Aquatic Ecology Series

Peter G. Beninger *Editor*

Mudflat Ecology

Springer

Aquatic Ecology Series

Volume 7

Editor

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Mudflat Ecology

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Aquatic Ecology Series
ISBN 978-3-319-99192-4 ISBN 978-3-319-99194-8 (eBook)
https://doi.org/10.1007/978-3-319-99194-8

Library of Congress Control Number: 2018960276

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Photo PG Beninger

Mud is Beauty in the making,

Mud is melody awaking…

Mud is mankind in the moulding,

Heaven's mystery unfolding…

- Robert William Service

For three wonderful women who have enriched my life immensely: my wife Li Jin, and our daughters Amelia and Cordelia.

For my brother Ian, without whom none of this would have been possible.

Foreword

By any measure, and despite visual appearances, mudflats constitute a highly diverse scientific subject, posing a great challenge for the student or researcher of this ecosystem. Embedded within this disciplinary diversity is the extraordinary biological diversity of mudflats, once again belying their visual appearance. Mudflats have existed since the oldest sediments were formed, and hosted Earth's earliest life, unambiguously already evolved in 3.48-billion-year-old rocks. Let me add that they are one of Earth's largest ecosystems, lining thousands of miles of our worldwide coastlines. From this point of view, it is astonishing that scientific exploration, while proficient in heading to remote areas such as Mars, seemingly is still in its infancy when it comes to the understanding of the mucky and wet mudflats so close to us.

Perhaps it is indeed the seemingly inhospitable nature of mudflats that has kept research efforts at bay? Or perhaps, since mainstream research in the ocean and Earth sciences focuses on topics of either the marine or the terrestrial realm, the very hybrid character of mudflats, bridging the terrestrial and marine environments, has created a subconscious 'confusion barrier'? Funding agencies, methodological approaches, and terminology commonly serve only one or the other environment, so it requires those with a strong heart to overcome at times significant disciplinary barriers. And then there is the intrinsic problem that ecosystem research faces by definition: tracking an ecosystem's individual components is a slippery endeavour, because they constantly interact and affect each other.

This well-composed book discusses the fundamental ecology of mudflats, as well as the human impact of the Anthropocene on this environment. Human impact includes the introduction of invasive species, the harvesting of natural and cultured populations by the growing human population, and the overprint of the natural setting by these and other human activities. While effects on macroscopic organisms such as birds may be easier to document, the complexity of the immensely fine network between microorganisms, and their effect on physical and chemical properties of the sediment and water, is beyond our comprehension at this time. In order to analyse a complex ecosystem such as mudflats, it is imperative that scientists of various disciplines work together. This inspirational volume will greatly contribute to this discussion and assist the student/scientist drawn to interdisciplinary research in acquiring the indispensable overview of the many facets of mudflat ecosystems, the status quo of research, and the most interesting challenges for the future.

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Nora Noffke

Preface

Historically, our efforts to understand the natural world have been the most fruitful when we proceeded to carve it up into cognitively manageable units—whether geological epochs, locations in the periodic table of the elements, taxonomic categories, or whole fields of study. Over the course of its history, the field of marine biology has itself progressively subdivided with the growth of its knowledge base; today, it is no more surprising to find coral reef or deep-sea ecologists than it is to find forest or grassland ecologists in the terrestrial system.

Perhaps due to its particular 'charisma', the mudflat habitat has not yet been ennobled by a study field label. Yet although it shares some features with the soft-substrate sublittoral environment, the mudflat is nonetheless a distinct habitat, with specific and ecologically far-reaching particularities. Previously scattered throughout the marine biology literature, the multiple facets of mudflat ecology are brought together for the first time in this work; we thereby hope to establish mudflat ecology as a true, diverse, yet intrinsically and necessarily coherent, field of study.

We are fortunate that such talented researchers as those assembled here have made their contributions to this work. Some of them will be very familiar to those who follow the literature, while others may be less well known, and this is because they may be younger scientists replete with promise. We are also indebted to their equally talented peers who have agreed to review chapters within their specialties:

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Chapter 1
Introduction: Mudflat Basics

Peter G. Beninger and David M. Paterson

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Abstract The study of mudflats should logically start with the type of intertidal depositional shore we consider to be true mudflats, and then an overview of their global distribution. Their dominant feature being mud, we then consider the etymology and cognitive associations of the word 'mud', the basics of sediment composition and its living matrix, and the concept of mudflats as systems of superposed emergent properties. Equipped with these basics, we may then proceed to a proper geological consideration of mudflats, our next chapter.

1 Mudflat Distribution

Intertidal depositional shores composed of fine sediments are a familiar environment to most marine biologists. The most commonly recognised parts of such coasts consist of either salt marshes (temperate zones) or mangrove systems (tropical zones). Indeed, mangrove systems occupy approximately 170,000 km^2, or 75% of

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P. G. Beninger (ed.), *Mudflat Ecology*, Aquatic Ecology Series 7,
https://doi.org/10.1007/978-3-319-99194-8_1

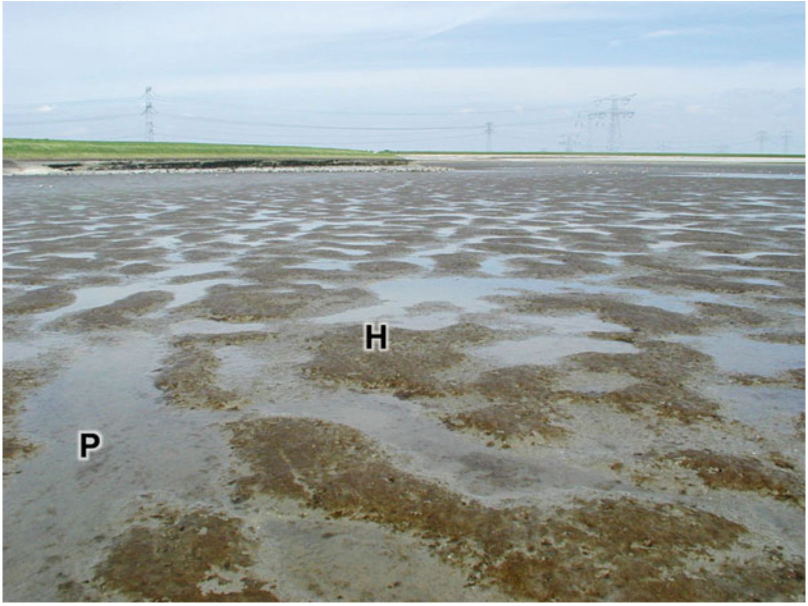

Fig. 1.1 A mudflat in the Netherlands, showing low-grade topography, with alternating pools (P) and hummocks (H). Microphytobenthos (light brown pigmentation) is evident on the crests of the hummocks. Photo J. van der Koppel.

all tropical coastline (Flemming 2002). In contrast to these extensively-vegetated habitats, true intertidal mudflats are vegetationally depauperate, and also generally lacking in visible macrofauna, such that the term ‘mudflat’ is very apt to describe their appearance: muddy, with very little three-dimensional complexity (Fig. 1.1). Although intertidal mudflats are commonly understood to be ‘distributed widely along the world’s coastlines’ (Gao 2009), estimations of the total area occupied by these environments are conspicuously lacking. A remarkable, although incomplete, survey of the world’s mudflats identified 350 major sites, with 79 greater than 5 kha (Deppe 1999). Of these, 19 were from 5–20 kha, 28 from 20–80 kha, and 26 were larger than 80 kha. Most (84%) mudflats were situated in protected topographical formations such as estuaries, bays, and behind barrier islands. The two largest and well-known examples are the Yellow Sea and the Wadden Sea mudflats (Fig. 1.2). An unknown number of mudflats remain undocumented in poorly-mapped regions of the globe (Deppe 1999).

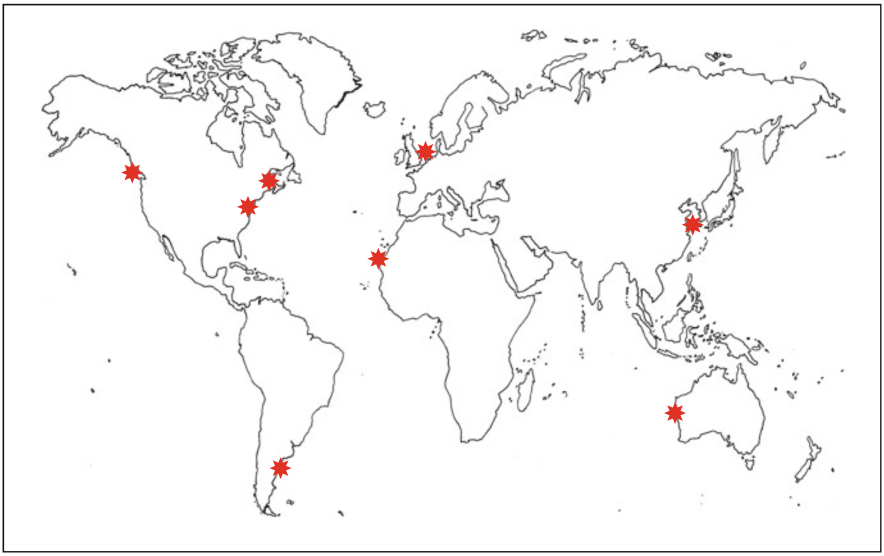

Fig. 1.2 Locations of some notable mudflats mentioned in the present volume. From west to east: Roberts Bank, Canada; Chesapeake Bay, USA; Bahía Blanca Estuary, Argentina; and Bay of Fundy, Canada; Banc d'Arguin, Mauritania; Wadden Sea, Netherlands; Shark Bay, Australia; Jiangsu (Yellow Sea), China. Original artwork, PG Beninger.

2 What Is Mud? Etymology and Cognitive Associations

At the outset, it is useful to define the term 'mud'. The full-size, multi-volume Oxford Dictionary devotes over 20 columns of very fine print to the word 'mud', its derivatives, and its etymological history. What emerges from this exposition is, first, that mud is a mixture of rock particles and water, varying in consistency from a semi-liquid to a plastic solid (much of the present volume will show how mudflat 'mud' is much more complex than this simple definition), and second, that the description as 'mud' or 'muddy' is a "loaded" term at several levels, persistently incorporating connotations of uncleanliness. It conveys a state lacking clarity, indeed, of almost complete opacity, and this may even be brought about intentionally ('muddying the waters'). It is used to describe confused thought ('muddled thinking'; 'clear as mud'). It has been used repeatedly to denote the worst of anything ('Scum of the mud of hell!', 'the mud of all races'). It characterizes an uninteresting person ('a stick in the mud'). It symbolizes spreading insults ('a mud slinger'). It describes a state of utter abjection ('your name is mud'). It is used to refer to the drug opium, due to its mud-like appearance (Simpson and Weiner 1989).

Amid all these negative associations with mud, there are some more positive ones. The Douay-Rheims version of the Bible translates Genesis 2: 7 as '. . .the Lord God formed man of the *slime* of the earth' (rather than the 'dust' in other versions).

Fig. 1.3 Making measurements and obtaining samples from extensive areas of mudflat can be logistically challenging, potentially dangerous, and exhausting. (NERC CBESS Project, Image E. Paterson).

Certainty can be declared ‘as sure as mud’. And the popular toast ‘here’s mud in your eye’ probably refers to the New Testament Siloam episode, where a man’s sight was restored when Jesus put mud over his eyes (John 9: 7). However, even the knowledge that mud was the probable cradle of life (Cairns-Smith 1965; Ponnamperuma et al. 1982; Cairns-Smith and Hartman 1986; Sami and Tewari 2009; Noffke et al. 2013; Yang et al. 2013) has had comparatively little popular echo. Similarly, the probable role of mudflats in prehistoric human sedentarization (as sources of relatively easily-captured animal food) is largely unrecognized, despite the fact that they probably led to the establishment of the first settlements, and ultimately to the cities of today (the ‘coastal zone’ has a population density three times that of inland areas) (Jackson et al. 2001; Crossland et al. 2005). These examples illustrate our complex cognitive relationship with the term ‘mud’, and, together with the difficult working conditions imposed by mud (Fig. 1.3), may explain why mudflat ecology has not previously been widely considered a *bona fide* field of study.

Table 1.1 Mud-sediment grain sizes and corresponding sediment type

Grain size (μm)	Φ Value	Wentworth size class (Wentworth 1922)
6.25 to 3.1	4–5	Coarse silt
3.1 to 1.56	5–6	Medium silt
1.56–0.78	6–7	Fine silt
0.78–0.39	7–8	Very fine silt
<0.39		Clay

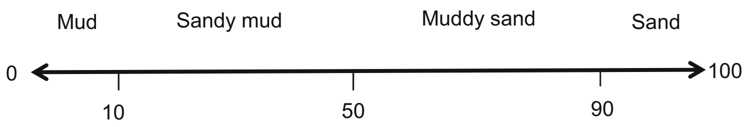

Fig. 1.4 Classification of sediments according to percent sand content (after Folk et al. 1970, modified and re-drawn, PG Beninger).

3 What Is Mud? Sediment Composition

Although a thorough treatment of mudflat geology is provided in Chap. 2, a brief definition of the terms of reference is warranted here. First of all, mud is chiefly *siliclastic*, i.e. composed of silicate particles eroded from rocks. Geologists classify sediments using the numerically-convenient phi size scale (Krumbein and Pettijohn 1938), based on the log ratio of grain size to a reference grain size (1 mm): $\Phi = \text{Log}_2\ D/D_0$, where Φ is the phi-scale value, D is the grain size, and D_0 is the reference size (1 mm). Use of this numerically-convenient scale explains why the grain size class boundaries consist of non-rounded millimetric measurements; thus, mud-containing sediments are defined as non-indurated moist sediments with grain sizes <0.063 mm (very fine sand). At the finest extreme, the silt-clay boundary is fixed at 3.9 μm (Table 1.1).

Mudflats contain various proportions of these grain size classes, in addition to various proportions of larger-grained sand, and corresponding to the familiar classification of mud, sandy mud, muddy sand, and sand (Folk et al. 1970; Fig. 1.4).

4 What Is Mud? The Living Matrix

Microbes have been colonizing muddy sediments for billions of years (Noffke et al. 2013), and their activities have greatly contributed to the physical, chemical, geological, and biological properties of this substratum. The terminology used to refer to the living mud matrix is more precise in the geological literature, and more ‘loose’ in the biological, and especially the ecological, literature. As most of the following chapters will make reference to this matrix, it is necessary to define a set of descriptive terms at the outset:

Fig. 1.5 An empty cockle shell (*Cerastoderma edule*), deposited on the surface of an intertidal mudflat (Dee Estuary, UK) which has the brown coloration of a transient epibenthic biofilm (Photo D.M. Paterson).

Biofilm A population of microorganisms, typically at a solid-liquid interface, surrounded by a matrix of extracellular polymeric substance (EPS = mucopolysaccharides). At the microscopic level, biofilms may form around individual sediment particles; on mudflats, we (rather loosely) refer to the macroscopic patches of microbes and EPS on top of sediments as ‘biofilm’, when in fact we mean either ‘transient epibenthic biofilm’ or ‘epibenthic microbial mat’, or both (see below). While many workers generally understand ‘biofilm’ as microscopic and ‘mats’ as macroscopic, many others understand it as a catch-all term (whose convenience is matched by its ambiguity).

Transient Epibenthic Biofilm Characteristic of muddy habitats, epipelic (see below) microbes often migrate to the sediment surface during periods of daylight low tides and form visible patches (biofilms) on the sediment surface (Fig. 1.5). These patches disappear just before the return of the tide, (although they probably leave behind EPS and other microbes), hence the term “transient” (Consalvey et al. 2004).

Epibenthic Microbial Mat This EPS-rich mat develops within the first millimeters of muddy to sandy sediments in the lower supratidal zone, just above the upper intertidal zone. This zone can be quite large, given the low grade of the mudflat slope, especially on macrotidal flats (Noffke 2010). The epibenthic microbial mat separates the sediment from the water column when immerged, and from the atmosphere when emerged. When subjected to currents, sediment biostabilization is up to 12 times higher compared to that of equivalent barren sediment (Noffke and Krumbein 1999; Noffke 2010); this property will be seen to be crucial to the formation and function of geomorphological features on mudflats (Chap. 9). Epibenthic microbial mats form over several months and are functionally and structurally different from transient epibenthic biofilms, in that they are supratidal, anchored to the sediment, persist between strong tides, and are of a thicker and more coherent structure. If never eroded by strong storms, they can occur at the same location for many years (Noffke 2010).

Endobenthic Microbial Mat This type of mat develops in the upper few mm of the more sandy [*sensu* Folk et al. (1970) ‘sandy mud’] sediment of the upper intertidal

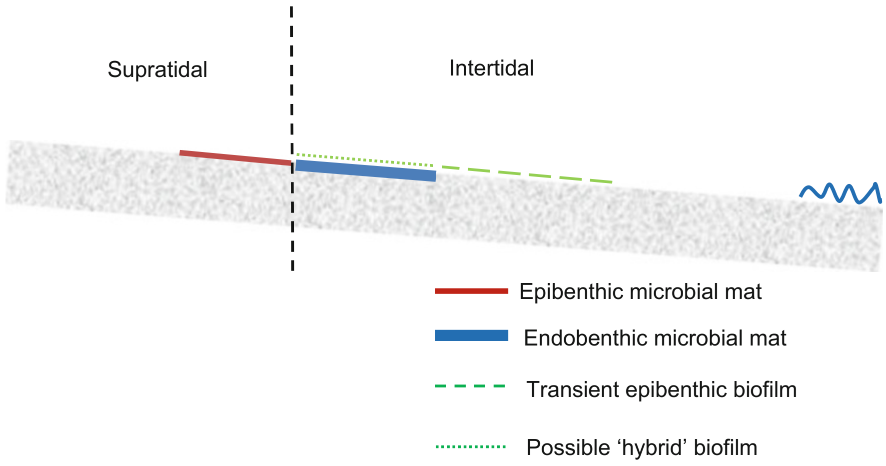

Fig. 1.6 Profile of a mudflat at low tide, showing locations where different microbial mats and biofilms develop. Original artwork, PG Beninger.

zone, and contains comparatively much less EPS than does the epibenthic microbial mat. Sediment biostabilization is about five times that of barren sediment (Noffke and Krumbein 1999). These mats can form within several hours (Noffke 2010). Their relation to the transient epibenthic biofilm is not yet clear; some of the same organisms may colonize both structures. In contrast to the transient epibenthic biofilm, the endobenthic microbial mat is not characterized by vertical migration.

Many mudflat ecologists do not indicate what type of biofilm or mat they report; any pigmented, superficially-visible patch is often simply termed a 'biofilm'.

Microphytobenthos (MBP) MBP designates the photosynthetic eukaryotic and prokaryotic (mainly diatoms and cyanobacteria) microorganisms that grow within and upon the upper several millimeters of the sediment bed. They are major components of microbial mats and transient biofilms.

Epipelic The term 'epipelic' denotes any organism living on top or migrating through the surface layers of muddy sediment, e.g. epipelic diatoms.

Endopsammic The term 'endopsammic' denotes any organism living within sandy sediment.

The zones wherein may be found the epibenthic and endobenthic microbial mats, as well as the transient epibenthic biofilms, are shown in Fig. 1.6.

5 Mudflats as Systems of Superposed Emergent Properties

As geologists themselves emphasize, mudflats are much more than just mud! In the following chapters, we will see that, beginning with the lowest level of organization (the physical, geological, and chemical), increasing levels of organization emerge from this mud, along with increasingly intricate properties. Mudflats harbour prolific unicellular assemblages which profoundly influence their physical, geological, chemical, and biological features, including the redox reactions driving the system energetics. Although we might expect the sedimentary mosaic of electrochemical gradients to be conducive to the metazoan chemosymbioses which are so characteristic of other mud-dominant marine habitats, such symbioses are found mainly among the meiofauna, and are intriguingly rare in the macrofauna. In the upper sedimentary layers, however, complex biofilms containing unicellular microphytobenthic organisms assemble and set the stage for geomorphological and ecological self-organization, which in turn largely determines the feeding and spatial distributions of both endobenthic and epibenthic invertebrates. These spatially-organized organisms may then influence vertebrate feeding distributions. All of these organisms harbour and transmit parasites, an important yet often overlooked component of trophic webs on mudflats. The combination of these living and nonliving features promote ecological engineering and the provision of ecological services. Mudflat geological and biological complexity affects the dynamics of colonization and invasion, as well as the multiple interactions with migratory shorebirds, which export mudflat production over thousands of kilometers. Spatially-organized living resources are exploited on mudflats through fishing and aquaculture. These themes are set out and explored in the chapters of the present work. Although certain study techniques are specific to each of these dimensions of mudflat ecology, some quantitative techniques and approaches are necessary and common to most of them; these are presented in the final chapter.

It is hoped that in bringing together the various disciplines which have been applied to the study of mudflats for decades, the present volume will provide the foundation for an integrated perspective of this important, yet understudied, environment.

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Chapter 2
Geological, Physical and Chemical Foundations

Jerónimo Pan, Paula D. Pratolongo, and Diana G. Cuadrado

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P. G. Beninger (ed.), *Mudflat Ecology*, Aquatic Ecology Series 7,
https://doi.org/10.1007/978-3-319-99194-8_2

Abstract Modern tidal flats are coastal geomorphological features with a recent geologic history (Holocene period, 10,000 YBP) that are found globally, under different climatic, hydrodynamic and sedimentological regimes. They are primarily characterized by fine-grained sedimentary deposits (silt and clay) that present unique physical and chemical properties, in comparison to other sediment types. The input of sediments to mudflats can be either riverine, from offshore, and/or from the erosion of coastal sedimentary deposits. Tides and tidal currents are the dominant hydrodynamic forces shaping mudflats, with wave action playing a secondary role. The occurrence of intermittent or temporary flooding and the presence of variable redox (oxidation-reduction) conditions are typical features of mudflat sediments. The temporally and spatially variable changes from aerobic, oxidized states of mudflat sediment and porewater to anaerobic, reduced states drive particular redox reactions that govern the characteristic chemical processes and biogeochemical functioning that distinguish mudflats from other coastal settings. Mudflat sediments are not inert; the high surface area:volume ratio of fine-grained sediment particles offers a vast and structurally-complex landscape for colonization by microbes that rely on surface-adhesion processes. Photosynthetic microalgae belonging to several taxonomic groups (collectively known as microphytobenthos MPB) are the dominant microorganisms growing in association with sedimentary particles, and forming a biofilm layer on top. In addition to physical forces, living benthic communities modify sediment properties as part of their normal physiology (micro- and macro-biota) and feeding, movement, and burrowing activity (meio- and macrofauna), especially in relation to stabilization and destabilization processes. These may ultimately have marked effects on sediment stability and geomorphology. The interplay between such biological processes and sediments in mudflats is currently an active field of research.

1 Geological Foundations

1.1 Mudflat Formation: Their Evolution in Geologic Time and Space

Modern mudflats, along with many other coastal geomorphological features, became well established during the mid-Holocene, with the rate of sediment supply and changes in sea level becoming the most important factors contributing to the formation of mudflats. Geologically-stable coasts accumulate erosional sediments on the continental margin, thus leading to the formation of sandy or muddy shores (Bertness 1999). The formation of soft-sediment habitats and the long-term fate of mudflats are dictated by the interplay of sediment supply and transport processes.

The Scientific Committee on Ocean Research (SCOR) established Working Group 106 to assess the impacts of relative sea-level change on muddy coasts, convening for the first time in China in 1995, and then in Germany in 1997. The task required a better understanding of the physical and biological processes acting in the formation of muddy coasts, something that, in comparison to sandy coasts, was poorly understood at the time. The Working Group first established a clear definition of *muddy coasts* as "*a sedimentary-morphodynamic type characterized primarily by fine-grained sedimentary deposits—predominantly silts and clays—within a coastal sedimentary environment. Such deposits tend to form rather flat surfaces, and are often, but not exclusively, associated with broad tidal flats*" (Wang and Healy 2002). Mud is further defined as a mixture of mainly fine-grained clay- and silt-sized sediments (and sometimes a minor sand fraction), organic matter and porewater. Such deposits typically display cohesive properties derived from water tension and the charged surfaces of clay minerals, enhanced by the chemical properties of the organic matter, that together dominate the overall rheological behavior of the mudflat. Mudflats also generally contain enough fine sediment that permeability is low and prevents draining at low tide, keeping the deposits perpetually saturated even when aerially exposed.

1.2 Sediment Classification and Characteristics

As mentioned previously (Chap. 1), the term "mud" or "fine grain" collectively refers to inorganic sediment <62.5 μm [4 phi, in Folk's (1968) sedimentological classification], that comprise mineral material in the silt (62.5–3.9 μm) and clay (3.9–0.5 μm) size-ranges. Clay minerals are ubiquitous components of marine sediments, produced by chemical weathering of terrestrial rocks and the authigenic reactions that occur in seawater. Clays are aluminosilicates (i.e. constituted primarily by oxygen and hydroxyl-bound aluminum and silicon), with the most abundant mineral forms being illite, kaolinite, smectite and chlorite. One feature shared by all clay minerals is the tetrahedral (Si) and octahedral (Al) crystalline structure of their base units that self-arrange in sheets or layers, so as to form a platy, or sheet-like, structure (Grim 1968) (Fig. 2.1). Most clay minerals comprise double-sheets (combined tetrahedral-octahedral-tetrahedral layers) that are bound together by various cations (e.g. Na^+, K^+ Ca^{2+}, Mg^{2+}, etc.) that themselves can exist in differing states of hydration or coordination. Differences in these cationic binding layers are what largely distinguish the different clay minerals and their physicochemical behavior. Weathering and varying environmental conditions can also drive the diagenetic alteration of clays between the different clay-mineral types, and even the intermediate states such as the regularly occurring mixed-layer illite-smectite (Libes 1992). The variability, alteration, and reactivity of clay minerals all exert a strong influence on the chemical and physical behavior of mudflat settings.

Mud has different and significant properties in comparison to other sediments. In addition to its cohesiveness, other important rheological properties include its viscoelastic behavior that is defined by mud's strain-dependent change between a particle-supported solid and a highly viscous, non-Newtonian fluid (Metha 2002). Furthermore, when mud is comprised of significant proportions of small clays (<2 μm), electrochemical processes become important and particles bind together, forming an adhesive floc. Due to their net negative surface charge, clay minerals

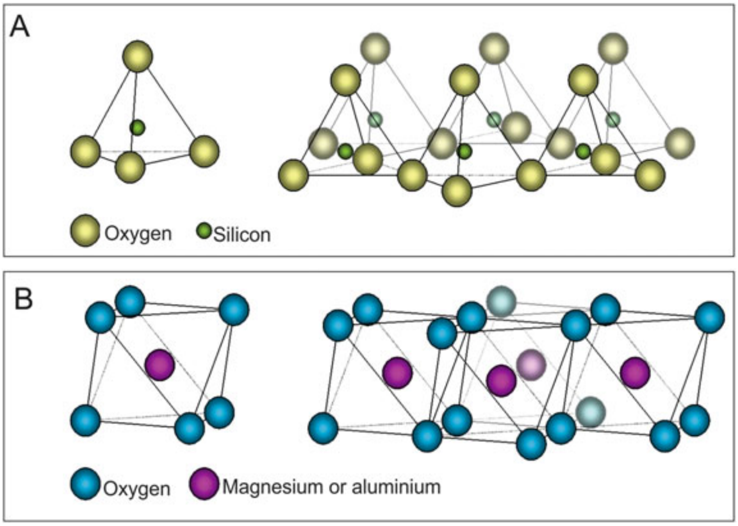

Fig. 2.1 Schematic molecular structural units of clay minerals, and their arrangement into (**a**) tetrahedral and (**b**) octahedral crystalline models.

adsorb cations and organic matter, which, upon settling, are carried to sedimentary deposits (Libes 1992). The adsorption of compounds such as pollutants, pesticides and heavy metals leads to the accumulation of these in sediments, which is particularly intense in some human-impacted coastal areas.

1.3 Sediment Supply

The supply of fine-grained sediments is one of the most important factors behind the formation of mudflats. Sediment can be eroded or accumulated by a number of physical processes, and muddy deposits persist where the provision of fine sediment exceeds the rate of removal by hydrodynamic processes. The source of sediments may either be riverine, from offshore, and/or the erosion of coastal sedimentary deposits. A coastal sedimentary environment is subject to erosion, transport and deposition processes due to coastal and estuarine mechanisms. High concentrations of fine-grained suspended loads carried by rivers contribute to the formation of muddy deposits at the river mouth and adjacent coast, such as the Amazon River where the suspended sediment discharge influences the geomorphology and sediment dynamics over a 1500 km-long stretch of coast along northeastern South America (Lisboa Cohen et al. 2012; Anthony et al. 2013). Similar delivery and transport of river-derived fine-grained sediments support the tide-dominated region in the Bengal Delta formed by three great rivers (Ganges, Brahmaputra, and Meghna). Shifting of the river mouths eastward over the late Holocene has diminished the direct supply of river-borne sediment in the distal portions of the delta, but tidal processes and

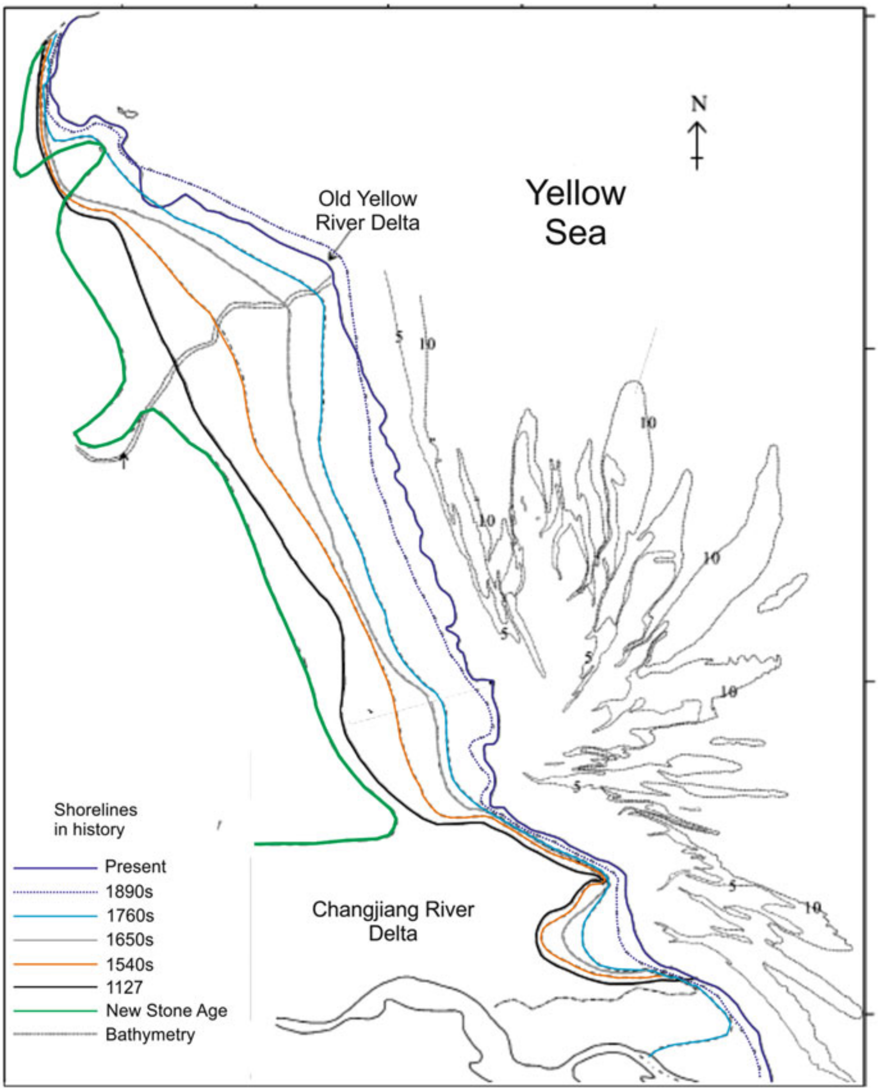

Fig. 2.2 Coastal plain of Jiangsu province, eastern China (modified from Gao 2009). The historical progradation of the shoreline from the New Stone Age (*ca.* 10,000 BC) to the present is shown.

alongshore currents have continued to sustain the coast through onshore transport of mud onto intertidal mangrove flats (Rogers and Goodbred 2014). Conversely, changes in sediment supply can have important consequences in coastal geomorphology; for example, the sediment discharge from the Yellow River in China formed large mudflats until 1855, after which its course was shifted and the shoreline retreated as a response to the reduced supply of particulate material (Gao and Zhu 1988) (Fig. 2.2).

1.4 Geographical Distribution

Mudflats are found globally, under different climatic, hydrodynamic and sedimentological regimes. A detailed distribution of fine cohesive sediment deposits around the world was compiled in Flemming (2002) and mapped at a 1:100,000 scale. A characteristic shared by all mudflats is the extremely low slope of the aggraded terrain, producing a tidal intrusion of as much as several km, and often being backed by low-lying saltmarsh or mangrove areas.

The Atlantic coast of North America is dominated in part by barrier islands associated with sheltered muddy backbarrier lagoons and large estuaries such as Chesapeake Bay, Delaware Bay, Long Island Sound, Narragansett Bay, and the Bay of Fundy, ranging from micro- to macrotidal regimes (Fig. 2.3a). Muddy deposits are present in sheltered embayments of many estuaries in northwestern Europe, including the British Isles, France, and the Netherlands (Flemming 2002; Carling et al. 2009). In the Wadden Sea the mudflats are sheltered by a chain of barrier islands, and the sediment source is mainly provided by the North Sea rather than river input (Pejrup et al. 1997) (Fig. 2.3b). On the Chinese coast (Fig. 2.3c), the Yellow River has the largest suspended sediment load in the world, forming extensive mudflats (Wang 1983), with Jiangsu province having the widest and most concentrated mudflats on Earth (Yao 2013; Zhang et al. 2016). A multi-decadal satellite-imagery reconstruction of mudflat accretion in Jiangsu province not only documented the seaward expansion of the coastline due to a combination of natural siltation and human activities, but also the significant changes in coastal land-use that took place over a ~20 year period (Yao 2013). As is typical of tropical regions, the Ganges-Brahmaputra-Meghna Delta on the Bengal Basin harbors the Sundarbans (Fig. 2.3d), the largest area of mangroves in the world, shared by India and Bangladesh (Wilson and Goodbred 2015). In the macrotidal coast of northern and northwestern Australia, large tidal flows entrain considerable volumes of mud which are carried in suspension to sediment-retaining mangroves (Wolanski 2006).

Methodological Approaches for Sediment Grain-Size Analysis

Traditionally, the methods for estimating the distribution of sediment grain sizes from a sample were sieve analysis and sedimentation analysis. The first method used different sieves on samples composed of particles with intermediate diameters (63 μm to 16 mm; i.e. fine sand to fine gravel) in order to separate them, based on their size (Ingram 1971) (Fig. 2.4a, b). Sedimentation analysis was based on Stoke's law of settling velocities (Galehouse 1971), and has been widely used for samples with particles in the 0.5–50 μm diameter range (i.e. clay and silt). The so-called "pipette" analysis, the most widely used of sedimentation techniques, basically consists of letting sedimentary particles with differential settling velocities settle in a graduated cylinder, and then sampling the different fractions with pipettes at specific settling times (known for each fraction in a

(continued)

suspension medium) (Fig. 2.4c). These sub-samples then are resuspended into graduated cylinders with a liquid medium of known density, and the pipetting process is reiterated. Thus, the different sediment fractions are separated by the sequential time-specific pipetting and resuspension; the proportions of the different size-fractions are then estimated by weighing. Although these traditional techniques require a considerable amount of time and effort, the training is relatively simple and the specific laboratory equipment is inexpensive.

Since the 1970s, a variety of automated devices based on the principle of measuring the angular distribution of forward-scattered light have been developed and popularized for the estimation of particle grain-size distributions. In the UK, Malvern Instruments developed one such automated particle-counter based on the principle that particles of a given size diffract light through a given angle, the angle increasing with decreasing size (McCave et al. 1986) (Fig. 2.4d). A narrow beam of monochromatic light from a laser is passed through a suspension and the diffracted light is focused onto a detector that senses the angular distribution of scattered light energy. Particles in suspension are made to pass through a laminar flow. Laser-diffraction-size analysis not only gives particle counts, but also size distributions with more accurate, efficient, and reproducible results than the traditional pipette and sieve analyses, especially for the clay fraction (Konert and Vandenberghe 1997), which represents the major advantage of this method. Besides laser diffraction, there are other technical approaches to automated particle counting that, analogously to the sedimentation analysis, start from a suspension of particles and measure the absorption of either X-radiation by settling particles (e.g. the X-ray sedigraph—Micromeritics Instrument Corporation, USA); or changes in the electrical resistance caused by particles passing through a microchannel (e.g. the Coulter counter—Beckman Coulter Inc., USA). Given that automated counters yield a tremendous amount of data from a single sample, versatile and user-friendly computer programs capable of processing this information and providing graphical outputs are routinely used, such as Gradistat (Blott and Pye 2001). Automated particle-counting techniques require a certain level of specific training, and familiarity of the operator with the equipment and the principles behind it.

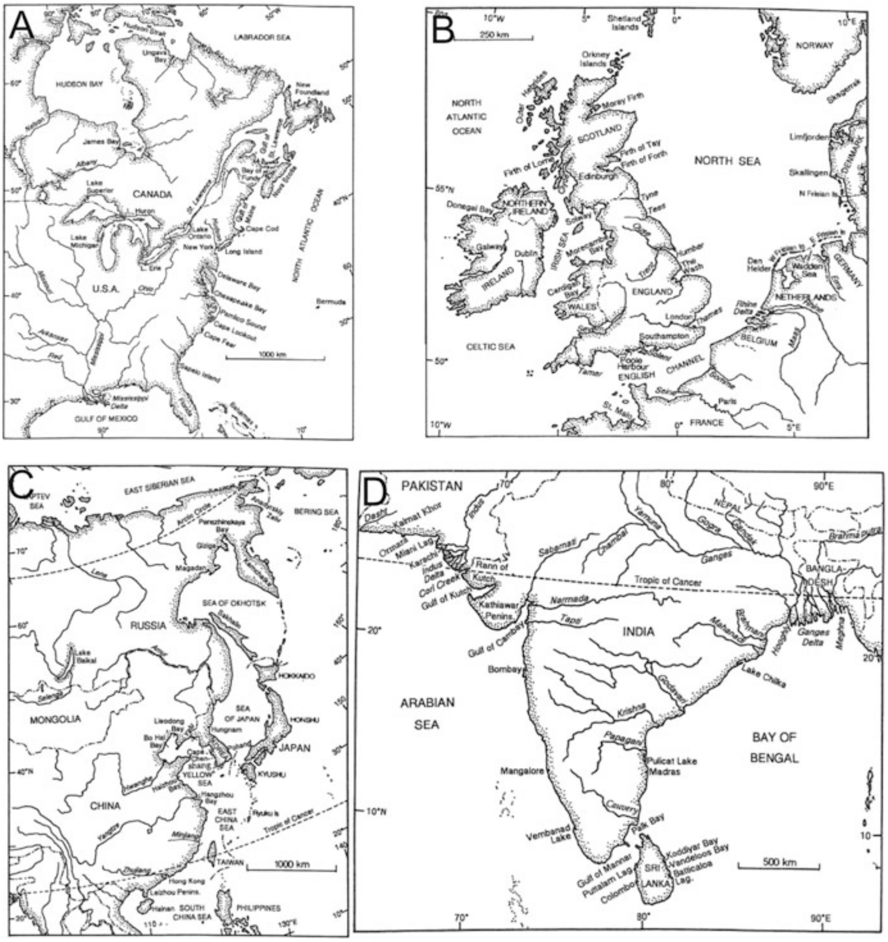

Fig. 2.3 Examples of world coastlines where significant continental sediment input has created extensive mudflats (modified from Flemming 2002). (**a**) Atlantic coast of North America dominated in part by barrier islands associated with sheltered muddy coasts, and large estuaries. (**b**) Mudflats are formed on sheltered embayments across many northwestern European estuaries. (**c**) The Yellow River has the largest suspended sediment load, creating the widest mudflats on Earth in Jiangsu province (China). (**d**) The Ganges-Brahmaputra-Meghna Delta on the Bengal Basin harbors the Sundarbans mudflats.

Fig. 2.4 Equipment for the estimation of sediment grain-size distributions. (**a**) Sieves of different mesh sizes are routinely used in the sieving method. (**b**) Stacked sieves and vibrating siever. (**c**) Fine sediment fraction resuspended in distilled water at room temperature, and settling in graduated cylinders, as used in pipette analysis. (**d**) An automated particle-size counter (Malvern Mastersizer 2000), which measures particle size distributions based on laser diffraction.

2 Physical Processes

2.1 Tidal Range

Studies by Kirby (1992, 2000) and Dyer (1998), attempted to gain an empirical understanding of the external forces shaping mudflat morphology; until then, the study of mudflats had been overlooked in comparison to sandy beaches. Various field programs have been carried out since, such as the INTRMUD Project (Morphological Development of Intertidal Mudflats), which studied the physical, biological and morphological characteristics of individual mudflats across 18 northwest European

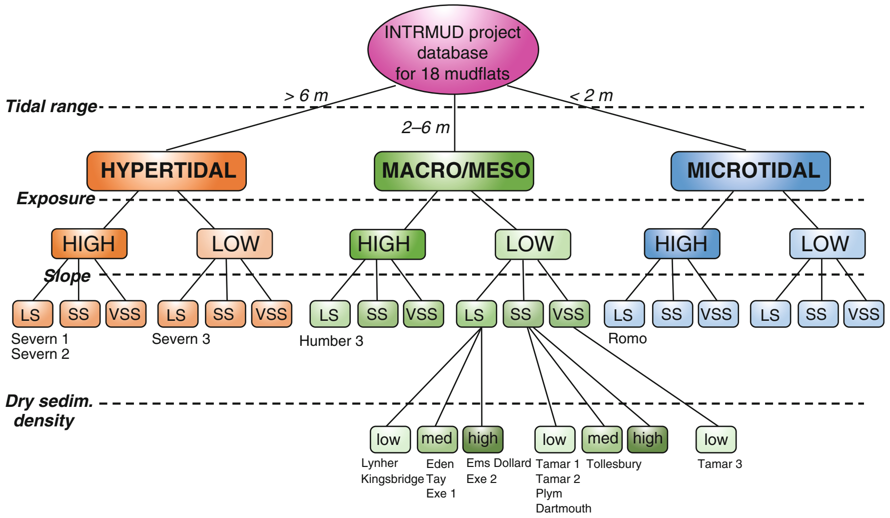

Fig. 2.5 Classification scheme for 18 North-west European mudflats, based on tidal range, wave exposure, mudflat slope [LS: low slope (<0.04); SS: steep slope (>0.04); VSS: very steep slope (~0.16)], and density of dry sediments (kg m^{-3}); examples of systems upon which the classification was constructed are included (modified from Dyer et al. 2000).

estuaries (see *Continental Shelf Research* Special Volume 20, 2000). This comprehensive study helped identify the variables that exert the largest influence in mudflat development and evolution. Dyer et al. (2000) classified parameters from independent variables, which is a challenge for those working in mudflats, since many variables are interdependent. They identified tidal range, exposure to waves and slope as the most important external driving variables (Fig. 2.5). Wave exposure was a resultant of the relationship between the orientation of the flat relative to the prevailing wind and maximum fetch, and the slope was calculated as the mean tidal range/mean flat width. The effect of the slope depends on the tidal range and width of the mudflat, considering 1:750 as a boundary between flat and steep mudflats.

On the other hand, Flemming (2012; Fig. 2.6) updated the original scheme proposed by Hayes (1979) of global distribution of tidal shores based on tidal range, as microtidal <1.0 m; lower mesotidal 1.0–2.0 m; upper mesotidal 2.0–3.5 m; lower macrotidal 3.5–5.0 m; and upper macrotidal >5.0 m; and the areas where back-barrier tidal mudflats are developed. As there is a positive correlation between intertidal mudflat extent and tidal range (Wang and Healy 2002), in microtidal areas, mudflats may form in sheltered embayments where wave action is of secondary importance in comparison to tidal currents. In high-energy, tidally-dominated settings, the deposition of fine-grained sediments onto mudflats can occur in a well-mixed estuary with low river discharge and strong tidal currents, where shoreline erosion and seabed erosion or resuspension provide muddy sediments to form mudflats (Shchepetkina et al. 2016). Archer (2013) gives other examples of mudflats in hypertidal coastal settings in North- and South America, and Europe.

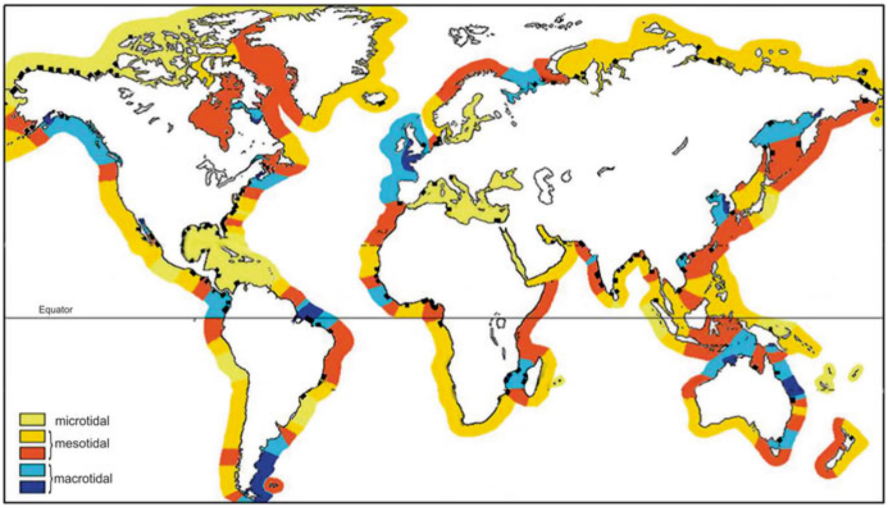

Fig. 2.6 Global tidal range distribution pattern (colors) and coastal barriers backed by mudflats or lagoons (black dots; modified from Flemming 2012).

The suspended river load can be alternately deposited and entrained on each tidal cycle. Deloffre et al. (2006) studied physical benthic-pelagic coupling and sedimentation processes on tidal flats along the Seine, a macrotidal estuary in France. A long-term (22 months) study of high frequency (1 measurement $\cdot$ 10 min^{-1}) and high resolution (0.6 mm) altimeter data, showed that during the largest spring tides (tidal range >7.1 m), sedimentation on the mudflat was predominantly controlled by vertical transfer of fine particles (<63 μm) from the turbidity maximum to the bed. Deposition of suspended particulate matter during high tide was favored by low current velocities at the mudflat bed (<0.4 m s^{-1}). Conversely, during periods of wave activity and periods of increased river discharge, the mudflat surface experienced erosion, also characterized by a vertical transfer of fine-grained material, from the mudflat bed back into the turbidity maximum. On average, 25–40% of the maximum mass of suspended particulate matter held within the turbidity maximum is temporarily deposited on the mudflat.

Wolanski et al. (1988) developed a model to explain the lutocline that separates a clear upper layer from an extremely turbid bottom layer during ebb tide in the South Alligator River (Northern Territory, Australia). In this model, sediment is entrained from the bottom and mixed vertically upward by eddy diffusion, but sediment-induced buoyancy effects inhibit vertical mixing, thus forming the two layers of comparable thickness.

The interface at which fresh- and saltwater enter into contact, such as the heads of estuaries, experiences significant changes in water biogeochemistry, over short horizontal scales, due to the high ionic strength of seawater (Libes 1992). In such areas, flocculation of suspended particles and dissolved organic matter (DOM) and colloids may represent a significant input of both inorganic and organic particles, from the water column to bottom sediments. Although organic compounds constitute a relatively small reservoir in the ocean, they play a central role in marine biogeochemical cycles; except for humic acids, all of these naturally-occurring compounds are synthesized by marine organisms (Libes 1992). Flocs are formed by a combination of two groups of processes, those bringing particles together, and those keeping them together. The first group is related to the flow conditions in the water, the coagulation of bacteria and plankton onto surfaces and each other (Libes 1992), and to organisms that clog particles into faeces or pseudofaeces or otherwise bind them in mucus. The second is related to the formation of sticky organic matter by a variety of organisms (phytoplankton, bacteria; Eisma 1986) to produce *bioflocculation* (Manning et al. 2010). Verney et al. (2009) presented experimental evidence that flocculation is mainly influenced by the constituents of suspended sediments and on the content and concentration of particulate organic matter (POM) rather than salinity changes. These authors found that diatom blooms in estuaries strongly enhanced flocculation speed and, to a lesser extent, efficiency.

Two main types of flocs have been described; *microflocs* with a diameter up to 125 μm, and *macroflocs* with a maximum size of 3–4 mm (Eisma 1986). The microflocs, together with single mineral particles, are the basic building units of macroflocs. Macroflocs are fragile, and formed in the water under conditions of viscous flow. Some flocs remain suspended in seawater, whereas others continue to aggregate until they become dense enough to sink, adsorbing metals during their transit through the water column (Libes 1992). Wells and Shanks (1987) studied flocs (therein termed “marine snow”) in a shallow coastal environment, and concluded that it is geologically significant due to its high settling rates (in the order of 50 to 200 m per day), and responsible for much of the vertical mass flux to coastal and estuarine fluid mud deposits. Flocs may thus represent a significant input of small sediment particles, organic matter and metals, from the water column to the sediments. The rate of vertical floc transport and incorporation into sediments depends upon several factors. The basic problem in floc settling relates to the variable degree of flocculation that makes settling velocity, size and density non-constant (Manning et al. 2010); the variation in settling velocity is the result of turbulence-induced aggregation and floc breakup processes (Winterwerp 2002).

In the Severn estuary in the UK, a secondary consequence of flocculation is the formation of mud : sand mixtures in turbid suspensions (Manning et al. 2010). The Severn Estuary contains both muddy and sandy sediments and they are often considered individually. However, mud and sand in estuaries can be deposited either as alternating layers or mixtures; the interaction of mud: sand mixtures can significantly affect the deposition, erodibility and transport characteristics within an estuarine system, far beyond their individual behaviors.

2.2 Wave Action

With the exception of those mudflats sheltered within estuarine environments, most mudflats are influenced by the action of waves that can mobilize and transport sediments, most significantly during storms (Le Hir et al. 2000).

Under normal conditions, the waves that arrive on the mudflat are attenuated by bed friction, and non-breaking waves lose 93–96% of their energy across shallow mudflat environments (Komar 1998). Regardless of the energy dissipation, wind waves in shallow water can resuspend fine sediment and transport it shoreward by tidal action. While sand particles settle at faster rates and travel shorter distances, muds are often maintained in suspension much longer and thus travel longer distances. Pereira et al. (2011) studied the episodic attenuation of the surface wave spectra due to the presence of fluid muds along the fine-grained sandy beach of Cassino (Brazil), and were able to describe how fluid mud overlays the sandy bottom episodically. On the other hand, during exceptional events such as storms, the wave disruption can produce a net difference in mud and sand transport. For instance, for the Louisiana coast, Draut et al. (2005) found that under certain conditions (i.e. abundant supply of fine-grained fluvial sediment and wave-induced resuspension that maintains an unconsolidated sea floor; dominant onshore wind direction during energetic conditions; and low tidal range), mudflat accretion can occur during energetic atmospheric activity episodes. Yang et al. (2015) developed an integrated model for the simulation of cohesive sediment transport during storm events where winds, currents, and waves play an important role in wave-induced shear stress.

The shear rate created by wave loading over a mud layer is highly phase-dependent (in turn, this is explained by the rheological properties of mud); thus a mud layer produces wave attenuation (Hsu et al. 2013b). Applying this principle to the field, it has been shown for the South American coast between the Amazon and the Orinoco river mouths that the interaction of muddy banks with waves results in complex and fluctuating shorelines (Anthony et al. 2010). Bank zones are protected from offshore wave attack as a result of wave-energy dampening by a fluidized mud layer that absorbs wave energy, and as a consequence, significant (albeit temporary) coastal accretion accompanied by rapid mangrove colonization is possible.

Wells (1983) compared intertidal and subtidal fluid muds in low-, moderate-, and high-tide-range environments, and found similarities in process-response behavior despite the wide range in tidal energy. The main findings in this study were the extreme wave attenuation produced by mudflats, and the rapid migration of soft muds. Muds are made "soft" by a wave-mediated process of fluidization. Small waves play a significant part in mud fluidization (Wells 1983), but tidal mixing may also be important in some estuaries [as discussed in the previous section, regarding the Wolanski et al. (1988) study].

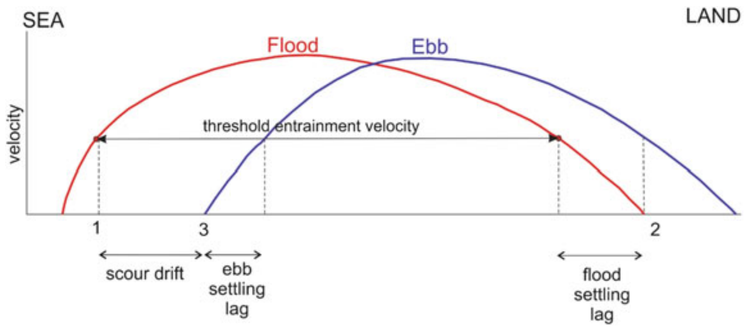

Fig. 2.7 Postma (1961) schematic diagram for net landward particle transport (modified by Carter 2013). A particle at point 1 is entrained into suspension and remains in suspension as long as it is over the threshold entrainment velocity. Thereafter it settles resting in point 2 after a flood settling lag. The particle then becomes re-entrained on the ebb tide settling out at point 3 after an ebb settling lag. The distance between point 1 and 3 represents the net landward movement over a tidal cycle.

2.3 Sediment Transport

The process of sediment transport comprises three stages, erosion (i.e. initiation of sediment motion), transport and deposition. While the non-cohesive sediment is transported as bedload (i.e. rolling or sliding along the sediment bed), the fine cohesive sediments and sand-sized particles are transported mainly as a suspended load (i.e. sediment uplifted in the water column by the flow), and are deposited under calm conditions during slack tides (i.e. net tide velocity = 0 m s^{-1}). A detailed explanation of sediment transport principles can be found in Wang (2012).

The greatest amount of sediment transport takes place in the intertidal zone, where the level of the water coincides with the stronger tides in the middle of the tidal cycle. Mudflat accretion occurs due to an onshore transport of fine material. As previously mentioned, this sediment is transported largely in suspension, and a lag effect is associated with the time required for the suspended sediment to adjust to changes in fluid velocity (Pritchard and Hogg 2003). This “scour lag” is based on the model proposed by Postma (1961) to explain the accumulation of fine sediment landward, where a hydrodynamic asymmetry is present, and takes into consideration the slow settling velocity of fine sediments. Basically, this model considers the lag that a suspended particle takes to be deposited (after the current velocity is below the threshold velocity for deposition) while it is carried landward by the flood tide for some distance (Fig. 2.7). Then, the particle is re-entrained when the threshold ebb tide velocity is reached. The mechanism is accentuated if the threshold velocity for the erosion of sediment is higher than the threshold velocity for deposition. Recent contributions on this topic have attempted to quantify the relative importance of mud properties and hydrodynamics (Roberts et al. 2000; Pritchard 2005; Chernetsky et al. 2010; Hsu et al. 2013a; van Maren and Winterwerp 2013).

While fine sediments are primarily deposited during slack (high and low) tides, coarse sediment particles (typically sand) can be deposited during ebb and flood tides or during strong storm events. This mechanism results in a lamination which is a diagnostic feature of tidal influence in the geologic record. This lamination may be promoted and maintained by biostabilization (see also Chaps. 3, 4, 5, 8, and 10). The resulting alternation of sand and mud forms the tidal bedding, i.e. a sequence of sediments produced by the above-mentioned cyclic conditions (Davies 2012).

The net sediment budget is often reflected in mudflat morphology by the occurrence of erosion or deposition patterns that generate either a convex-upward shape of the shore profile (indicating a stable state), or a concave-upward profile associated with wave action that causes erosion and a coarsening of the underlying sediment (Metha 2002). In the case of a concave profile, the maximum slope is often located towards the upper mudflat and frequently a small ridge occurs (Fig. 2.8a), as a consequence of wave erosion at high tide during storm episodes, in conjunction with the formation of a saltmarsh (Kirby 2000). Deposition rates on tidal flats are greatest for concave profiles (van Maren and Winterwerp 2013). In contrast, in a convex upward profile, the maximum slope is closer to the low water level and sediment transport is dominated by tidal currents (Fig. 2.8b). The convex curvature in an accreting bed profile attenuates wave-induced shear stress. Often, mudflats may evidence erosion and deposition throughout their extension, and both types of profiles can be observed simultaneously on different parts of the flat (Wang 1983), such as in the inner zone of the Bahía Blanca Estuary (Argentina) depicted in Fig. 2.8.

Accretion-dominated muddy coasts occur when sediment supply exceeds the rate of erosion and the destabilizing forces are smaller than sediment-stabilizing hydraulic forcing (Kirby 2002). However, an exception to this has been described for the Louisiana coast (USA—Draut et al. 2005), also discussed in the previous section. An anomalous case of mudflat accretion was detected in the study of a 17-year meteorological record; while the area experiences widespread land loss due to rapid relative sea-level rise, the abundant supply of fine-grained fluvial sediment combined with a dominant onshore wind direction during energetic atmospheric activity (i.e. winter cold fronts and tropical-depression storms) produce mudflat accretion with a low tidal range in this system.

Given the multiple and shifting processes that govern sediment transport in mudflats, the evolution of modern mudflats can sometimes be difficult to reconstruct, although there exist good methodological approaches, such as the study of the record of sea-level fluctuations left in transgressive deposition and regressive events. Chang et al. (2006) studied sediment cores from the East Frisian Wadden Sea (Germany), and interpreted sea regressions through indicators such as the presence of peat; in this way, they were able to reconstruct the evolution of what originated as a back-barrier tidal basin.

Fig. 2.8 Evidence of erosion and deposition throughout the extension of a mudflat; inner zone of the Bahía Blanca Estuary. (**a**) A convex-upward shape profile can be discerned at ebb tide. A narrow tidal channel (with water) and creeks incise the mudflat, while the upper mudflats favor the settling of cordgrass (note different coloration) forming a salt marsh interspersed among unvegetated mudflats. The city of Bahía Blanca can be seen in the background. (**b**) Small ridge (~1 m-high) in the upper mudflat formed by wave erosion during storm events caused when strong winds (in coincidence with wave fetch or blowing at a small angle with the coast) accumulate seawater in the inner estuary.

3 Chemical Processes

3.1 The Electrochemical Environment

The occurrence of intermittent or temporary flooding and the presence of anoxic conditions are typical features of mudflat sediments. The change from an aerobic and oxidized state to an anaerobic and reduced state generates particular redox reactions that govern many of the chemical processes occurring in mudflats, and controls, to a large degree, their biological functions (Mitsch and Gosselink 2000; see also Chaps. 3 and 7).

Redox reactions transfer electrons among atoms and many of these reactions in mudflats are based on organic decomposition. The loss of electrons from an atom is known as oxidation, while the gain of electrons by an atom is called reduction. Each complete redox reaction contains an oxidation and a reduction component called *half-reactions*. One important result of the oxidation and reduction processes is the frequent phase changes of the atoms in the sediment, such as causing solid minerals to dissolve and re-precipitate or dissolved ions to become gases. The basic oxidation half-reactions in mudflats are promoted by the chemical products of microorganism respiration. Oxidation occurs when organic tissues are decomposed by heterotrophic microorganisms, mainly bacteria. When tissues are oxidized, the released electrons are used in reducing reactions (Vepraskas and Faulkner 2001). The special case of organic decomposition will be considered in detail in Sect. 3.2.

The substances reduced in redox reactions are called electron acceptors, and oxygen is the primary electron acceptor in aerobic sediments. However, when oxygen is not present, anaerobic bacteria use alternative electron acceptors to continue their respiration. These alternative electron acceptors are used in a thermodynamically determined order or "thermodynamic sorting" (Richards 1965). In order of favorability, nitrate is utilized first, followed by manganese, iron, sulfate, and finally CO_2. It should be noted that different microbial species reduce each of the electron acceptors in a sequence known as a redox cascade. If nitrate, sulfate, and organic matter are present in anoxic sediments, a group of specialized bacteria (denitrifiers) will reduce all the available nitrate, and then sulfate reducers begin sulfate reduction (Fenchel and Jørgensen 1977; Reddy and DeLaune 2008).

On mudflats, the tidal regime results in alternating flooding and drying events, which have a determinant influence on the biogeochemical functioning of mudflats, leading to a highly variable temporal dynamics in the redox status of sediments. Extensive anoxic areas commonly develop below the surface because of reduced oxygen availability. The transition from predominantly oxidizing to reducing conditions is commonly termed the redox potential discontinuity (RPD) layer (Fenchel and Riedl 1970; Sturdivant et al. 2012). Under anoxic conditions, ferric iron and sulfate are reduced by microbial activity and the accumulation of reduced compounds produces a grey/green or black layer below the surface (Bloomfield 1952; Valdemarsen et al. 2009) that can be easily differentiated from the oxygenated orange-brown layer above it. This transition is often used as a relative measure of oxygen penetration into the sediment (e.g. Sundby et al. 1986; Moodley et al. 1998; Diaz and Trefry 2006). The depth of the RPD can vary extensively in time and space and is influenced by physical and biological factors like temperature, sediment particle size, hydrodynamic conditions, organic content, bacterial activity, and the presence of burrowing animals. Finer sediment particles and higher organic content, subject to warm conditions, promote microbial activity and proliferation. In such conditions, there is an increased anaerobic degradation, and the anoxic zone may extend almost to the sediment surface. Faunal irrigation and bioturbation, on the other hand, allow oxygenated water to penetrate deeper into the sediment, creating a three-dimensional mosaic of redox conditions (Kristensen 2000; Solan and Kennedy 2002; Hunting and Kampfraath 2013).

3.2 Sources of Organic Matter and Biogeochemical Cycles

The fixation of atmospheric carbon through photosynthesis is the major source of carbon to most terrestrial and aquatic ecosystems, and light penetration is sufficient in intertidal mudflats to allow photosynthesis and net primary production of organic carbon by benthic microalgae belonging to several taxonomic groups, and collectively known as microphytobenthos (MPB; MacIntyre et al. 1996). However, most of the organic matter in mudflats comes from allochthonous sources, through sedimentation from the water column (Mann 2009). Depending on the environmental parameters, different sources of organic matter may be dominant, e.g. sedimentation of phytoplankton, continental inputs from rivers, detritus of salt marsh macrophytes, or POM transported by tides. Invertebrate deposit feeders play a significant role in the processing of the organic matter settling on the mudflat surface. In the process of bioturbation, deposit feeders such as polychaete worms, crabs, and mollusks can mix sediments to a depth of several centimeters, burying organic matter below the upper well-aerated layer, into the deeper anaerobic sediments (Rosenberg et al. 2008; see also Chaps. 5, 6, and 10).

From an ecosystem perspective, a major function of mudflats is the regeneration of nutrients through the complete decomposition of organic matter from different sources (Sundbäck et al. 2003) into soluble forms of nitrogen, phosphorous and carbon. In the aerobic layer, organic matter is rapidly colonized by aerobic bacteria, and the end products of aerobic decomposition are CO_2 and inorganic nutrients like ammonium and phosphate, which are released back to the water column. Degradation of organically combined nitrogen involves two important biological transformations: ammonification (Fig. 2.9b), that oxidizes organic nitrogen to ammonium under either aerobic or anaerobic conditions; and nitrification, which transforms ammonium to nitrate under aerobic conditions (ZoBell and Feltham 1942; Owens et al. 1979; Reddy and DeLaune 2008). Nitrification is a two-step oxidation reaction that involves two different groups of bacteria: first the oxidation of ammonium to nitrite, and second the oxidation of nitrite to nitrate (Fig. 2.9c).

In anaerobic conditions, different groups of bacteria use alternative electron acceptors to decompose organic matter and generate energy. The most important groups are fermenters, nitrate reducers, sulfate reducers, and methanogens. In fermentation, water-soluble substances are degraded to low-molecular-weight organic compounds like lactate, acetate, propionate, or alcohol. Fermenting bacteria are mostly obligate anaerobes, and can derive a relatively small amount of energy through partial oxidation of organic substrates using specific organic compounds present in the bacterial cell as electron acceptors (Molongoski and Klug 1976).

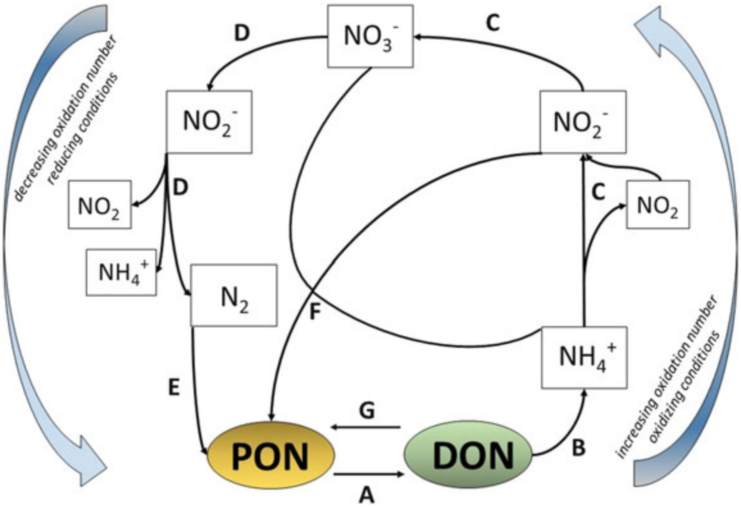

Fig. 2.9 Schematic representation of the biogeochemical nitrogen cycle. Relevant processes: (A) remineralization; (B) ammonification; (C) nitrification; (D) DNRA (dissimilatory nitrate reduction to ammonia); (E) nitrogen fixation; (F) assimilatory nitrogen reduction; (G) assimilation of DON. *DON* dissolved organic nitrogen, *PON* particulate organic nitrogen (modified from Libes 1992).

Nitrate reducers are the microbial group involved in N cycling. Denitrification and dissimilatory nitrate reduction to ammonia (DNRA; Fig. 2.9d) are two very important processes of microbially-facilitated nitrate reduction that occur under low oxygen concentrations (Tiedje et al. 1982). Denitrifiers are mainly facultative aerobic bacteria that oxidize organic compounds, including the end products of fermentation, by reducing nitrate to gaseous N_2. This reaction occurs under moderately reduced conditions, in the absence of oxygen (Ljungdahl and Eriksson 1985). On mudflats, the coupling of aerobic and anaerobic processes is enhanced (as shown in Fig. 2.9), and much of the nitrate formed during nitrification under aerobic conditions is rapidly consumed by denitrifiers in adjacent anaerobic micro-environments.

Dissimilatory reduction of nitrate to ammonia is performed by obligate and facultative anaerobes (Tiedje 1988). While denitrification removes N_2 from the system as a gaseous product, thereby reducing the potential for eutrophication, DNRA recycles nitrate into ammonium, retaining nitrogen within the mudflat. Intertidal sediments are hotspots of DNRA, and recent studies suggest that tidal pumping may sustain this nitrate-reducing pathway (Zheng et al. 2016).

Nitrogen reduction under anoxic conditions can also occur through anaerobic ammonium oxidation (*anammox*), a process that was not identified until 1995 (Mulder et al. 1995). In the presence of nitrite, the anammox process also produces N_2, by using nitrite as an electron acceptor to oxidize ammonium (Keunen 2008). Anammox makes a great contribution to N_2 formation in the continental shelf (Thamdrup and Dalsgaard 2002). In intertidal environments, a coupling between nitrification and anammox has been proposed; similarly to nitrification-denitrification coupling, anammox would be enhanced by high rates of nitrification in aerobic zones and accumulation of nitrate, which can diffuse into anaerobic zones. If denitrification is nitrate-saturated, some of the formed nitrite may support the anammox process (Dalsgaard et al. 2005). Intertidal sediments with an aerobic-anaerobic interface and redox oscillations provide an interesting system for the estimation of anammox rates, and for the evaluation of a possible coupling between nitrification and denitrification, as well as with anammox (Oliveira Fernandes et al. 2016).

Sulfate-reducing bacteria are obligate anaerobes that reduce the terminal electron acceptor sulfate to sulfides during the degradation of organic compounds (Muyzer and Stams 2008). Sulfur cycling largely regulates many microbial communities and redox reactions, and sulfate reducers have been extensively studied in mudflats and salt marshes. Thermodynamically, sulfate is a much less favorable electron acceptor than nitrate, manganese and iron oxides, but sulfates are widely available in the marine environment. Sulfur cycling processes are similar to those of nitrogen. In dissimilative sulfate reductions, obligate anaerobes reduce sulfate to sulfide to obtain energy. In assimilative sulfate reduction, sulfate is reduced to organic sulfhydryl groups by organisms that assimilate sulfate and sulfide for the synthesis of cellular constituents. In desulfuration, organic-bound sulfur is desulfurated, producing hydrogen sulfide gas. Hydrogen sulfide can be oxidized to elemental sulfur by sulfide oxidation, a process carried out by photosynthetic green and purple bacteria and some chemolithotrophs. Sulfur oxidizers produce sulfate by oxidizing sulfur, and elemental sulfur may be reduced to hydrogen sulfide through dissimilatory sulfur reduction (Reddy and DeLaune 2008).

In aerobic environments, most of the energy trapped in organic matter is released during decay. In anaerobic decomposition, on the contrary, a comparatively low amount of energy is released, and most of the remaining energy is conserved in high-energy reduced sulfur compounds such as soluble sulfides, iron monosulfides, pyrite, elemental sulfur, thiosulfate, and polythionite. When these reduced inorganic compounds are subsequently reoxidized, the energy is released. Thus, sulfur is a key element in the recycling of the energy in anaerobic environments, and accounts for a significant portion of the total respiration in intertidal sediments (Hansen 1994).

Dimethylsulfoniopropionate (DMSP) is a sulfur compound produced in great amounts by certain species of marine algae through osmoregulation. When released into the marine environment as dissolved DMSP, it is readily degraded to dimethylsulfide (DMS) by chemoheterotrophic bacteria, serving as a link between primary production and microbial food webs (Kiene 1990). The biogeochemical significance of these compounds was first suggested in 1972, when global DMS emissions from coastal waters and mudflats were found to be significant, and considered a key step in the global sulfur cycle (Lovelock et al. 1972).

Methanogenesis is the dominant process in organic matter degradation in anaerobic sediments with low levels of sulfate. The organisms capable of producing methane (Archaea) use carbon as the terminal electron acceptor in respiration (Figure 2.10c evidences methanogens in mudflat sediments). There is competition for electron donors between methanogens and sulfate reducers, and sulfate reduction

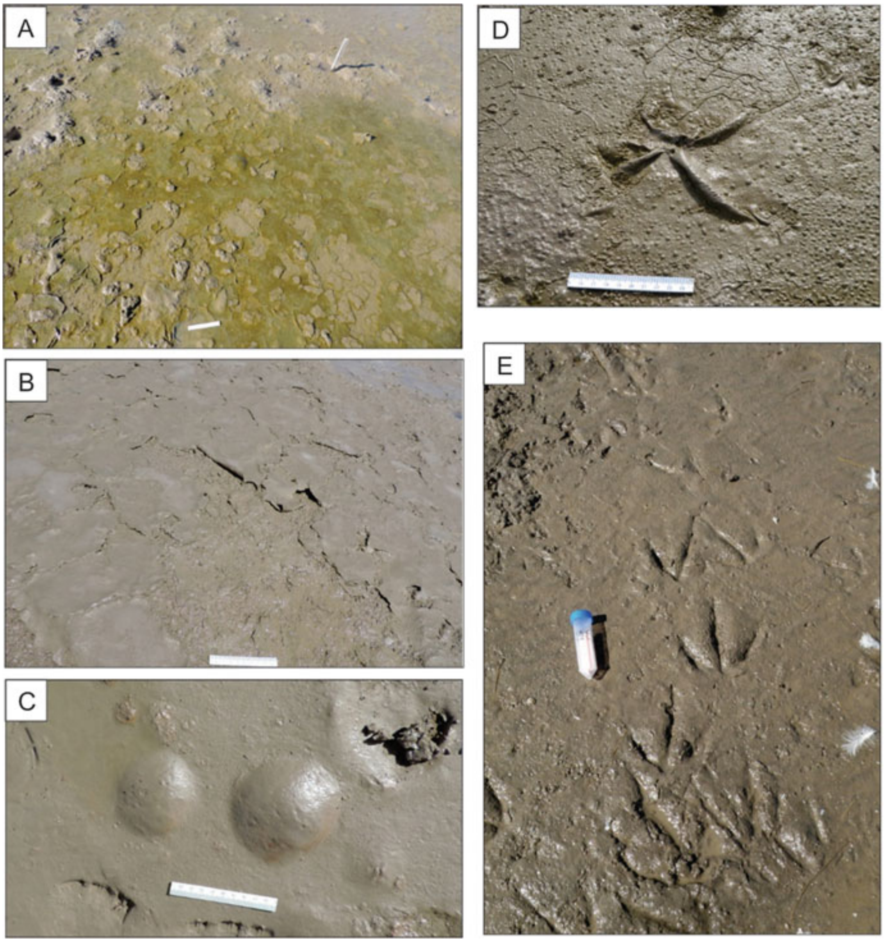

Fig. 2.10 Biologically-colonized surface sediments in mudflats of the Bahía Blanca Estuary. (**a**) Diatom-containing biofilms confer a characteristic golden-brown coloration; note interspersed microbial-mat chips. (**b**) Torn microbial mats covering muddy sediments, evidencing physical deformation as a product of wave shear stress; some of them have been flipped-over by wave action. (**c**) Gas domes (putatively, methane), indicative of microbial metabolic activity in underlying sediments. (**d**) A collapsed gas dome; there are also numerous gas bubbles trapped under the microbial mat. (**e**) Bird footprint preservation in biostabilized muddy sediments due to the presence of microbial mats. Field scales = 10.0 cm; except tube in (**e**) = 11.5 cm.

results in the liberation of more energy than methanogenesis. Therefore, in the anaerobic layer of mudflats and salt marshes, sulfate reduction is considered the most important process in organic matter remineralization (Llobet-Brossa et al. 2002), and methanogenesis becomes the dominant oxidation process when sulfate is depleted.