Review

Yeasts in marine and estuarine environments

Kathiresan Kandasamy*, Nabeel M. Alikunhi and Manivannan Subramanian

Centre of Advanced Study in Marine Biology, Annamalai University, Parangipettai: 608502, Tamil Nadu, India.

Accepted 14 July, 2011

Yeasts and other fungi are prevalent in marine and estuarine ecosystems where they play an important role in the food web. Marine yeasts are unique in performing fermentations under high salt concentrations. The mechanism underlying the high salt tolerance involves the ability to accumulate high concentrations of sodium without becoming intoxicated, and the exclusion of excessive sodium from the cytoplasm. Overall, the yeasts play major roles in fermentation, enzyme technology, pollution control, micro sensors, and in some medicinal and medical applications.

Key words: Marine yeast, deep sea, estuarine, mangrove, association.

INTRODUCTION

Yeasts are unicellular micro-fungi, capable of self perpetuating their populations in terrestrial and aquatic environments (Kurtzman and Fell, 1998). A key characteristic is the ability to ferment sugars for ethanol production. They live as saprophytes on plant or animal materials, where they preferentially catabolize sugars but can also utilize polyols, alcohols, organic acids, and amino acids as carbon and sources of energy (Spencer and Spencer, 1997). To promote efficient decomposition of substrates, many yeasts produce filaments or pseudohyphae and also produce hydrolytic enzymes. Research on yeasts has played a major role in the development of a number of modern scientific disciplines and much work is being carried out in studying their physiology, metabolism, genetics, and molecular biology and developing new applications for industry and medicine (Barnett, and Barnett, 2011). Although, a large number of studies about terrestrial and aquatic yeasts are available there are only few reports about marine and estuarine yeasts, and hence is the need for this review.

DISTRIBUTION OF MARINE YEASTS

Most studies on yeasts in estuaries and near-shore seawater was performed in Europe and north America

(Fell et al., 1960; Roth et al., 1962; Fell and Van Uden, 1963; Van Uden and Castelo-Granco, 1963; Taysi and Van Uden, 1964; Norkrans, 1966; Ahearn et al., 1968; Van Uden and Fell, 1968; Hoppe, 1972; Ahearn, 1973; Barnett and Pankhurst, 1974; Buck, 1975).

Marine and estuarine habitats

Marine yeasts display a high salt tolerance and the ability to perform fermentation. In general, yeast cell numbers decrease with increasing salt concentration and total organic carbon in the estuarine environment (Urano et al., 2001). Due to sewage pollution and terrestrial run-off in this environment, some species of yeasts are more prevalent in estuaries, as compared to open seas (Lazarus and Koburger, 1974). Yeast and other fungi are prevalent in salt marsh and mangrove ecosystems where they play an important role in the detritus food web of the coastal environment (Mayers et al., 1975; Hyde, 2002).

Yeasts in estuarine waters vary widely both in number and species. The most frequently isolated genera of yeasts are *Debaryomyces, Candida, Rhodotorula, Cryptococcus* and *Kloeckera*. While studying the yeast flora of the Suwannee River estuary in Florida, Lazarus and Koburger (I974) obtained highest yeast densities in low saline areas, and highest species diversity in the sewage-polluted waters in the estuaries. However, no ascosporogenous yeasts have been isolated from the areas of low salinity (Lazarus and Koburger, I974). The researchers from University of Miami have isolated one

^{*}Corresponding author. E- mail: kathirsum@rediffmail.com. Tel: + 91 4144 238419 (Res.), + 91 4144 243223. Fax: + 91 4144 243555

ascomycetous yeast, *Lachancea meyersii* from the mangroves of the Bahamas (Fell et al., 2004).

Offshore and deep-sea environments

Only a few studies on yeasts from oceanic regions have been published in the last decades. This may be due to the high costs involved in offshore and oceanic sampling (Fell, 1976). Among the ascomycetous yeasts, the halotolerant species Debaryomyces hansenii is a typical ubiquitous species in oceanic regions as well as in other aquatic environments. Among the basidiomycetous veasts, some species of Cryptococcus, Rhodotorula, Sporobolomyces and their teleomorphs are widespread across various oceanic regions. Generally, basidiomycetous yeasts often account for the majority of the total yeast population in oligotrophic oceanic water. Candida species also occur, but at lower frequencies than in the inshore or polluted freshwater regions. Some of the Candida species are only evident in the oceanic regions around Antarctica along with psychrophilic species such as Leucosporidium spp. and Sympodiomyces parvus.

They are probably autochthonous marine species (Lachance and Starmer 1998). *Metschnikowia* species are known to be associated with seawater, freshwater, algae, invertebrates and fish. Phylogenetic relationship analysis shows that *M. australis*, *M. bicuspidata var. bicuspidata*, *M. bicuspidate var. chathamia*, *M. krissii* and *M. zobellii*, prevalent in marine environments are monophyletic. However, the less prevalent aquatic species such as *M. reukaufii* and *M. pulcherrima* are phylogenetically distant (Mendonça-Hagler et al., 1993)... The latter two are usually found to associate with natural substrates of terrestrial origin such as flowers, fruits and insects. The monophyly of the marine species suggests that their divergence has evolved in the course of association with marine environments.

The ubiquitous species in various marine habitats are regarded allochthonous, usually as as many basidiomycetous types of yeast are often found to associate with the phyllosphere of terrestrial plants and their marine prevalence is believed to be due to run-off from the phylloplane (Hagler and Ahearn, 1987; Lachance and Starmer, 1998). The yeasts of the ballistosporogenous genera - Sporobolomyces and Bullera - and their teleomorphs are typical inhabitants of phylloplane. The yeasts of the genera the Sporobolomyces and Bullera – are the most commonly encountered in the Pacific Ocean off Mexico (Hernandez-Saavedra et al., 1992). Interestingly, the frequencies of occurrence of the veasts increase with increasing distance from the coastline and increasing depth of coastal sea. The yeasts of ballistosporogenous genera are also present in benthic invertebrates collected from deep-sea floors in the Pacific Ocean off Japan

(Nagahama et al., 2001b). These facts indicate that ballistosporogenous yeasts are not effluents from terrestrial plant foliages but are indigenous to the sea.

Basidiomycetous types of yeasts are present in the seawater of the Atlantic Ocean off Faro in the south of Portugal (Gadanho et al., 2003). *Rhodosporidium babjevae* and *Rhodosporidium diobovatum* (the two possible species previously identified as *Rhodosporidium glutinis*, and *Sakaguchia dacryoides*) and *Pseudozyma aphidis* (ustilaginomycetous yeast) are the most frequently occurring yeasts among the basidiomycetous yeasts (Gadanho et al., 2003).

Yeast-like cells are reportedly abundant in deep-sea sediment around the Pacific Ocean. The most frequently surveyed site is around a cold seep at a depth of about 880 to 1,200 m near Hatsushima Island, Sagami Bay. Other less frequently surveyed sites include Suruga Bay (380 to 2,500 m), the Japan Trench (4,500 to 7,500 m) and Iheya Ridge (990 to 1,400 m). The sites surveyed only once include Kagoshima Bay, 220 to 260 m; the Mariana Trench, about 11,000 m; the Palau–Yap Trench, 3,700 to 6,500 m; and the Manus Basin, 1,600 to 1,900 m. The Iheya Ridge and the Manus Basin are biologically fertile spots owing to the hydrothermal vent ecosystem (Alongi 1992, Nagahama et al., 2001a, b, 2003a, b).

The species which occur most frequently in the above sites are Rhodosporidium sphaerocarpum, Williopsis saturnus and Candida pseudolambica, but their distribution is limited mostly to the sediments of Suruga Bay and Kagoshima Bay. D. hansenii occurs only in the sediments of Sagami Bay and Suruga Bay, although it is known to be the most common ascomycete in marine Ahearn 1987). Almost all waters (Hagler and ascomvcetous veasts have been isolated from sediments. with the exception of Kloeckera nonfermentans, which is common to both sediments and benthic invertebrates, specifically in Sagami and Suruga Bay. In contrast, Rhodosporidium diobovatum and Rhodotorula mucilaginosa are widely prevalent in the various locations and sources.

The frequency of occurrence of each corresponding phylogenetic taxon is obviously different according to the source and geographical origin. The ascomycetous yeasts constitute the majority of the total yeast population in the sediments of Sagami Bay, Suruga Bay and Kagoshima Bay, and these sites are relatively inshore (5 to 20 km) near urban and industrial areas and where the sea floors are affected by human activity. Species in the *Erythrobasidium* clade have been isolated mostly from the benthic invertebrates, and the initial isolates from the sediments of the Manus Basin are considered to give clues about the hydrothermal ecosystems. Many of these species belong to the *Occultifur* lineage although some are novel species yet to be classified (Nagahama et al., 2001a, 2003a).

The association with animals is probably favourable for yeasts, owing to the abundance of nutrients (Hagler

and Ahearn, 1987). However, the reasons why the number of species associated with animals is low is yet to be known. Hymenomycetous species, mostly assigned to the genus Cryptococcus, are localized in the Japan Trench, Sagami Bay and Suruga Bay, and the genus does not appear farther southwest. Species of Sporidiobolales are present at all of the sites.

Marine yeasts are believed to have physiological adaptations but are not scientifically validated. In general, yeasts from both terrestrial and marine origins are moderately pressure-tolerant. However, the response of yeasts to elevated hydrostatic pressure has not been properly studied (ZoBell and Johnson, 1949; Yamasato et al., 1974).

The carotenogenic basidiomycetous yeasts such as *Rhodotorula* and *Rhodosporidium* are psychro-tolerant and pressure-tolerant (Davenport, 1980). *Rhodotorula* species grown at 20 MPa (equivalent to 2,000 m depth) are not significantly different as compared to those grown at 0.1 MPa; however, growth is reduced to 20 to 30% when the species is grown at 40 MPa (Lorenz and Molitoris, 1997).

The yeasts isolated from seafloors deeper than 4,000 m do not grow well under hydrostatic pressures corresponding to the sources at which they have been collected (2 to 4° C, > 40 MPa).

This may be due to the specifications of compressed incubation system, which allows sharp pressure changes and insufficient oxygen supply. Psychrophilic strains have not been found so far in the deep sea, but many isolates are psychrotolerant growing well at < 4°C (Lorenz and Molitoris, 1997).

Hypersaline habitats

Yeasts occur in hypersaline habitats world-wide (Butinar et al., 2005) and include *Rhodosporidium sphaerocarpus*, *R. babjevae*, *Rhodotorula larynges*, *Trichosporon mucoides*, *Candida parapsilosis C. glabrata*, *Pichia guilliermondii*, *Debaryomyces hansenii*, *Trimmatostroma* and *Yarrowia lipolytica*. Interestingly ascomycetous yeast, *Metschnikowia bicuspidate* is known to be a parasite of the brine shrimp and it occurs as a free-living form from the Great Salt Lake brine.

Antarctic habitats

The first *Candida*-like *Leucosporidium* species was isolated in the I960's from Antarctic soil and seawater (Di Menna, I960; Sinclair and Stokes, I965; Fell et al., I969; Watson and Arthur, I976; Ray et al., I992). *Leucosporidium antarcticum* is endemic to Antarctica. This yeast species can weakly utilize both sucrose and maltose, and is extremely sensitive to temperatures above 20°C.

Marine plant-associated yeasts

Yeasts are epiphytic on seaweeds, abundant on Chlorophytes and Rhodophytes, but of low abundance on Phaeophytes due to the release of growth-inhibitory phenolics from the brown seaweeds (Raja Seshadri and Sieburth, 1971).

The yeasts also associate with phytoplankton (Kriss and Novozhilova, 1954) and decaying seaweeds (Bunt, 1955; Suchiro and Tomiyasu, 1962; Van Uden and Castelo Granco, 1963). However, no specific association has been established for yeasts with marine algae and seagrasses (Roth et al., 1962).

Yeast communities of polluted estuary and mangrove ecosystems in subtropical marine environments are extremely diverse. Yeasts are prevalent in salt marshes or mangrove ecosystems where the yeasts play an important role in the detrital food web and they are food source for some marine invertebrates including zooplankton (Meyers et al., 1975). *L. meyersii* sp. nov. (type strain NRRL Y 27269, CBS 8951, ML 3925) is described from 18 strains collected from mangrove habitats in the northern Bahamas Islands.

This species is homothallic, producing spherical ascospores in asci that become deliquescent, and is delineated from other ascomycetous yeasts by sequence analysis of the D1/D2 domains of the large subunit ribosomal DNA.

The species can be distinguished from other members of the genus *Lachancea* by lack of growth on galactose and by growth on maltose.

This new species is named in honor of Professor Samuel P. Meyers in recognition of his pioneering research with marine fungi (Fell et al., 2004). Candida hansenii, intermedia, D. Issatchenkia occidentalis (Candida sorbosa), Pichia guillier- mondii and Pichia membranifaciens (Candida valida) are the ubiquitous ascomycetous species at the Sepetiba Bay, Japan (De Araujo et al., 1995; Soares et al., 1997). The identity of the yeast community in the subtropical mangrove ecosystem is unclear, owing phenotypic to characterization yielding ambiguous taxonomic results.

Yeast species, *Kluyveromyces aestuarii* is associated with detritus-feeding invertebrates and sediments within mangrove areas (De Araujo et al., 1995; Soares et al., 1997). The aquatic strains of *Kluyveromyces lactis* are isolated from rhizosphere sediments of the marine marsh lands (Naumova et al., 2004; *hansenii* Meyer et al., 1971; De Araujo et al., 1995; Soares et al., 1997).

Plant-associated yeasts on bromeliads in mangrove areas are distinct from those typical of polluted areas, and comprise a larger number of species and isolates with basidiomycetous affinities (Hagler et al., 1993). Two yeast species *Kluyveromyces lactis* and *Pichia spartinae* are prevalent in the outer- or intra-culm (fistulous stalk) cells and tissues of the saltmarsh grass, *Spartina alterniflora* (Buchan et al., 2002).

Human-associated marine yeasts

Yeasts can cause infection in humans. *Candida albicans* causes candidasis, resulting in vaginal infections and also diaper rash and thrush of the mouth and throat. *Debaryomyces hansenii* is generally considered a non-pathogenic yeast species; however, it is associated with one case of bone infection and is identified in several clinical isolates associated with bone infection, fever and chronic bronchitis (Wong et al., 1982; Nishikawa et al., 1996).

Human pathogenic yeasts can be found in coastal areas. For example, C. albicans is an obligate saprophyte of warm-blooded animals, occurring rarely in host-free environments and surviving in nature for only short periods outside of animals. C. albicans with sparse filamentation and weak fermentation has been reported to occur at the surface micro-layer of the North Sea, but not in subsurface waters. It is found sporadically in marine and fresh waters and is common in faeces and raw sewage. Human pathogenic yeasts enter and aggregate in the bivalve mollusks due to the filter feeding mechanism of these animals (Buck et al., 1977). C. parapsilosis, Candida tropicalis and Torulopsis glabrata are the human-associated yeasts most frequently isolated from bivalve shellfish (oysters and mussels) collected from estuarine areas (Dabrowa et al., 1964; Kobayashi et al., 1953; Buck et al., 1977). These pathogenic yeast are selectively inhibited in sewage filtrates by water soluble substances produced by bacterial strains of Bacillus (Coleman et al., 1975).

Water temperature and pollution are important factors that influence the distribution of human-associated yeasts. Temperatures lower than that of the human host may dictate the abundance of intestinal yeasts. Incubation of cultures at 37°C eliminated many saprophytic types of yeast but encouraged humanassociated yeast. The samples closest to sources of domestic pollution have the greatest abundance and survival of C. albicans in seawater (Dzawachiszwili et al., 1964; Madri et al., 1966; Madri, 1968; Ahearn, 1973). The C. albicans population is greatest during colder months in the heavily polluted waters. The pumping rates of bivalves are minimal at low water temperatures. This does not kill yeasts, but the slow rate of pumping may account for the survival of human-associated yeast and other yeasts in bivalves in the winter (Tripp, 1960; Galtsoff, 1964; Buck et al., 1977). In oysters, internal phagocytosis and migration are the main processes by which yeast cells (Saccharomyces cerevisiae) are removed.

When raw shellfish containing pathogenic yeasts are consumed, human health can be affected. However, the infective dosages of the yeasts are still not known. Individuals who repeatedly handle contaminated shellfish with cut or damaged hands are most at risk from yeast infections. Potentially pathogenic microorganisms are therefore, a serious consideration in the assessment of water and shellfish quality of near-shore recreational areas (Buck et al., 1977).

CULTURAL CHARACTERISTICS OF MARINE YEASTS

In the marine environment, bacteria are usually more numerous than yeasts. For the selective isolation of veasts from the environment, bacterial inhibitors such as chloramphenicol, chlorotetracycline and streptomycin are generally used in the culture medium either alone or in combination. Antibiotics are used at concentrations up to 50 times greater than that required for bacterial inhibition (Ahearn et al., 1968; Richards and Elliott, 1966). The indiscriminate use of antibiotics to suppress bacteria may inhibit some yeast. The low pH of many media may inhibit acid-sensitive yeasts growing in alkaline seawater. Thus, the media commonly used for the detection and enumeration of marine yeasts have their limitations (Meyer et al., 1967; Ahearn et al., 1968; Van Uden and Fell, 1968). Employing temperature - gradient gel electrophoresis. Gadanho and Sampaio (2004) have studied yeast diversity in the estuary of the Tagus River, Portugal. This molecular detection method is carried out directly from water samples in parallel with cultivation of the yeasts using enrichment media. The number of species detected after enrichment is higher than the number of taxa found using the direct detection method. The most common species detected in marine environments is D. hansenii, an ascomycetous yeast (Hagler and Ahearn, 1987), probably because of its broad salinity tolerance and ability to utilize a wide range of carbon sources (Yadav and Loper, 1999).

PHYSIOLOGICAL ADAPTATIONS OF MARINE YEASTS

Yeasts from seawater are of two types; obligate and facultative. The obligate marine yeasts originate from the marine and inhabit the seawater throughout their lives. The facultative marine yeasts originate from other environments such as rivers, soils, woods, or the surface of animals and are transported to the marine environment. The obligate yeasts have inherently high NaCl tolerance as well as fermentative activities under high salt conditions (Urano et al., 1998). The facultative marine yeasts have weak salt tolerance acquiring high NaCl tolerance gradually over long periods. Repeated cultivation of weak salt tolerant yeasts in NaCl-rich media transforms them to high salt tolerant organisms (Urano et al., 2001).

Microorganisms differ in their tolerance to osmotic stress, but in general yeasts and fungi are more tolerant than bacteria (Brown, 1978). Among yeasts, strains of *D. hansenii* and *S. rouxii* are highly osmotolerant and Table 1. Potential of m ar i n e yeasts for industrial processes and biotechnology.

High value products/Application	Yeast	Source
Pollution degradation or algae blooms controlling yeasts	Candida, Rhodotorula, Torulopsis, Hanseniaspora, Hagle Debaryomyces, and	er and Hagler, 1981
	Trichosporon	
Gycerol kinase	D. hansenii	Nilsson and Adler, 1990
Biotransformation of aromatic polycyclic hydrocarbons	Trichosporon penicillatum	Ronald and Shiaris ,1993
Membranes - surfactants for pharmaceuticals	C. bombicola	Shepherd et al., 1995; Guilmano et al., 2002
Convert prawn shell waste into microbial biomass protein	Candida species	Rhishipal and Rosamma Philip, I998
Organic acids and amino acids-regulating the acidity of the remented product, and also provides lipolytic and proteolytic activity contributing to flavour development	Debaryomyces hansenii	Urano et al., 1998
Superoxide dismutases-anti-inflammatory activities	D. hanseii	Gonzalez and Ochoa, 1999
Superoxide dismutase	Saccharomyces cerevisiae	Hernandez Saavedra and Ochoa
Microbialsensor-rapid measurements of bio-degradable substances.	Arxula adeninivorans	Tag et al., 2000
Glucoamylase gene Glycerol, compatible solutes	C. magnolia	Wartmann and Kunze, 200 Rothschild and Mancinelli, 2001; Sahoo and Agarwal, 2001
Lipids- liposomes for drug delivery and cosmetic packaging		Cavicchioli and Torsten, 2000
Waste transformation and degradation	C. utilis	Cavicchioli and Torsten, 2000; Zheng et al., 2005
Hydrocarbon degradation Prolyl aminopeptidase (PAP)- role in meat fermentation	Yarrowia lipolytica D. hansenii	Oswal et al., 2002 Bolumar et al., 2003
Carotene-food colouring	Rhodotorula mucilaginosa, Arxula adeninivorans	Libkind et al., 2004
/iable cells- bioremediation of TNT polluted marine	Y. lipolytica	Jain et al., 2004
glucosidases- facilitating assimilation of β -ructofuranosides and α glucopyranosides	Leucosporidium antaracticum	Turkiewics et al., 2005
mmunostimulant	Fenneropenaeus indicus	Sajeevan et al., 2006
Microorganism-useful to improve the final quality of ermented sausages	D. hansenii	Bolumar and Sanz, 2006
Protease	Aureobasidium pullulans	Chi et al., 2007
nulinase	Cryptococcus aureus	Sheng et al., 2007
Reducing post harvest decay of tomatoes caused by Alternaria alternate	Rhodosporidium paludigenum	Wang et al., 2008

Table 1. Continued.

Silver nanoparticles	Candida albicans, C. tropicals, Debaryomyces hansenii, Geotrichum sp., Pichia capsulata, Pichia fermentans, Manivannan et al., 2010 Pichia salicaria, Rhodotorula minuta, Cryptococcus dimennae and Yarrowia lipolylica
Bio-ethanol production	Candida albicans, C. tropicals, Debaryomyces hansenii, Geotrichum sp., Pichia capsulata, Pichia fermentans, Pichia salicaria, Rhodotorula minuta, Cryptococcus dimennae and Yarrowia lipolylica

capable of growth in media containing up to about 4 M NaCl (Onishi, 1963; Norkrans, 1966). S. cerevisiae is limited by NaCl concentrations above 1.7 M (Onishi, 1963). When D. hansenii is subjected to increased NaCl stress, intracellular K⁺ decreases and intracellular Na⁺ increases (Norkrans, 1968). However, the total salt level in the cells is not sufficient to balance the water potential of the medium; this is why additional osmotically active solutes such as polyols accumulate intracellularly when exposed to osmotic stress (Brown and Simpson, 1972; Gustafsson and Norkrans, 1976; Brown, 1978; Adler et al., 1985). Tolerance for a sudden osmotic dehydration is also better in cells having an increased amount of intracellular polyols (Adler and Gustafsson, 1980). Two polyols are produced and accumulated in D. hansenii; glycerol, which is the major internal solute in exponentially growing cells, and arabinitol, which predominates in stationary-phase cells (Adler and Gustafsson, 1980). A positive correlation exists between internal glycerol level and salinity of the surrounding medium (Adler et al., 1985; Andre et al., 1988). Glycerol is the major osmoticum, as its concentration may reach molar levels under strongly saline conditions (Gustafsson and Norkrans, 1976). The enzymes that control glycerol catabolism are glycerol kinase and mitochondrial glycerol 3-phosphate dehydrogenase (Gancedo et al., 1968; Sprague and Cronan, 1977; Adler et al., 1985). In yeasts lacking glycerol kinase, the presence of an NAD-

dependent glycerol dehydrogenase and a dihydroxyacetone kinase is an alternative pathway (Babel and Hofmann, 1982; May et al., 1982).

Among several marine yeasts, *D. hansenii* accumulates high amounts of Na^+ , and in this yeast, Na^+ is not more

toxic than K^+ (Ross and Morris, 1962; Norkrans, I966; Prista, 1997). Besides Na⁺, glycerol plays a role as a compatible solute for a glycerol/Na⁺ symporter with homeosmotic function in this yeast species (Lages et al., I999; Lucas et al., I990). Increased transport activities might be needed in addition to the maintenance of a high osmotic pressure within the cell. In addition, existence of sodium efflux process may also be involved in saline tolerance. The mechanism for extrusion of Na⁺ across the plasma membrane might be carried out via the function of Na⁺ -ATPase or Na⁺/H⁺ antiporters (Ramos, I999).

POTENTIAL OF MARINE YEASTS

Yeasts are used in many industrial processes, such as the production of alcoholic beverages, food, fodder yeasts and for the synthesis of various metabolic products. The last category includes enzymes, vitamins, polysaccharides, carotenoids, polyhydric alcohols, lipids, glycolipids, citric acid, ethanol and compounds synthesized by the introduction of recombinant DNA into yeasts. Some of these products are produced commercially, while others are potentially valuable in biotechnology. Some uses of marine yeasts in the food, beverage and fermentation industries are shown in Table 1.

CONCLUSION

Even after five decades of research, the potential of marine yeasts to contribute to biotechnological

applications has not been fully realized or exploited. By virtue of their occurrence in extreme environmental conditions, the marine yeasts have superior qualities over their terrestrial counterparts with regards to salt tolerance, enzyme production, biosynthetic potential, pollution abatement, and ethanol and other fermentative processes, and hence deserve further investigation. Although much work has been carried out on molecular aspects of yeasts, such efforts for marine yeasts are lacking. There are no proper culture collections for marine yeasts. Only a few marine habitats have been investigated for yeast species and many additional species await discovery. Based on the fact that yeasts of terrestrial origin are widely used in traditional and modern biotechnology, the exploration for new species of marine origin should lead to additional novel technologies.

ACKNOWLEDGEMENTS

The authors are thankful to the authorities of Annamalai University for providing facilities and the Ministry of Environment and Forests, Govt. of India, New Delhi for financial support.

REFERENCES

- Adler L, Blomberg A, Nilsson A (1985). Glycerol metabolism and osmoregulation in the salt-tolerant yeast *Debaryomyces hansenii*. J. Bacteriol. 162:300-306.
- Adler L, Gustafsson L (1980). Polyhydric alcohol production and intracellular amino acid pool in relation to halotolerance of the yeast *Debaryomyces hansenii*. Arch. Microbiol. 124:123-130.
- Ahearn DG (1973). Effects of environmental stress on aquatic yeast populations, pp:. 433-439. In L. H. Stevenson and R. R. Colwell (ed.). Estuarine Microbiology Ecology.
- Ahearn DG (1973). Effects of environmental stress on aquatic yeast populations, pp:. 433-439. In L. H. Stevenson and R. R. Colwell (ed.). Estuarine Microbial Ecology..
- Ahearn DG, Roth Jr FJ, Meyers SP (1968). Ecology and characterization of yeasts from aquatic regions of South Florida. Mar. Biol. 1: 291-308.
- Alongi DM (1992). Bathymetric patterns of deep-sea benthic communities from bathyal to abyssal depths in the western South Pacific (Solomon and Coral Seas). Deep Sea Res. 39: 549-565.
- Andre L, Nilsson A, Adler L (1988). The role of glycerol in osmotolerance of the yeast *Debaryomyces hansenii*. J. Gen. Microbiol. 134: 669-677.
- Babel W, Hofmann KH (1982). The relation between the assimilation of methanol and glycerol in yeasts. Arch. Microbiol. 132:179-184.
- Barnett JA, Barnett L (2011). Yeast Research: a Historical Overview. American Society for Microbiology Press, 392.
- Barnett JA, Pankhurst RJ (1974). A new key to the yeasts. American Elsevier, New York.
- Bolumar T, Sanz Y (2006). Sensory improvement of dry fermented sausage by the addition of cell free extracts from *Dabaryomyces hansenii* and *Lactobacillus sakei*. Meat Sci. 72:457-466.
- Bolumar T, Sanz Y, Aristoy MC, Toldra F (2003). Purification and Characterization of a prolyl aminopeptidase from *Debaryomyces hansenii*. Appl. Environ. Microbiol. 69:227-232.
- Brown AD, Simpson JR (1972). Water relations of sugar-tolerant yeasts: the role of intracellular polyols. J. Gen. Microbiol. 72:589-591.
- Brown AD (1978). Compatible solutes and extreme water stress in eukaryotic microorganisms. Microb. Physiol. 17:181-242.

- Buchan A, Newell SY, Moreta JI, Moran MA (2002). Analysis of internal transcribed spacer (ITS) regions of rRNA genes in fungal communities in a southeastern U.S. salt marsh. Microb. Ecol. 43:329-340.
- Buck JD (1975). Distribution of aquatic yeasts-effect of incubation temperature and chloramphenicol concentration on isolation. Mycopathologia 56:73-79.
- Buck JD, Bubucis PM, Combs TJ (1977). Occurrence of Human-Associated Yeasts in Bivalve Shellfish from Long Island Sound. Appl. Environ. Microbiol. 33:370-378.
- Bunt JS (1955). The importance of bacteria and other microorganisms in the sea water at MacQuarie Island. Aust. J. Mar. Fresh. Res. 6:60-65.
- Burke RM, Jennings DH (1990). Effect of growth characteristics of the marine yeast *Debaryomyces hansenii* in batch and continuous culture under carbon and potassium limitation. Mycol. Res. 94:378-388.
- Butinar L, Santos S, Spencer-Martins I, Oren A, Gunde N (2005). Yeast diversity in hyper saline habitats FEMS Microbiol. Lett. 244:229-234.
- Cavicchioli R, Torsten T (2000). Extremophiles. In: Lederberg J (ed) Encyclopedia of microbiology, vol 2, 2nd edn. Academic, San Diego, pp. 317-337.
- Chand GP, Eckert JW (1996). Studies on transformation of *Candida* cephila and *Debaryomyces hansenii* with plasmids. Phytopathology 86:S34.
- Chi Z, Ma C, Wang P, Li HF (2007). Optimization of medium and cultivation conditions for alkaline protease production by the marine yeast *Aureobasidium pullulans*. Bioresour. Technol. 98:534-538.
- Coleman A, Cook WL, Ahearn DG (1975). Abstr. Annu. Meet. Am. Soc. Microbiol. N20:187.
- Dabrowa N, Landau JW, Newcomer VD, Plunkett OA (1964). A survey of tide-washed areas of Southern California for fungi potentially pathogenic to man. Mycopathol. Mycol. Appl. 24:137-150.
- Davenport RR (1980). Cold-tolerant yeasts and yeast-like organisms. In: Davenport RR (ed) Biology and activity of yeasts. Academic, London, UK, pp. 215-230.
- De Araujo FV, Soares CA, Hagler AN, Mendonça-Hagler LC (1995). Ascomycetous yeast communities of marine invertebrates in a southeast Brazilian mangrove ecosystem. Antonie van Leeuwenhoek 68:91-99.
- Di Menna, ME (1960). Yeast from Antarctica. J. Gen. Microbiol. 7:295-300.
- Dzawachiszwili N, Landau JW, Newcomer VD, Plunkett OA (1964). The effect of sea water and sodium chloride on the growth of fungi pathogenic to man. J. Invest. Dermatol. 43:103-109.
- Fedorak PM, Semple KM, Westlake DWS (1984). Oil degrading capabilities of yeasts and fungi isolated from coastal marine environment. Can. J. Microbiol. 30:565-571.
- Fell JW, Kurtzman CP (1990). Nucleotide sequence analysis of the large subunit rRNA for identification of marine occurring yeasts. Curr. Microbiol. 21:295-300.
- Fell JW, Van Uden N (1963). Yeasts in marine environments, pp 329-340. In C. H. Oppenheimer [ed.], Symposium on marine microbiology. Charles C Thomas, Publisher, Springfield, III.
- Fell JW (1976). Yeasts in oceanic regions. In: Jones EBG (ed) Recent advances in aquatic mycology. Elec, London, pp. 93-124.
- Fell JW, Statzell-Tallman A, Luit MJ, Kurtzman CP (1992). Partial rRNA sequences in marine yeasts-a model for identification of marine eukaryotes. Mol. Mar. Biol. 1:175-186.
- Fell JW, Tallman AS, Kurtzman CP (2004). *Lachencea meyersii* sp. nov., an ascosporogenous yeast from mangrove region in the Bahama Islands. Stud. Mycol. 50:359-363.
- Fell JW, Ahearn DG, Meyers SP, Roth Jr FJ (1960). Isolation of yeasts from Biscayne Bay, Florida and adjacent benthic areas. Limnol. Oceanogr. 4:366-371.
- Fell JW, Statzell JW, Hunter IL, Phaff HJ (1969). *Leucosporidium gen. nov., the* heterobasidiomycetous stage of several yeasts of the genus *Candida.* Antonie Van Leeuwenhoek. 35:433-462.
- Fukumaki T, Inoue A, Moriya K (1994). Isolation of marine yeast that degrades hydrocarbon in the presence of organic solvent. Biosci. Biotechnol. Biochem. 58:1784-1788.
- Gadanho M, Sampaio JP (2004). Application of temperature gradient gel electrophoresis to the study of yeast diversity in the estuary of

the Tagus river, Portugal. FEMS Yeast Res. 5:253-261.

- Gadanho M, Almeida JM,Sampaio JP (2003). Assessment of yeast diversity in a marine environment in the south of Portugal by microsatellite-primed PCR. Antonie van Leeuwenhoek 84:217-227.
- Gadd, GM, Edwards SW (1986). Heavy-metal-induced flavin production by *Debaryomyces hansenii* and possible connections with ion metabolism. Trans. Br. Mycol. Soc. 87:533-542.
- Galtsoff PS (1964). The American oyster, *Crassostrea virginica* Gmelin. Fish. Bull. 64:1-480.
- Gancedo C, Gancedo JM, Sols A (1968). Glycerol metabolism in yeasts. Pathways of utilization and production. Eur. J. Biochem. 5:165-172.
- González AG, Ochoa JL (1999). Anti-Inflammatory activity of Debaryomyces hansenii Cu, Zn-SOD. Arch. Med. Res. 1:69-73.
- Govind NS, McNally KL, Trench RK (1992). Isolation and sequence analysis of the small subunit ribosomal RNA gene from the euryhaline yeast *Debaryomyces hansenii*. Curr. Gen. 22:191-195.
- Guilmanov V, Ballistreri A, Impallomeni G,Gross RA (2002). Oxygen transfer rate and sophorose lipid production by *Candida bombicola*. Biotechnol. Bioeng. 77:489-494.
- Gustafsson, L, Norkrans B (1976). On the mechanism of salt tolerance. Production of glycerol and heat during growth of *Debaryomyces hansenii*. Arch. Microbiol. 110:177-183.
- Hagler AN, Ahearn DG (1987). Ecology of aquatic yeasts. In: Rose A.H, Harrison J.S (ed) The yeasts, vol 2, Yeasts and the environment. Academic, London, pp. 181-205.
- Hagler AN, Hagler LCM (1981). Yeasts from marine and estuarine waters with different levels of pollution in the state of Rio de Janeiro, Brazil. Appl. Environ. Microbiol. 41:173-178.
- Hagler AN, Rosa Morais PB, Hagler LCM, Franco GMO, Araujo FV, Soares CAG (1993). Yeasts and coliform bacteria of water accumulated in bromeliads of mangrove and sand dune ecosystems of southeast Brazil. Can. J. Microbiol. 39:973-977.
- Hernandez-Saavedra, NY, Hernandez-Saavedr D, Ochoa JL (1992). Distribution of *Sporobolomyces* (Kluyver et van Niel) Genus in the Western Coast of Baja California Sur, Mexico. Syst. Appl. Microbiol. 15:319-322.
- Hernandez-Saavedra, NY, Ochoa JL, Vazquez- Dulhalt R (1994). Effect of salinity in the growth of the marine yeast *Rhodotorula rubra*. Microbiology 80:99-106.
- Hernendez Savedra, NY, Ochoa JL (1999). Copper zinc superoxide dismutase from the marine yeast *Debaryomyces hansenii*. Yeast 15:657-668.
- Hirayama K (1992). Part VI. Physiology in growth. In: Jap. Soc.Fisheries Sci. (ed.). The rotifer *Brauchionus plicatilis*-biology and mass culture, pp. 52-68. (In Japanese).
- Hyde KD (2002). Fungi in marine environments. Fungal Diversity Press, Hong Kong. Kimura, T., K. Hayashi and I. Sugahara, 1985. Studies on C1- compounds-utilizing yeasts from coastal water and sediments. Bull. Fac. Fish. Mie Univ. 12:61-67.
- Jain MR, Zinjarde SS, Deobagkar DD, Deobagkar DN (2004). 2,4,6-Trinitrotoluene transformation by a tropical marine yeast, Yarrowia lipolytica NCIM 3589. Mar. Poll. Bull. 49:783-788.
- Kathiresan K, Saravanakumar K, Senthilraja P (2011). Bio-ethanol production by marine yeasts isolated from coastal mangrove sediment. Int. Multidiscip. Res. J. 1:19-24.
- Kobayashi Y, Tsubaki K, Soneda M (1953). Marine yeasts isolated from little-neck clam. Bull. Nat. Sci. Mus. 33:47-52.
- Kriss AE, Novozhilova MI (1954). Are yeast organisms inhabitants of seas and oceans? Mikrobiologia. 23:669-683.
- Lachance MA, Starmer WT (1998). Ecology and Yeasts. In: Kurtzman CP, Fell JW (eds) The yeasts a taxonomic study, 4th edn. Elsevier, Amsterdam, pp. 21-30.
- Lages F, Silva-Grac M, Lucas C (1999). Active glycerol uptake is a mechanism underlying halotolerance in yeasts: a study of 42 species. Microbiol. 145:2577-2585.
- Lazarus CR, Koburger JA (1974). Identification of yeasts from the Suwannee River Florida estuary. Appl. Environ. Microbiol. 27:1108-1111.
- Li Z, Obita H, Kamishima S, Fukuda S, Kakita H, Kobayashi Y, Higashihara T (1995). Improvement of immobilization conditions for biodegradation of floating oil by a bio-system, co-immobilizing marine

oil-degrading yeast *Candida* sp. and nutrients. Seibutsu Kogaku Kaishi, 73:295-299 (in Japanese).

- Libkind D, Brizzio S, van Broock M (2004). *Rhodotorula mucilaginosa*, a carotenoid producing yeast strain from a Patagonian high-altitude lake. Folia Microbiol. 49:19-25.
- Lorenz R, Molitoris HP (1997). Cultivation of fungi under simulated deep sea conditions. Mycol. Res. 101:1355-1365.
- Lucas C, Da-Costa M, Van-Uden N (1990). Osmoregulatory active sodium-glycerol co-transport in the halotolerant yeast *Debaryomyces* hansenii. Yeast 6:187-191.
- Madri P (1968). Factors influencing growth and morphology of *Candida albicans* in a marine environment. Bot. Mar. 11:31-35.
- Madri P, Claus G, Moss EE (1966). Infectivity of pathogenic fungi in a simulated marine environment. Rev. Biol. 5:371-381.
- Manivannan S, Alikunhi NM, Kandasamy K (2010). *In vitro* Synthesis of Silver Nanoparticles by Marine Yeasts from Coastal Mangrove Sediment. Adv. Sci. Lett. 3:1-6.
- Marija V, Goran M, Ivanka P (1993). Capability for degradation of crude oil hydrocarbons by sea water yeasts and bacteria from Kvarner Bay. Period. Biol. 94:169-177.
- May JW, Marshall JH,Sloan J (1982). Glycerol utilization by *Schizosaccharomyces pombe*: phosphorylation of dihydroxyacetone by a specific kinase as the second step. J. Gen. Microbiol. 128:1763-1766.
- Mayers SP, Ahearn DG, Alexander S, Cook W (1975). *Pichia spartinae*, a dominant yeast of the *Spartina* salt marsh. Dev. Ind. Microbiol. 16:262-267.
- Mendonça-Hagler LC, Hagler AN, Kurtzman CP (1993). Phylogeny of Metschnikowia species estimated from partial rRNA sequences. Int. J. Syst. Bacteriol. 43:368-373.
- Meyers SP, Ahearn DG, Miles P (1971). Characterization of yeasts in Baratara Bay. La St. Univ. Coastal Stud. Bull. 6:7-15.
- Meyers SP, Ahearn DG, Gunkel W,Roth Jr, FJ (1967). Yeasts from the North Sea. Mar. Biol. 1:118-123.
- Morita K, Usami R, Horikoshi K (1994). Marine killer yeasts isolated from deep sea and their properties. J. Mar. Biotechnol. 2:135-138.
- Morris EO (1968). Yeasts of marine origin. Oceanogr. Mar. Biol. Annu. Rev. 6:201-230.
- Nagahama T, Hamamoto M, Nakase T, Takami H, Horikoshi K (2001a). Distribution and identification of red yeasts in deep-sea environments around the northwest Pacific Ocean. Antonie van Leeuwenhoek 80:101-110.
- Nagahama T, Hamamoto M, Nakase T, Horikoshi K (2001b). *Rhodotorula lamellibrachii* sp. nov., a new yeast species from a tubeworm collected at the deep-sea floor in Sagami bay and its phylogenetic analysis. Antonie van Leeuwenhoek 80:317-323.
- Nagahama T, Hamamoto M, Nakase T, Horikoshi K (2003a). *Rhodotorula benthica* sp. nov. and *Rhodotorula calyptogenae* sp. nov., novel yeast species from animals collected from the deep-sea floor, and *Rhodotorula lysiniphila* sp. nov., which is related phylogenetically. Int. J. Syst. Evol. Microbiol. 53:897-903.
- Nagahama T, Hamamoto M, Nakase T, Takaki Y, Horikoshi K (2003b). *Cryptococcus surugaensis* sp. nov., a novel yeast species from sediment collected on the deep-sea floor of Suruga Bay. Int. J. Syst. Evol. Microbiol. 53:2095-2098.
- Naumova ES, Sukhotina NN, Naumov GI (2004). Molecular-genetic differentiation of the dairy yeast *Kluyveromyces lactis* and its closest wild relatives. FEMS Yeast Res. 5:263-269.
- Nilsson A, Adler L (1990). Purification and characterization of glycerol-3-phosphate dehydrogenase (NAD⁺) in the salt-tolerant yeast *Debaryomyces hansenii*. Biochim. Biophy. Acta. *16:180*-185.
- Nishikawa A, Tomomatsu H, Sugita T, Ikeda R and Shinoda T (1996). Taxonamic position of clinical isolates of *Candida famata*. J. Med. Vet. Mycol. 34:411-419.
- Norkrans B (1966). Studies on marine occurring yeasts: growth related to *p*H, NaCl concentration and temperature. Arch. Microbiol. 54:374-392.
- Norkrans B (1968). Studies on marine occurring yeasts: respiration, fermentation and salt tolerance. Arch. Microbiol. 62:358-372.
- Onishi H (1963). Osmophilic yeasts. Adv. Food Res. 12:53-94.
- Oswal N, Sarma PM, Zinjarde SS, Pant A (2002). Palm oil mill effluent treatment by tropical marine yeast. Bioresour. Technol. 85:35-37.

Prista C, Almagro A, Loureiro-Dias MC, Ramos J (1997). Physiological basis for the highs tolerance of *Debaryomyces hansenii*. Appl. Environ. Microbiol. 63:4005-4009.

Ramos J (1999). Contrasting salt tolerance mechanism in *Saccharomyces cerevisiae* and *Debaryomyces hansenii*, pp. 377-390. In, S.G.Pandalai(ed) in recent research developments in Microbiology. Research Signpost Publication, Trivandrum, India.

Ranu G (1994). Emulsifying activity of hydrocarbonoclastic marine yeast. Nutr. Bioact. Subst. Aquat. Org. Pap. Symp. pp. 276-285.

- Ray MK, Uma DK, Seshu KG, Shivai S (1992). Extra cellular protease from the Antarctic yeast *Candida humicola*. Appl. Environ. Microbiol. 58:1918-1923.
- Rhishipal R, Philip R (1998). Selection of marine yeasts for the generation of single cell protein from prawn-shell waste. Bioresour. Technol. 65: 255-256.
- Ricaurte ML, Govind NS (1999). Construction of plasmid vectors and transformation of marine yeast *Debaryomyces hansenii*. Mar. Biotechnol. 1:15-19.
- Richards M, Elliott FR (1966). Inhibition of yeast growth by streptomycin. Nature 209:536.
- Ronald MA, Shiaris MP (1993). Biotransformation of Polycyclic Aromatic Hydrocarbons by Yeasts Isolated from Coastal Sediments. Appl. Environ. Microbiol. 59:1613-1618.
- Ross SS, Morris EO (1962). Effect of sodium chloride on the growth of certain yeasts of marine origin. J. Sci. Food Agr. 13:467-475.
- Roth FJ, Ahearn DG, Fell JW, Meyers SP, Meyers SA (1962). Ecology and taxonomy of yeasts isolated from various marine substrates. Limnol. Oceanogr. 7:178-185.
- Rothschild LJ, Mancinelli RL (2001). Life in extreme environments. Nature 409:1092-1101.
- Sahoo DK, Agarwal GP (2001). An investigation on glycerol biosynthesis by an osmophilic yeast in a bioreactor. Process Biochem. 36:839-846.
- Sajeevan TP, Philip R,Bright Singh IS (2006). Immunostimulatory effect of a marine yeast *Candida sake* S165 in *Fenneropenaeus indicus*. Aquaculture 257:150-155.
- Seshadri R, Sieburth JM (1971). Cultural Estimation of Yeasts on Seaweeds, Appl. Microbiol. 22:507-512.
- Sheng J, Chi Z, Li J, Gao L,Gong F, (2007). Inulinase production by the marine yeast *Cryptococcus aureus* G7a and inulin hydrolysis by the crude inulinase. Proc. Biochem. 42:805-811.
- Shepherd R, Rockey J, Sutherland IW, Roller S (1995) Novel bioemulsifiers from microorganisms for use in foods. J. Biotechnol. 40:207-217.
- Sinclair NA, Stokes JL (1965). Obligatory psychrophilic yeast from the Polar Regions. Can. J. Microbiol. 11:259-269.
- Soares CAG, Maury M, Pagnocca EC, Araujo EV, Mendonca-Hagler LC, Hagler AN, (1997). Ascomycetous yeasts from tropical intertidal dark mud of southeast Brazilian estuaries. J. Gen. Appl. Microbiol. 43:265-272.
- Sprague GF, Cronan JE (1977). Isolation and characterization of Saccharomyces cerevisiae mutants defective in glycerol catabolism. J. Bacteriol. 129:1335-1342.
- Suchiro S, Tomiyasu Y (1962). Studies on the marine yeasts. V. yeasts isolated from sea weed. J. Fac. Agric. 12:163-169.

- Tag K, Lehmann M, Chan C, Renneberg R, Riedel K, Kunze G (2000). Measurement of biodegradable substances with a mycelia-sensor based on the salt tolerant yeast *Arxula adenini forans* LS3. Sens. Actuat. B. 67:142-148.
- Taysi I, Van-Uden N (1964). Occurrence and population densities of yeast species in an estuarine-marine area. Limnol. Oceanogr. 9:42-45.
- Tripp MR (1960). Mechanisms of removal of injected microorganisms from the American Oyster, *Crassostrea virginica* (Gmelin). Biol. Bull. 119:273-282.
- Turkiewicz M, Pazgier M, Donachie SP, Kalinowska H (2005). Invertase and _-glucosidase production by the endemic Antarctic marine yeast *Leucosporidium antarcticum.* Pol. Polar Res. 26:125-136.
- Urano N, Hirai H, Ishida M, Kimura S (1998). Characterization of ethanol-producing marine yeasts isolated from coastal water. Fish. Sci. 64:633-637.
- Urano N, Yamazaki M, Ueno R (2001). Distribution of Halotolerant and/or Fermentative Yeasts in Aquatic Environments. J. Tokyo Univ. Fish. 87:23-29.
- Van Uden N, Fell JW (1968). Marine yeasts, pp. 167-201. In M. R. Droop and E. J. F. Wood (ed.), Advances in microbiology of the sea, vol. 1. Academic Press Inc., New York.
- Van Uden N, Castelo-Granco R (1963). Distribution and population densities of yeast species in Pacific water, air animals and kelp off Southern California. Limnol. Oceanogr. 8:323-329.
- Wartmann T, Kunze G (2000). Genetic transformation and biotechnological application of the yeast *Arxula adeninivorans*. Appl. Microbiol. Biotechnol. 54:619-624.
- Watson K, Arthur H (1976). *Leucosporidium* yeasts: obligate psychrophiles which alter mem- brane-lipid and cytochrome composition with temperature. J. Gen. Microbiol. 97: 11–-18.
- Wong B, Kiehn TE, Edwards F, Bernard EM, Marcove RC, De Haven E, Armstrong D (1982). Bone infection caused by *Debaryomyces hansenii* in a normal host: a case report. J. Clin. Microbiol. 16:545-548.
- Yadav JS, Loper JC (1999). Multiple P450 alk (cytochrome P450 alkane hydroxylase) genr from the halotolerant yeast *Dabaryomyces hansenii*. Gene. 226:139-146.
- Yamasato K, Goto S, Ohwada K, Okuno D, Araki H, Iizaka H (1974). Yeasts from the Pacific Ocean. J. Gen. Appl. Microbiol. 20:289-307.
- Yifei W, Bao Y, Shen D, Feng W, Yu T, Zhang J, Zheng XD (2008). Biocontrol of Alternaria alternata on cherry tomato fruit by use of marine yeast Rhodosporidium paludigenum Fell & Tallman. Int. J. Food Microbiol. 123:234-239.
- Zheng S, Yang M, Yang Z (2005). Biomass production of yeast isolate from salad oil manufacturing wastewater. Bioresour. Technol. 96:1183-1187.
- ZoBell CE, Johnson FH (1949). The influence of hydrostatic pressure on the growth and viability of terrestrial and marine bacteria. J. Bacteriol. 57:179-189.