Chapter 1
Yeasts in Continental and Seawater

Diego Libkind, Pietro Buzzini, Benedetta Turchetti, and Carlos A. Rosa

Abstract Even though yeasts are normal inhabitants of almost any type of aquatic environment, in comparison to other type of substrates, relatively little research has been carried out on the factors affecting their biodiversity and distribution patterns. The distinction of a yeast species as transient or resident element of an aquatic habitat has long been challenging and has been one of the main difficulties in the study of yeast diversity in, for example, continental lakes and rivers. The present chapter will provide an overview of our current knowledge on yeast diversity and ecology in continental freshwater and marine environments; in particular habitats like tropical and temperate rivers and lakes, seawater, and glacial melting water bodies will be reviewed. Water temperature and trophic state are major factors determining the yeast community composition in water bodies, and as they get more extreme due to the increase of stress factors such as cold temperatures, UV radiation, and scarce nutrient availability, the prevalence of basidiomycetous yeast gets more notorious. As a result of the evolutionary adaptation to extreme conditions, certain biotechnologically relevant traits became evident in extremophilic aquatic yeasts such as the production of carotenoid pigments, UV sunscreens, extracellular cold-adapted enzymes, etc.

Keywords Aquatic environments • Biodiversity • Ecology • Taxonomy

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P. Buzzini et al. (eds.), *Yeasts in Natural Ecosystems: Diversity*,
DOI 10.1007/978-3-319-62683-3_1

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1.1 Introduction

Yeasts, single-celled and free-floating, occur in water habitats, attached to substrates or within animal hosts (Jones and Slooff 1966; Pore and Sorenson 1990; Libkind et al. 2003; Kurtzman and Fell 2006; Yamaguchi et al. 2009). Yeasts are common inhabitants of aquatic environments and their population density, and species diversity depends on the water type and purity (Hagler and Mendoça-Hagler 1981). The biodiversity and distribution of yeasts have been largely overlooked, partly because of the prevailing ideas among microbiologists about the ubiquity of microorganisms (Reche et al. 2005; Yurkov 2017). As a result, yeasts are poorly documented in most reviews regarding freshwater fungi (e.g., Goh and Hyde 1996; Shearer et al. 2007; Wurzbacher et al. 2010). But it is now recognized that yeasts are among the taxa that deserve urgent research on aspects such as species richness and distribution patterns in most ecosystems (Lachance and Starmer 1998). Freshwater lakes and streams, brackish water, sewage-contaminated water, glacier meltwater, and wastewater have been the source of many basidiomycetous yeasts (Cooke 1976; Pore and Sorenson 1990; de García et al. 2010a, b, 2015; Jones et al. 2014) and made them the prevailing taxonomic group of yeasts in surveys of many aquatic ecosystems (de García et al. 2007; Brandão et al. 2011a, b).

Studies on the geographic distribution of aquatic yeast species are scarce, and most of them are focused on polluted water (Nagahama 2006). Yeast species exclusively associated with aquatic habitats are not numerous. For example, the most common ascomycetous yeast isolated from marine waters is *Debaryomyces hansenii*, a yeast species considered ubiquitous and isolated from many different environments and regions. Other ubiquitous species frequently observed also in aquatic habitats are *Aureobasidium pullulans*, *Rhodotorula mucilaginosa*, and

Vishniacozyma victoriae (former *Cryptococcus victoriae*) (Vaz et al. 2011; Brandão et al. 2011a, b, 2017; Buzzini et al. 2012; de García et al. 2012). Some species are endemic to determined regions: for example, *Metschnikowia australis* is associated with algae, marine invertebrates, and seawater in Antarctica (Lachance 2011b; Furbino et al. 2014). These observations suggest that geographical patterns and local conditions could influence the ecological distribution of aquatic yeast communities. An overview of geographic distribution patterns of yeasts has been recently published (Yurkov 2017).

Although many of the yeast species collected from water bodies may be truly aquatic species (i.e., autochthonous species), it is also conceivable that some species reached the aquatic environment through runoff from the surrounding watershed (i.e., allochthonous species). For yeasts recovered from aquatic environments, such distinction is always challenging, mainly because of our lack of understanding of factors limiting the distribution of most taxa.

The present chapter will provide an overview of yeast diversity and ecology in continental freshwater (lakes and rivers) and in seawater environments.

1.2 Yeasts in Freshwater of Tropical Rivers and Lakes

1.2.1 General Aspects of Tropical Lakes

There is a high diversity in different aquatic environments in tropical ecosystems. These water bodies can be surrounded by forests with huge species richness, or be situated in altitudinal regions with low plant diversity. In addition, these aquatic environments can be located near cities, resulting in a high anthropogenic influence in their water bodies. Lakes and rivers located in protected areas harbor yeast communities where the species composition reflects inputs from terrestrial sources such as soil and plant debris (Medeiros et al. 2008). These yeasts contribute to the recycling of the plant litter in these environments, through the action of extracellular enzymes, obtaining low weight organic carbon and making them available also to other organisms (Medeiros et al. 2012). According to Hagler and Ahearn (1987), oligotrophic clean lakes usually contain less than 100 yeasts l^{-1}, and mesotrophic lakes and rivers have total yeast counts in the range of 100–500 yeasts l^{-1}, whereas eutrophic aquatic environments usually have more than 10^3 yeast cells l^{-1}. However, Medeiros et al. (2008) reported counts around 3.5×10^3 yeasts l^{-1} in a pristine lake of Southeastern Brazil. This result suggests that the yeast populations in clean lake waters could be influenced by the influx of allochthonous organic matter in these environments. The majority of species isolated from tropical lakes and rivers are polytrophic generalists (i.e., species which assimilate a wide range of carbon sources). Nutritionally versatile yeasts are likely to colonize aquatic environments with low nutrient concentrations more efficiently (Rosa et al. 1995). In eutrophic water bodies, yeasts with narrow nutritional profiles may occur in high densities due to utilization of simple carbon sources available in these environments. Species as *Pichia kudriavzevii* (former *Candida krusei* = *Issatchenkia orientalis*), *Pichia membranifaciens*, *Candida glabrata* (*Nakaseomyces* clade), and *Hanseniaspora guilliermondii* may be prevalent in eutrophic aquatic environments (Medeiros et al. 2008; Brandão et al. 2010). These species assimilate a low number of carbon sources and probably survive and grow in eutrophic aquatic environments using simple sugars as glucose, fructose, and sucrose.

In eutrophic tropical lakes, the total yeast counts have been suggested as an indicator of anthropogenic eutrophication, i.e., organic matter concentration (Hagler et al. 1986; Brandão et al. 2010; Carneiro et al. 2015). The densities of total culturable yeasts also correlate positively with the abundance of *Escherichia coli* and of total coliform bacteria in several tropical water bodies, suggesting that total culturable yeast counts could be considered indicator of the abundance of these bacteria and, as consequence, of fecal pollution in freshwater habitats (Hagler et al. 1986; Brandão et al. 2010; Medeiros et al. 2012; Stone et al. 2012; Carneiro et al. 2015).

The most limiting nutrients in tropical lakes are nitrogen and phosphorus (Lewis 2000). The availability of these compounds can influence the colonization of these environments by yeasts. Rosa et al. (1990, 1995) reported significant positive correlation between total yeast counts and total dissolved phosphate in a paleo-karstic (i.e., karstified rock or area that has been buried by later sediments) tropical lake in Brazil. The species *A. pullulans*, *Deb. hansenii*, *Naganishia albida* (*Cryptococcus albidus*), *Papiliotrema laurentii*, *Rhodotorula glutinis*, *Rh. mucilaginosa*, and *Cutaneotrichosporon cutaneum* occurred in the highest frequencies, and a higher yeast diversity occurred during August and February, corresponding to the end of the isothermal and the beginning of the stratification periods in this tropical lake (Rosa et al. 1995). Morais et al. (1996) reported that the yeast species diversity decreased in the other paleo-karstic tropical lake with depth probably due to the absence of fermentative metabolism of most of the predominant species that could limit their distribution to the highly oxygenated surface waters. A probable correlation could exist between yeast counts and zones of nutrient accumulation determined by the thermal stratification of the water column of the lake. Yeasts are heterotrophic microorganisms that tend to be more prominent in habitats where nutrients are available. According to Morais et al. (1996), the predominance of oxidative polytrophic yeasts and pigmented species suggested that these microorganisms were probably carried from soils and foliar surfaces.

The yeast species richness in lakes and rivers is in general higher in tropical than in temperate and cold environments. This highest species richness could probably be related to the occurrence of dense and diverse surrounding plant communities (Fig. 1.1).

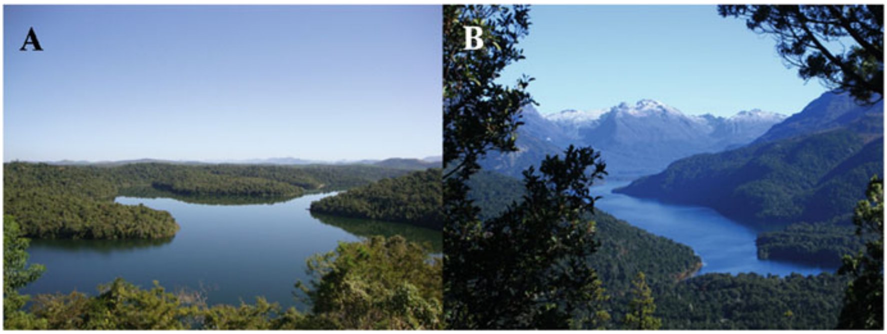

Fig. 1.1 Pictures of an Atlantic rain forest (**a**) and a glacially originated (**b**) lakes in Brazil (Dom Helvécio lake) and Argentina (Steffen lake), respectively. The latter photograph courtesy of Andrea Trochine

1.2.2 Yeast Communities Associated with Tropical Lakes and Rivers

Several works determined the yeast communities associated with tropical freshwater environments using morphological and physiological tests to identify these microorganisms. Most of these studies were done before the year 2000 (Hagler and Mendonça-Hagler 1981; Hagler et al. 1986; Rosa et al. 1995; Morais et al. 1996), and probably several species were misidentified (or not distinguished), becoming difficult to estimate the species richness in these environments. After the sequencing methodologies utilizing regions of the rRNA gene for identification of yeast species become routine, some works determining yeast species richness and diversity in tropical lakes and rivers were published (Medeiros et al. 2008, 2012; Brandão et al. 2010, 2017; Silva-Bedoya et al. 2014). These papers showed that the yeast communities from tropical lakes are dominated by basidiomycetous yeasts, mainly from the genera *Apiotrichum*, *Hannaella*, *Moesziomyces*, *Naganishia*, and *Papiliotrema*, as well as to the former polyphyletic genera *Rhodotorula* and *Sporobolomyces* (Medeiros et al. 2008; Brandão et al. 2011b, 2017). Ascomycetous yeasts occur in minor densities and are mainly represented by the genera *Aureobasidium*, *Debaryomyces*, *Meyerozyma*, and *Pichia* (mainly *P. kudriavzevii*) and species of the clade *Candida albicans*/*Lodderomyces*. Most common yeast species isolated from tropical freshwaters are *A. pullulans*, *Deb. hansenii*, *P. kudriavzevii*, *Pa. laurentii*, *Rh. mucilaginosa*, and *Sporobolomyces japonicus* (Medeiros et al. 2008; Silva-Bedoya et al. 2014; Brandão et al. 2017). These species correspond to around 50% of the total yeast isolates of the freshwater environments studied until now. Other species occur in minor frequencies but are consistently isolated from freshwater bodies, i.e., *Hannaella luteola*, *Hannaella pagnoccae*, *Meyerozyma guilliermondii*, *Moesziomyces aphidis*, *Na. albida*, and *Rhynchogastrema complexa* (Medeiros et al. 2008; Brandão et al. 2010, 2017; Silva-Bedoya et al. 2014). Most of the prevalent yeast species isolated from tropical freshwater are considered ubiquitous because they are not restricted to water but found in different environments and sampling sites. These yeasts are also frequently isolated from phyllosphere of terrestrial plants and soils, and their occurrence in the adjacent lakes and rivers might be the result of runoff from surrounding plants and soil particles. Higher occurrence of basidiomycetous (over ascomycetous) yeasts in these environments could be explained by the metabolic versatility of these yeasts, assimilating on average a broader range of carbon sources and being more tolerant to the variation of the physicochemical properties of these water bodies (Brandão et al. 2011b, 2017).

The presence or absence of some yeast species in tropical water bodies has been related to the anthropogenic impact on these environments. The species *Kluyveromyces aestuarii* is a marine organism and was observed in very high numbers in mangroves in Rio de Janeiro, so that could be considered an indicator species typical for mangroves; its presence in a specific environmental sample suggests the influence of the mangrove habitat, while its absence in mangroves could be related to a non-fecal pollution or other habitat alterations that modify the natural environment (Araújo and Hagler 2011). For example, *C. albicans* has been isolated on CHROMagar *Candida* from tropical lakes and rivers subjected to fecal pollution in Southeastern Brazil (Rosa, unpublished data). This species occurred in counts around 5.0 CFU ml^{-1} in rivers subjected to fecal pollution, and it was absent in lakes and rivers located in protected ecological reserves. Brandão et al. (2010) studied the yeast occurrence in three lakes of Southeastern Brazil and reported that the yeast densities, determined by the multiple-tube fermentation technique, were significantly correlated only with the density of fecal coliforms. Clinically relevant yeasts, *P. kudriavzevii*, *Mey. guilliermondii*, and *Candida tropicalis*, were the most frequently isolated species in this work and are associated with fecal contamination of water by warm-blooded animals.

Medeiros et al. (2008) and Brandão et al. (2010) tested the yeasts isolated at 37 °C in relation to their susceptibility to commonly used antifungal drugs: ketoconazole, fluconazole, itraconazol, and amphotericin B. These authors verified that several species were resistant to all antifungals tested, and approximately 20% of the isolates were resistant to amphotericin B. Several species isolated from lakes and rivers in Southeastern Brazil showed the virulence factors such as production of proteinases and phospholipases and were able to adhere to human buccal epithelial cells (Rosa, unpublished data). The presence of yeast strains resistant to commonly used antifungal drugs and isolation of strains producing virulence factors suggest that these environments, when affected by fecal pollution, can pose potential health risks for people utilizing these waters for recreation.

Some new species were recently described based on isolates obtained from tropical aquatic environments. For example, *Saturnispora serradocipensis* was isolated as a minor component of a yeast community from leaf detritus immersed in a tropical stream in the National Park of the Serra do Cipó, Minas Gerais State, Brazil (Canelhas et al. 2011). *Rhynchogastrema* (originally *Bandoniozyma*) *aquatica* was isolated from a freshwater lake surrounded by Atlantic Rain Forest, whereas *Rhy.* (*Bandoniozyma*) *complexa* was isolated in two lakes of the

Amazonian region and other substrates, including bromeliad leaves (Valente et al. 2012). *Yarrowia porcina* was obtained from sediment of a tropical freshwater river in Southeastern Brazil (Nagy et al. 2014). This river was exposed to different types of human influence, namely, cattle farming, mining, and domestic and industrial effluents (Medeiros et al. 2008; Nagy et al. 2014).

1.3 Yeasts in Freshwater of Temperate Lakes and Rivers

1.3.1 Yeast Diversity in Temperate Lakes and Lagoons

Due to a combination of solar heating and wind mixing of surface water layers, most lakes and lagoons in temperate regions are characterized by a fairly predictable seasonal pattern, with alternate cycles of layering and complete mixing. A number of studies investigated the yeast diversity in temperate lakes and lagoons using both culture-dependent and culture-independent approaches. The occurrence of yeasts in lake and lagoon ecosystems is common and is frequently influenced by allochthonous species external sources, including living and decaying plants and animals (Kurtzman and Fell 2004). The complete list of yeast species found in habitats associated with temperate lakes and lagoons is reported in Table 1.1. None of the papers reported the dominance of either Ascomycota or Basidiomycota phyla.

European lakes and lagoons were studied since the early 2000s. Bogusławska-Was and Dabrowski (2001) investigated the yeast diversity in strongly eutrophic waters and bottom sediments sampled in the Szczecin Lagoon, Poland. Yeast abundance in sediments and waters reached maximum in May and July, respectively. A total of 21 species of fungi including yeasts and yeastlike dimorphic fungi were found: most species were shared between both environments, while *A. pullulans* was only observed in water samples, and *Candida inconspicua*, *Candida utilis* (now *Cyberlindnera jadinii*), and *Pichia carsonii* (*Priceomyces carsonii*) were characteristic of bottom sediments only. *Candida famata* (*Deb. hansenii*) and *Rh. mucilaginosa* were the dominant species.

Culture-independent approaches were also used to study yeasts in aquatic samples. A 18S rRNA PCR survey was applied to study the eukaryotic community of the Lake Pavin, France. Of the 16 environmental fungal sequences, two were putatively identified as belonging to the basidiomycetous species *Rhodosporidium diobovatum* (currently *Rhodotorula diobovata*) and *Filobasidium globisporum* and one close to the ascomycetous yeast *Taphrina letifera* (Lefèvre et al. 2007). More recently, Monchy et al. (2011) studied fungal diversity in lake waters collected along transects from the shore to the center of Lake Pavin and Lake Aydat, France, using a twofold approach, including both cloning/sequencing of the 18S, ITS1, 5.8S, ITS2, and partial 28S region and the pyrosequencing of 18S rRNA hypervariable V2, V3, and V5 regions. Fungi represented about 50% of the total operational

Table 1.1 Diversity of yeasts and yeastlike dimorphic fungi in freshwater of temperate lakes, lagoons, and ponds

Species	Original taxonomic designation	Source	Locality	References
Ascomycetous yeasts				
Candida pseudolambica		Freshwater marshes	Florida Everglades—USA	Fell et al. (2011)
Barnettozyma californica	*Hansenula californica*, *Williopsis californica*	Lake and pond water	Iberian Pyrite Belt, Sao Domingos, Portugal; St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b), Gadanho et al. (2006)
Candida sp.		Pond water	Lake St. Clair, Canada; Iberian Pyrite Belt, Sao Domingos, Portugal	Kwasniewska (1988), Gadanho et al. (2006)
Candida amphicis	*Candida amphixiae*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Candida carpophila		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Candida dendronema		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Candida fluviatilis		pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Candida fructus	*Candida musae*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Candida glabrata		Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Candida inconspicua		Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Candida maris		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Candida melibiosica		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Candida norvegica	*Torulopsis norwegica*, *Torulopsis vanzylii*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Candida parapsilosis		Lake and lagoon water	Douglas Lake, Cheboygan County, Michigan, USA; St. Lawrence, Quebec, Canada; Szczecin Lagoon, Poland	van Uden and Ahearn (1963), Simard and Blackwood (1971a, b), Bogusławska-Was and Dabrowski (2001)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Candida pini	*Torulopsis pinus*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Candida rancensis		Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Candida sake	*Torulopsis sake*	Lake and lagoon water	St. Lawrence, Quebec, Canada; Szczecin Lagoon, Poland	Simard and Blackwood (1971a, b), Bogusławska-Was and Dabrowski (2001)
Candida sharkiensis		Freshwater marshes	Florida Everglades—USA	Fell et al. (2011)
Candida silvanorum		Freshwater marshes	Florida Everglades—USA	Fell et al. (2011)
Candida tenuis		Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Candida tropicalis		Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Candida versatilis	*Torulopsis anomala*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Candida zeylanoides		Lagoon water, freshwater marshes	Szczecin Lagoon, Poland; Florida Everglades—USA	Bogusławska-Was and Dabrowski (2001), Fell et al. (2011)
Cyberlindnera saturnus	*Hansenula saturnus*, *Williopsis saturnus*	lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Debaryomyces sp.		Lake water	Douglas Lake, Cheboygan County, Michigan, USA; Lake St. Clair, Canada	van Uden and Ahearn (1963), Kwasniewska (1988)
Debaryomyces hansenii[b]	*Candida famata*, *Torulopsis famata*	Lake, lagoon and pond water	St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland; Iberian Pyrite Belt, Sao Domingos, Portugal; Lake Biwa, Japan	Simard and Blackwood (1971a, b), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001), Gadanho et al. (2006), Ishida et al. (2015)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Debaryomyces maramus	*Debaryomyces marama*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Galactomyces candidus	*Geotrichum candidum*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Hanseniaspora guilliermondii	*Kloeckera apis*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Hanseniaspora uvarum	*Kloeckera apiculata*	Lake water, freshwater marshes	Lowland Zahorie, Bratislava, Slovakia; Florida Everglades, USA	Sláviková et al. (1992), Fell et al. (2011)
Hyphopichia burtonii		Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Kluyveromyces aestuarii		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Kluyveromyces lactis var. *drosophilarum*	*Kluyveromyces marxianus* var. *drosophilarum*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Kregervanrija fluxuum		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Lachancea kluyveri	*Saccharomyces kluyveri*	Lake and lagoon water	Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland	Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001)
Lachancea meyersii		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Lindnera jadinii	*Candida utilis* (anamorph)	Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Magnusiomyces capitatus	*Trichosporon capitatum*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Martiniozyma asiatica	*Candida asiatica*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Metschnikowia pulcherrima	*Candida pulcherrima*	Lake water	Douglas Lake, Cheboygan County, Michigan, USA; Lowland Zahorie, Bratislava, Slovakia	van Uden and Ahearn (1963), Sláviková et al. (1992)
Meyerozyma guilliermondii	*Candida guilliermondii*, *Pichia guilliermondii*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Nakazawaea ernobii	*Torulopsis ernobii*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Nakazawaea holstii	*Candida silvicola*, *Hansenula holstii*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Pichia fermentans	*Candida lambica*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Pichia kluyveri		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Pichia kudriavzevii	*Candida krusei*, *Issatchenkia orientalis*	Lake and pond water, freshwater marshes	Florida Everglades, USA; Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992), Fell et al. (2011)
Priceomyces carsonii	*Pichia carsonii*	Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Saccharomyces cerevisiae	*Saccharomyces italicus*	Lake and lagoon water	St. Lawrence, Quebec, Canada; Szczecin Lagoon, Poland	Simard and Blackwood (1971a, b), Bogusławska-Was and Dabrowski (2001)
Saccharomycopsis fibuligera		Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Saturnispora silvae	*Candida silvae*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Schwanniomyces vanrijiae		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Taphrina letifera[a]		Lake water	Lake Pavin, Massif Central, France	Lefèvre et al. (2007)
Torulaspora delbrueckii	*Candida colliculosa*	Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Trichomonascus ciferrii	*Candida ciferrii*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Wickerhamiella domercqiae	*Torulopsis saccharum*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Wickerhamomyces anomalus	*Hansenula anomala*, *Pichia anomala*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Wickerhamomyces bovis	*Pichia bovis*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Wickerhamomyces hampshirensis		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Wickerhamomyces sydowiorum		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Yarrowia lipolytica	*Candida lipolytica*	Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Basidiomycetous yeasts				
Anthracocystis flocculosa	*Pseudozyma flocculosa*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Buckleyzyma aurantiaca	*Rhodotorula aurantiaca*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Bullera alba		Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Bullera unica		Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Cryptococcus sp.		Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Cryptococcus neoformans		Lagoon water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Cutaneotrichosporon curvatus	*Candida curvata*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Cutaneotrichosporon cutaneum	*Trichosporon cutaneum*	Lake water	Szczecin Lagoon, Poland	Bogusławska-Was and Dabrowski (2001)
Cystobasidium sp.	*Rhodotorula cassiicola*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Cystobasidium laryngis	*Rhodotorula laryngis*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Cystobasidium minutum	*Rhodotorula minuta*	Lake water, deep igneous rock aquifers, freshwater marshes	Lowland Zahorie, Bratislava, Slovakia; Lake St. Clair, Canada; Aspo HRL, Sweden; Florida Everglades, USA	Kwasniewska (1988), Sláviková et al. (1992), Ekendahl et al. (2003), Fell et al. (2011)
Cystobasidium slooffiae	*Rhodotorula slooffiae*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Cystofilobasidium bisporidii		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Cystofilobasidium macerans	*Rhodotorula macerans*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Dioszegia zsoltii		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Filobasidium floriforme		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Filobasidium globisporum[a]		Lake water	Lake Pavin, Massif Central, France	Lefèvre et al. (2007)
Filobasidium magnum	*Cryptococcus ater*, *Cryptococcus magnus*	Lake water, freshwater marshes	Lowland Zahorie, Bratislava, Slovakia; Florida Everglades, USA	Sláviková et al. (1992), Fell et al. (2011)
Hannaella luteola	*Cryptococcus luteolus*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Hannaella sinensis	*Bullera sinensis*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Hasegawazyma lactosa	*Rhodotorula lactosa*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Leucosporidium muscorum	*Candida muscorum*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Leucosporidium scottii	*Candida scottii*	Lake water	St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slovakia; Iberian Pyrite Belt, Rio Tinto, Spain	Simard and Blackwood (1971a, b), Sláviková et al. (1992), Gadanho et al. (2006)
Moesziomyces aphidis	*Pseudozyma aphidis*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Moesziomyces parantarcticus	*Pseudozyma parantarctica*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Mrakia aquatica	*Candida aquatica*	Lake water scums	Malham Tarn, Yorkshire, UK	Jones and Slooff (1966)
Naganishia albida	*Cryptococcus albidus*, *Cryptococcus albidus* var. *albidus*	Lake and lagoon water, pond water	Florida Everglades, USA; Lake Okeechobee, Florida, USA; St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland	van Uden and Ahearn (1963), Simard and Blackwood (1971a, b), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Naganishia albidosimilis	*Cryptococcus albidosimilis*	Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Naganishia diffluens	*Cryptococcus diffluens*	Lake water, freshwater marshes	Douglas Lake, Cheboygan County, Michigan, USA; Florida Everglades, USA	van Uden and Ahearn (1963), Fell et al. (2011)
Naganishia gastrica	*Cryptococcus gastricus*	Lake water	Douglas Lake, Cheboygan County, Michigan, USA	van Uden and Ahearn (1963)
Naganishia globosa	*Hansenula amylofaciens*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Naganishia liquefaciens	*Cryptococcus liquefaciens*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Papiliotrema flavescens	*Cryptococcus flavescens*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Papiliotrema laurentii	*Cryptococcus laurentii*	Lake and lagoon water, pond water, freshwater marshes	Douglas Lake, Cheboygan County, Michigan, USA; Florida Everglades, USA; St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland; Florida Everglades, USA	van Uden and Ahearn (1963), Simard and Blackwood (1971a, b), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001), Bogusławska-Was and Dabrowski (2001), Fell et al. (2011)
Papiliotrema pseudoalba	*Bullera pseudoalba*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Papiliotrema taeanensis	*Cryptococcus taeanensis*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Piskurozyma capsuligena	*Filobasidium capsuligenum*, *Candida japonica*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Pseudohyphozyma bogoriensis	*Rhodotorula bogoriensis*	Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Rhodosporidiobolus ruineniae	*Sporidiobolus ruineniae*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Rhodotorula sp.		Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Rhodotorula babjevae	*Rhodosporidium babjevae*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Rhodotorula diobovata[b]	*Rhodosporidium diobovatum*	Lake water, freshwater marshes	Lake Pavin, Massif Central, France; Florida Everglades, USA	Lefèvre et al. (2007), Fell et al. (2011)
Rhodotorula evergladiensis		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Rhodotorula glutinis		Lake and lagoon water, pond water	Douglas Lake, Cheboygan County, Michigan, USA; Florida Everglades, USA; St. Lawrence, Quebec, Canada; Lake St. Clair, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland	van Uden and Ahearn (1963), Ahearn et al. (1968), Simard and Blackwood (1971a, b), Kwasniewska (1988), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001)
Rhodotorula graminis		Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Rhodotorula mucilaginosa	*Rhodotorula pilimanae*, *Rhodotorula rubra*	Lake and lagoon water, pond water, freshwater marshes	Douglas Lake, Cheboygan County, Michigan, USA; Florida Everglades, USA; St. Lawrence, Quebec, Canada; Lake St. Clair, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland; Iberian Pyrite Belt, Sao Domingos, Portugal	van Uden and Ahearn (1963), Simard and Blackwood (1971a, b), Kwasniewska (1988), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001), Gadanho et al. (2006), Fell et al. (2011)
Rhodotorula paludigena	*Rhodosporidium paludigenum*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Rhodotorula toruloides		Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Sakaguchia cladiensis	*Rhodotorula cladiensis*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sampaiozyma ingeniosa	*Torulopsis ingeniosa*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Sampaiozyma vanillica	*Rhodotorula vanillica*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Solicoccozyma aeria	*Cryptococcus albidus* var. *aerius*, *Cryptococcus aerius*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Solicoccozyma terreus	*Cryptococcus terreus*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporidiobolus pararoseus		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces sp.		Lake water	Lake St. Clair, Canada	Kwasniewska (1988)
Sporobolomyces beijingensis		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces blumeae		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces carnicolor		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces japonicus		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces roseus		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces ruberrimus		Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Sporobolomyces salmonicolor	*Sporidiobolus salmonicolor*	Lake water	Lowland Zahorie, Bratislava, Slovakia	Sláviková et al. (1992)
Symmetrospora marina	*Rhodotorula marina*	Lake water; freshwater marshes	St. Lawrence, Quebec, Canada; Florida Everglades, USA	Simard and Blackwood (1971a, b), Fell et al. (2011)
Udeniomyces pyricola	*Bullera pyricola*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Vanrija humicola	*Candida humicola*	Lake water	St. Lawrence, Quebec, Canada	Simard and Blackwood (1971a, b)
Vishniacozyma tephrensis	*Cryptococcus tephrensis*	Freshwater marshes	Florida Everglades, USA	Fell et al. (2011)
Yeastlike dimorphic fungi				

(continued)

Table 1.1 (continued)

Species	Original taxonomic designation	Source	Locality	References
Aureobasidium pullulans	*Pullularia pullulans*	Lake and lagoon water, fresh-water marshes	St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slovakia; Szczecin Lagoon, Poland; Florida Everglades, USA	Simard and Blackwood (1971a, b), Kwasniewska (1988), Sláviková et al. (1992), Bogusławska-Was and Dabrowski (2001), Fell et al. (2011)

[a] Only non-culturable
[b] Both culturable and non-culturable

taxonomic units (OTUs) identified in Lake Pavin and 30% in Lake Aydat and were dominated by sequences of Chytridiomycota. Pyrosequencing yielded Saccharomycetales as the sole Ascomycota in both lakes, while Basidiomycota sequences were mainly retrieved in the riparian areas of Lake Aydat.

Yeasts and filamentous fungi were collected from a number of stations throughout Lake St. Clair, Canada. The predominant basidiomycetous yeast isolates were identified as *Rh. mucilaginosa*, *Cystobasidium minutum* (*Rhodotorula minuta*), *Rh. glutinis*, and *Sporobolomyces* sp. (Kwasniewska 1988). Besides, Ishida et al. (2015) studied eukaryotic diversity of mesotrophic Lake Biwa and eutrophic Lake Inba, Japan. Results revealed that aquatic fungi included not only members of Chytridiomycota but also members of Aphelida, Cryptomycota, and yeasts, in particular the species *Deb. hansenii*, which was found on the surface of diatom cells from Lake Biwa (Ishida et al. 2015).

1.3.2 Yeast Diversity in Temperate Rivers and Creeks

Although a number of studies have found yeasts in temperate rivers and creeks, the identification of autochthonous populations was sometimes problematic because several yeast species seem to be very versatile, and, therefore, their isolation is not considered sufficient to infer any type of ecological association with aquatic sources. Yeasts represent a regular component of eukaryotic populations in freshwaters of temperate rivers and creeks (Kurtzman and Fell 2004). The complete list of yeast species found in temperate rivers and creeks (and associated habitats) is reported in Table 1.2.

Table 1.2 Diversity of yeasts and yeastlike dimorphic fungi in temperate rivers and creeks

Species	Original taxonomic designation	Source	Locality	References
Ascomycetous yeasts				
Barnettozyma californica	*Hansenula californica*, *Williopsis californica*	River and creek water	Danube, Bratislava, Slovakia; Iberian Pyrite Belt, Sao Domingos, Portugal; Iberian Pyrite Belt, Rio Tinto, Spain	Sláviková and Vadkertiová (1997), Gadanho et al. (2006)
Candida sp.		Creek water	Iberian Pyrite Belt, Sao Domingos, Portugal; Tagus river, Portugal	Gadanho et al. (2006), Coelho et al. (2010)
Candida bertae		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida boidinii		River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Coelho et al. (2010)
Candida etchellsii		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida fluviatilis		River and creek water	Iberian Pyrite Belt, Sao Domingos, Portugal; Iberian Pyrite Belt, Rio Tinto, Spain	Gadanho et al. (2006)
Candida glabrata		River water	Tagus river, Portugal	Coelho et al. (2010)
Candida haemulonis	*Candida haemulonii*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida inconspicua		River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Candida intermedia		River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), de Almeida (2005)
Candida maltosa		River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Candida oleophila		River water	Iberian Pyrite Belt, Rio Tinto, Spain; Tagus river, Portugal	Gadanho et al. (2006), Coelho et al. (2010)
Candida palmioleophila		River water	Tagus river, Portugal	Coelho et al. (2010)
Candida parapsilosis		River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), de Almeida (2005), Coelho et al. (2010)
Candida pseudoglaebosa		River water	Iberian Pyrite Belt, Rio Tinto, Spain	Gadanho et al. (2006)
Candida pseudointermedia		River water	Tagus river, Portugal	Coelho et al. (2010)
Candida pseudolambica		River water	Tagus river, Portugal	Coelho et al. (2010)
Candida rancensis		Creek water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Candida saitoana		River water	Tagus river, Portugal	Gadanho and Sampaio (2004)
Candida sake	*Torulopsis sake*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida tropicalis		River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Candida vartiovaarae		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida versatilis		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Candida zeylanoides		River water	Tagus river, Portugal	Coelho et al. (2010)
Citeromyces matritensis		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Clavispora lusitaniae		River water	Tagus river, Portugal	de Almeida (2005), Coelho et al. (2010)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Cyberlindnera saturnus	*Hansenula saturnus*, *Williopsis saturnus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Debaryomyces hansenii	*Candida famata*, *Torulopsis famata*	River and creek water, leaves submerged in a stream	Danube, Bratislava, Slovakia; Tagus river, Portugal; Iberian Pyrite Belt, Sao Domingos, Portugal; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Gadanho and Sampaio (2004), Gadanho et al. (2006), Sampaio et al. (2007), Coelho et al. (2010)
Diutina catenulata	*Candida catenulata*	River water	Tagus river, Portugal	de Almeida (2005)
Galactomyces candidum	*Geotrichum candidum*	River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Galactomyces geotrichum		River water	Tagus river, Portugal	Gadanho and Sampaio (2004)
Geotrichum klebahnii		River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Hanseniaspora guilliermondii		River water	Tagus river, Portugal	Gadanho and Sampaio (2004)
Hanseniaspora uvarum	*Kloeckera apiculata*	River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Gadanho and Sampaio (2004)
Hyphopichia burtonii		River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Kluyveromyces lactis		River water	Tagus river, Portugal	Coelho et al. (2010)
Kluyveromyces marxianus		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Lipomyces tetrasporus		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Metschnikowia bicuspidata		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Metschnikowia pulcherrima	*Candida pulcherrima*	River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Meyerozyma caribbica	*Candida fermentati*	River water	Tagus river, Portugal	Coelho et al. (2010)
Meyerozyma guilliermondii	*Candida guilliermondii*, *Pichia guilliermondii*	River water	Tagus river, Portugal	Gadanho and Sampaio (2004), de Almeida (2005), Coelho et al. (2010)
Nakazawaea ishiwadae	*Candida ishiwadae*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Pichia sp.		River water	Tagus river, Portugal	Coelho et al. (2010)
Pichia fermentans	*Candida lambica*	River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Pichia kudriavzevii	*Candida krusei*, *Issatchenkia orientalis*	River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Coelho et al. (2010)
Saccharomyces cerevisiae	*Saccharomyces italicus*	River water	Danube, Bratislava, Slovakia; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Coelho et al. (2010)
Schwanniomyces occidentalis	*Debaryomyces occidentalis*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Sugiyamaella castrensis	*Candida castrensis*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Sugiyamaella valdiviana	*Candida valdiviana*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Wickerhamiella domercqiae	*Torulopsis saccharum*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Wickerhamomyces anomalus	*Hansenula anomala*, *Pichia anomala*	River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007), Coelho et al. (2010)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Yarrowia lipolytica	*Candida lipolytica*	River water	Tagus river, Portugal	Coelho et al. (2010)
Basidiomycetous yeasts				
Buckleyzyma aurantiaca	*Rhodotorula aurantiaca*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Bullera alba		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Bullera penniseticola		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Bullera unica		Creek water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Colacogloea foliorum	*Rhodotorula foliorum*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cryptococcus sp.		River and creek water	Iberian Pyrite Belt, Rio Tinto, Spain; Iberian Pyrite Belt, Sao Domingos, Portugal; Tagus river, Portugal	Gadanho et al. (2006), Coelho et al. (2010)
Cryptococcus amylolentus		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cryptococcus neoformans	*Filobasidiella neoformans*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Curvibasidium cygneicollum	*Rhodotorula fujisanensis*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cutaneotrichosporon cutaneum	*Trichosporon cutaneum*	River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Cutaneotrichosporon cutaneum	*Trichosporon cutaneum*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cutaneotrichosporon moniliiforme	*Trichosporon moniliiforme*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cutaneotrichosporon mucoides	*Trichosporon mucoides*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Cystobasidium minutum	*Rhodotorula minuta*	River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007)
Cystofilobasidium sp.		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cystofilobasidium bisporidii		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cystofilobasidium capitatum		River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007)
Cystofilobasidium ferigula	*Cryptococcus ferigula*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cystofilobasidium infirmominiatum	*Rhodotorula infirmo-miniata*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Cystofilobasidium macerans	*Cryptococcus macerans*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Derxomyces mrakii	*Bullera mrakii*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Fellomyces polyborus		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Fibulobasidium inconspicuum		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Filobasidium floriforme		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Filobasidium oeirense	*Cryptococcus oeirensis*	River water	Tagus river, Portugal	Coelho et al. (2010)
Filobasidium uniguttulatum		River water	Tagus river, Portugal	Coelho et al. (2010)
Hannaella luteola	*Cryptococcus luteolus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Leucosporidium creatinivorum	*Rhodotorula creatinovora*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Leucosporidium fragarium	*Rhodotorula fragaria*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Leucosporidium scottii	*Candida scottii*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Leucosporidium yakuticum	*Rhodotorula yakutica*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Microstroma phylloplanum	*Rhodotorula hinnulea*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Naganishia albida	*Cryptococcus albidus*	River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007), Coelho et al. (2010)
Naganishia albidosimilis	*Cryptococcus albidosimilis*	River and creek water, leaves submerged in a stream	Iberian Pyrite Belt, Sao Domingos, Portugal; River Olo, Alvao Natural Park, Portugal	Gadanho et al. (2006), Sampaio et al. (2007)
Papiliotrema laurentii	*Cryptococcus laurentii*	River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007), Coelho et al. (2010)
Phaeotremella pseudofoliacea	*Tremella foliacea*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Phaeotremella skinneri	*Cryptococcus skinneri*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Pseudohyphozyma bogoriensis	*Rhodotorula bogoriensis*	Creek water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Rhodosporidiobolus colostri	*Rhodotorula colostri*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Rhodotorula sp.		River and creek water	Iberian Pyrite Belt, Sao Domingos, Portugal; Iberian Pyrite Belt, Rio Tinto, Spain; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Gadanho et al. (2006), Coelho et al. (2010)
Rhodotorula babjevae	*Rhodosporidium babjevae*	River water, leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sampaio et al. (2007), Coelho et al. (2010)
Rhodotorula diobovata	*Rhodosporidium diobovatum*	River water	Tagus river, Portugal	de Almeida (2005), Coelho et al. (2010)
Rhodotorula glutinis		River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007), Coelho et al. (2010)
Rhodotorula graminis		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Rhodotorula kratochvilovae	*Rhodosporidium kratochvilovae*	River water	Tagus river, Portugal	Coelho et al. (2010)
Rhodotorula mucilaginosa	*Rhodotorula rubra*	River and creek water, leaves submerged in a stream	Danube, Bratislava, Slovakia; Tagus river, Portugal; Tagus river, Portugal; River Olo, Alvao Natural Park, Portugal; Iberian Pyrite Belt, Sao Domingos, Portugal; Iberian Pyrite Belt, Rio Tinto, Spain	Slávikóvá and Vadkertiová (1997), Gadanho and Sampaio (2004), de Almeida (2005), Gadanho et al. (2006), Sampaio et al. (2007), Coelho et al. (2010)
Rhodotorula sphaerocarpa	*Rhodosporidium sphaerocarpum*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Rhodotorula toruloides	*Rhodosporidium toruloides*	Creek water, leaves submerged in a stream	Iberian Pyrite Belt, Sao Domingos, Portugal; River Olo, Alvao Natural Park, Portugal	Gadanho et al. (2006), Sampaio et al. (2007)
Saitozyma podzolica	*Cryptococcus podzolicus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Solicoccozyma aeria	*Cryptococcus albidus* var. *aerius*, *Cryptococcus aerius*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Solicoccozyma fuscescens	*Cryptococcus fuscescens*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Solicoccozyma terreus	*Cryptococcus terreus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Spencerozyma crocea	*Rhodotorula crocea*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Sporobolomyces sp.		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sampaio et al. (2007), Coelho et al. (2010)
Sporobolomyces roseus		River water, leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal; Tagus river, Portugal	Sampaio et al. (2007), Coelho et al. (2010)
Sporobolomyces salmonicolor	*Sporidiobolus salmonicolor*	River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007)
Sporobolomyces shibatanus		River water	Danube, Bratislava, Slovakia	Sláviková and Vadkertiová (1997)
Sterigmatosporidium polymorphum		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Trigonosporomyces hylophilus	*Rhodotorula hylophila*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Udeniomyces megalosporus	*Bullera megalosporus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)

(continued)

Table 1.2 (continued)

Species	Original taxonomic designation	Source	Locality	References
Udeniomyces pyricola	*Bullera pyricola*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Vanrija humicola	*Cryptococcus humicolus*	Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Vanrija longa	*Cryptococcus longus*	River water	Tagus river, Portugal	Gadanho and Sampaio (2004)
Xanthophyllomyces dendrorhous		Leaves submerged in a stream	River Olo, Alvao Natural Park, Portugal	Sampaio et al. (2007)
Yeastlike dimorphic fungi				
Aureobasidium pullulans		River water, leaves submerged in a stream	Danube, Bratislava, Slovakia; River Olo, Alvao Natural Park, Portugal	Sláviková and Vadkertiová (1997), Sampaio et al. (2007)

[a] Both culturable and non-culturable

The first studies on yeast diversity in temperate rivers and creeks are dated back to the early 1970s. Simard and Blackwood (1971a, b) found that culturable yeast abundance in water samples collected at St. Lawrence River, Canada, was considerably higher in July and somewhat higher in September. A wide range of ascomycetous and basidiomycetous yeasts was identified with no phylum prevalence. In particular species belonging to the polyphyletic genera *Candida* and *Rhodotorula* were the most abundant, and the species *Rh. glutinis* was the most frequently found (about 58% of the total isolates). However, the taxonomical identity of these isolates should be analyzed with care given that the correct identification of those species is only possible using molecular techniques.

The Danube is the second longest European river and is located in Central and Eastern Europe. Slávikova and Vadkertiová (1997) studied the culturable yeast diversity in water samples of Danube collected in the area of Bratislava. Yeast abundance ranged from 10^2 to 10^3 CFU l^{-1}. The species *A. pullulans*, *Candida maltosa*, *C. krusei* (*P. kudriavzevii*), *Geotrichum candidum* (*Galactomyces candidum*), and *Saccharomyces cerevisiae* among Ascomycota and *Cystofilobasidium capitatum* and *Rh. glutinis* among Basidiomycota were the most frequently found. Among them, *S. cerevisiae* was the dominant species (isolated from 50% of samples and about 25% of isolates). However, it should be kept in mind that the eutrophy of the Danube passing through different cities along the course could have influenced the natural composition of yeast communities.

Some rivers and creeks of the Iberian Peninsula have received particular attention since the 2000s. The Tagus is the longest river on the Iberian Peninsula. It is 1038 km long and spans 716 km in Spain, 47 km along the border between Portugal and Spain, and 275 km in Portugal, where it flows into the Atlantic Ocean. Temperature gradient gel electrophoresis (TGGE), including nested PCR to obtain fungal amplicons containing the D2 domain of the 26S rRNA gene, TGGE band extraction, re-amplification, and sequencing, was used for assessing yeast diversity in the estuary of the Tagus. Fourteen fungal taxa were detected and all except one were yeasts. Most yeast sequences corresponded to members of the Ascomycota and only three belonged to the Basidiomycota. The dominant species were *Deb. hansenii*, *Rh. mucilaginosa*, and *Cryptococcus longus* (currently *Vanrija longa*) (Gadanho and Sampaio 2004). More recently, de Almeida (2005) found that yeast occurrence in waters sampled at the Tagus estuary did not seem to depend upon tides, but river discharge had a dramatic impact on both the density and diversity of the community. Seasonal changes and yeast abundance were the highest around February/March as the result of the winter peak of the river flow. The main species found were *Candida catenulata* (currently *Diutina catenulata*), *Candida intermedia*, *Candida parapsilosis*, *Clavispora lusitaniae*, *Deb. hansenii*, and *Pichia guilliermondii* (currently *Mey. guilliermondii*) among Ascomycota and *Rh. mucilaginosa* and *Rhodosp. diobovatum* (currently *Rh. diobovata*) among Basidiomycota. Interestingly, Coelho et al. (2010) found a correlation between the occurrence of both *C. parapsilosis* and *P. guilliermondii* and the incidence of the bacterial fecal species *E. coli* in waters sampled in Tagus estuary.

Other Iberian rivers have been also taken into consideration. Sampaio et al. (2007) studied the culturable yeast populations occurring on submerged leaves (alder, eucalyptus, and oak) in a natural mountain stream of River Olo, Portugal. Seventy-two yeast taxa were found, and basidiomycetous species predominated over ascomycetous ones. In all leaf litter types, three ubiquitous yeast species, such as *Cr. albidus* (*Na. albida*), *Deb. hansenii*, and *Rh. glutinis*, were found.

The occurrence and diversity of culturable yeasts in water sampled in River Tinto, which is located in the Iberian Pyrite Belt, a vast geographical area with particular geological features that stretches along much of the south of the Iberian Peninsula, from Portugal to Spain, was studied. In the Iberian Pyrite Belt, acid rock drainage gives rise to aquatic habitats with low pH and high concentrations of heavy metals and causes important environmental peculiarities. Twenty-seven yeast species were detected, 48% of which represented undescribed taxa. A few species, namely, *Candida fluviatilis* and *Rhodosporidium toruloides* (currently *Rhodotorula toruloides*), occurred in situations of intermediate environmental stress (Gadanho et al. 2006). Comparable results were found in a similar environment but in this case of volcanic origin, the River Agrio as described by Russo et al. (2008). Several species/lineages were common to both acidic rivers and showed interesting physiological adaptations to such extreme environments (Gadanho et al. 2006; Russo et al. 2008, 2010, 2016).

1.4 Yeast Diversity in Seawater

1.4.1 General Aspects

The presence of yeasts has been recognized in all worldwide oceans, from coastal regions to offshore environments (including oceanic surface, deep waters, and sediments). Marine fungi including yeasts are known to inhabit a wide variety of habitats within the marine environments (Mouton et al. 2012). The first observation of yeasts in marine water was reported by Fischer and Brebeck (1894). Marine yeasts are believed to have physiological adaptations to overcome the adverse effect of salinity and high hydrostatic pressure and to grow and interact with other microbial marine communities (Lorenz and Molitoris 1997; Kandasamy et al. 2012; Rédou et al. 2015). However, the ecological significance of the presence of viable yeast cells in these habitats as the result of a mere survival under the harsh environmental conditions occurring in seawater environment or, on the contrary, the result of their ability to play an active role in this niche (or even a combination of both) is still an open question (Mouton et al. 2012). Researches on ecology and diversity of marine yeasts have been reviewed in recent years (Kutty and Philip 2008; Nagano et al. 2010; Fell 2012; Kandasamy et al. 2012). The genera and species found in worldwide marine habitats are reported in Table 1.3.

1.4.2 Yeasts in Coastal Marine Environments

Coastal marine waters are subjected to terrestrial influxes due to natural drainage and human activities, and most fungi, including yeasts, can be considered as facultative marine fungi with a presumably terrestrial origin. Terrestrial and human-associated allochthonous yeasts are introduced into these waters by rains and rivers, and their persistence is related to the ability to sustain the saline conditions occurring in seawater. The cell abundance in some cases can be as high as thousands of cells l^{-1} (Fell 2012). A number of ascomycetous and basidiomycetous yeasts have been found as inhabitant of both terrestrial and nearshore marine environments. The most frequently isolated species were *C. parapsilosis*, *Deb. hansenii*, and a few members of the genus *Malassezia* (Gao et al. 2008; Fell 2012) (Table 1.3). Many of these species were most likely introduced from the surrounding terrestrial vegetation, including mangrove habitats (Statzell-Tallman et al. 2008). The yeast diversity in aquatic ecotone habitats (estuaries, mangroves, salt marshes, bogs, and phytotelmata) is also reported in Chap. 2 of this book.

Some species have been regularly found in coastal marine habitats, namely, *Cryptococcus marinus* (currently *Bandonia marina*) and *K. aestuarii* (van Uden and ZoBell 1962; Fonseca et al. 2011), while a few *Metschnikowia* species, namely, *M. australis*, *Metschnikowia bicuspidata*, and *Metschnikowia krissii*, are either endemic or restricted to marine nearshore habitats, sometimes associated with

Table 1.3 Diversity of yeasts and yeastlike dimorphic fungi in marine environments

Species	Original taxonomic designation	Isolation source	Locality	References
Ascomycetous yeasts				
Barnettozyma californica	*Williopsis californica*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Blastobotrys adeninivorans	*Trichosporon adeninivorans*	Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Brettanomyces anomalus		Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Brettanomyces bruxellensis		Seawater; beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Brettanomyces custersianus		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida sp.^{b}		Sea sediment; shrimp; hydrothermal vent; mussel	Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise; Sagami Bay, Japan; Pacific Ocean	Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Bass et al. (2007), Takishita et al. (2007), Burgaud et al. (2010), Xu et al. (2014, 2016)
Candida albicans		Sea sediment; seawater; beach sand	Indian Ocean; Southwest cost of India; Greece; Pernambuco, Brazil; Florida, USA	Fell (1967), Prabhakaran and Gupta (1991), Papadakis et al. (1997), Loureiro et al. (2005), Vogel et al. (2007)
Candida aquaetextoris		Seawater	Arabian Sea	Babu et al. (2013)
Candida atlantica	*Trichosporon atlanticum*	Shrimp; mussel; seawater, hydrothermal vent	Azores Archipelago; North Atlantic Ocean; Portugal; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise	Siepmann and Hohnk (1962), Gadanho et al. (2003), Gadanho and Sampaio (2005), Burgaud et al. (2010)
Candida atmosphaerica		Seawater; seafish	Indian Ocean and Island of Mauritius; Azores Archipelago	Fell (1967), Gadanho and Sampaio (2005)
Candida blankii		Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Candida boidinii		Seawater	Faro, Portugal	Gadanho et al. (2003)

Candida diddensiae		Seawater	Pacific Ocean (equator); Pernambuco, Brazil	Yamasato et al. (1974), Loureiro et al. (2005)
Candida etchellsii[a]		Sediment	East Indian Ocean	Zhang et al. (2014)
Candida fennica		Seawater; beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida geochares		Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Candida glabrata	*Torulopsis glabrata*	Seawater; sea sediment	Sepetiba Bay, Rio de Janeiro, Brazil; Greece; Taiwan	Pagnocca et al. (1989), Papadakis et al. (1997), Chen et al. (2009)
Candida inconspicua[a]		Sediment	East Indian Ocean	Zhang et al. (2014)
Candida intermedia		Seawater; sediment; shrimp	Sepetiba Bay, Rio de Janeiro, Brazil; Pernambuco, Brazil	Pagnocca et al. (1989), Loureiro et al. (2005)
Candida maltosa		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida maris	*Torulopsis maris*	Seawater	Torres Strait, Australia	van Uden and ZoBell (1962)
Candida maritima		Seawater	Greece	Papadakis et al. (1997)
Candida melibiosica		Seawater; beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida membranifaciens subsp. *flavinogenie*		Seawater	China Eastern Sea	Wang et al. (2008)
Candida metapsilosis[a]		Sediment	Pacific Ocean	Xu et al. (2014)
Candida naeodendra		Beach sand	Florida, USA	Vogel et al. (2007)
Candida oceani		Hydrothermal vent	Mid-Atlantic Ridge	Burgaud et al. (2011)
Candida orthopsilosis[a]		Sediment	Central Indian Basin	Singh et al. (2012b)
Candida palmioleophila		Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Candida parapsilosis[b]		Sea sediment; seawater; beach sand; sea fish; seaweeds; sediment shrimp	Biscayne Bay, Florida, USA; Indian Ocean; Sepetiba Bay, Rio de Janeiro, Brazil; Camp Varnum, Rhode Island, USA; Southwest cost of India; Greece; Faro, Portugal; Azores Archipelago; Pernambuco, Brazil; Pacific Ocean, close to Japan	Roth et al. (1962), Fell (1967), Seshadri and Sieburth (1971), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Papadakis et al. (1997), Gadanho et al. (2003), Gadanho and Sampaio (2005),

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
				Loureiro et al. (2005), Nagano et al. (2010)
Candida pseudointermedia		Seawater; sediment	Sepetiba Bay, Rio de Janeiro, Brazil	Pagnocca et al. (1989)
Candida rhagii		Seawater; beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida rugopelliculosa		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida saitoana	*Torulopsis candida*	Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Candida sake[b]	*Candida salmonicola*	Seawater; beach sand; sediment	Greece; Pernambuco, Brazil; East Indian Ocean	Papadakis et al. (1997), Loureiro et al. (2005), Zhang et al. (2014)
Candida sorboxylosa		Seawater	Faro, Portugal	Gadanho et al. (2003)
Candida tenuis		Seawater and sea fish	Indian Ocean	Fell (1967)
Candida torresii	*Torulopsis torresii*	Seawater	Torres Strait, Australia	van Uden and ZoBell (1962)
Candida tropicalis[b]		Seawater; sea fish; beach sand; sea sediment; shrimp; marine sponge	Biscayne Bay, Florida, USA; Indian Ocean; Southwest cost of India; Sepetiba Bay, Rio de Janeiro, Brazil; Greece; Florida, USA; Island of Oahu, Hawaii; Taiwan	Roth et al. (1962), Fell (1967), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Papadakis et al. (1997), Vogel et al. (2007), Gao et al. (2008), Chen et al. (2009)
Candida vaccinii		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Candida viswanathii	*Candida lodderae*	Sea fish; seawater; shrimp; mussel; hydrothermal vent	Indian Ocean; Azores Archipelago; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise	Fell (1967), Gadanho and Sampaio (2005), Burgaud et al. (2010)
Candida xylopsoci[a]		Sediment	East Indian Ocean	Zhang et al. (2014)
Candida zeylanoides	*Candida krissii*	Seaweeds; seawater	Camp Varnum, Rhode Island, USA; Pacific Ocean (equator); Greece	Seshadri and Sieburth (1971), Yamasato et al. (1974), Papadakis et al. (1997)

Clavispora lusitaniae		Beach sand	Florida, USA	Vogel et al. (2007)
Cutaneotrichosporon curvatus[a]	*Cryptococcus curvatus*	Sediment	East Indian Ocean	Zhang et al. (2014)
Cutaneotrichosporon moniliiforme[a]	*Trichosporon moniliiforme*	Sediment	East Indian Ocean	Zhang et al. (2014)
Debaryomyces hansenii[b]	*Candida famata*; *Debaryomyces nicotianae*; *Debaryomyces kloeckerii*; *Torulopsis famata*	Seawater; sea fish; sea sediment; shrimp; mussel; hydrothermal vent	Biscayne Bay, Florida, USA; Indian Ocean and Island of Mauritius; Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Faro, Portugal; China South Sea; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise; Central Indian Basin	Roth et al. (1962), Fell (1967), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Gadanho et al. (2003), Bass et al. (2007), Gao et al. (2007), Burgaud et al. (2010), Singh et al. (2012a)
Dipodascus australiensis[a]		Sediment	East Indian Ocean	Zhang et al. (2014)
Diutina catenulata	*Candida catenulata*	Seawater; beach sand	Greece; Pernambuco, Brazil; Florida, USA	Papadakis et al. (1997), Loureiro et al. (2005), Zhang et al. (2014), Vogel et al. (2007)
Diutina rugosa	*Candida rugosa*	Seawater; beach sand	Indian Ocean; Greece	Fell (1967), Papadakis et al. (1997)
Galactomyces sp.		beach sand	Florida, USA	Vogel et al. (2007)
Geotrichum sp.		Seawater; sediment; shrimp	Sepetiba Bay, Rio de Janeiro, Brazil	Pagnocca et al. (1989)
Geotrichum candidum[b]		Sea sediment	Southwest cost of India; East Indian Ocean	Prabhakaran and Gupta (1991); Zhang et al. (2014)
Hanseniaspora uvarum	*Kloeckera apiculata*	Sea fish; seawater; sediment; shrimp	Biscayne Bay, Florida, USA, USA; Indian Ocean; Sepetiba Bay, Rio de Janeiro, Brazil; Taiwan	Roth et al. (1962), Fell (1967), Pagnocca et al. (1989), Chen et al. (2009)
Kazachstania sp.[a]	*Kazachstania zonata* like	Sediment	Worldwide Seas	Bass et al. (2007)
Kazachstania humilis	*Candida milleri*	Seawater	Pernambuco, Brazil	Loureiro et al. (2005)

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
Kazachstania jiainica	*Kazachstania jiainicus*	Seawater	Taiwan	Chen et al. (2009)
Kazachstania yakushimaensis	*Saccharomyces yakushimaensis*	Seawater	Taiwan	Chen et al. (2009)
Kluyveromyces aestuarii	*Saccharomyces aestuarii*	Marine mud; seawater	Biscayne Bay, Florida, USA; Torres Strait, Portugal; Shroud Cay, Bahamas	Fell (1961), Lachance (2011a)
Kluyveromyces nonfermentans		Sediment	Suruga or Sagami Bay, Japan	Nagahama et al. (1999)
Kodamaea sp.[a]		Sediment	Arabian Sea	Jebaraj et al. (2010)
Kodamaea ohmeri		Beach sand; seafish; seawater	Florida, USA; Pacific Ocean; Taiwan	Vogel et al. (2007), Li et al. (2008), Chen et al. (2009), Dong et al. (2015)
Kregervanrija fluxuum	*Candida mycoderma*	Seawater	Indian Ocean	Fell (1967)
Metschnikowia sp.[a]		Sediment	Pacific Ocean, close to Japan	Nagano et al. (2010)
Metschnikowia bicuspidata		Beach sand; seawater	Florida, USA; Point Reyes, California	Vogel et al. (2007), Lachance (2011b)
Metschnikowia krissii		Seawater	La Jolla, California, USA	Lachance (2011b)
Metschnikowia reukaufii		Sediment	South China Sea	Li et al. (2010a)
Metschnikowia zobellii		Seawater	La Jolla, California, USA; Clyde estuary, Scotland	van Uden and Castelo-Branco (1961), Miller and Phaff (1998)
Meyerozyma sp.[a]		Sediment	Pacific Ocean	Xu et al. (2016)
Meyerozyma guilliermondii[b]	*Candida guilliermondii*; *Pichia guilliermondii*	Seawater; sea fish; sediment; shrimp; beach sand; marine algae; mussel; hydrothermal vent	Biscayne Bay, Florida, USA; Indian Ocean and Island of Mauritius; Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Greece; Azores Archipelago; Qingdao, China; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise; Pacific Ocean; Canterbury Basin, New Zealand	Roth et al. (1962), Fell (1967), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Papadakis et al. (1997), Gadanho and Sampaio (2005), Gao et al. (2007), Burgaud et al. (2010), Xu et al. (2014), Rédou et al. (2015)

Nakazawaea ishiwadae	*Candida ishiwadae*	Beach sand	Florida, USA	Vogel et al. (2007)
Pichia sp.[b]		Seawater; sediment	Sepetiba Bay, Rio de Janeiro, Brazil	Pagnocca et al. (1989), Bass et al. (2007)
Pichia fermentans		Seawater	Indian Ocean	Fell (1967)
Pichia kudriavzevii	*Candida krusei*; *Issatchenkia orientalis*	Seawater; sediment; shrimp; beach sand	Sepetiba Bay, Rio de Janeiro, Brazil; Greece; Florida, USA; Taiwan	Pagnocca et al. (1989), Papadakis et al. (1997), Vogel et al. (2007), Chen et al. (2009)
Pichia membranifaciens	*Candida valida*	Sea sediment	Sepetiba Bay, Rio de Janeiro, Brazil	Pagnocca et al. (1989)
Pichia occidentalis	*Candida sorbosa*	Sea sediment; shrimp	Sepetiba Bay, Rio de Janeiro, Brazil	Pagnocca et al. (1989)
Saccharomyces sp.[b]		Sea sediment	Southwest cost of India; Central Indian Basin	Prabhakaran and Gupta (1991), Singh et al. (2012a)
Saccharomyces cerevisiae	*Saccharomyces fructuum*; *Saccharomyces steineri*	Seawater	Indian Ocean	Fell (1967)
Scheffersomyces spartinae	*Pichia spartinae*	Oyster grass (*Spartina alterniflora*) marshes	Barataria Bay, Louisiana, USA	Meyers et al. (1975)
Starmerella bombicola	*Candida bombicola*	Seawater	Pernambuco, Brazil	Loureiro et al. (2005)
Torulaspora delbrueckii	*Saccharomyces rosei; Torulopsis colliculosa*	Seawater; beach sand	Greece; Florida, USA; Taiwan	Papadakis et al. (1997), Vogel et al. (2007), Chen et al. (2009)
Wickerhamomyces anomalus	*Hansenula anomala*; *Pichia anomala*	Sea fish; seawater; sediment; shrimp; beach sand; gut of Sea squirts	Biscayne Bay, Florida, USA; Island of Mauritius; Sepetiba Bay, Rio de Janeiro, Brazil; Florida, USA; Taiwan; Coast of Yantai, China	Roth et al. (1962), Fell (1967), Pagnocca et al. (1989), Vogel et al. (2007), Chen et al. (2009), Guo et al. (2013)
Wickerhamomyces onychis	*Pichia onychis*	Beach sand	Florida, USA	Vogel et al. (2007)

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
Wickerhamomyces pijperi	*Pichia pijperi*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Yamadazyma barbieri		Seawater	Ipanema beach, Rio de Janeiro, Brazil; mid-Atlantic ridge	Burgaud et al. (2016)
Yamadazyma triangularis	*Candida polymorpha*	Seawater	Indian Ocean; Island of Mauritius	Fell (1967)
Yarrowia divulgata		Seawater and ocean fish		Nagy et al. (2013)
Yarrowia keelungensis		Seawater	Keelung City off the northern coast of Taiwan	Chang et al. (2013)
Yarrowia lipolytica		Beach sand; marine algae; seawater; sediment	Florida, USA; Qingdao, China; Persian Gulf, Iran; St. Helena Bay, South Africa	Vogel et al. (2007), Hassanshahian et al. (2012), Mouton et al. (2012)
Basidiomycetous yeasts				
Apiotrichum dulcitum	*Trichosporon dulcitum*	Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Bandonia marina	*Candida marina*	Seawater	Torres Strait, Australia	van Uden and ZoBell (1962)
Bensingtonia sp.		Seawater	Faro, Portugal	Gadanho et al. (2003)
Buckleyzyma aurantiaca	*Rhodotorula aurantiaca*	Sediment	Pacific Ocean	Nagahama et al. (2001a)
Bullera alba		Seawater	Faro, Portugal	Gadanho et al. (2003)
Bullera unica		Sediment	Canterbury Basin, New Zealand	Rédou et al. (2015)
Cryptococcus sp.[b]		Seawater; sediment	Faro, Portugal; Pacific Ocean	Gadanho et al. (2003), Xu et al. (2014, 2016)
Cutaneotrichosporon curvatus[b]	*Candida curvata; Cryptococcus curvatus*	Seawater; sediment; cold methane seep	Greece; Kuroshima Knoll, Japan; Sagami Bay, Japan	Papadakis et al. (1997), Takishita et al. (2006, 2007)

Cutaneotrichosporon cutaneum	*Trichosporon cutaneum*	Sea fish	Biscayne Bay, Florida, USA	Roth et al. (1962)
Cutaneotrichosporon dermatis[b]	*Trichosporon dermatis*	Seawater; sediment	Azores Archipelago; Pacific Ocean	Gadanho and Sampaio (2005), Xu et al. (2014)
Cutaneotrichosporon mucoides[a]	*Trichosporon mucoides*	Sediment	Pacific Ocean, close to Japan	Nagano et al. (2010)
Cystobasidium sp.[a]		Sediment	Arabian Sea; Pacific Ocean, close to Japan	Jebaraj et al. (2010), Nagano et al. (2010)
Cystobasidium benthicum	*Rhodotorula benthica*	Tubeworm	Sagami Bay and Iheya Ridge, Japan	Nagahama et al. (2003a)
Cystobasidium calyptogenae[b]	*Rhodotorula calyptogenae*	Clam; sediment	Sagami Bay, Japan; Central Indian Basin	Nagahama et al. (2003a), Singh et al. (2012b)
Cystobasidium minutum	*Rhodotorula minuta*	Sea fish; sediment; seawater; tubeworm; beach sand	Biscayne Bay, Florida, USA; Southwest cost of India; Pacific Ocean; Faro, Portugal; Sagami Bay and Iheya Ridge, Japan; Pernambuco, Brazil	Roth et al. (1962), Prabhakaran and Gupta (1991), Nagahama et al. (2001a, 2003a), Gadanho et al. (2003), Loureiro et al. (2005)
Cystobasidium pallidum	*Rhodotorula pallida*	Seawater	Indian Ocean	Fell (1967)
Cystobasidium slooffiae[b]	*Rhodotorula slooffiae*	Clam; sediment	Sagami Bay, Japan; Central Indian Basin; Pacific Ocean	Nagahama et al. (2003a), Singh et al. (2012a), Xu et al. (2014)
Cystofilobasidium sp.[a]	*Cystofilobasidium infirmominiatum like*	Sediment	Worldwide Seas	Bass et al. (2007)
Dioszegia antarctica		Rock surface	Vailulu'u active submarine volcano, Samoan volcanic chain	Jebaraj et al. (2010)
Filobasidium sp.[a]		Sediment	Worldwide Seas	Bass et al. (2007)
Filobasidium magnum	*Cryptococcus magnus*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Filobasidium uniguttulatum	*Cryptococcus uniguttulatus*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Goffeauzyma sp.[a]		Marine sponge	Yongxing Island, South China Sea	Jin et al. (2014)

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
Hannaella surugaensis	*Cryptococcus surugaensis*	Sediment	Suruga Bay, Japan	Nagahama et al. (2003b)
Hasegawazyma lactosa	*Rhodotorula lactosa*	Seaweeds	Camp Varnum, Rhode Island, USA	Seshadri and Sieburth (1971)
Kondoa malvinella	*Rhodosporidium malvinellum*	Seawater	Southern Pacific; Indian Ocean	Sampaio (2011)
Leucosporidium scottii		Hydrothermal vent	Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise	Burgaud et al. (2010)
Malassezia sp.[a]		Sediment; marine sponge	Island of Oahu, Hawaii; Arabian Sea; Pacific Ocean	Bass et al. (2007), Gao et al. (2008), Jebaraj et al. (2010), Xu et al. (2014, 2016)
Malassezia furfur	*Pityrosporum orbiculare*	Seawater; beach sand	Greece	Papadakis et al. (1997)
Malassezia restricta[a]		Sediment	Central Indian Basin	Singh et al. (2012a)
Malassezia slooffiae[a]		Sediment	Central Indian Basin	Singh et al. (2012a)
Moesziomyces aphidis	*Pseudozyma aphidis*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Naganishia sp.[a]	*Cryptococcus vishniacii* like	Sediment	Worldwide Seas	Bass et al. (2007)
Naganishia albida	*Cryptococcus albidus*	Sediment; seawater	Indian Ocean; Pacific Ocean; Sepetiba Bay, Rio de Janeiro, Brazil; Greece; Japanb Trench; Faro, Portugal	Fell (1967), Yamasato et al. (1974), Pagnocca et al. (1989), Papadakis et al. (1997), Abe et al. (2001), Gadanho et al. (2003)
Naganishia globosa	*Cryptococcus saitoi*	Rock surface	Vailulu'u active submarine volcano, Samoan volcanic chain	Jebaraj et al. (2010)
Naganishia liquefaciens	*Cryptococcus liquefaciens*	Sediment	Japan Trench; Pacific Ocean	Abe et al. (2006), Xu et al. (2014)
Naganishia uzbekistanensis	*Cryptococcus uzbekistanensis*	Hydrothermal vent	Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise	Burgaud et al. (2010)

Papiliotrema aurea	*Cryptococcus aureus*	Sediment	China South Sea	Gao et al. (2007)
Papiliotrema laurentii	*Cryptococcus laurentii*	Seawater	Island of Mauritius; Sepetiba Bay, Rio de Janeiro, Brazil; Faro, Portugal; Pacific Ocean, close to Japan	Fell (1967), Pagnocca et al. (1989); Gadanho et al. (2003), Nagano et al. (2010)
Phaeotremella sp.[a]		Sediment	Pacific Ocean, close to Japan	Nagano et al. (2010)
Rhodosporidium sp.[a]		Sediment	Pacific Ocean	Xu et al. (2016)
Rhodotorula sp.[b]	*Rhodosporidium diobovatum* like; *Rhodotorula mucilaginosa* like	Sediment; seawater	Zhanjiang, China; Central Indian Basin; Pacific Ocean	Yang et al. (2011), Singh et al. (2012a, b), Xu et al. (2016)
Rhodotorula babjevae	*Rhodosporidium babjevae*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Rhodotorula diobovata	*Rhodosporidium diobovatum*	Seawater; shrimp; mussel; hydrothermal vent	Faro, Portugal; Azores Archipelago; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise; Zhanjiang, China	Gadanho et al. (2003); Gadanho and Sampaio (2005), Burgaud et al. (2010), Yang et al. (2011)
Rhodotorula glutinis		Sea fish; seawater; sediment; beach sand; shrimp	Biscayne Bay, Florida, USA; Indian Ocean; Pacific Ocean; Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Azores, Portugal; Florida, USA; Pernambuco, Brazil; Zhanjiang, China	Roth et al. (1962), Fell (1967), Yamasato et al. (1974), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Nagahama et al. (2001a), Gadanho and Sampaio (2002), Loureiro et al. (2005), Yang et al. (2011)
Rhodotorula graminis		Seawater; sediment	Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Atlantic Ocean	Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Gadanho and Sampaio (2002)
Rhodotorula kratochvilovae	*Rhodosporidium kratochvilovae*	Seawater	Arrabida, Portugal; Faro, Portugal	Gadanho and Sampaio (2002), Gadanho et al. (2003)

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
Rhodotorula mucilaginosa[b]	*Rhodotorula pilimanae*; *Rhodotorula rubra*	Seawater; sediment; seaweeds; shrimp; mussel; hydrothermal vent; beach sand; sea fish;	Biscayne Bay, Florida, USA; Indian Ocean; Camp Varnum, Rhode Island, USA; Sepetiba Bay, Rio de Janeiro, Brazil; Southwest cost of India; Pacific Ocean; Faro, Portugal; Azores Archipelago; Pernambuco, Brazil; Queenscliff region, Victoria, Australia; Mid-Atlantic Ridge; South Pacific Basins; East Pacific Rise; Bohai Sea, China; St. Helena Bay, South Africa; Zhanjiang, China; Canterbury Basin, New Zealand; Central Indian Basin	Roth et al. (1962), Fell (1967), Seshadri and Sieburth (1971), Yamasato et al. (1974), Pagnocca et al. (1989), Prabhakaran and Gupta (1991), Nagahama et al. (2001a), Gadanho et al. (2003), Gadanho and Sampaio (2005), Loureiro et al. (2005), Vogel et al. (2007), Burgaud et al. (2010), Li et al. (2010b), Yang et al. (2011), Gupta et al. (2012), Mouton et al. (2012), Xu et al. (2014), Rédou et al. (2015), Singh et al. (2012a)
Rhodotorula nothofagi		Seawater	Faro, Portugal	Gadanho et al. (2003)
Rhodotorula pacifica		Sediment	Pacific Ocean	Nagahama et al. (2006)
Rhodotorula paludigena	*Rhodosporidium paludigenum*	Beach sand; seawater and shrimp	Florida, USA; Zhanjiang, China	Vogel et al. (2007), Yang et al. (2011)
Rhodotorula sphaerocarpa	*Rhodosporidium sphaerocarpum*	Seawater; shrimp	Faro, Portugal; Azores Archipelago; Florida, USA; Bahamas, USA; Zhanjiang, China	Gadanho et al. (2003), Gadanho and Sampaio (2005), Sampaio (2011), Yang et al. (2011)
Rhodotorula toruloides	*Rhodosporidium toruloides*	Seawater; shrimp	Azores Archipelago; Southern Ocean; Zhanjiang, China	Gadanho and Sampaio (2005), Sampaio (2011), Yang et al. (2011)
Saitozyma podzolica[a]	*Cryptococcus podzolicus*	Sediment	East Indian Ocean	Zhang et al. (2014)
Sakaguchia dacryoidea		Seawater	Faro, Portugal	Gadanho et al. (2003)
Sakaguchia lamellibrachiae	*Rhodotorula lamellibrachiae*	Sediment; deep-sea floor; tubeworm	Sagami Bay, Japan	Nagahama et al. (2001b, 2003a)
Sampaiozyma ingeniosa	*Rhodotorula ingeniosa*	Seawater	Pernambuco, Brazil	Loureiro et al. (2005)

Spencerozyma crocea	*Rhodotorula crocea*	Seawater	Indian Ocean	Fell (1967)
Sporidiobolus pararoseus		Shrimp	Zhanjiang, China	Yang et al. (2011)
Sporobolomyces lactosus[a]		Sediment	East Indian Ocean	Zhang et al. (2014)
Sporobolomyces roseus		Shrimp; mussel	Faro, Portugal	Gadanho et al. (2003)
Sporobolomyces salmonicolor	*Sporobolomyces odorus*; *Sporobolomyces hispanicus*	Seawater; sediment	Indian Ocean; Pacific Ocean	Fell (1967), Nagahama et al. (2001a)
Sporobolomyces shibatanus		Sediment	Pacific Ocean	Nagahama et al. (2001a)
Sterigmatomyces halophilus[b]		Seawater	Indian Ocean; Pacific Ocean	Fell (1967, 1970), Xu et al. (2014)
Sterigmatomyces sp.[a]		Sediment	Pacific Ocean	Xu et al. (2016)
Symmetrospora marina	*Rhodotorula marina*	Seawater	Pacific Ocean (equator)	Yamasato et al. (1974)
Tausonia sp.[a]	*Trichosporon pullulans* like	Sediment	Worldwide Seas	Bass et al. (2007)
Tausonia pullulans[a]	*Trichosporon pullulans*	Sediment	Pacific Ocean	Xu et al. (2014)
Trichosporon sp.[b]		Seawater; shrimp; sediment	Sepetiba Bay, Rio de Janeiro, Brazil; Pacific Ocean	Pagnocca et al. (1989), Xu et al. (2016)
Trichosporon aquatile		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Trichosporon asahii[b]		Beach sand; sediment	Florida, USA; Central Indian Basin	Vogel et al. (2007), Singh et al. (2012a, b)
Trichosporon beigelii		Beach sand	Pernambuco, Brazil	Loureiro et al. (2005)
Trichosporon coremiiforme		Beach sand	Florida, USA	Vogel et al. (2007)

(continued)

Table 1.3 (continued)

Species	Original taxonomic designation	Isolation source	Locality	References
Vanrija fragicola[a]	*Cryptococcus fragicola*	Sediment	East Indian Ocean	Zhang et al. (2014)
Vishniacozyma sp.[a]	*Cryptococcus carnescens* like	Sediment	Pacific Ocean	Bass et al. (2007), Xu et al. (2014)
Vishniacozyma victoriae	*Cryptococcus victoriae*	Seawater	Faro, Portugal	Gadanho et al. (2003)
Yeastlike microorganisms				
Aureobasidium sp.[a]		Sediment; marine sponge	Island of Oahu, Hawaii; Yongxing Island, South China Sea; Pacific Ocean	Bass et al. (2007), Gao et al. (2008), Jin et al. (2014), Xu et al. (2016)
Aureobasidium pullulans[b]		Sediment	Pacific Ocean	Xu et al. (2014)
Exophiala sp.[b]		Sediment	Pacific Ocean; Canterbury Basin, New Zealand	Xu et al. (2014, 2016), Rédou et al. (2015)
Exophiala dermatitidis		Seawater; sediment	Azores Archipelago	Gadanho and Sampaio (2005), Xu et al. (2014)
Sympodiomycopsis sp.[a]		Sediment	Pacific Ocean	Xu et al. (2016)

[a] Only non-culturable

[b] Both culturable and non-culturable

marine invertebrates and fishes (Fell and Hunter 1968; Seki and Fulton 1969; Donachie and Zdanowski 1998; Ebert et al. 2000a, b; Moore and Strom 2003; Wang et al. 2008; Lachance 2011b).

Coastal marine sediments represent peculiar environmental niches. Mouton et al. (2012) studied several fungal isolates obtained from marine sediments collected close to St. Helena Bay Western Cape, South Africa. Among them, *Rh. mucilaginosa* and *Yarrowia lipolytica* were found. More recently, Hassanshahian et al. (2012) isolated some *Y. lipolytica* strains from oil-polluted sediment and seawater samples collected in the Persian Gulf (Iran). The strains showed a high ability to degrade aliphatic hydrocarbons.

Several studies also reported the direct pollution of marine nearshore habitats with clinically important yeasts: *C. albicans*, *C. tropicalis*, and some *Trichosporon* spp. strains including *Trichosporon asahii* were isolated from worldwide bathing beaches (Velegraki-Abel et al. 1987; Papadakis et al. 1997; Vogel et al. 2007; Chen et al. 2009; Sabino et al. 2011) and polluted sediments and shrimps (Hagler et al. 1986; Pagnocca et al. 1989; Soares et al. 1997).

1.4.3 Yeasts in Offshore and Deep-Sea Marine Environments

Due to the high costs involved in offshore sampling, oceanographic studies are limited in number. Although the frequency of occurrence is depending on the source and geographical origin of samples, Kandasamy et al. (2012) reported that the yeast abundance increases with increasing distance from the coastline and increasing depth of coastal sea. Conversely, Fell (2012) reported that in offshore regions there is a reduction in the diversity of species and population densities. Bass et al. (2007) postulated that yeasts are the prevalent form of fungi in the deep sea, as revealed with a culture-independent assay. This hypothesis is consistent with that reported by Fell (2012) who suggested that the unicellular lifestyle is apparently better adapted to the aqueous environment than fungal hyphae. Numerically, yeast cells in open ocean waters ranged from 0 to 10 cells l^{-1}, although regions of high organic activity can result in intensive yeast proliferation (Fell 2012). The yeast genera and species found in worldwide offshore marine water are reported in Table 1.3.

Generally, basidiomycetous yeasts account for the majority of the total yeast population in oligotrophic oceanic water, while the ascomycetous yeasts constitute the majority of the total yeast population in the offshore marine sediments (Kandasamy et al. 2012). For example, a number of basidiomycetous yeasts were isolated in seawater collected in the Atlantic Ocean (southern Portugal). Specifically, *Rhodosporidium babjevae*, *Rhodosp. diobovatum* (currently *Rhodotorula babjevae* and *Rh. diobovata*, respectively), and *Pseudozyma aphidis* (currently *Moesz. aphidis*) were the most frequently found species (Gadanho et al. 2003). Among the ascomycetes, some *Candida* species and *Deb. hansenii* were found as inhabitant of offshore and deep-sea oceanic habitats (Kandasamy et al. 2012), in agreement with the early study of Hagler and Ahearn (1987), who postulated that *Deb. hansenii* can be considered the most common ascomycete in marine waters.

Although they have been occasionally isolated from nonmarine sources, some species were found to inhabit specific water masses or oceanographic regions. Among them, *Blastobotrys parvus* (formerly *Sympodiomyces parvus*) was found in warmed Antarctic and sub-Antarctic waters (Fell and Statzell-Tallman 1971), *Candida natalensis* was isolated in the Indo-Pacific ocean (Fell 2012), and *Candida norvegica* was found in a narrow geographical area southward from the polar front (Fell 2012). Strains of the species *Leucosporidium antarcticum* (currently *Glaciozyma antarctica*) have been isolated in Antarctic waters adjacent to the ice pack (Fell 2012). The yeast diversity in cold Polar, sub-Polar, and non-Polar habitats is also reviewed in Chaps. 11 and 12 of this book.

Nagano et al. (2010) investigated deep-sea sediments (1200–10,000 m) collected off the coast of Japan by a culture-independent approach. A number of unknown species together with OTUs (operational taxonomic units) close to *C. parapsilosis*, *Cryptococcus skinneri* (currently *Phaeotremella skinneri*), *Metschnikowia colocasiae*, *Metschnikowia continentalis*, and *Metschnikowia kamakouana* were found. Singh et al. (2012a) investigated fungal diversity in two deep-sea (5000 m) sediment cores collected in the Central Indian Basin by both culture-dependent and culture-independent approaches. A total of 19 culturable fungi including yeasts and 46 OTUs were found. The most represented yeast species were *Deb. hansenii*, *Rhodotorula slooffiae* (currently *Cystobasidium slooffiae*), *Rh. mucilaginosa*, and the black yeast *Hortaea* sp. The detection of amplicon sequences belonging to Exobasidiomycetes and Cystobasidiomycetes from deep-sea samples was also reported (Singh et al. 2012b). Zhang et al. (2014) studied yeast diversity of deep-sea sediment samples collected in the East Indian Ocean. OTUs were related to some yeast species, namely, *Candida etchellsii*, *C. inconspicua*, *Candida sake*, *Candida xylopsoci*, *Dipodascus australiensis*, and *Gal. candidum* among Ascomycota and *Cryptococcus curvatus*, *Cryptococcus fragicola*, *Cryptococcus podzolicus* (currently *Cutaneotrichosporon curvatus*, *Vanrija fragicola*, and *Saitozyma podzolica*, respectively), *Guehomyces pullulans* (*Tausonia pullulans*), *Cyst. slooffiae*, *Sporobolomyces lactosus*, *Sterigmatomyces halophilus*, and *Trichosporon moniliiforme* (currently *Cutaneotrichosporon moniliiforme*) among Basidiomycota and the black yeast *Hortaea werneckii*. A recent study on fungi and yeast diversity in the deep-sea biosphere (water depth ranging from about 5000 to 7000 m) of the Pacific Ocean also reported that the 38.5% of environmental sequences were closely related to phylogenetic lineages comprised by yeasts, namely, to the genera *Candida*, *Erythrobasidium*, *Meyerozyma*, *Tilletiopsis*, *Rhodotorula*, and unspecified members of the former polyphyletic genera *Cryptococcus* and *Rhodotorula*. Several OTUs were also classified as species of the genera *Malassezia*, *Trichosporon* (*Cutaneotrichosporon*), and *Sterigmatomyces*, which are well-known pathogens or parasites of marine animals (Zhang et al. 2014; Xu et al. 2016). Yeasts as parasites of animals, plants, and other fungi have been recently reviewed (Begerow et al. 2017).

Hydrothermal vents are fissures in a planet's surface from which geothermally heated water issues. Their presence strongly affects chemistry and biology of the adjacent habitats. The yeast diversity found in marine hydrothermal vents is reported in Table 1.3. Gadanho and Sampaio (2005) explored the culturable yeast diversity in thermal systems of the Mid-Atlantic Ridge. Species identifications reported both marine- and terrestrially associated species. Unknown species represented 33% of the total yeast taxa. The authors reported some species frequently found in marine waters, namely, *Candida atlantica*, *Candida atmosphaerica*, *C. parapsilosis*, *Rh. diobovata*, and *Rhodosporidium sphaerocarpum* (currently *Rhodotorula sphaerocarpa*). Similar results were obtained by Burgaud et al. (2010) from a series of studies at vents in the Mid-Atlantic Ridge, South Pacific Basins, and East Pacific Rise (Table 1.3). On the contrary, Le Calvez et al. (2009) observed the predominant presence of unknown fungal groups, including species of the former polyphyletic genera *Cryptococcus* and *Filobasidium* in vents of the Pacific and Atlantic Oceans.

Jin et al. (2014) studied fungal diversity in two South China Sea sponges (*Theonella swinhoei* and *Xestospongia testudinaria*) which resulted in 26 OTUs that were assigned to Ascomycota, Basidiomycota, and Blastocladiomycota, including a taxon closely related to the yeast species *Cryptococcus gastricus* (currently *Goffeauzyma gastrica*). The fungal composition of both sponges was significantly different from that of seawater.

A few new species inhabiting different offshore marine habitats were recently described. For example, *Yarrowia keelungensis* was isolated from the sea-surface micro-layer off the northern coast of Taiwan (Chang et al. 2013), while *Yamadazyma barbieri* was isolated from Mid-Atlantic Ridge ocean water samples located in the direct vicinity of black smokers near the Rainbow deep-sea hydrothermal vent and one from Brazilian marine water samples off the Ipanema beach (Burgaud et al. 2016). Also, *Yam. barbieri* is phylogenetically related to a few species of the *Yamadazyma* clade, which were isolated from marine habitats including deep-sea hydrothermal vents, i.e., *C. atmosphaerica*, *C. atlantica*, *Candida oceani*, *Candida spencermartinsiae*, and *Candida taylorii*. These species are widespread in marine habitats and represent an ecologically and phylogenetically defined cluster of marine species in the *Yamadazyma* clade (Burgaud et al. 2016).

1.5 Glacially Originated Water Bodies

1.5.1 General Aspects

Glacial ice is the largest reservoir of freshwater on Earth and many glaciers, because seasonal climates store water as ice during the colder seasons and release it later in the form of meltwater when warmer summer temperatures occur. As glaciers retreats, many water bodies (lakes, ponds, etc.) are left behind and retain direct connection to the glacier through rivers or streams. Even though most glacial ice is located in the polar regions, continental glaciers may be also found in mountain ranges between 35°N and 35°S like the Himalayas, Andes, Rocky Mountains, and in a few other high mountains, being Greenland and Patagonia the biggest expanses of continental glaciers. When a glacier erodes the land, and then melts, it fills the hole or space that it has created originating glacial lakes. In tropical areas, glacial meltwater is an important water resource for major cities (Cook et al. 2016). As glaciers retreat, which is a global tendency, ice-marginal lakes (or proglacial lakes) become distant water bodies which in most cases remain connected by rivers and streams. Most glacial lakes are in elevated locations and this increases in lower latitudes. Normally they are in remote or even protected areas, with little human influences, such as local pollution or land use change, and can be considerate open systems with surface in- and outflow. Most of these aquatic environments considered oligotrophic are characterized by the presence of very low nutrient levels and low rates of external supply.

1.5.2 Yeast Diversity and Ecology in Patagonian Glacial Water Bodies

An interesting example of oligotrophic water bodies is lakes and rivers of Andean Patagonia in South America. Patagonia, the southernmost region of the United States, extends approximately from 40°S—where the width of the continent is about 1000 km—and gradually narrows southward until it disappears in Cape Horn at 56°S (Coronato 2016). These lakes are mostly of glacial origin, reaching in the case of lakes, depths frequently greater than 100 m. They are extremely transparent due to their oligotrophic or even ultra-oligotrophic condition and have an extended euphotic zone (i.e., layer of seawater that receives enough sunlight for photosynthesis to occur) of about 50 m (Modenutti et al. 1998). Quirós and Drago (1985) classified Andean lakes as warm monomictic with a period of summer stratification. Their characteristic low nutrient concentrations is a consequence of the low chemical weathering of the dominant igneous bedrock, as well as low rates of atmospheric deposition. It has been reported that the presence of marine cyclic cations, dissolved inorganic nitrogen, is much lower than the world average (Pedrozo et al. 1993). Microorganisms thriving in such glacial-originated water bodies are typically exposed to multiple stress factors, namely, low temperatures, lack of nutrients, and increased UV exposure as a result of high elevation and transparency.

An additional description of South American cold habitats and a comprehensive list of psychrophilic and psychrotolerant yeast species recovered from such environments are given in Chap. 12 of this book. In this paragraph, we will focus on specific interesting cases illustrating diversity and ecology of yeasts in the northern Andean Patagonia (Argentina) where a great variety of glacially formed water bodies exist. They are characterized by ultra-oligotrophic to mesotrophic conditions and range from small to large lakes, including small high elevation lakes, sometimes surrounded by dense forest (Quirós and Drago 1985; Díaz et al. 2000) (Fig. 1.1). These habitats are normally exposed to extended daylight (at latitude 41–42°S) and consequently increased UV radiation, due also to ozone layer depletion and a clean atmosphere. As already mentioned, these aquatic environments are highly transparent due to their ultra-oligotrophic character and, thus, substantially affected by UV radiation (Villafañe et al. 2001). It is expected then that yeasts autochthonous to these habitats should display cold tolerance and nutritional plasticity and possess efficient strategies for photoprotection. Thus, although yeasts are ubiquitous components of these aquatic environments, they are often present at much lower concentrations than can be expected in terrestrial habitats, such as soils (10^3–10^4 cells g^{-1}) (Spencer and Spencer 1997; Slávikova and Vadkertiova 2000) and phylloplane [10^2–10^4 cells $(cm^2)^{-1}$] (Last and Price 1969; Inácio et al. 2002). Yeasts inhabiting soils and phylloplane are reviewed in Chaps. 3, 4, 6, and 7 of this book.

Even though a portion of the yeast species present in a water body might be native to the aquatic system, it is known that a significant proportion of the yeasts present in a water sample had reached the aquatic environment through runoff from the surrounding watershed (Hagler and Ahearn 1987). If this is entirely true, and assuming the absence of microbial growth in the water column, a few hypotheses can be drawn for the yeast cell dynamics in the water column of ultra-oligotrophic and pristine lakes like those discussed here. First, a higher number of yeast cells might be expected in coastal areas than in open waters (pelagic sites) due to dilution effect and higher availability of the organic matter. Second, allochthonous species can be expected to be more abundant in small lakes having a low lake-area-watershed-area ratio, as well as in the littoral (as opposite to pelagic) areas of larger lakes. One can speculate that the proportion of these allochthonous yeasts should be higher in coastal waters, as well as in small lakes having a low lake-area-watershed-area ratio. In contrast, the proportion of autochthonous species must be higher in the pelagic zone of large lakes given they are better adapted to the harsh conditions and can prevail. Finally, if photoprotective compounds (i.e., carotenoids and mycosporines, MYCs) provide adaptation advantages in the pelagic zone of a highly UV-exposed region, then differences in the proportion of species producing either carotenoids or MYCs between these two types of habitats can also be expected.

During studies of several water bodies in Northwestern Patagonia, including lakes, rivers, and ponds, yeasts were found in almost all samples (Libkind et al. 2003, 2009a; Brandão et al. 2011a, 2017), and they normally presented average abundances around 220 ± 389 CFU l^{-1}. Average yeast abundances ranged from 2 to 250 CFU l^{-1}, rarely exceeding 200 CFU l^{-1}, and these numbers are consistent with those reported for other clear lakes (Hagler and Ahearn 1987). A few exception were found in the high-altitude lake Laguna Negra (890 CFU l^{-1}, 93% of red yeasts) and in a few samples from an anthropogenically impacted coast (1668 CFU l^{-1}). The former case cannot be attributed to a high anthropogenic influence because of the secluded location of this lake, but given 87.5% of the pigmented yeasts were *Rh. mucilaginosa*, it is conceivable that an occasional surge of organic matter caused a temporary increase of this red yeast population (Libkind et al. 2009a) and the carotenoid pigments probably provided this yeast photoprotection (Moliné et al. 2010). In fact, a strain of *Rh. mucilaginosa* from a high-altitude lake was found as a good carotenoid producer for applied purposes (Libkind et al. 2004a). The latter case (coastal water) showed yeast counts characteristic of eutrophic waters (Simard and Blackwood 1971a, b; Meyers et al. 1970; Hagler and Ahearn 1987) and might indicate an increased availability of organic matter due to the coastal condition (higher availability of vegetal and animal residues). Though in a minor scale, a higher level of viable yeasts was found in anthropogenically affected coastal sites located at San Carlos Bariloche City, coast in the Nahuel Huapi Lake. These sites had higher yeast values (97–141 CFU l^{-1}) than other ones far off the influence of the city (22–73 CFU l^{-1}). Even though further studies should be performed in order to confirm this observation, for oligotrophic lakes such as those from Andean Patagonia, it seems that the total number of yeasts in the water sample serve as a good indicator of anthropogenic impact, given that normally unpolluted waters have very low numbers of yeasts. All other Andean lakes surveyed showed yeast values typical for open waters of non-polluted lakes (Hagler and Ahearn 1987; Nagahama 2006). In a yet unpublished work, 20 water bodies were pooled into two groups depending on whether they were coastal (8) or pelagic sites (12) (Libkind et al. unpublished data). The former group showed higher yeast numbers (442 ± 558 CFU l^{-1}) than the latter group (71 ± 62 CFU l^{-1}). Other studies reported also that open waters of clear lakes yield generally yeast counts below 100 CFU l^{-1} (van Uden and Ahearn 1963; Meyers et al. 1970; Hagler and Ahearn 1987) and that this value increases with the proximity to the coast (Hagler and Ahearn 1987).

Basidiomycetous yeasts are the predominant group in these type of aquatic cold environments (Libkind et al. 2003, 2005b, 2009b, 2010; de García et al. 2007, 2012; Brandão et al. 2011a). This is similar to other cold habitats and an exhaustive overview of the biodiversity of cold-adapted yeasts (see Chap. 12 of this book). A few authors have suggested that this could be due to a higher nutritional versatility and a higher tolerance to extreme environmental conditions of the basidiomycetous compared to ascomycetous yeasts (Sampaio 2004; Frisvad 2008). As already stated above, UV radiation is a major environmental factor in clear lakes and even more pronounced in Patagonian lakes. Thus, we compared the UV susceptibility of a large representative set of ascomycetous and basidiomycetous yeasts using different culture media (Moliné 2004). Even though results were greatly influenced by the nutritional level of the media, in general ascomycetous yeasts were significantly less tolerant to any of the radiation treatments used in the experiment (PAR, PAR + UVA, and PAR + UVB). This study also suggested that the carotenoid-accumulating yeasts (often referred to as red yeasts) were generally more tolerant than nonpigmented species. Later, using naturally occurring albino strains of *Sporobolomyces ruberrimus* and *Cystofil. capitatum* (two species typically found in glacially originated water bodies in Patagonia), Moliné et al. (2009)

demonstrated that carotenoid pigments provide protection against UVB. Further experimental evidence of the utility of carotenoids as photoprotectants arose from studies performed with one of the prevailing yeasts in aquatic environments of glacial origin: the ubiquitous red yeast *Rh. mucilaginosa* (Moliné et al. 2010). In this work, the accumulation of carotenoids, in particular torularhodin, was demonstrated to contribute substantially to enhance UVB tolerance in yeasts. The protective mechanism was shown to be indirect, probably by quenching reactive oxygen species (ROS) as a result of the antioxidant properties of carotenoid pigments. The ability of certain yeast species to synthesize mycosporines, compounds able to directly protect cells from UV radiation (natural sunscreens), was discovered for the first time studying glacially formed aquatic environments (Libkind et al. 2004b, 2006). Mycosporines are water-soluble compounds composed of a cyclohexenone attached to an amino acid (or amino alcohol). Fungal mycosporines absorb light in the UV spectrum with a maximum at 310 nm wavelength (UVB). The primary role assigned to mycosporines was to act as photoprotective UV filters (Shick and Dunlap 2002; Torres et al. 2004), although other roles were also attributed including antioxidant activity, osmoregulation, resistance to thermal stress, and to serve as intracellular nitrogen storage (Oren and Gunde-Cimerman 2007). Most basidiomycetous yeasts isolated from Patagonian lakes were found to synthesize a UV-absorbing compound when grown under photosynthetically active radiation (Libkind et al. 2004b), and this occurred more frequently in species of the subphylum Pucciniomycotina (Libkind et al. 2011b) and Agaricomycotina (Libkind et al. 2005a, 2011c). The main mycosporine found in yeast so far is mycosporine-glutaminol-glucoside (MGG) (Sommaruga et al. 2004) for which the UVB photoprotective role was recently experimentally demonstrated (Moliné 2010; Moliné et al. 2011). Biochemical characterization of yeast MGG further revealed that possesses high photostability and antioxidant properties (Moliné et al. 2011) and thus showing its value as natural UV protectants and as biotechnological relevant compound (Colabella et al. 2014; Libkind et al. 2016).

The occurrence of MGG-positive yeast in glacially originated water bodies goes through a wide range, from 14% to near 90% of total cultivable yeast community (Libkind et al. 2006, 2009a; Brandão et al. 2011a). MGG synthesis was more frequent in yeasts that were not able to accumulate carotenoid pigments such as *Cr. albidus* (currently *Na. albida*), *Cryptococcus antarcticus* (*Naganishia antarctica*), *Cryptococcus saitoi* (*Naganishia globosa*), *Cryptococcus festucosus* (*Holtermanniella festucosa*), *Cryptococcus adeliensis* (*Naganishia adeliensis*), *Cryptococcus magnus* (*Filobasidium magnum*), *Gu. pullulans* (*Ta. pullulans*), and *A. pullulans* (Libkind et al. 2009a; Brandão et al. 2011a), and red yeasts capable to produce MGG were *Cyst. minutum* (*Rh. minuta*), *Cystobasidium laryngis* (*Rhodotorula laryngis*), and *Dioszegia* spp. Like for red yeasts, the proportion of mycosporine-positive species was higher for lakes with higher transparency or in pelagic zones (Brandão et al. 2011a). In glaciers meltwater and ice, yeasts, which are able to synthesize MGG, are less frequent and include species like *Dioszegia crocea* and *Dioszegia fristingensis* as the most important ones (de García et al. 2012). *Dioszegia* species were proven to be considerably higher resistant to UVB damage than most other aquatic yeasts (Moliné 2004; Libkind et al. 2009a), probably as a result of its particular carotenoid composition (plectaniaxanthin) (Madhour et al. 2005) and the high levels of MGG they accumulate (Libkind et al. 2005a, 2009a), both explaining their ability to thrive and prevail in extreme environments like those described in this paragraph.

A few studies reported yeasts biodiversity indices (e.g., Shannon-Weaver index; see also Yurkov and Pozo (2017)) of aquatic biotopes in Patagonia and showed that the yeast diversity in these environments (expressed as Shannon diversity index values) seems comparable or even higher than the ones of some in Patagonian forest soils or from tropical lakes (Brandão et al. 2011a, 2017; Mestre et al. 2011; de García et al. 2012). Yeast biodiversity in Patagonian aquatic environments comprises a large number of species. Among carotenoid-producing yeasts, the ubiquitous species *Rh. mucilaginosa* was the most frequent and commonly found species (Libkind et al. 2003, 2008). Species of the genera *Cystofilobasidium*, *Dioszegia*, *Rhodosporidiobolus*, *Rhodotorula*, *Sporidiobolus*, and *Sporobolomyces* were also isolated, though less frequently. Interestingly, ballistospore-producing yeasts (a characteristic typical for yeasts living on leaf surfaces) were more frequent in aquatic environments under relatively low human impact and in lakes surrounded with dense forest (Libkind et al. 2003). Nonpigmented yeasts were studied in a less extent, but species belonging to the genera *Candida* and *Torulaspora*, as well as to the former polyphyletic genus *Cryptococcus*, were found (Brizzio and van Broock 1998). Other genera like *Cutaneotrichosporon*, *Debaryomyces*, *Hanseniaspora*, *Leucosporidium*, and *Pichia* may also occur in waters (de García et al. 2007; Libkind et al. 2009a; Brandão et al. 2011a, 2017). The majority of these species have been already reported to be present in other aquatic environments; however, several novel species of the genera *Sporobolomyces* and *Cystofilobasidium* have been described (for recent review, see Buzzini et al. 2012; de García et al. 2014). Recently, *Cystobasidium psychroaquaticum* was described from psychrophilic aquatic habitats, including oligotrophic lakes and swamps, although a few strains were also found in terrestrial habitats (Yurkov et al. 2015). To be specially mentioned is the finding in coastal areas of glacially formed water bodies of a few isolates of biotechnologically relevant yeasts such as *Saccharomyces eubayanus* (brewing) and *Phaffia rhodozyma* (astaxanthin) (Libkind et al. 2007; Brandão et al. 2011a), although these yeasts relevant to the beer and aquaculture industries, respectively, are clearly related to forest substrates rather than water and thus represent an allochthonous species in aquatic environments (Libkind et al. 2011a, d).

1.6 Concluding Remarks

Most yeasts recovered from water samples are actually associated with plants and soils and arrive to the aquatic ecosystems through runoff phenomena, rather than being true aquatic yeasts. This is why quantitative analysis of aquatic yeast communities is complicated due to large variability of data and a large fraction of presumably transient microbiota. The proportion of allochthonous yeasts is influenced by the trophic state of the lake, the surrounding vegetation, water body size, and the number and type of effluents, among other factors. Despite these complications, various interesting niches are present in aquatic environments, especially in marine environments, that deserve special attention due to its fundamental relevance or to the lack of available knowledge. For example, yeasts associated to deep sea (i.e., hydrothermal vents) have been mostly overlooked, and the few studies performed revealed promising results (Gadanho and Sampaio 2005). Macroalgae-associated yeasts are also an interesting topic of research given that species like *M. australis* show a strong association with this substrate in Antarctica (Godinho et al. 2013). The potential ecoclade (Gadanho and Sampaio 2009) of the genus *Yamadazyma* is also interesting given these yeast species are mostly found in seawater (Burgaud et al. 2016), and there is evidence that they might be metabolically active, participating in the carbon cycle in these ecosystems.

The application of culture-independent strategies (metagenomics) will allow to have a more clear picture of yeast diversity in aquatic environments. The low number of yeast cells found in many aquatic habitats (10–100 CFU l^{-1}), mostly oligotrophic or ultra-oligotrophic, complicates the use of metagenomic approaches and the achievement of a comprehensive picture of the yeast community. However, these might still be useful for the detection of novel taxa and the relative quantification of the main species of yeasts.

Yeasts inhabiting aquatic environments can be very often subjected to multiple stress factors such as cold temperatures, UV radiation, ultra-oligotrophicity, salinity, etc. Species adapted to one or several of these factors have naturally developed mechanisms to reduce the negative effects of the harsh environmental conditions. Metabolic and physiological characterization of isolated yeasts represents a valuable tool for the identification of potentially autochthonous species and the detection of biotechnologically relevant traits such as the production of carotenoid pigments, UV sunscreens, extracellular cold-adapted enzymes, etc. In the present chapter, we have shown that aquatic environments can act as reservoir of many yeast species bearing physiological adaptations interesting from both fundamental and applied perspectives and that many additional yeast diversity studies are needed in order to increase our incipient knowledge on the factors affecting yeast distribution and composition in water habitats.

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