically associated to organic matter enrichment (Jassby et al., 1993; Carlson, 2002; Mulholland, 2003; Bianchi, 2007; Wolanski, 2007; see Chapter 6.02), and may therefore promote bacterial growth rates. Local, tidal forcing, and lateral transport processes are also important for the transport of DOM and particulate organic matter, whereas wind forcing is relevant for the advection of floating organic detritus (Wolanski, 2007). Aspects related to climate (e.g., precipitation–evaporation balance, frequency of storms, and rainfall intensity), landscape topography (e.g., area-to-volume ratio, ratio of wetland area, catchment, and channel slopes), sediment quality (e.g., pH, oxygen, temperature, and degree of wetting), and habitat interconnectivity in adjacent watersheds are also primary determinants of organic matter fluxes into estuarine and nearshore coastal ecosystems (Alongi, 1998; Mulholland, 2003; Wolanski et al., 2004; Wolanski, 2007). Moreover, processes that control the biological production of DOM and particulate organic matter or modify its biological lability (e.g., ultraviolet radiation) are also significant with regard to bottom-up control of bacterial growth rates. The majority of these processes are, in effect, related to climate and hydrology (see

Section 10.02.2.1.1; Moran et al., 2000; Moran and Zepp, 2000; Carlson, 2002; Bianchi 2007).

The relevance of DOM as a determinant of bacterial growth rates in estuarine and coastal ecosystems is unequivocal, and may be inspected using data derived from specific experimental approaches and field studies over different spatial and temporal scales. Comparative studies have shown that bacterial biomass or production is positively correlated to phytoplankton biomass or production, within and across aquatic ecosystems (see empirical models by Cole et al. (1988), White et al. (1991); Figure 5). These relationships are usually interpreted as evidence for bottom-up control of bacterial growth by organic substrates directly or indirectly provided by phytoplankton (Nagata, 2000). As phytoplankton are strongly driven by climatic and hydrologic features (see Section 10.02.2.1), positive relationships between heterotrophic bacteria and phytoplankton inherently imply strong, indirect linkages between bacteria, climate, and hydrologic drivers.

Strong interactions between heterotrophic bacteria and phytoplankton are also apparent within individual coastal ecosystems, at different spatial and temporal scales. Episodic increases of bacterial biomass and production during or after the demise of phytoplankton blooms are widely reported for estuarine (Cloern, 1996; Mulholland et al., 2009) and upwelling coastal systems (Barbosa et al., 2001). These events traduce the relevance of phytoplankton or their grazers as sources of labile organic substrates to heterotrophic bacteria, and also the importance of climatic and hydrodynamic processes. In meso- and macrotidal estuaries, periodic short-term changes in bacterial biomass and production are usually coupled to tidal forcing. The effects of semidiurnal and fortnightly tidal cycles on heterotrophic bacteria vary across and within ecosystems, and have been related to multiple top-down (see next section)

Figure 5 Relationships between chlorophyll *a* concentration and production of heterotrophic bacterioplankton (BP_e) in the Ria Formosa coastal lagoon (SE Portugal) during the period 1991–93 (with adjusted regression line and regression equation). Dotted and dashed lines represent empirical models based on cross-system comparisons of aquatic ecosystems (Cole et al., 1988) and estuarine and coastal ecosystems (White et al., 1991). Note that for any given chlorophyll *a* concentration, estuarine ecosystems mostly have higher bacterial production rates than other aquatic ecosystems, suggesting the relevance of other sources of organic matter. Both phytoplankton and other autochthonous and allochthonous sources of organic matter usually are under climate and hydrologic regulation (see text). Data derived from Barbosa, A.B., 2006. *Estrutura e dinâmica da teia alimentar microbiana na Ria Formosa*. Ph.D. Thesis, Universidade do Algarve, 517 pp.

and bottom-up control mechanisms. Among the latter, tidally induced changes in phytoplankton (see Section 10.02.2.1.2; Ducklow, 1982; Eldridge and Sieracki, 1993), DOM fluxes from sediments into overlying waters and resuspension of particulate organic matter were referred as mechanisms underlying tidal variability in heterotrophic bacterioplankton (Morales-Zamorano et al., 1991; Guenther et al., 2008; Chauchan et al., 2009).

Annual patterns of heterotrophic bacterioplankton in estuarine and coastal systems also provide opportunities to examine direct and indirect interactions between hydrodynamic processes and bacterial growth. Annual cycles of bacterial biomass and production in estuarine ecosystems usually show highest values during the spring–summer period, namely in temperate systems (Hoch and Kirchman, 1993; Shiah and Ducklow, 1995; Cloern, 1996; Murrell et al., 1999; Ziegler and Benner, 1999; Revilla et al., 2000; Murrell, 2003; McManus et al., 2004; Staroscik and Smith, 2004; Barbosa, 2006; Alonso-Saéz et al., 2008). In some ecosystems (see Ria Formosa coastal lagoon, Figure 5), bacterial seasonality is coupled to phytoplankton biomass or activity, indicating that phytoplankton apparently constitutes a relevant source of labile DOM (Cloern, 1996; Goosen et al., 1997).

However, annual cycles of heterotrophic bacterioplankton and phytoplankton are frequently weakly coupled or uncoupled in many estuarine and coastal ecosystems (Findlay et al., 1991; Ducklow and Shiah, 1993; Schultz et al., 2003; Gocke et al., 2004; Alonso-Saéz et al., 2008). This apparent uncoupling has been attributed to a series of factors such as (1) inefficient DOM consumption due to inorganic nutrient limitation; (2) regulation of bacterial growth by other environmental drivers (see later); (3) temporal lags between DOM production by phytoplankton and bacterial consumption (see Barbosa et al., 2001); (4) effects of bacterial mortality (see next section); (5) strong resuspension of bacteria from the sediment (Gocke et al., 2004); (6) consumption of other autochthonously derived DOM; and (7) consumption of allochthonously derived DOM (Barbosa et al., 2001; Schultz et al., 2003).

In estuarine and nearshore ecosystems, bacterial production frequently represents a large proportion of phytoplankton production, thus implying bacterial assimilation of other autochthonously derived DOM or allochthonous sources (see Ducklow and Carlson, 1992). Bacterial isotopic signatures as well as bacterial annual dynamics suggest that microphytobenthos and macrophytes (e.g., seagrasses, salt-marshes, mangroves, and macroalgae), hydrologically sensitive groups, are relevant nonphytoplanktonic autochthonous sources of both DOM and particulate organic substrates for heterotrophic bacteria (Chin-Leo and Benner, 1991; Jassby et al., 1993; Bano et al., 1997; Alongi, 1998; Hopkinson et al., 1998; Ziegler and Benner, 1999; Mann, 2000; Barbosa, 2006; Grami et al., 2008; Barrera-Alba et al., 2009; Barbosa, 2010). Heterotrophic bacterioplankton and their predators possibly play a pivotal role in channeling primary production of macrophytes to metazoans (Ziegler and Benner, 1999; Grami et al., 2008; Barbosa, in press).

In some estuarine and coastal ecosystems, bacterial growth rates are clearly supported by allochthonous labile sources of DOM. Episodic meteorological events (e.g., wind storms and high rainflow episodes), for example, stimulate heterotrophic bacterioplankton due to increased availability of organic

matter and/or inorganic nutrients associated to increased continental runoff or benthic resuspension (Cotner et al., 2000; Grémare et al., 2003; Alonso-Saéz et al., 2008; Solic et al., 2009). Variability in river discharge rates, usually considered a proxy for organic carbon flux into estuarine systems (Jassby et al., 1993), is also positively related to bacterial production and growth over seasonal (Murrell et al., 1999; Schultz et al., 2003) and interannual time scales (Murrell, 2003; Shiah et al., 2006; Barrera-Alba et al., 2009). In some estuaries, a shift in ecosystem metabolism toward heterotrophic dominance is observed under increased freshwater discharge rates (see Hitchcock et al., 2010). Yet, it is worth noting that direct relationships between bacterial growth and river flow may be explained by different causal mechanisms: a bacterial growth stimulation by riverine DOM, by phytoplankton-derived DOM, or both (see Figure 6). The former explanation probably applies to the East China Sea ecosystem (see Figure 6(b); Shiah et al., 2006).

The assimilation of allochthonous (riverine) or resuspended organic matter by heterotrophic bacterioplankton is fundamental for estuarine food-web dynamics and

Figure 6 Evidence for hydrologic regulation of heterotrophic bacterioplankton growth rates in estuarine and coastal ecosystems: (a) relationships between the Escambia River flow and specific bacterial growth rates ± 1 SE (temperature normalized to 25 °C) in the subtropical estuary Pensacola Bay (Florida, USA), during years of low and regular river flow and (b) relationships between the Chang Jiang River discharge index and specific bacterial growth rates (± 1 SD), normalized by chlorophyll *a* concentration (Slope of BGR vs. Chl), in the coastal mixing zone and adjacent oceanic area; minimum river discharge (year 2003) reflects the completion of the Three Gorges Dam. (a) From Murrell, M.C., 2003. Bacterioplankton dynamics in a subtropical estuary: evidence for substrate limitation. *Aquatic Microbial Ecology* 32, 239–250. (b) From Shiah, F.-K., Gong, G.-C., Xiao, T., 2006. Effects of Chang Jiang River summer discharge on bottom-up control on coastal bacterial growth. *Aquatic Microbial Ecology* 44, 105–113.

biogeochemical cycling within periods (e.g., winter), ecosystems (e.g., turbid and heterotrophic systems) or locations (e.g., estuarine maximum turbidity zones) of reduced primary production (Cotner et al., 2000; David et al., 2006; Barrera-Alba et al., 2009). The establishment and evaluation of flood-management practices should take into account that river-flow patterns affect not only phytoplankton (primary producers) but also heterotrophic bacteria (consumers). Indeed, the construction of the Three Gorges Dam and related river-discharge reduction was recently associated to a significant decrease of bacterial growth rates in adjacent coastal and oceanic ecosystems waters (East China Sea; see Figure 6(b); Shiah et al., 2006).

Regardless of the source of autochthonous (e.g., phytoplankton, microphytobenthos, and macrophytes) and allochthonous (e.g., continental runoff, riverine inputs, and atmospheric deposition) organic carbon assimilated by heterotrophic bacterioplankton, climate, and hydrodynamic processes are, inevitably, fundamental determinants of DOM fluxes into estuarine and coastal ecosystems. In case of bacterial growth limitation by inorganic dissolved nutrients (Kirchman, 2000b; Farjalla et al., 2002; Church, 2008; Hitchcock et al., 2010), climate and hydrology are, again, relevant environmental drivers of bacterial growth (see Section 10.02.2.1.1).

In addition to DOM and inorganic nutrients, bacterial growth rates are also regulated by other hydrologic variables (e.g., temperature, turbulence, salinity, oxygen, toxic compounds, and ultraviolet radiation). These are, in turn, controlled by climatic and hydrodynamic processes (see Section 10.02.2.1.1; White et al., 1991; Shiah and Ducklow, 1995; Moran and Zepp, 2000; Malits et al., 2004). Due to a relative excess of autochthonous and allochthonous organic matter and inorganic nutrients, bacterial growth is frequently limited by temperature, not by substrate supply, within many estuarine systems (Hoch and Kirchman, 1993; Shiah and Ducklow, 1994, 1995; Goosen et al., 1997; Revilla et al., 2000; Murrell, 2003; Schultz et al., 2003; McManus et al., 2004; Staroscik and Smith, 2004). Yet, in some ecosystems, temperature control of bacterial growth is apparently stronger below some threshold temperature value and above some chlorophyll concentration (see review White et al., 1991). When temperature rises above this threshold, other factors, namely substrate availability became increasingly important (Wikner and Hagstrom, 1991; Hoch and Kirchman, 1993; Shiah and Ducklow, 1993, 1995). Beyond its direct effect on bacterial growth, temperature might also affect heterotrophic bacteria indirectly, through its impact on biologic DOM sources (e.g., phytoplankton, see Section 10.02.2.1.1) and bacterivores (see next section). Indeed, remote interannual changes in strong atmospheric drivers (air temperature and precipitation) were apparently propagated to heterotrophic bacterioplankton, indirectly, through trophic connections via phytoplankton (Li and Harrison, 2008).

10.02.2.2.2 Hydrologic control of bacterial loss rates

Loss rates of heterotrophic bacterioplankton include those due to physically driven processes, such as advective losses and sinking in association with aggregates, and biological processes such as viral-induced lyses (Fuhrman, 2000; Suttle, 2007; Breitbart et al., 2008; Wilhelm and Matteson, 2008) and predation. Bacterial predators include a wide variety of unicellular

organisms (phagotrophic protists and *Bdelovibrio*-like organisms; Jurgens and Massana, 2008; Chauchan et al., 2009) and multicellular organisms (e.g., meroplankton and benthic suspension feeders; Douillet, 1993; Newell and Krambeck, 1995; Bak et al., 1998).

Due to their small size, bacterial sinking losses are usually considered negligible, namely in shallow coastal ecosystems (Jurgens and Massana, 2008). Hydrodynamic processes (e.g., tidal forcing, wind mixing, and river discharge) and circulation patterns regulate vertical and horizontal advection of water masses and associated heterotrophic bacterioplankton. In estuaries, bacterial cells are longitudinally advected, by river-driven transport, from upper- to lower estuarine locations, and eventually exported into adjacent coastal ecosystems (Cunha et al., 2001; Barbosa, 2006). Advective washout losses of heterotrophic bacteria are more pronounced within ecosystems and habitats or during periods of low hydraulic residence times (Shiah and Ducklow, 1995; Painchaud et al., 1996; Crump et al., 2004; McManus et al., 2004; Barbosa, 2006). Tidal forcing induces substantial horizontal and vertical mixing, as well as the displacement of bacterioplankton along estuarine axis. The effects of semidiurnal and fortnightly tidal cycles on heterotrophic bacteria vary across and within ecosystems. Mechanical effects coupled to advective transport of bacterial cells (Wright and Coffin, 1983; Chrzanowski and Zingmark, 1989; Thottathil et al., 2008) and bacterial resuspension from sediments (Wilson and Stevenson, 1980; Kirchman et al., 1984; Painchaud et al., 1995; Sosa-Ávalos et al., 1997; Shimeta et al., 2003; Chauchan et al., 2009) have been used to explain, to some extent, tidal variability of bacterioplankton (but see previous section).

Biological processes, namely predation by phagotrophic protists and viral lyses, are considered prime bacterial loss processes. Grazing by phagotrophic protists, namely planktonic aplastidic nanoflagellates and ciliates, is currently considered the major loss process being responsible for the removal of a substantial fraction of daily bacterial production (Strom, 2000; Jurgens and Massana, 2008). As previously referred, both viral activity and grazing rates of phagotrophic protists are directly affected by hydrologic processes and properties (see Section 10.02.2.1.2; see Jurgens and Massana, 2008; Montagnes et al., 2008a). Temperature and prey concentration are relevant predictors of bacterivory exerted by phagotrophic protists (see empirical model by Vaqué et al., 1994). Indeed, increased water temperature is sometimes used to explain seasonal bacterivory maxima observed in estuarine and coastal ecosystems during summer (e.g., Staroscik and Smith, 2004; Barbosa, 2006; Solic et al., 2009).

Some hydrological processes may also control bacterivory indirectly, due to their action upon bacterivores or other prey types (Eldridge and Sieracki, 1993). Hydrologically mediated changes in the abundance of phagotrophic protists, such as periodic resuspension events associated to spring-neap tidal cycles (Shimeta et al., 2003) or the effects of riverflow and storms on phagotrophic protists (Reaugh et al., 2007; Wetz and Paerl, 2008b), may potentially reverberate through the food web, and affect bacterial mortality losses. Moreover, tidally driven changes in bacteriophages (Almeida et al., 2001) and other bacterial predators (*Bdelovibrio*-like organisms, Chauchan et al., 2009) might also illustrate the hydrologic control of bacterioplankton loss rates in estuarine and coastal ecosystems.

10.02.2.2.3 Hydrologic control of bacterial composition

On the whole, bottom-up and top-down factors jointly control the composition of the assemblages of heterotrophic bacterioplankton, and their succession (Chauchan et al., 2009). Therefore, climate- and hydrodynamic-driven environmental changes might potentially affect not only bacterioplankton biomass, growth, and mortality, but also their composition. Changes in the heterotrophic bacterioplankton community composition along longitudinal estuarine axis (Bouvier and del Giorgio, 2002), and bacterial successions over tidal (Chauchan et al., 2009), seasonal, and interannual timescales (Kan et al., 2006; see Crump et al., 2009) further demonstrate the relevance of climatic and hydrodynamic processes as drivers of bacterioplankton composition in estuarine and coastal ecosystems. From an ecosystem perspective, these alterations in bacterial composition probably imply concurrent changes in ecosystem biodiversity, resilience, and biogeochemical functioning (see review Höfle et al., 2008).

Globally, climatic- and hydrologic-driven alterations in heterotrophic bacterioplankton biomass, composition, growth, and mortality, occurring at different timescales, are propagated to higher trophic levels, affecting trophodynamics, nutrient biogeochemical cycling processes, and global ecosystem functioning (Höfle et al., 2008; Barrera-Alba et al., 2009; Hitchcock et al., 2010).

10.02.3 Hydrologic Regulation of Metazoans in Estuarine and Nearshore Coastal Ecosystems

Aquatic metazoans include a wide diversity of organisms that share a common structure, cells organized into tissues and organs, and are consumers of microbes and other metazoans. Due to this complex structural organization and a larger size, metazoans are usually more independent of their surrounding environment than microbes. Moreover, advanced mobility strategies are used by metazoans to actively search for more favorable environmental conditions and resources. Planktonic larval phases of fish, for example, may present a higher swimming performance than some nektonic organisms (Leis, 2006). This section will address, in turn, the effects of hydrologic variables and processes upon different functional groups of aquatic metazoans, metazooplankton, nekton, and benthic organisms. Metazooplankton are drifting organisms with swimming speeds usually lower than the surrounding currents (Day et al., 1989). The metazooplankton section will include holoplanktonic organisms, such as copepods, and meroplanktonic larval phases of invertebrates and early stages of fish (eggs and preflexion stages). Nekton include actively free-swimming organisms able to move independently of water currents, and both advanced fish larval phases (micronekton) and typical nektonic organisms, such as adult fish and shrimps, will be considered. Zoobenthic communities have usually low or restricted mobility, and include a broad group of organisms having an intimate relationship with the substrate bottom (Little, 2000).

Most metazoans, such as verms, jellyfishes, bivalve mollusks, crustaceans, and fishes, are ectothermic and, therefore, are affected by water temperature, a major hydrologic variable. The effects of temperature and other meteorologic and

hydrologic variables and processes, namely salinity, turbulence, and freshwater flow, on aquatic metazoans will be addressed, considering both effects at individual (growth and reproduction) and community levels (specific composition).

10.02.3.1 Metazooplankton

10.02.3.1.1 Hydrologic control of metazooplankton growth and biomass

Spatial and temporal distribution patterns of structural (biomass) and functional (metabolic rates) properties of zooplankton are closely linked to hydrologic features, namely hydrodynamic physical structures (Alcaraz et al., 2007). Calanoid copepods commonly represent the dominant fraction of net holoplankton during most seasons (70–90% of the biomass) within most estuarine ecosystems, independent of their location (polar, cold or warm temperate, and tropical), geomorphology, and freshwater and tidal influence (Heip and Herman, 1995). Meroplanktonic larval stages are regularly the second most abundant group, and the contribution of other holoplanktonic groups is usually minor, except for periodic occurrences of huge blooms of jellyfish (Purcell, 2005). Estuarine meroplankton is much more diverse than holoplankton because a large number of otherwise benthic or pelagic species spend their larval and/or juvenile stages in the plankton (Little, 2000). Holoplanktonic organisms permanently live in the very variable pelagic environment, and have developed high growth rates, broad physiological tolerances, and curious behavioral patterns that allow them to survive this dynamic, hydrologic-driven environment (Day et al., 1989).

Planktonic copepods are usually considered relevant herbivores (Nybakken, 2001) and vital agents in biogeochemical cycles of carbon and other elements in estuarine and nearshore ecosystems (Hernández-León and Ikeda, 2005; Buitenhuis et al., 2006). Copepods and their developing progeny form the main food supply for many planktonic predators, such as pelagic fish and medusa (Hay, 1995). According to Day et al. (1989), the copepod genus *Acartia* is not only the most abundant metazooplanktonic species, but also the most widespread. *Acartia* distribution ranges from nearly fresh to hypersaline waters, from 0 to 40 °C, clear to turbid, shallow to deep, and polar to tropical estuarine and coastal ecosystems (Sautour and Castel, 1995). For these reasons, interactions between hydrology and *Acartia* will be examined in great detail.

Estimates of copepod secondary production using the copepod egg production method (EPR) or the product of growth rate and biomass are extremely important to evaluate global organic matter fluxes in aquatic ecosystems, and species-specific responses of zooplankton to hydrologic variability. Such estimates of production integrate recent feeding history and physiological adaptations to environmental variability (Hay, 1995). EPR can be applied to free-spawning copepods that release their eggs into the water column, such as *Acartia*, but are not applicable to species that carry their egg in the abdomen (Figure 7). Some calanoid species inhabiting relatively shallow temperate habitats also present diapause eggs (e.g., Marcus, 1984, 1996), probably to cope with extreme annual ranges in key environmental factors within these areas (Holste and Peck, 2005).

Figure 7 Estuarine copepods with different spawning strategies: (a) *Acartia* sp. during free spawning of normal eggs and (b) *Oithona* sp. carrying eggs in the abdomen. Bar: 100 μm .

In temperate estuaries and nearshore areas, temperature not only affects the copepod EPR but also the hatching success (HST) for copepods (Chinnery and Williams, 2004; Holste and Peck, 2005). Temperature-specific responses in the production of diapause eggs may explain the lack of hatching observed at cold temperatures, although other interpretations are also possible (i.e., temperature effects on egg quality; Holste and Peck, 2005). Relatively few studies have examined the effects of salinity on the HST of calanoid copepod eggs, which is surprising given the high abundance of members of this family within

estuarine and brackish waters (Paffenhöfer and Stearns, 1988). In case of *Acartia congens*, the hatching success (HST) increases with increasing salinity, and is maximal at 25. However, a marked decline in HSS below a salinity threshold of 17 indicates a nonlinear relationship (Holste and Peck, 2005). In addition to their individual effects, temperature and salinity interactions are also important, especially with regard to physiological tolerances affecting vital rates. For example, pelagic invertebrates often have higher tolerance to lower salinities at higher temperatures (Jeffries, 1962; Kinne, 1970). Comparisons of *in situ* *Acartia* EPRs between two temperate and close coastal ecosystems (SE Portugal), the Guadiana estuary (brackish) and the Ria Formosa coastal lagoon (marine), support *in vitro* results obtained by Peck and Holste (2006), showing higher EPR for estuarine system (Figure 8). However, high temporal and spatial variability in the abundance of calanoid copepods within estuaries and confined coastal ecosystems may be explained by direct hydrologic forcing on growth and reproduction, and also by alterations in biologic forcing variables, such as food availability and predation pressure. The copepod *Acartia* is restricted to nearshore environments because it is adapted to high food concentrations, which it encounters in estuaries and upwelled waters (Paffenhöfer and Stearns, 1988).

Jellyfish and ctenophore populations are relevant mortality sources for metazooplanktonic crustaceans in estuarine and coastal ecosystems. Few long-term records of jellyfish are currently available, and most records are semi-quantitative. However, these records are extremely valuable to examine the

Figure 8 Copepod (*Acartia*) egg production rates ($\pm 1\text{SE}$) in a coastal lagoon (a) and an estuary (b) connected to the Gulf of Cadiz (NE Atlantic). Legend: ■ – inner location; □ – outer location. Data derived from Encarnação (2009) and Joana Cruz et al. (unpublished data).

interactions between jellyfish abundance and hydrologic and climate variability. Due to their short generation times (usually ≤ 1 year), gelatinous zooplanktonic species appear to respond to climate forcing without a time lag (Lynam et al., 2004). Annual cycles of jellyfish production in temperate and boreal regions usually peak during spring. The cues triggering medusa production have not been definitively determined for most species, but apparently include a seasonal progression or combination of environmental changes in temperature, salinity, food availability and light, and vary between species (Purcell, 2005). Due to rearing difficulties, few experimental data are currently available to understand how environmental drivers effectively affect medusa physiology (Ma and Purcell, 2005a, 2005b). Temperature and salinity directly affect physiological processes, and both low and high temperatures can disable enzymes and transport systems, which physiologically restricts organisms to specific temperature ranges (Kinne, 1970). Within suitable physiologic ranges, high temperatures usually accelerate metabolism and reproduction. Direct effects of salinity changes occurring in the Atlantic and Pacific coasts were shown to affect estuarine scyphozoans, which cannot osmoregulate at salinities below 5 (Purcell, 2005). Moreover, rainfall and riverflow into the Chesapeake Bay (NE USA) are inversely correlated to visual counts of medusa, at both annual (January–June; see Figure 9) and interannual timescales (1960–86). Salinity reductions within several Asian coastal ecosystems (western Japan, Po Hai, Yellow Sea, and the East and South China Seas) were also related to reduced survival in different medusa species (Purcell, 2005). However, most experiments referred were designed to test the environmental factors responsible for the initiation of medusa's productive period and not to determine their effects on jellyfish population size.

Direct effects of water motion on zooplankton depend on the spatial and temporal scales considered and organism size. Large- to macroscale fluid motions cannot be sensed by zooplankton. However, small- to microscale fluid motions (i.e., small-scale turbulence) can affect individual behavior for organisms as small as 1 mm (Alcaraz et al., 2007). Turbulence

is an intrinsic and ubiquitous characteristic of aquatic environments, and plays a pivotal role in shaping the structural and functional properties of planktonic systems. In estuaries, tidal forcing is responsible for strong diurnal and fortnightly changes in turbulence intensity, with higher turbulence levels at spring tides in relation to neap tides, particularly in shallow meso- and macrotidal estuaries (Trevethan et al., 2008). In estuaries and coastal ecosystems, turbulence sources are related to various climate and hydrodynamic features, including tides, winds, waves, and freshwater discharges, and affect metazooplanktonic organisms at the individual, population, and community levels (Figure 10). As a whole, turbulence effects on zooplankton appear analogous to those resulting from an increase of temperature, as described by Van't Hoff's and Bergman's laws or by the Arrhenius equation (Alcaraz et al., 1994; Margalef, 1997). Increased particle encounter rates under intensified turbulence, a consequence of the hydrodynamic disorder, has analogies with the enhanced collision of molecules induced by temperature increases (entropy or molecular disorder). Turbulence effects on zooplankton feeding activity depend on turbulence intensity. High turbulence levels can interfere with prey detection and capture resulting in dome-shaped feeding responses as the result of the tradeoff between positive (increased encounter rate) and negative aspects (e.g., eroding feeding currents and impairing prey detection; Singarajah, 1975; Saiz and Kiørboe 1995). The enhancement of the encounter rates due to small-scale turbulence (Saiz and Kiørboe, 1995) has significant consequences at the individual level. For predator–prey interactions implying low relative velocities, such is the case of ambush and pause-and-travel predators (Caparroy et al., 1998), it can mean a significant increase of ingestion rates, whereas suspension feeders are less benefited (Saiz and Kiørboe, 1995). Turbulence-induced changes at individual levels (e.g., enhancement of metabolic and development rates of specific taxa) may accumulate and modify the structural and functional properties of zooplankton communities (see Figure 10; Alcaraz et al., 2007).

10.02.3.1.2 Hydrologic control of metazooplankton communities

Estuarine and coastal communities of metazooplankton are influenced by physical forcing, and are quite reactive to inter-annual changes in the freshwater flow (Holden and Green, 1960; Kimmerer, 2002) due to their effects upon hydraulic residence time, salinity, and temperature (Champalbert et al., 2007). Low winter abundance and biomass of metazooplanktonic organisms in temperate estuaries and tropical areas affected by monsoons are usually explained by their increased advective flushing and decreased growth due to lower salinities under high river-discharge rates (Iyothibabu et al., 2006). As noted earlier, most of the estuarine copepods live in the salinity close 25, and such salinities can be expected only in the vicinity of estuarine mouths or adjacent bays.

Changes in river flow can also indirectly impact zooplankton, through stimulation of primary production and its propagation up the trophic web. Phytoplankton constitutes a relevant food source for metazooplankton and its concentration is strongly hydrologically regulated (see Section 10.02.2.1). Yet, food availability to estuarine and coastal zooplankton consists of a broad spectrum of particles that differ in size,

Figure 9 Relationship between freshwater discharge (January–June, $\text{m}^3 \text{s}^{-1}$) into the Chesapeake Bay (SE USA) and counts of *Chrysaora quinquecirrha* medusae in the mesohaline Chesapeake Bay during July and August (1960–86). From Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of Marine Biology Association United Kingdom* 85, 461–476.

Figure 10 Sources of small-scale turbulence in estuarine and nearshore ecosystems and integration of turbulence effects from individual to ecosystem levels.

shape, chemical composition, and nutritional quality. Globally, zooplankton food is strictly connected to hydrological conditions that affect the fluxes of nutrients and organic matter from connected catchment basins into estuarine and adjoining coastal waters (see Sections 10.02.2.1 and 10.02.2.2). An ability to discriminate between particles of high and low quality is energetically advantageous, especially in estuarine and nearshore ecosystems, which are frequently dominated by low-quality, suspended matter. Copepods do discriminate successfully between living phytoplankton cells and nonliving detritus (Paffenhöfer and Stearns, 1988).

In estuaries and coastal waters, freshwater outflows and tidal forcing may create prominent turbidity areas, namely estuarine turbidity maximum (ETM) and coastal freshwater plumes. ETM zones are located at the head of estuaries and constitute a freshwater-brackish interface, with high concentrations of organic and inorganic particulate material. Mesozooplankton associated to ETM zones are often dominated by copepods, such as *Acartia* and *Eurytemora*, which probably exploit the detrital food web, and amphipods, mysids, polychaetes, and cirripedia larvae (Baker and Wolff, 1987; Sautour and Castel, 1995). Suspended particulate matter within coastal freshwater plumes originates from adjoining catchment basins (riparian vegetation, salt marshes, mangroves, and seagrasses), and also includes relevant contributions from phytoplankton (Simenstad et al., 1994). Conceptually, increased biomass of metazooplankton within coastal freshwater plumes are supported by two trophic pathways: consumption of fresh marine phytoplankton production stimulated by riverine nutrients; and consumption of allochthonously derived organic detritus and associated heterotrophic microorganisms (see Section 10.02.2.2). Multiple

stable isotopes were recently used to evaluate the importance of these two trophic pathways in an estuary and coastal freshwater plume in eastern Australia (Figure 11; Schlacher et al., 2009). At the lower estuary, terrestrial and estuarine carbon sources only made a sizeable contribution (47%) to the carbon demand of zooplankton during pulsed freshwater flow periods (freshets). By contrast, phytoplankton supplied up to 90% of the dietary carbon zooplankton feeding in the plumes developed in nearshore coastal waters even during freshets.

Increased freshwater runoff during winter is also related to the enhancement of water-column salinity stratification, and the shallowing of the mixed layer. This scenario is frequently related to the occurrence of phytoplankton blooms, well before the amount of solar radiation is able to induce thermal stratification (see Section 10.02.2.1.1). Early onset of phytoplankton blooms may anticipate annual zooplankton cycles, and eventually impact fish larvae using these areas (Esteves et al., 2000). In fact, the nursery function of estuarine systems (Beck et al., 2001) is also linked, among other factors (see Section 10.02.3.3, Nekton), to higher food availability. Copepod and mysid populations, in particular, are major prey items for different pelagic fish species (Baldó and Drake, 2002).

Despite the positive effects of high concentrations of suspended matter, increased turbidity may also negatively affect estuarine fauna. High turbidity may interfere with the food-collecting abilities of moderate-sized zooplanktonic species, such as copepods and some mysids, reducing their fecundity and causing global ecosystem deterioration. Moreover, high and persistent turbidity events (HPTE) caused by strong and sudden freshwater discharges, preceded by long periods of very low freshwater inflow, may also directly affect marine recruits by increasing larval mortality and reducing the

Figure 11 (a) Conceptual model of trophic pathways supporting zooplankton consumers in freshwater coastal plumes; (b) stable isotope ratios (C and N) of zooplankton at an offshore reference station, a lower estuarine location, and a freshwater plume off the estuarine mouth, during three phases of plume development; (c) variability in rainfall (1), chlorophyll a concentration (2), and carbon isotopic signature of the organic fraction of suspended particles, SPOM (3) in the lower estuary and freshwater plume region off an eastern Australian estuary. From **Figures 1, 2, and 3**, Schlacher, T.A., Connolly, A.R.M., Skillington, A.A.J., Gaston, T.F., 2009. Can export of organic matter from estuaries support zooplankton in nearshore, marine plumes? *Aquatic Ecology* 43, 383–393.

physiological condition of estuarine individuals (Griffin et al., 2009). Time series obtained in the Guadalquivir estuary (SE Spain) show that the extension of HPTEs into estuarine nursery grounds caused a strong reduction in mysid populations (see **Figure 12**; González-Ortegón et al., 2010). This occurrence is connected to global climate variability over the area, as illustrated by the variability in the North Atlantic Oscillation (NAO) winter index. In fact, NAO winter index during 1999–2000 and 2007–2008 attained exceptionally high values (max. 2.8), consequently leading to concurrent reductions in rainfall and river flow over southern Europe Chicharro et al. (2006). Other alternative or complementary hypotheses to explain sudden decreases in estuarine zooplanktonic populations, such as those reported by González-Ortegón et al. (2010) and Chicharro et al. (2009), are jellyfish blooms (Xian et al., 2005). According to Boero et al. (2008), oscillations in zooplankton abundance may sometimes be explained by concurrent changes in the abundance of native and nonindigenous gelatinous species of medusa and ctenophores. Gelatinous zooplankton play a pivotal role in shaping estuarine and coastal zooplanktonic communities through predation and competitive interactions (**Figure 13**). Gelatinous zooplankton are well known for their erratic occurrence (Boero et al., 2004). However, estuarine medusa may be closely linked to freshwater discharge rates (**Figure 9**). In specific locations over the North Atlantic, interannual changes in the abundance of scyphomedusae are also explained by the NAO winter index variability patterns, and associated changes in sea-surface temperature and winter precipitation (Lynam et al., 2004).

Under regular river discharge periods, short episodic freshwater pulses may increase the diversity of zooplanktonic assemblages, minimizing the occurrence of phytoplankton blooms. During a freshet disturbance, changes in physical-chemical conditions improve the success of hatching of resting stages of zooplankton, increasing directly zooplanktonic diversity. Furthermore, nutrient inputs may also promote phytoplankton diversity, thereby directly contributing to a more diverse prey assemblage, and indirectly to increased zooplankton diversity due to the suppression of competitive exclusion processes (Hutchinson, 1951, 1961; Holden and Green, 1960; Reynolds, 1984; Roelke, 2000). Despite the positive effects of freshwater discharges, strong riverflow events may evidently contribute to increased seaward advection of zooplankton (Champalbert et al., 2007). Moreover, water fluxes associated to diurnal tidal cycles in meso- and macrotidal estuarine systems are commonly much higher, often by a factor of 10–100, than the volume flux due to riverine inflow (Wolanski, 2007). In fact, net seaward flow often poses a retention problem to estuarine endemic zooplankton populations, although their continuous existence provides evidence that they can successfully resist displacement forces. Mechanisms must therefore exist to prevent, or compensate for, catastrophic transport of these animals seaward.

Several theories have been formulated to explain the maintenance of zooplankton communities in estuaries, based on passive or active mechanisms. The former mechanisms include (Little, 2002) (1) the presence of gyres and eddies in estuarine water, which rarely flow directly seaward; instead, they circulate

Figure 12 Yearly, monthly, or daily mean values for hydrologic variables (water temperature, salinity, rainfall, freshwater inflow, and turbidity), mysid densities and NAO winter index values in the Guadalquivir estuary, SE Spain. Legend: F, February; M, May; A, August; and N, November. Shaded symbols represent samples collected during high and persistent turbidity periods. Reproduced from [González-Ortegón, E., Subida, M.D., Cuesta, J.A., Arias, A.M., Fernández-Delgado, C., Drake, P., 2010. The impact of extreme turbidity events on the nursery function of a temperate European estuary with regulated freshwater inflow. Estuarine, Coastal Shelf Science 87, 311–324.](#)

Figure 13 Relationship between nonnative medusae and zooplanktonic diversity and density in the Guadiana middle estuary (SE Portugal). Data derived from Chícharo, M.A., Leitão T., Range, P. Gutierrez, C. Morales, J. Morais, P., Chícharo, L., 2009. Alien species in the Guadiana Estuary (SE-Portugal/SW-Spain): *Blackfordia virginica* (Cnidaria, Hydrozoa) and *Palaemon macrodactylus* (Crustacea, Decapoda): Potential impacts and mitigation measures. *Aquatic Invasions* 4 (3), 501–506.

in large rotatory gyres or mixes in turbulent eddies; (2) high residence time of estuarine water, namely in middle and upper areas (up to several weeks), comparable to planktonic life cycles of some invertebrates, especially in tropical or warm temperate estuaries; and (3) an exposure time in lower estuarine areas higher than the residence time because organisms and water particles that leave an estuary during ebb tide re-enter the estuary at a later time, possibly at the next flood tide (Wolanski, 2007). Particle-trapping processes at the estuarine turbidity maximum zones may also passively contribute to the retention of zooplankton (Simenstad et al., 1994). In some species, larval anatomy and nonfree eggs (e.g., copepod *Oithona*, Figure 7) may also prevent organisms from being flushed out. Different complexes of traits could present alternative adaptive solutions to the problems presented by a given hydrological regime. In zoobenthic organisms with lecithotrophic development, such as bryozoans or nereid polychaetes, with a limited-feeding larval phase, the length of pelagic period is constrained and thus the export of larvae from estuaries is also limited (Strathmann, 1982).

With respect to active retention mechanisms, metazooplankton exhibit the amazing ability for vertical migrations, which may allow them to be retained inside estuaries and nearshore areas, or dispersed offshore according to life-cycle strategies. Vertical distribution is under strong behavioral control from the time of hatching, if not before, and can have a decisive, if indirect, influence on dispersal trajectories (Leis, 2006). Tidal forcing is a key determinant of hydrodynamics in meso- and macrotidal estuarine and nearshore ecosystems (Alvera-Azcárate et al., 2003). A vertical swimming speed of $0.3\text{--}1.0\text{ cm s}^{-1}$ “would substantially enhance shoalward displacement” in most estuarine ecosystems (Smith and Stoner, 1993). Swimming speeds up to 0.5 cm s^{-1} , recorded in copepods (Katona, 1973), would be sufficient to carry them into,

and out of, faster-moving upper-water layers on a tidal basis. Copepods are able to jump up to $200\text{--}400$ body lengths per second ($20\text{--}40\text{ cm s}^{-1}$), eliciting one of the greatest work outputs per gram of muscle measured in the animal kingdom (Lenz et al., 2000). Swimming speeds of crustacean decapod larva, up to 1 cm s^{-1} , are relevant to avoid off-shore advection during upwelling events (Chia et al., 1984). A distinct example of an active retention strategy is the tidally timed vertical migration of estuarine copepods, which swim upward into the water column during flood periods and sink to deeper waters during ebb periods (Hough and Naylor, 1991). This particular behavior is apparently driven by salinity changes and implies a circa-tidal endogenous swimming rhythm. Similar tidally timed migrations were also reported for estuarine larvae of crabs and oysters (Cronin, 1982).

In coastal lagoons with reduced freshwater inputs, the environmental cues allowing the retention of zooplanktonic organisms are evidently different. In a mesotidal coastal lagoon (SE Portugal) the abundance of bivalve larvae exhibits large, short-term oscillations. A strong reduction is observed during spring-tide periods, when water exchange with adjacent coastal water is amplified, due to increased offshore advection into flood currents (Chícharo and Chícharo, 2001). This variability pattern is common to different bivalve larval stages, and is particularly well defined during the spawning period. Semilunar spawning cycles, with spawning at neap-tide periods, are described for several bivalve species, crustaceans, and fishes. This spawning pattern is considered a strategy to take advantage of high food availability for larvae growth and avoid advection of larvae into unfavorable habitats (Figure 14; Sinclair, 1987).

Contrary to the retention strategies linked to tides, rhythmicity of larval release during ebb tides is recognized as a

Figure 14 (a) Tidal variability in the abundance of *Ruditapes decussatus* bivalve larvae in a coastal lagoon (Ria Formosa, SE Portugal) considering all larval phases (veliger and pediveliger); (b) larval shell microstructure showing intense growth during two consecutive spring tide periods. Data derived from Chícharo L., Chícharo M.A., 2000. Estimation of life history parameters of *Mytilus galloprovincialis* (Lamarck) larvae in a coastal lagoon (Ria Formosa- South Portugal). *Journal of Experimental Marine Biology and Ecology* 243, 81–94.

phenomenon to insure the transport and dispersion of estuarine decapod larvae from estuarine to coastal areas (Strathmann, 1982). Larval-releasing activity during ebb tides promotes a quick export of the first zoeae out of the estuary. Most of the larval development will then take place within adjacent coastal habitats, avoiding predation. The megalopae stage reinvests estuarine ecosystems, using the flood currents (Little and Epifanio, 1991; Queiroga et al., 1994; Sprung, 2001; dos Santos et al., 2008).

Several flatfish species spawn in marine waters and their pelagic larvae are transported inshore to settle into nursery habitats, located in shallow estuarine and coastal ecosystems (Yamashita et al., 2003). Given the strong tidal currents, what is the ecological importance of swimming abilities for estuarine species? Soleid larvae are unable to swim against typical tidal current speeds (Leis, 2006); hence, passive transport is probably the most common way of entering estuarine ecosystems. However, larvae actively select their position in the water column, using predominantly areas of low-velocity currents, to swim against. Current velocity usually drops almost to zero in the vicinity of the benthic boundary layer. Thus, flatfish larvae occupying this boundary layer will be subject to a much

reduced advection in comparison to larvae that remain above it, and the current climate within the water column will not affect their dispersal. An interaction between physical conditions, namely local topography, currents, tidal dynamics, and temperature, and vertical and horizontal behavior might explain why early fish larvae are not flushed away from estuarine systems (Cowen and Sponaugle, 2009).

10.02.3.2 Benthos

10.02.3.2.1 Hydrologic control of benthos growth and biomass

Linkages between benthic and pelagic domains, along with terrigenous inputs, play a major role in determining the production and biological structure of shallow coastal ecosystems. Hydrologic features are key determinants for benthic–pelagic coupling. Physically driven resuspension events increase the concentrations of phytoplankton and detritus, enhancing food availability to benthic suspension feeders. Moreover, turbulence may also affect other benthic food items, such as copepods. Recent field experiments estimating mussel stomach content, and grazing experiments measuring zooplankton

predation by bivalves have shown that mussels are capable of ingesting copepods (Davenport et al., 2000), especially in turbulent environments (see Table 1; Jonsson et al., 2009).

Benthic resting stages, a life form that enables organism survival under adverse environmental conditions (Marcus and Boero, 1998), are also affected by hydrologic variables such as turbulence and salinity (Ma and Purcell, 2005b) (Figure 15). Polyps usually have a tolerance to low-oxygen conditions greater than other benthic organisms, ensuring that jellyfish survive, and even reproduce, during hypoxic events, which other benthic organisms are unable to do (Richardson et al., 2009). The increase of available hard substrates in estuaries (e.g., dams, artificial reefs, and shells from bivalve aquaculture) enhances the chance for suitable planula settlement and subsequent ephyra/polyp production (Boero et al., 2008).

As discussed in the last section, most benthic macrofauna living in coastal systems have planktonic larvae illustrating, again, another aspect of benthic–pelagic coupling. The timing and location of invertebrate settlement are regulated by hydrological variables, such as currents, temperature, salinity, and turbulence. According to Pearce et al. (1998), high turbulence levels negatively and transiently affect meiofauna settlement rates. After settlement, organisms first became part of temporary meiofauna, living among sediment particles. Permanent meiofauna (protists excluded) within estuarine habitats are mainly dominated by nematodes and harpacticoid copepods. Sandy sediments located at estuarine mouths usually have low

densities of meiofauna due to high turbulence and periodic sediment re-working. Hydrological properties and processes, such as tidal flushing and currents, usually determine whether or not sediment hypoxia occurs. The tolerance of meiofauna to oxygen depletion or anoxia is species specific, being higher for nematodes than harpacticoid copepods (Coull, 1999).

Salinity is usually considered an overall controller of the biomass of estuarine and nearshore macrobenthic organisms. Yet, salinity fluctuations may be more important than absolute salinity values (Little, 2002). Brackish waters, located between marine and freshwater habitats (e.g., estuarine turbidity maximum zones) have also other properties particularly challenging for benthic organisms (Figure 16), such as oxygen depletion. Direct effects of current speed or 'bed stress' also affect benthic estuarine organisms. Excluding oligohaline regions (salinity <5), most benthic animals inhabiting estuarine ecosystems are euryhaline species of marine origin. Nevertheless, salinity may have important effects on the life-style of estuarine animals, particularly when it changes. Many infaunal animals retreat into the substratum when salinity suddenly falls or rises. This reaction protects them from sudden salinity changes because there is a considerable time lag in salinity changes along few centimeters down in mud or sand. Hard-shelled organisms close their shells for the same purpose. In both cases, body fluids can reach a new equilibrium with the overlaying water over a protracted period. Possibly for this reason, marine euryhaline species penetrate more easily into

Table 1(a) Grid speeds of the copepod *Acartia tonsa* used in experiments, turbulent dissipation rates (ϵ), and wind speeds required in nature to produce equivalent dissipation rates

<i>Turbulence level</i>	<i>Grid speed</i> (cm s^{-1})	ϵ ($\text{cm}^2 \text{s}^{-3}$)	<i>Wind speed</i> (cm s^{-1})	<i>Meteorological classification</i>
Low	0	10^{-5}	Calm	Calm
	0.19	5.2×10^{-5}	1.5	Light air
Intermediate	0.32	2.4×10^{-4}	2.5	Light breeze
	0.44	6.7×10^{-4}	3.5	Gentle breeze
	0.63	2.0×10^{-3}	5.1	Gentle breeze
	0.95	6.6×10^{-3}	7.8	Moderate breeze
High	1.90	5.4×10^{-2}	16.2	Near gale
	3.80	4.3×10^{-1}	33.3	Hurricane

Data based on Kjørboe, T., Saiz, E., 1995. Planktivorous feeding in calm and turbulent environments with emphasis on copepods. *Marine Ecology Progress Series* 122, 135–145.

Table 1(b) Escape coefficients of different life stages of the copepod *Acartia tonsa* (± 1 SE) from mussels, their predators, when subjected to different turbulence intensities (low, intermediate and high)

<i>Experiment</i>	<i>Escape coefficient</i>		
	<i>Low</i>	<i>Intermediate</i>	<i>High</i>
Early nauplii	1.7 ± 0.1	1.1 ± 0.1	1.1 ± 0.1
Late nauplii	1.6 ± 0.1	1.3 ± 0.1	1.2 ± 0.0
Early copepodites	2.8 ± 0.6	2.0 ± 0.3	1.1 ± 0.1
Adults	4.1 ± 0.6	2.3 ± 0.3	2.4 ± 0.2

Data based on Jonsson, A., Gissel Nielsen, T., Hrubenja, I., Maar, M., Petersen, J. K., 2009. Eating your competitor: functional triangle between turbulence, copepod escape behaviour and predation from mussels. *Marine Ecology Progress Series* 376, 143–151.

Figure 15 Relationship between hydrology and life-cycle strategies of estuarine medusae, showing a permanent presence in the benthos either as resting phases or as actively feeding colonies. Both benthic stages will produce planktonic medusae during next generations.

regions of low salinity where salinity is stable. In the presence of density stratification due to salinity (e.g., under a river plume) or temperature (e.g., nearly stagnant estuary), oxygen diffusion to bottom waters is hindered, exacerbating hypoxia and anoxia in bottom waters and sediments (Little, 2002). Resident animals die if the concentration of dissolved oxygen falls below 1 mg l^{-1} . Hypoxia and anoxia events displace pelagic organisms and wipe out demersal and benthic organisms; entire taxa may be lost. Recovery occurs only if the anoxic zone is removed. Turbulence and mixing caused by large storms can break up anoxic zones (Wolanski, 2007), but these events can also increase turbidity, thus leading to negative effects on benthic organisms.

Turbidity is, in fact, a relevant hydrologic variable affecting benthic organisms. It is closely related to substrate properties

and hydrodynamic processes affecting the overlaying water column (e.g., currents, wind velocity and fetch, and tidal forcing). Increased turbidity has usually detrimental effects upon benthic organisms as it affects feeding and respiratory processes. Muddy marine snow flocs are also most harmful to small benthic organisms, such as barnacles and polyps, because flocs stick on them and literally choke them to death. The extreme paucity of some suspension feeders, such as tunicates, hydroids, and sponges, in turbid estuaries is probably related to the clogging of their feeding apparatus with silt. In effect, clean and less turbid estuaries usually have dense coverages of bryozoans, tunicates, and sponges associated to rocky sublittoral substrates (Heip and Herman, 1995). Negative effects of turbidity are also evident in nearshore coastal ecosystems. Mud can be resuspended by wind waves and exported into coastal waters as a bottom-tagging nepheloid layer. Mud escaping from estuarine mud banks and reclamation areas can be transported over long distances, and impact sensitive benthic ecosystems, such as seagrasses and coral reefs, due to increased turbidity (Wolanski, 2007). Yet, exported mud can also be beneficial, supporting penaeid shrimps in offshore mud banks (Alongi and Robertson, 1995).

The salinity tolerance of epibenthic organisms can also affect their grazing potential and feeding grounds. Some predators, such as *Carcinus maenas*, are euryhaline and penetrate far into estuarine systems, whereas stenohaline predators are spatially more restricted. Thus, the relative distribution of euryhaline and stenohaline epibenthic predator species will directly impact their putative prey (Little, 2002).

A recent example illustrating the relevance of temperature as a driver of benthic organisms is related to bivalves in the Wadden Sea. In this case, elevated temperatures negatively affected *Macoma balthica* populations due to several detrimental effects on recruitment, mortality, and growth (Beukema et al., 2009).

Figure 16 Hydrology and biota interactions affecting the distribution of benthic estuarine fauna.

10.02.3.2.2 Hydrologic control of benthic communities

Estuaries have long been regarded as stressful environments for benthic communities due to a high degree of variability in hydrologic variables (e.g., water dissolved oxygen, temperature and salinity, and bed-sediment dynamics). However, estuarine biota are well adapted to cope with these environmental stresses, thus making estuarine communities resilient to estuarine inherent variability. This ability to absorb stress without adverse effects is regarded as 'environmental homeostasis' (Elliott and Quintino, 2007). In the case of estuarine organisms, estuarine instability and variability are regarded as a subsidy whereby they successfully capitalize on the stressful conditions. Yet, estuaries should be regarded as stressful environments for marine- and freshwater-adapted organisms.

Numerous hypotheses involving hydrologic regulation have been proposed to explain distribution patterns of the biomass, density, species richness and productivity of macrofaunal assemblages in localized estuarine areas. These include (1) nutrient loading and primary production (e.g., Heip et al., 1995); (2) periodic anoxia (Diaz and Rosenberg, 1995); (3) freshwater flushing and salinity (e.g., Ardisson and Bourget, 1997); and (4) sediment grain size (e.g., Mannino and Montagna, 1997). While each hypothesis may be appropriate to specific locations, their general relevance can be partly assessed by examining community variability patterns over different spatial and temporal scales. Temporal fluctuations in density and species richness of benthic fauna over days and weeks are very small (Edgara and Barrett, 2002). Fluctuations over monthly, seasonal, and interannual scales are generally inferior to spatial variation over distances of hundreds of

meters. At large spatial scales, faunal biomass and productivity primarily vary across estuaries rather than between localities within estuaries. Hence, general characteristics of each estuary appear to have overriding influences on these variables (Edgara and Barrett, 2002).

Among four different hydrologic factors proposed to account for variation in faunal biomass (see above mentioned hypotheses), only the former is apparently supported by this data set (Edgara and Barrett, 2002). Indeed, spatial patterns of faunal biomass and productivity and the relatively low levels of intrannual variability were consistent with the first hypothesis that relates faunal biomass and productivity to estuarine nutrient loading and primary productivity. Anoxia and sediment grain size would be expected to show substantial axial variation within estuaries, whereas periodic defaunation caused by freshwater flushing and anoxia should cause substantial intrannual variation (Table 2). Potentially relevant variables related to primary productivity at the estuary and nearshore scale include nutrient loading, turbidity, and light penetration, and flux of allochthonous organic matter (Edgara and Barrett, 2002). According to Dahlhoff (2004), differences in nearshore primary productivity and subsequent delivery of high-quality phytoplankton associated to upwelling events, induce notorious spatial differences in benthic community structures.

Estuarine benthic communities are impacted by episodic, meteorologic events, such as hurricanes, and are thought to be resilient to habitat alterations. Post-hurricane benthic communities show significant reductions in the number of taxa, diversity, and abundance, as well as shifts in composition and

Table 2 Synopsis on the relationships between freshwater discharge and the abundance of different species of nektonic and benthic organisms in estuarine and nearshore ecosystems. Significant positive and negative relationships between variables are represented by + and -, respectively, and explanatory hypothesis are presented inside brackets

River	Freshwater discharges	Species	Relationship/Hypothesis	Lag (years)	Source
Coastal and large estuarine environments:					
St. Lawrence	Annual mean	Lobster	+	6	Sutcliffe (1972)
		Halibut	+	10	Sutcliffe (1972)
		Haddock	+	8	Sutcliffe (1972)
		Soft-shell clam	+	5	Sutcliffe (1972)
Zambezi	Inter-annual	Shrimps	+ (Recruitment enhancement; Dispersion; turbidity)	0	Gammelsrød (1992)
Guadiana	Annual mean	Community	+ (Food web)	0	Erzini (2005)
Ebro	Monthly mean	Anchovy	+ (Food web; recruitment)	1	Lloret et al. (2005)
Sheltered estuarine environments:					
Southampton	Water Monthly mean (summer)	Hard-shell clam	- (Recruitment; larval flushing)	0	Mitchel (1976)
Loxahatchee	Daily	Benthic community	+ (Shift from a pelagic to a benthic food web)	0	Nichols (1985)
Berre Lagoon	Monthly mean	Benthic community	- (Community structure; Changes physiological stress)	0	Stora and Arnoux (1988)
Guadiana	Monthly mean	Anchovy	+ (planktonic food availability)	0	Chicharo et al. (2006)

Figure 17 Submarine groundwater discharge within intertidal areas of an estuarine ecosystem under Mediterranean climate influence, at low tide (a) and high tide (b), showing biota aggregations in the discharge area (c).

ranking of dominant taxa. These effects are not associated with changes in chemical contamination, organic enrichment of sediments, or hypoxia, but are likely due to hurricane-related scouring and changes in salinity (Engle et al., 2009).

Submarine groundwater discharge rates are commonly much smaller than surface flows. Nevertheless, groundwater inflows cannot be neglected because they impact sediment and water properties in the vicinity of discharge areas, especially salinity, therefore affecting planktonic and benthic communities. Groundwater discharges into saltmarshes are quite swift, being enhanced by bioturbation, decaying vegetation, and turbulence (Figure 17), and there is evidence that they interact with benthic boundary layer (Westbrook et al., 2002; Shi et al., 2006). The benthic boundary layer is composed by the water layer immediately adjacent to the bottom substrate. This zone is of considerable interest due to steep gradients of energy, dissolved and particulate chemical components, suspended matter and resident biological communities.

The benthic boundary layer also occurs in hard substrates, such as coral reefs, and cryptobenthic fishes are especially important within these areas. They play a relevant role in the recycling of macrophytes' primary production through detrital pathways, to higher trophic levels. Wave exposure is a pivotal determinant of the structure of cryptobenthic reef-fish assemblages (Depczynski and Bellwood, 2003).

10.02.3.3 Nekton

10.02.3.3.1 Hydrologic control of nekton physiology and behaviour

For nektonic organisms, hydrological conditions such as strong tidal currents, extremely high or low temperatures, intense freshwater discharges, and depletion of dissolved oxygen, which commonly occur in estuarine habitats, may be stressful. In well-mixed estuaries, much of the spatial and temporal distribution of aquatic organisms can be

explained by reference to the salinity gradient (Kimmerer, 2002). For marine fish and crustaceans, the extent of penetration and residence times in estuaries depends primarily on their salinity tolerance (Whitfield et al., 2006). Estuarine fishes are stressed by salinity changes, and they adapt to those changes through osmotic regulation, an energy-demanding process (Malloy et al., 1996). Thus, brackish-water organisms are usually smaller than their marine relatives (Yamashita et al., 2003). In fact, the whole-body cortisol concentration, a stress indicator (Wendelaar Bonga, 1997), is approximately 4 times higher in fish from estuarine than nearshore sites. This elevated cortisol level is possibly attributable to the much higher diel fluctuations in temperature and salinity observed in estuarine habitats than in nearshore habitats, where both environmental variables are comparatively stable. However, elevated growth rates, feeding conditions, and densities overall indicate that elevated cortisol levels are within a physiologically tolerable range, and do not impair fish performance (Yamashita et al., 2003).

Fish performance in estuarine ecosystems is also strongly regulated by fish swimming abilities. According to Wakeman and Wohlschlag (1981), for pelagic estuarine fishes, least-cost swimming speeds in length-specific terms are less for larger fish than for smaller fish, especially with respect to micronektonic larval phases (Leis, 2006). A relationship between ecophysiological performance measured by the RNA:DNA ratio (Chícharo and Chícharo, 2008), and swimming abilities of different post-flexion fish larval stages, has recently been established for different species (see Figure 18; Faria et al., 2011; Chícharo, unpublished data). In fact, at the end of the pelagic period, and for a time prior to this, fish larvae are both morphologically and behaviorally well developed. They are one or more centimeters in length, have all or nearly all their fins, functional sensory organs that can detect predators, and they swim faster than ambient currents in many cases (Leis, 2006). During this period, post-flexion larvae constitute gross violations of the simplifying assumption that classify them as passive particles and they are clearly nektonic. The boundaries for this classification are dependent on marine ecosystems. Indeed, effective swimming is obviously easier to achieve in nearshore areas, with low mean current speeds (e.g., 10 cm s^{-1} , dos Santos et al., 2008) than in meso- and macrotidal estuaries with threefold higher current speeds ($\sim 30 \text{ cm s}^{-1}$, Alvera-Azcaratea et al., 2003). Globally, comparison of *in situ* swimming speeds of fish larvae and water velocity evidence abilities to swim against current during several periods (see Table 3).

Temperature is also a crucial variable, especially in highly variable ecosystems, such as estuaries. Temperature has two effects on swimming performance in fish. First, fish are ectotherms, and fish muscle cells operate more efficiently at higher temperatures. Second, the seawater viscosity increases as temperature decreases, which means that either higher speed or greater size are required to reach a given Reynolds number at cooler temperatures. This viscosity effect of temperature is greatest for smaller fish and at lower water temperatures. At cooler temperatures, greater speeds are required to reach an inertial environment, and the increased swimming efficiency. Both of these effects contribute to increased swimming efficiency at higher temperatures,

Figure 18 Relationship between RNA:DNA ratio, an indicator of nutritional status and growth rate, and U_{crit} indicator of swimming abilities (see text for details) in fish larvae of *Solea senegalensis*, *Sparus aurata*, and *Argyrosomus regius* during ontogeny and rearing, at similar water-temperature conditions. Each symbol represents results for individual larvae. Data derived from Faria, A.M., Muha, T., Morote, E., Chicharo, M.A., 2011. Influence of starvation on the critical swimming behaviour of the Senegalese sole *Solea senegalensis* and its relationship with RNA/DNA ratios during ontogeny. Scientia Marina 75:87-94. (unpublished data).

Table 3 Mean speed over bottom for post-flexion fish larvae of different families and mean ambient current speed. Values derived from in situ studies that examined if fish larvae movement could overcome the passive drift induced by ambient current speed

Family	Habitat	Water depth (m)	Mean ambient current speed $cm. s^{-1}$	Mean fish speed over bottom $cm. s^{-1}$	Source
Blenniidae	Warm temperate island	5-6	7-12 (drifting beads)	15-17	Ninos (1984)
Sillaginidae	Temperate bay	2-7	7-12 (drogue, current meter)	2-13	Hindell et al. (2003)
Pomacentridae	Tropical island	8-35	10-16 (drogue)	15-20	Leis and Carson-Ewart (2003)
Chaetodontidae	Tropical island	8-35	10-16 (drogue)	16-21	Leis and Carson-Ewart (2003)

although, within natural temperature ranges, the effects of viscosity may outweigh the effects of muscle efficiency. It is clear that larvae can swim faster and more efficiently in warmer waters, namely in nearshore tropical coral reefs. There is a typical assumption that temperate fish larvae are poor swimmers compared to tropical estuarine fishes. This theory, although not fully proved, may be due, in part, to differences in water temperature. It is well known that temperature influences both the physiology of fish larvae and the physics of the hydrodynamic environment in which larvae are swimming. Mean, *in situ* swimming speeds of settlement-stage tropical reef fish larvae range between 2 and $66 cm s^{-1}$, whereas those of settlement-stage wild temperate larvae are $5-15 cm s^{-1}$, at the slow end of the range of tropical species (Leis, 2006).

10.02.3.3.2 Hydrologic control of nektonic communities

Several mechanisms have been proposed to explain positive effects of freshwater discharge changes upon estuarine nektonic communities. Positive effects to resident species appear to operate mainly through the stimulation of primary production, with effects propagating up the food web (Wolanski, 2007), or the alteration of attributes of their physical habitat (Kimmerer, 2002).

All major resident or temporary nektonic communities inhabiting estuaries are influenced by hydrological forcing. Estuarine ecosystems respond most strongly to interannual timescales. Episodic, climatically induced resource pulses, related to hurricanes also affect community structure through a combination of physical and chemical habitat changes, as nektonic communities often return quickly to pre-hurricane conditions (Piazza and Peyre, 2009).

In temperate estuaries, nektonic production peaks during spring and summer in response to increased solar radiation, warmer waters, and possibly higher food availability. In tropical estuaries, peak productivity occurs during the post-monsoon season, when riverine nutrients are still abundant and water clarity and light availability have improved after high-turbidity peaks linked to high river flow in the monsoon season (Alongi, 1998). A likely explanation for the influence of river flow on fish and crustacean biomass is a river-flow-induced enhancement of the recruitment success. Possible causal mechanisms to support this hypothesis include (1) a greater primary and bacterial production resulting from increased nutrient loading, organic matter loading, and estuarine stratification during high river flow periods; (2) a greater larval and juvenile survival due to reduced predation rates under higher turbidity conditions associated with greater riverine sediment loads; (3) increased survival of early life-history stages due to increased dispersion or retention; and (4) the extension of nursery habitat with increased river flow (Kimmerer, 2002).

For temporary fish species, highly turbid freshwater plumes may constitute important cues to find spawning or nursery areas. In fact, according to Kingsford and Suthers (1994), low-inflow years, in association to the reduction of turbidity plumes, hampers the orientation of adult fishes during their search for suitable spawning and nursery areas. Moreover, freshwater input insures well-developed ETM areas that pelagic fish use as nursery or feeding grounds based on the abundance of copepods. Fish eggs and larvae retained within the ETM regions may face (1) a zone of increased zooplankton biomass and production (Simenstad et al., 1994); (2) a predation refuge due to high turbidity; and (3) optimal temperature or salinity conditions (Strathmann, 1982). Episodic river flow and storm events during the fish spawning season may alter circulation patterns within the ETM regions, causing loss of eggs and larvae from the ETM nursery areas, with negative consequences for fish survival (North and Houde, 2001; Morais et al., 2010; Figure 19).

Despite its seasonality, high productivity of estuarine ecosystems is also a cue for attraction of fish and crustaceans into these nursery areas. Shallow-water habitats in estuaries, including tidal wetlands and seagrass beds, offer food and shelter from predators to fish juveniles. Owing to high habitat diversity, structural complexity, and varying

turbidity, resources are partitioned, thus providing ecological stability.

For resident nektonic species, population connectivity is also a key factor. Instructive examples are endemic fishes from the California's delta that are currently at risk of extinction. The decadal scale coherence between population collapses of fish and their zooplankton food suggests that reduced production of supporting food webs is one mechanism of diminished carrying capacity. The magnitude of aquatic habitat loss and fragmentation is well established: virtually all of the delta's original 1400 km² of tidal marsh have been drained or diked (Nichols et al., 1986) and the tributary rivers have been dammed, channelized, and disconnected from their floodplains. Cloern (2007) recently showed how disruption of habitat connectivity might influence production in pelagic food webs supporting secondary consumers, such as planktivorous fish. In fact, habitat connectivity can amplify rates of nutrient regeneration and primary and secondary production, affecting global ecosystem functioning. Many efforts to restore aquatic communities and sustain depleted stocks of individual species have failed for unknown reasons (Thompson et al., 2001). Connectivity of functionally variable habitats may be a key to the design of actions for sustaining populations of harvested species and biological diversity across increasingly fragmented landscapes (Cloern, 2007).

10.02.4 Biologic Regulation of Estuarine and Nearshore Hydrology

Aquatic organisms impact a wide diversity of hydrologic variables and processes within their habitats (Wolanski et al., 2004; Wolanski, 2007). External sources of energy (e.g., light, reduced inorganic compounds and organic compounds), dissolved inorganic macro- and micronutrients (e.g., C, N, P, and Fe), and electron acceptors (e.g., O₂, NO₃⁻, and SO₄²⁻) are required for maintenance, growth, and reproduction of aquatic organisms. Except for light, these elements are biologically removed from the water column or sediment pore water, metabolized, and transformed. Most metabolic pathways, physiologic processes, prey-predator interactions, and parasite-host interactions in aquatic food-webs generate by-products, which are usually released into the water (e.g., CO₂, O₂, dissolved inorganic nutrients, DOM, and particulate organic matter). All compounds used as resources and electron acceptors or

Figure 19 Schematic representation of the migration patterns of anchovy (*Engraulis encrasicolus*) in an estuary under Mediterranean climate influence (Guadiana Estuary) and adjacent coastal waters, taking advantage of estuarine turbidity maximum (ETM) region.

produced as metabolic by-products are actively affected by biological activity. Other biologically produced compounds (e.g., pheromones, siderophores, antibiotics, toxins, and exoenzymes) are also released into the water column, thus globally affecting chemical properties in aquatic ecosystems. Aquatic organisms may also passively regulate hydrologic features. Benthic bioturbators and ecosystem engineers (e.g., bivalve reefs and submerged and emergent aquatic vegetation), for instance, modify their physical environment, affecting water circulation, turbidity, sediment accretion, and wave attenuation (Bianchi, 2007; Wolanski, 2007).

This section will examine how pelagic and benthic organisms regulate key hydrologic attributes in estuarine and nearshore coastal ecosystems, specifying how these changes are propagated into ecosystem functioning. For the sake of simplicity, we will consider, in turn, how biota impact the concentration of chemical elements needed for organism growth (dissolved gases, inorganic nutrients, and organic matter), biological contaminants, non-nutrient bioactive compounds, turbidity, and water flow. In view of the major aims of ecohydrology, which include the use of combined physical and biological manipulations to increase ecosystem robustness and its ability to cope with human stresses (Wolanski et al., 2004; Wolanski, 2007), this section will also specify how aquatic organisms might contribute to ecosystem remediation (e.g., eutrophication, HABs, fecal contamination, and chemical contamination). The consequences of various human activities for the functioning of estuarine and coastal ecosystems are specifically addressed by Elliot and Kennish (see Chapter 8.01).

10.02.4.1 Biologic Control of Dissolved Gases

Carbon dioxide is a relevant, climatically active compound. As other gases, it is controlled by various physical (e.g., wave and sea roughness, wind, temperature, salinity, rainfall, and surfactants) and biological factors. Yet, the latter are usually recognized as fundamental drivers of carbon dioxide distribution in estuarine and nearshore ecosystems aquatic ecosystems (e.g., Upstill-Goddard, 2006). Uptake of carbon dioxide by photo- and chemoautotrophic organisms, and its release by aerobic respiration are major biological processes controlling CO₂ concentration in the water. Heterotrophic bacteria are the most relevant contributors to CO₂ release accounting, on average, for approximately 50% of global community respiration (Kaiser et al., 2005; Kirchman, 2008; Robinson, 2008), and are commonly limited by the availability of organic substrates and temperature (see del Giorgio and Williams, 2005). Increased respiration of anthropogenic sources of organic carbon, following urbanization and industrialization, is mainly responsible for CO₂ supersaturation, leading to net heterotrophy, oxygen depletion, and CO₂ effluxes into the atmosphere (see Gupta et al., 2009). Additionally, precipitation and dissolution of calcium carbonate associated to calcareous organisms (e.g., zoobenthic species such as bivalves) are also biogenic sources of CO₂. The contribution of calcareous organisms as CO₂ source is probably increasing due to the global translocation of bivalves and their successful colonization of estuarine habitats (see Chauvad et al., 2003).

Dissolved oxygen concentration in estuarine and coastal ecosystems is controlled by physical and biological processes

as well, but the latter usually explain most of the variability on oxygen dynamics (e.g., Borges and Frankignoulle, 2001; Quinones-Rivera et al., 2010). Oxygen is the electron acceptor used during aerobic respiration, and is also a product of oxygenic photosynthesis. Globally, oxygen concentration in the water column or sediment pore water reflects the balance between respiration and photosynthesis and is, therefore, strongly dependent on the availability of light and organic substrates (del Giorgio and Williams, 2005). Periods or ecosystem locations with increased organic matter loads and reduced hydrodynamics (e.g., temperature or saline stratification) usually have lower oxygen concentrations, namely at bottom waters (Mallin, 1994; Fenchel et al., 1998; Wolanski, 2007; Barbosa, 2010). Particularly steep and dynamic vertical oxygen gradients may be established at the sediment surface (see Kuhl and Polerecky, 2008). In salt marshes and mangroves, benthic bioturbators may decrease, to some extent, the probability of hypoxic or anoxic events. In fact, bioturbation associated to biodiffusers, regenerators, and gallery diffusers form important conduits for the circulation of water, and aerate the sediment deeper in the substrate (Kaiser et al., 2005; Bianchi, 2007; Wolanski, 2007). Increased sediment aeration by mangrove crab activity, for instance, is related to declines in sulphide and ammonium concentrations within the sediment, enhancing the reproductive output and productivity of mangrove forests (Smith et al., 1991).

Anthropogenic eutrophication is associated to increased loads of organic and inorganic nutrients into estuarine and coastal ecosystems, leading to phytoplankton and macroalgal blooms (Burkholder et al., 2007). As a result of oxygen production by photosynthesis, oxygen oversaturation may occur during daytime. Yet, increased oxygen consumption by respiration is frequently related to water-column and sediment hypoxia, and occasionally anoxia, during the night. Oxygen depletion, strongly mediated by bacterial respiration, is obviously more severe and frequent in estuarine and coastal ecosystems with high water residence times and high organic matter loads (e.g., microtidal fjords, enclosed bays, choked coastal lagoons, the Adriatic, Baltic, Black and North Seas, and Gulf of Mexico; Cloern, 2001). Hypoxic and anoxic events are often associated to buildup of toxic compounds, such as by-products of anaerobic respiration (e.g., hydrogen sulfides), and decline and mortality of benthic and some pelagic species, ultimately leading to extensive dead zones (Alongi, 1998; Kaiser et al., 2005; Calleja et al., 2007; Wolanski, 2007). Restoration of stressed ecosystems usually involves diminishing the water residence times by dredging to deepen channels or opening or relocating new inlets or river mouths. In dammed rivers, the establishment of minimum environmental river discharge rates and the generation of occasional man-made freshets from dams were also suggested (Wolanski et al., 2006; Wolanski, 2007).

10.02.4.2 Biologic Control of Dissolved Inorganic Nutrients

Dissolved inorganic nutrients (e.g., nitrates, ammonium, phosphates, and silicates for diatoms) are key elements for all autotrophic organisms, being removed by photoautotrophs (e.g., phytoplankton, microphytobenthos, and macrophytes) and chemoautotrophs (e.g., nitrifying bacteria, and anaerobic ammonia oxidizers). Moreover, some strict or facultative

anaerobic heterotrophic bacteria use nitrate, instead of oxygen, as an electron acceptor under anaerobic conditions (dissimilative nitrate reduction). Heterotrophic bacteria might also assimilate dissolved inorganic macro- and micronutrients, if the quality and stoichiometry of organic matter are not suitable to their elemental and biochemical composition, thereby directly competing with primary producers (Kirchman, 2000b; Church, 2008). Denitrifying and anaerobic ammonium-oxidizing bacteria are particularly interesting, as they uptake nitrate from the water, and reduce it to nitrogen gas (N_2), which may escape into the atmosphere (Rheinheimer, 1994; Kirchman, 2008).

Biologic processes are also relevant sources of dissolved inorganic nutrients within aquatic ecosystems. The remineralization of organic matter into inorganic nutrients undertaken by heterotrophic bacteria, and phosphate and ammonium excretion by bacterivores, mostly phagotrophic protists, are currently considered major biologic sources of inorganic nutrients (Ducklow, 2008; Sherr and Sherr, 2008). In shallow coastal ecosystems, benthic organisms (e.g., bivalve mollusks) may also constitute relevant sources of phosphate and ammonia (Dame and Libes, 1993; Chapelle et al., 2000; Wolanski, 2007). Biologic sources of inorganic nutrients (regenerated) are particularly relevant for ecosystems (e.g., tropical ocean) or periods of reduced mechanical energy inputs, when (new) nutrients derived from allochthonous or deep water sources are negligible (Legendre and Rassoulzadegan, 1995; Kaiser et al., 2005). In temperate estuaries and nearshore coasts, the relevance of biologic benthic and pelagic sources of nutrients is stronger during the summer, when high phytoplankton production is strongly based on regenerated nutrients (Mallin, 1994; Sin et al., 1999; Chapelle et al., 2000). On such occasions, vertical diel migrations of zooplankton may provide significant nocturnal inputs of recycled nutrients to surface waters (Alcaraz et al., 2007).

Anthropogenic pressures are usually associated to increased nutrient loading into estuarine and coastal ecosystems, frequently leading to severe deleterious effects (see previous Section). Management strategies to minimize or remediate environmental problems related to anthropogenic eutrophication usually involve reducing anthropogenic nutrient inputs to the watersheds, diminishing the water residence times, and promoting biologic communities that effectively remove dissolved inorganic nutrients (CCME, 2000; Cloern, 2001; Wolanski, 2007). In this context, the maintenance, restoration, transplantation, and creation of wetland areas, including emergent and submerged vegetation, mudflats, and macroalgae beds, have been extensively proposed as eco-hydrological tools to control nitrogen and phosphorus in aquatic ecosystems (Wolanski et al., 2004; Wolanski, 2007; Xu et al., 2008; Weisner and Thiere, 2010). Furthermore, the enhancement of denitrifying and ammonia-oxidizing bacteria within natural and constructed wetlands is also used to diminish excessive nutrient levels in aquatic ecosystems (Bednarek and Zalewski, 2007; Wickramasinghe et al., 2009; Yin et al., 2009).

10.02.4.3 Biologic Control of Dissolved Organic Matter

DOM is continuously being produced within aquatic ecosystems through physical-chemical and biological processes

(see Section 10.02.2.2.1), but the latter are usually predominant. Biologic production of DOM is associated to a wide variety of processes, including extracellular release by primary producers, grazer-mediated processes (excretion, egestion, and sloppy feeding), molting, programmed cell death, parasite-induced cell lyses, production of mucous polymers, and particle solubilization via exoenzymatic activity (Nagata, 2000; Carlson, 2002; Bertilsson and Jones, 2003). Globally, any pelagic or benthic organism, independently of its size or nutritional strategy, contributes to the DOM pool. Although DOM may be used by different organisms, including some phytoplankton and metazoan groups, heterotrophic bacteria are, undoubtedly, the dominant consumers of DOM in aquatic ecosystems. Aquatic fungi play a relevant role in the decomposition of dissolved and particulate organic detritus only within particular ecosystem habitats, namely salt marshes and mangroves (Alongi, 1998; Mann, 2000; Kaiser et al., 2005).

As heterotrophic bacteria are often substrate limited, biologic production of labile dissolved organic substrates usually enhances bacterial growth and production rates. Positive relationships between phytoplankton and heterotrophic bacteria, observed at different spatial and temporal scales (e.g., annual cycles, and upwelling episodes), illustrate the relevance of phytoplankton as a source of labile DOM (see Section 10.02.2.2.1; see Figure 5). When biological production rates of DOM exceed uptake rates, a net accumulation might occur, eventually leading to DOM export to adjoining ecosystems (Barbosa et al., 2001). Net accumulation of DOM within estuarine and coastal ecosystems may constitute a relevant energy reservoir, sustaining aquatic food webs during periods of lower primary production (see Barbosa et al., 2001).

At the level of ecosystem functioning, biologic production of DOM and particulate organic matter and their assimilation by heterotrophic bacteria is particularly relevant within ecosystems where most of the primary production is not directly consumed by herbivores, but instead is processed through detrital pathways. Such is the case with mangroves, salt marshes, seagrass meadows, and macroalgae forests, where the largest fraction of the primary production (up to 90%) is channeled into the ecosystem as organic detritus (Duarte and Cebrián, 1996; Alongi, 1998; Mann, 2000). Moreover, non-macrophyte-dominated ecosystems also display clear heterotrophic phases, when primary production rates are diminished and organic detritus are clearly fueling benthic and pelagic food webs (Legendre and Rassoulzadegan, 1995; Kaiser et al., 2005; Barbosa, 2006; David et al., 2006).

Anthropogenic eutrophication of estuarine and coastal ecosystems is associated to direct and indirect increases in the concentration of organic matter that typically result in oxygen deficiency and increased production of hydrogen sulfide by sulfate-reducing bacteria (Alongi, 1998; Wolanski, 2007). The natural self-purification of natural waters, strongly mediated by heterotrophic bacteria and bacterivores, is a relevant microbial service to ecosystem functioning (Rheinheimer, 1994; Ducklow, 2008). However, in shallow estuarine systems, excess biomass of macrophytes is sometimes harvested annually to prevent further accumulation of organic matter, and oxygen deficiency (e.g., Sfriso et al., 2003; Wolanski, 2007).

10.02.4.4 Biologic Control of Biological Contaminants

Phagotrophic organisms, including strictly heterotrophic and mixotrophic protists and metazoans, mostly ingest living particulate organic matter. Phagotrophic protists and metazoans exhibit a wide variety of feeding strategies and prey types, and usually display a quite selective feeding behavior (Montagnes et al., 2008a; see Section 10.02.3). Globally, phagotrophic protists and metazoans may effectively control the concentration and composition of suspended particles in estuarine and coastal ecosystems, including phytoplankton. Phytoplankton usually represent the dominant primary producers in most aquatic ecosystems. Their composition and activity largely control essential biochemical pathways, energy efficiency transferences and efficiencies of energy and essential biochemicals, and the respiration rates within aquatic ecosystems (Cloern and Dufford, 2005; del Giorgio and Williams, 2005). There are, however, certain phytoplankton taxa that form HABs, and constitute a global environmental problem. HABs present several deleterious effects including (1) risks for human health due to algal toxins and its accumulation within living aquatic resources (e.g., bivalve mollusks and fish); (2) direct impacts on living aquatic resources due to algal toxins, mucilage, or mechanical effects; (3) impacts on tourism and on the recreational use of estuarine and coastal waters; and (4) damage to estuarine and coastal ecosystems due to global environmental degradation, including oxygen depletion and hydrogen sulfide production (Paerl, 1988; Zingone and Enevoldsen, 2000). HABs are controlled by a combination of hydrological, chemical, and biologic factors (see Figure 20;

Figure 20 Schematic representation of the potential for harmful algal blooms along habitat gradients in irradiance (I_0), nutrient concentration ($[S]$), and hydraulic flushing (expressed as the residence time, τ). In addition to physical-chemical regulation, bloom occurrence is further controlled by biologic loss sources, such as predation and viral-induced lyses. The differential between phytoplankton growth and loss rates, not only growth rates, will effectively determine if a bloom will occur. Reproduced from Smayda, T.J., 2008, Complexity in the eutrophication-harmful algal bloom relationship, with comment on the importance of grazing. *Harmful Algae* 8, 140–151.

Paerl, 1988; Smayda, 1997). The fundamental ecological roles of phytoplankton, as well as their putative detrimental effects, make the analyses of biologic controls of phytoplankton a particularly relevant aspect for ecosystem management and remediation.

A wide diversity of benthic and pelagic protists and metazoans is responsible for phytoplankton removal (including HAB species) in estuarine and coastal ecosystems (Paerl, 1988), but phagotrophic protists are usually the dominant phytoplankton grazers (Calbet and Landry, 2004). Protist grazers are capable of growing as fast as their phytoplankton prey, thus minimizing the occurrence and duration of phytoplankton blooms (Calbet and Landry, 2004). Both experimental approaches and field studies have shown that phagotrophic protists may be responsible, to some extent, for the dissipation or absence of harmful phytoplankton blooms in inland, estuarine, and coastal areas (Jeong and Shim, 1996; Calbet et al., 2003; Rosetta and McManus, 2003; Gobler et al., 2007; Jeong et al., 2008; Stoecker et al., 2008). Other biologic processes, namely viral-, bacterial- and eukaryotic-induced lyses may also contribute to the demise of HABs (Hare et al., 2005; Frazier et al., 2007; Montagnes et al., 2008b; Smayda, 2008).

Benthic suspension feeders (e.g., bivalve mollusks, sponges, tunicates, and polychaetes) may also exert a strong top-down control on phytoplankton assemblages in shallow coastal ecosystems (Cloern, 2001; Wong et al., 2003; Petersen, 2004). Natural assemblages of phytoplankton and benthic bivalves (both native and introduced species) within freshwater and estuarine ecosystems are inversely related, at different time-scales, implying a strong grazing control by benthic predators (see Cloern, 2001; Petersen, 2004; Caraco et al., 2006; Gulati et al., 2008). Experimental mesocosm experiments using natural assemblages have shown that suspension-feeding bivalves apparently also control outbreaks of toxic algal blooms (see Figure 21; Cerrato et al., 2004; Smayda, 2008). In addition to reducing phytoplankton biomass and HAB species, benthic predators can also control other hydrologic properties. Benthic suspension feeders accelerate the sedimentation of suspended food particles by pelletization. Enhanced sedimentation contributes to the removal of nutrients from the water column, thus decreasing turbidity and pelagic nutrient and oxygen demand (Soucho et al., 2001; Nelson et al., 2004; Wolanski, 2007). These biologically mediated hydrologic alterations in the water column can also affect benthic biogeochemical fluxes, enhance microphytobenthos and macrophytes, and eventually exert a positive feedback on phytoplankton growth. Moreover, bivalve reefs also constitute a structural refuge for benthic invertebrates and fishes (Prins et al., 1998; Soucho et al., 2001; Porter et al., 2004; Gulati et al., 2008).

Globally, benthic bivalves are frequently used to control phytoplankton biomass and blooms, improve water quality, and mitigate eutrophication impacts within estuarine and coastal ecosystems (Prins et al., 1998; Nelson et al., 2004; Caraco et al., 2006; Wolanski, 2007). HABs constitute a serious environmental threat to estuarine and coastal ecosystems, and several physical-chemical methods have been proposed to control and mitigate these events (e.g., clay flocculation, Sengco and Anderson, 2004). However, the repercussions of these control strategies still remain a concern (Frazier et al., 2007). Bivalve mollusks, namely native species, have also been

Figure 21 Changes in the biomass and composition of phytoplankton for different experimental treatments, during a 9-day mesocosm experiment designed to examine the effect of the bivalve mollusk *Mercenaria mercenaria* on blooms of a brown tide algae: (a) concentration of chlorophyll *a*, as a proxy for phytoplankton biomass; (b) abundance of the harmful algal species *Aureococcus anophagefferens* (cell size, ca. 2–4 μm); and (c) relative contribution of *A. anophagefferens* to total phytoplankton biomass. Values are means ($\pm 1\text{SE}$). Note that bivalves not only prevented an increase of total phytoplankton biomass but also induced a shift in phytoplankton composition, to the detriment of the harmful algae. Reproduced from Cerrato, R.M., Caron, D.A., Lonsdale, D.J., Rose, J.M., Schaffner, R.A., 2004. Effect of the northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide *Aureococcus anophagefferens*. *Marine Ecology Progress Series* 281, 93–108.

proposed as biofilters to remove or reduce HABs in freshwater and estuarine ecosystems (Chícharo et al., 2006; Wolanski, 2007; Gulati et al., 2008). Although there is some ingestion of harmful algae by bivalves, the responses of bivalve species to different harmful algae are species specific, indicating that generalizations about removal of harmful algae by bivalves cannot easily be made (Dionísio Pires et al., 2007; Hegaret et al., 2007; Liu et al., 2009). It is worth noting that benthic suspension feeders, namely bivalves, are embedded within a greater, overarching grazing cascade (see Smayda, 2008). Benthic grazing may potentially affect phytoplankton and harmful algae indirectly, by changing the abundance of their predators (e.g., phagotrophic protists, micrometazoans, and mesozooplankton) or direct competitors (Dupuy et al., 2000; Wong et al., 2003; Cerrato et al., 2004; Maar et al., 2008; Trotter et al., 2008). Other potential biological tools to circumvent and/or remediate HABs involve the use of macrophytes to reduce the concentration of inorganic nutrients (Wolanski, 2007), algicidal bacteria (Frazier et al., 2007), phagotrophic

ciliates (Jeong et al., 2008), and specific viruses (Nagasaki et al., 2009).

Aquatic organisms may also be used to control or remediate other biological contaminants, such as fecal and pathogenic bacteria and vectors of water-related human diseases (e.g., malaria and schistosomiasis; see Wolanski, 2007). The survival time for most fecal and pathogenic bacteria in estuarine and coastal ecosystems is relatively low, and is affected by a wide range of physical, chemical, and biological factors (Rheinheimer, 1994). Yet, natural assemblages of phagotrophic protists, namely aplastidic nanoflagellates, are considered predominantly responsible for the elimination of enteric bacteria from natural estuarine and coastal ecosystems (see Gonzalez et al., 1992). Management and restoration strategies to minimize fecal pollution involve passive, physical manipulations to reduce water residence time and enhance marine influence (Portnoy and Allen, 2006), and also biologic manipulations using zooremediation with specific animal species, for example polychaetes and sponges (see Gifford et al., 2006; Licciano et al., 2007).

10.02.4.5 Biologic Control of Bioactive Compounds

Aquatic organisms produce a wide variety of nonnutrient bioactive compounds, which are directly released into the water, thus globally affecting chemical properties in aquatic ecosystems. These compounds include chemicals with varying functions, such as pheromones, siderophores, antibiotics, toxins, exoenzymes, anti-grazing molecules, and other allelopathic substances, that may either promote or inhibit biological activity. Bioactive compounds produced by aquatic microbes are commonly involved in competitive interactions or used as grazing deterrents (e.g., Rheinheimer, 1994; Smayda, 1997). In case of aquatic metazoans, chemical cues mediate many critical life processes, such as feeding, reproduction, and benthic settling (see Webster and Weissburg, 2009). Some natural bioactive compounds, such as phytoplankton toxins released into the water by healthy cells or after cell rupture, pose serious health hazards to aquatic ecosystems and humans (Zingone and Enevoldsen, 2000). Natural assemblages of cyanotoxin-biodegrading bacteria (Edwards and Lawton, 2009), probably enhanced by bacterivores, are successfully applied to remove or detoxify contaminated waters (Bourne et al., 2006).

Estuarine and nearshore coastal ecosystems are frequently subjected to strong anthropogenic pressures, leading to increases in the concentration of various nonnutrient inorganic and organic contaminants, such as pesticides, herbicides, dioxins, polychlorinated biphenyls, heavy metals, and hydrocarbons (e.g., Wolanski et al., 2004; Wolanski, 2007). Although these molecules constitute a threat to most aquatic organisms, eventually suffering bioaccumulation and bioamplification along the food web, in some cases organisms may use and transform these chemical contaminants into less damaging chemical species. Biodegradation of anthropogenically derived chemical contaminants, as well as natural contaminants, is usually partitioned by different bacterial taxa, which together, as a community, can remediate complex contaminant mixtures in polluted estuarine and coastal environments (Rheinheimer, 1994; Gallego et al., 2006; McKew et al., 2007). Bacterial degradation of chemical contaminants is usually promoted by specific environmental factors, and bioremediation strategies usually optimize contaminant-degradation pathways. For instance, bacterial bioremediation of hydrocarbons is usually stimulated after addition of inorganic nutrients or mycolic acids (Mills et al., 2004; Gallego et al., 2006; Alonso-Gutierrez et al., 2009).

Although bacteria are usually taken as major biodegradation agents, other organisms, such as phytoplankton and macroalgae (phycoremediation), vascular plants (phytoremediation), and benthic metazoans (zooremediation) are also involved in natural bioremediation of chemical contaminants (Gifford et al., 2006; Hong et al., 2008). Vascular plants (e.g., salt marshes and mangroves) transform organic pollutants into less toxic compounds, bioaccumulate heavy metals, and inhibit pollutant migration in shallow ecosystems. They are, therefore, used as ecohydrologic tools to minimize pollution impacts in estuarine and coastal waters (Wolanski et al., 2004; Gifford et al., 2006; Wolanski, 2007). Aquatic animals are also effective remediation agents of heavy metals, hydrocarbons, and persistent pollutants (see review Gifford et al., 2006).

10.02.4.6 Biologic Control of Water Flow, Turbidity, and Habitat Structure

Water flow is an important, sometimes dominant, factor shaping the ecology of aquatic ecosystems (Paterson and Black, 1999). However, to enhance our perception of ecosystem functioning, the influences of estuarine and nearshore biota on hydrodynamic and sedimentologic properties should be also considered. Despite the growing interest in the functional role of biota as a hydrology driver, when, compared to food-web analyses, the conceptual understanding of biota – hydrology interactions is still in its infancy.

Epibenthic communities living in nearshore coastal ecosystems can effectively decrease current speeds in their habitats. For example, maximum current speeds are small ($\leq 0.08 \text{ m s}^{-1}$) in wetland vegetated areas, but peak velocities at adjacent (10 m) wetland-fringed tidal creeks are clearly higher ($\approx 1 \text{ m s}^{-1}$). Within tidal creeks, fully nonlinear, open water hydrodynamics prevail, whereas of in the vegetated wetlands, the currents are reduced by friction of the flow around the vegetation (Wolanski, 2007). Endobenthic organisms, such as cockles, can affect the properties of the benthic boundary layer, causing steeper velocity gradients and increasing the mixing intensity over the cockle beds in comparison to bare sediments (Fernandes et al., 2007).

Planktonic communities regulate turbidity, and can either reduce it due to the consumption of suspended matter by protists and metazooplanktonic organisms, or increase it when feeding on organic matter flocs. Suspended large flocs are usually broken up into small-sized flocs, decreasing their settling velocity. Planktonic organisms also play a key role in the production of marine snow. Marine snow consists of flocs or organic and inorganic fractions, including dead plankton, fecal pellets, and macroscopic aggregates of biological origin, bound by organic material such as transparent exopolymeric particles (TEPs). TEPs are mostly composed of polysaccharides, predominantly exuded by bacteria and diatoms (Figure 22). In estuaries, small mud flocs are aggregated and bound by TEP into very large flocs, called 'muddy snow flocs'. In very turbid estuarine and coastal ecosystems (suspended matter concentration $> 500 \text{ mg l}^{-1}$), marine snow is usually scarce due to the lack of light for photosynthesis. As a result, flocs are largely inorganic and generally small. In less turbid ecosystems, TEPs are common, resulting in large muddy marine snow flocs. Muddy marine snow flocs are very porous, and floc size generally increases with increasing availability of TEP. The location of the muddy marine snow zone varies across estuaries,

Figure 22 Suspended aggregates containing diverse inorganic and organic particules, including dead plankton, fecal pellets, and living phytoplanktonic colonies. Bar = 100 μm .

depending on their turbidity. A concentration of suspended particulate matter less than 100 mg l^{-1} is typically required for sufficient light penetration to allow photosynthesis (Wolanski, 2007).

Some benthic suspension feeders have been shown to capture large quantities of particles and might directly regulate suspended matter and chlorophyll in estuaries and nearshore areas (see Section 10.02.4.3; Gili and Coma, 1998). In fact, the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea was related to huge blooms of diatoms (Beukema and Cadeé, 1990).

Plant and animal mats, associated to mangroves, salt marshes, seagrasses, macroalgae beds, and bivalve reefs, may also decrease water flow speed. This biologically mediated flow reduction enhances sedimentation and sediment accretion rates, minimizing sediment erosion (Bos et al., 2007). Suspension feeding by bivalve reefs also accelerates the deposition of suspended matter by fecal pelletization. Settling is also enhanced by pelletization of flocs filtered out of suspension by feeding bivalves. Conversely, benthic mud burrowers, such as the mud snails, contribute to mud stabilization by compacting it into fecal pellets, but also destabilize the consolidated mud making it more erodible. Likewise, bioturbation exerted by detritivorous invertebrates, such as amphipods that feed on benthic diatoms attached to sediment particles, reduces sediment cohesion, increasing sediment erodibility. Consequently, birds feeding on detritivorous amphipods contribute to sediment stabilization and preservation. Microphytobenthos also contribute to sediment stabilization in estuarine and nearshore ecosystems, and increased stability of crests of bedforms in respect to troughs is usually attributed to the biostabilization effect of benthic diatoms in the former (Bouma et al., 2009).

Suspension feeders develop dense, three-dimensional communities whose structural complexity depends on flow speed. It has been postulated that these communities can self-organize to enhance food capture, establishing boundary systems capable of successfully exploiting a less-structured system, namely the plankton (Gili and Coma, 1998). Ecosystem-engineering species (e.g., marsh plants, seagrasses, epibenthic algae, and endobenthic invertebrates) tend to be most dominant in stressful environments, such as estuaries and nearshore areas (Bouma et al., 2009), where they create more favorable conditions and resources not only for themselves, but also for other organisms. These effects of bioengineers play a crucial role for habitat structure, providing niches for associated and dependent organisms, and affecting biodiversity. The primarily autogenic structures of epibenthos achieve high diversity at the expense of endobenthos, while allogenic sediment reworking by infauna may facilitate other infauna and inhibit epibenthos. On a larger scale, these antagonistic processes generate patchiness and habitat diversity. Due to their functional characteristics, ecosystem engineers can exert a strong influence on ecosystem properties, exceeding what could be expected from their relative abundance alone (Hooper et al., 2005). Although conceptually it may be easily understood (Figure 23), understanding the underlying mechanisms by which these biodiversity effects occur is complex, and may involve the combination of different ecosystem properties, namely productivity, disturbance intensity, and habitat complexity.

Figure 23 Schematic representation of the multiple impacts of bioengineers on hydrology and ecosystem biodiversity. Ecosystem engineers are represented by an endobenthic organism ((a) – bivalve) and an epibenthic organism ((b) – macrophyte). Established ecosystem engineers modify hydrologic features (see arrow 2); the extent of habitat modification depends on organism traits, in combination with abiotic conditions (level of environmental stress; see arrow 3). This habitat modification will affect the ability of both the ecosystem engineers of (see arrow 1), and other species (see arrow 4), to live in such engineered area. This habitat change may facilitate and inhibit different species, impacting global ecosystem biodiversity (see arrow 5).

10.02.5 Conclusions

This study examined the interactions between biologic and hydrologic processes in estuarine and nearshore coastal ecosystems, and their relevance to ecosystem functioning. Hydrologic variables and processes occurring within an ecosystem, connected ecosystems, and their catchment basins have strong impacts on most aquatic organisms, including phytoplankton, heterotrophic bacteria, phagotrophic protists, metazooplankton, nekton, and benthic communities. Hydrologic impacts on biota include not only bottom-up effects, related to growth regulation, but also top-down effects related to biomass or mortality regulation. On the whole, bottom-up and top-down factors, both under climate, hydrologic, and biologic control, jointly control the composition of biological communities and their succession at different spatial and temporal scales.

Temperature, light, inorganic nutrients, organic matter, and turbulence are key determinants of biologic activity and ecosystem dynamics, and are clearly under climatic and hydrologic control. Temperature, for instance, directly affects the growth, reproduction, and swimming behavior of most aquatic organisms. Yet, temperature has also indirect impacts mostly through its effects on nutrient regeneration rates, water-column stratification, and predator's activity. Thus, depending on specific ecosystems properties and organism limitations and controls, a given temperature change may elicit quite contrasting effects on planktonic communities. Turbulence, light, and inorganic

nutrients are particularly relevant as they directly control primary production rates, and indirectly regulate fluxes of autochthonous organic matter and secondary production of pelagic and benthic communities. In the case of inorganic nutrients, DOM and particulate organic matter, as well, both autochthonous and allochthonous sources, associated to riverine-, groundwater discharges, and atmospheric and oceanic inputs, should be considered. Turbulence-induced changes at individual levels (e.g., metabolic and developmental rates and feeding activity) may also accumulate and modify structural and functional properties of planktonic and benthic organisms, reverberating into community and ecosystem functioning. It is worth noting that estuarine and nearshore communities are sensitive not only to local, natural, and anthropogenic influences, but also to far-field processes, regulated by global climate variability and oceanic dynamics. Changes in the abundance, growth rate, mortality, composition, and recruitment of planktonic, nektonic, and benthic communities along longitudinal estuarine and nearshore gradients, and over different timescales (e.g., episodic events and diurnal, annual, and interannual scales) illustrate the relevance of climate and hydrologic forcing as drivers of biological processes.

Conversely, fundamental hydrological properties and processes are clearly under biologic control. Planktonic, nektonic, and benthic organisms directly and indirectly shape hydrologic features, such as dissolved gases, inorganic nutrients, and non-nutrient bioactive compounds, through their production, uptake, or transformation. At the level of ecosystem functioning, biological production of regenerated inorganic nutrients is mostly relevant for ecosystems or periods of reduced mechanical energy inputs, when nutrients derived from allochthonous or deep water sources are negligible. Biological production of organic matter, and its assimilation via microheterotrophic detrital pathways, is particularly important within ecosystems where most of the primary production is not directly consumed by herbivores, or during heterotrophic periods of low primary production rates. Organisms may also actively (e.g., consumption) and passively (e.g., bioturbation) modify the concentration and composition of suspended particulate matter, thereby modulating turbidity, phytoplankton biomass (including harmful algae), and water-flow regime. In addition to these impacts, ecosystem engineers actively shape habitat structure, providing multiple ecological niches for resident and temporary organisms, and affecting ecosystem biodiversity.

Biologic- and hydrologic-induced changes interact within estuarine and nearshore ecosystems over different spatial and temporal scales, and reverberate into ecosystem trophodynamics, biogeochemical cycling processes, biodiversity, resilience, and global ecosystem functioning. Our efforts to understand ecosystem functioning and establish effective management and remediation practices should evidently consider the multiple feedbacks between hydrology and biota within estuaries, coastal ecosystems and connected watersheds. Ecohydrology science offers a number of solutions, including top-down and bottom-up physical and biological manipulations, based on modeling approaches, to help restore the health of estuarine and coastal ecosystems. Nevertheless, long-lasting ecohydrology solutions can only be based on a profound understanding of hydrology–biota interactions, which requires

long-time series of *in situ* observations. Thus, comprehensive understanding of hydrology–biota interactions may also constitute promising opportunities for restoration of estuarine and nearshore coastal ecosystems.

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