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Common benthic algae and cyanobacteria in southern California tidal wetlands

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Abstract

Benthic algae and photosynthetic bacteria are important components of coastal wetlands, contributing to primary productivity, nutrient cycling, and other ecosystem functions. Despite their key roles in mudflat and salt marsh food webs, the extent and patterns of diversity of these organisms is poorly known. Sediments from intertidal marshes in San Diego County, California host a variety of cyanobacteria, diatoms, and multi-cellular algae. This flora describes approximately 40 taxa of common and notable cyanobacteria, microalgae and macroalgae observed in wetland sediments, principally from a small tidal marsh in Mission Bay. Cyanobacteria included coccoid and heterocyte and non-heterocyte bearing filamentous genera. A phylogenetically-diverse assemblage of pennate and centric diatoms, euglenoids, green algae, red algae, tribophytes and brown seaweeds was also observed. Most taxa are illustrated with photographs.

Key words

alpha diversity • cyanobacteria • diatoms • euglenoids • Kendall-Frost Mission Bay Marsh Reserve • macroalgae • microphytobenthos • salt marsh • Tijuana Estuary • *Vaucheria*

Introduction

The sediments of coastal marine wetlands in California are inhabited by a variety of algal and bacterial primary producers in addition to the more conspicuous vascular plants that provide most of the physical structure of coastal salt marshes and seagrass meadows. The non-vascular plant flora includes microscopic cyanobacteria, anoxygenic phototrophic bacteria, diatoms, and euglenoids, often collectively known as "microphytobenthos" (Sullivan and Currin 2000). Larger green algae, red and brown seaweeds, and the macroscopic tribophyte, *Vaucheria* are also residents of these ecosystems (Barnhardt et al. 1992).

Ecologically, sediment-associated algae and photosynthetic bacteria are key components of wetland food webs (Sullivan and Moncreiff 1990, Page 1997). They account for a substantial fraction of ecosystem primary productivity in California (Zedler 1980) and in other regions (Fejes et al. 2005). While understanding of the ecological roles and spatio-temporal dynamics of these organisms has improved, the diversity and natural history of the micro- and macroalgae of salt marshes and mudflats from the northeastern Pacific, including southern California, are still poorly understood. Lack of a deeper understanding of the diversity of these organisms within and between estuaries and estuarine habitat types impedes efforts to understand how spatio-temporal variation in the composition of benthic assemblages may affect ecosystem functions or how changes in assemblages may relate to anthropogenic impacts to wetlands.

To date no comprehensive floristic account of wetland algae and photosynthetic bacteria in California has been produced by the phycological community. However, some taxonomic information on these organisms exists in scattered sources. Early research on the taxonomy of wetland algae began with William Setchell, Nathaniel Gardner, and George Hollenberg. These phycologists produced lists and/or descriptions of cyanobacteria and macroalgae from salt marshes and mudflats in several publications, but the accounts principally focused on either rocky shore cyanobacteria (Gardner 1918, Setchell and Gardner 1919) or wetland vascular plant floras (Purer 1942). Several decades later, Zedler (1982) published a list of cyanobacteria, diatoms, and green algae collected from Tijuana Estuary at the southern extreme of the state. She recorded 32 species of diatoms, four cyanobacterial taxa, and the green algal genera *Rhizoclonium* and *Enteromorpha*, but noted that her account was not comprehensive. Wilson (1980) and Carpelan (1978) studied benthic diatoms from Mugu Lagoon and pelagic diatoms in four lagoons in northern San Diego County respectively. Records of wetland macroalgae have been compiled for Humboldt Bay in northern California (Barnhardt et al. 1992), and for Newport Bay in southern California

(Vogl 1966). Stewart's (1991) treatment of San Diego County seaweeds also notes wetland occurrences of marine macroalgae.

There are formidable obstacles to producing a comprehensive flora of tidal wetland algae for any localized region. First, the phylogenetic breadth of photosynthetic organisms in tidal wetland habitats requires a diversity of specialists, employing an array of tools from electron microscopy (to observe diatom frustule ornamentation for species identification; Round et al. 1990) to culturing techniques (for cyanobacteria and anoxygenic photosynthetic bacteria) to standard phycological methods for macroalgal identification and preservation. As Sullivan and Currin (2000) note, funding for such an endeavor is likely to be difficult to acquire. Moreover, the systematics of many groups of these organisms is in flux. In particular, study of the cyanobacteria is complicated by the existence of competing bacteriological and morphological classification schemes and by widely differing approaches to using morphology to delineate species (Sullivan and Currin 2000, Whitton and Potts 2000). An additional consideration is that application of names to microalgal and cyanobacterial taxa for a given locality is at least somewhat dependent on decisions made in other geographic regions or habitats since detailed taxonomic studies are haphazardly distributed in space and time. For instance, some important cyanobacterial reference sources either treat distant geographic areas (e.g., Komárek and Anagnostidis 1999) or describe primarily freshwater and terrestrial organisms (e.g., Desikachary 1959).

Despite these challenges, floristic and systematic work on wetland microalgae and seaweeds provides the foundation for progress in basic biodiversity research. In addition to the possibility that cryptic taxa may be discovered in the flora, algae are excellent systems for investigation of molecular versus morphologically-based phylogenies (Whitton and Potts 2000). Better knowledge of the diversity of microproducers present in coastal wetland habitats should also enable a better understanding of ecological interactions between microphytobenthos and other wetland organisms and facilitate the use of biodiversity metrics as a means of assessing ecosystem health and dynamics.

In this paper the common benthic cyanobacteria, microalgae, and seaweeds associated with sediments from tidal wetlands in southern California are described and illustrated. The goal is to provide preliminary (though not comprehensive) documentation of the local flora and add to the fragmentary knowledge of these organisms in the region. The paper focuses on new collections made from Mission Bay and Tijuana Estuary in San Diego County, but also includes some records of species previously recorded from wetlands throughout southern California (Point Conception to the US/Mexico border). Organisms included here were assigned tentative genus (and sometimes species) names based on morphological features visible by eye or by light microscopy. Supporting references pertinent to the identification of taxa, their local distribution, and (where possible) their natural history, are also included. Of the various taxa treated, documentation of the cyanobacteria is most thorough, partly filling the significant gap in information on these common inhabitants of tidal wetlands in the region.

Materials and methods

Benthic sediment samples and macroscopic algae were collected between 1999 and 2005 at the Kendall-Frost Mission Bay Marsh Reserve and adjacent Northern Wildlife Preserve in northern Mission Bay (32°47′ N, 117°13′ W) and during 2000 and 2001 at Tijuana Estuary (32°34′ N, 117°7′ W) in San Diego County, California. Various types of intertidal wetland habitats were present within these estuaries including mudflat, un-vegetated intertidal channels, and salt marshes dominated by vascular plants such as *Spartina foliosa, Distichlis spicata, Salicornia bigelovii, Sarcocornia pacifica, Batis maritima*, and *Limonium californicum*. Prior to significant urban development along the San Diego coastline, Mission Bay supported much more extensive areas of salt marsh habitat, including a large expanse of marsh along the entire southern portion of the bay (USGS 1930, 1967). Although historical maps suggest that the Kendall-Frost Reserve and immediately adjacent areas have long been vegetated marsh, habitat area appears to have decreased in size since the 1930s. Tijuana Estuary has been less impacted by urban encroachment and today remains one of the largest estuarine ecosystems in southern California.

Observations and photographic documentation were made on live organisms, or occasionally on organisms grown in culture. Specimens were often kept alive by transferring moist field sediment to incubation in the laboratory. Field sediment and cultures were maintained at about room temperature (usually 21-22°C) with illumination (13 hr light exposure of ~70 μ E m⁻² s⁻¹). Cultured organisms were grown on sterilized f/2 media prepared in artificial seawater with or without sterilized glass particles (13-44 μ m diameter) as a substrate. Organisms living on field-collected sediment were kept and observed up to about seven months following removal from the field (living taxa were still apparently abundant on these sediments although proportional abundances and the composition of taxa likely changed over time). Photographs were taken with a digital camera through compound microscopes (usually at 160 or 400x magnification).

Diatoms were identified to genus where possible using Round et al. (1990). Cyanobacterial taxa were generally identified to genus (occasionally to species level) using the recent taxonomic treatments in Anagnostidis and Komárek (1988), Komárek and Anagnostidis (1989), and Boone and Castenholz (2001). Humm and Wicks (1979), Desikachary (1959), and Setchell and Gardner (1919) were also consulted for identification and nomenclatural purposes.

Macroalgae attached to sediment-associated substrates or occurring loosely in wetland habitats were pressed fresh on herbarium paper and dried. Identification and current nomenclature of macroalgae follows Abbott and Hollenberg (1976) and Gabrielson et al. (2004).

The flora

CYANOBACTERIA

Worldwide, cyanobacteria are frequently found in a variety of coastal habitats such as mudflats, salt marshes, hypersaline lagoons, and the rocky intertidal (Fogg et al. 1973). They comprise an important component of the microscopic flora of southern California salt marshes and mudflats (Zedler 1982), but are often patchy in their spatial distribution (Janousek 2005). Habitats with warm hypersaline water or low grazing pressure may be more conducive to extensive cyanobacterial populations (Pinckney and Paerl 1997, Nübel et al. 1999, Stal 2000).

Previously published records of cyanobacteria from tidal wetlands in southern California document the presence of only a few taxa, all in the botanical order Oscillatoriales (Purer 1942, Zedler 1982; Table 1). Setchell and Gardner (1919) list many additional species for the northeastern Pacific coast, but it is uncertain which of their taxa were present in wetland habitats from southern California. Zedler (1982) listed three "Schizothrix" species from Tijuana Estuary (apparently using Drouet's taxonomic system), but did not include descriptions or illustrations, so reassignment of these species using more modern classification schemes is not possible. In this paper, at least 15 "morphospecies" are described from collections made in San Diego County.

Table 1. Benthic cyanobacteria from tidal wetland habitats in southern California. Subsection (ordinal) classification is after Boone and Castenholz (2001). The three *Schizothrix* species listed in Zedler (1982) have not been included in the table since they apparently reflect the radically condensed classification system of Drouet. * Tentative identification.

Subsection (order) and species	Local distribution	Reference
Subsection I (Chroococcales)		
Chamaesiphon *	Mission Bay	this study
Chroococcus turgidus	Mission Bay	this study
Chroococcus sp(p).	Mission Bay	this study
Gloeocapsa sp(p).	Mission Bay	this study
Synechocystis *	Mission Bay	this study
Johannesbaptistia pellucida	Mission Bay	this study
Subsection II (Pleurocapsales)		
Chroococidiopsis *	Mission Bay	this study
Subsection III (Oscillatoriales)		
Spirulina subsalsa	Mission Bay	this study
Spirulina labyrinthiformis	Mission Bay	this study
Microcoleus lyngbyaceus	Tijuana Estuary	Zedler 1982
Microcoloeus sp.	Mission Bay	this study
Oscillatoria sp. 1	Mission Bay	this study
Oscillatoria sp. 2	Mission Bay	this study
Oscillatoria sp. 3	Mission Bay	this study
Lyngbya aestuarii f. ferruginea		Purer 1942
Phormidioideae, unknown species	Mission Bay	this study
Leptolyngbya *	Mission Bay	this study
Subsection IV (Nostocales)		
Anabaena sp. 1 *	Mission Bay	this study
Anabaena sp. 2 *	Mission Bay	this study

ORDER CHROOCOCCALES

Coccoid cyanobacteria characterized by only binary fission as a means of cellular division are placed in the Chroococcales (equivalent to *subsection I* of Boone and Castenholz 2001).

Chamaesiphon (?)

As recently defined, *Chamaesiphon* is a genus of unicellular cyanobacteria generally found attached to substrates in freshwater habitats (Komárek and Anagnostidis 1999, Herdman et al. 2001a). Daughter cells are produced from the larger mother cells by a budding-like type of binary fission.

Chamaesiphon-like organisms were observed in raw sediment samples and were also brought into culture (on f/2 media). Cultured cells seemingly did not form clusters of more than about two cells. These observations suggest either that Chamaesiphon is also found from saline habitats or that these organisms represent a morphologically-similar taxon in possible need of a new taxonomic identity.

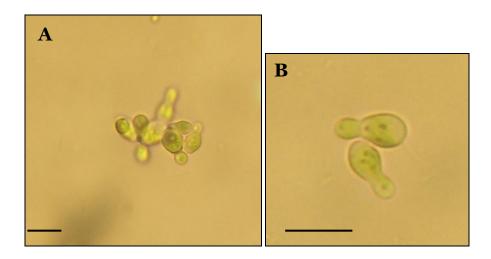


Figure 1. Chamaesiphon-like cyanobacteria from Mission Bay sediments. **A.** A large aggregation of cells; bar = $8.3 \mu m$. **B.** Clusters of two cells; bar = $10 \mu m$. Both photographs are of sediment-associated material collected during October 2003 and kept in the lab under incubation for about six months.

Chroococcus

Chroococcus species inhabit both freshwater and marine habitats and occur as colonies of 1-4 large hemispherical cells (Rippka et al. 2001a). The genus is morphologically similar to *Gloeocapsa*, but differs by having larger cell diameters, a more tightly appressed sheath, and more hemi-spherical cells (Herdman et al. 2001b). Molecular evidence supports the morphologically-based distinction between the two genera (Rippka et al. 2001a), although separation of the genera by size is not followed by all workers (e.g., Silva and Pienaar 2000). Organisms with cell diameters greater than 20 µm are herein assigned to *Chroococcus* while those with diameters less than about 10 µm diameter are placed in *Gloeocapsa* in accordance with recent bacteriological taxonomic schemes (Herdman et al. 2001b). The ability to fix nitrogen has been determined in two of the three cultured isolates of *Chroococcus* (Rippka et al. 2001a).

Both *Chroococcus* and *Gloeocapsa* are frequently reported from salt marsh habitats worldwide. The large-celled type species of *Chroococcus*, *C. turgidus*, has been previously reported from rocky habitat in California (Setchell and Gardner 1919), but the organism depicted below (Figure 2A) may be the first record from salt marsh sediments in California.

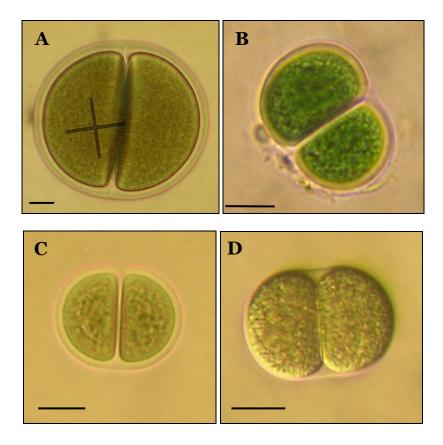


Figure 2. Salt marsh *Chroococcus* spp. from Mission Bay. **A.** *C. turgidus* from sediments collected during August 2004. **B.** *Chroococcus* sp., collected October 2003. **C.** A smaller *Chroococcus* colony collected during summer 2004. **D.** *Chroococcus* specimen with tightly appressed sheath, collected October 2003. All bars = $10 \mu m$.

Gloeocapsa

The clusters of cyanobacteria depicted in Figure 3 have been tentatively assigned to *Gloeocapsa*, based on cellular diameters and the presence of wider, loosely appressed sheaths (Herdman et al. 2001b). Komárek and Anagnostidis (1999) recognize more than 30 species in this genus from Europe alone. Nitrogen fixation has been observed in at least one member of the genus (Wyatt and Silvey 1969).

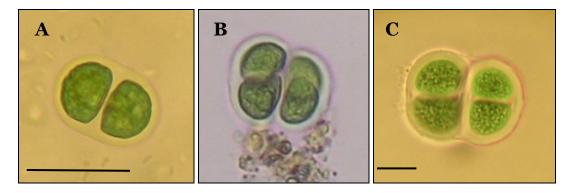


Figure 3. Examples of coccoid cyanobacteria attributable to the genus *Gloeocapsa*. **A.** Organism from sediments in lightly vegetated salt marsh; sheath thickness ~2.5 μ m; bar = 24 μ m. **B.** Four (possibly five) celled colony ~33 μ m long. **C.** Specimen collected from vegetated marsh during summer 2004; bar = 10 μ m.

Synechocystis (?)

Loosely-organized clusters of coccoid cyanobacteria were occasionally observed in sediments samples. The organisms below are tentatively assigned to the genus *Synechocystis* based on their cellular diameter, apparent cell division in three dimensions, and absence of a well-structured sheath or gas-filled vesicles (Herdman et al. 2001c).



Figure 4. A *Synechocystis*-like colony consisting of coccoid to egg-shaped cells with diameters of approximately 5 μ m; bar = 10 μ m.

Johannesbaptistia pellucida

This species was only observed once in a sediment collection from vegetated salt marsh in Mission Bay during the summer of 2004. The organism in Figure 5 is similar in morphology to *Johannesbaptistia* as illustrated in Humm and Wicks (1980) and Potts (1980). Cells are arranged in a pseudo-filament (Humm and Wicks 1980) with a relatively thick sheath. This species has been found worldwide from lower latitudes, but is apparently not found in abundance (Umezaki 1961). Sage and Sullivan (1978) record this taxon for North American salt marsh habitats.



Figure 5. Portion of a filament of *Johannesbaptistia pellucida* collected from Mission Bay salt marsh. The sheath was approximately 2.5 μ m thick; bar = 10 μ m.

ORDER PLEUROCAPSALES

The Pleurocapsales (*subsection II* of Boone and Castenholz 2001) are coccoid cyanobacteria reproducing via multiple fission (Rippka et al. 2001b).

Chroococidiopsis (?)

Sediment material incubated for a short time in the laboratory following collection from the field yielded abundant coccoid cyanobacteria growing on glass. Based on apparent patterns of cellular division, these organisms were tentatively assigned to *Chrococidiopsis*.

One or more greenish-yellow cells are present per cluster within a common sheath. There is large variation in cellular size (from ~ 1.7 to $> 24 \mu m$).

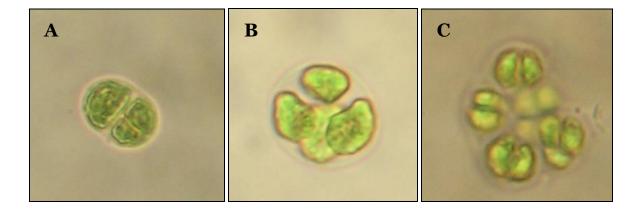


Figure 6. Cells tentatively assigned to *Chroococidiopsis*. **A.** Cluster length \sim 14.5 μ m. **B.** Tetrahedral-like cell division in 4 cell cluster of \sim 16 μ m diameter. **C.** Length of cell cluster \sim 22 μ m.

OSCILLATORIALES

The Oscillatoriales (*subsection III* of Boone and Castenholz 2001) are common in tidal wetlands. Species in the order are characterized by unbranched, cylindrical trichomes lacking heterocytes. Members of the Oscillatoriales may reproduce via short filaments termed hormogonia.

Microcoleus

Microcoleus (usually the species *M. chthonoplastes*) occurs in salt marsh sediments and other marine habitats worldwide (Karsten and Garcia-Pichel 1996, Nübel et al. 1999). Multiple filaments often occupy a single sheath. Cell lengths are slightly longer than widths. Apical cells may be terminally rounded (Figure 7B, C) or conical (not shown). The taxon appears to be very common in sediments from both Mission Bay and Tijuana Estuary. Zedler (1982) noted that *M. lyngbyaceus* was a very common species at Tijuana Estuary, present in the summer in *Spartina* marsh.

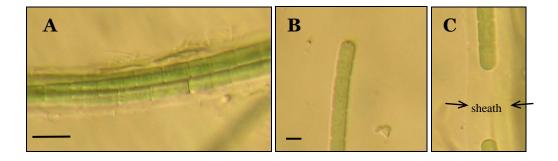


Figure 7. *Microcoleus* sp. **A.** Bundle of filaments from Mission Bay salt marsh habitat, collected during April 2004; bar $\sim 8.33 \, \mu m$. **B.** Single filament from a cyanobacterial mat in Mission Bay, April 2004; bar $= 4 \, \mu m$. **C.** Single filament in a larger sheath (faintly visible), collected in October 2003 from salt marsh.

Oscillatoria sp. 1

Filamentous, unbranched cyanobacteria with cell length to width ratios <1 are assigned to either *Lyngbya* or *Oscillatoria* (Boone and Castenholz 2001). Both genera may be present in Mission Bay, with up to several species present. *Lyngbya* can be distinguished from *Oscillatoria* by a relatively thicker sheath (Castenholz et al. 2001a).

The morphological diversity of *Oscillatoria*-like cyanobacteria from Mission Bay sediments is significant. This is similar to the large number of species (~10) that Setchell and Gardner (1919) recorded from wetland habitats along the Pacific coast, though it is unknown how many of their taxa were from southern California.

In Figure 8 (*Oscillatoria* sp. 1), filaments are brownish and are approximately 5-6 µm in diameter. Terminal cells are rounded. Constrictions between individual cells are fairly distinct in this taxon, although it should be noted that cellular constrictions are largely absent in recent conceptions of the genus.

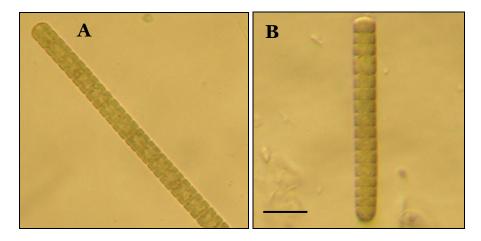


Figure 8. Oscillatoria sp. 1. **A.** Specimen from lightly vegetated salt marsh at Mission Bay, October 2003. Filament width \sim 6 μ m. **B.** Specimen from a cyanobacterial mat in lightly vegetated salt marsh. Trichome width \sim 5 μ m; bar = 10 μ m.

Oscillatoria sp. 2

Cells in Oscillatoria sp. 2 are distinctly granular and are several times wider than they are long.

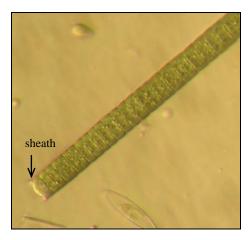


Figure 9. Oscillatoria sp. 2. Filament \sim 9 µm wide; cells \sim 2.5 µm long. A transparent sheath can be seen protruding beyond the rounded terminal cell.

Oscillatoria sp. 3

This is the widest cyanobacterium observed in sediments that appears to correspond with the generic description of *Oscillatoria*.

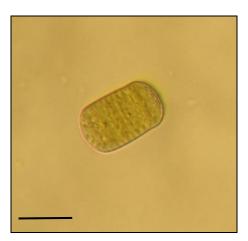


Figure 10. Oscillatoria sp. 3. Cellular cross walls are faintly visible. Specimen collected during April 2004; bar $\sim 13 \ \mu m$.

Leptolyngbya (?)

Thin (<3 µm wide) filamentous cyanobacteria were common in collections from Mission Bay and Tijuana Estuary. Several species may be present in the local flora but because of their small size, discernment of taxonomically-useful characters was difficult via light microscopy. In one specimen below (Figure 11A), cell length to width ratios were approximately two. The specimen is tentatively assigned to the "provisional" genus, *Leptolyngbya* (Castenholz et al. 2001b), but may need reassignment upon further study. Similar cyanobacteria of ~2.5 µm diameter (Figure 11B) were brought into culture on f/2 growth media and grew prolifically under incubation. Cultured organisms were motile.

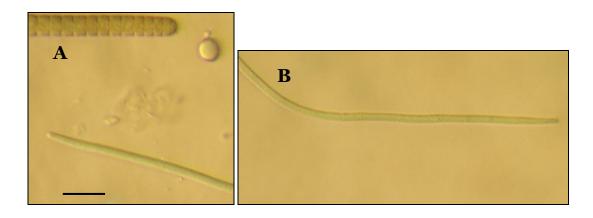


Figure 11. Leptolyngbya (?) **A.** Specimen from Mission Bay sediments, October 2003; bar = $10 \mu m$. **B.** Specimen from culture.

Spirulina spp.

Three genera of regularly helical cyanobacteria have been reported from marine environments: *Spirulina*, *Arthrospira* and *Halospirulina*. *Spirulina* is distinguished from *Arthrospira* by having smaller cell diameters, a more compact coil (as opposed to the loose coil of *Arthrospira*), and cell walls barely visible under light microscopy (Castenholz et al. 2001c, d). However, a number of other taxonomic studies place both loose and tight-coiled cyanobacteria in *Spirulina* (e.g., Umezaki 1961, Silva and Pienaar 2000). Members of this genus may have coil diameters up to 12 µm (Castenholz et al. 2001c). Individual filaments exhibit movement either by rotating about the filament axis or by waving the terminal end of the filament from side to side (Castenholz et al. 2001c).

Traditionally, at least two species of *Spirulina* have been recognized from marine habitats, these differentiated by cellular and spiral diameters: *S. subsalsa* and *S. labyrinthiformis* (Desikachary 1959, Umezaki 1961). The organisms in Figures 12A and 12B correspond closely with the morphological description of *S. subsalsa*, whereas Figure 12C can tentatively be assigned to *S. labyrinthiformis*.

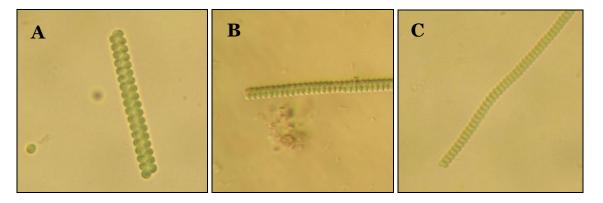


Figure 12. *Spirulina* spp. from Mission Bay, October 2003. **A.** *S. subsalsa*; filament diameter \sim 4 μ m. **B.** *S. subsalsa*; coil diameter \sim 4.75 μ m. **C.** *S. labyrinthiformis*; coil diameter \sim 2.4 μ m.

Phormidioideae, sp. 1

Cells of this taxon are approximately isodiametric with shallow constrictions between cells. A relatively inconspicuous sheath also appears to be present. Generic placement is difficult because of the lack of observations, however the presence of a sheath appears to preclude placement in *Geitlerinema* (Anagnostidis 1989).

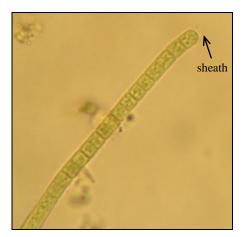


Figure 13. Unidentified cyanobacterial filament from Mission Bay, of probable affinity with the subfamily Phormidioideae; width of the trichome \sim 4.75 μ m.

NOSTOCALES

The Nostocales (*subsection IV* of Boone and Castenholz 2001) include unbranched, heterocytebearing cyanobacteria in both traditional and more recent classifications. Several heterocyte-bearing forms were collected from Tijuana Estuary and Mission Bay but were never observed in great abundance in sediments. A few species may be present in the southern California flora including several *Nodularia*-like taxa and *Anabaena*. Notably, heteropolar Rivulariaceae such as *Calothrix* were not collected nor have other records from southern California coastal wetlands been located in the literature, although they are known from a number of sedimentary intertidal habitats including *Spartina* shoots (Currin and Paerl 1998) and sandflats (Stal et al. 1985). No records of Nostocales in southern California salt marshes or mudflats appear to have been published to date.

Anabaena sp 1. (?)

The most common Nostocales observed were filaments composed of roughly spherical to compressed (discoid) cells with heterocytes of not much larger diameter than vegetative cells. Despite the presence of variable degrees of compression of vegetative cells in some specimens (which might suggest alignment with *Nodularia*; Komárek and K. Anagnostidis 1989), heterocytes were spherical, suggesting placement in *Anabaena*. Moreover, the specimens in Figure 14 may correspond better with *Nostoc*, but since akinetes were not observed in any field material, it was nearly impossible to decide between the two genera.

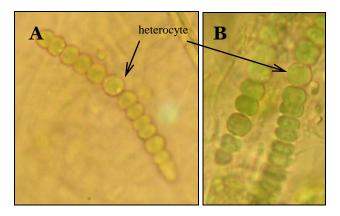


Figure 14. Heterocyte bearing cyanobacteria from Mission Bay wetlands tentatively placed in *Anabaena*. **A.** Short filament bearing a single heterocyte collected from Mission Bay in October 2003. **B.** Filaments epiphytic on *Ulva* (Chlorophyta).

Anabaena sp. 2 (?)

The specimen illustrated in Figure 15 is distinct from other collections of Nostocales because the heterocytes were enlarged relative to vegetative cells. Like the specimens above (Figure 14), it may also be more accurately placed in *Nostoc*.

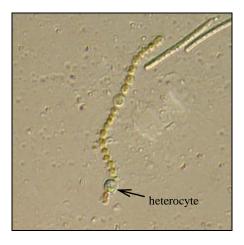


Figure 15. A single collection of this species made in Mission Bay from a pool near salt marsh during April 2002; no scale available.

BACILLARIOPHYCEAE

Diatoms are the most common members of the microalgal flora in southern California wetlands, often substantially outnumbering cyanobacteria and green algae in terms of species richness and numerical abundance. This is consistent with studies from various temperate salt marshes and mudflats around the world that show overall diatom dominance (Underwood 1994, Peletier 1996, Sundbäck et al. 1996, Brotas and Plante-Cuny 1998, Thornton et al. 2002, Zheng et al. 2004). Pennate forms dominate the benthic flora, but centric diatoms (e.g., *Melosira*) may also be present either as permanent residents of surface sediments or as settled phytoplankton (Admiraal 1984, Round et al. 1990).

Cocconeis sp(p).

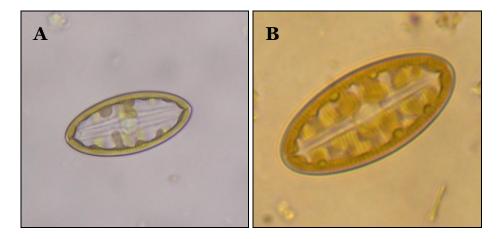


Figure 16. *Cocconeis* specimens from Mission Bay salt marsh sediments. **A.** Length of cell = $38 \mu m$. **B.** specimen collected from lightly vegetated salt marsh in Mission Bay, October 2003.

Amphora

A number of *Amphora* species are listed for southern California tidal wetlands. Zedler (1982) lists three species for Tijuana Estuary and Wilson (1980) records 17 taxa for Mugu Lagoon in Los Angeles County.

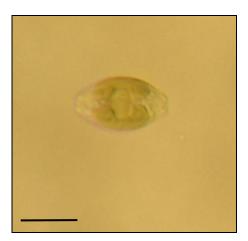


Figure 17. Amphora specimen from culture, originally isolated from Mission May sediments; bar = $10 \mu m$.

Entomoneis

Entomoneis is a diverse genus of pennate diatoms, usually found in saline waters (Round et al. 1990). Twisted valves render the organisms bilobate in appearance.

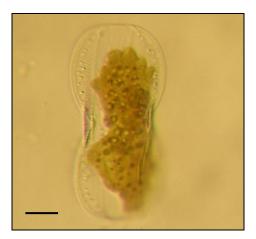


Figure 18. *Entomoneis* collected from a cyanobacterial mat in Mission Bay salt marsh, October 2003; $bar = 10 \mu m$.

Diploneis

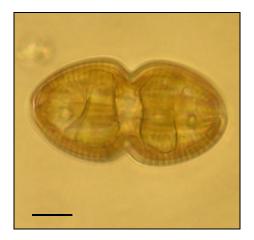


Figure 19. *Diploneis* collected from Mission Bay vegetated marsh during summer 2004. This was the only observed specimen of this taxon; bar = $10 \mu m$.

Unknown chain diatom

Tube-dwelling chain diatoms such as the specimens in Figure 20 were observed occasionally in sediments.

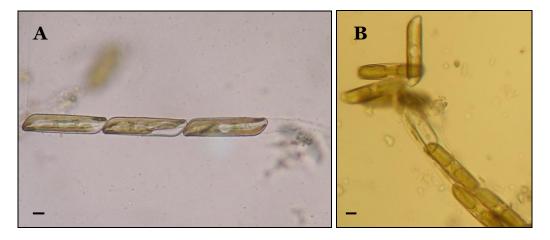


Figure 20. Chained diatoms. **A.** Specimen collected from lightly vegetated salt marsh, October 2003; bar = $10 \mu m$. **B.** Specimen collected during July 2004 from salt marsh vegetated with *Salicornia*, *Batis* and *Triglochin*; bar = $10 \mu m$.

Pleurosigma

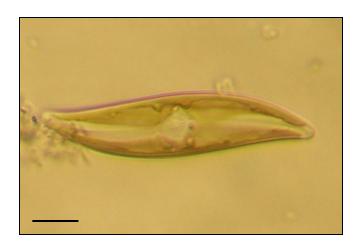


Figure 21. *Pleurosigma*, collected during summer 2004 from salt marsh in Mission Bay vegetated with *Salicornia* and *Batis* in Mission Bay; bar = $10 \mu m$.

Gyrosigma

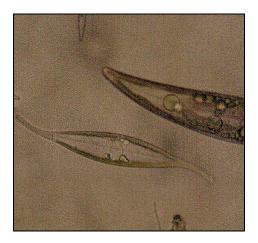


Figure 22. *Gyrosigma*, collected from Tijuana Estuary; no scale available. The organism to the above right of *Gyrosigma* is *Pleurosigma*.

Cylindrotheca

Cylindrotheca was observed in both Mission Bay and Tijuana Estuary sediments; cells were motile.

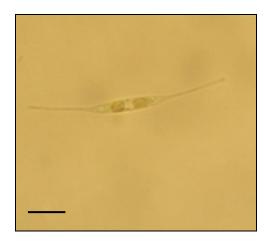


Figure 23. This organism was collected from a cyanobacterial mat in the Kendall-Frost Reserve, Mission Bay during April 2004. Total cell length = $53.5 \mu m$; bar = $10 \mu m$.

Navicula spp.

Navicula is a large genus of pennate diatoms frequently reported from many wetlands worldwide (Peletier 1996). Zedler (1982) lists three species in the local flora and Wilson (1980) recognized 22 taxa from Mugu Lagoon.

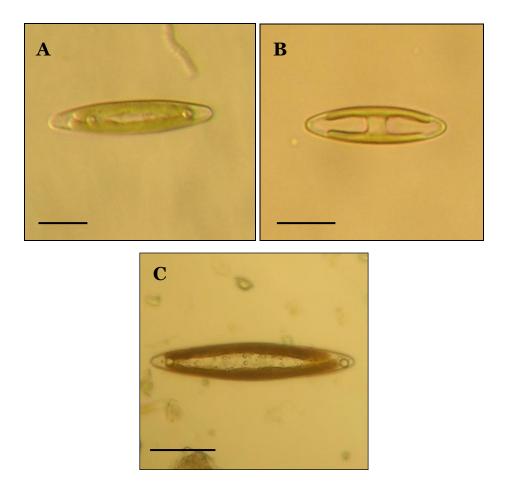


Figure 24. A. *Navicula* from a cyanobacterial mat in salt marsh in Mission Bay, October 2003; cell length = 33.3 μ m; bar = 10 μ m. **B.** Cell from a cyanobacterial mat in Mission Bay salt marsh, April 2004; frustule length ~24 μ m; bar = 10 μ m. **C.** Large *Navicula* collected during summer 2004 from mixed halophyte salt marsh in Mission Bay; cell length = 156 μ m; bar = 50 μ m.

Melosira

Melosira, though a centric diatom, is found in the benthos of both saline and freshwater ecosystems (Admiraal 1984).



Figure 25. *Melosira* collected from Mission Bay during April 2002; bar = $10 \mu m$.

Nitzschia

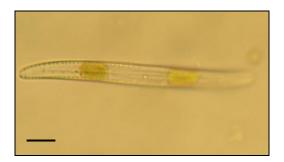


Figure 26. Nitzschia sp. collected from a salt marsh cyanobacterial mat, April 2004; cell length = $81~\mu m$; bar = $10~\mu m$.

Cymbella

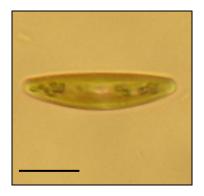


Figure 27. Cymbella collected during October 2003 from lightly vegetated salt marsh; bar = $10 \mu m$.

Unidentified pennate diatoms

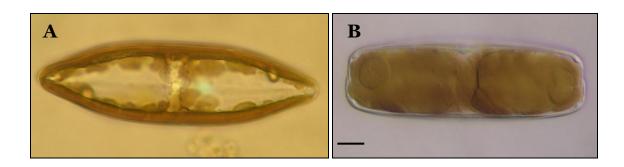


Figure 28. Unidentified diatoms collected from Mission Bay sediments. **A.** Diatom resembling the freshwater genus *Stauroneis* (Round et al. 1990), collected in October 2003 from lightly vegetated salt marsh. **B.** Large pennate diatom seen in girdle view, obtained from salt marsh in October 2003; bar = $10 \mu m$.

CHLOROPHYTA

Green macroalgae are relatively common in southern California's tidal wetlands. Many belong to the speciose genus *Ulva*, but additional taxa such as *Rhizoclonium* are found (Table 2). In California, Chlorophyta are proportionally relatively well represented in wetlands compared with the state's rocky shorelines where red and brown seaweeds tend to dominate. Nübel et al. (1999) found the unicellular green alga *Dunaliella* in hypersaline sediments of Ojo de Liebra Lagoon (Baja California), but no published records of this species have yet been encountered for San Diego County coastal wetlands.

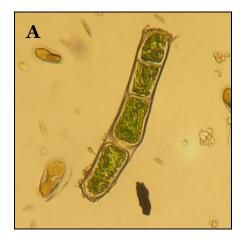
Table 2. Records of macroalgae from southern California wetlands. Attribution of *Enteromorpha* species in Purer (1942) to contemporary binomials was not attempted, although all such species should now be in the genus *Ulva* (Hayden et al. 2003). * Tentative identification.

Division and species	Local distribution	References
Chlorophyta (green seaweeds)		
Bryopsis hypnoides	Mission Bay	this study
Chaetomorpha spiralis	Mission Bay	Stewart 1991
Cladophora sp(p).	San Diego Co.	Purer 1942, Vogl 1966
Derbesia marina	San Diego River	Stewart 1991
Rhizoclonium riparium *	Mission Bay	this study
R. tortuosum	San Diego Co.	Purer 1942
Ulva clathrata	Tijuana Estuary	this study
U. flexuosa	Tijuana Estuary	Purer 1942; this study
U. intestinalis	San Diego Co.	Purer 1942
U. prolifera	Tijuana Estuary	this study (see p.76)
Enteromorpha crinita	San Diego Co.	Purer 1942
E. expansa	Tijuana Estuary	Stewart 1991
E. latissima	San Diego Co.	Purer 1942
E. salina	San Diego Co.	Purer 1942
E. tubulosa	San Diego Co.	Purer 1942
Phaeophyta (brown seaweeds)		
Ectocarpaceae	San Diego River	Stewart 1991
Sargassum muticum	Mission Bay	this study
Rhodophyta (red seaweeds)		
A. cordatum	San Diego Bay	Stewart 1991
Gracilaria pacifica *	Mission Bay	this study
Dasya sinicola var. californica *	Mission Bay	this study
Tribophyta (yellow-green algae)	-	
Vaucheria sp.	Mission Bay	Stewart 1991

Rhizoclonium spp.

Gabrielson et al. (2004) recognize two *Rhizoclonium* species from the California and Oregon flora: *R. riparium* (Roth) Harvey, with roughly isodiametric cells and widths usually not exceeding 30 μ m and *R. tortuosum* (Dillwyn) Kützing with cells several times longer than wide and filament widths of approximately 35-40 μ m.

Stewart (1991) and Zedler (1982) recorded *R. riparium* from Tijuana Estuary. The specimens in Figure 29 are from Mission Bay. A variety of cellular morphologies are evident. For instance, Mission Bay material shows variation in cell shape, the thickness of cell walls, and cell length to width ratios, which renders species-level assignment based on morphology alone difficult.



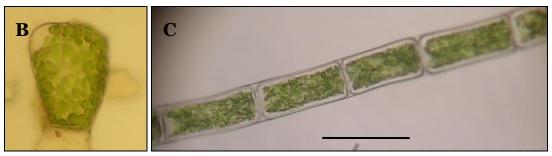


Figure 29. *Rhizoclonium* spp. from Mission Bay. **A, B.** Short filaments roughly corresponding to *R. riparium*. **C.** *R. tortuosum* from salt marsh sediments collected February 2005; bar = $73 \mu m$.

A number of *Ulva* and *Enteromorpha* species have been recorded from wetlands in southern California. *Enteromorpha* species were recently transferred to *Ulva* because the genus is not monophyletic using molecular characters (Hayden et al. 2003). I have observed both sheet-like and tubular thalli in Mission Bay wetlands and the following species have been identified in this paper: *U. prolifera*, *U. flexuosa* and *U. clathrata*. Additional records from the literature are given in Table 2.

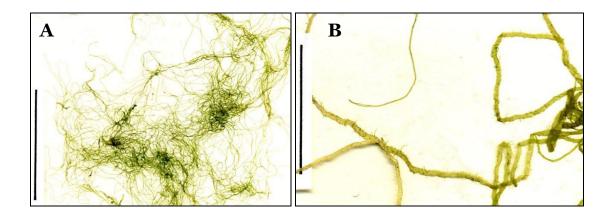


Figure 30. *Ulva* spp. **A.** Thalli of *U. flexuosa* collected from a restored wetland in Tijuana Estuary, February 2000; bar = 5 cm. **B.** Thalli of *U. clathrata* collected from Mission Bay, November 1999.

Bryopsis hypnoides Lamouroux

A single specimen of *Bryopsis* was collected from a tidal marsh channel in Mission Bay; it is tentatively assigned to *B. hypnoides*. Stewart (1991) does not mention the presence of this species in the county's wetlands.

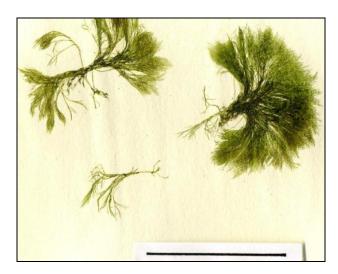


Figure 31. Herbarium specimen of *B. hypnoides* collected from Mission Bay, November 1999; bar = 5 cm.

PHAEOPHYTA

Macroscopic brown algae are generally rare in temperate wetland habitats. In southern California, only unspecified members of the Ectocarpales have been recorded from soft sediment habitats along the coast (Stewart 1991). Giant kelp wrack (*Macrocystis pyrifera*) is frequently found in mudflats and marshes, but it is not a component of the living flora. *Fucus* sometimes occurs in the upper intertidal of estuaries in other regions (Gabrielson et al. 2004).

Sargassum muticum (Yendo) Fensholt

A single collection of *Sargassum muticum* was made in an intertidal channel in Mission Bay salt marsh habitat. It is an invasive species from Japan that has spread throughout the west coast of the United States (Abbott and Hollenberg 1976). It is very common in the intertidal of the outer coast but has also apparently penetrated Mission Bay. Lack of hard substrates at lower intertidal elevations in the local wetlands probably prevents its widespread occurrence in these coastal habitats.



Figure 32. A portion of a *Sargassum muticum* thallus from a Mission Bay salt marsh creek, November 1999; bar = 5 cm.

RHODOPHYTA

Red algae are very diverse in rocky habitats of temperate and sub-tropical marine coastlines, but tend to be more poorly represented in temperate wetland habitats. A few species occur in mudflat/seagrass habitat in Mission Bay and San Diego Bay (Stewart 1991), but none have apparently been recorded from the local salt marshes. Stewart (1991) lists *Aglaothamnium cordatum* from mudflats in southern San Diego Bay and *Gracilaria* spp. from bays in San Diego County. *Dasya sinicola* var. *californica* (Gardner) Dawson has been recorded from Newport Bay (Abbott and Hollenberg 1976) and from San Diego Bay (Stewart 1991)

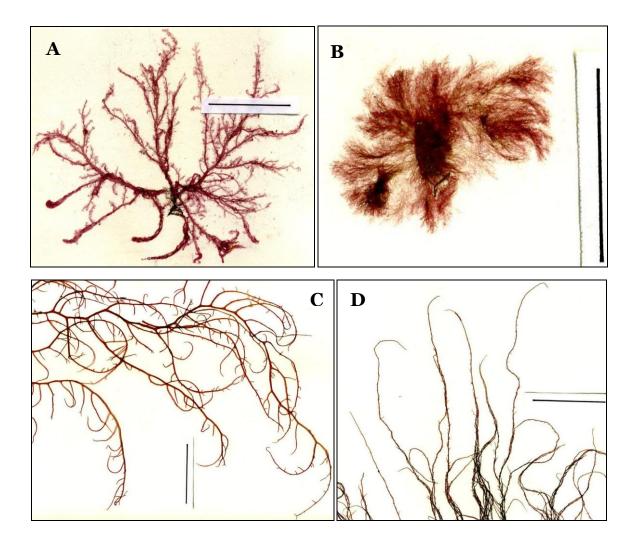


Figure 33. Red algae collected from non-salt marsh Mission Bay wetlands during November 1999. **A.** *Dasya sinicola* var. *californica* (tentative identification). **B.** Filamentous thallus potentially belonging to *Aglaothamnion*, *Callithamnion* or *Pleonosporium*. **C, D.** *Gracilaria pacifica* Abbott-like thalli (*G. verrucosa* of Abbott and Hollenberg [1976]). All bars = 5 cm.

TRIBOPHYTA

The benthic tribophyte, *Vaucheria* is known from marine wetlands worldwide. It is a single celled (coenocytic) dark green alga occurring in moss-like patches on the surface of sediments. Specimens attributable to the genus have been found in Tijuana Estuary, southern San Diego Bay, Mission Bay, and in the San Diego River channel (Stewart 1991). *V. longicaulis* specifically has been reported from Elkhorn Slough in Monterey County (Abbott and Hollenberg 1976), but it is unclear if the local specimens should be assigned to this species. In Mission Bay, *Vaucheria* appears to favor mudflats, especially near the edge of marsh vegetation.

EULENOPHYTA

Euglena or Eutreptia

Euglenoids were occasionally observed from wetland sediments in Tijuana Estuary and Mission Bay. Underwood (1994) noted the presence of *Euglena deses* in sediments from the UK, a species that lacks a flagellum. One of the specimens in Figure 34 appears to have at least one flagellum, but flagellar shape and number were not elucidated in these specimens.

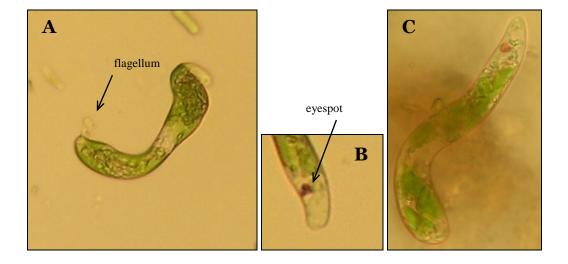


Figure 34. A, B. An unidentified euglenoid collected from a cyanobacterial mat in Mission Bay, October 2003. **C.** Euglenoid collected from vegetated salt marsh in Mission Bay, summer 2004.

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