Pietro Buzzini · Marc-André Lachance
Andrey Yurkov *Editors*

Yeasts in Natural Ecosystems: Diversity

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Preface

Since the pioneer investigations of Pasteur in the 1860s, the study of the yeast world has seen important advances, especially in terms of their phenotypic, taxonomic, and genetic characterization and commercial exploitation. Research on the application of yeasts in traditional and advanced biotechnologies or their use as model organisms in science overshadows taxonomic studies and assessments of biodiversity. As a result, yeasts are often equated with the species *Saccharomyces cerevisiae* (baker's yeast), and the primary role of yeasts is thus reduced to the production of fermented foods and beverages. The truth is that the domesticated species represents only a tiny fragment of the vast diversity of the yeast world, especially those genera and species inhabiting natural ecosystems. Progress in the discovery of new species and the application of modern techniques for the rapid detection and identification of yeasts are only beginning to change the situation.

Yeasts are widely distributed throughout all biomes and most of the world's ecosystems, where they occur together in communities or guilds of species that share similar ecosystem functions, properties, and interactions. Yeasts participate in the degradation of complex organic substances but also synthesize, accumulate, and release organic molecules into the environment and act as primary and secondary decomposers in ecosystems. This volume reviews the diversity and distribution of yeasts across different habitats, including but not limited to nutrient-rich sources such as fruits, flower nectar, and decaying cactus tissues. Aquatic habitats are extremely diverse in size and properties and may well harbor the largest pool of yeast cells as suggested by recent studies. Soil has been among the first substrates sampled for yeasts. Although yeasts often occur in soils in low numbers, the global species diversity in this habitat is likely to be large in view of the wide range of soil properties and vegetation. Numerous species-rich communities associated with living plants undergo successional changes as senescence and decomposition proceed. As a result, the number of yeast cells in the phylloplane and decaying plant material is possibly as large as in water. Yeasts are also common inhabitants of extreme environments such as hypersaline habitats and cold polar and nonpolar regions. A large proportion of yeasts are associated with invertebrate animals and birds that may reflect the co-evolution and physiological adaptations of yeasts and their vectors.

The book presents a comprehensive overview of yeast diversity in natural ecosystems and constitutes the second volume of a whole monograph on *Yeasts in Natural Ecosystems*, of which the first volume (assembled by the same editors) is dedicated to yeast ecology. Several books and book series such as *The Life of Yeasts* (Phaff, Miller, Mrak), *The Yeasts* (Rose and Harrison), *Yeasts in Natural and Artificial Habitats* (Spencer and Spencer), and *Biodiversity and Ecophysiology of Yeasts* (Rosa and Péter) published in the last four decades covered major advances in yeast biodiversity. With this book, we attempt to give an update to topics covered in previous books, introduce new subjects, and provide novel views on selected aspects of yeast diversity in natural ecosystems. We hope that the book will introduce readers to the history, tools, and most recent developments in this field.

In view of rapid decline of many natural habitats due to anthropogenic activities (agriculture, deforestation, urbanization) and climate change, the need to study biodiversity is pressing. Rising temperatures threaten species inhabiting cold and aquatic environments, and species in terrestrial ecosystems are endangered by habitat fragmentation or loss. Soil erosion (i.e., topsoil degradation or loss) is an important concern to the global community since it affects both below- and aboveground communities, including soil-related habitats, as well as invertebrate and plant associates. Soil erosion leads to increased pollution and eutrophication of water bodies, thereby changing local communities and sometimes favoring unwanted or pathogenic species. The protection of genetic resources and their natural habitats is a priority of current conservation activities. However, unlike animals and plants, microscopic organisms and fungi are rarely, if ever, considered in conservation programs. The most common practice today is to conserve microbial species ex situ, namely, to preserve pure cultures or consortia in culture collections. Most of our knowledge of intrinsic properties (autoecology) of yeasts reported throughout this book is derived from laboratory experiments with pure cultures. Accordingly, the importance of culture collections for ecological studies is highlighted by presenting an overview of worldwide available yeast strains and their origins.

The chapters of this book review the knowledge accumulated during more than 60 years of yeast biodiversity research. Yeast species cited in these works were often identified by different techniques and criteria that may not be as accurate as the current sequence-based approaches. Many species names cited in the early literature are not current. Accordingly, all original taxonomic designations reported in the cited references were checked and, if necessary, updated following the latest taxonomic guidelines published in Kurtzman et al. (2011), Liu et al. (2015), Wang et al. (2015a, b), or more recent literature. A unified list of abbreviations was prepared to assist readers in following species names throughout the book.

The selection of topics and invitation of potential contributors were made by the three editors. Chapters were edited and managed by P. Buzzini and A. Yurkov. The editors thank all the authors for their excellent contributions. We also acknowledge researchers for granting access to public repositories of publications and sharing unpublished results.

P. Buzzini is grateful to Ann Vaughan-Martini and dedicates this book to the memory of his teacher (and friend) Alessandro Martini.

A. Yurkov is grateful to his teachers, soil microbiologists, and yeast ecologists Inna Babjeva and Ivan Chernov. A few sections of the book review their work and are dedicated to the memory of Ivan Chernov, who studied distribution of yeasts across many terrestrial biomes.

A. Yurkov acknowledges the research network of yeast scientists promoted by the van Uden International Advanced Course on Molecular Ecology, Taxonomy and Identification of Yeasts. Many of the authors of this book were participants and later lecturers in this course in various years.

M. A. Lachance is grateful to P. Buzzini and A. Yurkov for their invitation to join the editorial team in a mostly advisory capacity.

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Abbreviations

The following abbreviations are used for names of microbial genera (including synonyms) cited in the text.

Apiotrichum	*Ap.*
Aureobasidium	*A.*
Barnettozyma	*Barn.*
Bullera	*B.*
Candida	*C.*
Citeromyces	*Cit.*
Clavispora	*Cl.*
Colletotrichum	*Coll.*
Cryptococcus	*Cr.*
Cutaneotrichosporon	*Cut.*
Cyberlindnera	*Cyb.*
Cystobasidium	*Cyst.*
Cystofilobasidium	*Cystofil.*
Debaryomyces	*Deb.*
Dipodascus	*Dip.*
Diutina	*Diut.*
Escherichia	*E.*
Exophiala	*Ex.*
Filobasidium	*F.*
Galactomyces	*Gal.*
Ganoderma	*Gan.*
Goffeauzyma	*Goff.*
Guehomyces	*Gu.*
Hannaella	*Hann.*
Hanseniaspora	*H'spora*
Hortaea	*Ho.*

Kazachstania	*Kaz.*
Kluyveromyces	*K.*
Kodamaea	*Kod.*
Lachancea	*Lach.*
Leucosporidium	*Leuc.*
Lipomyces	*L.*
Magnusiomyces	*Magn.*
Metschnikowia	*M.*
Meyerozyma	*Mey.*
Middelhovenomyces	*Midd.*
Millerozyma	*Mill.*
Moesziomyces	*Moesz.*
Mrakia	*Mr.*
Myxozyma	*Myx.*
Naganishia	*Na.*
Ogataea	*O.*
Ophiocordyceps	*Oph.*
Papiliotrema	*Pa.*
Phaeotheca	*Phaeoth.*
Phaffia	*Ph.*
Phaffomyces	*Phaff.*
Phenoliferia	*Phen.*
Pichia	*P.*
Rhinocladiella	*Rhin.*
Rhodosporidiobolus	*Rhod.*
Rhodosporidium	*Rhodosp.*
Rhodotorula	*Rh.*
Rhynchogastrema	*Rhy.*
Saccharomyces	*S.*
Saitozyma	*Sa.*
Scheffersomyces	*Scheff.*
Schwanniomyces	*Schw.*
Solicoccozyma	*Sol.*
Spathaspora	*Spath.*
Spencermartinsiella	*Spenc.*
Sporidiobolus	*Sporid.*
Sporobolomyces	*Sp.*
Sporopachydermia	*Sporop.*
Starmera	*Starm.*
Sterigmatomyces	*Sterig.*
Sugiyamaella	*Sug.*
Suhomyces	*Su.*
Symbiotaphrina	*Symb.*
Tausonia	*Ta.*
Tortispora	*Tort.*
Torulaspora	*T'spora*

Trichosporon	*Tr.*
Trimmatostroma	*Trimm.*
Vanrija	*Va.*
Vishniacozyma	*Vishn.*
Wickerhamomyces	*W.*
Xylona	*Xyl.*
Yamadazyma	*Yam.*
Yarrowia	*Y.*
Zygosaccharomyces	*Zygosacch.*

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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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 paleokarstic (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).

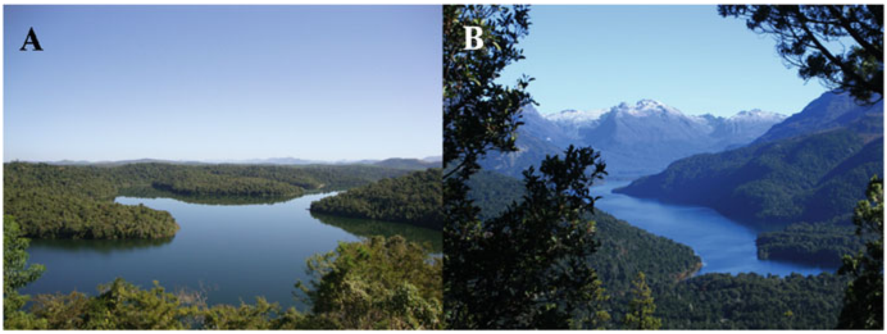

Fig. 1.1 Pictures of an Atlantic rain forest (**a**) and a glacially originated (**b**) lakes in Brazil (Dom Helvécio lake) and Argentina (Steffen lake), respectively. The latter photograph courtesy of Andrea Trochine

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, fresh-water marshes	Douglas Lake, Cheboygan County, Michigan, USA; Florida Everglades, USA; St. Lawrence, Quebec, Canada; Lowland Zahorie, Bratislava, Slova-kia; 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)
Pseudohyphoz-yma bogoriensis	*Rhodotorula bogoriensis*	Pond water	Iberian Pyrite Belt, Sao Domingos, Portugal	Gadanho et al. (2006)
Rhodosporidi-obolus 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, fresh-water 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.